T H E S I S.

ON THE ANATOMY AND DEVELOPMENT OF CASSIOPEA XAMACHANA, *sp.n.*

A THESIS

Presented to the Board of University Studies in the Johns Hopkins University For the Degree of Doctor of Philosophy

By

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Baltimore, April, 1892.

C O N T E N T S.

I N T R O D U C T I O N.

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In the Island of Jamaica, at the west side of the mouth of Kingston Harbor, there is a large pond of salt water completely separated from the sea by a sand beach, which at its narrowest part is several rods in width. It is said, however, by those who live near, that in times of storm or freshet this barrier is sometimes broken through.

One morning in June, 1891, Dr. G. W. Field while hunting birds along the seaward shore of this pond, came upon a little bay connected with it by a narrow inlet. This bay is overhung by low cashaw and mangrove trees. At one side is a sunny, sandy spot, where a crocodile had made its bed and from this there was a fresh zigzag mark left by its tail when it last slid into the water. Upon the submerged roots of the mangroves were to be found barnacles and sea anemones, but the most interesting thing observed was a collection of beautiful rhizostomatous medusae, that, at one end of the bay, completely covered the bottom, to the very edge of the water. A few very small specimens might be seen swimming about, but most of the medusae, especially the larger ones, would not leave the bottom unless they were disturbed. They lay there upon their backs with their voluminous, branching mouth parts spread out over their

disks, which were motionless except for occasional flaps of their margins. If any of these animals were stirred up they would swim about like ordinary medusae but it would not be long before they would settle down again and assume their usual attitude upon the bottom. Within this limited area there were countless numbers of them, and in many places they were so thickly spread that their margins touched upon all sides, or even overlapped.

In order that the rest of us might know something of this marvel, Mr. Field dipped up a number of these medusae in a pail and brought them into the Marine Laboratory of the Johns Hopkins University, which was stationed at this time at Fort Henderson, about two miles away. Upon examination of the medusae they were found to belong, all of them, to a single new species of Cassiopea, a genus not known before outside of the Red Sea, Indian Ocean and south-west Pacific; and this pailful, taken up at random, contained both adults and young in many stages of growth. Of some of these Professor Brooks made drawings. Subsequently I visited the Salt Pond to obtain more of the young medusae and with them I collected at random submerged bits of wood and stems of plants, in the hope of finding scyphistomas. On returning to the laboratory, I was de-

lighted to find some of these [illegible] places in the larvae for which I was looking. I was still more delighted when in one of the largest of these larvae I noticed certain glistening spots in the bases of the tentacles and found on examining them with a microscope that these spots were, as I suspected, unmistakably masses of crystals that would form parts of future marginal sense organs. After this discovery, I entered, with the advice of Professor Brooks, into an investigation of this material, the results of which are embodied in the present paper. I wish to express my thanks to him for his help and encouragement during this work and I am also indebted to him for suggesting the name by which I propose to call this species. It is derived from Xaymaca, which was the name used by the aborigines for the island that we now know as Jamaica.

A single monstrous specimen with but two subgenital cavities, with extraordinarily large oral vesicles, and otherwise misshapen, that perhaps belongs to this species, was found in the harbor near Port Royal. Except for this doubtful specimen, the only locality in which this species has been found is the lagoon that I have described. Although the adults were few, the young in nearly all stages were present at this place in such

great numbers searches for males and for females with ripe eggs were equally fruitless. The great abundance of young and the range in their apparent ages was, therefore, surprising, until I found a method of budding in the scyphistomas, to be described later, which easily accounts for these phenomena.

The full grown medusae could be kept in good condition in aquaria for a number of days and could be kept alive for weeks, while the young medusae and scyphistomas would thrive there an indefinite time if there was a little pond ooze at the bottom of the aquarium, and the water was changed twice a day. Indeed the growth and multiplication of the scyphistomas would proceed actively under these conditions. By keeping the larvae in shallow dishes I was able to watch the whole course of non-sexual development, but the development from eggs remains unknown to me because of the impossibility of finding any that would develop.

I shall first give a systematic description of the species, with an account of the anatomy of the adult, and follow this with what I have learned of the development, from observation of the living animals while in Jamaica, and by study of sections of the preserved material since my return to Baltimore.

T E C H N I Q U E.

For preservation of the material I used a one-quarter saturated solution of picric acid with 2% of sodium chloride added, Erlicki's fluid with the same addition ; and 1/2% osmic acid followed by Erlicki's fluid. The last two methods preserve external structures and the general shape of the animal very well, but the first method is much better for internal structures.

S Y S T E M A T I C P A R T.

Cassiopea Xamachana, species nova.

Diagnosis. The umbrella is concave on the aboral side forming a sucking disk. The number of rhopalia is regularly 16, but often from 17 to 23. When there are 16 rhopalia there are 80 short obtuse lobes in the margin of the umbrella, separated by deep grooves on the surface of the umbrella (in each of the 16 parameres 3 velar lobes between 2 ocular ones.) The exumbrella is marked by a white circle at the periphery of the concavity ; from this there extends outward a white band along each marginal lobe, and in the radius of each rhopalium there is also a white band tapering centrally from this circle to a

point about half way to the stomach. These radiating bands are not always connected with the circle of white. The eight oral arms are rounded and slender, never angular, with 10 to 15 alternate primary branches and numerous secondary ones. The distance from the centre of the oral disk to the tip of an extended arm nearly equals the diameter of the umbrella. In the axil of each branch there is a flattened oval or linear vesicle varying in length with the size of the adjoining branch the length of the eight largest ones (one in the axil of the chief branch of each arm) may be one to three centimeters, but many do not exceed the size of one of the oral funnels. There are also 5 to 13 large vesicles on the oral disk, the one in the centre being the longest, sometimes equalling 1/4 the diameter of the umbrella. In full grown individuals there are no oscula, or oral funnels, on the oral disk, except near its margin. Their place is taken by a great number of very small, oval vesicles.

Comparison with Other Species.

This species is very similar to Cassiopea Andromeda, Esch. and to C. polypoides, Keller. It differs from the first as described and figured by Tilesius, in the shape of the umbrella ; in having much longer and stouter oral arms, with ten or

more primary branches that are never triangular in section ; in having much larger oral vesicles ; and never anything corresponding to the flattened condition of the ultimate branches figured by Tilesius and mentioned by Haeckel. The arrangement of the white spots and other color markings is also somewhat different. It is distinguished from the second by having fewer of the large oral vesicles and having these of a smaller size ; by having more slender and graceful oral arms than those figured by Keller, with a greater number of primary branches ; and by a difference in the coloration.

It is readily distinguished from C. ornata, Haeckel, by its large oral vesicles and from C. Mertensi, Brandt, C. depressa, Haeckel, and C. picte, Vanhoffen, by the number of marginal lobes.

GENERAL DESCRIPTION.

Form of the Body.

To one who has only seen the Cyaneas, Aurelias, and the like, of our northern coast, the shape of this medusa appears very strange. The aboral or exumbrella surface, instead of being convex, as one would expect, is concave when at rest, except for a slight convexity over the stomach, and except in the region of the thinner marginal part of the umbrella, where

it is also convex. The surface of the subumbrella, on the other hand, is convex except in this same thinner marginal area. This is evidently an adaptation to the animal's habit of resting on the bottom with its oral side uppermost.

The gelatinous layer of the exumbrella is firm and elastic and when the animal comes to rest on a flat surface and the subumbrellar muscles are relaxed, this jelly tends to assume its normal shape and the slight suction which is thus produced gives the animal something of a hold on the bottom, and makes it less liable to be disturbed by the action of waves and currents. The marginal zone of jelly is much thinner and is capable of motion independently of the central concave disk, and it is by its frequent movements that currents of water are kept up bringing food and oxygen to the animal.

<u>Structure of the Jelly</u>.

Keller's description (1883) of the structure of the jelly in <u>C. polypoides</u> would apply equally well to our species. Besides connective tissue fibres the jelly contains several kinds of elements. First there are scattered through it many star-shaped cells that remind one of osteoblasts and are probably analogous to them. Hamann (1881) speaks of them as Colloblasts. Then there are great numbers of the so-called green cells, especially in the subumbrella. These may be isolated

or in clusters. Each is a sphere with a well marked cell wall and contains one or two nuclei that stain deeply, and a number of what appear to be chlorophyl bodies. Although these cells have every appearance of being unicellular algae, Keller thinks they are not algae but that they are essential elements of the "mesoderm," for according to his experiments they do not have cellulose in their cell walls.

There are also in certain regions peculiar little vesicles the nature of which is not clear, and which appear in the fresh tissue to be highly refractile granules. There is a nucleus to one side of the vesicle, otherwise it is empty in the preserved specimens. According to Keller, the cell is clear and colorless at the centre while its periphery is thickly filled with minute scales or granules.

Color Markings.

The coloring of this semi-transparent animal consists of certain white markings together with shadings of subdued tints of brown, green and blue that are often very beautiful. This is largely due to the last two of the elements in the jelly that I have just described. The green cells give a general greenish brown color to the entire animal, while the refractile granules produce the white pattern that is so characteristic of this genus and the related Polyclonia.

If we turn the aboral side of the animal towards us we find often a brownish band produced by the green cells encircling the disk at the periphery of the concavity. This shades off on both sides. Deeper in the jelly beneath this there is a much wider white circle, and from this there are white bands extending outward along the marginal ridges of the jelly, one nearly to the tip of each marginal lobe. The bands to the rhopalial lobes are interrupted, however, by a roughly circular, transparent area over each rhopalium ; and in young specimens the other bands are not fused with the circle. On the inner side of this circle there are, deep in the jelly, a number of white areas tapering towards the centre. Each one is in the radius of a rhopalium, and extends to a point about half way from the periphery of the concavity to the edge of the stomach. These areas, like the marginal spots, are not always continuous with the circle. At the centre of the umbrella the stomach and subgenital cavities may be seen through the jelly as a reddish brown circular area with a diameter of about one-seventh of the total diameter of the disk, while surrounding the stomach there is a deep blue halo with points that extend outward between the last mentioned bands of white.

