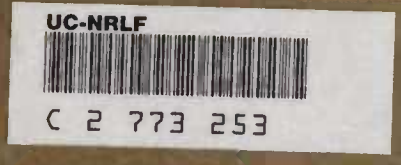
QL
377
H9B5



MEMOIRS

OF THE

BOSTON SOCIETY OF NATURAL HISTORY;

VOLUME 5, NUMBER 6.

THE ANATOMY AND DEVELOPMENT OF CASSIOPEA XAMACHANA.

By ROBERT PAYNE BIGELOW.

BOSTON:
PUBLISHED BY THE SOCIETY.
AUGUST, 1906.

EXCHANGE

SIGILLVM · VNIVERSITATIS · CALIFORNIENSIS

FIAT LVX

MDCCCLXVIII

EX LIBRIS

Univ. Calif. Zoology Dept

BIOLOGY
LIBRARY
G

Main Lib.
Zool. Dept.

QL 377
H 9735
BIOLOGY
LIBRARY
G
UNIV. OF
CALIFORNIA

6. The Anatomy and Development of Cassiopea xamachana.[1]

By Robert Payne Bigelow.

Introduction.

During the summer of 1891 the Marine Laboratory of the Johns Hopkins University was stationed in the Island of Jamaica. It was at Port Henderson, — a little hamlet situated at the west side of the mouth of Kingston Harbor, at the point where the Salt Pond Hill, eight hundred feet high, descends to the salinas and mangrove swamps surrounding the mouth of the Rio Cobre. On the other side of the hill, and to the south of it, there is a considerable body of salt water, known as the Great Salt Pond. It is completely separated from the sea, but only by a beach of sand, which at its narrowest part is not more than a few rods in width; and it is said by those who live near that in times of storm or freshet this barrier may be broken through.

One morning in June Dr. G. W. Field was hunting birds along the seaward shore of this pond, and came upon a little bay that forms a deep indentation in the barrier and is connected with the pond by a narrow inlet. The 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 a fresh zigzag mark showed where it had recently slid into the water. A school of fish was circling about in the clear water, and barnacles and sea-anemones spread their tentacles from the submerged roots of the mangroves, while the bottom at the inner end of the bay was completely carpeted by a colony of beautiful rhizostomatous medusae.

A few very small specimens might be seen swimming about, but most of the medusae, especially the larger ones, would not ordinarily leave the bottom. They lay there upon their backs, with their voluminous, branching mouth parts spread out over their discs, which were motionless, except for occasional flaps of their margins. If any of these animals were disturbed, they would, however, swim about like ordinary medusae; but before long they would settle down again and assume their usual attitude upon the bottom.

[1] An earlier draft of this paper was accepted in May, 1892, by the Board of University Studies in the Johns Hopkins University as a thesis for the Degree of Doctor of Philosophy. During the years 1891–92 and 1892–93 I held the Adam T. Bruce Fellowship in the Johns Hopkins University, and was thus enabled to make a second journey to Jamaica. Publication has been delayed in order that the results of this journey might be incorporated in the paper, and it is hoped that the greater accuracy and completeness thus obtained have added materially to its value.

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.

The spectacle presented by this collection of medusae was truly marvelous; and in order to show something of it to the rest of us, Dr. Field gathered a pailful of specimens and brought them to the laboratory. Upon examination they were all found to belong to a single new species of Cassiopea, — a genus of which only one species was known to occur outside of the Red Sea, Indian Ocean, and southwest Pacific;[1] and this pailful, taken up at random, contained both adults and young in various stages of growth.

Professor Brooks made drawings of some of these, and then I made a visit to the Salt Pond to obtain more of the young medusae, and at the same time I collected submerged bits of wood and stems of plants. My hopes were more than realized when, upon examining these objects in the laboratory, I found them thickly studded in places with scyphistomas in various stages of development. I was particularly delighted when I noticed in one of the largest larvae certain glistening spots in the bases of the tentacles and found, on putting them under the microscope, that they were unmistakably masses of calcareous bodies that would form part of the marginal sense organs of the adult. They excited my interest, especially as I had been studying the development of these structures in Discomedusae ('90), and had been unable hitherto to obtain the early stages.

