XIV. The Life-History of the Hydromedusæ: A Discussion of the Origin of the Medusæ, and of the Significance of Metagenesis.

By W. K. Brooks, Johns Hopkins University, Baltimore, Md.

(Read Oct. 7, 1885.)

MOST recent writers upon the origin of the sexual Medusæ which are set free from communities of sessile hydroids, and upon the relation between them and the hydroids, agree in the opinion that the sessile community is the primitive form from which the medusæ have been derived, and that the medusæ have originated through the gradual specialization of the reproductive members of a polymorphic hydroid-cormus.

This opinion is generally, but not universally, accepted for Böhm (9) has given his reasons for believing that the medusæ have arisen from floating, rather than fixed hydroids; and Claus has advanced the opinion that the medusa is older than the polymorphic hydroid-cormus, that the hydra is simply a medusa-larva, and that the alternation of generations has originated through the power to multiply asexually which this larva possesses; and that the alternation of generations is therefore a secondary modification of a life-history which was originally simple and direct.

Neither of these writers refers to the life-history of the Narcomedusæ and Trachomedusæ, and the purpose of the present paper is to show that the metamorphosis of these medusæ furnishes direct disproof of the polymorphism-hypothesis, and completely establishes the explanation advanced by Böhm and Claus, through evidence which neither of these authors discusses.

I may also be allowed to state that I was led, several years ago, by the study of the development of the Trachomedusæ and Narcomedusæ, to the conclusions which are here given, before I was aware that Böhm and Claus had also arrived at the same view of the relation between the medusa and the hydra. As this is my first opportunity to publish the illustrations which are necessary for demonstrating the correctness of this conclusion, I now select, from notes which I have made on the Medusæ of Beaufort during the past six years at the Marine Laboratory of the Johns Hopkins University, those observations which are best adapted for illustrating my view of the origin and significance of alternation of generations or metagenesis in the Hydromedusæ. This paper therefore contains an account of the life-history of a Narcomedusa, *Cunocantha* *octonaria;* a Trachomedusa, *Liriope scutigera;* an Anthomedusa, *Turritopsis nutricula;* and a Leptomedusa, *Eutima mira.* I give detailed accounts of these four life-histories, as I believe that in each case I have enough new facts to warrant their publication as purely descriptive work, independently of their usefulness as illustrations.

I take this opportunity to express my indebtedness to Messrs. A. Hoen & Co. of Baltimore; who, prompted by their interest in the advancement of science, have warmly seconded my efforts to obtain satisfactory photo-lithographs from pen drawings, and have permitted me to draw at will upon their technical knowledge, and upon the resources of their establishment.

The four species which I have selected are among the most abundant and characteristic medusæ of our southern coast, and as no figures of the adult *Cunocantha octonaria,* or *Liriope scutigera* have ever been published, and as nothing whatever has ever been known of the life-history of Turritopsis or Eutima, I have made use of the opportunities which have been afforded by a residence of several summers on our southern coast to obtain a thorough knowledge of these common species.

In a recent paper (1), A. Agassiz says that "Haeckel's work shows how much progress could be made in our knowledge of Acalephs by selecting a few properly placed stations where Medusæ could be studied advantageously," and I hope that this paper will also serve to exhibit the value of such stations.

The four species which I have studied have all been accurately described by McCrady (48), but as my daily familiarity with them for several seasons has enabled me to add many new points, and to correct the few errors which occur in his writings, it seems best to preface my account of the development by a brief revision of the systematic zoology of each species. This is the more necessary as an unfortunate accident destroyed nearly the whole edition of McCrady's papers soon after they were printed, and they are now almost unattainable by the student; and while his descriptions are very graphic, later writers have often given his specific names to other Medusæ than those which he studied.

Section I. The Narcomedusæ.

Plates 43, 44.

Although Cunina and its allies have, in times past, been regarded as Discophoræ rather than Hydromedusæ, chiefly on the account of the fact that the gelatinous substance of the bell is lobed, and also on account of the very striking resemblance between a Cunina and an Ephyra, I think that naturalists are now almost universally disposed to agree that these resemblances are superficial and that the Cuninas and Æginas are true veiled Medusæ. The establishment of a correct view of their affinities is due in great part to the careful study of their anatomical structure, which Haeckel was led to undertake on account of his remarkable hypothesis that they are genetically related to the Geryonidæ, and that the two forms are stages in the same life-cycle; and we can well afford to overlook this error since its fortunate result has been a clearer insight into the affinities of the most instructive of all the Hydromedusæ. His conclusions regarding their relationship to the Craspedotæ are so generally received that it is unnecessary to discuss the subject, nor do I believe that any one doubts the propriety of establishing for these forms a distinct order of Hydromedusæ. Cunina then is a representative of Haeckel's fourth order of Hydromedusæ, the Narcomedusæ, or veiled medusæ with free tentacular auditory organs, with endodermal otolith cells on the bell margin ; with ocelli usually absent, and the tentacles inserted on the dorsal surface of the umbrella, and connected by peronia with the free edge, which is thus divided into a number of lobes. Radial canals absent, or present as flat radial stomach pockets, in the sub-umbral walls of which the reproductive elements are developed. Circular canal obliterated or converted into a series of festoon canals, which fringe the edges of the lobes. The number of radial organs is very variable, seldom four, usually eight, and often as many as thirty-two. Velum thin and wide. Ontogeny, so far as observed, a metamorphosis, with metagenesis in a few exceptional forms. Cunina belongs to the first of Haeckel's four families, the *Cunanthidæ*, or Narcomedusæ with broad, radial stomach-pockets, which are united to the circular canal by double peronial canals; with otoporpæ or ciliated centripetal stripes, and with nettle cells at the bases of the auditory tentacles. Our species, *Cunina octonaria*, McCrady, belongs to Haeckel's genus Cunocantha, which includes species with only eight tentacles, while the true Cuninas have more than eight ; and these eight tentacles are inserted into the ends of the eight stomach pockets, while Cunoctina, which also has eight tentacles, has them inserted into deep notches which divide each pocket into two.

Cunocantha octonaria, *Haeckel.*

Plates 43 and 44.

Cunina octonaria, McCrady, 1857. Gymnophthalmata of Charleston Harbor, p. 109, pl. 12, fig. 4 (young specimen).

Foveolia octonaria, A. Agassiz, 1865. N. A. Acalephæ, p. 57.

Cunocantha octonaria, Haeckel, 1879. Das System der Medusen, p. 316.

Species-Diagnosis. Umbrella lens-shaped, more than twice as wide as high. The eight lobes semicircular, and about two-thirds as long as radius of central portion of umbrella. Stomach pendent, reaching nearly to level of veil, with a wide base and a small circular contractile mouth. Stomach pockets a little wider at distal than at proximal ends, with reproductive elements developed over the whole sub-umbral surface, two-thirds as long as the radius of central portion of umbrella. The tips of the eight equal tentacles project only a little beyond the bell margin. Three auditory tentacles on each of the eight lobes, the central one largest.

Color. Stomach pockets and tentacles golden brown.

Size. Diameter 12 mm. Height, 5 mm.

Ontogeny. Metamorphosis together with asexual multiplication of the larvæ, which are parasitic in the bell cavity of Turritopsis.

Habitat. Charleston, S. C., McCrady; Beaufort, N. C., Brooks; Hampton Roads, Virginia, Brooks.

While the larvæ are said by McCrady to be quite common at Charleston, he found no mature specimens, and only one which had the adult characteristics. He figures this specimen in his Pl. 12, fig. 4, and this figure is copied as fig. 3 of Pl. 44, of this paper. The figures of the adult which are here given, Pl. 44, figs. 4 and 5, are the only ones which have ever been published. Adult specimens are quite common at Beaufort during September and October, but I have found very few during the last weeks of August, or earlier, nor do the specimens of Turritopsis which are captured early in August contain the larvæ, although these are present in about one-third of the specimens which are captured after the Cuninas make their appearance.

By actually rearing the larvæ and medusæ, I have verified McCrady's conjecture that the parasitic form found in the bell of Turritopsis is the young of this species; and while there was no reason to doubt this conclusion, the extremely great interest of the subject, and the very perplexing character of most of our information regarding the parasitic Cuninas, rendered this direct proof very desirable.

One other species of Cunina, *C. discoides*, Fewkes (21), is a very rare visitor at Beaufort, and I have found only a single immature specimen, which was captured outside the bar on Sept. 2, 1882.

The Life-History of Cunocantha octonaria.

The Narcomedusæ are unquestionably the most primitive of the Hydromedusæ, and we might therefore expect their ontogenetic development to throw light upon the more complicated life-histories of the other members of the group, and I shall try to show that this actually is the case, and that the series of species which have been carefully studied does present us with the successive steps through which metamorphosis has become converted into metagenesis or alternation of generations. Our species furnishes one very important link in this chain, and as I have been able to verify all the points in McCrady's classic, but almost inaccessible paper, and to add many new ones, I shall give as complete an account as possible of the metamorphosis, using my own material as well as McCrady's description.

The life-history is illustrated by Plates 43 and 44. Figs. 2 and 5 of Pl. 43, and figs. 3 and 6 of Pl. 44, are copied from McCrady, while the others are original drawings from nature.

McCrady gives (49, p. 10) the following account of the discovery of the larvæ. "In the early part of July, I found the first full-grown specimens of Turritopsis. Among them was one somewhat larger, perhaps, than the rest, which I took with the bell inverted. When placed under the microscope, conceive my astonishment to find, clinging to the bell and sides of the proboscis, numerous little animals of singular aspect, each of which appeared to be sustaining his hold by a four-legged pedestal, and to be writhing about in the water a long appendage, the meaning of which I could not understand. * * * It was not until the 15th of August, that I again encountered the same phenomenon, in a smaller size of Turritopsis, of which quite a number were taken. I found the cavity of the bell around the proboscis again occupied by these larvæ" (see Pl. 44, fig. 6, which is copied from McCrady's Pl. 5, fig. 28), "but besides these formerly observed, were others, which were gradually becoming Medusæ, and still others which had assumed the Medusa-form already, and, lastly, to complete my satisfaction, I saw them, after expulsion from their former abode, swimming about freely in the water, with the rhythmical contractions of Medusæ. It was quite plain from this, that expulsion had taken place, but still I had not seen the expelled animals until some time after the occurrence, and it was not until a later date, Sept. 18th, that I had an opportunity of observing the condition of the larva at the time of expulsion. From this I learned that shortly after assuming independence the larva changes the Medusa-form, under which it is first freed, for another which is more persistent."

Although McCrady believed, at the time his first paper was written, that the larvæ were the young of Turritopsis, he discovered that their position inside the bell is not their primitive one, and the youngest larvæ which he found, and of which he gives the following description, were on the bell-margin among the tentacles. He says of this stage, "It was proboscidian and apparently unprovided with tentacles. * * * It was clinging to the tentaculiferous border of the parents' disk, by means of the extremity of its own proboscis. This circumstance also was peculiar, since in no other instance have I seen the larva to use the proboscis as even a means of temporary adherence for the purpose of locomotion. Its position, also, at the border of the disk, is worthy of especial notice, for the habitual position of the tentaculated larva, is on the sides of the proboscis of the parent, or clinging to the inner surface of the upper part of the swim-bell, and in no other instance have I been able to satisfy myself that there was any adhesion to the tentaculiferous border. Just within the cavity, and almost on the border of the veil, it clung with such tenacity that, notwithstanding the powerful contractions of the parent, by which it would be thrown, now within and now without the opening of the swim-bell, its hold was never lost. Yet it appeared to be in contracted condition from the constant irritation to which, by its position, it was subjected. From the same cause I was prevented from making anything but an outline." This rough outline seems to show that this larva was like, or perhaps a little younger than, the one shown in Pl. 43, fig. 1.

This also was found on the bell-margin, and consisted of a body with two short stout tentacles, ending in rounded batteries of lasso cells, and a very long proboscis with a very small mouth. The digestive cavity, *c*, is lined by large ciliated endoderm cells, *f*, and the mouth may be closed until it is almost invisible, or it may be widely opened. The ectoderm, which contains scattered lasso cells and spots of brown pigment, is thin everywhere, except at the tips of the tentacles and at the aboral end, between the bases of the tentacles, where it forms a thickened pad, *g*.

When detached it swims or glides slowly through the water, and as floating particles are driven away from the surface, there can be no doubt that the ectoderm is covered with small cilia, although I was not able to see them. McCrady says that his specimens had no mouth or tentacles, but his figures show that the larva was essentially like the one which I have drawn, although the tentacles may possibly have been a little shorter.

The very close similarity between this larva and the larva of Polyxenia which Metschnikoff has studied (51), renders it probable that the egg in this case also gives rise to a ciliated planula which floats in the water, and acquires a stomach and a mouth, and that two opposite tentacles are then developed, either just before or just after it fixes itself to the Turritopsis. The rhizopod-like stage, which Metschnikoff (52) has described in the parasitic Cunina-larva which is found on Carmarina, is probably absent in our species, and the planula undoubtedly becomes directly converted into the larva shown in fig. 1.

The larva next makes its way into the bell cavity where it fastens itself by the tips of the tentacles, as shown in Pl. 44, fig. 6. Its proboscis now becomes enormously lengthened, as shown in Pl. 44, fig. 1, and its enlarged tip is inserted into the mouth of the Turritopsis, while two new tentacles are developed between the first two, and soon become equal to them in length, and the aboral end of the body becomes a little elongated, between the bases of the tentacles, as shown in fig. 1.

The interesting fact that the larva shown in Pl. 44, fig. 1, is a true hydra, differing from the actinula larva of Tubularia only in the length of its proboscis and the small number of tentacles, has been almost completely overlooked by all recent writers, although it did not escape McCrady's attention. He says in his second paper, in his diagnosis of the genus Cunina (48, p. 108), "Larva a free hydra, like the free stage of the Tubularia," and on p. 12 of his first paper (49), "The resemblance of these beings to the free young hydra of Tubularia was unmistakable." Very soon after the larva fastens itself by its tentacles, and either before or soon after the two secondary tentacles are developed, it begins to multiply asexually by budding from the aboral process between the bases of the tentacles, and thus forms little communities, like the one shown in Pl. 43, fig. 2, which is copied from McCrady, who calls attention on p. 21, to the obvious fact that this method of budding from an area which is aboral to the tentacles is directly comparable with what occurs in the fixed hydroids, when this part of the body becomes the stem or root. On p. 14, he states his belief that no more than two buds are ever developed at one time, but this is an error, as communities like the one shown in fig. 3, consisting of six or seven larvæ, are frequently met with. This figure will also serve to illustrate the changes through which the larva passes during its development and conversion into the medusa. The young buds have, at first, no tentacles and no mouth, but the proboscis soon lengthens, the mouth appears at its tip, and two opposite tentacles grow out from its base, and are soon followed by two more, alternating with, and at first shorter than the primary tentacles. A rim or flange now grows out from the wall of the body, and in the zone which is occupied by the bases of the tentacles. This zone which is to become the umbrella of the medusa occupies the same position as the inter-tentacular web of such hydroids as the Campanopsis-larva of Eutima, although, unlike the inter-tentacular web, it is composed of both layers of the body wall, and contains a circular diverticulum from the digestive cavity. Four more tentacles now make their appearance, alternating with the first four, and the circular rim becomes notched or infolded opposite the base of each tentacle, or more strictly the free edge between the tentacles grows faster than it does elsewhere, and thus converts the rim into eight marginal lobes, each of which contains a pocket or diverticulum from the central digestive cavity. The tentacles are at first on the rim, in the notches between the lobes, but they very soon begin their migration towards the aboral pole of the body. It is important to note that the lobes are at first directly comparable to the marginal lobes of an Ephyra, inasmuch as their free edges are entirely separated from each other. As the tentacles retreat however, and the notches deepen, the endoderm alone is infolded, thus leaving the bottom of each notch spanned over by a double layer of ectoderm, the radial string of the adult. A sensory tentacle, with a single otolith now grows out from the tip of each lobe, and the free edges of the lobes bend down towards the mouth, thus forming a shallow circular sub-umbrella around the base of the proboscis, and at this stage the larva detaches itself and escapes into the water as a medusa, fig. 4, with an enormously long proboscis, a shallow sub-umbrella, four long and four short tentacles, and alternating with the tentacles, eight marginal lobes, each of which ends in an auditory tentacle, and contains a spacious diverticulum from the central stomach. I have not been able to study the manner in which this cavity becomes converted into the "festoon-canal," but this is probably formed by the growth of an area of adhesion in the centre of each lobe, between the sub-umbral and the ex-umbral endoderm. The pockets of the young medusæ shown in Pl. 43, fig. 4, must not be compared with those of the adult Cunina which are of much later origin. After the medusa is set free the umbrella grows very rapidly, while the proboscis remains without change, so that the animal soon assumes the form shown in Pl. 43, fig. 5, which is an aboral view, copied from McCrady. The lateral pockets of the digestive cavity have now disappeared and the central digestive cavity is nearly circular, but it soon becomes folded in at its edge, between the bases of the tentacles, as shown in Pl. 44, fig. 2, in which figure the right half is an oral, and the left an aboral view. The eight inter-tentacular notches on the free edge of the stomach now deepen rapidly as shown in fig. 3 (copied from McCrady), and thus give rise to the eight stomach pockets of the adult, while a thickening on the oral surface around the circumference of the stomach marks the rudimentary reproductive organs, which soon spread over the whole oral surface of the pockets. The long proboscis of the larva soon disappears, so that the stomach becomes a flat pouch with a contractile mouth in its centre, but in the adult the oral wall of the stomach again becomes drawn downwards to form a pendent proboscis.

The life-history of *Cunocantha octonaria* may now be briefly summarized as follows:

The larva is a ciliated swimming organism, with a mouth, a long proboscis and two opposite tentacles. It soon develops two more tentacles, loses its cilia, and becomes a hydra with a greatly developed proboscis and with its aboral extremity reduced to a small prominence, from which other hydras are budded. There is no sessile stage, but the locomotor hydra makes its way into the bell of a Turritopsis, where it fastens itself by its tentacles, and lives as a parasite. It then becomes directly converted into a medusa by the outgrowth of an umbrella around its tentacular zone, and escaping into the water begins its medusan life. Before it becomes a medusa it produces other larvæ by budding, and all these become medusæ. The state of our knowledge of the development of other Narcomedusæ, especially of Polyxenia and Æginopsis, indicates that the parasitic habit of the larvæ is not primitive but recently acquired, and the tendency to multiply asexually has probably been also secondarily acquired by the larva as an adaptation to its parasitic life. In the case of our Cunocantha all the larvæ become medusæ, and there is therefore no true alternation of generations, but in the case of the Cunina studied by Uljanin (60), and afterwards by Metschnikoff, the adaptation to a parasitic habit is much more perfect, and the larva which hatches from the egg and gains access to the Carmarina, never becomes converted into a perfect medusa, but remains as a degraded nurse, from which other larva are budded, and as Uljanin points out, we have in this case a true alternation of generations.

The Evolution of our Knowledge of the Life-History of the Narcomedusæ.

The growth of our knowledge of the Narcomedusæ forms one of the most remarkable chapters in the history of zoology, and I shall review it at some length, in order to exhibit the life-history of our American *Cunina octonaria* in its true relations, and also to show by what slight increments our knowledge has grown. The life of an animal which passes part of its time inside the body of another as a parasite, and then, assuming quite a different form swims at large in the water, presents a very perplexing puzzle, which becomes still more confusing when, as in the Narcomedusæ, some species are parasitic and others are not. Each observation then becomes important, and I shall refer to many papers which contain very small additions to our positive knowledge, the present state of which may be summarized as follows:

1. Some of the Narcomedusæ develop directly from the egg, without asexual multiplication.

2. In other species the ciliated larva becomes a parasite upon the body of a totally different medusa, gaining access to the sub-umbrella of Turritopsis, or to the digestive cavity of a Geryonid. It there multiplies asexually; producing, by budding from an aboral stolon, other larvæ which are at first hydras. These hydra larvæ become converted into medusæ by direct metamorphosis.

3. Similar Cunina larvæ are found in the stomachs of many species of Cunina. In some cases the larvæ become converted into Cuninas with the specific characteristics of the adult which carries them, but in other cases they differ in the number of tentacles and sense organs, and in other particulars. The youngest of these larvæ are free and ciliated, while the older ones are attached and produce buds from an aboral stolon.

4. No one has shown, by careful examination, that any adult Cunina produces buds from its stomach or from any other part of its body, and there is every reason for believing that the Cunina larvæ found in their stomachs are parasites, like those found in Turritopsis and in Geryonids, and that a Cunina larva, found in the stomach of an adult Cunina, does not necessarily belong to the same species with the adult.

So far as I am aware Krohn was the first to observe a Cunina larva. In a paper which was published in 1861 (41), he says that he found at Messina, in 1843, great numbers of tentaculated larvæ, fastened by their aboral surfaces to the protruded gastrostyle of a Geryonid, *Geryonia proboscidalis.* He gives few details, and appears to regard the larvæ as the asexual progeny of the Geryonia.

In 1851, Johannes Müller (71) captured at the surface of the ocean at Marseilles great numbers of small ciliated larvæ, and a series of older stages which were sufficiently complete to satisfy him that the larva is the young of a very simply organized Narcomedusa, *Æginopsis* (*Solmundella*) *mediterranea.*

As the youngest larvæ are ciliated, he believed that they are newly-hatched egg-embryos, and as each one of them becomes converted into a medusa, he suggests that

Æginopsis will probably be found to develop directly from the egg without alternation; a prophecy which was verified twenty-five years later by Metschnikoff (51).

The youngest larva which Müller figures, Pl. XI, fig. 1, is a hydra essentially like the one shown in our Pl. 43, fig. 1. The position of the tentacles is different, but he says in the text, that they are often carried as they are shown in our figure.

In the autumn of the following year, 1852, three young naturalists, Gegenbaur, Kölliker and H. Müller, met at Messina to spend a few months in zoological research at the seashore, and their fruitful harvest furnishes one with the earliest evidences of the value of marine zoological stations.

Kölliker, who studied the lower invertebrates, made many interesting observations on the medusæ, one of the most important being the discovery of young Cuninas in the stomach of an old one, which he names *Eurystoma rubiginosum* (*Cunina rubiginosa*, Haeck.).

The oldest larvæ are so similar to another Cunina which he found at the same place, and named *Stenogaster complanatus*, that he decided that they were the young of this species. He says nothing about budding from the stomach, and adopts the view, which is undoubtedly correct, that they had gained access to the stomach from outside, although he supposes that they had been swallowed by the Eurystoma as food.

In 1854, Gegenbaur (24) found small bud-like bodies, each with four tentacles, attached to the walls of the stomach of a Cunina, which he named *Cunina prolifera*, since he supposed, from the fact that the larvæ became adults of the same species, that they are produced by budding.

The observations which come next in historical order (1856) are by an American naturalist, McCrady (48, 49), and they will always remain a monument to the accuracy of this sharp-sighted observer, for they give for the first time a pretty complete history of the life of a Cunina, which is accurately illustrated and vividly described. McCrady's papers are very different from the brief notices which have been referred to above, and they are by far the most important which have ever appeared upon the subject. They not only serve to throw a flood of light upon the significance of earlier observations, but they also contain a record of facts which should have prevented the confusion which later writers have introduced. Unfortunately the edition of his paper was almost completely destroyed before it was distributed, and reference to it is now nearly impossible, and although proper credit is now given to the author, a desire to place the facts which it contains within the reach of all was as strong an inducement to the preparation of this paper as my desire to publish my own additions to the subject. I have illustrated some stages which he did not obtain, and my figures exhibit many points which are not shown in his much smaller ones, but I have also copied a few of his original figures, and I have embodied all the leading points of his paper, the chief results of which are as follows:

1. The young *Cunina octonaria* is a parasite inside the bell of a Hydromedusa, Turritopsis.
2. The larva is a hydra.
3. It multiplies asexually by budding from an aboral stolon, and gives rise to other larvæ like itself.

4. Each larva finally becomes metamorphosed into a medusa, and there is no alternation of generations.

McCrady's papers were published in 1856 and 1857, and at about the same time (1856) Leuckart (47) figured and described a Cunina larva under the name *Pyxidium truncatum* (Pl. 11, fig. 7), but he gives no account of its history.

In 1860, Keferstein and Ehlers (72) repeated Gegenbaur's observations upon a Cunina which they call *Ægineta gemmifera*, but which is probably the same as *Ægineta* (*Cunina*) *prolifera*, Gegenb. They were ignorant of McCrady's work, and believed with Gegenbaur that the larvæ are formed as buds from the wall of the stomach.

In 1861, Krohn published the observation above referred to, made in 1843, to the effect that peculiar bud-like bodies are sometimes found on the gastrostyle of Geryonids, and the same volume of the Archiv f. Naturgeschichte contained a paper by Fritz Müller (56), in which he says that, in 1860, he found on the gastrostyle of a Brazilian Geryonid, *Liriope catherinensis*, a group of medusa-buds, each of which became metamorphosed into a young Cunina closely resembling an adult Brazilian Cunina which he names *Cunina Köllikeri*. In the same paper he says that in 1859 he found in the stomachs of male specimens of the Cunina, young ciliated larvæ which became young Cuninas, differing from *C. Köllikeri*, in the number of tentacles. He holds that the larvæ found in the stomach of the adult Cunina are asexual buds from the walls of the stomach, while he believes that those found in the stomach of the Geryonid have been swallowed as food.

In 1865, Noschin published a paper (57), in which he states that he has found on the gastrostyle of *Geryonia* (*Carmarina*) *hastata*, bud-like larvæ which became medusæ which he identifies as young specimens of Keferstein and Ehlers' *Cunina discoidalis*. He regards this as a case of alternation of generations, and advances the astonishing hypothesis that the Geryonid, a Trachomedusa, and Cunina, a Narcomedusa, belong to the same cycle, and that the buds which become Cuninas are produced by the Carmarina.

In the same year Haeckel published a brief preliminary abstract and two fully illustrated papers (29, 30), in which he describes the same facts, and advances, independently, the same astonishing hypothesis, but the mistake is the more remarkable in this case since Haeckel had himself traced the metamorphosis of Carmarina from a very young and small larval medusa, which, as he correctly conjectures, is an egg-embryo (30 *d*). If we believe that the Cunina buds are also produced by the Carmarina, we are compelled to believe that this medusa has two methods of reproduction, producing Geryonids like itself from eggs, and producing Cuninas from internal buds. Haeckel boldly accepts this hypothesis (30 *a*, p. 184), and says on p. 293, "I do not doubt that what I have here described as a remarkable exception will in time be found to be a widely distributed occurrence, at least among the lower medusæ, especially the Æginidæ. Allotriogenesis or alloeogenesis, as this form of reproduction may be called, is very essentially different from all forms of alternation of generations." Haeckel's papers are beautifully illustrated, and his figures show that although the proboscis of his larva is shorter than that of *Cunina octonaria*, and the number of buds which are produced very much greater, there is, in all other respects the closest resemblance to the American larva as described by McCrady, with whose work Haeckel was not acquainted.

