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THE CNIDARIA AND THEIR EVOLUTION
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THE EVOLUTION OF THE HYDROZOA

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SUMMARY

The various ideas concerning the origin of the Cnidaria are briefly reviewed and an attempt is made to discover the characteristics of a basic cnidarian. By elimination this is reduced to a gastrula which probably evolved into an actinula-like organism. This appears to be basic to the whole of the Cnidaria and radiation in the direction of the different classes would appear to depend on habitat. The ancestors of the Hydrozoa probably became planktonic, evolving into medusae with a direct development (Trachymedusae). In the Narcomedusae, also planktonic, asexual budding in the larva and the beginnings of a true metagenesis (in some species) indicate the pattern that was evolved into an alternation of a hydroid and a medusa phase in the so-called Hydroida. In this group (Anthomedusae, Leptomedusae and Limnomedusae) the more primitive forms (where metagenesis is already well established) are found in the families Moerisiidae and Corymorphidae.

INTRODUCTION

In recent years there has been a lively interest in the evolution of the Metazoa and whether the Cnidaria form a starting point for metazoan evolution or whether they are descended by retrogressive evolution from Turbellaria and are consequently not in the main stream of evolution.

It has also been suggested by several authors that the Actinozoa are the primitive Cnidaria and the Hydrozoa the most specialized. The ideas concerning these are briefly reviewed before proceeding to consider the origins of the Hydrozoa.

Here it will be shown that the most likely ancestor of the Hydrozoa was an actinula which became planktonic and evolved into a medusa and that the hydroid phase has arisen through the budding and colonization from an asexual larva.

HAECKEL'S GASTRAEA THEORY

The Metazoa were derived by Haeckel (1874) from hollow Volvocine flagellated colonies and this idea of a hollow spherical ball of cells, the blastaea, has long been believed to be repeated in the development of the Metazoa and has been called the blastula stage. From this blastaea Haeckel derived the gastraea—a hypothetical larval stage

formed by invagination at one end of the blastaea forming a two-layered, cup-shaped structure—thus, in effect, arriving at the basic structure of the Cnidaria.

These ideas of Haeckel were challenged by Metschnikoff who pointed out that digestion is intracellular and phagocytic in many lower Metazoa and a mouth with digestive sac would not be needed. He favoured an inwandering of cells that would fill the blastula cavity, creating what is today known as a gastrula in cnidarian development. Metschnikoff and his contemporaries pointed out that the hollow gastrula is not found in ontogeny of primitive Metazoa like Coelenterates (but see p. 202). Certainly the inwandering of ectodermal cells to form endoderm is a more common process in Cnidaria than its formation by invagination (Fig. 1).

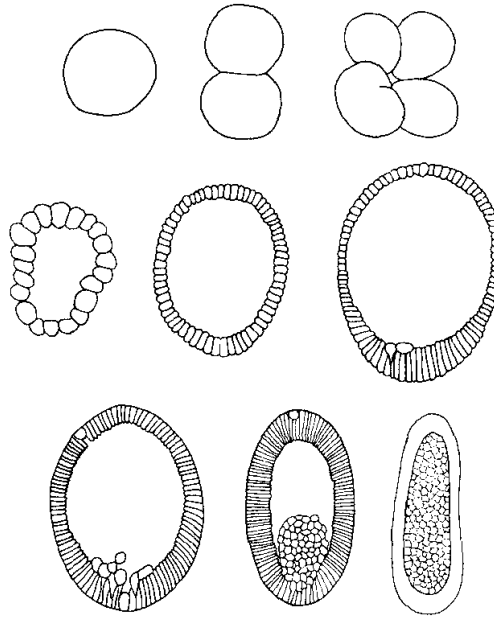


FIG. 1. Gastrulation by polar invagination in the development of the hydroid *Clytia hemisphaericum* (L.) from egg to planula. (After Metschnikoff, 1886.)

Metschnikoff's ancestral flagellated, diploblastic larva, termed by him parenchymula and planula by Dalyell, has often been regarded as the common ancestor of coelenterates and flatworms (Fig. 2). Hyman favours this planuloid origin in a slightly modified form in which she supposed that "the Metazoa arose from an axiatic hollow spherical flagellated colony in which there occurred first a differentiation into somatic and reproductive cells and then a differentiation into locomotor-perceptive and nutritive types, through the wandering of the latter into the interior. In this parenchymula or stereogastrula, food was caught by the surface cells in protozoan fashion and passed into the

interior amoeboid cells for digestion. The sex cells were also relegated to the interior and received food supplies from the amoeboid cells, as still happens in many lower metazoans. The anterior pole probably bore special sensory cells or a tuft of sensory cilia. Such an organism may be considered the common ancestor of the coelenterates and flatworms."

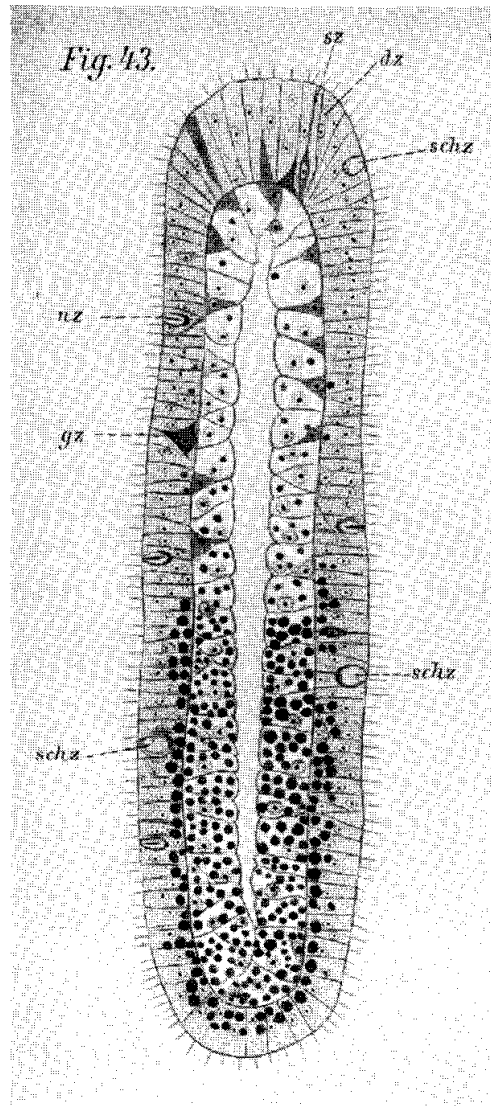


FIG. 2. Longitudinal section of a planula of the thecate hydroid *Gonothyrax loveni* Allman. *dz*, Gland cell; *gz*, ganglion cell; *nz*, nurse cell; *schz*, mucus cell; *sz*, sensory cell. (After Wulfert, 1902.)

However, Hyman (1940, 1942, 1959) believes that the ancestral cnidarian was a primitive medusa developed from an actinula larva. The medusoid origin of the Hydrozoa had also been suggested by Rees (1957) and by Hand (1959).

JÄGERSTEN'S BILATEROGASTRAEA THEORY

Jägersten (1955), however, points out that although inwandering of cells during gastrulation is probably predominant in the Cnidaria, being entirely dominant in the Hydrozoa, "invagination also occurs in Cnidaria (both in Anthozoa and Scyphozoa)". Jägersten argues that as this latter process is found in such widely separated groups as Cnidaria, Annelida, Chaetognatha and Acrania, "*The common ancestor possessed invagination, i.e., was simply a Gastraea.*"

Jägersten supposes that Haeckel's blastaea, which was assumed to be planktonic, turned to living near the bottom on account of more favourable feeding, finally becoming a bottom-dweller gliding forwards over the substratum with the aid of flagella. He adds: "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."

With this change from a planktonic to a benthonic habit, Jägersten assumes that phagocytosis became limited to the cells of the ventral side and when some larger dead organisms were encountered the animal arched its body over the food and gradually "this occasional 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 gastraea stage in the evolution of the Metazoa was reached." This Jägersten called a bilaterogastraea (Fig. 3).