After this discovery I began, with the advice of Professor Brooks, to make a careful study of this species, with the intention of carrying the investigation of its anatomy and development as far as the limited amount of time at my command would allow. Preliminary accounts of my results were published in 1892 (Bigelow, '92, *a*, *b* and *c*). In the spring of 1893 I had another opportunity to visit Port Henderson with a party from the Johns Hopkins University, and was able to make important additions to my earlier observations.

During the first visit to Jamaica I was unable to find Cassiopea outside of the one locality that I have described, and, although both the adults and 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 that the scyphistomas were multiplying freely by budding, in a manner to be described later on. During my second visit I found this species as abundant as ever in this locality, and I also found a number of adult specimens in several of the small shallow lagoons among the mangroves in the rear of Port Royal. But these were all females, and it was still impossible to obtain males or eggs that would develop.

[1] Although Fewkes ('82) identifies his *Cassiopea frondosa* Lamarck, of Key West and the Tortugas, with *Polyclonia frondosa* Ag., it is nevertheless a true Cassiopea, not a Polyclonia.

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 were a little pond ooze at the bottom of the aquarium and the water were 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. It was not until a few days before we left Jamaica in 1891 that I discovered the habit that the very young free-swimming larvae have of hiding beneath the bits of bark and the like to which the scyphistomas in the aquarium were attached, and therefore the greater part of my work on the early stages of development was done during the second expedition.

After a few words concerning technique I shall begin with a systematic description of the species, followed by an account of the anatomy of the adult, and the remaining part of the paper will contain what I have learned of the development from the observation of the living animals while in Jamaica, and by the study of sections of preserved material, carried on chiefly at the Biological Laboratory of the Johns Hopkins University, but in part also at the Marine Biological Laboratory of Woods Hole and at the Biological Laboratory of the U. S. Fish Commission in the same place.

I wish to express my thanks to Professor W. K. Brooks for the advice and encouragement that he gave me while I was doing this work as one of his students, and I am also indebted to Professor C. O. Whitman, to the Hon. George M. Bowers, and to Professor H. C. Bumpus for the many courtesies received while at Woods Hole.

Technique.

For the preservation of the very young larvae a one quarter saturated solution of picric acid, with 2% of sodium chloride added, gave good results. Erlicki's fluid with the same addition, and ½% osmic acid followed by Erlicki's fluid, did fairly well for scyphistomas, but the best specimens obtained were those killed in the following mixture:

10% solution copper sulphate	100 c. c.
saturated solution corrosive sublimate	10 c. c.

As soon as they were killed, the specimens were placed in 5% bichromate of potassium and left there until hardened, after which they were washed in 35% alcohol containing a trace of hydrochloric acid and preserved in 70% alcohol. Excellent preparations of the medusae were obtained by this same method, and Flemming's fluid also gave good results.

SYSTEMATIC PART.

Genus **Cassiopea** PÉRON and LESUEUR (*1809*).—This genus, as limited by Haeckel ('80), may be defined as follows: Discomedusae without tentacles and without a central mouth opening; provided, instead of the latter, with numerous oral funnels attached to the ventral, or axial, side of the *eight oral arms*, which are *pinnately or trichotomously branched*, have a *subcylindrical*, or *subconical*, *gelatinous support continuous to the tips of the principal branches*, are provided with *numerous club-shaped vesicles* among the oral funnels, and are without appendages on the dorsal, or abaxial, side; also with four interradial gonads in the aboral wall of the four separate subgenital cavities; *sixteen marginal sense organs* (*rhopalia*); and *thirty-two radial canals* connected by a network of anastomosing branches.

For the sake of clearness this definition is made to include the characters of the family Toreumidae Haeckel, to which this genus belongs, and the purely generic characters are italicized.

Cassiopea xamachana.[1]

Cassiopea xamachana BIGELOW, Zool. Anzeiger, no. 393, 1892, pp. 212–214.

(?) *C. frondosa* FEWKES, Bull. mus. comp. zool., vol. 9, no. 7, 1882, pp. 254–259.