If now the animal be allowed to return to its usual position, the subumbrellar surface will be found to be pretty even-

ly stippled by the greenish brown cells in the jelly. Apparently beneath this stippling there is a blue color forming a circle around the margin of the stomach and extending outward in broad bands, one along each interrhopalial radius nearly or quite to a large, more or less distinct patch of blue, that lies close to the margin between every two rhopalia. The radial canals and the fine connecting network of tubes appear as rather indistinct opaque white lines.

The jelly of the oral arms is transparent and colorless, except for an opaque white stripe beneath the dorsal surface of each arm of the same character as the white markings of the umbrella. There is a similar stripe on the dorsal side of each of the larger branches which may, or may not, be continuous with the stripe on the main stem. The bases of the oral funnels are of a delicate blue color, which often extends on to the brachial canal. The margin of each funnel is a deep brown, that shades off over the blue, while the small tentacles, or digitella, that spring from this margin are pure white. The larger, tongue-shaped vesicles on the arms and oral disk have a greenish yellow color with a bluish green, longitudinal stripe. The smaller vesicles on the arms are colored in a similar way and are inconspicuous, but the cluster of very small vesicles that occupies the greater part of the oral disk have

a very different appearance, being lightly tinted by fine, reddish brown pigment spots.

Variability of Marginal Structures.

One of the most striking peculiarities of this species is its great variability. Undoubtedly sixteen is the normal number of the parameres, but we as often find specimens with seventeen or eighteen. The number of rhopalia does not always correspond to the number of parameres. There are often seventeen or eighteen of these and specimens have been found with as many as twenty-three, Fig. 22. The introduction of additional rhopalia seems to be a process analogous to the formation of double monsters in higher animals. We find all stages from a bifurcated rhopalium to two complete parameres in the place normally occupied by one. Indeed, we may trace the process further back to forked tentacles in the scyphistoma larva.

As in all Rhizostomae there are no marginal tentacles. The margin of the disk is, when regular, divided into sixteen scollops, the sinuses separating these being the sensory niches. Each of these primary lobes is divided into five secondary ones, (forming the 80 marginal lobes mentioned in the diagnosis) and from each of the shallow notches separating these

there is a groove running towards the centre for a centimeter or more along the aboral surface of the umbrella. in the bottom of each groove the gelatinous layer is extremely thin.

Structure of the Marginal Sense Organs.

The rhopalia have each a pigment spot on the aboral side near the extremity and each one lies in a deep sensory niche. The dorsal sensory groove common in the Pelagidae, Aurelia, etc. is entirely lacking, although Keller found in C. polypoides a slightly depressed thickening of the ectoderm that corresponds to it. The sensory niche and rhopalium are, with the exception of the pigment spot, similar in all essential particulars to what is found in Pelagia. The rhopalium is the only organ in the sensory niche, Fig. 44. It is a hollow, finger-like projection attached by its base to a low ridge that runs along the roof to the central wall of the niche. This ridge is penetrated longitudinally by the continuation of a radial canal from the stomach and into the distal end of this canal the lumen of the rhopalium opens. In the distal half of the rhopalium the lumen is nearly obliterated by the increase in thickness of its entodermal lining. Here the entoderm, instead of being a columnar epithelium as elsewhere, is a mass of parenchyma-like cells each of which contains a large calca-

reous concretion, a so-called otolith. A thin supporting membrane separates the entoderm from the ectoderm. At the distal extremity of the rhopalium the ectoderm is a thin cuboidal epithelium, while over the rest of the surface it is a thick sensory epithelium resting on a thick network of fine nerve fibres. This, in turn, rests on the supporting membrane. I have observed no ganglion cells in this layer of nerve fibres, which is continued under the epithelium of the rhopalial ridge to the central wall of the niche where it becomes imperceptible. There are no thickened bands of these fibres running to ciliated pockets such as I found (1890) in Dactylometra, and these fibres probably spread out finally into a thin network underlying the general epithelium of the subumbrella.

The one feature in which this rhopalium differs from what is found in Pelagia is the presence of the pigment spot, already mentioned as lying on the aboral side of the rhopalium immediately above the centre of the mass of concretions. This is an area sensitive to light and only differs from the rest of the sensory epithelium in that here the superficial cells are deeply colored by a yellowish brown pigment. A more careful examination would undoubtedly show the histology of this structure to be similar to what Schewakoff (1889) has found in Aurelia.

The Oral Arms and their Branches.

The eight oral arms (Fig. 26) arise from the central oral disk at about equal intervals and, when an arm is extended, the distance from the centre of the oral disk to the tip of the arm about equals the diameter of the umbrella. But the arms are very contractile and may be shortened to half this length. The arms are slender and graceful in shape, the jelly tapering very gradually to the tips of the finest branches. The branches are arranged alternately. The largest one, which is the one first formed, is at a point about two-thirds the length of the arm from its base. From this point the branches gradually decrease towards the base of the arm, and rapidly decrease towards its apex. The general outline of the arm, therefore, including its branches, is roughly spatulate.

The Oral Funnels and Brachial Appendages.

Just below the surface of the oral side of each arm, there is a longitudinal tube, the brachial canal, that ramifies to each branch and finally opens to the exterior by funnel-shaped oscula (os. Fig. 26) at the tips of the numerous ultimate branches, and at many places along the course of the tube. The margins of these oscula, or oral funnels are provided with short, tentacle-like projections, or digitella. These are covered by an epithelium containing nettle cells and each has

an axis of jelly in which there are transverse plates of greater density than the rest of the jelly, and these give the structure the cellular appearance first described by Hamann (1881). The epithelium lining the funnels and tubes is ciliated.

There open also into the brachial canals the lumena of the oral vesicles, (v. Fig. 26). These structures, as already stated in the diagnosis, have their points of attachment in the axils of the branches. All except the smallest are flattened laterally. The smaller ones are oval in outline, the larger ones linear. At one side near the apex there is a cluster of short processes that Hamann has homologized with digitella.

The Oral Disk.

Although the eight oral arms seem to be placed at equal distances and to be alike, they are morphylogically in pairs, each pair being homologous to one of the four lips of an Aurelia, for example. The line that separates two members of a pair is therefore according to Haeckel's nomenclature a perradius. The brachial canals from each pair of arms on entering the oral disk converge and unite into a single tube that is continued to the centre of the disk, where it unites with the other three. In this way the course of the tubes on the oral disk forms a pattern that resembles a Maltese cross. At the

centre of the cross there is attached the large central vesicle. In a living specimen 11 cm. in diameter this measured 3 cm. in length. There are four other vesicles that most nearly approach the central one in size and these arise from the arms of the cross near the junction of the brachial canals. In full grown individuals there are eight more vesicles, a little smaller, one on each canal distal to the junction. It is only near the periphery of the disk that the canals are provided with oral funnels. For most of their course on the disk, the canals give rise to the very small vesicles finely speckled with a reddish brown pigment that have already been mentioned. These have nettle batteries at their tips and are so numerous as to completely cover the greater part of the disk and to hide the course of the canals. This mass of small vesicles is not acquired, however, until late. Specimens as much as 6 cm. in diameter will be found to be without them. In such specimens we have the five largest vesicles and a number of oral funnels are scattered along the canals just as they are upon the arms.

<u>The Subgenital Cavities and the Digestive Tract.</u>

At each of the four points of junction of the brachial canals there is a slit-like passage dipping vertically into the jelly of the disk and opening into the stomach. This is a lens-shaped cavity. It has a gently arched roof and its floor

consists chiefly of four lozenge-shaped areas where the body wall is very thin and pleated in radial folds. (s g. Fig.26.) These thin parts of the body wall form the roofs of the subgenital cavities, which open to the exterior, each by an eliptical orifice in the side of the oral disk near the subumbrella and in the angle between two pairs of arms. The ovary appears as a band crossing this membrane tangentially at its greatest width. Just central to each ovary there is a multiple series of very small gastric filaments. These are ciliated and provided with nettle and gland cells. I say "ovary" because of the many individuals that I examined, every one was without exception a female. It is a curious coincidence that of a number of specimens of Polyclonia that we found in the harbor near Port Royal all, on the other hand, were males. The portion of the floor of the stomach not made up of these lozenge-shaped membranes is bounded by the firm jelly of the oral disk. This area has the shape of a Maltese cross, and it is in the arms of this cross between the subgenital cavities that the passages from the oral canals open into the stomach. Fig. 26.

Near its periphery the floor of the stomach is marked by radial grooves. These are continued, each into one of the radial canals, that extend outward from the edge of the circular stomach to the marginal region of the umbrella. There are

regularly thirty-two of these, sixteen in the radii of the rhopalia, and sixteen interrhopalial. When the number of rhopalia is increased the number of radial canals may or may not increase in proportion. There are often thirty-four or thirty-six of them. The rhopalial radial canals are larger and more nearly straight than the interrhopalial ones and all are connected by a fine network of anastomosing canals, among which no distinct circular canal can be recognized. The meshes in the network of canals are not free from entoderm, for in these areas the entoderm of adjacent canals is connected by a plate of entodermal cells, the entodermal lamella. This lamella is also in contact with the subumbrellar ectoderm along a line encircling the umbrella a short distance from its margin, so that there is a complete sheet of entoderm separating the exumbrellar from the subumbrellar jelly.

O N T O G E N Y.

Historical Review.

Goette in his well known work on the embryology of Aurelia and Cotylorhiza (1887) attacked the previous work of Claus (1883). In 1890 Claus replied by an article embodying the results of more recent research on Cotylorhiza. In this some of Goette's conclusions are confirmed, notably the one as to the origin of the septal muscles, and the ectodermal nature of the lining of the proboscis, but in general the author maintains his previous views. This paper has been followed quite recently by a pamphlet from Goette (1891) in which, instead of presenting any new facts, he makes an elaborate attempt to prove from Claus' own words that in almost all points Claus has receded (1890) from his former position (1883) and now, while really agreeing with him, seeks to mask this by ambiguity of language and by casting reflection upon him. The chief difference between these two authors is that Goette regards the scyphistoma as essentially an actinian, while Claus compares it to a hydroid. Besides this Goette believes the entoderm to arise by multipolar immigration of the blastula cells, the septal funnels of the scyphistoma to pass into the subgenital cav-

ities of the adult, and the rhopalia to be new structures. While Claus, on the other hand, maintains that in Aurelia the entoderm is formed by invagination, the septal funnels have nothing to do with the subgenital cavities, and the rhopalia are then developed in the basal portion of tentacles.