Among the reasons that forced Jägersten to propose the bilaterogastraea was his belief that in the Anthozoa "The inner bilateral symmetry prevailing here is, in my opinion, incompatible with the current opinion that the Cnidaria are primarily a radially symmetrical group". Following this up Jägersten felt compelled to derive them from some bilaterosymmetrical ancestor (Fig. 4) and in consequence reverses the order Hydrozoa—Scyphozoa—Anthozoa, regarding the last mentioned as the primitive group and the Hydrozoa as the most modified (Jägersten, 1955, 1959).

In support of his ideas he points out the bilateral arrangement of mesenteries, directives and siphonoglyphs and regards as primitive their gastrulation by invagination and the absence of a medusoid generation. He also indicates that the nematocysts are most simple and uniform in the Anthozoa, compared with the diversity found in the Hydrozoa.

Hyman (1959, p. 751) in reviewing Jägersten's ideas does not deny that the tendency to bilaterality is deep-rooted in the Anthozoa but

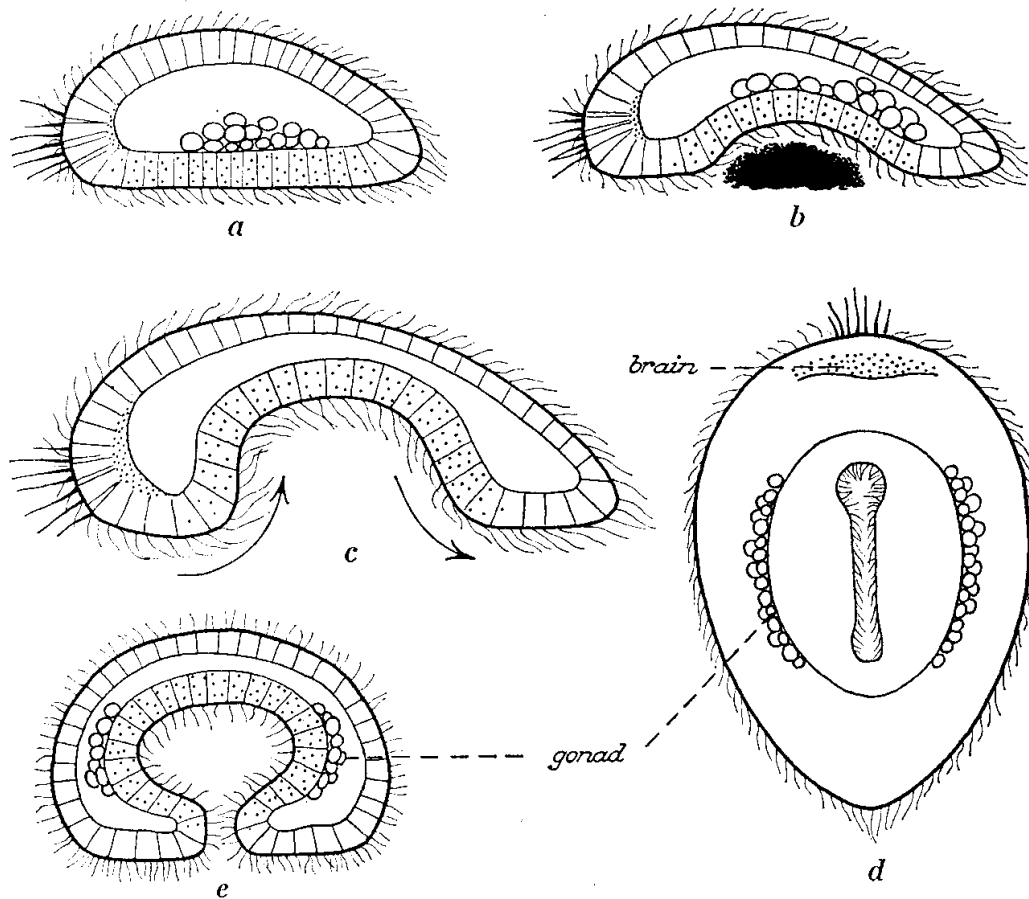


FIG. 3. Diagrammatic representations of a bilaterogastraea (a) Early bilaterogastraea; (b) later bilaterogastraea feeding, curved over a large particle of food; (c-d) late bilaterogastraea in longitudinal section (c); ventral view (d); transverse section (e). (After Jägersten, 1955.)

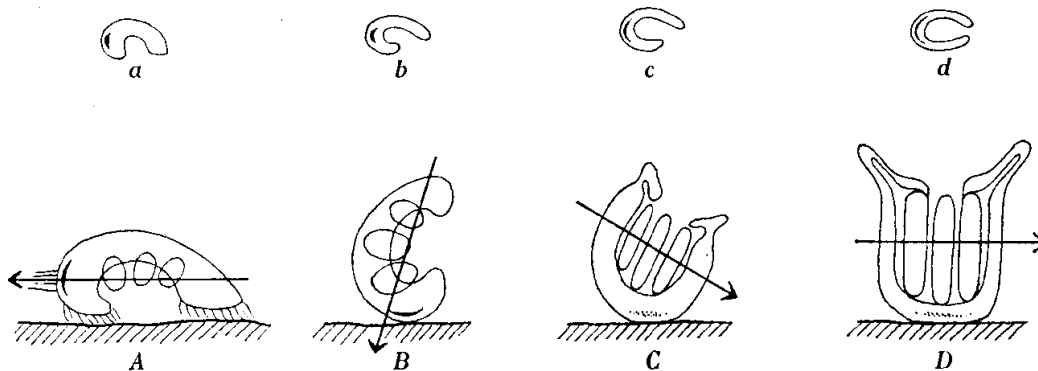


FIG. 4. Diagrams illustrating the presumed evolution from the bilaterogastraea to the primitive cnidarian. A-D, Adults; a-d, the corresponding larval stages. The intestinal pockets of one side are projected into the median plane and the position of the brain is marked in all diagrams, although it is reduced in C and D. (After Jägersten, 1959.)

does not see that it necessarily follows that it is obligatory to invent a bilateral ancestor. As she sees it deviations of radial symmetry into bilateral symmetry are common and points to such occurrences in hydroids as in *Branchiocerianthus* and in the sertularian, plumularian and aglaophenian families. Here it is necessary to correct some impressions of *Branchiocerianthus* and *Corymorpha nutans*, created by Jägersten (1959). The former is clearly adapted for feeding in slow currents and the drooping hydranth of the latter in dredged specimens is due simply to loss of hydrostatic pressure. Many of the more specialized hydrozoans like *Proboscidactyla*, *Plumularia*, *Dinotheca* and *Aglaophenia* exhibit a high degree of bilaterality (Fig. 5); all are

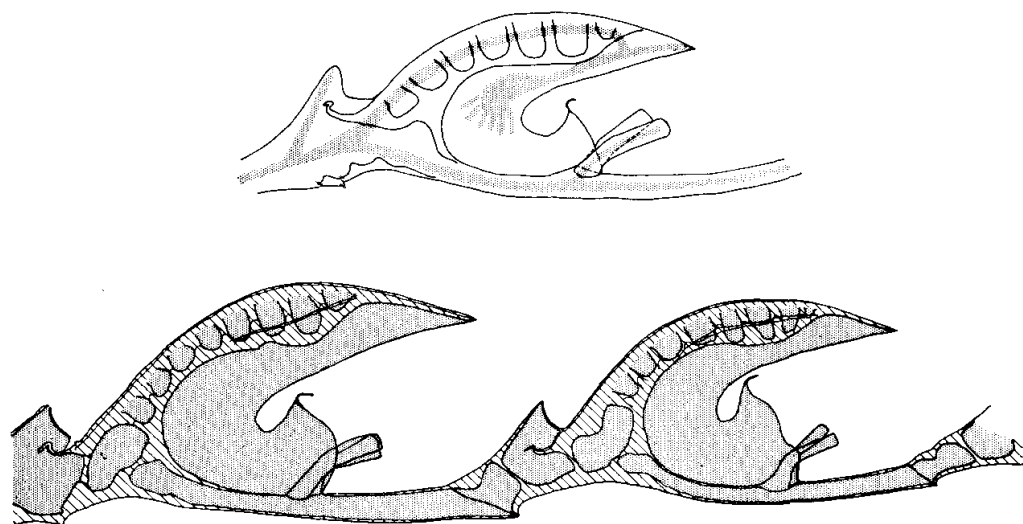


FIG. 5. Portion of a hydrocladial branch of the aglaophenid hydroid, *Dinotheca dofteini* Stechow to show the advanced bilateral symmetry of the thecae; the upper diagram shows the position of the hydranth, its retractor, the long coenosarcal branch connecting it with the main branch and the connexions to the nematophores.

admirably adapted to their ecological niches in the same way as *Antipathes* and Gorgonians are adapted to theirs.