Diagnosis.—A Cassiopea with a disc-like umbrella, concave on the aboral side; when regular, with eighty short and obtuse marginal lobes separated by deep grooves on the surface of the exumbrella (in each of the sixteen parameres three velar lobes between two ocular ones); white markings on the exumbrella, consisting of a circular band with a diameter somewhat greater than that of the concavity, within this sixteen oval or eliptical spots lying in the radii of the rhopalia, and on the outer side eighty marginal spots, one for each marginal lobe; oral arms rounded and slender, never angular, exceeding the radius of the umbrella by at least one half of its length, and bearing nine to fifteen primary branches which are, in turn, copiously branched, giving the whole appendage a spatulate outline; very numerous small oval vesicles attached at the axils of the small branches and thickly massed upon the oral disc of adult females, and many small and a few large, flattened, linear vesicles attached one at the axil of each of the larger branches

[1] This name, suggested by Professor Brooks, must stand as printed in the preliminary description of the species, according to the current rules of nomenclature, followed by the Boston Society of Natural History. But it should have been written *xamaycana*, from *Xamayca* (the *x* is pronounced like *ch* in the German *ach*), the Indian name for the island of Jamaica, as written by the early Spanish historians (see Herrera, Novi orbis pars duodecima, sive descriptio Indiæ occidentalis, 1624; also Encycl. Brit., 9th ed., article, Jamaica). The form *Xaymaca* given by Bridges, Annals of Jamaica, 1827, and followed by several subsequent authors, is probably a misprint.

and to the canals on the oral disc, the thirteen largest vesicles being one at the axil of the largest branch on each arm and one at each junction of the canals on the oral disc; oral funnels entirely wanting on the oral disc in adult females, but present in immature specimens.

Special description. — A detailed account of the anatomy of this species will be given in the anatomical portion of this paper. It is intended here to call attention merely to the features that distinguish our species from its nearest allies. *Cassiopea xamachana* resembles very closely two medusae that inhabit the Red Sea and Indian Ocean, *Cassiopea andromeda* Eschscholtz and *C. polypoides* Keller ('83), but it seems, nevertheless, to be distinct from either.

Upon comparison with the descriptions of *Cassiopea andromeda* given by Tilesius ('29), Haeckel ('79), and Vanhöffen ('88), and with the figures of Tilesius ('29) and Forskål (1776), *C. xamachana* appears to differ from this species in the following particulars: The exumbrella is not merely flat, but is concave; besides the ninety-six white spots on the exumbrella, there is a broad circular band of white more or less connected with all of the marginal spots (Fig. 35), the oral arms are more thickly branched and are longer, exceeding by one half to two fifths the radius of the umbrella, instead of being only one third longer; moreover the arms have none of the flattened appearance figured by Tilesius and mentioned by Haeckel.

C. xamachana differs from *C. polypoides* in having more slender oral arms, with five to seven pairs of branches instead of three, and with fewer very large vesicles, and these apparently not so large and always flattened. The color pattern in the two species is nearly the same, except that in *C. xamachana* the three white spots on the three velar lobes of each paramere are seldom widely separated from the circular band of white. The colors in the pattern, however, differ considerably in the two species. The ground color in *C. xamachana* is never light brown, but is always much darker, a greenish brown, usually with a distinct shade of blue on the subumbrella. The large oral vesicles are never sky-blue, rose-colored nor white, but are yellowish green, often with a bluish green stripe; and, while the margins of the oral funnels are deep brown, they are always fringed with the white digitella.

C. xamachana is easily distinguished from *C. ornata* Haeckel by the presence of large oral vesicles and by the more extensive branching of the arms; and it differs from *C. mertensii* Brandt ('38), *C. depressa* Haeckel ('80), and *C. picta* Vanhöffen ('88), in the number of marginal lobes on the umbrella. *C. ndrosia* Agassiz and Mayer ('99) differs also in number of marginal lobes and in coloring. Fewkes ('82) has described a medusa from Key West and the Tortugas under the name "*Cassiopea frondosa* Lamarck," which he regards as identical with *Polyclonia frondosa* Agassiz. From the description given by

Fewkes it is impossible to identify his species positively. But a comparison of his figures with living specimens of both sexes of *P. frondosa* shows at once that the two species are distinct; while a comparison with *C. xamachana* shows so close a resemblance that I am inclined to think that Fewkes has discovered one of the varieties of our species, described in the next section. Not only is *P. frondosa* perfectly distinct from *C. xamachana*, but I think we are justified in retaining the former, for the present at least, in a separate genus; and there can be little doubt that Lamarck's *Cassiopea frondosa* dwelling in the "Ocean of the Antilles" with its "*margine decem-lobata*" is none other than Agassiz's *Polyclonia frondosa*. Therefore, even if it should be proved that the form described by Fewkes is the same as the subject of the present memoir, the name that I have given to it will hold, nevertheless, as the designation of the species.