On the whole Haeckel's error was a fortunate one for science, for it led him to make a very thorough comparative study of the adult Geryonid and Cunina, and this comparison resulted in his two valuable and beautifully illustrated papers (30), and showed conclusively that the Cuninas are veiled medusæ, not very different in structure from the Geryonidæ, through which they are related to the ordinary Hydromedusæ. The Cuninas and their allies had previously been regarded as Acraspeda, but Haeckel's results, which are now almost universally accepted, form a valuable addition to positive science, although they were based upon this strange hypothesis.

The next paper in historical order contains no new observations, and is simply an attempt by Allman (6) to bring Haeckel's hypothesis into harmony with our knowledge of other hydroids. He accepts without question Haeckel's opinion that a Geryonid may give rise to Cuninas by budding, and he sees nothing remarkable in such an occurrence. On p. 469, he says "While the observations of Haeckel, however, can scarcely be too highly estimated for the light they throw upon the relation between the Geryonidæ and Æginidæ, it appears to me that he *greatly overrates* the difference between the genetic phenomena which are here presented and those already well known among the Hydroida." He then gives a series of diagrams by the aid of which he attempts to show that the production of medusæ by budding from the wall of the stomach of a medusa of a totally distinct order, which also reproduces itself normally by eggs, is no more than the analogy of Hydractinia would lead us to expect. He makes no reference to McCrady's paper, with which he does not seem to be acquainted. It is rather strange to find that while he accepts without question the statement that a Geryonid may produce Cuninas by budding, he is half disposed to believe that the Cunina buds found in Cuninas by Gegenbaur, Keferstein and Fritz Müller, are to be regarded as "suggesting parasitism rather than gemmation" (p. 474).

Metschnikoff's papers (30 *a*, *b*, and *c*), which come next in historical order (1874), are, with the exception of McCrady's papers, the most important ones which have appeared, for he gives for the first time a complete life-history of two Cuninas, *Ægineta* (*Solmoneta*) *flavescens*, and *Æginopsis* (*Solmundella*) *mediterranea*. He proves, by rearing these medusæ from the egg, the correctness of the prophecy Johannes Müller made twenty-five years before, that, in these two species at least, there is no alternation of generations, no sessile hydra-stage, and no asexual multiplication. In a third paper (30 *a*), he shows, as Fol had done a few months before, that *Geryonia* (*Carmarina*) *hastata* also develops directly from the egg without alternation or budding. In a third paper (30 *c*), he gives an illustrated account of the development of the Cunina larvæ which are found in the stomach of Cunina, and although he calls attention to the close similarity between the youngest of these larvæ and those which he reared from the eggs of Ægineta and Æginopsis, and although the youngest larvæ were found swimming in the stomach, not fastened to its walls, he regards them as buds from the wall of the stomach. His account shows that the history of the larva is very much like that of the one which McCrady studied; that the larva is a hydra; that it multiplies by budding from an aboral stolon, and that the hydra-larvæ which are thus produced change into medusæ by metamorphosis. He does not refer to McCrady, but it seems strange that he was not led to question the origin of the larvæ by budding from the stomach, by his knowledge of the fact that Fritz Müller and Haeckel had observed similar proliferating Cunina larvæ in the stomachs of Geryonids.

In 1875, Uljanin (60, 61) proved that there is no genetic connection between the Geryonid and the Cunina larvæ found in its stomach, but that they gain entrance from outside and then multiply asexually, and that they are sometimes found on the inside of the bell, as well as in the stomach. He does not refer to McCrady, whose papers were published twenty years before, but he shows that the history of the parasitic larvæ found in Carmarina is essentially like that of the one which McCrady had found in Turritopsis.

There is one interesting difference, however, for in his species the original larva never becomes a medusa, but permanently retains its larval nature, budding off numerous larvæ which become medusæ. He calls attention to the fact that this is a true alternation of generations, the egg-larvæ being the first, and the larvæ which are budded from it the second generation.

This discovery, and his verification of McCrady's discovery that the larvæ are parasites, entitle his paper to an honorable position, but I cannot believe that his account of the minute structure and of the mode of development of the larva is correct, as it conflicts with all our knowledge of the subject. He says that the tentacles are developed on the edge of the mouth, that the buds are formed at the oral end, that the digestive cavity is formed by a peculiar infolding and splitting of the endoderm, and he figures the embryo as a two-layered gastrula, with an aboral mouth which has nothing to do with the definitive mouth of the larva; and as this account cannot be reconciled with our general knowledge of the subject, or with the careful observations which Metschnikoff made (52) several years later, I am compelled to believe that he has failed to interpret his observations correctly.

In the same year, 1875, Schulze showed (58) that there is no organic connection between the Geryonid and the larvæ found on its gastrostyle, and he therefore decides that the Cunina embryo originates outside the Geryonid, and after fastening itself to its gastrostyle, gives rise to new larvæ by budding, as Uljanin also shows to be the case.

In December, 1881, Metschnikoff published an illustrated paper (52), in which he traced the embryology of the parasitic larva found in Carmarina, showing that the group of medusa-buds is formed by budding from the aboral surface of a ciliated egg-embryo, which gains access to the digestive cavity and there multiplies asexually. In this species, *Cunocantha parasitica*, Haeck., the egg-embryo, which in all probability corresponds to the *mother bud* of *Cunina rhododactyla* and to the larva shown in our figure 1, is very much degraded. It fastens itself to its host by means of pseudopodia which are thrown out at the oral end from a very peculiar large cell, which fills its digestive tract. It develops tentacles, but never acquires an umbrella or a proboscis, and soon begins to produce medusa-buds from an aboral stolon.

As Uljanin has shown, it does not become converted into a medusa, but is simply a nurse for the production of medusa-buds. This species therefore presents an example of a true alternation of generations, since the embryo which hatches from the egg remains as a larva and never becomes a medusa, although it gives rise to buds which do become medusæ.

In many respects Metschnikoff's observations upon the structure of the egg-embryo are in conflict with Uljanin's account; but as it is impossible to reconcile the statements of the latter writer with our general knowledge of the subject, I think we may safely conclude that Metschnikoff's account is the more trustworthy.

Both authors agree that the egg-embryo of the species which occurs in the stomach of Carmarina is degraded and has no umbrella, while Metschnikoff shows that the proboscis also is absent.

The next paper in historical order is a short one which Fewkes published in 1884 (19). He gives a brief account, with one figure, of Cunina larvæ which he found at Villafranca, attached to the gastrostyle of Carmarina, and he verifies Uljanin's statement that the larvæ are sometimes found on other parts of the medusa. He has observed them on the umbrella.

The youngest larva which he found was attached to the tip of the gastrostyle. It was solitary and he regards it as an egg-embryo destined to develop a stolon and to give rise to medusa-buds. He states that it was furnished with a long proboscis and a diminutive bell, and was almost identical with the youngest larva figured by McCrady, which, however, has a short proboscis and no bell, and it is impossible to reconcile his account with the observations by Uljanin and Metschnikoff, which show that the nurse is, in the species which they found in Carmarina, greatly degraded and has neither proboscis nor umbrella. His description is inaccurate, or else his species is a new one; and if the latter is the case it is to be hoped that his drawings and a more minute description will soon be published.

Fewkes attempts to show that there is a morphological similarity between a Siphonophore and the clusters of Cunina buds which are found in Carmarina. In support of this view he states that "these clusters or colonies of young Cuninæ, as is well known, ultimately dissolve their connection with the stolon and swim away as free medusæ." If he means by this sentence that the *clusters or colonies* swim away, the phenomenon is neither "well known" nor supported by a single published observation. If he means simply that each medusa-bud is detached from the stolon and becomes a free medusa, there is little resemblance to a Siphonophore; nor does our knowledge of the subject furnish any basis for his statement, p. 305, that the stolon which carries the buds is a modified proboscis.

He says "Cunina has become degenerated by its parasitism or commensalism so that the proboscis with young budding from it alone remains. Its bell has gone, the mouth opening is no longer functional, and the proboscis, which has elongated into a stolon attached to the body of a host, is closely crowded with the young;" but Metschnikoff's account of this particular form, shows that here, as in all other Cuninas which have been studied, the stolon arises from the aboral surface and has nothing to do with the proboscis.

This paper completes the long list of observations upon this interesting subject, and it may now be well to summarize the history of research regarding the parasitism of Cunina.

1. In Ægineta and Æginopsis the egg gives rise to the ciliated planula, which acquires a mouth, a short proboscis and tentacles, and thus becomes a free hydra or actinula, which is directly metamorphosed into a medusa. One egg gives rise to a

single larva and this becomes converted into a single adult. There is no asexual multiplication, no parasitism and no alternation of generations.

2. In *Cunina octonaria*, the hydra embryo, while still ciliated like a planula, but furnished with a mouth and two tentacles, gains access to the bell of a Hydromedusa, Turritopsis, where it lives as a parasite, and produces other larvæ, like itself, by budding. The first larva, like all the others, becomes a medusa, so that we have budding and parasitism, but no alternation.

3. The Cunina larva, which inhabits Geryonids, is essentially similar, but the first larva or egg-embryo does not become a medusa, so that we have alternation as well as budding and parasitism.

4. As no one has proved that the Cunina larvæ found in Cuninas do not pass in from outside, and as their history is like that of the species above noticed, there is every reason for believing that they also are parasites.

Section II. The Trachomedusæ.

Plates 41, 42.

Liriope is a representative of the third of the four orders into which Haeckel divides the Hydromedusæ; the *Trachomedusæ*, or veiled medusæ, with auditory tentacles, which are either free on the bell margin or inclosed in auditory vesicles, with endodermal otolith-cells. Ocelli on tentacular bases usually absent. Reproductive organs on the course of the radial canals, which are four, six or eight in number, often with blind centripetal canals between them. Veil, thin and wide. Ontogeny, as far as it is known, hypogenesis or direct development without alternation, but usually with metamorphosis.

It is a representative of his fourth family or the *Geryonidæ:* Trachomedusæ with four or six radial canals, with broad, leaf-like reproductive organs; a long proboscis, eight or twelve peronia, and closed auditory vesicles, which lie on the axial sides of the peronia in the gelatinous substance of the umbrella-margin; and to the first subfamily, the Liriopidæ, or Geryonidæ with four radial canals, four reproductive organs and eight auditory vesicles. He divides the subfamily into two genera: Lirantha with eight permanent tentacles in the adult; and Liriope, with only four; and he places our species in the first genus.

Haeckel has undertaken the very perplexing and laborious task of introducing order and system into the confused mass of fragmentary observations which have been printed regarding the Geryonidæ, and as his writings upon the subject introduce order where all had been confusion, and as he himself is more familiar than any other naturalist with the species and genera of the family, I hesitate to depart in any particular from his system: but inasmuch as specimens of our *Liriope scutigera* are sometimes found with four, five, six or seven tentacles, as well as specimens with the unusual number eight, I cannot believe that his two genera Liriantha and Liriope are natural, and I therefore retain the generic name Liriope for our species. Fewkes' statement (Acalephs from the Tortugas, Bull. Mus. Comp. Zool., IX, No. 1, p. 279) that Haeckel bases his two genera upon the presence or absence of blind centripetal canals is inaccurate, as a reference to Haeckel will show.

The large figure at the top of Pl. 42, which is a photolithograph of a pen drawing made from nature, is the only figure of *Liriope scutigera* which has ever been published.

Liriope scutigera, *McCrady.*

Liriope scutigera, McCrady, 1857; Gymnophthalmata of Charleston Harbor, p. 106.
Liriope scutigera, L. Agassiz, 1862; Contributions IV, p. 365.
Liriope scutigera, Brooks, 1883; Studies, II, p. 475.
Liriantha scutigera, Haeckel, 1879; Medusen, p. 287.
Xanthea scutigera, Haeckel, 1864; Geryoniden, p. 24.

Species-Diagnosis. Umbrella, when relaxed in swimming or floating, about half as high as wide: but sub-spherical or almost cubical when violently contracted. Gastric peduncle conical, thick, about as long as diameter of umbrella, gradually diminishing in size from the base to the proximal end, where it terminates in a pointed, tongue-like process, which may be protruded from the mouth, which is quadrate, without lips. Reproductive organs nearly square with rounded corners, extending from near circular tube to top of sub-umbrella, and nearly meeting along the inter-radii. Four perradial flexible, contractile hollow tentacles, three or four times as long as the diameter of the umbrella, and four short stiff interradial tentacles, which are absent in a few exceptional adults. Eight sensory vesicles, one at the base of each interradial tentacle, and one a short distance from the base of each perradial tentacle.

Color. By transmitted light, the tip of the proboscis is purple; by reflected light it is green and the ovaries red.

Size. About one-third of an inch in diameter.

Habitat. Abundant all through the summer in Hampton Roads, Virginia; at Beaufort, North Carolina, and at Charleston, South Carolina. It is one of the most characteristic medusæ of our southern coast.

Ontogeny. Hypogenesis with metamorphosis.

Haeckel's diagnosis of the species, which is abstracted from McCrady's account, is in the main correct, but it contains several statements which are not strictly accurate, such as the statement that the umbrella is nearly spherical, that there is no tongue-like process and that the reproductive organs are round. The species is distinguished from Fritz Müller's *Liriope catherinensis* (Arch. f. Naturges. xxv, p. 310, pl. 11) by the fact that the reproductive organs are nearly square, instead of being elliptical, and by the fact that they reach nearly to the circular tube, while Müller's figures show quite an interval between them and the circular tube. The primary radial tentacles of the young also lack the terminal flagellum or hook which is shown in Müller's figures.

Haeckel has shown that Agassiz's *Liriope scutigera* (N. A. Acalephs, p. 60, fig. 87) is quite different from McCrady species, and this is also true of Fewkes' *Liriope scutigera,* (Studies of the jelly-fishes of Narragansett Bay, Bull. Mus. Comp. Zool., VIII, 8, p. 126, Pl. 6, figs. 7, 10, 11, 1881). There is a lack of agreement between the text and the figures of Fewkes' paper, as he says there are only four otocysts, while his figure shows four on one-half of the umbrella, but neither the text nor the figures correctly represent *L. scutigera*, McCrady.

Special Description. McCrady's description of this species is so very vivid and minute, that, although he gives no figures, there is not the least difficulty in identifying the species, thousands of specimens of which may be procured at any point between Charleston and the Chesapeake Bay. His account of the habits of the animal is so graphic that I quote it: "This species is evidently gregarious, great numbers being found together in nearly every instance when I have found it at all. It is bold and rapid in its movements and very rapacious. I have seen one of this species, so extremely diaphanous as to make the impression of nothing but a set of outlines, seize upon a small fish fully thrice as large as itself, and securing itself by spreading out its lips upon it, making them act as suckers, and then entangling about the poor animal its four long tentaculæ, hang on in this manner despite the violent struggles of the fish which, alarmed, swam violently about the jar, until at last apparently from sheer exhaustion, it was evident he was dying. At last changing color, the fish turned over on his side and expired." McCrady speaks of the great size and circular form of the reproductive organs, but their shape may be more exactly described as square with rounded corners. He gives the following very accurate account of their general appearance. "They are four in number, and are so large that they very nearly touch each other laterally, and stretch very nearly from top to bottom of the disk-cavity, thus occupying almost the whole inner surface of the bell. When viewed from above their unyielding structure gives the disk a quadrate outline, and viewed in profile they appear as large, circular shields especially when at the death of the animal they assume a marked white coloration." The quadrate outline, however, is only apparent, except when the violent contraction of a freshly caught or a dying specimen causes the substance of the umbrella to conform to the shape of the distended ovaries. McCrady's account of the sense organs is somewhat misleading, owing to the fact that it is founded, in part, upon an examination of immature specimens. He says "the concretionary capsules are of two sorts, a small round vesicle containing a concretionary corpuscle at each of the shorter and complex tentacula, and at each of the longer and simple tentacula, a *double* capsule consisting of two cysts, one above the other, and connected by an intermediate (tubular?) thread, apparently a continuation of the membrane of the cysts." This second cyst, with its connecting thread, is really the degenerated primary radial tentacle of the young medusa. It must not be confused with the interradial club-shaped structure described and figured by Fewkes (Pl. vi, figs. 7 and 11.)

THE EMBRYOLOGY AND METAMORPHOSIS OF *Liriope scutigera*, MCCRADY, AND THE LIFE-HISTORY OF THE GERYONIDÆ.

Since the publication, in 1856, of Leuckart's observation on the metamorphosis of *Geryonia exigua* (47) naturalists have been aware that the young Geryonid is quite different from the adult, and that, during its youth, it undergoes a complicated metamorphosis.

It is generally stated in the monographs as well as in the text books that although the young medusa is unlike the adult, there are no true larval stages, since the egg gives rise directly to a medusa, which becomes metamorphosed, through a series of changes, into the adult.

This is, as I shall show, an erroneous interpretation of the facts, for the published accounts, when rightly interpreted, show that the larva actually passes, like other hydromedusæ, through a planula stage and a hydra stage, although naturalists have been misled by the fact that the hydra-larva is locomotive, and as it does not multiply asexually the fact that it is a true hydra has been entirely overlooked; and, so far as I am aware, not a single naturalist has noticed the existence of a hydra stage.

Most writers in fact have been so firmly impressed with the belief that medusæ have originated from sessile hydroid communities, that they have not only overlooked this stage in the development of the Geryonidæ, but they have expressly stated that it has disappeared. Thus Balfour states (65, p. 153) that The Trachomedusæ are * * * "probably derived from gonophores in which the trophosome disappeared from the developmental cycle," and Haeckel says (31) of the development of the Trachomedusae: "This form of ontogenesis is to be regarded as a secondary or cenogenetic process, which has originated from the primitive metagenetic mode of development through the loss of the polyp generation." See also Lendenfeld (46, p. 448).

So far as I am aware, Böhm is the only writer who has recognized the possibility of any other explanation, and he dismisses the subject very briefly and makes no reference to the Trachomedusæ, although he does not believe that alternation of generations is primitive, and suggests (9, p. 158) that "Lucernaria, the Ctenophora, the free Siphonophora (*and possibly some of the medusæ without a polyp-generation?*) may be the direct descendants of a free ancestral form without the intervention of a sessile stage."

The total absence of anything like alternation of generations gives especial importance to the occurrence of a hydra stage in the life-history of the Geryonidæ, and furnishes a key for the interpretation of the more complicated life-histories of other Hydromedusæ, proving, as I think, the correctness of the view so briefly hinted by Böhm; and I therefore give in Pl. 41 figures of various stages in the life of *Liriope scutigera*. The development of this species has never been described, although we have in Fol's paper on the embryology of *Geryonia fungiformis* (22) and those by Metschnikoff (51, 52) on *Geryonia fungiformis*, *Geryonia hastata* and *Liriope eurybia*, a very complete history of closely allied species.

Ray Lankester has stated in a recent paper that Fol, in his well known and valuable monograph "has completely failed to give even an approximately correct account of them atter" and that Metschnikoff's description is "erroneous" (45). As my own observations on our American Liriope agree in every essential particular with the accounts by Fol and Metschnikoff it seems proper to give, in detail, my verification of the excellent researches which are thus sweepingly condemned.

I have been able to add a few points, such as the origin of the mouth, and of the radial canals, but my observations show that the development of our Liriope is, in all essentials, like that of the European Geryonidæ.

Our species appears to be very regular in its breeding habits, and specimens captured at all hours of the day laid their eggs at about 8 P. M., the eggs passing out of the mouth. Fol says that when he kept female specimens of *Geryonia fungiformis* by themselves they did not lay their eggs, but that as soon as a mature male was placed with them and discharged the contents of his reproductive organs into the water, the females at once deposited their eggs (22).

This was not the case with our species, for when I placed a single female by itself it discharged its eggs promptly at the proper hour. In two or three cases these eggs were not fertilized and soon died, without exhibiting any evidence of vitality, but in other cases the eggs laid by an isolated female developed normally. Schulze has shown, however, that hermaphrodite Geryonidæ sometimes occur, and these females may possibly have been hermaphrodites; but the occurrence or absence of fertilization makes no difference in the time of oviposition.

The eggs develop very rapidly and at six o'clock the next morning the embryos are in the stage shown in Pl. 9, fig. 3, so that it is necessary to keep them under observation all night in order to study the early stages. The segmentation of the egg and the formation of the ciliated embryo have been correctly and very minutely described by Fol (22) and by Metschnikoff; and, as is well known, the origin of the germ-layers is very peculiar and without any exact parallel. The transparent spherical egg, which consists of a peripheral layer of granular protoplasm, and a central less granular portion, in which the protoplasm is finely reticulated, undergoes total regular segmentation, and gives rise to a spherical embryo, composed of a single layer of larger cells, arranged around a small central segmentation cavity.

Each of these cells consists of an internal transparent reticulated portion, and an outer more granular portion, Pl. 41, fig. 1, $a+b$. Soon the outer granular portion, fig. 1, *a*, separates from the transparent portion *b*, leaving this as an independent endoderm cell inside the layer of ectoderm, which is formed from the outer granular ends of the blastoderm cells. This division of each blastoderm cell into a central endodermal cell, and an outer ectodermal one, does not take place in all parts of the egg at the same time, and eggs may easily be found in the stage which is shown in fig. 1, where two distinct layers are present on one side only. The central cavity, the segmentation cavity, persists, and ultimately becomes converted into the chymiferous tubes, and the stomach of the adult medusa. Before the delamination of the blastoderm cells is completed, the ectoderm cells begin to multiply by division, and the ectoderm cells of the young embryo are therefore more numerous than the endoderm cells, which divide more slowly. At the end of the process of delamination, the embryo, fig. 2, consists of a continuous hollow spherical layer or shell of granular and slightly flattened ectoderm cells, fig. 2 *a*, and within this, and in contact with its inner surface, a second concentric hollow sphere, *c*, of large transparent rounded endoderm cells, with reticulated protoplasm, surrounding a small central digestive cavity, *d*. The gelatinous substance of the umbrella now begins to appear between the ectodermal shell and the endodermal one, thus stretching and flattening the ectoderm cells, which continue to increase in number and soon form a very thin layer of pavement epithelium, fig. 3, upon the outer surface of the gelatinous umbrella, *b*.

According to Fol, the gelatinous substance is not homogeneous, but is marked by fine striations, which radiate through it in all directions from the surfaces of the endoderm cells. The latter also increase in number, and become flattened as at *c*, in fig. 3, while the digestive cavity, fig. 3 *d*, becomes correspondingly enlarged. The endoderm cells preserve their reticulated structure, which is visible until after the tentacles of the medusa appear. When the gelatinous substance first appears, and for some time after, it is uniformly thick and almost perfectly spherical, and the endodermal shell is also spherical, concentric with the outer surface, and separated from the ectoderm at all points; but it soon approaches, and finally touches the ectoderm, at a point which is to become the oral pole of the medusa, and which is below in fig. 3. The gelatinous substance, which lies between the two layers, is absorbed at the oral pole during this process, and Fol makes the very satisfactory conjecture, that the force which pushes the endodermal sac to one side of the spherical embryo is produced by the more rapid secretion of the gelatinous substance at the aboral than at the oral pole. The embryo now changes its shape a little, and becomes slightly flattened at the ends of the principal or oral-aboral axis, and the cells of both layers become thickened around the oral pole, to form an oral area or *peristome*, *a'*, *c'*. At this period the embryo rises from the bottom and floats in the water, apparently at rest. Under the microscope, however, it is easy to see that it does not simply float, but swims about with a very slow uniform motion, and although I was not able to see any cilia, small floating particles were thrown away as if by the action of cilia, which are undoubtedly present upon part if not the whole of the ectoderm. Fol states (22, page 482) that, at this stage in the development of the very much larger embryo of *Geryonia fungiformis*, scattered cilia make their appearance over the whole ectoderm, and cilia are visible upon the oral area of our species at a later stage, as shown at *c*, in figs. 4 and 5.

The spherical larva, with its two concentric layers of cells separated from each other by a gelatinous umbrella, without a mouth or any other passage into its spacious digestive cavity, and swimming by means of ectodermal cilia, is at first sight very different from the embryos of other medusæ; but its peculiar appearance is due to the very early formation of the gelatinous substance of the umbrella. If this were absent or if it made its appearance at a later stage, the embryo would be a ciliated, mouthless, two-layered planula, almost exactly like an ordinary planula, after the endoderm and digestive cavity have made their appearance, but before the mouth has been formed. The Geryonidæ accordingly pass through a planula stage, directly comparable with the same stage in other hydroids, but complicated by the accelerated development of the digestive cavity and the gelatinous umbrella.

The origin of the endoderm, at a very early stage of segmentation, by the simultaneous delamination of the inner ends of all the blastoderm cells is clearly a modification of what occurs in ordinary hydroid planulæ, although the segmentation cavity persists as the digestive cavity, and the endoderm never forms a solid mass, as it certainly does in the planulæ of Hydractinia and Tubularia. In Eutima however the segmentation cavity persists as it does in Liriope, and this is no doubt true also of other hydroids.

The two naturalists who first described the development of the Geryonidæ, Fritz Müller (55) and Haeckel (30) published their accounts at a time when embryological knowledge was much less advanced than it is to-day and when comparatively little was known of the histological structure and significance of the hydroid larva. They both fell into the error of regarding the central capsule of cells as the sub-umbrella, and believed that the digestive cavity, and its endodermal walls originated at a much later period; but our present comparative knowledge of the embryology of other organisms would now lead us, even in the absence of any record of its later history, to regard the central cells as an endoderm, for the hypothesis that they are the ectoderm of the sub-umbrella implies that the Geryonoid embryo is fundamentally different from all other known hydroid embryos.

At the present day the fact that the central cells of an ordinary planula become the cells of the digestive cavity is, in itself, an evidence that the central cells of the Liriope embryo are their homologue and equivalent, and the later history of the embryo fully bears out this view of their nature, and puts out of question the acceptance of Fritz Müller's and Haeckel's interpretation.

The next change which takes place, the formation of the mouth, is shown in figs. 4 and 5. The cells of the oral area or peristome become ciliated and a depression appears in the centre of the outer or ectodermal area, and a similar internal one is found in the endoderm, as shown at *e* in fig. 4. These two depressions soon meet, and break through to form the mouth, fig. 5, *c*, the edges of which become ciliated. Food is now swept into the digestive cavity, although little growth takes place until the larva is much older. If the gelatinous substance at the stage shown in fig. 5 were absent, the larva would be identical in structure with a typical gastrula; but it is quite clear, from the account of its origin which I have given, that it is essentially different from the invaginate gastrulæ of ordinary metazoa, and that the mouth is not an orifice of invagination, but a younger structure than the digestive cavity. At this and the following stages there is a noteworthy difference between our species and those which were studied by Fol and Metschnikoff. In our species the endodermal capsule, fig. 5, *c* and fig. 7, which is now a stomach, retains its rounded outline, and ultimately becomes elongated along the principal axis, fig. 7, *d*. Metschnikoff says that, in *Geryonia hastata*, it becomes flattened so that its aboral wall is almost in contact with its oral (52, Pl. 11, figs. 10, 11 and 14), while in *Geryonia fungiformis*, according to Fol, the aboral side becomes pushed down into the oral half, so that it forms a double cup, with a very thin cup-shaped cavity. The absence of this flattening, in the American Liriope, shows that it has no important morphological significance.