Marcus (1958, p. 26) agrees with Jägersten that the common ancestor of the Metazoa was simply a gastraea and further that flagellates with cnidotrichocysts stood at the root of the Cnidaria. He is also in agreement with Ulrich (1950), Remane (1954) and Jägersten in reversing the order Hydrozoa—Scyphozoa—Anthozoa. Here we may note that none of these authors has specialized on the Cnidaria and from a specialist's point of view cannot have a sufficiently profound knowledge of the group.

Marcus also agrees with Korshelt and Heider (1890) and Remane (1954) that a tetra- or radiate polyp with four gastric pouches separated

by septa may have been the ancestral cnidarian—this giving rise along different lines to medusae and metagenesis and to the Anthozoa. This author thinks that bilateral symmetry in the Anthozoa is a retained adaptive innovation and that “the early phylogeny of the Metazoa can be understood without the premise of Jägersten’s bilaterogastrula”.

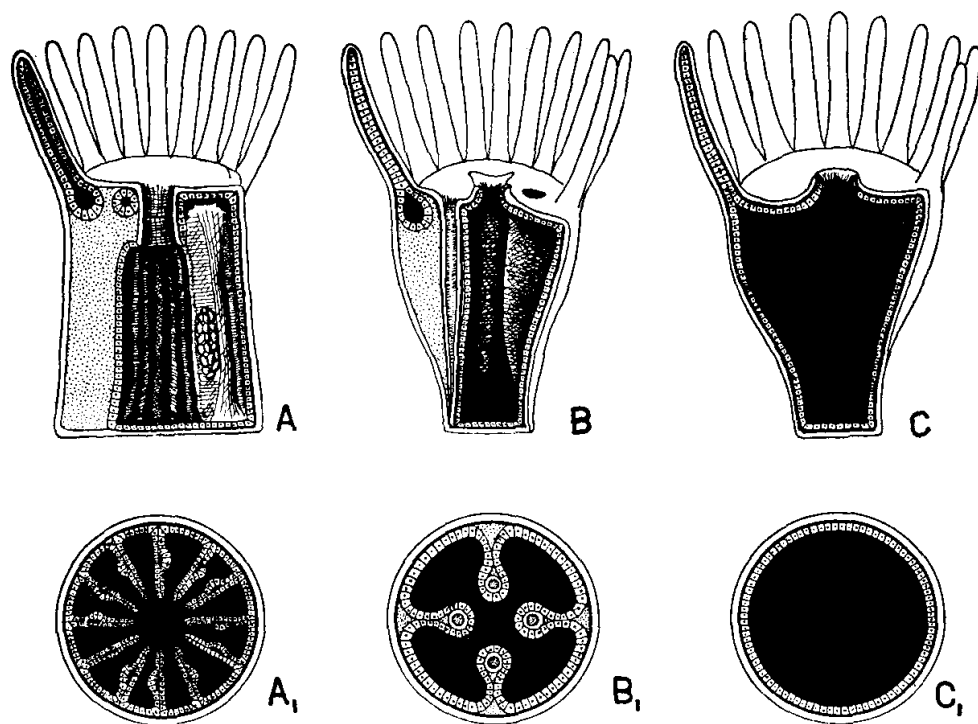


FIG. 6. Diagrammatic representation of three kinds of cnidarian polyps. (After Hadži, 1963.)

THE CELLULARIZATION THEORY

Many authors from von Jhering (1877) to de Beer (1954) are agreed that the most probable ancestor of the Eumetazoa was a multinucleate, ciliated protozoan and that the primitive metazoan would be an acoelous turbellarian, derived by internal cellularization (Fig. 7). This theory has been adapted by Hadži (1944, 1953, 1963) to account for the origin of all cnidarians from rhabdocoel turbellarians that in turn had been derived from acoelous ones. It followed that the primitive cnidarians would be bilaterally symmetrical and for this reason Hadži selects the Anthozoa as the more primitive and the Hydrozoa as the more specialized. This theory which has been popularized by de Beer, postulates that the Cnidaria have arisen by retrogressive evolution and the reduction of what mesoderm these primitive Turbellaria possess.

Hadži's notions on evolution *within* the Cnidaria (1963) apparently all stem from the internal bilateral symmetry of Anthozoa—"a most unpleasant fact for all the adherents of the old interpretation". From all the verbiage it is difficult to extract any other arguments that cannot be reversed and that can be used to show that the Anthozoa are the most advanced Cnidaria. It must be said that Hadži fails to weigh up the evidence on both sides of the fence—he skims over and discards ideas not in line with his own theory as *wrong interpretation* and *absurd*.

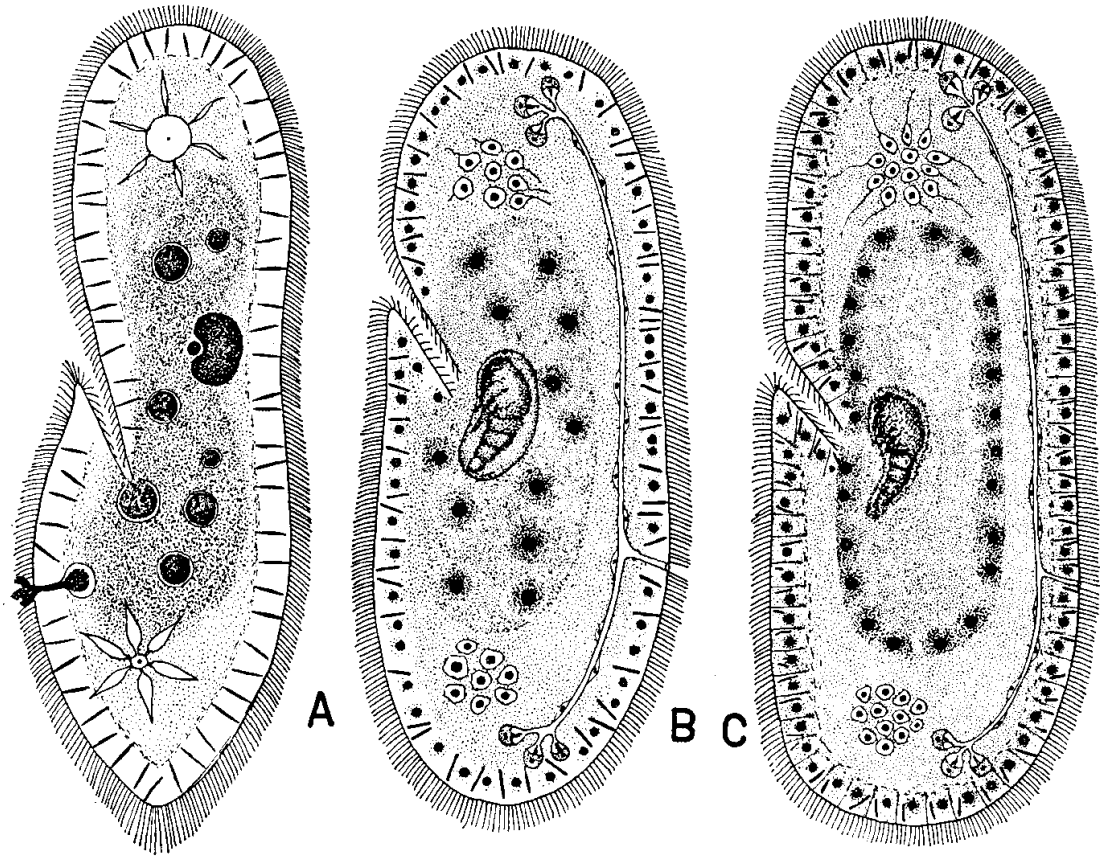


FIG. 7. The hypothetical evolution of a primitive turbellarian from a ciliate by internal cellularization. A, Ciliate; B, transitional stage; C, primitive turbellarian, with nervous system and musculature omitted. (After Hadži, 1963.)