Variations. — If we compare the average dimensions of various organs, expressed in thousandths of the diameter, with the maxima and minima, as may be done by examining the third, fourth, and fifth columns in Table 1, p. 201, it becomes evident that there is a very considerable amount of variation in the relative size of parts of *C. xamachana*.

In the oral arms, not only does the relative size vary, but the number and the arrangement of the branches are both variable. Moreover this variability exists between the different individuals. In nineteen specimens examined the maximum number of branches found on one arm was sixteen, the minimum nine, and the greatest difference on any one individual was four.

The most striking variations in *C. xamachana*, however, are to be found in the structures at the margin of the umbrella. These are highly variable in this species, and have been found to be variable, although to a less extent, in other medusae. It is unfortunate, therefore, that in his beautiful systematic work on the medusae Haeckel should have found himself forced to distinguish the genera chiefly by differences in the marginal structures. He himself notes the variability in the number of parameres of *Polyclonia frondosa*. Agassiz and Mayer ('99) found in one specimen of *C. ndrosia* eighteen rhopalia, and in another twenty-two.

The number of rhopalia was counted in twenty-seven specimens of *C. xamachana*. Of these ten were found to have sixteen, the typical number for the genus, and twelve had more than sixteen, three having seventeen, and three more, eighteen. The largest number on one individual was twenty-three. There were five specimens with fewer than sixteen rhopalia, but only two had less than fifteen, and both of these showed correlated abnormalities in the mouth parts and subgenital cavities. One had fourteen rhopalia, four oral arms, and two subgenital cavities and gonads. The other had ten rhopalia, only five oral arms, with three oesophageal canals leading from the stomach to the canal system of the arms, and three normal subgenital cavities and one very small vestigial one (Fig. A.).

Redundancy of mouth parts is not nearly as common as of the marginal structures. Only two cases were observed. One specimen with an additional pair of oral arms in one interradius had seventeen rhopalia. The other had eleven arms, with five subgenital spaces and gonads, and this one had twenty-two rhopalia. On the other hand, five specimens were found with twenty or more rhopalia, and perfectly normal mouth parts.

It will be seen, then, that the number of rhopalia, which has been taken as the principal generic character in the group, is a highly variable one. The number of

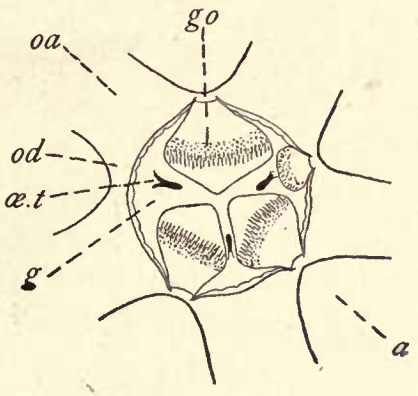


Fig. A. Section through the stomach of a specimen with only 10 rhopalia and 5 oral arms, to show the abnormal arrangement of gonadia and oesophageal canals. In the region marked *a* the margin of the umbrella presents a wide space in which there are no rhopalia. *go* = gonad. For explanation of the other lettering see Explanation of Plates.

marginal lobes in each paramere has been taken as one of the principal specific characters, and this is, likewise, highly variable. The variation consists principally in the interpolation of a small secondary lobe between two typical ones. Even in a regular and typical specimen, such as is shown in Fig. 35, the position that would be taken by these secondary lobes is indicated by small ridges on the dorsal surface. A specimen with a large number of rhopalia is as likely to have the marginal lobes in each paramere arranged typically as one having a smaller number. Conversely, a specimen with fifteen to seventeen parameres is as likely as not to vary from the typical form. The variation may consist in the addition of two secondary lobes in the paramere, the addition of four lobes, or in a quite irregular arrangement; and this modification may affect all of the parameres alike or only a portion of them.