The tentacles, *f*, now begin to grow out around the edge of the peristome, as shown in an oral view in fig. 6, and, in an oblique view in fig. 5. Two of them probably appear before the others, and in the stage shown in fig. 6, there are three: two, which are probably primary, opposite each other; and a third, 90° from these. A fourth soon appears opposite the third, and Fritz Müller's figures show that they are the primary radial tentacles, figs. 9, 10 and 11 *f*, of the medusa. They are solid, and consist of a layer of ectoderm, continuous at the base of the tentacle with the ectoderm of the edge of the peristome, and a solid endodermal axis, which may, in our species, be clearly seen to be continuous with the endodermal portion of the edge of the peristome. Fol says, (22, page 484) that he found it difficult to trace, in his larger embryos, any visible continuity between the endoderm cells of the tentacles and the wall of the stomach, but in our species there is no such difficulty. The endodermal origin of the axial cells of the tentacles of hydroids and medusæ is such a firmly established fact, that the presence of tentacles at this stage is, in itself, a proof that the digestive cavity is present, and would in the present condition of embryological science compel us to regard the central structure as an endoderm rather than an ectodermal sub-umbrella. The tentacles, fig. 8, *f* now rapidly elongate and their tips become enlarged and crowded with lasso-cells. Fritz Müller, Haeckel, Fol and Metschnikoff figure at this stage peculiar hook-like appendages which project beyond the enlarged tips of the tentacles, but I have not observed anything of the sort in our species.

The larva shown in fig. 8 is a very interesting one, for it is in all essential points a hydra with a gelatinous deposit between the ectoderm and the endoderm. It has a mouth, a peristome, and solid tentacles, but no bell cavity; and if the thick umbrella were absent, and the endoderm and ectoderm in contact, it would be almost exactly like the floating, solitary actinula of Tubularia. It swims through the water, and its ectoderm is probably ciliated, and I think that comparison will convince any one that the hydra-like stage is actually represented in the life-history of the Geryonidæ; and that the Actinula, the Geryonid larva, and the Polyxenia larva shown in Metschnikoff's Pl. 3, fig. 11 (51) are modifications of the same type, a free, solitary, swimming hydra with solid tentacles. It is well known that the solid tentacles of the Geryonidæ are transitory larval organs, and that the persistent radial tentacles of the adult, Pl. 42, fig. 1, are hollow, like those of ordinary Anthomedusæ and Leptomedusæ. This difference is in perfect harmony with the view that the larval tentacles are hydra tentacles, while those which persist are medusa tentacles.

According to Fol, who has given a very careful account of the changes which now follow, from the study of an embryo which is much larger than ours, and, therefore, more convenient for study, the periphery of the mouth area now thickens to form a circular rim, from which the ectoderm of the tentacles is derived; while the rim itself becomes the free edge of the umbrella, and gives rise on its inner side to a circular fold of ectoderm, which becomes the veil. The ectoderm cells of the peristome, between the rim and the mouth, become the epithelium of the sub-umbrella, which meets the endoderm around the mouth, where the line of demarcation between the two layers can be clearly seen.

Metschnikoff's account is like Fol's in all essentials, as he also says that the periphery of the mouth area becomes the free edge of the umbrella, and gives rise to the tentacles and velum, while the area between the velum and the mouth becomes the epithelium of the sub-umbrella; but Lankester states (45) that there is a "substantial disagreement" between Metschnikoff's statement (52, page 20), that "Der Centraltheil der Scheibe stülpt sich dagagen weiter in's Innere ein, um die äussere Bedeckung der Schirmhöhle darzustellen," and Fol's account. The two authors studied different genera, and we should not expect to find an exact agreement in every point, but I fail to discern any reason for questioning either of them, and certainly do not perceive any difference regarding any significant points. Lankester's claim, that the two accounts conflict with each other, seems to be the result of his desire to show that neither of them is correct, but that his own very different explanation of the process is the true one; and I, therefore, quote the words of Fol's account, for comparison with the statement which I have quoted from Metschnikoff.

He says (22, p. 485), "Der anfangs fast kugelige Schirm breitet sich mehr nach unten und aussen aus, und nimmt bald eine wirklich schirmförmige Gestalt an. Der Rand des Schirmes nimmt der Randwulst ein, welcher sich schnell ausdehnt und zugleich relative verdünnt.

Der Magen tritt dabei verhältnissmässig immer mehr in die Höhe, so dass er in den Grund einer, anfangs seichten, trichterförmigen, später tiefen, glockenförmigen Höhle zu liegen kommt. Letztere ist die wachsende Schirmhöhle. Ein Epithel kleidet ihre Wände aus, welches direct von der oralen Ectodermscheibe abstammt. Am Mundrande sieht man immer noch die Grenze zwichen Ento- und Ectoderm, welche ihrer verschiedenen Beschaffenheit wegen noch unterscheidbar sind."

For all morphological purposes it is a matter of no consequence whether the bell cavity is formed by a pushing in at its centre, or by the growth of its edges, or in both ways, and it is easy to understand that closely allied species may differ in this respect. This difference upon a minor detail is therefore no reason for doubting the accuracy of either Fol's or Metschnikoff's account.

The youngest medusa which I obtained in the open water is shown in Pl. 41, fig. 9. It is peculiarly interesting on account of the simple structure of its digestive cavity, and it presents a very early stage in the formation of the chymiferous tubes, the origin of which has never been traced.

It is true that Haeckel gives an account of the origin of these structures, and says that they are formed by differentiation of the epithelium of the sub-umbrella; but as we now know that the sub-umbrella is lined by ectoderm, no one would, at the present time, believe, without very conclusive evidence, that endodermal structures originate in this way, although, at the time Haeckel's paper was published, such an error was not unnatural.

Haeckel says (30 *b*, p. 136): "The gastrovascular system is differentiated from the cells which cover the velum and line the cavity of the bell as a sub-umbrella. This differentiation takes place in such a way that, on the bell margin, at the junction of the velum and the sub-umbrella, a broad strip of larger and thicker-walled cells becomes specialized as the embryonic circular tube. At the same time two similar strips, crossing each other in the middle of the arch of the sub-umbrella, and joining the bases of two opposite tentacles, are differentiated from the general surface of the sub-umbrella."

"These are the four radial canals, which, like the circular canal, are at first so wide that only four small four-sided areas of the sub-umbrella remain free and covered with the smaller, flatter and thin-walled epithelial cells."

According to Ray Lankester (45) Haeckel alone has given a correct account of the origin of the sub-umbrella; but I doubt whether any other embryologist would at the present day credit the statement that the endodermal chymiferous tubes are formed from the epithelium of the sub-umbrella, although such a statement was not, twenty years ago, intrinsically improbable.

My own observations show that Haeckel really observed the origin of the chymiferous tubes, although he failed to discover that they are formed by the differentiation of the walls of the digestive cavity, instead of those of the sub-umbrella.

At the stage shown in fig. 9, the oral layer of endoderm has been pushed in, by the formation of the sub-umbrella, until it is nearly in contact with the aboral wall, and the digestive cavity is thus reduced to a thin dome which is concentric with the sub-umbrella and extends to the bell margin. At four points on the four inter-radii and near the bell margin, the two layers of endoderm have come into contact with each other and fused to form four shield-shaped areas of adhesion, fig. 9, *i*. The stomach is thus divided, by the four areas of adhesion, into first, a spacious axial chamber or stomach proper, which reaches more than half-way down the bell; second, four short, wide, radial canals, *l*; and third, four short arcs of the circular tube, *m*, which unite the distal ends of the radial tubes with each other.

In older medusæ I have traced the gradual extension of the four areas of adhesion, figs. 10 and 11, *i*, *i*, until four narrow, sharply defined radial canals, *l*, and a circular canal, *m*, are produced, and I think there can be no doubt that, in a younger medusa than the one shown in fig. 9, the areas of adhesion would be still smaller, and that, in a still younger medusa they would be entirely absent, while the stomach would extend to the bell margin as a continuous cavity without interruption.

While I have not found a larva in this condition, a reference to Fritz Müller's (55) and Haeckel's papers (30) will show that both these authors have seen and correctly figured this stage of development. The larva shown in Haeckel's Pl. 4, fig. 35, is like our fig. 9, except that the areas of adhesion have not yet appeared, and the four quadrate, interradial areas, of which Haeckel speaks on p. 136, are, beyond doubt, the areas of adhesion.

Although both Fritz Müller and Haeckel were led astray in their interpretations, I believe that their figures correctly represent the larvæ, but this is not true of the figures which have been given by other authors.

Drawings which are touched up at home, from sketches made at the seashore, are very apt to become conventionalized, and I cannot help believing that the sharply defined radial canals which are shown by Leuckart (47) and Fewkes (68, pl. 7, fig. 2) in young Geryonids at about the same age as our fig. 9, were introduced into the drawings upon theoretical grounds, rather than from observation. This is certainly the case with Gegenbaur's figure (25) for he represents the canals as interradial.

It is interesting to note that the endoderm cells do not completely disappear in the areas of adhesion, even in the adult. The Hertwigs give (69, Pl. 4) two sections, figs. 2 and 9, through the bell margin of *Carmarina hastata*, and in each section they show a double layer of endoderm cells, r', t', in contact with each other, running up toward the axis of the bell from the oral side of the circular tube, with the epithelium of which they are continuous, although the cavity of the tube does not extend between them.

The observations here given show the correctness of Balfour's conjecture (65, p. 130) that "while the exact mode of formation of the gastrovascular canals of Geryonia has never been worked out, the presence in the adult of hypoblastic lamellæ, and the mode of formation in medusa-buds, justify us in believing, with the Hertwigs, that they are the remnants of a once continuous gastric cavity."

The metamorphosis of the young medusa has been well described by Fritz Müller and Haeckel. The bell gradually becomes flattened, as shown in fig. 11 and in Pl. 42, and the gastrostyle gradually grows down from the apex of the sub-umbrella, carrying with it the stomach and the oral ends of the radial canals, until, in the adult, the mouth and stomach are far below the level of the veil. At various stages in its life the medusa has three sets of tentacles, four in each, or twelve in all. Of these, one set is radial and larval, soon disappearing with the growth of the medusa. The second set, figs. 9 and 10, *h*, next appear, and in some species persist throughout life, while they are absent in the sexually mature medusæ of other species. They are interradial. The third set, fig. 10, *g*, fig. 11, *g*, are radial; and are the long tentacles of the adult medusa.

The primary radial tentacles, figs. 9, 10, 11, are larval organs. They are the first to make their appearance and they are present in very young medusæ. They are solid, consisting of a central axis of very large cartilage-like endoderm cells, and a surface layer of ectoderm which is thickened at the tip of the tentacle, to form a knob or bulb, which is crowded with lasso-cells.

When these tentacles first appear in the larva they are situated at the edge of the peristome, and when this becomes pushed in, to form the sub-umbrella, the tentacles spring from the edge of the umbrella, just outside the velum, and their endoderm is continuous with that of the circular edge of the digestive cavity; but as the medusæ grow, they are carried out on to the outer surface of the umbrella, some distance from its edge, as shown in fig. 9. A string of degenerated endoderm cells persists for some time between the base of the tentacle and the circular tube, and thus marks out the line along which the tentacle has migrated. There is also an ectodermal ridge, "Schirmspang," on the surface of the umbrella, running from its free edge to the base of the tentacle. These tentacles drop off before the medusa attains to its full size, and they are entirely absent in the adult.

The four primary interradial tentacles are the next to appear, figs. 9, 10, 11, *h*. They also are solid, but they are distinguished from the primary radials by the fact that the ectoderm of the axial side is thickened to form a number of ridges or incomplete rings, each of which is filled with large, oval lasso-cells. The stiff interradials are usually, carried turned up against the outer surface of the umbrella, with thin rings of lasso-cells facing outwards. They are, at first, situated on the bell margin, but they migrate, like the primary radials, and in the adult they are separated from the bell margin by an interval which is somewhat greater than the diameter of the circular tube, with which a row of degenerated endoderm cells connects the base of each tentacle, and there is also an ectodermal ridge or "Mantelspang" with large lasso-cells running from the axial surface of the base of the tentacle to the bell margin. According to Haeckel, the Geryonidæ are divided into two great groups: one group including those species in which the interradial tentacles are retained by the adult, and the other including those in which they disappear before maturity is reached.

In our species, however, there is no invariable rule. Most adults retain all four of them; but individuals with only three, two, one, or with none at all are sometimes found. It is possible, and in fact probable, that this is true of other species also, and that the presence or absence of these tentacles cannot be used as a diagnostic characteristic.

The third set of tentacles, the secondary radials, are always present in the adult. They appear as small buds, fig. 9, *g*, in the young medusa, and grow throughout life. They are very elastic and may be stretched out to four or five times the diameter of the bell, and they are seldom contracted to less than twice this diameter. They are hollow and their lasso-cells are arranged in prominent rings along the whole length of the tentacle.

Summary of the Development of Liriope.

The following features in the life-history of Liriope are especially important as a basis for comparison with other hydromedusæ in the attempt to trace the origin of alternation.

1. Each egg gives rise to no more than one adult medusa, and there is no alternation of generations or asexual process of multiplication.

2. The segmentation cavity persists as the digestive cavity, and the embryo is not a solid mass of cells at any stage of its development.

3. The process of delamination which results in the formation of the two germ layers takes place rapidly over the whole of the spherical blastoderm.

4. The metamorphosis is gradual and is not divided into well-marked stages separated from each other by sudden changes; but it may be divided into a planula period, a hydra period and a medusa period, although certain characteristics of the medusa appear during the planula and hydra periods, and certain characteristics of the hydra are retained after the medusa period is reached.

5. During the planula period the spherical embryo consists of a ciliated ectoderm, and a capacious digestive cavity which has no opening to the exterior and is bounded by a single spherical layer of endoderm cells concentric with the ectoderm, but separated from it by the gelatinous umbrella which is at first spherical and of uniform thickness.

6. The planula is converted into a hydra by the union of the ectoderm and endoderm at the oral pole, where the two layers become perforated to form the mouth, around which the ectoderm cells become differentiated into a sharply defined oral area or peristome, on the periphery of which four solid hydra-tentacles are developed. The hydra is free, does not multiply asexually and has a gelatinous umbrella. If this were absent it would be very similar to the actinula of Tubularia.

7. As the hydra becomes converted into the medusa the peristome becomes pushed inwards to form the sub-umbrella, at the top of which the mouth is situated; while the digestive cavity becomes converted into a dome with its edge at the bell margin. The ex-umbral and sub-umbral layers of endoderm are thus brought close together and they

now unite with each other over four interradial areas of adhesion which increase in size and convert the peripheral portion of the digestive cavity into a circular tube and four radial tubes.

8. The veil is formed around the periphery of the peristome. The solid radial hydra-tentacles disappear and the solid interradial tentacles and the hollow radial medusa-tentacles are developed. The larval tentacles do not disappear until all the characteristics of the medusa are acquired, so that there is a period, before maturity is reached, when the animal is both a hydra and a medusa.

9. During the hydra period there are no marginal sense organs.

Literature of the Development of the Geryonidæ.

In 1856 Leuckart pointed out (47) the fact that the young Geryonid medusa is quite different from the adult, and that its growth is accompanied by metamorphosis; and in 1857 Gegenbaur figured and described (25, p. 247, Pl. 8, fig. 12) a young Geryonid under the name *Eurybiopsis anisostyla*. Fritz Müller's minute and amply illustrated account of *Liriope catherinensis*, published in 1859 (55), is the first in which the absence of an alternation of generations is established. He gives an account of the metamorphosis of the medusa, and shows that the young embryo is a double spherule of cells, and that the central capsule has, at first, no opening; and he also figures an older embryo with a mouth, but without tentacles, although he supposed that the central cavity was the sub-umbrella, that the mouth was the opening of the umbrella, that the peristome was the veil, and that the embryo has, at this stage, no mouth or digestive tract. In his classic monograph, published in 1866, Haeckel gives beautifully illustrated figures of the metamorphosis of *Glossocodon eurybea*, (30 *b*) and *Carmarina hastata* (30*d*); but he falls into Fritz Müller's error regarding the embryo, and describes the endoderm as the sub-umbrella, stating that the digestive tract and chymiferous tubes are formed, at a later stage, by the differentiation or specialization of the sub-umbral ectoderm. In 1873 Fol (22) reared *Carmarina fungiformis* from the egg, and gave a complete account of its development, illustrated by beautiful figures, showing that the central cavity is the digestive cavity and that its endodermal cells arise by delamination from the blastoderm, that the mouth appears later, and that the ectoderm around it becomes the sub-umbral epithelium, around the edges of which the veil and tentacles are developed. Metschnikoff states (52) that his observations (51) are a year earlier than Fol's, but as Fol's paper appeared Nov. 18, 1873, while Metschnikoff's was not published until Jan., 1884, the discovery belongs to Fol, although Metschnikoff's observations, which were made at Villafranca in 1870, agree with Fol's in all essential particulars.

Kowalevsky's Russian paper, which appeared in the same year, 1874, gives a totally different account of the early stages, as observed in *Carmarina hastata*. According to Metschnikoff's statement (52) and Leuckart's abstract in the Arch. f. Naturgeschichte, Kowalevsky observed the origin of the central capsule by delamination, but decides that its cells become converted into the gelatinous substance of the umbrella, and have nothing to do with the digestive tract, which originates by invagination at a later period.

We therefore have three irreconcilable statements as to the fate of the central capsule and the origin of the endoderm. Haeckel and Fritz Müller say that the central capsule becomes the sub-umbrella, from the walls of which the digestive tract is subsequently formed; Fol and Metschnikoff hold that the central capsule is the digestive cavity, and that the sub-umbrella is an ectodermal structure of later origin; while Kowalevsky claims that the central capsule is neither endoderm nor sub-umbrella, but that it breaks down and becomes the gelatinous substance of the bell.

In the summer of 1882 I studied the embryology of *Liriope scutigera* in order to decide between these conflicting views, and quickly satisfied myself of the correctness of the accounts of Fol and Metschnikoff.

While I was engaged in this work I received Metschnikoff's last paper (52) dated Dec. 30, 1881, giving an account of his renewed study at Naples of the embryology of *Liriope eurybea*, Haeckel, and *Carmarina fungiformis*, Haeckel, resulting in the complete verification of the account which he published in 1874.

The next paper in historical order, "On Young Stages of Limnocodium and Geryonia," by Ray Lankester (45), is a very noteworthy example of "deductive biology;" for while the title would lead us to expect new observations on the young stages of the Geryonidæ, the paper contains nothing to show that the author has ever seen a Geryonid, either young or adult, and his statement (44) that the tentacles of the Trachomedusæ are solid would hardly be made by any one who had examined an adult Geryonid; nor for that matter would any one who is familiar with Eucope venture the statement that the Leptomedusæ all have hollow tentacles. In this connection see Hamann (32) and the Hertwigs (69, p. 72).

It is true that the paper does contain diagrammatic figures, page 200, to illustrate the development of the Trachomedusæ, but they are purely imaginary and unlike anything which has ever been observed, for the author has undertaken the very dangerous task of constructing embryology upon general ground rather than from observation.

As his theoretical views bring him into conflict with the careful observations of Fol and Metschnikoff, he attempts to show that there is a "substantial disagreement" between their accounts, and he does not hesitate to assert that "Fol has completely failed to give even an approximately correct account of the matter," while Metschnikoff's account is "erroneous."

The same author had published, a few months before, an account of an interesting medusa which was found in very great numbers, at various stages of growth, in a tank in which tropical water plants were cultivated in England. The medusa, Limnocodium, is remarkable in many respects, as it is very different from all the known species, and has, so far as we know, no close allies. Ray Lankester regards it as a Trachomedusa, although Allman, who described it on the same day in another place (70), considers it a Leptomedusa.

In his second paper (45) Ray Lankester gives figures of young medusæ which were found in the water with the adults, all of which were males, and although the young are similar in all respects to the medusa-buds of hydroids, and quite unlike any medusa-embryo which has ever been reared from the egg, he regards them as egg-embryos, and constructs upon them a new view of the embryology of the Trachomedusæ, although he did not rear them from the egg, and gives no reason for believing that they are egg-embryos, except his opinion that the adult is a Trachomedusa, and must therefore develop directly from the egg, without the intervention of a hydra-stage.

The number of species of Trachomedusæ which have been reared from the egg is so small, and these are all so different from Limnocodium, that the argument from analogy affords very scanty grounds for rejecting all the published observations, and as a matter of fact, we may well doubt whether Limnocodium is a Trachomedusa at all, as none of his reasons are conclusive. The younger ones are exactly like medusa-buds, with a closed sub-umbrella, a mouth and a manubrium which have no functional importance, and four radial canals which appear before the opening of the sub-umbrella. In all these respects they agree with medusa-buds and differ from all egg-embryos which have ever been described. There is, therefore, good reason for believing that they are buds, which are detached from a fixed hydra, and this view furnishes an explanation of the fact, so puzzling to Lankester, that among thousands of specimens no females were found. In animals hatched from eggs, we should certainly expect to find both sexes, and when thousands of embryos occur, ripe females must be present, but a fixed hydroid community gives rise to medusæ of only one sex; and the occurrence in the tank, year after year, of thousands of male medusæ, at all stages of growth, without any females, is just what we should expect if they are all the progeny of a single hydroid community, which has been accidentally introduced into the tank, and there gives rise to medusæ by budding. The author does not hesitate to resort to hypothetical explanations, and he attempts to explain the absence of females (42) by the hypothesis that the females may be fixed while the males are free.

This may prove to be the case, but there is not a single fact in the history of the Hydromedusæ to give it the least support except his failure to find females and the fragmentary account of the life-history of Limnocodium is therefore an extremely narrow base upon which to construct the embryology of the Trachomedusæ in opposition to the observations of Fol and Metschnikoff.

Section III. The Anthomedusæ.

Plate 37.

Turritopsis is a craspedote or veiled medusa belonging to Haeckel's order ANTHOMEDUSÆ or veiled medusæ without marginal vesicles or otoliths, with ocelli on the bases of the tentacles, with the reproductive organs in the walls of the digestive cavity, and with (in most cases) four radiating tubes. The Anthomedusæ originate, by alternation, from Tubularian Hydroids.

In the order Anthomedusæ, Turritopsis is a representation of Haeckel's Family TIARIDÆ, or Anthomedusæ with four broad oral lips, four wide radiating canals, simple unbranched tentacles, four separate reproductive organs in the walls of the stomach, and it belongs to Haeckel's Sub-Family PANDÆIDÆ, or Tiaridæ with eight or more tentacles.

As a number of allied medusæ were unknown when McCrady's original diagnosis of the genus Turritopsis was published (48, p. 25) his characteristics of the genus include certain points which are now known to be shared by other genera, and others which are only of specific importance. Haeckel's diagnosis (31, p. 66) is based in part upon an erroneous interpretation of McCrady's account of our species, and I therefore give a new statement of the distinctive characteristics of the genus.

Genus-Diagnosis. Tiarid with numerous tentacles in a single row, and a single ocellus on the inner or axial side of the bulb of each. No gastric peduncle from the gelatinous substance of the umbrella, from which the digestive cavity is suspended by a cartilage-like mass, made up of the greatly enlarged endoderm cells of the radiating tubes. No mesenteries. Four simple perradial reproductive organs in the walls of the digestive cavity, separated by deep furrows with smooth surfaces. Oral lips fringed with stalked bunches of lasso-cells.

The stalk which suspends the digestive cavity of Turritopsis from the centre of the sub-umbrella is not a gelatinous prolongation from the umbrella, but a peculiar structure, made up of the greatly enlarged endoderm cells of the radiating tubes, which, in the adult, are pendent from the sub-umbrella, as in Haeckel's figures of Callitiara (3, Pl. 3) but so greatly thickened as to form a solid cartilage-like mass, through which the four small channels pass down to the digestive cavity, into which the chorda-cells also extend.

McCrady's figures and minute description of this structure are so very clear that there should be no room for mistake. He says (48, page 3) "The stomach surrounded by the ovaries occupies the lower half (of the peduncle), but above is *a mass of very large cells* filled with a clear substance like that in the upper part of the disk in Oceania. This portion is traversed by the four ascending chymiferous tubes, around which the large cells are arranged with much regularity, and which, on reaching the muscular disk, arch over it to descend through its substance as vertical tubes." On p. 5, he says, "Returning now to the vertical tubes, we find that before entering the tissues of the bell, they traverse the clear portion of the proboscis. Here they do not preserve the even, somewhat flattened form which they have in the disk, but assume a rather irregular outline. This appears to be due to the circumstance that the canal occupies the somewhat irregular cavity left between the juxtaposed ends of the large cells composing the transparent part of the proboscis. How these cells are arranged radiately is shown in a diagrammatic cross-section at fig. 7. A small quadrangular space is left between the four masses thus formed, which is, probably, filled with the same clear substance which fills the cells. The tissue so formed is not confined to the tubes, though it has there its greatest development; it spreads also downward over the several lobes, but in this portion the cells are very much smaller. Around the tubes the cells are of a somewhat pyramidal form, their bases turned outwards, the apices inwards, to meet the chymiferous canal."

Keferstein (36, p. 26) correctly describes the peduncle of his *Oceania polycirrha*, which is a true Turritopsis, as "made up of large transparent cells which look like a network;" but Haeckel (31, p. 66) misled, no doubt, by the close resemblance between Turritopsis and Callitiara, has described the structure as an ordinary gelatinous gastric stalk, although it is, in reality, a very different structure from the peduncle of Eutima or that of the Geryonidæ.

McCrady failed to discover that the cells are nothing more than the greatly thickened walls of the radiating tubes, but in other particulars his account is very accurate, although Fewkes states (21, page 153) under the heading *Turritopsis nutricola,* in his description of a medusa which he wrongly supposes to be a Turritopsis, that McCrady's description is "quite faulty," and that there is nothing which corresponds to his "long description of what he calls a cellular upper portion of the proboscis."

Distribution of the Genus. So far as our present knowledge goes, the genus is distributed as follows: Messina, Mediterranean (Kolliker, Gegenbaur, Keferstein, Ehlers, Haeckel); St. Vaast, Normandy (Keferstein); Australia (Peron & LeSueuer); Charleston, South Carolina, U. S. (McCrady); Beaufort, North Carolina (Brooks); Hampton Roads, Va. (Brooks); Naushon, Buzzard's Bay (A. Agassiz.)

Turritopsis nutricula, *McCrady.*

Turritopsis nutricula, McCrady, 1856. Description of *Oceania* (*Turritopsis*) *nutricula,* nov. spec. and the embryological history of a singular medusoid larva found in the cavity of its bell. Plates 4 & 5.

McCrady, 1857. Gymnophthalmata of Charleston Harbor, page 127, Plate 8.

L. Agassiz, 1865. Contributions IV, p. 347.

Haeckel, 1879. System der Medusen, p. 66.

Brooks, 1883. Studies Biol. Lab., 11, p. 465.

Oceania nutricula, McCrady, 1856. Description, etc.