He dismisses Jägersten's ideas with "This is a typical suitcase theory (*Koffertheorie*) which is so general and all embracing that with only a small modification it will explain anything". On Marcus, he adds "He and I speak two different languages and his line of thought remains unintelligible to me . . .". Hadži, too, avoids discussing ideas that are unpalatable for him and, for example, we find no mention of Brooks's classical paper on metagenesis in hydromedusae (1886)—a fundamental paper in any discussion of hydrozoan ancestry.

THE BASIC CNIDARIAN

As we have seen the Cnidaria have been derived by various authors from ciliates, flagellates with cnidotrichocysts, volvocine organisms and Turbellaria. Favourite contenders among the more immediate ancestors are planuloids, the gastraea, the bilaterogastraea and rhabdocoele turbellarians. We may note that all these are by implication active non-sedentary organisms—either planktonic or creeping benthic forms. Further, this proto-coelenterate would possess primitive nematocysts and would be ancestral to both Cnidaria and Ctenophora—the demonstration by Picard (1955b) that the nematocysts of the ctenophore *Euchlora rubra* are genuinely possessed by this form and are not kleptocnidae, points to a common but remote ancestry of two groups. The Ctenophora, however, need not concern us further except to mention that four gastric pouches appear in the ontogeny of this group.

Marcus (1958), in agreement with several other authors (Korschelt and Heider, 1890; Heider, 1914; Remane, 1954), believes that the ancestral cnidarian may have been a tetraradiate polyp with four gastric pouches separated by septa and with the germ cells located in the gastric pouches. This is as good a point as any to begin our search for an ancestral cnidarian. These authors have noted the four gastric pouches with intermediate septa both in the scyphopolyp and in the typical Scyphozoan medusa. They will also have noted the basic tetraradiate symmetry of the Actinozoa today, found usually in multiples of four (eight, twelve, sixteen, etc.). In the Hydrozoa the digestive gut shows no trace of the tetramerous symmetry in the hydroid but this is preserved in the medusa in the form of gastric pouches and in the radial canals. It is therefore reasonable to assume that a quadrate stomach could be a basic feature in cnidarian ancestry. The suggestion has also been made that the germ cells are situated in the gastric pouches—these presumably being undifferentiated cells analogous to the interstitial cells of *Hydra*.

If I interpret Marcus's thesis correctly, this tetraradiate polyp would be sedentary and fixed to the substratum and it appears that this has too many secondary features about it to be accepted as a basic cnidarian.

Sessility is always a secondary innovation and such an ancestor would be free-living either planktonic, benthoplanktonic or creeping over the substratum. We are not told whether this polyp would be tentaculate.

Granting this, and I am inclined to favour the benthoplanktonic habitat as the least specialized, the gastric sac would be a simple one

as we must also regard a quadrate stomach as a secondary manifestation.

An elongate polyp is usually associated with a sedentary habit and the ancestral form would probably be round or somewhat flattened, without tentacles and with a ventral central mouth very much as in Jägersten's bilaterogastraea and in the Turbellaria—an admirable position in a benthic or benthoplanktonic form. We are thus forced to

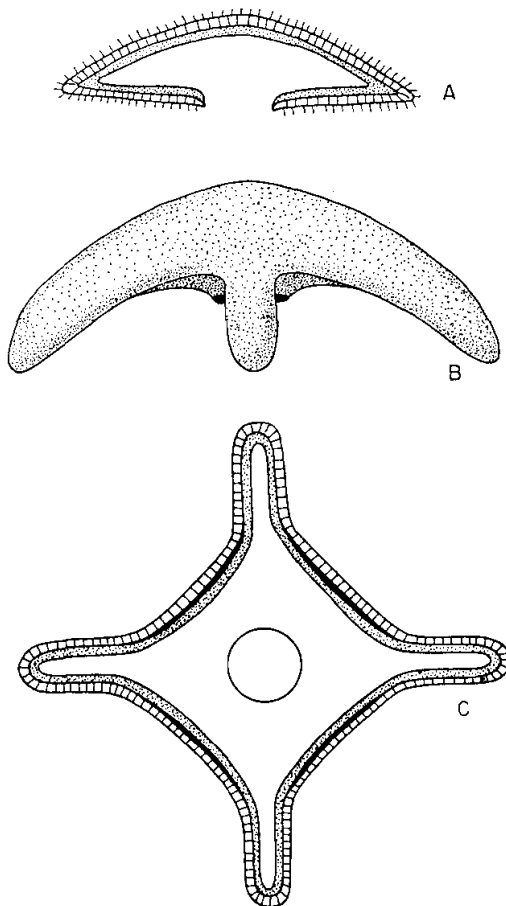


FIG. 8. Diagrammatic representation of hypothetical basic cnidarians. A, Proto-coelenterate (gastrula stage) in vertical section; B-C, proto-actinula with four hollow tentacles and tetra-rotate stomach.

return to a gastraea-like form as the basic cnidarian without necessarily accepting any of the theories concerning its earlier history.

This basic cnidarian is in effect a proto-actinuloid which was probably ciliated and armed with scattered nematocysts all over the ectoderm (Fig. 8A). A secondary development would be a greater concentration of nematocysts around the free edges and with further evolution at least four hollow tentacles would be developed, these being deployed

as offensive or defensive weapons and in assisting locomotion (Fig. 8B-C). The quadrate stomach would be a relatively late development associated with the increasing size of the actinuloid. The germ cells would probably arise from undifferentiated cells of the interstitial type between ectoderm and endoderm and they would be discharged into the stomach and through the mouth.

In effect this ancestral cnidarian would be a fertile actinula differing only in its ability to reproduce itself from the modern actinula larva. With the evolution of a quadrate stomach all the essential features for evolution into all three classes of Cnidaria would be present.

THE EVOLUTION OF THE HYDROZOA

Choice of habitat by the ancestral cnidarians would lead to radiation. Evolution along the actinozoan line would necessitate the adoption of a benthic or creeping habitat, but whether first into a bilateral larva

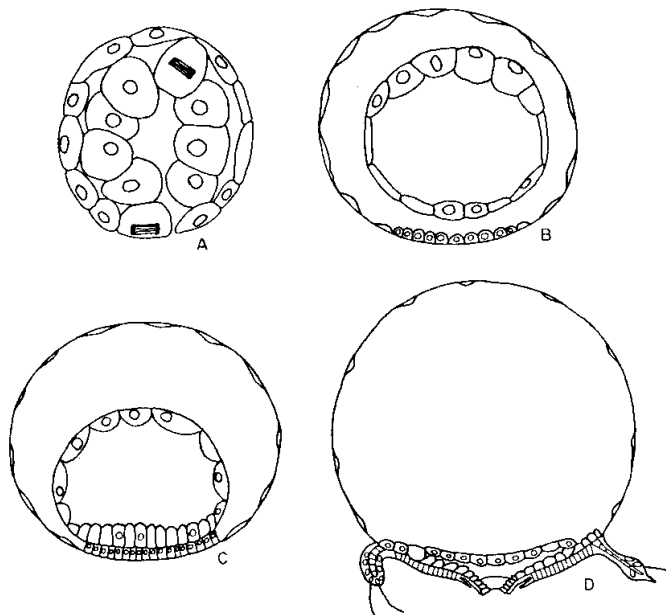


FIG. 9. The direct development of the embryo of the cosmopolitan trachymedusa *Liriope tetraphylla* (Chamisso and Eysenhardt); note the early development of the mesogloea. (Redrawn from Metschnikoff, 1886.)

(analogous to Jägersten's bilaterogastraea) or whether through a radial larva, with secondary internal bilateral symmetry developing later, is beyond the scope of this paper. All the evidence points to the non-existence of a medusoid phase in the history of the Actinozoa and suggests the early adoption of a sessile habit by the actinula.