Throughout all of these modifications of the margins there is manifested a constant regard, as it were, for the symmetry of the parts. It is very seldom that an additional rhopalium appears as if attached fortuitously in some irregular way. Almost always either it is in the midst of an entirely new paramere or else there is a distinct line of symmetry running between two adjacent rhopalia that evidently correspond to an originally single one. In other words, a paramere has been incompletely doubled, and the two parts are

bilaterally symmetrical to one another. We find all degrees of this doubling in the adult from a double-headed rhopalium [1] to two complete parameres, and the same process may be seen in the forked tentacles frequently found in the larvae (Figs. 14 and 21, *x*). With the exception of the forked tentacle and the double-headed rhopalium, these stages of duplication are well represented at *u*, *w*, *x*, *y* and *z* in Fig. 30.

The radially arranged stripes and spots on the exumbrella, which, with a circular band, form the color pattern described in the next section, vary in number with the rhopalia and marginal lobes. But when two rhopalia are close together there may be only one corresponding rhopalial stripe, and it will then occupy a position intermediate between the two. For example, in the specimen mentioned before as having only ten rhopalia, two of the rhopalia were very close together and there was but one rhopalial stripe corresponding to them. The other rhopalia were evenly spread, except that they were absent from one rather wide section of the circle. The rhopalial stripes, nine in all, were placed in a corresponding manner, and were absent from the corresponding area.

There is also a wide degree of variation in the extent of fusion between the circular band and the marginal spots. The spots on the velar lobes are usually not fused to the circular band in young specimens, and they frequently remain distinct in adults. It was found, however, that this is more usually true of specimens from the Salt Pond than of those from Port Royal. I thought that I could see, also, correlated differences in the sizes of certain of the mouth parts, and I was thus led to inquire if there were a division here of the species into two races. For this purpose Table 2, p. 201, was constructed. From this it will be seen that the specimens from the Salt Pond (var. *A*) have on the average longer oral arms and shorter vesicles than the ordinary specimens from Port Royal (var. *B*), while the stomach is of the same size in the two groups. Whether these slight differences are in any way connected with the probable difference in density of the water in the two localities, experiment alone can determine.

In the third column of this table dimensions are given of some specimens from Port Royal (var. *C*) that are so different from the rest that they might be regarded as of a distinct species.[2] Suspicion of their being merely sports is aroused, however, by the fact that only two specimens (female) were found living among a large number of the usual form.

The most striking peculiarity of these two specimens was the great number (forty to fifty) of uniformly large oral vesicles, two to four centimeters in length, scattered over

[1] Fewkes, ('82) has observed similar double-headed rhopalia, and it is on account of the variability of the marginal structures that he regards Polyclonia as merely an abnormal Cassiopea.

[2] It is possible that this variety may be the same as *Cassiopea frondosa* Lamarck of Fewkes, although his figures do not show any large vesicles on the proximal parts of the oral arms.

the whole extent of the mouth parts. Among them the central, radial, and primary vesicles were hardly distinguishable, although so easily recognized by their greater size in the typical form of the species.

Another peculiarity was a projection of the mesogloea on the oral side of each subgenital osteum, so that the interradial diameter of the oral disc was considerably longer than the radial diameter, as shown in the table. These specimens presented also some peculiarities of coloring, which will be noted in the next section.

Color.—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.

If we turn the aboral side (Fig. 35) of the medusa toward us we find often a brownish band encircling the disc at the periphery of the concavity and shading off gradually on both sides. Deeper within the mesogloea there is a much wider white circular band extending under the brownish one; and white bands, or spots, extend in a radial direction outward from this along the marginal ridges. There is one spot to each ridge, and it reaches nearly to the tip of the marginal lobe. The bands on the rhopalial lobes are interrupted, however, by a roughly circular, transparent area over each rhopalium; and in many specimens, especially young ones, the interrhopalial (velar) spots are not fused with the circle. On the inner side of the circular band of white there is a circle of large white spots, "rhopalial spots," or stripes, that lie deep in the substance of the exumbrella and are visible through the mesogloea, one in the radius of each rhopalium. The spot is elliptical in outline, and extends from the white band to a point about two fifths of the distance between the periphery of the concavity and the edge of the stomach. These spots, while usually continuous with the band, like the marginal spots, are not always so.

At the centre of the umbrella the stomach and subgenital cavities may be seen through the mesogloea as a reddish brown circular area with a diameter of about one fourth of the total diameter of the disc; while surrounding the stomach there is a deep blue halo with points that extend outward between the last-mentioned bands of white.