These persistent differences of opinion made it desirable that a third person should review the whole subject, and for this reason I was very anxious to obtain developing eggs and to rear the larvae of Cassiopea. I failed to obtain the eggs and, therefore, cannot touch upon the question of the origin of the entoderm or of the relation of the early scyphistoma to the actinians. But I did succeed in rearing scyphistomas from planula-like buds and was able to study larvae of nearly all stages from the bud to the fully formed medusa. It may be objected that as the larvae that I studied were probably all produced by budding they can furnish no evidence as to the course of development of egg embryos. The validity of this objection depends, it seems to me, upon the manner in which the bud is formed. In the case of the fission of an Actinian, naturally, neither of the two new individuals passes through any larval stage, nor would one expect a hydroid stage in a medusa bud that is produced directly on the body of a medusa, although one such case has been described. Again, it

would be unfair to expect the hydroid buds on a hydroid to pass through a planula stage or to have their entoderm produced by delamination, or immigration ; while, on the other hand, there is no apparent reason why after these buds are once established their future development should not proceed in the same way as in a larvae produced directly from an egg. In Cunoctantha, according to Brooks (1886), the hydra-like larva produces buds like itself on an aboral stolon and then all the hydras, the original sexually produced ones as well as the others, pass through a metamorphosis by which they become medusae. No difference was observed between the medusae formed from hydras that were produced directly from the egg and those from larvae that were produced indirectly by budding, and beginning with the hydra stage the steps in the development of the two sets of medusae are the same. It will be seen from what follows that the scyphistoma larvae of Cassiopea set free buds of a very simple structure, and that when these buds have become scyphistomas provided with eight tentacles they are essentially like larvae at a corresponding stage that are developed from the eggs of other Discomedusae. In the absence of any evidence to the contrary, it seems fair to assume, that we have here a case similar to Cunoctantha and that the subsequent development of this larva is the same as that of sexually produ-

ced larvae of the same species.

This, of course, is a mere assumption, but it gains in probability when we find that the development of these larvae corresponds in most particulars with what Claus has found to take place in the egg larvae of another Rhizostome, Cotylorhiza.

Up to this time the process of budding in the Discomedusae has received but little attention. In 1841 Sars described the budding in scyphistoma larvae that were supposed to be either Aurelia or Cyanea. The buds, according to this account, may grow directly out from the main part of the body of the larva, or they may be produced on stolons extending outward from the foot. In either case, several buds may apparently be formed in various positions on the scyphistoma at one time. The figures show the buds still attached to the parent and with a well developed crown of tentacles at the distal end. Agassiz (1860) also found a similar process of budding to occur occasionally in Aurelia. Goette (1887) has confirmed these observations and has also found that the larvae of Cotylorhiza tuberculata produce buds. In this species the process, as described by Goette, is peculiar. A bud is formed as an outgrowth from the body of the scyphistoma, and as this grows it gradually approaches the shape of its parent, but its relative position is just the reverse of what Sars found, for the dis-

tal end forms the stem and the proximal end begins to flatten out into a circumoral disk. In this condition, the bud is set free and swims about, rotating on its long axis with the stem pointing forward. The mouth is formed at the point where the constriction finally separated the bud from its parent, and the larva fixes itself by the opposite end.

In all the above cases this process of budding appears to be merely an incident in the life history of the individual. On the other hand, in Cassiopea Xamachana the process of budding is an important, if not the chief, factor in the perpetuation of the species.

Development of Cassiopea from Buds.

I. Formation of the Buds.

Usually on looking over a collection of the scyphistoma larvae, a considerable proportion will be found to be in the process of budding. Figs. 1 and 19. There is never any stolon such as is figured by Sars, but the bud first appears as a slight swelling on one side of the calyx just above where it tapers into the stem. It involves all three layers of the body wall. Fig. 27. At an early stage in the growth of the bud, the four septal muscles may be found as four slender cords of cells embedded in the jelly and apparently growing out from

a thickened area of the ectoderm at the apex of the bud. Fig. 28. At this point the supporting jelly is very thin, so that the entoderm and ectoderm are almost in contact. The bud gradually increases in size, becoming hemispherical and then elongating. As it elongates, a constriction appears close to the body of the scyphistoma, and now, while the bud continues to elongate, it alters its shape and the constriction deepens, cutting off the lumen of the bud from the digestive cavity of the scyphistoma. The result is an obversely pear-shaped body attached to the scyphistoma by a very narrow isthmus of supporting substance covered by ectoderm, Fig. 19. Sometimes a second bud will appear before the first one has dropped off. In this case the second bud has always the same point of origin as the first, so that in such specimens the first bud is attached to the apex of the second one, Fig. 1.

II. The Planula-like Larva.

The bud is finally constricted off while it is still a simple, pear-shaped, or perhaps more properly, acutely egg-shaped body, without trace of mouth or tentacles and immediately becomes a planula-like, free swimming larva. Like a planula, its whole surface is covered with cilia, and in swimming it rotates from right to left upon its long axis, which is parallel to its line of progression.

The outline of the larva at this stage is not at all rigid but a single larva may be seen to assume many shapes if watched attentively for only a few minutes. It may assume, indeed, any figure, from a very elongated oval to a short heart-shape. But, in any case, there is almost always one end that is more obtuse than the other, and this is always the forward end of the larva. Figs. 2a, b, and c.

To one watching a swimming larva it is very noticeable that one transverse diameter of the body is considerably shorter than the other. In fact, the larva is usually rather broadly eliptical in cross section, except when strongly contracted, when it may be irregularly quadrangular. Figs. 3 and 4.

In color the larva is white specked with a few greenish brown spots (the green cells) and it is very opaque. It swims usually close to the bottom with a varying speed that is sometimes quite rapid. When it strikes an obstacle it may, while in contact with it remain quiet or it may rotate slowly on its long axis. After a short time it will generally move away again. In the shallow dishes in which the scyphistomas were kept, the swimming larvae might often be found hiding, as it were, beneath bits of bark and wood to which the scyphistomas were attached, and when disturbed they would go swimming about.

This habit, which afforded a convenient way of collecting them, I unfortunately did not discover until my last week at the marine laboratory. These larvae not only have the appearance of planulae but their habits are the same. Agassiz' description of the habits of the planulae of Aurelia would apply very well to these non-sexual larvae of Cassiopea.

The structure of the larva at this stage may be seen in a longitudinal section, Fig. 29. The ectoderm is uniformly ciliated and consists of a rather deep layer of very narrow and closely packed columnar cells. Their nuclei are small and are arranged in several rows and the cells themselves are entirely filled with a very opaque substance. Beneath the ectoderm is a layer of supporting substance, containing a few green cells and, occasionally, a colloblast. In a small area, at what was the distal end of the bud, (D. Fig. 29) this layer is very thin; there is a thicker zone, which diminishes in thickness towards the equator, and in the proximal half of the animal the layer is again quite thin. In the distal end of the larva the four septal muscles (s. m.) are seen, each occupying a tube in the jelly and being directly continuous with the ectoderm. This is better shown in Fig. 28. The muscle fibres are already differentiated and line the wall of the tube, while the nuclei are more central. It is not usually possible to trace the muscles

for more than half the length of the bud, but I have one specimen, one just about to be detached from its parent, in which at least one of the muscles may be followed for the whole length of the bud from its distal to its proximal end. There is also a difference between the two poles of the larva to be noticed in the entoderm. Throughout, it is a columnar epithelium, but at the proximal end it is rather thin and gradually becomes much thicker at the equator. In this proximal half the cells are somewhat crowded and contain coarse granules. From the equator to the distal pole the cells gradually become broader and more clear, and the most distal cells are large and hyaline.

III. Formation of the Mouth.

The first change noticeable in the swimming larva is the formation of the mouth, and this does not occur until two or three days after the larva has been set free. At the time of its first appearance, the mouth is a minute opening in the posterior end of the larva. Figs. 3a and b. Whether this point is identical with the distal, or with the proximal end of the bud, it is difficult to say. The evidence points in both directions.

That this point was the distal apex of the bud seems probable, when we observe, in the first place, that in the comple-

ted bud it is generally the distal end that is the more acute. This is also true of the posterior end of the swimming larva, in which the mouth always arises. Better evidence is furnished, in the second place, by the position of the septal muscles. It is known that in larvae produced from eggs the septal muscles arise as ingrowths from the ectoderm of the peristome. In the buds of Cassiopea the septal muscles when first observed have the appearance of ingrowths from the ectoderm of the distal end of the bud, and it is impossible, at this time, to trace them to the proximal end. The earliest stage after the formation of the mouth of which I have sections, has the septal muscles continuous with the ectoderm of the peristome in the same way. Compare Figs. 28 and 2[illegible].

This seems conclusive, but, on the other hand, the fact must not be overlooked that in the stage last mentioned the septal muscles are also well developed in the aboral end of the larva. Moreover, in the bud when about to be set free, while the entoderm cells in the proximal part are somewhat granular, those on the distal end are clear and larger than the others, and thus come to be more like the entoderm in the stem of the scyphistoma. Fig. 29. This is directly opposed to what is indicated by the origin of the muscles and makes it possible therefore, that the distal end of the bud may, after all, be

aboral as Goette says it is in Cotylorhiza, and we should expect the two species to agree in this particular.