Modeeria multitentaculata, Fewkes, 1881. Bull. Mus. Comp. Zool., VIII, 8, page 149, Pl. 3, figs. 7, 8, 9.

Modeeria nutricola, Fewkes, 1882, Bull. Mus. Comp. Zool., IX, 8, page 295.

Species-Diagnosis. Umbrella nearly flat on top. In profile view the upper third is nearly rectangular, while the outline slopes outwards in lower two-thirds. Diameter of umbrella about three-fourths of height. The large proboscis nearly fills the upper portion of the sub-umbrella. The upper wider than the lower half, cubical, and made up of four masses of endoderm cells, perforated by the channels of the radiating tubes. Digestive cavity, making about half total length of proboscis, cubical, ending below in four simple large lips, fringed with stalked bunches of lasso-cells, and nearly reaching level of velum, or sometimes reaching below it. Four very large ovoidal reproductive organs, separated from each other by deep interradial furrows, rounded below but divided above into two lobes which run up for a short distance on sides of radiating tubes.

One hundred or more tentacles, placed close together around bell-margin, and consisting of an enlarged bulb, a long slender contractile shaft, and a slight terminal clavate enlargement. Tentacles capable of extension to three or four times diameter of umbrella and with a single ocellus on axial side of basal bulb.

Color. Umbrella transparent-reddish brown; reproductive organs, reddish orange; interradial furrows, deep lake; lips frosted, base and tip of tentacles red, shaft a very faint purple.

Size. About 6 mm. wide, and 8 mm. high.

Ontogeny. Larva a branching tubularian hydroid, with a fusiform body, and three irregular rows of short filliform tentacles. It is a member of Weismann's genus Dendroclava, and it is so very similar to his *D. Dohrnii*, as to render it probable that this also is the larva of a Turritopsis. Stems from 8 mm. to 12 mm. high. Hydranths, pale yellowish red. Medusa-buds originate on stem at base of hydranth. Young medusa has eight tentacles, a small gelatinous peduncle, and no cellular peduncle. Mouth of young medusa simple. Velum of young with four radial and four interradial hemispherical pouches.

Habitat. Charleston, S. C. (McCrady); Beaufort, N. C. (Brooks); HamptonRoads, Va. (Brooks); Naushon, Buzzard's Bay (A. Agassiz).

Remarks. The description and figures which have been given by A. Agassiz (2, p. 167, figs. 269-270), and which are referred to by Haeckel (31, p. 65) as giving all we know of the metamorphosis of the medusa, do not represent a Turritopsis at all, but a quite different medusa.

Fewkes's *Modeeria multitentaculata* (21, p. 149, Pl. 3, figs. 7, 8 and 9) is a true Turritopsis and so far as I can judge from the figure, which is copied from a sketch made by A. Agassiz of a single specimen which he found in 1865 near Naushon in Buzzard's Bay, an immature specimen of our southern *T. nutricula*.

This seems to be the only recorded instance of its occurrence north of the Chesapeake Bay, where it is very rare. Verrill states (62, page 454) in his "List of species taken at the surface of the water on the southern coast of New England" that it was found there at night from July to September, but as he refers on page 734, to A. Agassiz's description and figures, which are noticed above, I infer, in the absence of all description, that the medusa which he found was the one which A. Agassiz figures, and not a Turritopsis.

Fewkes (21, p. 153) describes and figures a medusa which he calls *Turritopsis nutricola*, but which he was able to reconcile with McCrady's figures and description, only on the supposition that they are quite faulty. In a later paper (20, p. 294) he corrects this error, proposing a new name for his Turritopsis, and stating, incidentally, that his *Modeeria multitentaculata* is probably the same as McCrady's *Turritopsis nutricula;* an opinion which is undoubtedly correct. He says, however, that "as the generic name Modeeria is older than Turritopsis, and as they seem to have been applied to similar jelly fishes, McCrady's medusa may later be known as *Modeeria nutricula;*" but as Forbes, who established the genus Modeeria, states (23) that it includes only medusæ with four tentacles, there seems to be no good reason why it should supplant McCrady's name for medusæ with more than a hundred tentacles.

Special Description. McCrady gives the following vivid and accurate description of the general appearance and habits of this interesting medusa, which may be readily recognized by its reddish brown color, its square outline and its rapid zigzag movements.

"*Turritopsis nutricula* is a lively animal swimming gaily about, near the surface of the water, with very regular rhythmical pulsations. * * * Its motion in swimming is peculiar; though it does not shoot forward so far at every stroke as Sarsia, yet each throb of the disk gives it a considerable impetus. Now if we examine a Thaumantias, Geryonia; or Turris while swimming, we see it propelled by many successive pulsations in a straight line, corresponding to the vertical axis of the animal, but this is not the case in Turritopsis. The pulsations here are slow, measured, powerful, each appearing to have a more special design in it, than the oft-repeated pulsations of Thaumantias, and each, instead of driving the animal directly forward toward the point whither its whole course tends, propels it in a direction crossing that line diagonally, like the course of a ship in tacking or traverse sailing. It is thus propelled first to one side of its course, and then to the other; its actual track being a zigzag. * * * This is the motion of Turritopsis when performing a long journey, but he may be often seen sporting about the surface, taking a few sidelong leaps like those described, and then, with the mouth of the bell downwards, expanding himself to the utmost, all his tentacula, which in progression were tightly curled up, now gradually disentangling and stretching themselves to their greatest length, turned upwards or horizontally, while the motionless parachute slowly sinks to the bottom (See Pl. 37, figs. *I* and *K*). However, the tentacula thus extended seem to be keenly alive to every passing particle, and every now and then, one or two or more of them may be seen to contract with great rapidity, as if they had come in contact with something to be seized or avoided. At this time the Turritopsis has spread all his snares, and his tentacula radiating on all sides, form a circle probably equally efficacious with the spider's web. Indeed I have found small Crustacea, their principal food, frequently dead or dying in the embrace of these tentacula, or rather simply hanging to them by invisible attachments, illustrating in another instance the deadly properties of these wonderful thread-cells. After, however, the Turritopsis has been sinking for some time (he may even allow himself to touch the bottom of the jar), he suddenly draws in, more or less, all his tentaculæ, and beats up again toward the surface in the same old zigzag way, now and then running along for a little distance in a horizontal direction, but generally going quite up to the surface, and then expanding himself, mouth downwards, again to sink slowly towards the bottom. The animal may continue fishing in this way a whole morning."

As it is a hardy species it thrives perfectly in an aquarium, where its active movements and the graceful curling and unfolding of its long hair-like tentacles, as well as its bright color, render it very attractive. A specimen may, if supplied with proper food, be kept all summer, but it is very voracious, and I have seen a small specimen kill and finally swallow a Sagitta more than half an inch long, the Sagitta being bent like a bow in the middle and distending the whole body of the Turritopsis.

At Beaufort a few specimens may be found throughout the whole summer, but it is not very abundant inside the inlet until the end of August, although we frequently obtained great numbers outside in June and July. When the south wind, which blows almost constantly during these months, comes to an end, near the end of August, Turritopsis makes its appearance inside the harbor, and with the continuance of calm weather, it becomes more and more abundant, and through September and October hundreds of specimens of all ages and sizes may be captured nearly every day. I infer from this, that the hydra lives in deep water off shore, and that the proper home of the medusa is in the open ocean. Indeed, we have taken them at the bottom outside with the trawl, at times when the water was so rough that none were found at the surface or inside the inlet. I have found only a single colony of the hydroid, and this was obtained inside the harbor.

Description of the Larva. In a previous paper (10, p. 495) I gave a brief account of the hydra and young medusa, which I am now able to supplement with illustrations and additional notes. Although I made many attempts to rear the young from the egg, I succeeded only once, and the planula is shown in Pl. 42, fig. 2. It is very opaque, and as I obtained very few, I did not sacrifice any of them for examination, and learned very little of the minute structure. In a living planula it is easy to make out, at the posterior end, an ectodermal invagination, which looks very much like the mouth of an invaginate gastrula, but this resemblance is misleading, for the careful study of a similar structure in the planula of Eutima shows that the invagination has no connection with the digestive cavity, but is an ectodermal gland for the attachment of the planula. My few planulæ of Turritopsis attached themselves in the angle at the bottom of the aquarium, where examination was impossible, and I was not able to displace them without destroying them. Finally, I broke the glass, and was fortunately able to secure, among the fragments, one specimen which was uninjured, and this I have figured in Pl. 42, fig. 3. The figure shows that the planula does not become converted into a hydranth but forms a root, *a*, from which the first hydranth, *h*, is formed as a bud. This has as yet no mouth nor tentacles, but its oral end is enlarged and filled with lasso-cells.

The only colony of the hydra which I obtained was scraped from the piles of the steamboat wharf at Morehead City, seven or eight feet below low tide mark. The tips of two of its branches are shown at *H*, in Pl. 37. It lived for two weeks in the house, and set free great numbers of hardy medusæ which were reared until they had acquired the characteristics of the genus.

The upright stems of the hydra, from 8 mm. to 12 mm. high, bore large terminal hydranths, as well as smaller ones which were scattered irregularly along the stem on short stalks. The long fusiform body of the hydranth carries from eighteen to twenty thick, short, filiform tentacles, which are arranged in three or more indefinite whorls. The medusa-buds, *B*, *B*, originate around the stem just below the hydranths, and they are themselves carried on short stems. The perisarc is not annulated, and it forms a loose cylindrical sheath around the main stem, and the short branches which carry the lateral hydranths and the young medusæ, while the latter are closely invested by a much thinner and more transparent capsule of perisarc. The sheath on the stems is thick and crusted with foreign matter. It terminates abruptly by a sharp collar just below each hydranth. The young hydranths and the medusæ are budded off above the collar, but they soon become entirely sheathed in perisarc by the growth of the stem. The pale yellowish-red hydranths, are very similar to those of Tubularia (Allman) and the hydroid is so similar to *Dendroclava Dohrnii* recently described by Weismann, that they undoubtedly belong in the same genus.

Metamorphosis of the Medusa. The little medusa remains attached to the stem, as shown in Pl. 37, *C*, for some time after the rupture of its capsule of perisarc. At this time it is nearly spherical and covered with large conspicuous ectoderm cells. Its eight short tentacles are thrown backwards in contact with the outer surface of the bell, and their tips are hooked or bent upon themselves in a very characteristic manner, which is shown in the figure. This position of the tentacle renders the bulb at the base, with its ocellus, very prominent.

The medusa when set free, Pl. 37, figs. *D* and *E*, has eight tentacles, a thin globular bell, and a short simple proboscis. When the animal is in active motion the tentacles are contracted, bent into hooks and thrown back against the umbrella, as shown in fig. *D*, and at each pulsation the bell is lengthened and emarginated during contraction, but when relaxed it is nearly globular. Fig. *D* shows a young medusa in the shape which it assumes while swimming, at each period of contraction, while E shows a medusa of the same age floating in a relaxed condition. When at rest the height of the umbrella is about equal to its diameter, and the shape is that of a spherical segment almost equal to a sphere. The tentacles are capable of extension to a length equal to about twice the diameter of the bell, and when the animal is at rest they are stretched out almost horizontally, and the distal half is bent downward a little at an obtuse angle near the middle of the tentacle. The four interradial tentacles, when thus extended, lie nearly in the plane of the velum, while the four perradial tentacles are carried a little lower. This peculiar bending and alternation of the tentacles, which is very characteristic, is well shown in fig. *E*, which, like all the other figures, is a careful study from life. Many hydroids carry their tentacles bent so as to form two cycles, and the resemblance to them which the young Turritopsis exhibits, seems to be an embryonic characteristic, for I have failed to observe anything of the sort in older medusæ. The tips of the extended tentacles are slightly clavate, each with a spot of dark orange pigment. The length of the proboscis of the young medusa is about two-thirds the height of the umbrella, and its upper and lower ends are smaller than the middle. The mouth of the medusa, when it is set free, and for several days afterwards, is simple and circular, and the endoderm of the oral end of the proboscis is thin; but, just below the aboral constriction, it becomes very thick and cartilage-like, and the thickened area arches out into the sub-umbral surfaces of the radiating tubes, as shown in fig. 7.

This thickening of the endodermal cells of the aboral end of the stomach is characteristic of the genus Turritopsis; and in a specimen a week old, fig. *H*, the whole upper half of the proboscis is made up of four great masses of very large, cartilage-like endoderm cells, which meet upon the central axis and run out for a short distance into the radiating tubes, which penetrate the masses of cells on their way to the stomach, the cavity of which lies below the cartilaginous peduncle. The singular structure which is thus formed is quite unlike anything which occurs in any other genus. It has been described by various authors as an ordinary gelatinous peduncle or gastrostyle, but it is not at all the same as the gelatinous projection from the substance of the umbrella which, in many medusæ, hangs down in the centre of the bell.

As the medusa grows the proximal ends of the radiating tubes are drawn down into the cavity of the umbrella, as shown in fig. *H*, until in specimens two weeks old the stomach is suspended some distance below the sub-umbrella by a transparent mass of large cells meeting in the central axis, and perforated by the four tubes. In the adult, figs. *I*, *J*, *K*, this body almost entirely fills the upper half of the cavity of the bell.

In a medusa a week old, fig. *H*, the four oral lobes or lips have made their appearance, and are fringed by the stalked bunches of large prominent lasso-cells which have been described in the adult by McCrady and others.

At about this time traces of the reproductive organs made their appearance in the walls of the proboscis at the lower ends of the masses of endoderm cells. The tentacles, at the stage shown in fig. *H*, are still carried in two cycles: the interradials being higher than the perradials. There are only eight, and no more were developed in the medusæ which I reared from the hydra, although I captured many specimens in the same state, and at all the following stages up to maturity.

In specimens from one to two weeks old the lower surface of the very wide velum, fig. *G*, is pushed out to form eight hemispherical pouches; four of them radial and four interradial, in the planes of the eight tentacles. They project so much that they are quite easily seen in a profile view, and I have represented them in fig. *H*. May they not be homologous with the pouches, which, in the ocellate medusæ become closed and converted into the marginal vesicles?

The adult medusa is shown in figs. *I*, *J* and *K*. When it is swimming up from the bottom the tentacles are carried tightly curled up close to the edge of the bell. When it reaches the surface they are suddenly extended on all sides, shown in fig. *K*. They are nearly straight, but their tips are a little bent and sometimes coiled. This attitude is preserved only for a few seconds and the medusa at once begins to sink towards the bottom, while the tentacles coil up at their tips and assume the position shown in fig. *I*. The bell also becomes flattened and nearly hemispherical, and before the animal reaches the bottom of the aquarium it usually assumes the appearance which is shown in fig. *J*. As it nears the bottom it suddenly draws in its tentacles and rises to the surface, and again extends them, as shown in fig. *K*.

The plate, which has been photo-lithographed from sketches and studies which were made from the living animals, may, I believe, be relied upon as a faithful picture of the life-history of Turritopsis, and I trust that this accuracy, which is often lacking in drawings which are carefully finished at home, may compensate for the roughness and lack of transparency which are unavoidable in a pen-and-ink sketch. The figures of the adult medusæ, *I*, *J*, *K*, are much less magnified than the others, which are all drawn to the same scale.

Eutima. Plates 38, 39, 40.

I have selected Eutima as an illustration of the life-history of the second of the four orders, into which Haeckel divides the Craspedota or veiled medusæ. This order, the LEPTOMEDUSÆ, includes the Craspedota which are set free as buds from an asexual Campanularian nurse and which have the reproductive organs on the radial canals. Ocelli on the bases of the tentacles are usually absent, and marginal vesicles are almost universally present, and are developed along the veil at its junction with the umbrella, and contain ectodermal otolith cells.

Haeckel divides the order into four families, in the third of which, the EUCOPIDÆ, or Leptomedusæ with marginal vesicles and four simple unbranched radial canals, Eutima is placed, being included in the third of Haeckel's sub-families, the EUTIMIDÆ or Eucopidæ with eight adradial marginal vesicles, and with the stomach at the end of a proboscis or peduncle.

The seventeen species which are enumerated by Haeckel are arranged by him in eight genera, five of which are new, and the eight genera are divided into two groups: the SAPHENIDÆ, or Eutimidæ with four reproductive organs, and the OCTORCHIDÆ or those with eight; but as the reproductive organs are sometimes four and sometimes eight in two of our species, we cannot regard this division as a natural one. Haeckel's genera differ in the number of reproductive organs, the presence or absence of marginal cirri, and the number of tentacles, but as all of these characteristics are either variable or subject to change during growth, it is possible that a more complete knowledge of the life-histories of species which have been described from single specimens will compel us to make a very considerable reduction in the number of genera.

Haeckel's personal familiarity with the medusæ undoubtedly exceeds that of any other writer, and all students must bear testimony to the great value of the laborious researches into the perplexing literature of the subject, the results of which he has given us in his "System der Medusen." My own studies have taught me the value of this work, and I hesitate to propose any change in Haeckel's classification; but his arrangement of the species of Eutimidæ is not even available as an artificial key, for his genus Eutima is characterized by the presence of only four reproductive organs and numerous marginal cirri, while all my specimens of *Eutima mira*, a species which he places in this genus, had eight reproductive organs, and while nearly all of them had marginal cirri a few had none. His genus Octorchandra is characterized by eight reproductive organs and numerous cirri; but McCrady says that our *Eutima variabilis* (*Octorchandra variabilis*, Haeckel) sometimes has only four reproductive organs, and my specimens had no marginal cirri.

The genus Eutima, as originally established by McCrady, is equivalent to Haeckel's family Eutimidæ, and as all the species are very closely related to each other, while several of them are as yet very imperfectly known, it does not seem practicable to divide them into a number of genera at present.

Genus-Diagnosis. Eucopidæ with eight adradial marginal vesicles, and with the stomach at the tip of a gelatinous peduncle from the apex of the umbrella. Reproductive organs linear in the course of the four radiating tubes, which themselves extend down the peduncle to the stomach.

Remarks. The reproductive organs are often disposed in two masses on each radiating tube, one on the sub-umbrella and one on the peduncle, as shown in Pl. 39, but McCrady states that some specimens bear them only on the peduncle, some only on the sub-umbrella and some in both positions, and I have found specimens of *Eutima mira* in which ova were scattered along the whole course of the tube, from near the bell margin to the base of the stomach, although as a rule they are divided into two sharply defined regions separated from each other by an area where the canal bears no ova. This area is often longer on one of the tubes than it is on the other, and the two ovaries in one quadrant are sometimes confluent, while those in the other quadrants are distinct. We must therefore agree with McCrady that, far from furnishing a basis for a division into genera, the number of reproductive organs cannot even be used to separate species; that they may be double or single, and that when single they may be placed either on the peduncle or on the sub-umbrella, or they may stretch over both regions without interruption, and that all their variations may occur in one and the same species. In the two species which have been traced to their hydra stage, this is a Campanopsis, or a Campanularia-like hydroid without a calyx.

Eutima mira, *McCrady.*

Eutima mira, McCrady, 1857. Gymnopthalmata of Charleston Harbor, p. 88, Pl. 2, figs. 8 and 9.

L. Agassiz, 1862. Contributions, IV, p. 363.

A. Agassiz, 1865. N. A. Acalephæ, p. 116.

Haeckel, 1879. System der Medusen, p. 191.

Brooks, Studies Biol. Lab. 1882, p.

Species-Diagnosis. Umbrella, when contracted in swimming, nearly hemispherical, about two-thirds as high as wide. Proboscis slender, slightly enlarged at base, four or five times as long as the diameter of the bell. Stomach of greater diameter than the peduncle at its junction with the stomach, about three times as long as wide, quadrate in cross section, and less than half as long as the height of the bell. Edges of the mouth folded to form four everted radial lips, separated from each other by four interradial inverted folds. Reproductive organs linear, sometimes extending from near the edge of the bell nearly to the base of the stomach, sometimes divided into a sub-umbral and a peduncular portion, either of which may be present alone. Four tentacles, with enlarged hollow bulbs, six or seven times as long as diameter of bell, sometimes with basal cirri, sometimes without. Numerous marginal tubercles, with or without cirri. Marginal vesicles with one large medium otolith and two or three pairs of smaller ones. Bases of tentacles covered by hood-like gelatinous projections from the umbrella.

Color. Almost perfectly transparent, endoderm of tentacular bulbs yellowish red.

Size. Umbrella 12 or 13 mm. in diameter and about 8 mm. high.

Habitat. Charleston, S. C., McCrady; Beaufort, N. C., Brooks.

Remarks. This is a very active and graceful species and the specimens which I kept in aquaria were seldom at rest. When swimming the tentacles and proboscis are usually extended to their full length, as shown in Pl. 39, fig. 2, but when the animal is floating at rest or sinking to the bottom, the tentacles are swept into graceful folds by the resistance of the water, as shown in fig. 7. As the animal rises rapidly from the bottom the tentacles are thrown into undulations by the flapping of the bell. When contracted in swimming, the outline of the umbrella is nearly hemispherical, but when at rest it is slightly emarginated, as shown in McCrady's figure. In an oral or an aboral view, the outline of the umbrella is not circular but produced to form four rounded, radial projections or hoods over the bases of the tentacles. The enlarged bulbs at the bases of the tentacles taper rapidly into the slender, hollow shafts, which may be extended to seven times the diameter of the bell, and are never completely retracted but lie around the medusa in loose, irregular coils when it lies at rest on the bottom. In nearly all the specimens which I examined, the radial canals anastomose with each other through an irregular plexus of canals around the base of the peduncle, as shown in Pl. 39, fig. 3. Some specimens have coiled accessory tentacles on each side of the bulb of each radial, but these as well as the marginal cirri are often absent.

The species is very abundant at Beaufort in August and September, and it is usually found in company with *Liriope scutigera*, to which it bears a close superficial resemblance which may possibly be due to mimicry. This resemblance led Eschscholtz to associate these and allied medusæ with the Geryonidæ and it is expressed by the name Geryonopsidæ proposed by Agassiz for the Eutimidæ, Eirenidæ and related medusæ.

Ontogeny. I have reared the hydroid from the egg laid by the medusa. It is a Campanopsis very similar to the one from which Claus obtained the young medusæ of *Octorchis* (*Eutima*) *Gegenbauri*. It has a prominent, rounded manubrium, a single circlet of ten tentacles, arranged in two alternating series, and an elongated cylindrical body, which is not covered by the perisarc which invests the unannulated stem, Pl. 38, fig. 10.

Eutima variabilis, *McCrady.*

Pl. 39, fig. 1; Pl. 40.

Eutima variabilis, McCrady, 1857. Gymnophthalmata of Charleston Harbor, p. 88.
L. Agassiz, 1862. Contributions IV, p. 363.
A. Agassiz, 1865. N. A. Acalephæ, p. 116.
Octorchandra variabilis, Haeckel, 1877. Prodrom. System Med., Nr. 211.
Haeckel, 1879. System der Medusen, p. 199.
Eutima sp., Brooks, Studies Biol. Lab. 1882.

Species-Diagnosis. Umbrella thick, flattened, more than three times as wide as high Peduncle about equal in length to radius of bell, and less than twice as long as its height. Stomach short, quadrate, much folded, and prolonged into four pointed, crenulated lips. Sixteen tentacles of equal length, with three or four marginal thickenings between adjacent tentacles. Eight marginal bodies with ten or twelve otoliths in each; the medium one largest and the others in pairs. Each marginal vesicle lies close to radial sides of bulb of tentacle next radial tentacle. Reproductive organs usually divided into a sub-umbral and a peduncular portion; the latter absent in the young. No marginal cirri or accessory tentacles.

Color. Umbrella and peduncle transparent and colorless. Stomach and endoderm of tentacular bulbs intense green by reflected light. Endoderm of tentacular bulbs bright pink, and ectoderm sky-blue by transmitted light. Ectoderm of tentacular bulbs colorless by reflected light.

Size. Diameter of bell about 30 mm. Height about 7 mm.

Habitat. Charleston, S. C., McCrady; Beaufort, N. C., Brooks. It is a rare species at Beaufort and most of the specimens which I obtained were captured outside in August and September.

Ontogeny. Although I obtained ripe eggs on several occasions they were not fertilized and we have no direct knowledge of the ontogeny, although there is no reason to suppose that the hydra is different from that of *Octorchis* (*Eutima*) *Gegenbauri* and *Eutima mira*.

Remarks. McCrady's specimens had only twelve tentacles, while all the mature specimens which I obtained had sixteen, but as the Beaufort specimens agree with his description in all other respects, their identity can hardly be doubted. The tentacles were all of equal length, and were arranged as in this diagram, where *R* stands for a radial tentacle and *O* for a marginal vesicle.

R T T T R T T T R
O O O O

If the middle tentacle of each quadrant is the youngest one, the stage which is shown in Pl. 40 must be preceded by a stage with only twelve tentacles. This plate, which is a photographic copy of a pen sketch made from the living medusa, is the only figure which has ever been published of this beautiful species.

The tentacles of the adult have well-marked bulbs; their long, slender shafts are usually extended to four or five times the diameter of the bell, and are never completely retracted, but when shortened they are thrown into zigzag folds.

On Aug. 7, 1880, I obtained a single specimen of a Eutima with a thick, flattened umbrella, and four long, slender tentacles. It is shown in Pl. 39, fig. 1. It was 8 mm. in diameter and although it differs in many respects from the adult *Eutima variabilis*, it shows so many points of resemblance that it is, in all probability, the four-tentacled stage of this species. The bell is very flat, about four times as wide ashigh, thick in the middle, and gradually becoming thin at the edges. The peduncle is longer than the diameter of the bell, while the stomach is very short and only a little longer than wide. Veil very narrow. The four tentacles have bulbs, which are covered by hood-like outgrowths from the umbrella, and their long, slender shafts are capable of very limited contraction; and, when extended to four times the diameter of the bell, are thrown into zigzag folds. The four ovaries are long, narrow and continuous, and they run from near the circular tube up into base of peduncle and down this for a short distance. There are no accessory tentacles on the tentacular bulbs, but between each pair of tentacles, there are nine or ten marginal enlargements, some of which have cirri. The lips are simple folds, and there are eight marginal vesicles, each with from three to nine otoliths.

It is possible that Agassiz's *Eutima pyramidalis* may be the young of this species, although he states that the bell is hemispherical, which is certainly not the case with any of the specimens which I have seen.

A. Agassiz's *Eutima limpida* (2) and Fewkes's *Eutima gracilis* (20) are, beyond question, distinct from the species found at Beaufort, so that we have, on our coast, four species of the genus.

Eutima mira, with a hemispherical bell, and a very long proboscis, with folded lips, and with four tentacles; *Eutima variabilis* with sixteen long tentacles, a short proboscis and a flattened bell; *Eutima limpida* with short tentacles without bulbs, and with simple lips; *Eutima gracilis* with a flattened bell, four tentacles with bulbs, large cirri, accessory tentacles and a globular stomach. The latter species, which is so far known from only a single specimen, is very similar to Keferstein's *Siphonorhynchus insignis* (36) with which it may prove to be identical.