The ancestors of both Hydrozoa and Scyphozoa differed in the adoption of a planktonic habitat and the evolution of the actinulae into

medusae. Here we have time only to consider the Hydrozoa. In this class the simplest kind of life cycle is found in the Trachymedusae in which the whole is spent in the plankton. In these the fertilized egg develops directly into an actinula larva which metamorphoses into a medusa. There is no asexual reproduction and the chief changes, apart from proportions and a number of tentacles, are the development of a thick layer of mesogloea and of statocysts—both associated with the life of the adult medusa in the plankton.

This simple life cycle is basic to the whole pattern of hydrozoan evolution; *Liriope tetraphylla* (Chamisso and Eysenhardt) (Fig. 9) and *Aglaura hemistoma* Péron and Lesueur (Fig. 10) are typical oceanic medusae whose development was followed by Metschnikoff (1886).

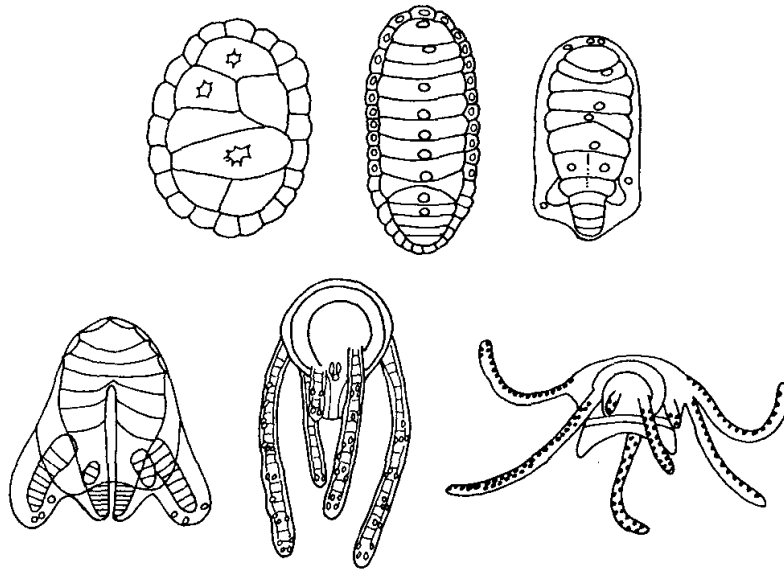


FIG. 10. Direct development in the trachymedusa *Aglaura hemistoma* Peron and Lesueur. (Redrawn from Metschnikoff, 1886.)

When we consider another order of pelagic Hydrozoa, the Narcomedusae, the medusae of some of these, notably the Aeginidae, have retained the tetra- or eight-fold symmetry, but here there is a development of bell structure both above and ventral to the point of origin of the tentacles (Fig. 11). Unfortunately we do not know much about the life cycle except in some rather advanced genera like *Pegántha* and *Cunina* where the larvae are usually epizoid on the manubria of other medusae (Brooks, 1886; Kramp, 1957).

In *Cunina octonaria*, McCrady (1857) and Brooks (1886) have shown that the actinulae may multiply asexually producing other larvae that in turn, together with the original larva, all grow up into adult medusae

(Fig. 12). Thus there is no persistent larva and therefore no metagenesis.

Some other larvae described by Kramp (1957, p. 87 *et seq.*) differ from those of other Narcomedusae as described above and are of considerable significance (Fig. 13). The larvae (whose adults are not known for certain) are described as: "collected in clusters attached to the subumbrella of the host by means of a number of threads, which are really the tentacles of the primary individual of the cluster. These tentacles are solid with an endoderm consisting of one row of disc-like

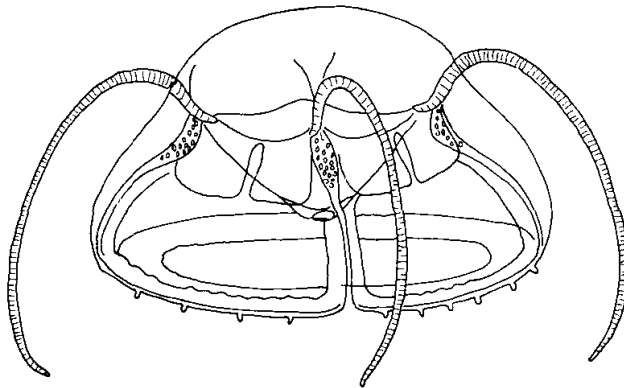


FIG. 11. The narcomedusa *Aeginea citrea* Eschscholtz showing the development of the umbrella both proximal and distal to the points of origin of the tentacles. (From Russell, 1953; after Mayer, 1910.)

cells and terminating in an adhesive, knob-like expansion studded with nematocysts. The body of the primary individual is merely a tiny knob with no indication of a medusoid structure; it acts as a stolo-prolifer from which other individuals arise by budding, and all these are successively developed into medusae . . . the primary individual remains in a polypoid stage. Accordingly the development must be regarded as a true metagenesis."

Before going on perhaps I should mention the Actinulida that have been so ably investigated by Dr. Swedmark and Professor Teissier; these have sometimes been looked upon as having arisen from Narcomedusae through loss of jelly and through adopting an interstitial habit, but these authors regard them as persistent actinulae specially adapted to their environment (Swedmark and Teissier, 1957 and p. 130).

The presence of true metagenesis in some Narcomedusae is highly significant and the implication is clear that the evolution of a hydroid phase has arisen through the elaboration of the asexual larva, its persistence and its gradual evolution into a colonial system, which becomes dominant in the higher families of the Hydrozoa like the Sertulariidae and the Plumulariidae.