The mouth is at first very small and is slightly funnel-shaped. It looks under the microscope like a pin hole in one end of the larva. Fig. 3b. There is no indication at the surface of any invagination of ectoderm to form an ectodermal oesophagus. The larva is, however, so very opaque that one cannot get an optical section of it at this stage. A larva at this stage swimming in a watch glass will every little while decrease in speed and turn its anterior end downwards until it strikes the glass. Its forward motion will then cease and it will for a short time remain attached to the glass, revolving very slowly on its long axis with its oral end turned upward. One may at such a time look down through the mouth into the entodermal cavity. After a little, the revolutions increase in frequency, and the larva turns over on to its side, and swims off. So far, then, as I was able to observe, there is a free passage from the enteric cavity to the exterior at the time of the first appearance of oral structures and there is apparently no previous invagination of ectoderm.

Soon after this, a slight circular concavity appears surrounding the oral region in such a way as to faintly outline the proboscis. Fig. 4a and b. Fig. 5 shows a larva a lit-

tle more advanced. Here the mouth is considerably larger than in the last stage and has become a narrow slit. A slight shoulder has developed a little above the equator of the larva, while the aboral end has become conical. There is apparently a thickening in the supporting membrane at the region of the shoulder, but the opacity of the larva prevents a clear view of it. This shoulder is the beginning of the peristome and the part of the animal posterior to it is the proboscis. There has been no invagination during the formation of the mouth, but it is possible that this proboscis arises by an outgrowth of the ectoderm between the mouth and the origin of the septal muscles. This seems the more probable when we remember that one of the few points on which Claus and Goette agree, is in regarding the lining of the proboscis as ectodermal.

IV. The Eight Tentacle Stage.

The period at which the larvae become attached varies considerably, but some larvae that were reared from buds and had recently become fixed, were found to be at a stage not greatly in advance of the last. Figs. 6 and 7. The mouth in these is circular and well opened. The peristome is distinctly formed and is eight angled, the four angles in what we may call the principal radii being somewhat more distinct than the other four. The stem is also distinctly formed, and in it the

entoderm has apparently begun to thicken.

The stage following this is usually as represented in Fig. 9. Here we see a large circular mouth. The eight angles of the peristome are produced into eight tentacles nearly of a size and still very small. The stem has begun to lengthen and to show its characteristic structure. Larvae at this stage, are normally quite firmly attached to some foreign body, but retain their swimming powers some time longer. When removed from its seat, such a larva will swim about as before, only more slowly, rotating on its long axis, with its stem end forward. An interesting exception to this rule was found in a larva Fig. 8, that while still actively swimming with stem undeveloped, had four of its tentacles of about the same size as in Fig. 9, while the four tentacles that alternate with these were twice as long. This arrangement of the tentacles reminds one of Aurelia, where four tentacle first appear and these are followed by four others alternating with them.

Fig. 30 is from an obliquely longitudinal section of a larva in the same stage as Fig. 9. This section cuts the larva in an adradial plane, that is, in a plane that bisects the angle between two tentacles, the eight tentacles being, four perradial and four interradial. Fig. 31 is another section of the same series. It cuts the larva tangentially and shows

the connection between one of the septal muscles and the peristome. The larva is covered by a single layer of epithelium composed of narrow columnar cells and this is throughout of nearly an even thickness. The supporting membrane, underlying this, is rather thin except in the short stem, where it is somewhat thicker. The entoderm is about twice as thick as the ectoderm, consists of larger columnar cells, apparently somewhat vacuolated, and is everywhere of about the same character. The stem is apparently entirely filled with the entoderm so as to be without a lumen. About the mouth the ectoderm is a little higher than elsewhere and grades imperceptibly into the entoderm within. Each of the eight short tentacles contains a plug of entoderm cells. The entodermal membrane follows the general contour of the whole animal except that that portion of the entiric cavity internal to the periphery of the peristome is divided into four very shallow pouches (g. p.) by four folds of the entoderm, the interradial septa. At the peripheral base of a fold the two layers of entoderm are in contact and are continuous with the entoderm of the interradial tentacle. More centrally, each fold of entoderm surrounds a plate of supporting substance that is continuous with the supporting membrane of both the oral and the aboral surfaces of the larva. Compare Figs. 31, 32, 33 and 34. As has been

already pointed out, the swimming larva is flattened laterally, just as is the sexually produced larva of Aurelia, and it is probable that these entodermal pouches have arisen at an earlier stage, two at a time, in nearly the same way that Goette (1887) found them to arise in that species.

We have, then, four tentacles in the planes of the septa and four in the intermediate planes, or perradii.

The four septal muscles have an interradial position. At the peristome they appear as cone-shaped thickenings of the ectoderm dipping into the supporting substance of the septa, Fig. 31. From the apex of each cone there is a slender cord of cells that penetrates the supporting membrane of the septum and continues through the jelly of the aboral part of the larva to the extremity of the stem, or foot, but it does not appear to have any direct connection with the ectoderm at this point. This aboral portion of the muscles is perhaps at this stage a little more differentiated than the rest.

Neither in the living animal nor in sections can any trace be seen of an oesophagus of the nature described by Goette, and the gastric pouches only resemble those of an Actinian very remotely.

V. The Sixteen Tentacle Stage.

While the eight tentacles of the first cycle are still quite short, eight tentacles of a second cycle make their appearance in the intervals between the tentacles of the first. Fig. 10. The animal shown in this figure was, two days before, a swimming planula-like larva. It is interesting as an example of how the irregular increase in the number of tentacles, that is so common, is brought about. Two tentacles of the first cycle have become bifurcated, so that in each of these places there are two tentacles where, if the larva were regular, there would be but one.

Figs. 32 and 36 are from a series of cross sections of a larva perhaps a little older than this one. Figs. 32, 33 and 34 are consecutive : The first two show the entodermal connection between two gastric pouches at the base of an interradial tentacle. In Fig. 34 the septum is complete. Fig. 35 is the second one from this and shows the gastric pouches opening into the central stomach. A section of the stem is seen in Fig. 36. The septa do not extend below the expanded part,what we may call the calyx of the scyphistoma. There is a very slight depression in the peristome in the region of each septal muscle, but no true septal funnels appear, Fig. 32.

The septal muscles are without a lumen and they each occupy a tube in the jelly. The wall of this tube is lined by a layer of longitudinal muscle fibres and within these there is a granular substance with scattered nuclei : Towards the end of the stem the muscles gradually become smaller and, the jelly becoming very thin, they are closely applied both to the entoderm and ectoderm. The ectoderm cells in this region become very flat and are covered by a cuticula, and there is now a marked differentiation between the entoderm of the calyx and that of the stem.

This is better shown in a longitudinal section of a little older larva, Fig. 57. The epithelium lining the proboscis is now very different from that covering its exterior. The lining epithelium is thick and composed of crowded narrowly columnar cells. At the septa this epithelium passes abruptly, and in the gastric pouches more gradually, into the entoderm of the calyx. This is likewise a deep columnar epithelium but the cells are larger, are vacuolated at their bases, and many appear to be gland cells containing coarse granules at their free ends. At the plane where the calyx joins the stem there is a rather sudden transition from this character of epithelium to the large, clear cells of the stem. The stem is hollow nearly to its base. The solid entodermal core of the tentacles

is composed of large clear cells with thick walls and apparently arranged in a single series, the chorda cells common in the tentacles of coelenterates The base of the stem by which the scyphistoma is attached to foreign bodies is broadened a little into a foot. The cuticula extends nearly half the length of the stem and is in very intimate contact with the tissue of the plant, or other body, to which the animal is attached. There are short, thread-like processes from the supporting substance of the foot into this part of the cuticula.

Fig. 11 will give an idea of the appearance of a scyphistoma with the sixteen tentacles well developed. They are now long and graceful and ornamented by clusters of nettle cells, that are scattered thickly over the surface, most thickly at the tip. The mouth is now becoming quadrate, Fig. 12, and there is a nice co-ordination between the movements of the tentacles and of the mouth. Food is captured by the tentacles. As soon as the tentacle attaches itself to its prey it is whipped quickly into the mouth, which simultaneously opens toward the tentacle affected. Once, I saw food taken by two tentacles at the same instant, and the mouth opened in both directions at one time.

VI. The Complete Scyphistoma.

With the increase in size of the scyphistoma the calyx is relatively more expanded and more tentacles are formed. Scyphistomas that are still quite small are found with twenty-four tentacles, and the full number of tentacles, thirty-two, is acquired long before the scyphistoma had attained its maximum size. The tentacles appear, when they are arranged symmetrically, in cycles of eight ; but the larva is as variable as is the adult, and the final number of tentacles, while never less than thirty-two, very often exceeds that number.

The interval between the acquisition of the full number of tentacles and the beginning of the next stage seems to be a long one. The great majority of scyphistomas were found in this stage, and it is during this time that the buds are given off. The four angles of the mouth are now very pronounced, and in the proboscis there are four deep longitudinal grooves corresponding with them. Fig. 46. Between the angles of the proboscis there are, in preserved specimens, four marked depressions in the peristome. These are shown in Figs. 46 and 47. The septal muscles do not arise from the bottom of these depressions but from high up on the outer sides, (Figs. 46 and 47.) It seems hardly possible that these depressions

are entirely due to muscular contraction but neither do they correspond with the septal funnels found in Aurelia.

The four gastric pouches are now much deeper than in the earlier stages and are in communication by means of a small perforation in each septum, close to the base of the interradial tentacle (c. s., Fig. 47). These perforations, together with the peripheral part of the gastric pouches, form the "Ringsinus" of German authors. There is a slight extension of the cavity of the "Ringsinus" into the base of each tentacle, Figs. 38 and 39. Beyond this the tentacle is solid and has the same structure as in earlier stages. The tentacles may in this, as in earlier stages, be divided into two series according to the position in which they are normally held, the one series being kept more erect, than the other that is nearer the longitudinal axis of the larva. The two series are equal in number and their members alternate. Figs. 11 and 13, or 14.