Now if the animal be allowed to return to its usual position, the subumbrellar surface will be found to be pretty evenly stippled by the greenish brown cells in the mesogloea. Apparently beneath this stippling there is a blue pigment 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 mesogloea 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 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 disc 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 occupy the greater part of the oral disc has a very different appearance, being lightly tinted by fine reddish brown pigment spots.

The two specimens that I have called variety *C*, are somewhat differently colored. The markings are yellowish white. The circular white band is indistinct. The rhopalial bands are interrupted at the margin of the concavity of the exumbrella, and stop short about half a centimeter from the rhopalial hood. At the margin of the umbrella there is a white spot on each rhopalial lobe and a strap-shaped spot on each velar lobe. The centre of the umbrella is whitish and opaque, so that the stomach does not show through. The oral arms are translucent, milky white tinged with brown, and without distinct white markings, except on the dorsal side of the principal branches. The large oral vesicles are yellow and greenish yellow, with a brown centre.

Size. — The diameter of the largest specimen found is 24 cm., while the smallest specimen that contained eggs measured 6.5 cm. The average diameter of twenty-three adult specimens was 13.7 cm. The relative sizes of the parts are exhibited in the following tables. Table 1 shows what may be regarded as the normal proportion for the species, though, to be sure, some of the measurements were made only on Port Royal specimens. Some of the dimensions were measured on a smaller number of specimens, and for these the average diameter of the umbrella of the specimens on which these measurements were made is given separately to show the correct proportions. Table 2 furnishes a means of comparing the proportions in the three varieties.

TABLE 1. DIMENSIONS OF SPECIMENS FROM BOTH SALT POND AND PORT ROYAL (VARIETIES *A* AND *B*.)

	Number of specimens measured	Average dimensions in centimeters	Average dimensions in thousandths of average diameter	Maximum (In thousandths of diameter unless otherwise noted)	Minimum	Remarks
Diameter of umbrella	21	14.33	1000	24 cm.	9 cm.	
Length of arms measured from centre of oral disc	21	11.21	782	888	642	Salt Pond and Port Royal specimens taken together.
Length of central vesicle	21	2.71	189	287	103	
Length of primary vesicle	21	1.82	126	190	71	
Diameter of umbrella	10	15.79	1000	24 cm.	12 cm.	Port Royal only.
Length of radial vesicle	10	3.01	190	250	117	
Diameter of umbrella	11	13.62	1000	16.3 cm.	6.3 cm.	Salt Pond and Port Royal.
Diameter of stomach	11	4.22	311	333	292	
Diameter of umbrella	3	18.66	1000	24 cm.	15 cm.	Port Royal.
Thickness of umbrella	3	1.33	71	73	70	
Total depth	3	3.59	191	212	173	
Diameter of umbrella	2	20.50	1000	24 cm.	17 cm.	Port Royal.
Diameter of oral disc	2	8.00	390	441	354	

TABLE 2. AVERAGE DIMENSIONS OF THE THREE VARIETIES, GIVEN IN THOUSANDTHS OF THE AVERAGE DIAMETER OF THE UMBRELLA.

	Variety *A*—Salt Pond	Variety *B*—Port Royal	Variety *C*—Port Royal
Length of arms	850	715	818
Length of central vesicle	157	217	—
Radial vesicle	—	190	163
Primary vesicle	112	138	167
Diameter of stomach	298	311	322
Thickness of umbrella	—	71	80
Total depth	—	191	213
Radial diameter of oral disc	—	390	394
Interradial diameter of oral disc	—	390	470

Locality. — Great Salt Pond, and mangrove swamps ("The Lakes") in the rear of Port Royal, Jamaica.— BIGELOW.

(?) Moat outside Fort Jefferson on Garden Key, Tortugas Islands, and Mangrove Keys, near Key West, Florida. — FEWKES.

Anatomy.

Form of the Body. — To one who is familiar with the cyaneas, aurelias, and the like, of our northern coast, the shape of this medusa appears very strange. The aboral, or exumbrellar surface (Fig. 35), instead of being convex in *Cassiopea xamachana*, as it is in the great majority of medusae, is concave when the animal is at rest, except for a slight convexity over the stomach, and except in the region of the thinner marginal part of the umbrella, where also it is convex. The surface of the subumbrella, on the other hand, is convex, except in this same thinner marginal area, where it is in turn concave. The umbrella thickens very gradually from its margin to the centre, and the elevations and depressions of its surface have very gentle slopes, so that its general shape is much nearer that of a flat disc than the dome-like form of most medusae (Fig. 35).