In June, 1879, I obtained at Beaufort several young specimens, about 5 mm. in diameter, of a young *Eutima* which agrees with A. Agassiz's description of *Eutima* *limpida* in so many respects that I am inclined to regard it as the young of that species. It is shown in Pl. 39, figs. 4, 5 and 6. It has a flattened, emarginated bell, simple lips and short tentacles without bulbs, and with accessory spiral tentacles. Specimens were also found at the same stage of growth in Aug., 1879 and Aug., 1880.

The Embryology and Metamorphosis of the Eutimidæ.

In 1881 Claus called attention to the fact that almost nothing is known regarding the life-history of Eutima or any of its nearest allies, and that the only observations upon the development of any of the Gerynopsidæ are those of A. Agassiz (2, p. 115, figs. 171 and 172) who has reared the planula of *Tima formosa* from the egg and has given a very brief description and a single figure of the hydra, although he did not observe the production of medusa-buds and says nothing about the very young stages of the medusa.

Except for Claus' paper, which will be noticed presently, the only addition to our knowledge of the subject is a very brief account by Merejkowsky (50) of the young embryo of Irene. In the spring of 1880, Claus (66) found a number of small hydroid communities in an aquarium, in which specimens of *Octorchis Gegenbauri*, *Irene pellucida* and *Æquora Forskalia* had been placed some time before. From these hydroids he obtained a number of young medusæ, which, however, he did not succeed in rearing; but, as he was able to collect in the open water series of young medusæ of each of the three species, he showed that those which he obtained from the hydroid were essentially different from young specimens of Irene and Æquora, while they were sufficiently like the youngest specimens of Octorchis which he obtained in the open ocean, to render it very probable that the hydroid belongs to this species, although the gap between the two is sufficiently great to render further information desirable. In the absence of any observations which connect the hydroid with its parent or the medusa-buds with adult medusæ, it is possible that the hydroid may not have been reared from the eggs of any one of the three species which were placed in the aquarium, as eggs or planulæ may have been introduced with the water. Claus' observations render it very probable that the hydroid is the larva of Octorchis, but they do not prove it beyond question, and I have been able to complete the story by actually rearing from the eggs of our *Eutima mira*, under constant observation, a hydroid which is so similar to the one which Claus figures, as to show beyond doubt that his conclusion is correct. Octorchis is a Eutima according to McCrady's definition of the genus, and the species which I studied is very closely related to the one which Claus observed. As I have observed the segmentation of the egg, the swimming life of the planula, its attachment and the origin of the hydroid, while Claus has described the medusa-buds and the metamorphosis of the medusa, the two accounts give a very complete life-history of the Eutimidæ.

The fertilized eggs of Eutima may be obtained by placing a few mature specimens in a small aquarium or a shallow dish of sea water. They usually lay their eggs the first night after they are captured, and if the species is very abundant, the water will often contain enough spermatozoa to fertilize them, even when only one specimen is used; but the result is much more certain if several specimens are placed in the same dish, for many of the eggs fail to develop if no males are present. Eutima is very regular in its breeding habits, and while my specimens were captured at all hours in the day, nearly all the eggs were laid between the hours of 7.30 and 8.30 P. M.

The tendency to lay eggs at a fixed hour of the day seems to be quite prevalent among marine animals, and a knowledge of this is of the greatest importance to naturalists, since a failure to procure the fertilized eggs of an animal may often be due to the fact that it has not been collected or observed at the proper hour. The phenomenon has received very little attention and I therefore give a few illustrations which have recently attracted my attention. Claus in 1882 (14) and Merejkowsky in 1883 (50) have shown that the young stages of Æquora and Obelia are found only in the morning, and Merejkowsky says that the successive steps in the formation of the planula of Obelia follow each other with such regularity that each stage is met with only at a definite hour in the morning. This author attributes the regularity to the direct influence of light, but he gives no proof of this and observations which have been made at Beaufort, under my direction, during the past three or four years, show that the periodicity is not due to any external influence, but that it is a specific characteristic determined within the organism. Wilson found at Beaufort that the eggs of Renilla, an Alcyonarian, which lives in the sand below low-tide mark, are always laid at or about 6 A. M. He observed only a single instance of spawning at 5.30 and it was never observed later than 7 A. M. The regularity is entirely independent of temperature, for the spawning hour was the same on cold and on warm days, although the rate at which the embryo develops does vary with the temperature. He says that the eggs of Leptogorgia are laid with the same regularity, although in this case the hour is 4 A. M. (67).

While Merejkowsky says that the eggs of Obelia are laid early in the morning, I find that several allied Beaufort medusæ spawn at night. Thus Eutima, Eirene, Turritopsis and Liriope discharge most of their eggs about 8 P. M., although captive specimens drop a few eggs irregularly at all hours. As one hydromedusa lays its eggs early in the morning, while other species lay them in the evening, the regulating influence can hardly be the supply of light.

While studying the development of a pelagic crustacean, Lucifer, I found that sexual union took place with great regularity, between 6 and 8 P. M.; while the eggs were laid between 8 and 10 P.M., so that the early stages can be studied only between 10 P. M. and 7 A. M.

Dr. H. H. Donaldson has observed at Beaufort that actiniæ of various genera are fully expanded only between the hours of 5 and 6 P. M. This is true of these animals in their natural homes, as well as in aquaria; and experiments showed that specimens which were kept in darkness expanded as promptly at the proper hour as those which were exposed to direct sunlight.

Among the animals which are here enumerated, some live at the surface, as Eutima and Obelia; some, such as the actinias, live near low-tide mark; some, Renilla for example, live in deeper water; and some, like Lucifer, are vigorous swimmers, while some, like Geryonia, are fixed. Wilson's observations show that the periodicity is not due to temperature, while Donaldson's experiments show that it is not the effect of light. There is no evidence to show that it is due in any way to the direct influence of surrounding conditions, and I think we must believe that it has been established in each species by natural selection on account of some advantage to the animals which exhibit it.

The fact that the hour for discharging the reproductive elements is, in so many species, a definite one, often in the night-time, shows the importance of marine observatories where the naturalist may keep his specimens under his eye at all hours of the day and night; for, as midnight collecting is usually impracticable, the early stages of many animals cannot be procured without facilities of this sort.

The eggs of *Eutima mira* develop rapidly, and the swimming planula stage is reached early in the morning after the eggs are laid.

Segmentation is total, but as shown in Pl. 38, fig. 1, it is not perfectly regular. A capacious segmentation cavity, fig. 8, *a*, soon makes its appearance, and the cells which are a little larger at one pole than they are at the other arrange themselves in a single layer, *b*, and continuing to subdivide soon become nearly uniform in size as shown in fig. 3. The embryo now becomes ciliated and, rising from the bottom, assumes the well-known pear-shaped outline of the hydroid planula, fig. 4, with a spacious segmentation cavity, surrounded by a single layer of ciliated cells, *b*, which are much thicker at the small end of the pear than over the rest of the body. While the blastoderm consists of only one layer of cells, the planula increases considerably in size, and appears to have some method of nourishing itself.

According to Merejkowsky. (50) the central cavity of the planula of Obelia communicates with the exterior through a great number of minute pores which are situated between the blastoderm cells. He says the pores are large enough to permit small infusoria to pass through them into the central cavity where he has seen small animals swimming actively. He believes that these small organisms serve as food, and, although I have not been able to discover the pores in Eutima, I have satisfied myself that the planula does obtain food in some way and increases in size.

The endoderm cells soon begin to make their appearance at the small or posterior end of the cavity and are set free, as shown at *c*, in fig. 4. They soon arrange themselves in a continuous layer or endoderm over the whole inner surface as shown at *c*, in fig. 6. According to Merejkowsky, they are not formed by the transverse division or delamination of the blastoderm cells, but by migration, in the manner which has been described by Schultze, Metschnikoff and others in the sponge planula. In a preliminary paper on the life-history of Eutima (11) I have stated that they are formed by delamination, but as I made no attempt to watch the changes of a single cell, I did not actually witness the process of division and it is possible that they are not formed in this way but by migration. The formation of the endoderm cells goes on rapidly and the planula soon appears to become a solid mass of cells, fig. 5, but careful examination will show that a small central digestive cavity, fig. 5, *g*, persists in the axis of the embryo, although it is rendered almost invisible in the living planula by the increasing capacity of the endoderm cells, which are apparently distended, so that they almost meet in the centre. In a specimen which has been killed with osmic acid and stained with picro-carmine, they are flatter than they are in the living animal, and it is easy to see that they are arranged in a single layer to form the walls of the digestive cavity. Fig. 6 is a stained specimen of the same age as the one shown in fig. 5. In a surface view, *c*, the rounded ectoderm cells are seen and by focussing a little deeper, the polygonal outlines of the granular endoderm cells, *c*, come into view, while still deeper focussing shows an empty space, *g*, the stomach, around the edges of which the single layer of endoderm cells is seen in sectional view.

There can, of course, be no doubt that in most hydroids, the planula is at first solid, and that the digestive cavity does not make its appearance until some time after the cells are specialized into an ectoderm and an endoderm, and I think that the persistence of the segmentation cavity of Eutima as the digestive cavity and the absence of a solid stage must be regarded as a secondary modification of the ancestral history, although it is not impossible that the manner in which the endoderm and digestive cavity are formed in the Geryonidæ (see below) may be the primitive one and the solid stage a secondary phenomenon.

The fact that a solid stage occurs in so many hydroids, in the Acraspeda (see Kowalevsky, 40) and in the Anthozoa (see Wilson, 67), as well as in the sponges, would seem however to indicate that the early appearance of the digestive cavity in Eutima and in the Geryonidæ is not primitive but secondary.

I shall not enter upon the discussion of the relation of the embryology of the Hydromedusæ to the gastrula theory, further than to point out that not a single hydroid gastrula has been observed; but that, in every species which has been studied, the digestive cavity has at first no opening to the exterior, and that the mouth is formed very much later than the stomach. Most writers believe, it is true, that the planula is a modified gastrula, and that its digestive cavity was originally invaginated from the exterior, but this is purely a deductive inference from the analogy of other animals. Thus Claus (14) describes the origin of the endoderm and digestive cavity of Æquora and Merejkowsky that of Obelia (50) as like that of Eutima, but both these writers state their opinion that the planula has originated through a modification of a primitive invaginate gastrula. Böhm says (p. 153) that it is natural to derive the Hydromedusæ and sponges from an ancestral gastrula, *since in no other group is descent from this form so certain.*

No one can question the resemblance between an adult hydroid or sponge, and the gastrula stage of the ordinary metazoa, and there is every reason for believing that the almost universal occurrence of this larval stage indicates that the cœlomatous metazoa are the descendants of an ancestral form which was essentially like the existing cœlenterates and that these themselves are the divergent modifications of a common type, the gastrula or two-layered metazoon, with stomach and mouth; but it is quite conceivable that the cœlenterates themselves may be the descendants of a form with a stomach, but without a mouth, and that the planula stage may be the ontogenetic representative of this just as the gastrula stage is the ontogenetic representative of the adult cœlenterate. Most writers have started however with the assumption that, as the hydroids must be the descendants of a gastrula, the planula must be a modified gastrula; and one writer (32) has, with the greatest simplicity, given us the chain of reasoning which has led him to supply a missing gastrula stage in the life of the hydroids. Hamann says in his section on "Segmentation and the formation of the Gastrula" that he was induced to study the subject by his belief that a planula stage did not exist and that the published accounts were wrong. He says, however, that in his studies of the embryos of Tubularia, Aglaophenia and several Plumularidæ, which were entered upon in this frame of mind, he was unable to find anything like the formation of a gastrula by invagination; that the paper by Ciamician, in which the invaginate gastrula of Tubularia is figured, is a conglomeration of errors, and that in all the forms which he himself has studied, the embryo becomes a planula like that which Schultze had described for Cordylophora; but while his appeal to nature leads him to these facts he says, "I hold that while the hydroid planula does in fact originate by delamination, without a segmentation cavity, nevertheless the planula is just as truly a gastrula as it would be if it originated by epibole or in any other manner," and that Balfour's view that the planula stage of development represents a free swimming ancestral form in the history of the Cœlenterata, in which the mouth and the digestive cavity were absent, is untenable.

If we believe that the gastrula stage of the higher metazoa is the representative of an ancestral form like the adult hydroid, we certainly should not expect to find a gastrula stage in the embryology of the hydroids themselves; and the analogy of the animals above the hydroids is no reason for supposing that the planula is a modified gastrula if we believe that these forms are the descendants of an ancestral form which was itself a divergent branch from the cœlenterate stem. The planula stage is certainly dominant among the sponges, and the so-called gastrula is here beyond doubt a secondary larva. Kowalevsky has shown that the embryo of Lucernaria is a planula (40) and Fol states (22) that his examination of the embryos of Pelagia has shown the need for a renewed examination of the alleged gastrula stage, while Wilson (67) shows that the Renilla embryo is certainly not a gastrula, and as there is not a single observation of a gastrula in the Hydromedusæ, we may, so far as this group is concerned, continue to speak of the larva as a planula.

Hamann says that since we have a planula in some hydroids, and *instead of this*, an actinula in others, we are compelled to believe that the life-history of the lower Cœlenterates is considerably modified and does not give us the primitive condition of things; but his own observations show that the actinula of Tubularia is not the equivalent of the planula of other hydroids, but that it is preceded by a planula stage, although this is not free but contained within the medusa-bud, and not being locomotor has no cilia.

Merejkowsky, who has given us a minute account of the planula of Obelia (50), says that he found a few embryos of Irene, in what seemed to him to be an invaginate gastrula stage, but he made no minute study of them and did not rear them. Irene is very closely related to Eutima, and it is interesting to note that, in Eutima, after the endoderm and the digestive cavity are formed, and before the appearance of the mouth, there is an ectodermal invagination which is possibly what he has seen in Irene, although the study of the late stages shows that it is not a mouth, but an ectodermal adhesive gland. · At the stage which is shown in fig. 6, there is a mouth-like aperture *f* at the small or posterior end of the planula, and in the living animal it is easy to see that this is formed by an invagination from the surface. In a specimen which has been killed with osmic acid and stained with picro-carmine, fig. 5, it is still more conspicuous, and is seen to be a spacious cavity, *f*, opening to the exterior and surrounded by a single layer of invaginated cells, which are continuous around the edge of the orifice with the ciliated cells of the surface of the body. As this invagination is very conspicuous while it is difficult to trace out the structure of the more opaque endoderm, the planula bears, at first sight, a very striking resemblance to an invaginate gastrula like that of the Echinoderms; but more careful examination shows that the digestive cavity, *g*, is already present, and surrounded by a continuous wall of endoderm cells, *c*, *c*, and that the endoderm as well as the ectoderm is infolded, and that the invagination does not communicate with the digestive cavity, and takes no part whatever in its formation. At a somewhat later stage, fig. 11, the endoderm becomes drawn away from the invagination, leaving this as an exclusively ectodermal structure.

I have observed a similar invagination at the small end of the planula of Turritopsis, Pl. 42, figs. 2 and 3, although the planula of this species is so opaque that the study of its internal structure is very difficult. The fact that the invagination is present in an Anthomedusa and a Leptomedusa gives a reason for believing that it occurs in other species as well and that future research may show that it is not at all unusual. At first, the orifice is terminal, as shown in figs. 5 and 6, and the invagination lies on the axis of the larva, but one lip or edge of the opening soon grows faster than the other and thus pushes the pouch on one side, fig. 11, *f*, which may be called ventral, since it is the surface by which the planula becomes attached; but, before attachment takes place, the whole structure is evaginated as shown in fig. 7, so that only a slight notch, *f*, remains to mark its position. Lasso-cells now begin to appear at the small end of the planula, the cilia are lost, and a delicate layer of transparent cement is thrown off from the ventral surface of the small end of the planula, as shown at *n* in fig. 8.

This soon hardens, and, entangling foreign particles, becomes the perisarc. When first attached, and for a short time after, the larva retains the shape which it had during the swimming stage, but it soon elongates, as shown in fig. 9, and becomes the sessile, creeping root, which ultimately produces a community of hydroids. For some time, its posterior end, figs. 9 and 10, *h*, is marked by a flattened pad of ectoderm cells, separated by a constriction from the ectoderm of the general surface of the body. This pad is the area which was invaginated during the swimming stage. The root has no mouth nor other opening to the exterior, and there is for some time no trace of the future hydranth; but a bud, fig. 9, soon grows out from the free end of the root and, developing a circlet of tentacles and a mouth, becomes the first hydranth, fig. 10. A second bud now grows out from the root on the proximal side or base of the first and this is soon followed by a third and so on. As the first hydranth is formed, like all the others, by budding from the root, the growth of the hydranth from the planula is rather a process of metagenesis than metamorphosis and this is not the only species of which this is true. The planula of Turritopsis, Pl. 42, figs. 2 and 3, also becomes a root from which the hydras bud, and I have observed the same thing in Hydractinia, where it has been frequently described; first by Wright (64) I believe. Merejkowsky shows that the hydranth of Obelia originates in the same way; that the planula becomes a star-shaped root from which the first hydranth grows out as a bud, and many other cases are recorded. In some forms the planula becomes directly converted into a single hydra, as in Tubularia, where there is no metagenesis, but in many other forms there is certainly a true alternation between the planula stage and the hydra stage.

The direct conversion of the ciliated, mouthless planula into the tentaculated stomatous hydra will, without doubt, be recognized as the primitive life-history; and the alternation of generations between the planula, or the root into which it becomes converted, and the hydras formed from it by budding, will, I think, be universally accepted as a secondary modification. I shall give, in the last section of this paper, my reasons for believing that the alternation of generations between the hydra and the medusa is not primitive but secondary, and that originally a tentaculated hydra-like larva became directly metamorphosed into a single medusa; and the fact that an alternation of generations between the planula and the hydra has been secondarily established in Hydractinia, Eutima and Obelia certainly shows that this view is not without the support of analogy.

The oldest hydranths of Eutima which I reared from the egg were like the large one in fig. 10. They had ten tentacles, five long ones alternating with five short ones, with their bases united by an intertentacular web, *k*, in the centre of which there is a rounded hemispherical manubrium, ending in a simple circular mouth, without oral tentacles.

Although the hydroid is Campanularia-like, the perisarc is not annulated and is confined to the root and stems and does not extend over the bodies of the hydranths, which therefore belong to Claus' genus Campanopsis (66) from which he has reared a medusa which is very closely related to Eutima, and which belongs to the same genus as originally established by McCrady. The metamorphosis of the young medusa has been well described by Claus for his species and there is no reason to suppose that ours is essentially different.

In the species which he studied, *Octorchis Gegenbauri,* the medusa-buds originate on the body of the hydranth, on short pedicels, and they are inclosed in mantles or capsules which are cellular and without a covering of perisarc. When set free, the bell of the medusa is deep, the height being somewhat greater than the radius. There is no peduncle, and the stomach, which is less than half as long as the depth of the sub-umbrella, ends in a simple mouth without lips. There are two opposite radial tentacles, the rudiments of two others, numerous solid marginal cirri, and eight adradial marginal vesicles, each with a single ocellus. Claus did not succeed in keeping the medusæ alive, but he traced in a series of captured specimens the gradual increase in the number of tentacles, the growth of the peduncle and lips and the development of the reproductive organs, the peduncular portions of which appear earlier than the sub-umbral portions.

The Origin of Alternation of Generations in the Hydromedusæ.

In the experimental sciences, the investigator seeks for the simplest manifestations of the natural law which he wishes to study, and divests it, as far as possible, of all secondary complications. In the natural sciences where experiment is usually impossible, the phenomena must be studied as they present themselves in nature; and the difficulties which any given problem presents depend, to a very great degree, upon the accidents which direct attention to examples and illustrations which are simple and easy to understand, or to those where the simple laws are obscured or hidden under secondary complications.

Just as Werner's geological speculations were colored by the peculiar nature of the region where he lived, so the speculations of zoologists upon the origin of the medusæ, and their relation to hydroids, have been complicated by the accident which has directed their attention to the wrong end of the problem and has caused the almost total neglect of the groups which furnish its solution.

The typical Hydromedusæ, the Tubularians or Anthomedusæ, and the Campanularians or Leptomedusæ, are found in abundance on every coast and the shortest visit at the seashore must bring them before the eyes of the naturalist; while the pelagic Trachomedusæ and Narcomedusæ, which are seldom found near the shore, are usually regarded as minor or aberrant groups and they usually occupy a very subordinate and secondary position in our general conception or mental picture of the Hydromedusæ, although they include nearly one-third of all the known species of Acraspeda and are, so far as diversity of structure is concerned, fully as important as the more familiar groups.

Most of the writers who have discussed the origin of the medusæ, and the significance of the alternation between them and the hydroids, have entirely ignored the Narcomedusæ and the Trachomedusæ; or else they have made only an incidental reference to these two groups, which actually furnish the clearest, simplest and most direct evidence which is attainable.

As soon as we perceive that there is no reason why we should believe that the medusæ which are set free from fixed hydroid communities are the most primitive, simply because they are the most familiar; and that Liriope, Ægina and Cunina are not, as Balfour (65) and Grobben (74) assert, medusæ which have lost their ancestral hydra stage, but simply solitary floating or swimming hydras which gradually grow into medusæ and which repeat, more or less exactly during their own ontogenetic development and gradual metamorphosis from the egg to the adult, the phylogenetic history of the medusa: the complicated problem disentangles itself and we feel at once that we have found the right end of the thread.

In Æginopsis, as Metschnikoff shows (30), the egg gives rise to a ciliated swimming planula, which acquires a mouth and tentacles and thus becomes directly and gradually converted into a floating hydra or *actinula* which is at first ciliated like the planula. The tentacular zone of the floating hydra now grows out into a flange or umbrella which carries the tentacles with it; sense organs and a veil are soon acquired and the hydra becomes a medusa.

The whole process is perfectly simple and direct; there is nothing like an alternation of generations and the single egg becomes a single medusa with an actinula stage, a floating hydra-like larval stage and a swimming medusa stage. The life-history is as simple and uninterrupted as that of any other animal which undergoes a metamorphosis, and it may be represented by the following simple diagram in which the sign of equality (=) denotes that the change is direct growth or metamorphosis rather than multiplication.

I. ÆGINOPSIS — *Egg* = *Planula* = *Actinula* = *Medusa* $\times <$ *Eggs*.

As the floating hydra stage of Tubularia is well known under the familiar name *Actinula* and as it seems desirable to use a special term for the free hydra stage of medusæ as distinguished from a sessile hydroid, I shall employ this word for this purpose, designating by it a free or floating hydra which may or may not be ciliated.

I have shown that we have in Liriope and its allies a life-history which is very similar to that of Æginopsis, with numerous secondary modifications, most of which are due to the fact that the gelatinous substance of the umbrella begins to be secreted between the endoderm and the ectoderm at a very early stage in the life of the embryo. The acceleration of the formation of the umbrella is exactly paralleled by innumerable similar phenomena in the lives of nearly all of the higher metazoa, and it therefore presents no difficulties; and if we imagine the gelatinous substance absent, the mouthless, untentaculated, ciliated Liriope larva, shown in Pl. 41, fig. 3, is obviously a planula with an outer layer of ectoderm and a central capsule of endoderm. It has a spacious digestive cavity; the two layers are separated by a gelatinous substance; and in our species, the cilia are restricted to a small part of the outer surface: but, in spite of these secondary modifications, it is clearly a planula. It soon acquires a mouth and four solid tentacles, and becomes converted into the floating hydra or actinula, shown in Pl. 41, fig. 8, with ectoderm, endoderm, stomach, mouth, lasso-cells, and four tentacles, but with neither sub-umbrella, sense organs nor veil. This larva becomes converted into an adult medusa by the growth of the tentacular zone into an umbrella, and by the acquisition of sense organs, precisely like the Æginopsis larva, and as each egg gives rise to only one adult the life-history is simple and direct, with a planula stage, a hydra stage and a final medusa stage, and it may therefore be represented by the same diagram as that which was used for Æginopsis.

II. LIRIOPE — *Egg* = *Planula* = *Actinula* = *Medusa* $\times <$ *Eggs*.

In our common American Narcomedusa, *Cunina octonaria*, the fact that the larva is a true hydra was long ago pointed out by McCrady. The planula stage of this species has never been observed, but the resemblance between the ciliated, bitentaculated hydra shown in our Pl. 43, fig. 1 and Metschnikoff's account of the Æginopsis larva at the same stage is so close that we have every reason for believing that, in this species also, the hydra stage is preceded by a planula stage without a mouth or tentacles. The hydra soon acquires two more tentacles and is then fundamentally like the four-tentacled hydra of Liriope. The number of tentacles soon increases to eight, and as is shown in our figs. 3, 8 and 4, the hydra becomes converted into a medusa by the outgrowth of the tentacular zone and the acquisition of sense organs. So far, the life-history of our Cunina is as simple as that of Æginopsis or Liriope, but it is complicated by the occurrence of a sexual multiplication in the larva and also by parasitism. The actinula, or floating ciliated hydra, after gaining access to the sub-umbrella of a Turritopsis, gives rise to buds from the aboral end of its body, behind the circlet of tentacles; each of these buds is a hydra like the parent and, like it, becomes directly converted into a medusa. As these secondary hydras originate as buds, they are at first sessile, but they become detached while in the hydra stage, or at least before they are completely converted into true medusæ: the time of detachment is not constant and although the larvæ are at first sessile, and, therefore, not actinulæ, they serve to show that the boundary line between a floating actinula and a sessile hydra is an extremely faint one.