The differentiation of the epithelium lining of the proboscis from the general entoderm is even more marked than before. The two grade into one another on the roofs of the gastric pouches, but on the septa the transition is quite abrupt, Fig.48. There is a slight prominence (g. f.) projecting from the margin of the septum into the stomach. This is covered by a continuation of the lining of the proboscis and in the angle on

its lower side the two kinds of epithelium meet. This projection is noticeable in all my sections of the septa, from this stage onward. It may be due to contraction of the muscles but from its position, its constance, and the kind of epithelium covering it, it seems probable that it is the rudiment (Anlage) of a gastric filament. Fig. 48 shows the histology of this region. The epithelium lining the proboscis and the oral side of the central stomach is composed of moderately deep columnar cells with a dense, granular contents, small nuclei, and indistinct cell walls. Among them there is occasionally a nettle cell. On what I suppose to be a gastric filament, the epithelium is of nearly the same character. Below this, it is very different. Here the cells are more than twice as deep, are vacuolated, have larger nuclei, and the free ends of most of them are filled with coarse granules that stain with safranin and are apparently composed of a secreted substance.

VII. The Strobila.

Development of the Rhopalia.

When the scyphistoma has reached a diameter of about two millimeters the first characters appear that are distinctive of the Strobila. The first noticeable change in this direction takes place at the bases of the tentacles of the more erect series.

This change may be regarded either as the outgrowth of a conical lobe from the margin of the peristome bearing the tentacle at its tip or as a conical widening of the basal portion of the tentacle. The former view is probably the better. At about this time there appear in the tentacle just beyond the apex of the cone from which it springs a few glistening white bodies. These are the so-called otoliths and mark the beginning of the formation of the rhopalium, Fig. 13. The tentacles containing them will be called the rhopalial tentacles.

These concretions, the so-called otoliths, increase in number until they form a conspicuous mass, while the basal cone begins to broaden laterally. This is now distinctly noncontractile and may be spoken of as a marginal lobe of the peristome. Figs. 14 and 14a show the part of the tentacle in which the concretions lie, to be covered with a thicker epithelium and to be a little wider than the distal part, but this may be due merely to the extended condition of the latter.

In the specimen shown in Fig. 15, we see the first indication of strobilization . The upper, expanded part of the calyx is separated from a conical, lower portion by a slight groove. The marginal lobes have become semi-circular in outline and a slight elevation is noticeable on the aboral side of each rhopalial tentacle immediately external to the mass of concretions.

The epithelium at this point is pigmented and forms the first rudiment of the eye, oc. Fig. 15a. Fig. 16 illustrates a more advanced stage where the proximal part of the tentacle is beginning to take on its final shape and is separated by a pronounced band from the distal part, which is still functional as a tentacle.

We come finally to a stage in which, while the long distal part of the tentacle retains its characteristic structure and remains completely functional, the short proximal part has become completely differentiated into a rhopalium. Fig. 40 is from a longitudinal section of such a tentacle. The rhopalial part has assumed nearly its final shape. The differentiation of its ectoderm into sensory epithelium, eye spot, and layer of nerve fibres, is complete. It has a lumen that extends outward to the solid chorda-like entoderm of the distal part of the tentacle and opens towards the centre into a gastric pocket. The entodermal lining of the lumen is a columnar epithelium, the more distal cells being deeper and containing the concretions. Compare Fig.40 with Figs.38 and 39 which, being interradial, are certainly destined to be rhopalial tentacles.

The growth of the marginal lobes, that when last mentioned were semicircular, has continued, and each lobe has now pro-

duced two secondary ones, one on each side of the rhopalial tentacle. These are connected by a slight ridge, that crosses the base of the tentacle on its aboral side. (h. Fig. 40) These secondary lobes are the rhopalial lobes of the margin of the umbrella (Flügellappen of German authors) and the connecting ridge is the hood (Deckplatte) that covers the rhopalium. These marginal structures may be seen in Fig. 17, and this brings us to another stage in the development of the rhopalium, the absorption of the distal part of the tentacle.

In the strobila shown in Fig. 17 the rhopalial tentacles have a very different appearance from what we have seen before. They are shorter than the other tentacles and are much swollen at a point just beyond the eye spot. The distal portion is beginning to degenerate. This process, when once begun, proceeds rapidly. During the few hours that were spent in making this drawing, the rhopalial tentacles were reduced in length nearly one half. The eye spots and concretions were conspicuous and in each of the former there was a slight cup-shaped depression. This is the earliest stage in which I observed slight medusa-like movements of the ephyra disk. Figs 41 and 42 are rather oblique sections at right angles to one another of rhopalia at about this stage. The tentacle is seen to be in a process of degeneration for about fifteen-hundredths

of a millimeter outward from the ocellus. In this area of degeneration the entoderm cells are broken down, the supporting membrane has disappeared, and the inner boundary of the ectoderm is indistinct. The axial mass of this part of the tentacle is made up of loose particles of a finely granular substance in which, in Fig. 42, we see many small and deeply stained nuclei. In Fig. 41 these nuclei are not so prominent and there are numbers of green cells that apparently escaped into the central mass when the supporting membrane broke down. There is evidently a free communication between this mass of disintegrating material and the digestive cavity through the rhopalial canal.

The method by which the shortening of the tentacles is brought about would seem to be as follows : The axial cells adjoining the cells that bear the concretion (Fig. 40) first break down. Why they should do so, and at this particular time, I cannot say. This disintegration proceeds centrifugally and it is accompanied by a dissolution of the supporting membrane. The ectodermal cells then either begin here and there to break down while still in place and the resulting debris is squeezed into the central cavity ; or else, the cells migrate, or are squeezed inward and then disintegrate. The continuity of the remaining ectoderm is maintained, how-

ever. The products of the degeneration probably pass through the rhopalial canal into the digestive tract. As this process continues, the inward movement of the ectoderm cells is more rapid than their disintegration, so that when the distal part of the tentacle is reduced to the size of the rhopalial part (Figs. 18 and 43) it is a solid mass of small cells with small nuclei that stain darkly. Some of these cells contain a large vacuole and have the nucleus pushed to one side. Scattered among the small cells, there are numbers of globular bodies as large as, or larger than, the green cells, and completely filled with coarse granules that stain deeply with safranin ; no nucleus is visible in them. The ocellus has now become distinctly cup-shaped. (Fig. 43.)

At about this time the interrhopalial tentacles begin to be absorbed in their turn. The umbrella margin has in the mean time grown out beyond the insertion of each interrhopalial tentacle and over its aboral side into two lobes with a hood between. (Figs. 18 and 19.) This structure, although smaller corresponds exactly to the rhopalial lobes and hood, and is further evidence for homology between the tentacles and the rhopalia. In the specimen illustrated by Fig. 18 the interrhopalial tentacles were in the process of absorption. The drawing was made between the hours of 11 A. M. and 2 P. M.

At 5 P. M. of that day the tentacles had been reduced to one-third the length shown in the figure and the absorption of the rhopalial tentacles was very nearly completed.

In the later stages of the absorption of the interrhopalial tentacles the broken down material is evidently forced in some way into the radial canal. This is well shown in Fig. 45, which is from a specimen at about the stage of Fig. 19. In Fig. 45 we see that the axis of what is left of the tentacle is filled with a confused mass of disintegrating cells, small nuclei, and cnedocysts, and some of this mass actually extends into the cavity of the radial canal.

The rhopalium(Fig. 44)is practically complete at this stage. The point (x) where the last trace of the tentacle proper disappeared, is still distinguishable in sections by the presence of small cells with indistinct cell walls, and by the absence of otoliths.

Other Phenomena of Strobilization.

While these changes are taking place in the margin of the disk, there are important changes in the general shape of the animal. The horizontal constriction first noticed in Fig.15 has deepened, while the fold below it has heightened. At the same time the upper disk has broadened and flattened until it assumes the shape shown in Figs. 18 and 19. The four depres-

sions in the peristome of the earlier stages have become nearly flattened out, all that remains of them being the hollows between the projecting angles, or pillars of the proboscis, that are now very prominent. The specimen from which Fig. 40 was taken shows a slight cavity (s. f.) in the peristome at the point where each septal muscle joins the general ectoderm. This is a little more marked in Fig. 49 and it is seen at its maximum development in Fig. 50 which is taken from a specimen in which the absorption of the tentacles is nearly complete. It is a funnel-shaped depression into the septal muscle and is a vestige of the septal funnel, which, according to Goette, is found well developed in Aurelia.

With the increase in width of the peripheral portion of the upper disk of the strobila, the orifices in the septa become relatively larger, until the septa are reduced to columnar pillars (c. Fig. 50) of supporting substance that connect the jelly of the peristome or subumbrella with the aboral disk of jelly, or exumbrella. They are clothed with entoderm, or perhaps partially with ectoderm, and are pierced longitudinally, each, by a septal muscle. We may speak of these structures now as columellae.

They are what the Germans call "Septalknoten." There is of course no adhesion of the two entodermal plates at these

points, and they are not homologous with the so-called Septalknoten, or areas of adhesion in the Peromedusae. The true columellae, or "Septalknoten" in the Peromedusae are separated, according to Haeckel's figures, from the areas of adhesion by spaces in which the gonadia lie, and are the walls of the large septal funnels where these pass through the stomach from the subumbrella to the exumbrella.

While the septa are shrinking to become the columellae, ridges appear opposite each other on walls of the peripheral part of the digestive tract between the bases of the tentacles. The entoderm at the summits of opposite ridges unites and thus there is formed a series of lines of adhesion extending inward from the periphery and dividing the space into a series of radial canals, each ending in a tentacle, whether it be rhopalial or interrhopalial. The two disks of jelly never fuse along these lines of adhesion but the entoderm remains between them as the entodermal lamella, or cathammal plate. At the stage of Fig. 40 the lines of adhesion occupy half the space from the margin to the columellae.

At this same stage eight curious nettle batteries appear arranged symmetrically on the proboscis. Perhaps it would be better to speak of them as special organs for the production of nettle cells. They are nearly spherical thickenings of the

ectoderm sunk into the supporting substance from the outer surface of the proboscis. In these structures nettle cells are to be found in all stages of development.