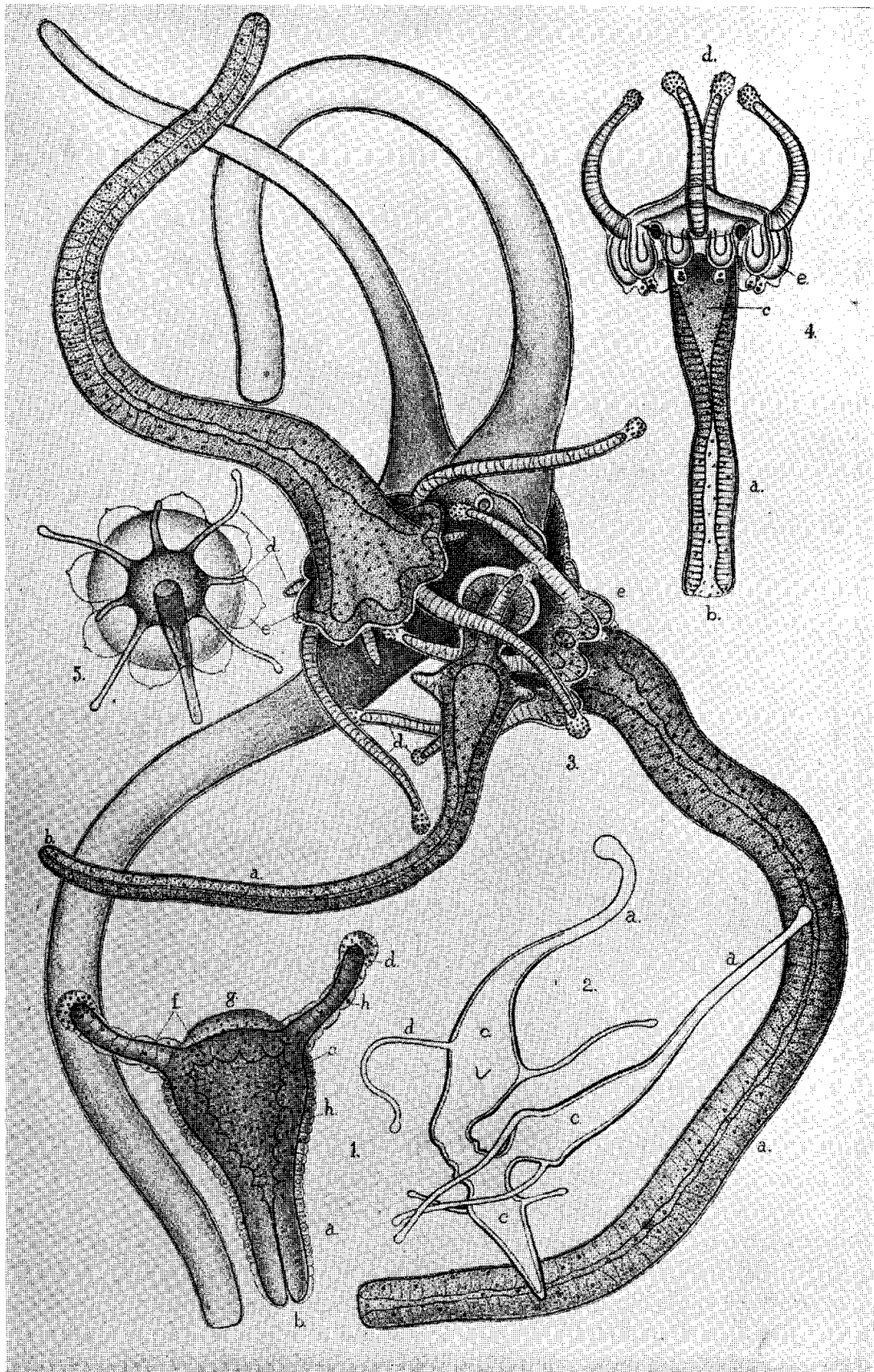


FIG. 12. Asexual reproduction of the actinula of *Cunina octonaria* McCrady, in which all the larvae, including the original one, develop into medusae. 1, Young actinula; 2, early stage in asexual budding, soon after attachment to host medusa; 3, later stage with several daughter actinulae; 4, actinula in process of metamorphosis into medusa. (All after Brooks, 1886.)

Mosaic evolution in hydroids and medusae has been discussed in an earlier paper (Rees, 1957), and in this type of evolution (which is very evident in the Anthomedusae and Leptomedusae) a medusa may evolve and result in a highly specialized organism, while its hydroid may remain simple and relatively unspecialized—or it may be the other way round, an elaborate hydroid and a simple medusa. All living Trachymedusae and Narcomedusae are very distinctive organisms and could not possibly have given rise to the hydromedusae but they appear to have common ancestors with them.

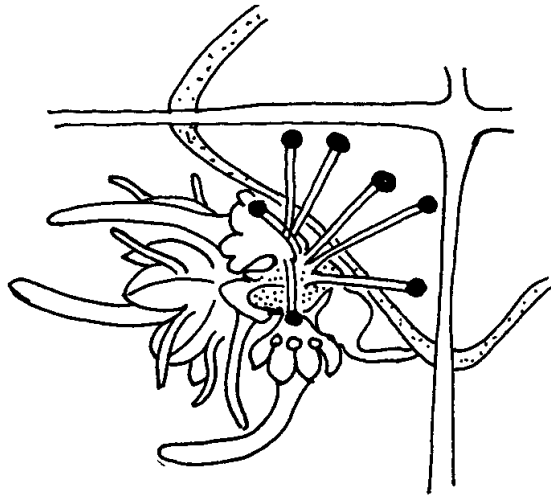


FIG. 13. Cluster of larvae of a narcomedusan thought to be *Pegantha triloba* Haeckel, attached to the manubrium of the hydromedusa *Bougainvillia platygaster* from latitude 22° 36' S., 30° 01' 30'' W. Note the stolon-prolifer with long capitate tentacles budding off medusae. (After Kramp, 1957.)

The fossil record, which has been discussed by Uchida (1963), gives no satisfactory evidence on the evolution of the Anthomedusae, Leptomedusae and the Limnomedusae, and the living tips of the evolutionary tree present us with a well developed alternation of a hydroid and a medusa phase that I have already discussed for the Capitata (Rees, 1957).

This actinula theory of the origin of metagenesis is not new. It was first put forward by Böhm (1878), lucidly elaborated by Brooks (1886) and later supported by Hyman (1940, 1959), Rees (1957) and Hand (1959). Kramp (1943) came to the conclusion "that the polypoid ancestor of the hydrozoa was first split into a pelagic and a fixed form (I have no idea as to which of them was the primary form)" but he adds "The Trachylina were developed from the pelagic polypoid progenitor in accordance with the actinula theory". Unfortunately he does not define precisely what he means by polypoid.

THE POLYP THEORY

The origin of the Hydrozoa from a fixed, solitary polyp was briefly outlined by Leuckart (1851) and supported by Balfour, Gegenbaur and also Grobben (1882). Sometimes called the division of labour theory, this postulates that the fixed polyp was fertile and possessed the ability to reproduce asexually by budding and form colonies. In time, with division of labour, sexual individuals became detached, free-swimming and became transformed into medusae. Further, according to Grobben (1882) they evolved along two distinct lines—some medusae becoming reduced and remaining attached in various degrees of degeneration to the hydroid, and in the other line the medusae became dominant and the hydroid almost suppressed to give rise to the Trachymedusae and Narcomedusae. Huxley (1877) thought that a medusoid was “in a morphological sense simply the detached generative organ of the hydrosoma on which it is developed”—in other words, merely a dispersal agent for gametes. Some writers of textbooks of general zoology still adhere to this view without presenting the student with the alternatives.

This theory has much to commend it to the followers of Hadži's Turbellaria theory but among Cnidarian specialists Naumov (1960) appears to be the only one who regards the medusa as merely a dispersal agent, this being reflected in his systematic studies on the group.

ANCESTRAL HYDROIDS AND MEDUSAE

The evidence for the medusoid origins of the hydroids and medusae have already been discussed by Rees (1957) and by Hand (1959) and the broad outlines of evolutionary trends in the Capitata (generally agreed to be the most primitive group of athecate hydroids) have been traced by the former. In that paper I drew a diagrammatic representation of a hypothetical ancestral codonid medusa, with its ring gonad, its four radial canals, its four exumbrellar nematocyst tracks and its hollow, tentacular bulbs with a moniliform arrangement of nematocyst batteries (Fig. 14). This, I believe still stands as an ancestral *codonid* (Tubularoidea), but subsequently I was able to study the Moerisiidae which had been placed in the order Limnomedusae by Kramp (1938) and Paspaleff (1938).

Species of the family Moerisiidae were examined by Picard (1951) who concluded that their relationships were with the “Tubularidae-Corynidae”; this was confirmed by Rees (1958) who transferred the

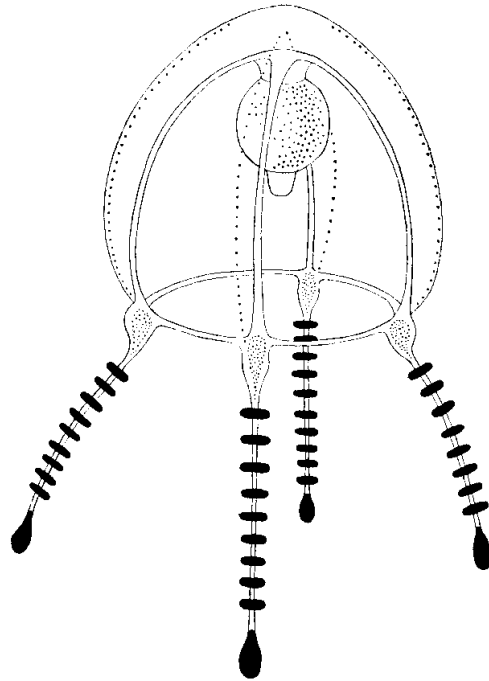


FIG. 14. Hypothetical ancestral codonid medusa, a basic type in the ancestry of the athecate superfamily Tubularoidea. (After Rees, 1957.)