Owing to the occurrence of asexual multiplication, each Cunina egg may give rise to an indefinite number of adult medusæ, but as each larva becomes directly converted into a medusa by a process of growth, there is no alternation and the life-history may be represented by the following diagram:

$$\text{III. CUNINA OCTONARIA } \textit{Egg} = \textit{Planula} = \begin{array}{c} \textit{Hydra} = \textit{Medusa} \times < \textit{Eggs}. \\ \times \\ \textit{Actinula} = \textit{Medusa} \times < \textit{Eggs}. \\ \times \\ \textit{Hydra} = \textit{Medusa} \times < \textit{Eggs}. \end{array}$$

Here we have asexual multiplication without alternation, but in the Cuninæ which Uljanin and Metschnikoff studied there is a true alternation which is obviously of secondary origin and undoubtedly due to a very slight modification of such a life-history as the one shown in diagram III. The planula itself is very peculiar and is furnished with an anomalous pseudopodial apparatus for clinging to and fastening upon the gastric process of the Geryonid within which it becomes a parasite; and the actinula, or primary hydra, into which it becomes converted, never completes its development into a perfect, free medusa. It remains as a brood-stock, from which other larvæ are budded, and these are set free and become converted into medusæ so that the life-history is represented by the following diagram, in which for the first time, we find a true alternation:

$$\text{IV. CUNINA (CUNOCANTHA) PARASITICA } \textit{Egg} = \textit{Planula} = \textit{Actinula} \times \left\{ \begin{array}{l} \textit{Hydra} = \textit{Medusa} \times < \textit{Eggs}. \\ \textit{Hydra} = \textit{Medusa} \times < \textit{Eggs}. \\ \textit{Hydra} = \textit{Medusa} \times < \textit{Eggs}. \end{array} \right.$$

A comparison of Metschnikoff's account of the development of *Cunina* (*Cunocantha*) *parasitica*, and that which I have given of *Cunina octonaria*, will bring out an interesting and significant difference between them which I have not yet pointed out. In the American *Cunina*, the hydra-stage is well marked in the larvæ which are produced by budding as well as in the one which hatches from the egg. In Metschnikoff's species, however, the characteristics of the adult medusa begin to make their appearance in the secondary buds, almost as soon as the buds themselves appear, and it would be difficult to recognize a hydra-stage in the life of this species if we were not acquainted with the simpler life-history of the American *Cunina*. In Metschnikoff's species, the primary hydra is also greatly modified to fit it for its parasitic life, but in other respects its life-history is very similar to that of the ordinary hydroids; and if the acquisition of the medusa characteristics by the secondary buds were a little more accelerated so that their hydra characteristics were entirely, instead of almost, crowded out, we should have a life-history like this:

$$\text{V.}\quad \textit{Egg} = \textit{Planula} = \textit{Actinula} \times \left\{\begin{array}{l} \textit{Medusa} \times < \textit{Eggs.} \\ \textit{Medusa} \times < \textit{Eggs.} \\ \textit{Medusa} \times < \textit{Eggs.} \end{array}\right.$$

I know of no hydra which presents this life-history without modification, but there are many Campanularians and Tubularians in which the only modification is the acquisition by the actinula or primary hydra of the power to produce, in addition to the buds which become medusæ, other buds which remain in the hydra condition, and share with their parent, the primary hydra, the power to produce both kinds of buds. Thus in Perigonomus (Stomatoca), the egg gives rise to a planula which becomes the first hydra, and this produces other hydras like itself and builds up a hydroid cormus; and ultimately all these hydras give rise to buds which become directly converted into medusæ, the hydra-like stage being completely suppressed, and we have a life-history like this:

$$\begin{array}{rcl} & \textit{Hydra} & \times \left\{\begin{array}{l} \textit{Medusa} \times < \textit{Eggs.} \\ \textit{Medusa} \times < \textit{Eggs.} \end{array}\right. \\ & \times & \\ & \textit{Hydra} & \times \left\{\begin{array}{l} \textit{Medusa} \times < \textit{Eggs.} \\ \textit{Medusa} \times < \textit{Eggs.} \end{array}\right. \\ & \times & \\ \text{VI.}\quad \textit{Egg} = \textit{Planula} = \textit{Actinula or} & \textit{Primary Hydra} & \times \left\{\begin{array}{l} \textit{Medusa} \times < \textit{Eggs.} \\ \textit{Medusa} \times < \textit{Eggs.} \end{array}\right. \\ & \times & \\ & \textit{Hydra} & \times \left\{\begin{array}{l} \textit{Medusa} \times < \textit{Eggs.} \\ \textit{Medusa} \times < \textit{Eggs.} \end{array}\right. \\ & \times & \\ & \textit{Hydra} & \times \left\{\begin{array}{l} \textit{Medusa} \times < \textit{Eggs.} \\ \textit{Medusa} \times < \textit{Eggs.} \end{array}\right. \end{array}$$

In Turritopsis we have essentially the same life-history, except that there is a secondary alternation between the primary hydra and the others. The planula does not become a hydra, but a mouthless, untentaculated root which is undoubtedly a degraded actinula or primary hydra. It does not give rise to medusa buds, but remains as a brood-stock or embryonic hydra from which fully developed hydras are formed by budding, and all of these produce medusa-buds, so the life-history is as follows:

$$\text{VII.}\quad \text{TURRITOPSIS } \textit{Egg} = \textit{Planula} = \textit{Root} \times \left\{\begin{array}{l} \textit{Hydra} \times \left\{\begin{array}{l} \textit{Medusa} \times < \textit{Eggs.} \\ \textit{Medusa} \times < \textit{Eggs.} \end{array}\right. \\ \textit{Hydra} \times \left\{\begin{array}{l} \textit{Medusa} \times < \textit{Eggs.} \\ \textit{Medusa} \times < \textit{Eggs.} \end{array}\right. \\ \textit{Hydra} \times \left\{\begin{array}{l} \textit{Medusa} \times < \textit{Eggs.} \\ \textit{Medusa} \times < \textit{Eggs.} \end{array}\right. \end{array}\right.$$

In the ordinary Campanularians, with free Medusæ, we have a new element of complexity, owing to the appearance of polymorphism. The ordinary hydras no longer give rise to medusa-buds, and these are produced only on the reproductive hydras or blastostyles. In Eutima, which I shall take as an example of this group, we have another complication, which is very significant. As in Turritopsis, there is a secondary alternation of generations, for as I have shown above, Pl. 36, fig. 9, the planula no longer becomes converted into a hydra but forms a root from which the primary hydra is budded like those which appear later.

As I have shown, this secondary alternation occurs in many hydroids, such as Hydractinia, Eutima, Turritopsis, Obelia (Merejkowsky) and others, and it was correctly described by Wright in Hydractinia in 1856; but, so far as I am aware, no one has pointed out that it is a true alternation, exactly like the alternation between the hydra and the medusa. It is certainly a secondary acquisition, as we may see from the fact that in Tubularia, Eudendrium and other hydroids, the planula becomes directly converted into a hydra. So far as this point is concerned, the life-history of Eutima or Hydractinia, and that of Tubularia or Eudendrium present the following contrast.

$$\begin{array}{rc} & \textit{Hydra} \\ & \times \\ \textsc{Tubularia}\ \textit{Egg} = \textit{Planula} = \textit{Actinula} = & \textit{Hydra} \\ & \times \\ & \textit{Hydra} \end{array}$$

with no alternation, while in the other forms we have

$$\textsc{Eutima}\ \textit{Egg} = \textit{Planula} = \textit{Root} \times \left\{ \begin{array}{l} \textit{Hydra} \\ \textit{Hydra} \\ \textit{Hydra} \end{array} \right.$$

with an alternation.

The complete life-history of Eutima with its double alternation between the root and the hydranths, between the hydranths and the medusæ, and its polymorphism, and division of the hydranths into nutritive persons and blastostyles, may be represented as follows:

$$\text{VIII.}\quad \textsc{Eutima}\ \textit{Egg} = \textit{Planula} = \textit{Root} \times \left\{ \begin{array}{l} \textit{Nutritive Hydra} \times \left\{ \begin{array}{l} \textit{Blastostyle} \times \left\{ \begin{array}{l} \textit{Medusa} < \textit{Eggs.} \\ \textit{Medusa} < \textit{Eggs.} \\ \textit{Medusa} < \textit{Eggs.} \end{array} \right. \\ \textit{Nutritive Hydra} \end{array} \right. \\ \\ \textit{Nutritive Hydra} \times \left\{ \begin{array}{l} \textit{Nutritive Hydra} \\ \textit{Blastostyle} \times \left\{ \begin{array}{l} \textit{Medusa} < \textit{Eggs.} \\ \textit{Medusa} < \textit{Eggs.} \\ \textit{Medusa} < \textit{Eggs.} \end{array} \right. \end{array} \right. \end{array} \right.$$

In Podocoryne (Dysmorphosa) we have an extremely complex life-history which, however, is readily derivable from one like that of Eutima as just given. There is a secondary alternation between the root and the hydranths as in Eutima, and the polymorphism between the hydranths is more specialized, as we find not only nutritive polyps and blastostyles but defensive polyps as well; and as each medusa, in addition to its sexual function, also possesses the power to produce other medusæ by budding, the number of sexual animals which may be derived from a single egg is unlimited.

The following diagram represents the life-history of this species, except that the first generation of medusæ, like the second, gives rise to reproductive elements.

IX. Podocryne
Egg = Planula = Root ×

- *Nutritive Hydra* × { *Nutritive Hydra*, *Blastostyle*, *Defensive Hydra* } ×
  - *Medusa* × { *Medusa* < *Eggs.* / *Medusa* < *Eggs.* }
  - *Medusa* × { *Medusa* < *Eggs.* / *Medusa* < *Eggs.* }

  ×
- *Nutritive Hydra* × { *Nutritive Hydra*, *Blastostyle*, *Defensive Hydra* } ×
  - *Medusa* × { *Medusa* < *Eggs.* / *Medusa* < *Eggs.* }
  - *Medusa* × { *Medusa* < *Eggs.* / *Medusa* < *Eggs.* }

  ×
- *Nutritive Hydra* × { *Nutritive Hydra*, *Blastostyle*, *Defensive Hydra* } ×
  - *Medusa* × { *Medusa* < *Eggs.* / *Medusa* < *Eggs.* }
  - *Medusa* × { *Medusa* < *Eggs.* / *Medusa* < *Eggs.* }
- *Nutritive Hydra* × { *Nutritive Hydra*, *Blastostyle*, *Defensive Hydra* } ×
  - *Medusa* × { *Medusa* < *Eggs.* / *Medusa* < *Eggs.* }
  - *Medusa* × { *Medusa* < *Eggs.* / *Medusa* < *Eggs.* }

  ×
- *Nutritive Hydra* × { *Nutritive Hydra*, *Blastostyle*, *Defensive Hydra* } ×
  - *Medusa* × { *Medusa* < *Eggs.* / *Medusa* < *Eggs.* }
  - *Medusa* × { *Medusa* < *Eggs.* / *Medusa* < *Eggs.* }

  ×
- *Nutritive Hydra* × { *Nutritive Hydra*, *Blastostyle*, *Defensive Hydra* } ×
  - *Medusa* × { *Medusa* < *Eggs.* / *Medusa* < *Eggs.* }
  - *Medusa* × { *Medusa* < *Eggs.* / *Medusa* < *Eggs.* }

It is very probable that future research will show that even this complex diagram is too simple for some of the Hydromedusæ, and that there is, in some cases, a secondary alternation between the first generation of free medusæ and those which are produced by budding from this generation. The life-history of these proliferous medusæ has not been studied, as they are seldom found near laboratories and appliances for research, but there is reason to suspect that in some of them only those medusæ which are budded from the bodies of the medusæ of the first generation become sexually mature; and if future research should prove this we should have still another alternation between the asexual proliferous medusæ and their sexual descendants.

In Hydractinia, the cormi of which are so similar to those of Podocoryne that a drawing of one will correctly represent the other, the life-history begins to simplify itself by the degradation of the sexual medusæ into sessile buds, or reproductive organs, which, however still retain traces of their former independent locomotor existence; traces which have almost totally disappeared in Eudendrium and in many of the Campanularians.

The life-history of Hydractinia may be represented as follows:

$$\text{X. HYDRACTINIA } \mathit{Egg} = \mathit{Planula} = \mathit{Root} \times \left\{\begin{array}{l} \mathit{Nutritive\ Hydra} \times \left\{\begin{array}{l}\mathit{Nutritive\ Hydra} \\ \mathit{Blastostyle} \\ \mathit{Defensive\ Hydra}\end{array}\right. \times \left\{\begin{array}{l}\mathit{Medusa\text{-}Bud} < \mathit{Eggs.} \\ \mathit{Medusa\text{-}Bud} < \mathit{Eggs.}\end{array}\right. \\ \mathit{Nutritive\ Hydra} \times \left\{\begin{array}{l}\mathit{Nutritive\ Hydra} \\ \mathit{Blastostyle} \\ \mathit{Defensive\ Hydra}\end{array}\right. \times \left\{\begin{array}{l}\mathit{Medusa\text{-}Bud} < \mathit{Eggs.} \\ \mathit{Medusa\text{-}Bud} < \mathit{Eggs.}\end{array}\right. \\ \mathit{Nutritive\ Hydra} \times \left\{\begin{array}{l}\mathit{Nutritive\ Hydra} \\ \mathit{Blastostyle} \\ \mathit{Defensive\ Hydra}\end{array}\right. \times \left\{\begin{array}{l}\mathit{Medusa\text{-}Bud} < \mathit{Eggs.} \\ \mathit{Medusa\text{-}Bud} < \mathit{Eggs.}\end{array}\right. \end{array}\right.$$

Now, what is the significance of this remarkable series of life-histories? Most of the facts have long been known, but the most conflicting interpretations of them have been advanced, and the student who seeks in the various monographs upon the subject an exposition of the relation between the direct development of a single adult from each egg, which is characteristic of most animals, and the circuitous history which is so remarkably exhibited by the medusæ, will find a speculative literature which is almost unlimited, but a total lack of agreement as to the true solution of this, the most interesting of all the problems involved in the life of these most interesting animals.

The view which I believe to be the true one is that the remote ancestor of the hydromedusæ was a solitary swimming hydra, or actinula, with no medusa stage, but probably with the power to multiply by budding. I believe that this pelagic animal gradually became more and more highly organized and more perfectly adapted for a swimming life, until it finally became converted into a medusa with a swimming bell and sense organs, developing directly from the egg without alternation, but exhibiting during its growth the stages through which it had passed during its evolution. After this stage of development had been reached I believe that the larva derived some advantage from attachment to other bodies, either as a parasite within other medusæ, or as what may perhaps be called a semi-parasite, upon other floating bodies such as the fronds of algæ; and that it multiplied asexually in this sessile condition, giving rise to other larvæ like itself, all of which became medusæ.

I believe that the sessile or attached mode of life of the larvæ proved so advantageous to the species, that it was perpetuated by natural selection, and that the primary larva then gradually lost its tendency to become a medusa, but remained a sessile hydra, giving birth by budding to other larvæ which became sexual medusæ; and that the medusa-characteristics of these secondary larvæ were accelerated, and that the primary larva gradually acquired, at the same time, the power to produce other larvæ which remained permanently, like itself, in the hydra-stage; that in this way the sessile hydra-communities with medusa-buds and free sexual medusæ were evolved; and that finally these communities became polymorphic by division of labor, and that the sessile habit proved so advantageous that the free medusæ became degraded into medusa-buds, or sexual buds on the bodies of the sessile hydras or on the blastostyles.

The view which is most generally accepted is the reverse of this. Thus Huxley (34) tells the student that the medusa is simply a reproductive organ which was originally sessile upon the body of the hydroid, and that it has gradually acquired its free habit of life and its power of locomotion in order to secure the diffusion of the reproductive elements. Gegenbaur (26) and Balfour (65) tell him that the medusa is not an organ but a person, homologous with a whole hydroid, not with a part of it as Huxley teaches; that the separation of the community into sessile nutritive hydra-persons and locomotor reproductive medusa-persons has been brought about by division of labor; that the hydra community is older than the medusa; that originally all the members of the community were alike; that gradually certain ones became set apart for reproduction; and that, finally, these latter were set free, and acquiring reproductive organs became locomotor medusæ and that this change was brought about in order to secure the diffusion of the reproductive elements. These authors also believe that after medusæ had been gradually evolved in this way for this purpose, circumstances changed in some unexplained way, so that the wide diffusion of the reproductive elements was no longer so essential and that the medusæ took the back track and retrograded into sessile medusa-buds.

Hamann (32) who also believes that the sessile community is the primitive form, and that the medusæ have been produced by the gradual specialization of certain members which were set apart as the reproductive members, holds that they gradually acquired the power of locomotion in order to secure cross-fertilization rather than the diffusion of the eggs.

In 1878 Böhm (9) showed that the opinion that the sessile community is the primitive form, presents insuperable difficulties and he points out many reasons for believing that both the fixed hydra and the locomotor medusa have been evolved from a floating actinula, and Claus, two years after (17), 1880, states very briefly his belief that the hydra-stage is a larva and the medusa simply the adult and that the alternation of generations is due to the fact that the larva has the power to multiply asexually and thus to produce a number of larvæ like itself. This view is identical with the one which I reached independently at about the same time, before I was acquainted with the conclusions of Böhm and Claus, from the evidence which I am now able to present in full with illustrations, and which is not the same as the evidence which led Claus and Böhm to the same result, for neither of these authors makes any special reference to the life-history of the Narcomedusæ and Trachomedusæ.

It seems to me that the facts which are given in this paper establish this view beyond controversy and I shall show in the review of the literature of the subject which is given farther on that it is the only hypothesis to which there are not insuperable objections. Even if this were not the case, I think that a comparison of the life-histories which are represented in the nine diagrams given above would convince every one that they stand in some derivative relation to each other, and it is surely simpler to believe that the complicated life-history shown in diagram VIII has been derived from a simple one like that shown in diagram I, than it is to believe with Balfour, Hamann and Grobben that the Narcomedusæ and Trachomedusæ have been produced as the reproductive members of polymorphic cormi and that they have afterwards lost all traces of this ancestry.

Most of the reasons which compel us to this conclusion will be brought out in the review of the literature of the subject, but I wish to call attention here to one argument which is not noticed elsewhere, although it seems to me to be entitled to great weight.

The union of the sexes is so important to animals which are not locomotor that, among the Arthropoda, a group which includes far more than half of all the animals known to us, the sessile barnacles are almost the only hermaphrodites.

If the medusæ have been formed by the specialization of members of a community, and if the sessile hydroid cormi are, as this hypothesis requires, very old and primitive, we should certainly expect to find them exhibiting the power to produce from a single cormus medusæ of both sexes, for Hydra, which is one of the most primitive hydroids, is hermaphrodite. The polymorphism hypothesis gives no explanation of the remarkable fact that, with the exception of Hydra, all the numerous descendants, often many thousand in number, of any particular planula, are of one sex; but we can readily understand how this might be the case if the fixed hydroid cormi have been produced as I suppose, for if the sexes are distinct in adult medusæ, the larva of any particular medusa must be either a male or a female, and there would be nothing strange in the fact that its gemmiparous offspring should resemble it in this respect.

Section VI.

A Review of the Literature on the Relation between the Hydra and the Medusa and on the Origin of Alternation of Generations.

The fundamental similarity between a hydra and a medusa is so obvious that it hardly seems necessary to dwell upon it, but the history of opinion upon the subject shows that this has been by no means uniform, although nearly all naturalists now agree that a single hydra is directly comparable or homologous with a single medusa, and that the various hydromedusæ are also directly comparable with each other; that both the hydra and the medusa are in that stage of individuality to designate which Haeckel's term "person" is now almost universally employed.

The general plan of structure is very much alike and the history of such forms as the Geryonidæ and Æginidæ, where the hydra-like larva becomes directly transformed into the adult, shows that a medusa is little more than a hydra with sense organs and a locomotor apparatus. The hydroids are not furnished with sense organs, although there is every reason to believe that the sense organs of the Narcomedusæ are modified tentacles, homologous with the solid tentacles of hydroids; and I know of only one writer who does not regard the cavity of the sub-umbrella of the medusa as the homologue of the space which lies on the oral side of the circlet of tentacles in such a hydroid as Eutima, Pl. 38, fig. 10. The mouth of the hydroid is homologous with the mouth of the medusa, and where this is mounted upon a proboscis or manubrium, this structure is directly comparable with the proboscis or pendent stomach of the medusa.

The ectoderm of the peristome of the hydroid, or the area included between the bases of the tentacles, is homologous with the ectoderm of the sub-umbrella and proboscis of the medusa; while the convex dorsal or aboral surface of the hydroid corresponds to the convex ex-umbrella of the medusa.

The oral tentacles of such a hydroid as Tubularia or Pennaria are to be compared with those of Margelis and I regard them as strictly homologous structures, while the zone which carries the circlet of tentacles of the Campanularian hydroids, or the aboral tentacles of Pennaria, is homologous with the bell margin of the medusa with its tentacles. The velum is not represented by any distinct hydroidean structure.

The digestive cavity of the medusa with its tubes or pouches is quite different from that of a hydroid, although the history of the origin of these parts in medusa-buds, or in the egg-embryo of Liriope or in Cunina, shows that the union of the ex-umbral and sub-umbral layers of endoderm has converted the peripheral portion of the simple digestive cavity of the hydroid into radial canals or pouches arranged around the central stomach of the medusa, which therefore does not correspond to the whole stomach of the hydroid, but only to its axial or central portion, while its peripheral portion is homologous with the canal system of the medusa. For a more extended statement of the subject see Koch (38) and Haeckel (78).

There can be no doubt that this, the generally accepted view, is correct, and the fact that the hydra-larva of the Trachomedusæ and Narcomedusæ becomes directly converted into a medusa, furnishes very direct and conclusive proof. I doubt, however, whether it could be so satisfactorily established if we were not acquainted with these forms; for many of the phenomena in the life of the Antho- and Leptomedusæ which are urged in proof of it are in themselves inconclusive. The retrograde metamorphosis, which according to Van Beneden (8), Hinks (33), Allman (6) and Merejkowsky (50) often results in the conversion of a medusa into a hydra-like organism, through the disappearance of the umbrella and the return to a sessile habit, seems to show that the two forms are mutually convertible; but Merejkowsky confirms Van Beneden's statement that in these cases of degeneration the resemblance to a hydra is entirely superficial.

The fact that the chymiferous tubes of a medusa-bud are formed by the development of areas of adhesion in the lateral portions of a digestive cavity which is at first continuous like the stomach of a hydra, is often adduced as evidence of fundamental similarity, but there is no reason for believing that the ontogenetic history of developing buds repeats the phylogenetic record. The history of Cunina and Liriope shows that the peristome of the hydra is the sub-umbrella of the medusa, and if bud-ontogeny were a recapitulation of phylogeny, we should expect the sub-umbrella of a budding medusa to arise as it does in Cunina; but we find, on the contrary, that in the medusa-buds of all the Campanularians and Tubularians, as well as in the Siphonophores, it originates as a bud nucleus, *Knospungskern*, which gives rise by splitting, before the mouth is formed, to the sub-umbrella, which has at first no opening to the exterior. It is therefore unsafe to trust any of the evidence furnished by bud-embryos; but the evidence from egg-embryology is not open to this doubt, for in all cases where there is no reason to suspect secondary modification, we may safely regard this as a recapitulation of phylogeny; and the life-history of those few medusæ which develop directly from the egg is therefore of the greatest importance as a basis for comparison of the medusa with the hydra.

In all these egg-embryos, the "bud-nucleus" is absent, the mouth appears before the bell cavity makes its appearance and this is never closed but is formed by the folding of the body; while the chymiferous tubes are formed by the modification of a simple digestive cavity as we should expect if the hydra and the medusa are representatives of the same fundamental type.

So far as I am aware, only one modern writer has advocated any other homology between the two forms than the one which I have stated. Ray Lankester has proposed (45) to homologize the sub-umbrella of a hydromedusa with the stomadæum of Anthozoa, Ctenophora and other Metazoa, basing this view upon the unproved and very improbable hypothesis that the young specimens of Limnocodium which he has described are egg-embryos. He does not state his view very clearly, but he must either believe that those Metazoa which are furnished with a stomadæum are the modified descendants of a form like an adult medusa, or else he must believe that the young Limnocodium represents the ancestral condition of the medusæ, and that the presence of a bell cavity is a very old characteristic. If he intends to advocate the latter view, it is plain that he cannot regard the medusa as an ordinary hydroid specialized for locomotion.

Many authors who have fully recognized the close similarity between the hydra and the medusa, and some who have been among the most important contributors to our knowledge of the subject, have nevertheless held that a medusa is not equivalent to a single hydra, but to a polymorphic hydroid community; that a medusa is not a person but a cormus.

This view has long been a favorite one, and it appears in many forms in the literature of the subject. The following extracts from my notes will serve to show how frequently it has been advanced, although I do not believe that the writers quoted are all who might be referred to. In 1854 W. Thompson compared the reproductive process of hydroids to that of plants and pointed out the resemblance between a medusa and a flower (59), and in 1860 Jäger (35) enlarged upon this familiar comparison and attempted to show that the medusa bears the same relation to the hydroid colony that the flower does to the plant, not only in position and in its reproductive function, but in its ultimate morphological structure also. He says it is made up, like the flower, of several circlets of individuals; that the tentacles, sense-organs, reproductive organs, etc., are all morphological individuals; that the swim-bells of Siphonophores are sterile flowers; that the medusa-buds of Hydractinia are flowers without calyces and that alternation of generations should more properly be called "*anthogenesis*."

In 1856 Wright advanced the opinion (63) that a veiled medusa is to be compared with a polymorphic hydroid community like Hydractinia, which he regards as a single person, not a cormus; that the umbrella is homologous with the flat, spreading root of Hydractinia, its chymiferous tubes with the canals of the root; that the stomach of the medusa is a nutritive hydranth, its tentacles spiral zooids, its reproductive organs medusa-buds, etc.

At a time when homology was not regarded as having any phylogenetic significance, there was little check upon such fancies as those of Jäger and Wright, but they are clearly of little more scientific value than Mörch's suggestion (53) that the Acalephs should be placed with the Mollusca on account of the imaginary resemblance between Lima and a medusa.

In 1856, Leuckart (47) in his account of the structure of a Trachomedusa, *Agalma Peronii*, figures and describes the reproductive organs. They form a circlet of eight hollow-stalked pouches, within the walls of which the eggs are developed; while their central chambers are outgrowths from the digestive cavity. The pouches are arranged in a circle around the base of the pendent stomach, and he calls attention to the marked resemblance between them and the medusa-buds, which are produced by many species in exactly the same situation. He therefore advances the hypothesis that the sexual pouches of Agalma are not organs but buds, which instead of becoming free sexual medusæ remain in a rudimentary or arrested condition; and, like the degraded medusa-buds of Hydractinia, give rise to ova or spermatozoa. He says "our *sexual organs* are therefore to be regarded as *sexual animals*, which, remaining sessile, form with the mother a polymorphic colony. The relation between these appendages and the medusa which carries them is in this species at bottom an alternation of generations." He is careful to state that he does not offer this as an interpretation of the reproductive organs of other species, and he says that while he is not prepared to decide whether the reproductive organs of Agalma are homologous with those of other medusæ, he inclines to the view that they are not.

Three years later Allman (3) advanced almost the same hypothesis, but in the form which he gives to it, the reproductive organs of Agalma and those of all the Anthomedusæ are simply organs, while the reproductive bodies of the Leptomedusæ are not organs but persons.

The fact that Leuckart first advanced the hypothesis as an explanation of the reproductive organs of Agalma while Allman excludes Agalma and brings forward the hypothesis as an explanation of the nature of the reproductive organs of quite different forms, is in itself enough to raise a suspicion that the whole conception is unscientific and fanciful.

As Böhm has shown in his valuable paper on the Leptomedusæ of Helgoland (9) that there is no such resemblance between the various stages in the development of a medusa-bud and the stages in the development of the reproductive organs of a Leptomedusa as Allman's hypothesis requires, it seems unnecessary to give any other reasons for rejecting it. Although Allman has devoted a paper to the attempt to show that the Geryonidæ are blastochemes (6), the life-history of Liriope, as I have detailed it, is absolutely irreconcilable with the belief that it is a cormus, and the hypothesis is completely overthrown by the recent discovery (76) that in many cases, the ova of the Leptomedusæ arise in the proboscis and migrate along the radiating canals to the ovaries.

One of the oldest opinions upon the relation between the hydra and the medusa is the one which Huxley adopts (34), that the medusa is a free locomotor reproductive organ. This is almost the opposite of Allman's view, that the reproductive organs of a medusa are themselves persons, and that the medusa is in reality a community. Huxley says (34, p. 149), "A medusoid, though it feeds and maintains itself, is in a morphological sense simply the detached generative organ of the hydrosoma on which it is developed," and on p. 34, "Morphologically the swarm of medusæ thus set free from a hydrozoon are as much organs of the latter as the multitudinous pinnules of a Comatula, with their genital glands, are organs of the echinoderm."