The lower disk of the strobila remains simply an annular fold of the body wall until the upper disk is nearly a complete medusa. The septal muscles in this region bend outward with the rest of the body wall. Fig. 49. At length, however, the entoderm grows out as four shallow pouches with gelatinous septa between containing the muscles, and very soon after the gelatinous septa are perforated so as to allow a fusion of the entoderm at at their upper angles. Fig. 50. This figure shows that the body wall has become very thin at the bottom of the groove that separates the disks, and the septal muscles in this region have become constricted. The body wall finally becomes so thin here that it is ruptured by the movements of the upper disk which is then set free, and at about the same time the columellae lose their connection with the exumbrella.

Fig. 19 represents an advanced strobila. The lower disk is drawn as it usually appeared, very much contracted. In occasional moments of relaxation a few small tentacles could be seen but they disappeared again before one could count them. The bud dropped off and began swimming about while I was taking a short rest from drawing. Pulsating contractions of the um-

brella are first noticed at the time when the rhopalial tentacles begin to be absorbed. They are then feeble and at long intervals. At the stage now before us, these movements are rapid and violent and the rhythm of movement is interrupted by few pauses, and these are short. The medusa was set free during the night after this drawing was made. The following morning the basal segment had the appearance shown in Fig. 20. It is a scyphistoma with seventeen tentacles, but the mouth is merely an orifice left after the detachment of the medusa. The proboscis is not formed yet. I found many scyphistomas that, from the large size of the stem and smallness of the calyx, I concluded had undergone strobilization and I have no doubt that regeneration and strobilization are repeated a number of times. At any rate, I am certain that the basal segment becomes a fully formed scyphistoma.

VIII. The Ephyrula.

The medusa that is set free from a strobila of Cassiopea has a very different appearance from the ephyrula stage in jelly-fish that have eight, the usual number of rhopalia. Cotylorhiza has an ephyrula resembling the same stage in the semostomatous medusae. Good figures of this are given by du Plessis and Claus and there is a striking difference between these figures and my Figs. 21 and 22 which are camera drawings of well preserved ephyrulas of Cassiopea mounted in balsam. Fig. 21 represents a young Cassiopea that has not long enjoyed a free existence. The general shape of the umbrella is like that of the adult, and there is the same concavity in the centre of the exumbrella, while the margin curves in the opposite direction, as in Fig. 52. The typical ephyrula of Aurelia or Cotylorhiza has eight marginal arms with two lobes at the end of each and between these, a rhopalium. In Casiopea structures corresponding to these arms are present to the number of sixteen, or often more. But these do not destroy the general circular outline of the animal for they are connected by thin areas in the jelly with an equal number of ridges alternating with them, which at an earlier stage bore the interrho-

palial tentacles on their under sides. We have, then, at this stage the marginal zone of the umbrella marked by a number of short radial ridges separated by an equal number of thin areas. The ridges are in line with the radial canals. At the principal end of each ridge the margin of the umbrella is produced into two lobes, those adjoining the rhopalia (sh.l.) being well marked, the others (i.l.) small and inconspicuous.

In Fig. 22 there are twenty-three rhopalia. This is an unusually large number and it will be noticed that the number of marginal lobes has not increased in proportion, so that irregularities of the margin occur in many places. Indeed I think if a bifurcated rhopalium were added that this one specimen would show all the irregularities of the margin that can occur in this stage of existence in a Cassiopea. In scyphistomas forked tentacles may occasionally be found, and bifurcated rhopalia are not uncommon in the medusae. Between the bifurcated rhopalium and two complete parameres in the place of one, we find all degrees of duplication: The first stage beyond the double rhopalium is seen at 1. in Fig. 22, at 3. or 4. there is a greater separation, while at 5. we have two nearly complete parameres. Except for this multiplication of marginal parts the specimen is perfectly normal.

At this stage the rhopalia have come to lie, as in the adult, wholly within the margin of the umbrella and project from its subumbrella surface. The interrhopalial tentacles have totally disappeared. The lines of adhesion separating the radial canals are faintly visible as radiating lines of greater transparency. The four lips of the mouth are spread out into a cross-shaped figure and one may look directly through the lumen of the oesophagus into the stomach, and see four gastric filaments, Fig. 21.

Each one of the four lips is nearly square and from its two outer angles there are two grooves that extend obliquely inward until they meet and form a V. The point of the V. is in an angle of the oesophagus along which there is a groove that is continuous with these other two grooves and extends into the stomach. On the interradial side of each of the eight labial grooves there may be seen a small roughly circular area that is less transparent than the rest. These areas are the nettle batteries first seen in earlier stages. The margins of the lips are provided with numerous small processes, the digitella. These are arranged in a single continuous series.

The medusa from the strobila Fig. 19, was examined a few

hours at most after it became free. The lips were a little less distinctly quadrate and the digitella were much smaller than in Fig. 22. On looking through the mouth one could see the four gastric filaments and an opening to the exterior through the roof of the stomach left by the rupture of the connection with the basal segment of the strobila. Fig. 51 is a section of an ephyrula at about this stage. In this the last vestige is to be seen of the connection between the columella (c.) and the roof of the stomach, and of the degenerated remnants of the septal muscles (s.m.) in the jelly near the aboral opening. The other end of one of these muscles is seen at s. m. on the right hand side of the figure. It extends for some distance into the jelly at the base of a gastric filament and it is penetrated from the exterior by a very narrow septal funnel (s. f.).

At a little later stage when the opening in the roof of the stomach has closed both the septal muscles and the septal funnels totally disappear. Sometimes one, sometimes the other, is the first to vanish.

IX. The Later Stages.

For the present I must pass very briefly over the later stages in the development of Cassiopea. While the umbrella

remains unchanged the two outer angles of each of the more or less quadrate lips are drawn out into extended lobes, Fig. 23. At the same time the pillars of the proboscis thicken and the jelly is continued outward along each of these lobes as a mid-rib. We have then eight oral arms each with a longitudinal groove, supported by a midrib and fringed with digitella ; arms very similar to those characteristic of the genus Aurosa, Haeckel (1879). But it is only the mouth parts of Cassiopea that may be said to pass through an Aurosa stage, for the comparison cannot, at this time at least, be carried to the other organs. As the gelatinous axes of the oral arms are thickened, their bases unite to form the oral disk.

Claus has described (1883) some of the principal stages in the metamorphosis of Pilema (Rhizostoma) and Cotylorhiza. He regards the formation of the eight oral arms as a different process in these forms from what occurs in Aurosa. There it is a splitting of the four oral arms, here it is an outgrowth of the corners of the ephyrula lips. This sounds to me like the same thing merely expressed in two different ways. the comparison that Claus makes between the process of formation of the eight arms and the foldings of these arms that results in the oscula seems hardly applicable in Cassiopea, as will ap-

pear later. Compare Figs. 2? and 25.

In the next stage we find two oral funnels, or oscula, and a small vesicle developed at the tip of each oral arm. The other portions of the arm are still open and fringed with digitella as before, but the outline is no longer a regular curve, for at intervals there are folds in the margin. The deepest folds are the most distal and they become progressively more shallow towards the base of the arm. The central mouth is still widely open. The subgenital cavities are well developed at this stage, Figs. 52, 53, and 54. Figs. 53 and 54 show how they are produced by the great increase in the thickness of the jelly of the pillars of the proboscis and of the oral arms. By the growth of these structures these cavities are necessarily produced. The only special adaptations are the subsequent growth and folding of the dorsal wall and the narrowing of the orifice. The marginal lobes of the umbrella now begin to broaden and thus approach the adult condition, but there is only a single "velar lobe" between two rhopalial ones.

At a little later stage when there are three oral funnels at the tips of the arms (Fig. 25) the re-entrant angles between the pillars of the proboscis have grown inward, met at

the centre, and fused, Fig. 24. In this way the lumen of the oesophagus is divided into four tubes (oe. t. Fig. 24) representing the grooves that were present in its angles in the earlier stages. In this case the fusion at the centre has gone so far as to involve the edges of the lips and the labial grooves of the different pairs of arms are not in open communication but a short cross-shaped tube connects them at the centre and the oral disk is now completed.

It is interesting to note that Claus has found a stage both in Pilema and in Cotylorhiza that, while showing the characteristic family differences, as also a certain resemblance to this stage in Cassiopea. In all three, the walls of the proboscis have fused so as to divide its lumen into tubes and the formation of oscula has begun at the tips of the arms in such a way that we have on each arm three oscula with a vesicle in the angles between them. The occurrence of this stage in the ontogeny of three so distinctly separated families must have some morphological significance and we may regard these eight primary vesicles as homologous in the three groups.

The mode of formation of the oral funnels becomes evident at this stage. They are not formed in Cassiopea simply by a series of fusions of the lips along the line of the labial groove, as Hamann found (1882) to be the case in Cotylorhiza(?).

It is more like the process in Pilema as described by Claus. Each of the primary funnels is represented at first by one of the folds in the margin of the lips referred to above, Fig.25. The fold deepens and its edges are brought together on the ventral side and fused, leaving an opening at the apex of the fold, the osculum. At the same time the labial groove in this region is converted into a canal by the fusion of the lips on its two sides. After the fusion all trace of what has occurred quickly disappears.

With the division of the oesophagus into four tubes and the completion of the oral disk our larva comes to be distinctly a rhizostomatous medusa. Further development of the mouth parts consists in the continued division of the labial or brachial groove into oral funnels and brachial canal, together with the development of oral veiscles. By the time two or three vesicles have been formed on the end of each arm a vesicle appears in the centre of the oral disk. Except for this interruption the development of the mouth parts proceeds regularly in a centripetal direction. The funnels and vesicles are formed first at the tips of the arms and then one after another in regular succession towards the centre. Each of these primary funnels is the rudiment of one of the primary branches of the arm. When the process of forming funnels has

reached to about half the length of the arm the distal funnels begin to subdivide. By this subdivision of the primary funnels, funnels are produced of which some are the rudiments of secondary branches, these subdivide again and so on as long as growth continues. The subdivision is not dicotymous, but takes place in such a way as to produce alternate branches. A vesicle is formed in some way at about the time of the completion of the fusion of the fold of the lip into a funnel. I have not been able to determine, so far, whether the vesicle is a funnel with the orifice closed as Hamann claims it to be, or whether it is an evagination from the pedicle of a vesicle as it seemed to me to be at first, and as Claus thinks it possibly is.