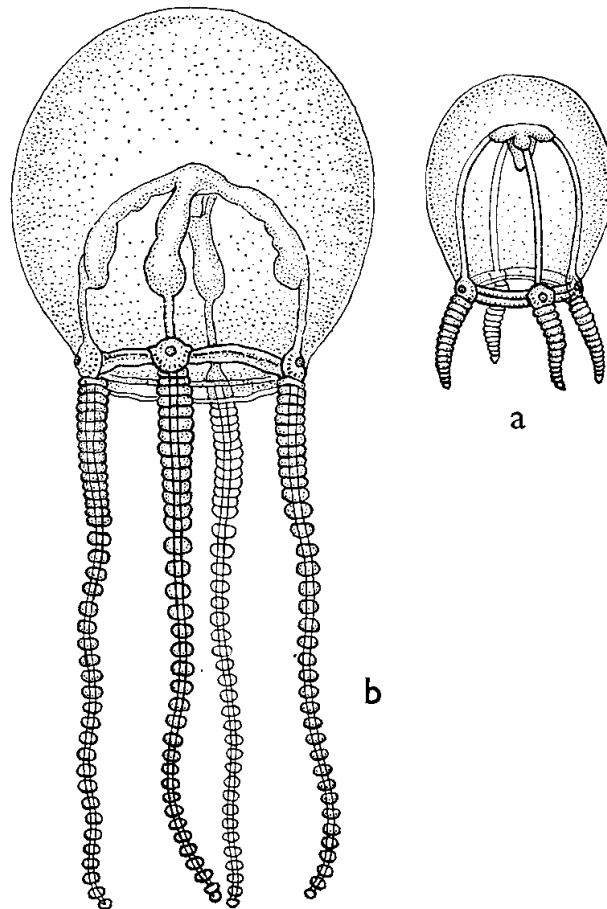


FIG. 15. Medusae of *Moerisia lyonsi* Boulenger, possibly the most primitive of living Anthomedusae. (a) Juvenile medusa; (b) adult male medusa. (Re-drawn from Boulenger, 1908.)

family to the Capitata in a superfamily of its own which he regarded as more primitive than the rest of the Capitata.

Compared with the primitive codonid medusa, the moerisiid has a quadrangular stomach on the radial extensions of which the mature

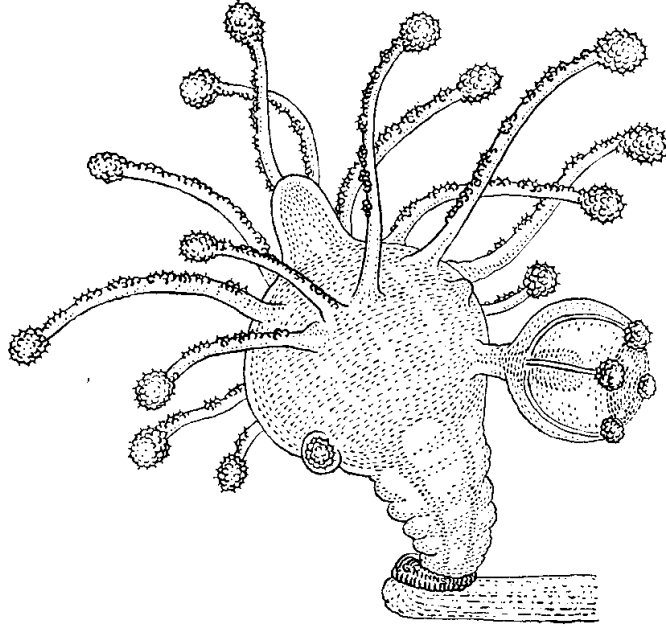


FIG. 16. Hydroid of the moerisiid hydroid, *Odessia maeotica* (Ostroumoff). (Re-drawn from Picard, 1951.)

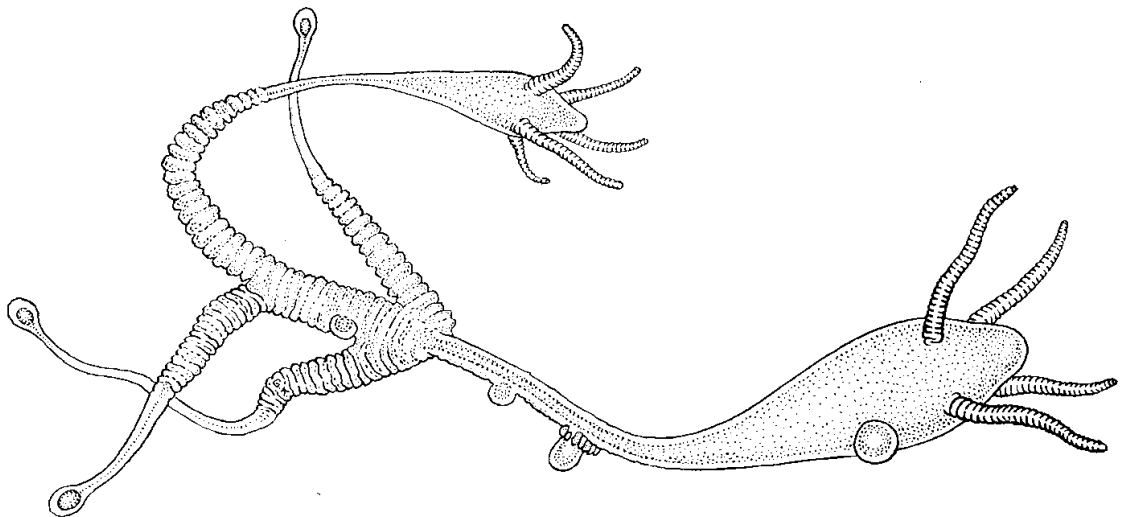


FIG. 17. The irregular growth of the hydroid *Moerisia lyonsi* Boulenger which exhibits a primitive colonial habit. (Re-drawn from Boulenger, 1908.)

gonads are found. In other respects the medusae are very similar except in the absence of nematocyst tracks on the exumbrella in the modern *Moerisia* (Fig. 15).

The *Moerisia* hydroids form a series *Moerisia*, *Odessia* and *Ostroumovia* with the last mentioned being more highly organized. Both *Odessia* (Fig. 16) and *Ostroumovia* are solitary but the latter forms podocysts from which new hydroids arise. *Moerisia* itself shows primitive colonization and there is a simple, irregular sheath over parts of the coenosarc (Fig. 17). Among the codonids (Tubularoidea) its affinities lie with primitive corymorphines like *Euphysa* (Rees, 1958).

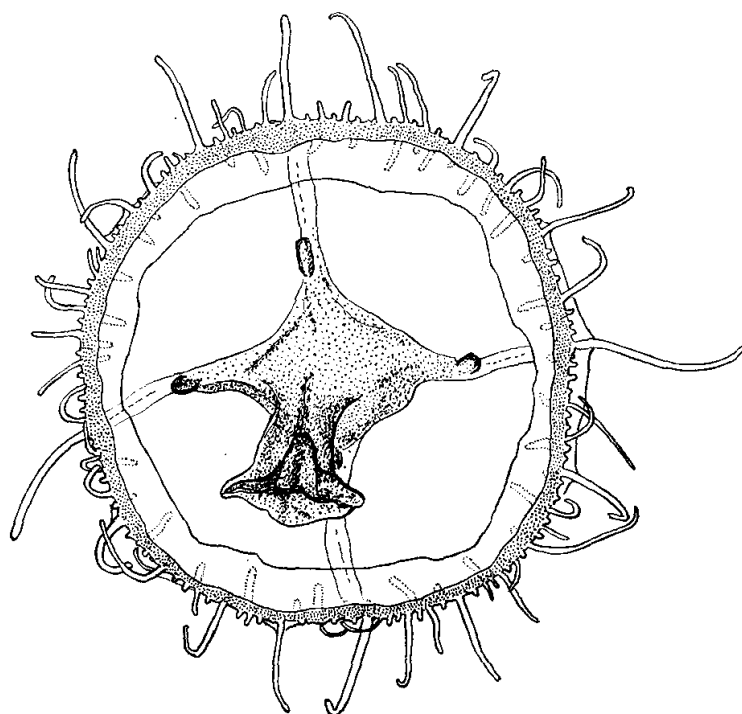


FIG. 18. The origin of the gonads from the corners of the quadrate stomach in the freshwater olindiid medusa *Craspedacusta sowerbyi* Lankester. (After Russell, 1953.)