The authors who have accepted this view have appealed to the fact that we have a complete series of species which present all the intermediate stages between the simple reproductive prominences of Hydra and the free sexual medusa of Turritopsis or Eutima. In Hydra the reproductive organ is simply a protrusion from the surface of the body; in Eudendrium it is more prominent and it contains a stomach-like outgrowth from the digestive cavity of the hydroid; in Hydractinia this outgrowth is a true proboscis or manubrium, which projects into a sub-umbral, ectodermal chamber opening to the exterior, and gives rise to a peripheral chamber which corresponds to the canal system of medusæ. In some species of Tubularia the peripheral chamber is not continuous, but is divided into four radiating canals and a circular canal, and in other species the opening of the umbrella is furnished with tentacles, so that we have all the characteristic structures of a locomotor medusa, although the medusa-buds of Tubularia are never set free, and serve simply to mature the eggs and embryos. In a closely related form, Ectopleura, the ova or spermatozoa are matured before the medusa is set free, as is the case in Tubularia, but the medusæ of Ectopleura are nevertheless set free, and live for some time as swimming medusæ, while in still other forms the reproductive elements are very immature at the time the medusa is set free, and are gradually developed and ripened during its swimming life.

The series of forms is so complete that we cannot doubt that there is a genetic relation between them, and that they are actually steps in a process of modification; and it at first seems natural to conclude that the simplest forms show us the first steps in this process, and the more complex forms the later stages, and that they therefore prove that the free locomotor medusa has been gradually evolved from the simple sexual organ; but we must remember that the process of modification may possibly have gone in the other direction, and that the simple reproductive buds of Hydractinia and Eudendrium may possibly be degraded medusæ which have gradually become sessile and have lost, by successive slight modifications, their locomotor apparatus.

So far as I am aware, Koch (38) was the first to point out, in 1873, that this is not only possible, but that there are facts which compel us to believe that it is actually true, such as the homology between a medusa and a hydroid and the fact that the medusæ of widely separated hydroids are fundamentally alike, while closely related species of hydroids may give rise to sexual buds which are very different from each other. For example, the hydroid communities of Hydractinia and Podocoryne (Dysmorphora) are so much alike that they can be distinguished only by the most careful examination, but Hydractinia produces sessile medusa-buds without radiating canals or tentacles, while Podocoryne sets free perfect locomotor medusæ. A very similar case is presented by Tubularia with its sessile medusa-buds and Ectopleura with its free medusæ; and the medusa-buds of Tubularia are essentially like those of Hydractinia, while the free medusæ of Ectopleura and Dysmorphora (Podocoryne) are again very much alike. If we put these facts into tabular form, we shall have something like this:

1	Hydractinia	Sessile buds	Tubularia	3
2	Podocoryne	Medusæ	Ectopleura	4

1 and 2 are much more closely related to each other than to either 3 or 4, while 3 and 4 stand in a similar relation to each other; and, if we believe that medusæ have been produced by the gradual specialization of reproductive buds, we must believe that 2 has

been produced by the modification of 1, and 4 by the modification of 3, and that the locomotor habits of 2 and 4 have been independently acquired.

In each case we have a pulsating, gelatinous bell, with sub-umbral muscles and a veil; a pendent stomach with ova or spermatozoa developed in its walls; four radial canals, a circular canal and hollow marginal tentacles; and the two medusæ are almost as much alike as the hydroids 1 and 2, or the hydroids 3 and 4. The chances are very greatly against the independent modification of the two forms along lines which are so perfectly parallel, and when we bear in mind that the hypothesis compels us to believe that this has taken place not in two but in many cases, the difficulty becomes a very great one; but, if we adopt the opposite hypothesis, and regard the medusa-bud as a degraded, sessile medusa, there is no such difficulty, for similar medusæ would give rise, by degradation and the loss of their locomotor apparatus, to similar medusa-buds. Then, too, if the medusa-buds are stages in the process which has led to the formation of free medusæ, we cannot account for the presence in buds which never became free, of structures which like the bell-cavity and velum are of functional importance only in the swimming medusæ, although we should expect these organs or their rudiments to be retained by medusæ which had lost their swimming habits and become sessile.

These and other facts have led most naturalists to believe with Koch that the medusæ are not specialized reproductive organs, but modified hydras, and that the sessile medusa-buds are degraded medusæ rather than stages in the evolution of medusæ. The life-history of Liriope seems to be totally irreconcilable with Huxley's view, for this would require us to believe that the egg here gives rise to nothing but a reproductive organ and that this process is continued generation after generation.

I think, therefore, that the facts justify the statement that our present knowledge of the subject disproves the view which Huxley advocates and that this view is now untenable. As a matter of fact, nearly all naturalists reject it in favor of the "polymorphism" hypothesis, which the student will find presented in the text-books of Gegenbaur and Balfour, but examination of the special literature will show that the various advocates of this hypothesis are by no means agreed as to the precise manner in which the two polymorphic forms, the hydra and the medusa, have been produced.

Balfour, for example (65), adopting essentially the views which had been brought forward many years before by Leuckart, says, "The chief interest of the occurrence of alternation of generations among the Hydromedusæ and Siphonophora is the fact that its origin can be traced to a division of labor in the colonial system of zooids so characteristic of these types. In the Hydromedusæ an interesting series of relations between alternation of generations and the division of the zooids into gonophores and trophosomes can be made out. In Hydra the generative and nutritive functions are united in the same individual. * * * A condition like that of Hydra in which the ovum directly gives rise to a form like its parent is no doubt the primitive one. * * * The relation of Hydra to the Tubularidæ and Campanularidæ may be best conceived by supposing that in Hydra most ordinary buds did not become detached so that a compound hydra became formed, but that at certain periods particular buds retained their primitive capacity of becoming detached and subsequently developed reproductive organs, while the ordinary buds lost their generative function. It would obviously be advantageous to the species that the detached buds with generative organs should be locomotive, so as to distribute the species as widely as possible, and such buds in connection with their free existence would naturally acquire a higher organization than their attached trophosomes. It is easy to see how, by a series of steps such as I have sketched out, a division of labor might take place, and it is obvious that the embryos produced by the highly organized gonophores would give rise to a fixed form from which the fixed colony would be budded. Thus an alternation of generations would be established as a necessary sequel to such division of labor." He goes on to state his belief that the sessile medusa-buds are degraded medusæ, and that the medusæ, which like Liriope develop directly from the egg, are forms in which the hydra stage has disappeared from the developmental cycle; and summing up his views he says that three types of development are presented by the Hydromedusæ.

1. No alternation of generations: permanent form a sexual hydra or hydra community. *Example:* Hydra.

2. Alternation of generations: hydroid stage fixed, medusa stage free. *Example:* most hydroids.

3. No alternation of generations: permanent form a sexual medusa. *Example:* Trachomedusæ.

But, in his explanation, which we have quoted, he recognizes the following six successive stages in the evolution of the Hydromedusæ.

1. Solitary hydra, no polymorphism, all buds detached, all persons sexual.

2. Community of sexual persons, giving rise also to detached buds which also become sexual persons.

3. Polymorphism, community of asexual nutritive persons, detaching buds which become sexual persons.

4. Same, detached sexual persons specialized as locomotor medusæ.

5. Polymorphic community consisting of nutritive asexual persons and sexual sessile medusæ-buds, or

6. Derived from 4, medusæ without a hydra stage.

Grobben (74) advocates a view which is very similar to that given by Balfour, and he believes that the alternation has been produced by the following series of steps:

1. Solitary hydroids, like Hydra.
2. Communities without polymorphism, each individual sexual, like Hydrella.
3. Communities, with polymorphism, with sexual and asexual persons, all sessile.
4. Same, with free reproductive persons.
5. Same, with free reproductive persons specialized as locomotor medusæ.
6. Same, with medusæ degraded to sessile reproductive buds.
7. Derived from 5, medusæ without a hydra stage.

While Balfour believes that certain members of the community first became free and afterwards became specialized for reproduction, Grobben believes that they became specialized for reproduction while sessile, and that the tendency to become free was afterwards acquired, but in other respects these two authors are in substantial agreement.

Hamann (32), however, adopts a somewhat different view and says that it was possible to believe that the alternation, or the origin of the medusa on the hydroid, came about through division of labor, so long as it was supposed that the reproductive elements originate in the medusæ; but the discovery that the eggs, in many cases, originate in the cœnosarc of the hydroid and migrate into the medusa-buds, shows, he says, that this is not the true view, and he advances another which was suggested to him in conversation with Weismann. Starting with a community in which the reproductive elements may originate in every part, he supposes that certain persons were set free from the stock as in Hydra or in Tiarella, and that the persons thus set free were at first driven about by wind and tide, obtaining their food by the use of their tentacles; that they were simply floating hydras. Those which became adapted to this new life would, retaining their power to produce eggs, give rise to fixed communities, in which locomotor persons would be set free earlier and earlier, until finally the reproductive function would become restricted to the free stage which would gradually acquire a locomotor apparatus and thus become a medusa.

These various opinions which are selected from a great number which might be quoted show that the "polymorphism" hypothesis, which is the one most generally accepted, is itself polymorphic and that authorities are far from an agreement as to the precise form which it should take and this lack of agreement is in itself sufficient to excite a suspicion that it may be merely an hypothesis unsupported by proof.

All these authors agree, however, in the opinion that the reason for the evolution of the locomotor medusa is the advantage which comes from the distribution of the sexual elements and embryos, and the analogy of the polymorphic hydroids seems at first sight to be a reason for believing that the medusa has originated according to the law of division of labor. The hydroid blastostyle is undoubtedly a hydranth which has in this way lost its nutritive function, and has become exclusively a reproductive zooid, while the ordinary hydranths have lost their reproductive function and have become simply nutritive persons, and there is every reason for believing that the polymorphism of such a hydroid as Hydractinia has been brought about by division of labor; but is there any real analogy between a blastostyle and a medusa? The medusa is very far from being, like the blastostyle, a reproductive zooid. The blastostyle has no mouth, but the medusa is a highly voracious animal, furnished with organs for perceiving and capturing its prey, and with highly developed digestive organs. There is nothing in the structure of a medusa to indicate that it is a reproductive zooid. It is true that in a few Tubularians such as the Eucopella, recently described by Lendenfeld, or in Corymorpha, it is simplified in structure and is little more than a locomotor reproductive pouch; but these cases are plainly the result of recent modification, and the typical medusa has all the characteristics of a perfect adult animal with all the powers necessary for a complete life, and in many species it produces other medusæ by budding. There is certainly nothing in its own structure to indicate that it has like a blastostyle originated by division of labor. It does not show any tendency to lose its nutritive function, and its locomotor and sensory functions are not lost, as we should expect them to be in a zooid specialized for reproduction, but they are, on the contrary, much more highly developed than they are in the nutritive hydra. It is true that the hydranths have, as the theory requires, no reproductive function, but this is no more than we should expect, if the hydra is a medusa larva.

Balfour says that "it would obviously be advantageous for the species that the detached buds with generative organs should be locomotive, so as to distribute the species as widely as possible, and such buds in connection with their free existence would naturally acquire a higher organization than the attached trophosomes." It seems at first sight as if this must be true, but more careful examination will give us many reasons for questioning whether the high organization of the medusa has been acquired for the purpose of distributing the species, rather than for the benefit of the individual. We know that, in many species, of all the great groups of hydroids, the medusæ have become degraded into sessile gonophores which have lost their locomotor power, and in many cases all their complicated organization as well. This degradation must be for the advantage of the species, and in view of its prevalence I think we must hesitate to believe that the production of free reproductive zooids would be for the good of the species, and that after such free zooids were produced, they might be expected to acquire a complicated organization and highly specialized locomotor and sensory organs. We know that changes in the opposite direction have been to the advantage of the species, since they have been preserved, and if sessile gonophores are so useful that free medusæ have been degraded into sessile gonophores, there is no *a priori* reason for believing that it would be to the advantage of the species for reproductive zooids to become locomotor. The distribution of the species is well provided for in the swimming planula and the habits of the medusa often carry it very far from any proper habitat for the hydra, and as a matter of fact, genera and species without free medusæ are as widely distributed as those in which the medusa is a perfect swimming organism. Eudendrium and Cordylophora have no means of dispersal except the cilia of the planula, yet Cordylophora is found on both sides of the Atlantic and from Boston to Baltimore, and Eudendrium is found all over the world. Turritopsis is an extremely active medusa, living in the open sea, and it is often swept by the gulf stream as far north as Cape Cod, yet its hydra has been found nowhere except upon the North Carolina coast.

I think that we may safely conclude that while the view that the complex structure of the medusa has been acquired as a means for distributing the species seems at first sight to be very plausible, more careful examination renders it probable that this is not the case, but that the purpose of the organization of the medusa is to enable it to live out its own life; that it has been acquired and preserved on account of its direct benefit, rather than from any indirect advantage to the species as a whole.

In 1871 Koch advanced an hypothesis which escapes this difficulty, since he believes that the medusa stage has been acquired to prevent self-fertilization rather than to secure the distribution of the species, and his hypothesis is therefore more satisfactory than those which have been noticed.

He says (38) that the ancestral form was a hydra, with solid scattered tentacles, reproducing both sexually and asexually, and that in some species the new buds were set free as in Hydra, while in others they remained attached and formed communities.

Those which were set free either fastened themselves like Hydra, or they remained floating in the water, and gradually became adapted to a free life, and thus furnished the initial point for the formation of the medusa, which as Koch clearly shows, as Claperède had also shown years before (13), is not essentially different from such a hydroid as Tubularia. In a species with both sessile and swimming persons, the latter, if both were sexually mature, would be much less likely to interbreed closely than the former, and the sessile forms would therefore gradually lose the power of sexual reproduction, while the swimming forms would become the reproductive persons of the species. This specialization of the reproductive function would tend to secure cross-fertilization and it would therefore become established on account of this advantage.

He then supposes that some of these hydroids with free medusæ became established in places where the locomotor medusæ were exposed to the danger of being swept out to sea, away from proper localities for the attachment and growth of the sessile hydras, before these were born. Natural selection would, under such circumstances, lead to the preservation and perpetuation of those medusæ which reproduced their young very early in their own life, and we should thus gradually obtain medusæ which became sexually mature before they were detached; and as these medusæ would derive no advantage from a locomotor life they would gradually become converted into sessile medusa-buds.

According to Leuckart, Gegenbaur, Hamann, Balfour and others, the locomotor organs have been acquired for the purpose of distributing the species, and the free persons first became the sexual members of the species, and then became locomotor, while Koch believes that the locomotor life has not been acquired for the purpose of distributing the species; and that the free persons became locomotor medusæ before they became specialized for reproduction, and that the reason for this specialization was not the need for distributing the species, but the advantage of crossing. So far as simple plausibility goes, this hypothesis is certainly a little more satisfactory than any of the others, but the test of the truth of an hypothesis is an appeal to fact, rather than its neatness.

While the various writers who have advocated the hypothesis of polymorphism differ so greatly in their accounts of the process by which the medusa has been evolved, by the specialization of persons detached from a hydroid community, the "proofs" which they advance in support of the belief that it has originated by such specialization are essentially the same. As the first step in the argument, they point out the homology between the hydra and the medusa, and justly claim that this proves that both are modifications of some common type, and they then proceed to make either on words or by implication the further assumption that this type must have been either a member of a hydroid community or a medusa. Thus Koch says, "in the attempt to study the relation between the hydra and the medusa in the light of the theory of descent, we have to decide between two hypotheses; *first*, that the medusa is primitive and that the hydroids are only larvæ which have been independently modified, or *second*, that the hydroids are primitive and that the medusæ have been derived from them. The fact that the hydra bears a close resemblance to many other organisms, such as sponges and corals, while the medusa shows no such resemblance to other groups, leads us to reject the first hypothesis and to adopt the second alternative." If we were compelled to accept one or the other of these alternatives, there is no doubt that this reasoning would be of great weight, but it is quite possible that neither hypothesis may be correct, and that the primitive form may have been neither a sessile hydra nor a highly specialized medusa, but something midway between; for example, a ciliated locomotor organism with simple hydra-like structure. But overlooking this third alternative, and deciding that the homology between the hydra and the medusa can only be explained on the hypothesis that one has been derived from the other, they go on to show, quite correctly, that the view that the medusæ have been produced by the gradual specialization of medusa-buds, or medusiform gonophores, leads us to a series of untenable positions, and that we are compelled to believe that the medusa-buds are degraded medusæ. They therefore conclude that the medusæ must have originated as modified hydroid persons, which have become adapted to a swimming life, and have assumed the function of sexual reproduction, which has at the same time been lost by the sessile unmodified hydras.

In the absence of all direct evidence, this reasoning could be termed "proof" only by showing that we are compelled to accept one of the two hypotheses, and a very great step was made towards the solution of the question when Böhm showed in 1878 (9, p. 153) that the primitive form may have been intermediate between medusæ and hydroids, and that both these forms may have been developed from this common form in two divergent directions.

Böhm points out that the long path from the slightly specialized sessile hydra to the highly complex swimming medusa is greatly shortened by the assumption that they are both derived from an intermediate form; and on p. 174 he says that an additional reason for the belief in such a form is to be found in the fact that in certain families, as in the Eucopidæ, the very simply organized medusæ are so much alike that it is difficult to find any distinctive specific characters, although the hydroids are often very different from each other, thus proving that they have diverged more than the medusæ.

As he justly remarks, it is much more difficult to understand the origin of locomotor medusæ by the modification of sessile polyps or the reverse, than it is to understand the origin of both from an intermediate form which has served as a basis for two lines of modification; and he therefore believes that both the hydra and the medusa are descended from a free, solitary hydra-like organism with solid tentacles and with lasso-cells, which were peculiarly abundant at the tips of the tentacles. The life-history of Liriope, as I have described it, furnishes us with a stage of development which is exactly like Böhm's hypothetical form in every particular, except that its endoderm and ectoderm are separated from each other by a thick gelatinous layer. The ciliated, tentaculated larvæ of Æginopsis and Ægineta which Metschnikoff has figured (51), and the Cunina larvæ shown in Plate 43 of this paper, are also free hydra-like larvæ which become directly converted into medusæ without the intervention of a sessile "nurse" stage, and without metagenesis. Böhm himself does not refer to the Trachomedusæ or the Narcomedusæ in this connection, although he calls attention on p. 162 to the fact that the actinula of Tubularia is an example of the persistent retention of this locomotor ancestral stage.

He says very little about the actinula larva, however, and he selects Eleutheria as the best modern representative of the hypothetical ancestral form, and treats of its structure at considerable length. This selection seems an unfortunate one to me, for Eleutheria itself has an alternation of generations, and the Eleutheria stage does not occur at the beginning of the life-history, but at the end. The Cladonemadæ are simply ordinary Anthomedusæ, with a tubularian hydra-stage and medusæ produced by budding; and it may be due to the unfortunate selection of Eleutheria as an illustration, that Böhm's view, the correctness of which seems to me to be proved by the occurrence of a locomotor solitary larval hydra stage in the Trachomedusæ, has attracted so little attention.

His contribution to the subject is a decided advance beyond the views which we have noted, for he shows clearly that we are not compelled to choose between the two alternatives which seemed to the other writers to be the only ones, but that the third, viz., that the primitive form was not a sessile community but a locomotor person, has much to commend it; and that we are not compelled to believe with Kleinenberg (75, p. 33) that the alternation is primitive, but that it may have been gradually and secondarily acquired (9, p. 159). Having thus cut himself partially loose from tradition, so far as the antiquity of the nurse stage in the history of the medusæ is concerned, he rests satisfied with the old explanation in other particulars, and states, on p. 159, his belief that the divergence from his stem-form, which resulted in the production of the sessile hydra and the locomotor medusa, was brought about by division of labor and polymorphism; he further says that the locomotor stem-forms multiplied asexually, and thus gave rise to cormi, and that some of the persons of the cormus then became gradually specialized for nutrition, and were thus converted into sessile hydras, while other persons became specialized for reproduction, and were gradually converted into true medusæ.

Böhm's paper was published in 1878, and in the same year Claus (15) also showed that the hydra and the medusa are modifications of a common type, of which the actinula is the living representative (p. 50), and in his Grundzüge der Zoologie, 1880, he advances an explanation of the origin of the alternation between the hydra generation and the medusa generation, which, so far as I am aware, had never before received attention, although there can, I think, be no doubt that it is the true one.

He discusses the subject very briefly and simply says, on p. 62, that alternation of generations may be between two stages with similar organization, or it may be *between the larva and the adult as in the Medusæ.* He goes on to point out that we must therefore recognize two distinct kinds of alternation which have originated genetically in two different ways, and have different explanations. We must believe that the second sort of metagenesis, that which resembles metamorphosis, has originated, in most cases, through the retention by the larva of the power to multiply asexually at a stage of development which, while it may be more or less subject to secondary modification, corresponds to a remote ancestral stage in the evolution of the species; and that a larva-like nurse stands in the same genetic relation as the larva itself, but the original stem-form, which is now represented by the larva, had in addition to the power of sexual reproduction, which is now restricted to the highly modified adult, the power of asexual multiplication by budding, which has been preserved by the larva in the course of the phylogenetic evolution of the species. On pp. 245–246 he also calls attention to the fact that the actinula larva of Tubularia is a modern representative of the ancestral stem-form, and *Tetrapteron volitans* a locomotor ciliated larva which is neither a hydroid nor a medusa, but an indifferent type which might be modified in either direction.

In his paper on Tetrapteron (16) he says that he has expressed his view of the manner in which alternation originated among the medusæ in his paper on Halistemma (15), but I am unable to find it there, or to find any statement of his view earlier than 1880.

A recent writer in Nature (28) states, p. 69, that Claus supports the view originally formulated by Leuckart, that alternation of generations has originated among the medusæ through polymorphism, rather than through a modification of metamorphosis, but he gives no references in support of his statement, which is probably an error like many others which occur in the paper.

In 1883 I published a paper in which I gave a very brief explanation of the origin of alternation in the medusæ. My view is identical with that which I have quoted from Claus, although I reached it independently and in ignorance of Böhm's and Claus' writings on the subject. The paper is a short abstract without illustrations, but my conclusion was based upon the life-history of the Narcomedusæ and Trachomedusæ, which seem to me to furnish much more conclusive proof than any which these writers bring forward.

The statement is as follows: "It is hardly possible that the form of development which we now find in most of the Hydromedusæ can bear any close resemblance to their primitive life-history, and there are many reasons for believing that alternation of generations has gradually arisen through the modification of 'metamorphosis.' In Cunina we seem to have the ancestral form of development: a direct metamorphosis without alternation * * * The larva of Cunina is a hydra with the power of asexual multiplication; but, instead of giving rise to medusa-buds, like an ordinary hydroid, it becomes directly converted into a medusa by a process of metamorphosis: it is a true larva and not an asexual generation, although the occurrence of asexual reproduction renders the gap between this form of development and true alternation very slight indeed.

In Cunina we have a series of this kind:

```
Egg
 |
Larva – Larva – Larva
 |        |       |
Adult   Adult   Adult
```