According to Haeckel (1879) the genus Archirhiza represents a form that was the ancestor of all the rhizostomatous medusae. Of this genus there are two known species, A. primordiatis, Haeckel, and A. aurosa, Haeckel. They agree in having four subgenital cavities and eight simple unbranched arms that are provided with a single zig-zag row of closely set oral funnels and are devoid of other appendages. Hamann says that a stage representing this condition is a feature of the ontogeny of rhizostomatous medusae. From what I have said it is evident that we have no such stage in the development of

Cassiopea Xamachana, for while the labial groove is still open in the proximal half of an oral arm, in its distal half the vesicles are formed and branches are in the process of formation.

The outline of the umbrellae margin has not changed essentially since the last stage. The areas of adhesion have become much wider than the radial canals they separate and in them there has appeared a network of anastomosing canals, while the gastric filaments have become numerous. In short we have now followed the larva of our Cassiopea from its first appearance as a bud, to a point where with the exception of the gonadia all the organs of the adult are outlined. Here we must take leave of it.

C O N C L U D I N G R E M A R K S.

In Cassiopea Xamachana, then, multiplication of individuals takes place largely by two kinds of non-sexual reproduction, strobilization and budding. In regard to the last, several interesting questions naturally suggest themselves, such as,— the origin of budding in the scyphomedusae, which of the known methods is nearer the primitive one, whether this has any relation to strobilization, and the like; but until much more evidence has been collected than we at present possess it will be impossible to give to them conclusive answers. It seems to me to be highly probable, however, that the mode of budding that occurs in Cassiopea will will be found to be the most highly specialized of those so far known. It seems to be an especial adaptation to overcome the unfavorable effect on the distribution of the species caused by the sedentary mode of life of the adult, a mode of life unusual with medusae. Dwelling as it does on the bottom in quiet lagoons and bays, its eggs stand little chance of wide distribution and the planulae would not probably swim very far from their mother before becoming fixed. The individual buds probably do not swim very far either, but the last one of a series of generations of buds may

be at a great distance from the parental, sexually produced scyphistoma.

The resemblance of the swimming bud of Cassiopea to the planula of Aurelia is extraordinary. Both are ciliated and have the same movements, the shape is the same, both being a slightly flattened oval with the more acute end posterior and it is at the posterior end in both that the mouth arises. It is only when these larvae are examined in sections that the difference appears. The bud has, in distinction from the planula, a thick supporting or gelatinous layer, and the four septal muscles already formed.

In the development from the bud to the scyphistoma there is no stage comparable to an anthozoan. This is not an argument, however, against Goette's theory of the descent of the scyphomedusa from an anthozoan-like ancestor, for one could not expect a step in the phylogeny to be recapitulated in a process of non-sexual development unless this process takes place during a relatively earlier ontogenetic stage and the budding in Cassiopea occurs on scyphistomas that have long lost their anthozoan characters, if they ever possessed any. Goette regards the early stages in the scyhphistoma as possessing essentially anthozoan characters, in the ectodermal oesophagus and the four gastric pouches. Claus admits the existence of

these structures but refuses to regard them in the same way that Goette does. Goette says (p. 26) that the scyphistoma maintains the typical structure of an anthozoan usually until the eight tentacle stage. It seems to me that this stage is much more transitory. The septal muscles arise in Aurelia according to Goette in the four tentacle stage and it is with the appearance of these very distinctively medusoid structures that I should say the larva loses its supposed anthozoan character. The septal muscles are peculiar to the scyphomedusae, they are found in no other group of animals and every scyphomedusa possesses them at some stage of its existence. In the buds of Cassiopea these are produced very early, while the bud is merely a hemispherical evagination on the side of the scyphistoma, and the bud could not, therefore, ever pass through an anthozoan stage.

The early development of these muscles is further evidence for the supposition that this planula-like bud is a modification of a phylogenetically earlier condition with mouth and tentacles, perhaps as in Aurelia.

It is to be expected that the organs of a non-sexually produced animal will be derived from the same germ layers that give rise to corresponding organs of a related animal that has

been produced by a sexual process.

Claus and Goette agree in regarding the lining of the proboscis as of ectodermal origin in Aurelia and Cotylorhiza. It is therefore probable that this is true also of Cassiopea and that the proboscis is formed as a crater-like fold of the ectoderm surrounding the mouth opening. If I were sure of this I would go a step farther than Goette and, judging from the histology, say that not only the interior of the proboscis but also parts of the septa are clothed with ectoderm. The parts of the septa referred to appear to give rise to the gastric filaments. This would be further confirmation of Goette's theory if it were not for the fact that these filaments are not developed in the Anthozoan stage but long afterward, at about the time that the medusa becomes free. I do not believe that there is any homology between the gastric filaments in the two groups, Anthozoa and Scyphomedusae.

At first there are eight tentacles, four of them in the radii of the septa and four interseptal. When the larva is regular the additional tentacles arise in cycles of eight, there being next sixteen, then twenty-four and finally thirty-two ; but the interpolation of other tentacles is very common.

Agassiz and Claus have stated that the rhopalia in Aurelia are developed in the basal portions of tentacles. This I find

to be true also for Cassiopea. In this species I have followed every stage in the development of the rhopalium from the first trace of such a structure to its completion and I have no hesitation in saying that Goette's account of this process, which he persistently upholds, is entirely erroneous. To show that the two views are essentially opposed I introduce Goette's Fig. 49 (Fig. 40a) in which the rhopalium appears as an evagination on the oral side of the margin and quite independent of the tentacle. The absorption of the tentacles is rapid and the rhopalial tentacles are absorbed before the rest, so that the process is easily overlooked if there is a scarcity of material. Goette's mistake is probably due to this cause. Goette says that generally the tentacles are constricted off but sometimes they are absorbed. I find the latter to be the only method in Cassiopea.

The gelatinous part of the septa is perforated at about the time of the appearance of the first tentacles. Later the septa become reduced to columellae and the radial canals are formed by lines of adhesion just as Goette found this to take place in Aurelia.

The relations of the septa and septal funnels are about as Claus found them to be in Cotylorhiza. Although the septal

muscles extend to the foot, the septa remain short, occupying only the upper part of the calyx. The septal funnels are abortive and do not become the subgenital cavities.

The strobilization is monodiscous and the basal segment is regenerated into a scyphistoma. In this I agree with Goette. The free segment is very different in appearance from an ordinary ephyrula. Stylorhiza must have a similar one. Lendenfeld (1884) found young specimens of this genus with twenty-four rhopalia. In older ones the number is reduced to sixteen and finally to eight. In Cassiopea the number of rhopalia is constant in each individual, and depends on the number of tentacles in the scyphistoma stage. There are, as a rule, half as many rhopalia as there were tentacles, every alternate tentacle having given rise to a rhopalium. The irregularities in the marginal structures of the adult that are so strikingly frequent, are to be referred back to irregularities in the arrangement of the tentacles of the larvae from which they are developed.

The young medusa has at first a simple quadrate mouth with slightly spreading lips. Later these are drawn out into eight lobes so that as far as the mouth parts are concerned we have an Aurosa stage.

There is no Archirhiza stage in Cassiopea but there is a

stage with the oesophagus reduced to four tubes and with three oscula and an oral vesicle on each arm, which it has in common with Pilema and Cotylorhiza.

A somewhat cursory examination of my material made to determine the mode of development of the oral funnels and vesicles, inclines me to the views on this point upheld by Claus, rather than to those of Hamann.

A synopsis of the principal characters of the adult medusa is given in the diagnosis of the species and the following section. What most strikes a casual observer, is the peculiar concave exumbrella and the animal's mode of life. The only other species that has been described as having a similar shape is *Cassiopea polypoides*, Keller, but I have observed that *Polyclonia frondosa* also approaches this condition. The habit of living in schools in shallow water and resting on the bottom with the mouth upwards has been noticed by a number of persons in other species of Cassiopea and in Polyclonia and seems to be common in these two genera.

L I S T O F P A P E R S R E F E R R E D T O.

1829. Tilesius. Zur Naturgeschichte der Medusen, Nova Acta Phys. Med. N. C. Vol. 15. p. 236.

1841. Sars. Uber die Entwicklung der Medusa aurita und Cyanea capillata, Arch. f. Natur. Vol. 7.

1849. Milne-Edwards. Les Zoophytes, Cuvier's Regne Animal illustré. Pl. 51.

1853. Frantzius. Uber die Jungen der Cephea (Cotylorhiza), Zeit. f. wiss. Zool. Vol. 4. p. 118.

1860 L. Agassiz. Contributions to the Natural History of the United States of America. Boston. Vols. 3 and 4.

1869. Haeckel. Crambessiden, Zeit. f. wiss. Zool. Vol. 19. p. 509.

1877. Claus. Die Polypen und Quallen der Adria. Wien.

1878. O. and R. Hertwig. Das Nervensystem und die Sinnesorgane der Medusen. Leipzig.

1879. O. and R. Hertwig. Die Actinian. Jena.

Haeckel. Das System der Medusen. Jena.

1881. A. Agassiz. Polyclonia frondosa. Nature Vol. 24. p. 509.

Archer. Medusae. Nature Vol. 24. p. 307.

Claus. Uber enige bislang noch unbekannte Larvens-

tadien von Rhizostoma. Zool. Anz. 1881. No. 78. p. 79.

Haeckel. Report on the Deep-Sea Medusae. Challenger Reports. Zoology. Vol. 4.

Hamann. Die Mundarme der Rhizostomen und ihre Anhangsorgane. Jena. Zeit. Vol. 15. p. 243.

du Plessis. Remarques sur les Metamorphoses de la Cassiopé bourbonnienne. Bull. Soc. Vaudois. Lausanne, 2nd series, Vol. 17.

1882. Guppy. Habits of Scyphomedusae Nature. Vol. 27. p. 31.

Fewkes. Notes on the Acalephs of the Tortugas. Bull. Mus. Com. Zool. Cambridge. Vol. 9. No. 7.