In the Anthomedusae (Filifera), the Leptomedusae and in the Olindiidae (the sole remaining family in the Limnomedusae), this quadrate stomach appears (or the gonads arise from the corners of the stomach) in some genera (Fig. 18) of which a short list is given below.

Order ANTHOMEDUSAE

Suborder FILIFERA

Family Hydractiniidae

Podocoryne areolata Alder

Family Bougainvillidae

Bougainvillia principis (Steenstrup)

Bougainvillia macloviana Lesson

Family Pandeidae

Annatiara affinis (Hartlaub)

Family Proboscidaetylidae

Proboscidaetyla Brandt

Order LEPTOMEDUSAE

Family Laodiceidae

Staurophora mertensi Brandt*Chromatonema rubrum* Fewkes*Modeeria rotunda* (Quoy and Gaimard)

Order LIMNOMEDUSAE

Family Olindiidae

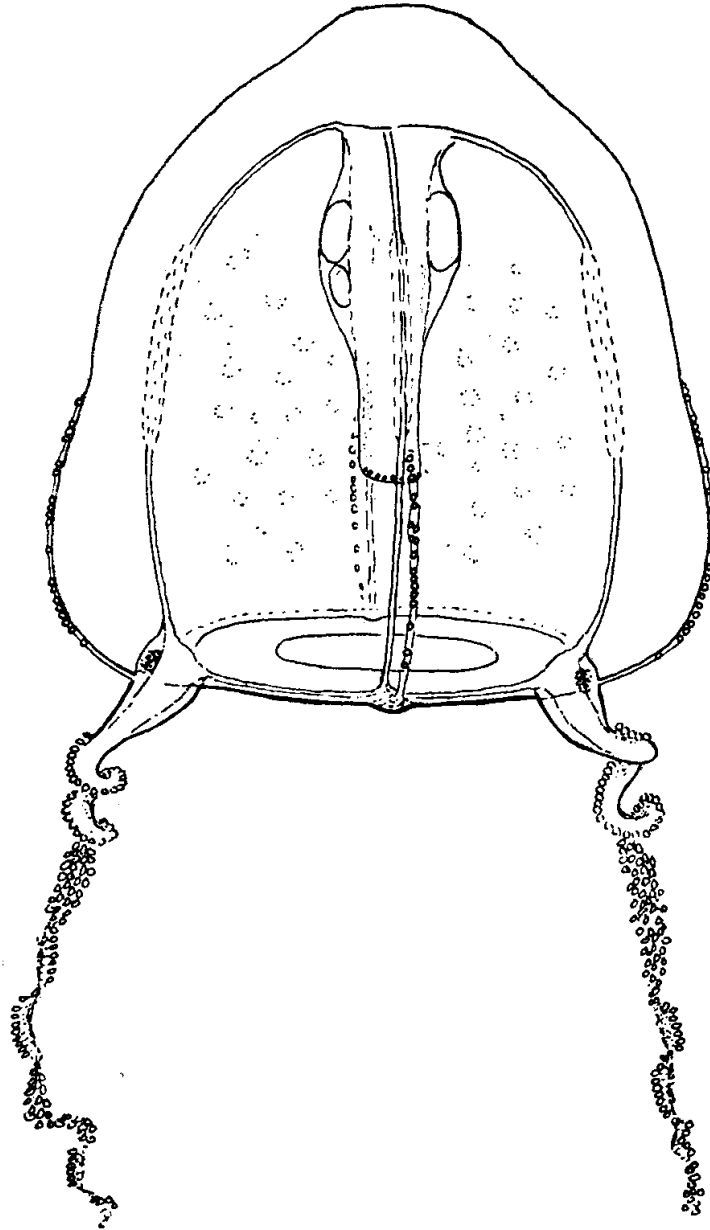
Craspedacusta sowerbyi Lankester

FIG. 19. Mature medusa of *Zanclea implexa* (Alder) with the linear swellings midway along the radial canals—here interpreted as vestiges of an ancestral quadrate stomach. (After Russell and Rees, 1936.)

The codonid and moerisiid stocks are among the most primitive of the Hydrozoa with a well developed metagenesis and both are apparently involved in the further evolution of this group.

There is an indication in some codonid medusae that these have been derived from ancestors with quadrate stomachs. The slight swellings that are found mid-way along the radial canals of *Dipurena halterata* (Forbes) and *Zanclea implexa* (Alder) can only be interpreted as vestigial indications of a quadrate stomach in the ancestry of these species (Fig. 19).

Although some very interesting theories have been put forward to account for the origin of the Cnidaria, my own personal view is that the idea of an actinula-like ancestor offers the best explanation of the origin of the three classes of Cnidaria. Hadži's notions, which have received an unwarranted amount of publicity, require far too many assumptions (and it must also be said that too many of his arguments are reversible) for them to be seriously considered. The whole trend of evolution within the Hydrozoa (and I do not think this is reversible) is the elaboration of the hydrosoma and the elimination of the free medusa in the higher categories—a clear indication at least as far as this group is concerned, that it cannot be fitted into Hadži's *Turbellaria theory*.

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DISCUSSION

HAND: You make it quite clear that you are in favour of thinking of Narcomedusae and Trachymedusae as primary forms or at least closer to the primitive forms of Hydrozoa than any of the others.

REES: Yes, but they are now rather specialized. I imagine that their ancestors had a common ancestry with the hydroids and medusae.

HAND: Do you really conceive of an actinuloid animal roaming around on the bottom of the oceans somewhere back in the history of this group?

REES: Yes, I think it is quite feasible—even stranger animals exist.

BRAVERMAN: I would like to take this opportunity to point out that the phrase "alternation of generation" seems to obscure a point of interest to the student of development: that what is involved is sexual differentiation, not very different in this phylum than in others, except for the rather elaborate vehicle provided for gamete transport.

REES: I fully agree, but it was a convenient term and has been in use for a long time. Dr. Braverman will remember that I used the expression "the

alternation of a hydroid phase with a sexual medusa phase". You have the same kind of life cycle in the trematodes where there is proliferation of the larvae and there is no difficulty there in deciding which is the adult.

D. CHAPMAN: Is asexual reproduction of planulae present as it is in the Scyphozoa?

REES: I have not seen asexual division in planulae in Hydrozoa; possibly Dr. Werner may have seen something.

WERNER: I have seen any number of the post-larval *Gonionemus* but nothing like that. You mean the reproduction of *Haliclystus*?

D. CHAPMAN: Yes, and even *Aurelia* will do this too. What I mean is that if planulae reproduce asexually, then there are two asexual generations (i.e. planula and polyp) before the sexual medusae.

REES: This is no different from what you find in sporocysts and rediae in the Trematoda.

WERNER: You think that the planula reproduces asexually?

D. CHAPMAN: Yes.

[Here a discussion between Dr. Werner and Dr. D. Chapman was unintelligible on the tape recording.]

REES: I assume that Dr. Werner means the frustulation in *Gonionemus* which is rather like the type of asexual reproduction you get in an *Obelia* with its long stolons and frustules.

WERNER: Yes, that is the same.

REES: Unfortunately you cannot compare the planula with a frustule.

WERNER: No, but I think I should like to compare it in the same way as asexual reproduction, but I do not believe that in the case of a probably accidental or occasional dividing of the planula one can speak of a true asexual reproduction.

THIEL: Have you had asexual reproduction of *Aurelia* in dishes in your laboratory, or outside?

D. CHAPMAN: In the laboratory in dishes.

THIEL: Yes, and you can stimulate this by unfavourable conditions.

D. CHAPMAN: It was only the large planulae that divided as if to maintain the normal size.

HAND: Did you ever see this in the wild?

D. CHAPMAN: No.

THIEL: If you require planula larvae from *Aurelia*, you need only take a mature medusa and put it upside down in a dish where the water does not fully cover the subumbrella. After some time you will find quite a brown circle at the margin of the umbrella, which is composed of planulae and slime. They can easily be taken off with a pipette. If the planulae would reproduce asexually under natural conditions, they would do so in the pockets of the mouth arms as well. The asexual reproduction in dishes seems to be induced by unfavourable conditions.