If the larva which is produced from the egg were to remain permanently in the hydra stage we should have a series like this

```
Egg
 |
Hydra – Hydra – Hydra
           |       |
        Medusa – Medusa
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and such a history would be a true alternation." (12).

A few months later, March 1884, Fewkes published a paper (19) in which he says "That exceptional form of development, called alternation of generations, which exists in the fixed hydroids may be regarded as the irregular not the normal method. It is an adaptation resulting from peculiar circumstances and a departure from a rule in one direction as that of the Siphonophores is in another. The Cunina colonies have resemblance with both fixed hydroids and Siphonophora, but have not departed as widely as either from the normal method in their older larval and adult condition" (p. 305).

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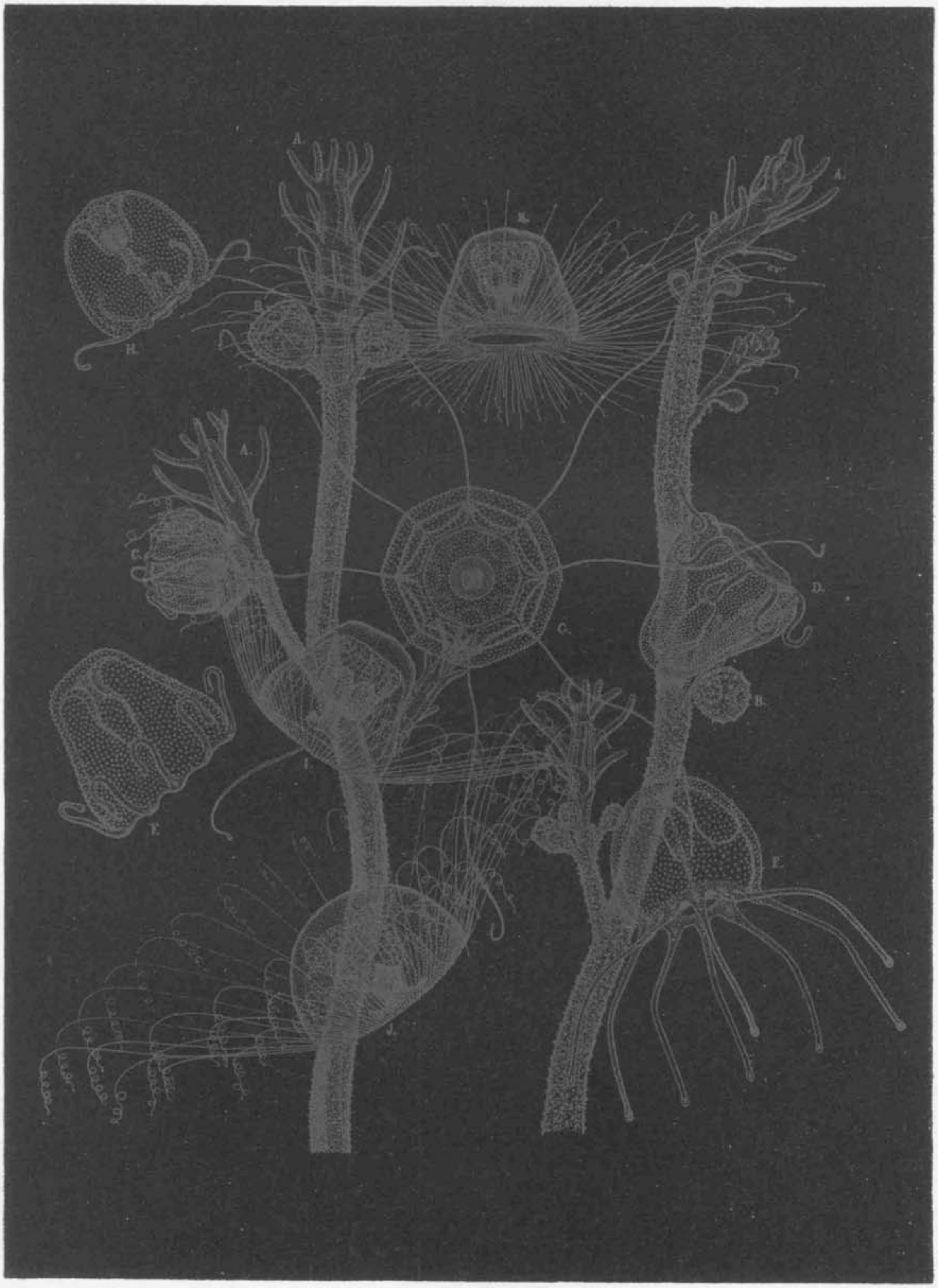

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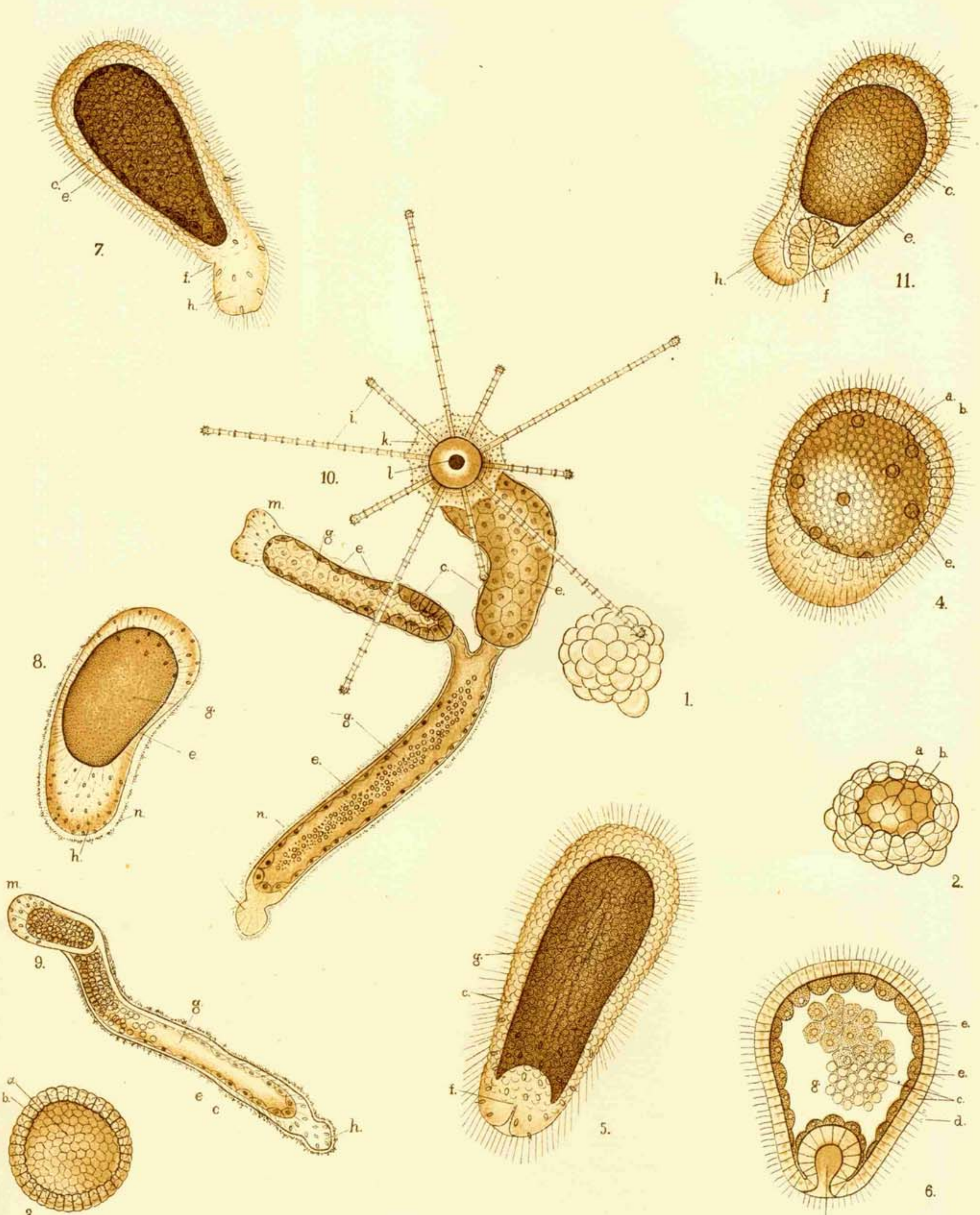

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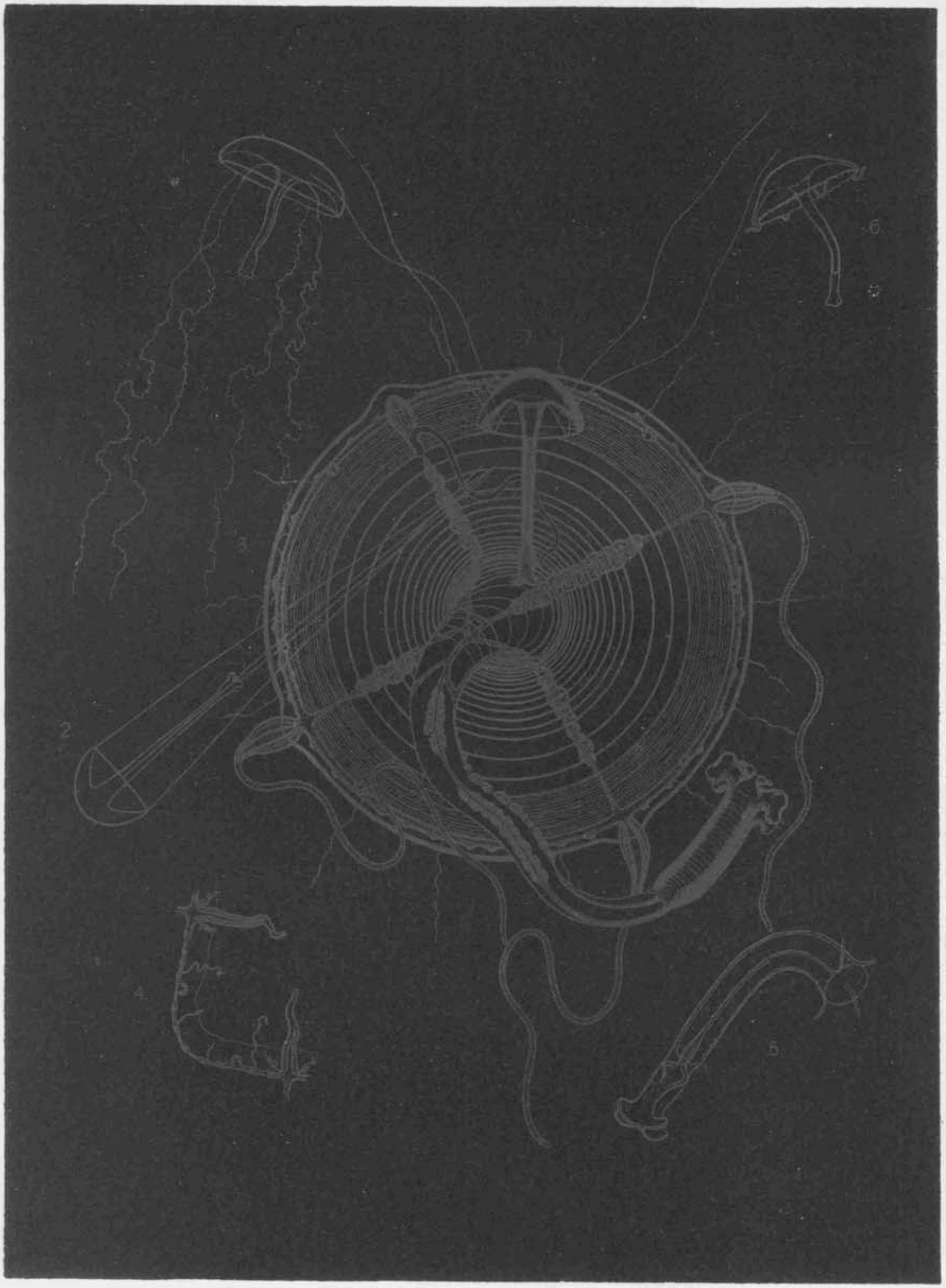

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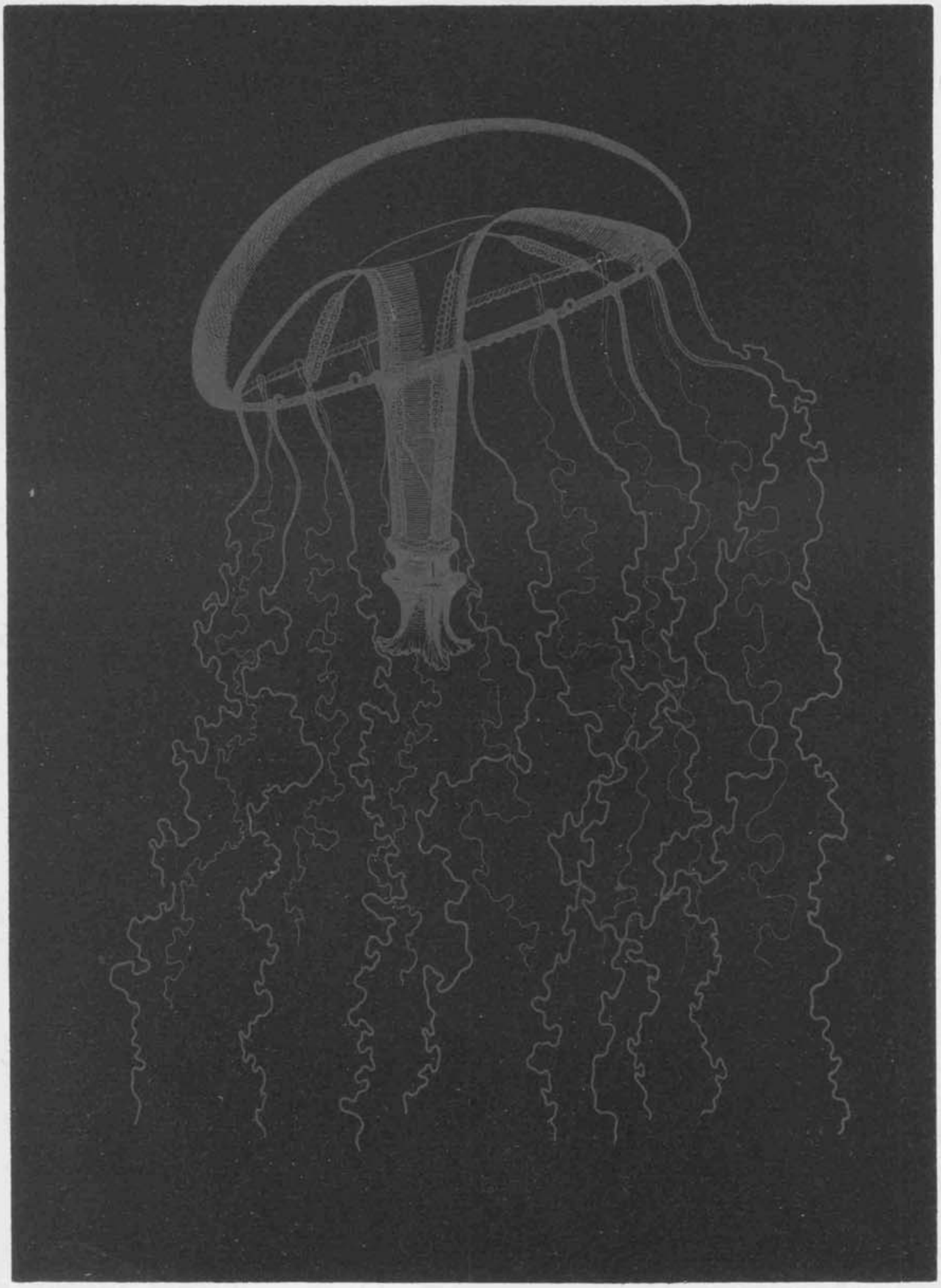

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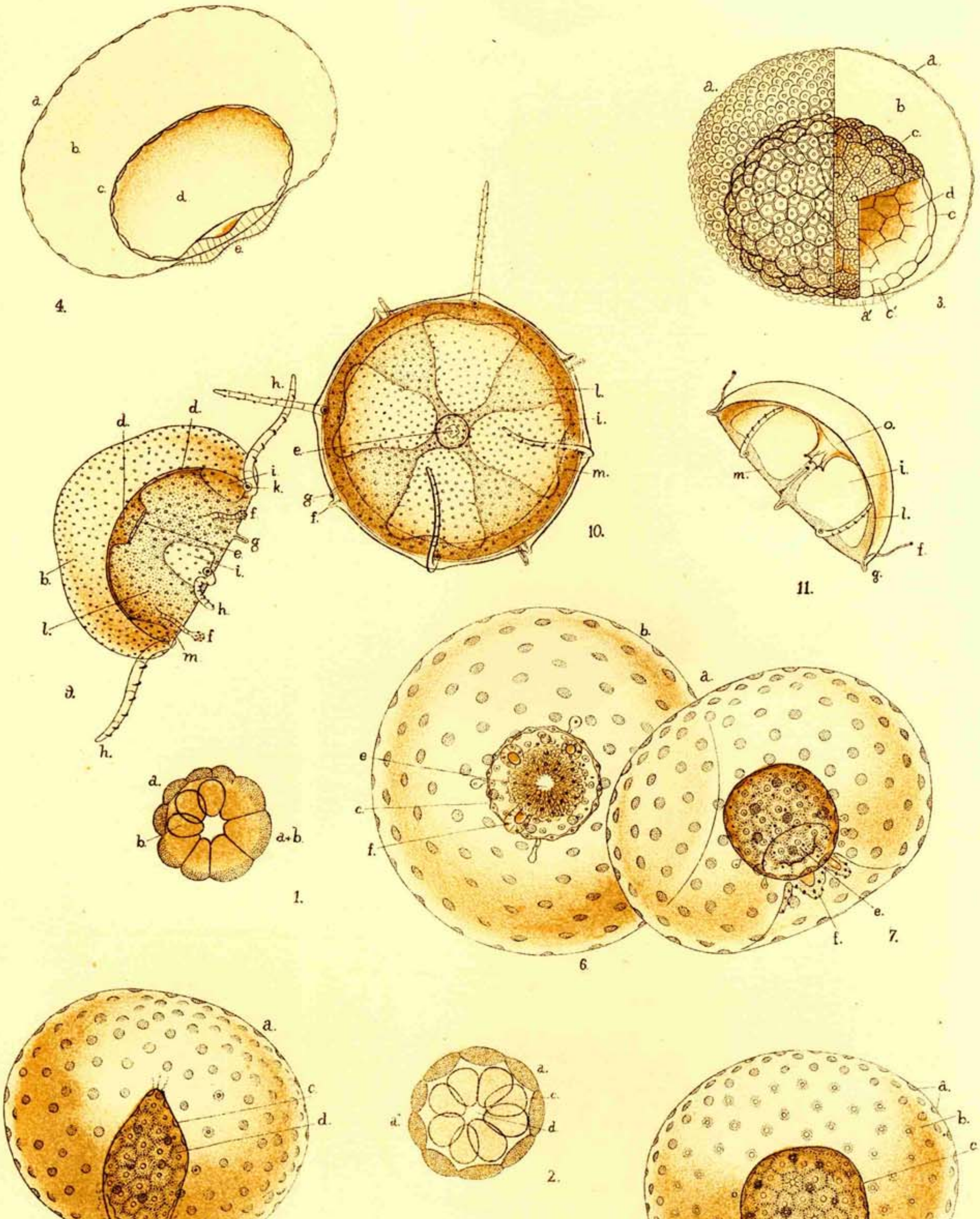

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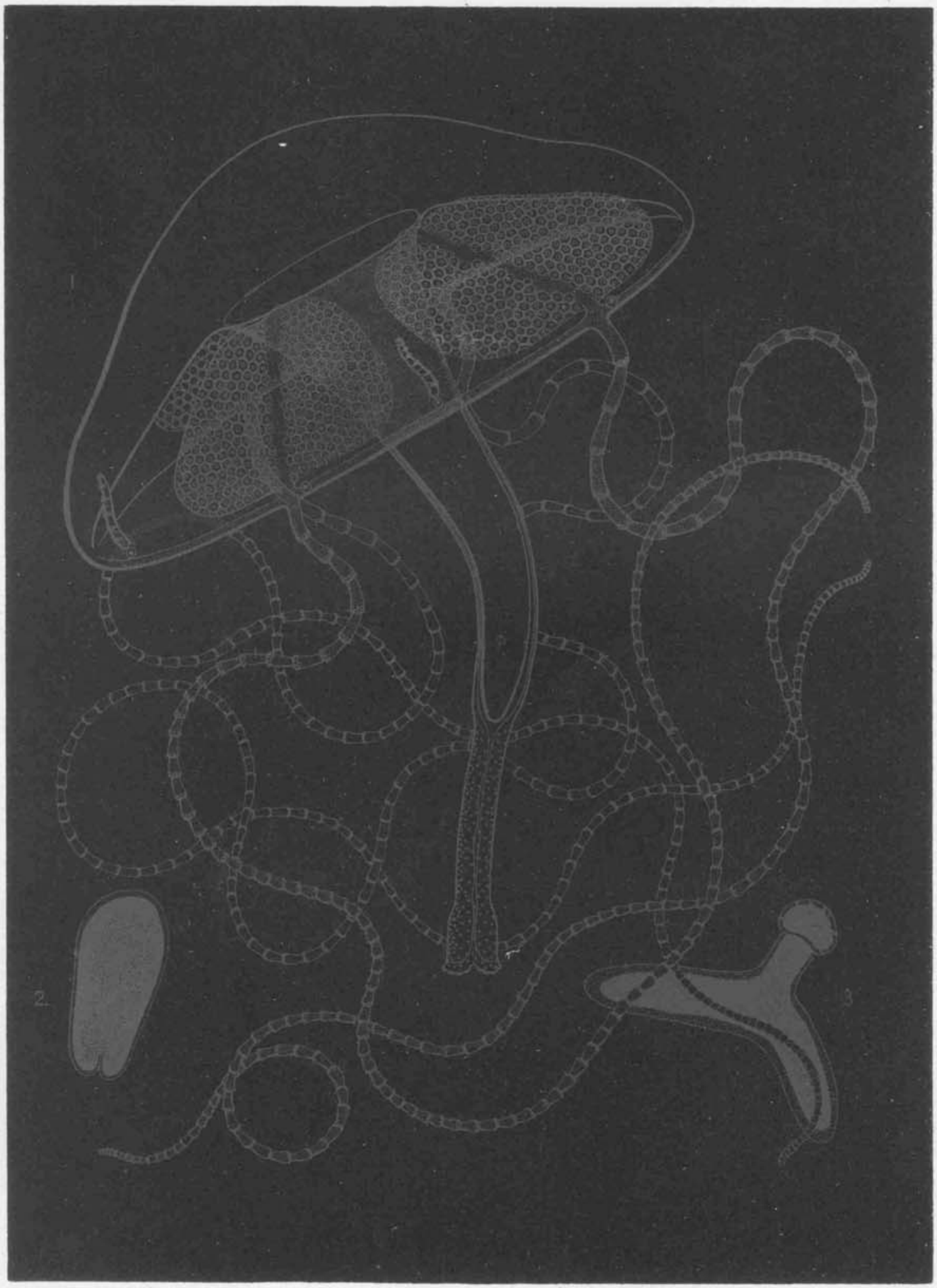

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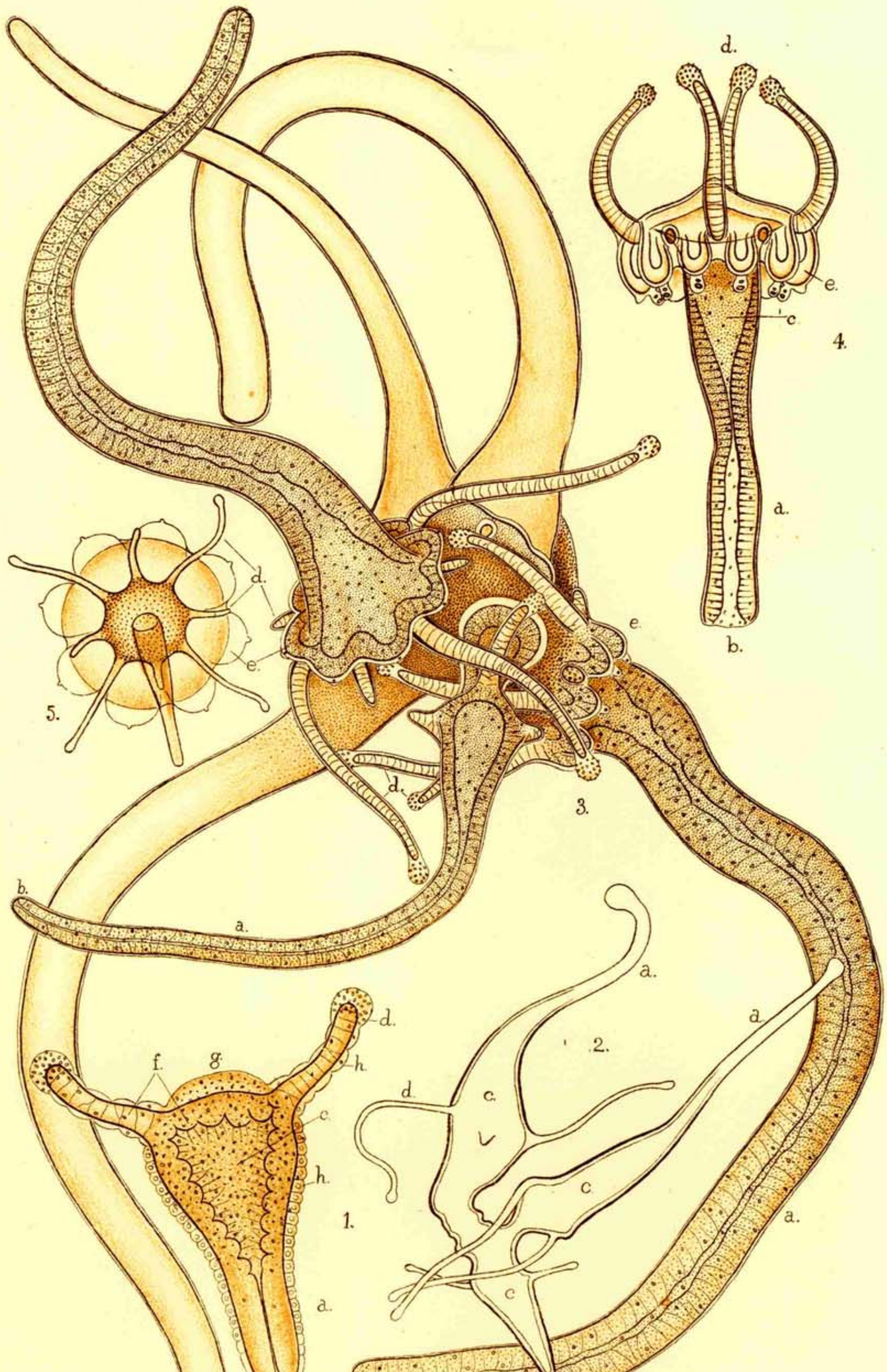

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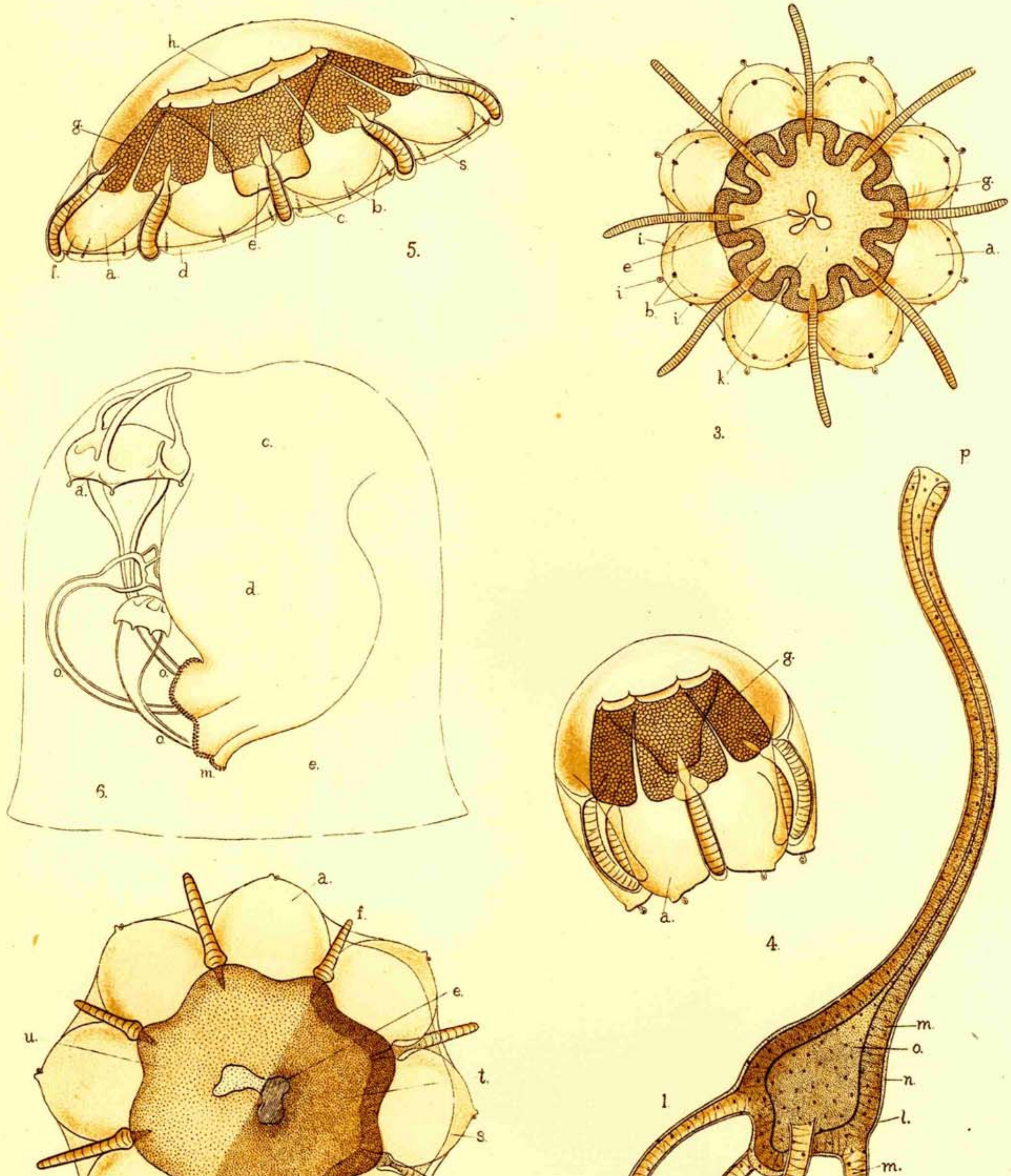

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