Lendenfeld. Über eine Übergan-sform zwischen Semostomen und Rhizostomen (Pseudorhiza). Zool. Anz. 5 Jhy. p. 380.

1883. Claus. Untersuchungen über die Organisation und Entwicklung der Medusen. Prag und Leipzig.

Keller. Untersuchungen über neue Medusen aus dem rothen Meere. Zeit. f. wiss. Zool. Vol. 38. p. 621.

1884. Claus. Die Ephyren von Cotylorhiza und Rhizostoma. Arb. zool. Inst. Wien. Vol. 5. p. 168.

Lendenfeld. Zur Metamorphose der Rhizostomen. Zool.

Auz. 7 J..., p. 29.

1885. Haacke. Pseudorhiza. Biol. Centrall. Vol. 4. p. 291.

1886. Metschnikoff. Embryologische Studien an Medusen. Wien.

Brooks. The Life History of Hydromedusae, a discussion of the origin of Medusae and of the significance of Metagenesis. Mem. Bost. Soc. Nat. Hist. Vol. 3. No. 12, also Mem. Biol. Lab. Johns Hopkins Univ. Vol. 1.

1887. Goette. Entwicklungsgeschichte des Aurilia aurita and Cotylorhiza tuberculata. Hamburg und Leipzig.

1888. Fisher. Scyphostomata of Acraspedote medusae. Abs. in Jour. Roy. Mic. Soc. 1888. p. 545.

Lendenfeld. Die Australischen rhizostomen Medusen. Zeit. f. wiss. Zool. Vol. 47. p. 201.

1889. Vanhoffen. Semaeostome und rhizostome Medusen. Leuckart und Chun's Biblioth. Zool. 3 Heft.

Schewiakoff. Zur Kenntness der Acalephenauges. Morph. Jahrb. Vol. 15. p. 25.

1890. Bigelow. The marginal sense organs in the Pelagiidae. Johns Hopkins Univ. Circ. Vol. 9. p. 65.

Claus. Über die Entwicklung des Scyphostoma von Coty-

lorhiza, Aurelia und Chrysaora. Arb. Zool. Inst. Wien. Vol. 9. p. 23.

1891. Goette. Claus und die Entwicklung der Scyphomedusen. Leipzig.

1892. Bigelow. On Reproduction by Budding in the Discomedusae. John Hopkins Univ. Circ. Vol. 11. p. 71.

Bigelow. On the Development of the Marginal Sense Organs of a Rhizostomatous Medusa. Johns Hopkins Univ. Circ. Vol. 11. p. 84.

EXPLANATION OF THE FIGURES.

All the figures from 1 to 20 and Fig. 2? are free hand drawings made from the living specimens. Figs. 21 to 25 are from well preserved specimens mounted in balsam and were outlined with the camera lucida. The remaining figures are camera lucida drawings of microtome sections.

Lettering common to all the Figures.

b.	bud
c.	columella
c. d.	circumoral disk or peristome
c. s.	circular sinus
cx.	calyx
d.	digitellum
ect.	ectoderm
e. l.	entodermal lamella
ent.	entoderm
e. u.	exumbrella
g.	stomach
g. f.	gastric filament
g. p.	gastric pouch
h.	hood

i. l.	intermrhopalial lobe
i. t.	intermrhopalial tentacle
j.	jelly or supporting membrane
m.	mouth
n. f.	nerve fibres
o. a.	oral arm
oc.	ocelus
o. d.	oral disk
oe.	oesophagus
oe. t.	oesophagial tube
os.	Osculum
ot.	rhopalial concretion (otolith)
p.	proboscis
p. p.	pillar of the proboscis
r. c.	radial canal
rh.	rhopalium
rh. c.	rhopalial canal
rh. t.	rhopalial tentacle
s.	stem
s. e.	sensory epithelium
sep.	septum
s. f.	septal funnel

s. g. subgenital cavity

s. m. septal muscle

s. u. subumbrella

t. tentacle

v. vesicle

Fig. 1. A scyphistoma in the process of budding. In this case a second bud ($b_{,,}$) has formed before the first ($b_{,}$) is set free.

Figs. 2a, b, and c. A planula-like larva showing the changes of shape assumed by one specimen during a few minutes. The arrow shows direction of motion.

Fig. 3a. A larva in which the mouth has just formed.

Fig. 3b. Oral aspect of the same specimen.

Figs. 4a and b. A slightly older specimen viewed in two planes at right angles to one another.

Fig. 5 Larva with first traces of the proboscis and circumoral disk.

Fig. 6. Scyphistoma very recently attached.

Fig. 7. Oral aspect of a similar larva.

Fig. 8. A scyphistoma with rudiments of eight tentacles but still swimming freely.

Fig. 9. An attached scyphistoma with rudiments of eight tentacles. More usual form.

Fig. 10. Scyphistoma with rudiments of the second set of eight tentacles.

Fig. 11. Scyphistoma with sixteen tentacles fully developed.

Fig. 12. Oral aspect of a similar specimen.

Fig. 13. Scyphistoma showing first traces of rhopalial structures.

Fig. 14. Scyphistoma at a slightly older stage.

Fig. 14a. Small part of the margin of a similar larva.

Fig. 15. An early stage in strobilization.

Fig. 15a. A rhopalial tentacle of the same specimen seen from the side.

Fig. 16. An older rhopalial tentacle.

Fig. 17. Strobila in which the rhopalial tentacles have begun to degenerate.

Fig. 18. One in which the interrhopalial tentacles have also begun to degenerate.

Fig. 19. A complete Strobila.

Fig. 20. The basal segment remaining after strobilization.

Fig. 21. An Ephyrula recently set free.

Fig. 22. A specimen of about the same age showing varia-

tions of the margin.

Fig. 23. Mouth parts of a young medusa in the Aurosa stage.

Fig. 24. Oral disk of an older specimen.

Fig. 25. One of the oral arms from the same specimen.

Fig. 26. Floor of the stomach and the oral arms of an adult viewed from the aboral side. The roof of one subgenital cavity is removed and a thread is represented as passing thro' the external orifice into this cavity.

Fig. 27. Section of a young bud. x 315.

Fig. 28. Section through the distal apex of an older bud showing the origin of a septal muscle. Zeiss H oc.2.

Fig. 29. Longitudinal section of a planula-like larva. Zeiss DD oc.2. D was the distal, P the proximal end before it was set free.

Fig. 30. Adradial section of a scyphistoma of the same age as Fig. 29. Zeiss DD oc.2.

Fig. 31. A tangential section of the same larva showing the connection of a septal muscle with the circumoral disk. Zeiss H. oc.2.

Figs. 32 to 34 are consecutive transverse sections of one individual. Fig. 32 shows the continuity between the ento-

derm of adjacent gastric pouches at the base of an interradial tentacle. Fig. 34 is lower and here the gelatinous septum completely separates the two pouches. Zeiss. H oc.2.

Figs. 35 and 36 are from the same series. Fig. 35 is the second section below Fig. 34. It just clears the oesophagus.

Fig. 36 is through the upper part of the stem. Zeiss. DD oc.2.

Fig. 37. Longitudinal section of a scyphistoma with sixteen tentacles, probably a little younger than Fig. 11. 490.

Figs. 38 to 44 illustrate the development of the rhopalia.

Fig. 38. A radial section through the base of an interradial tentacle in a fully developed scyphistoma. xH oc.2.

Fig. 39. A tangential section through the base of another interradial tentacle of the same larva. xH oc.2.

Fig. 40. A radial section from the base of a rhopalial tentacle somewhat older than Fig. 16. Zeiss H oc.2.

Fig. 40a. A copy of Goette's Fig. 49, introduced for comparison.

Fig. 41. A radial section through a rhopalial tentacle in the stage of Fig. 17. Zeiss H oc.2.

Fig. 42. A tangential section of a similar tentacle of the same age in the plane x y of Fig. 41. Zeiss H oc.2.

Fig. 43. Radial section of a rhopalium in the stage of Fig. 18. Zeiss H oc.2.

Fig. 44. Radial section of a rhopalium in about the stage of Fig. 19. Zeiss H oc.2.

Fig. 45. A similar section through the degenerated remnant of an interradial tentacle from the same specimen.

Fig. 46. A somewhat obliquely transverse section of a fully developed scyphistoma showing the relations of the septal muscles to the depressions in the circumoral disk. Zeiss. DD. oc.4.

Fig. 47. Section in the plane of an interradius from a similar larva. Zeiss. C oc.2.

Fig. 48. Part of the opposite side of a similar section of the same series, more highly magnified to show the histology of the parts. Zeiss. H oc.2.

Fig. 49. Radial section showing the course of a septal muscle in a strobila. X 313.

Fig. 50. A similar section from an older specimen. X Zeiss DD oc.2. X point of separation between the two disks.

Fig. 51. A median verticle section of a young medusa that has very recently become free X is opposite the opening that formerly lead into the lower disk of the strobila. Zeiss DD oc.2.

Figs. 52 to 54. Parallel sections from a single medusa intermediate in age between Figs. 23 and 24. The mouth opens freely to the exterior, while the formation of vesicles and oscula has begun at the tips of the oral arms.

Fig. 52 is nearly radial ; the other two are tangential.

V I T A.

The author of this thesis, Robert Payne Bigelow, is the son of Otis and Margaret Payne Bigelow, and was born in Baldwinsville, New York, July 10th, 1863. Since 1868 he has resided in the city of Washington, where he attended the public schools and afterwards studied for two years, until 1882, in the Preparatory School of Columbian University. A year was then spent as book-keeper for the firm of Otis Bigelow & Co., after which he entered the Scientific School at Harvard University, whence he was graduated in 1887, with the degree of Bachelor of Science, *magna cum laude*.

Another year was spent in business, and then he entered the Johns Hopkins University, taking Animal Morphology as his principal study, with Physiology and Botany as subordinate subjects. While in this University he has held the positions of University Scholar, Fellow, and Bruce Fellow.