A circular column arises from the centre of the oral surface of the umbrella. It is broad, but very short; and a few millimeters from the umbrella it loses its circular outline, owing to eight stout arms that spring from it at regular intervals (Fig. 34). These are smooth and rounded, except along a line on the oral side, where they bear the fringe of oral appendages, and they are long and much branched. This column is the *oral disc*, and its arms the *oral arms*.

The Structure of the Mesogloea. — By far the greater part of the mass of the oral arms and disc, as well as the umbrella, is composed of a firm, elastic, gelatinous substance, the *mesogloea*, and it is to this that the shape of the body is due.

The description given by Keller ('**83**), of the structure of the mesogloea in *C. polypoides* would apply almost equally well to our species. The mesogloea consists of a hyaline matrix, in which are imbedded certain fibres and three kinds of cellular elements. Most of the fibres appear to be analogous to connective tissue fibres, and take a general course through the mesogloea at right angles to the surface. Others seem to be protoplasmic. At any rate, they may be observed to proceed from the star-shaped cells that are scattered throughout the jelly.

The cellular elements are : the star-shaped cells, just mentioned; vesicular bodies, found in certain restricted localities; and the green cells, which, as it will be shown later, are symbiotic plants.

The star-shaped cells remind one of osteoblasts, and are probably analogous to them, in that they are concerned in the formation of the jelly. Hamann ('**81**) has called them *colloblasts*. They are small, often somewhat elongated, and have a well-marked nucleus.

The vesicular bodies give rise to the white markings that were mentioned in the description of the species. These vesicles are much larger than the colloblasts. Each one seems to be made up of a wall of exceedingly minute refractile granules, surrounding a clear space. That this body is a cell, however, is shown by the presence of a nucleus pressed closely against one side.

The green cells, or *zoanthelae*, are widely distributed throughout the mesogloea, but are most abundant in the umbrella. They are not infrequently found imbedded in the endodermal epithelium. The living cells have a greenish brown color, which they impart to the animal as a whole. They are of considerable size, are globular, without projections of any kind, and are generally to be found in clusters of two or more (*za*, Figs. 52, 56, and 63). Each one contains a nucleus and numerous granular bodies, and apparently is surrounded by a cell wall; but the latter is hard to distinguish from the edge of the adjacent matrix.

Keller thought that similar bodies in *C. polypoides* could not be algae, because he failed to find any evidence of a cellulose cell wall. He regarded them, therefore, as essential elements of the "mesoderm."

In those of my specimens, however, which have been killed in Erlicki's fluid and stained with borax carmine, the nucleus of these cells is found to be red, while the granular contents of the cell are bright green, and there are often one or two green bodies present that are as large or larger than the nucleus. They have all the appearance of chlorophyl bodies, and it is well known that the chlorophyl of some algae is not readily removed by alcohol. Moreover, in teased preparations treated with iodine solution these cells are found to be filled with granules that quickly turn deep blue, — evidently starch. The test for cellulose with iodine followed by sulphuric acid, gave, however, unsatisfactory results. The outline of the cell would become distinctly darker, but not recognizably blue. In the same way with chloriodide of zinc, a very marked reaction for starch was obtained, the granules becoming almost black; but so long as the object was viewed by direct transmitted light, no reaction for cellulose could be detected with certainty. On the other hand, when the light was thrown upon the object obliquely by means of a condenser with a central diaphragm, the effect was quite different. The starch granules became a deep ultramarine, and the parts of the cell not occupied by the starch appeared distinctly violet, showing without doubt the presence of cellulose.

Both starch and cellulose, as well as some form of chlorophyl, having been demonstrated in them, there can be no further question that the green cells in Cassiopea are symbiotic algae.

The Oral Arms and their Branches. — The eight oral arms (Fig. 34) arise from the central oral disc at about equal intervals; and when an arm is extended, the distance

from the centre of the oral disc to the tip of the arm about equals three quarters of 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 mesogloea tapering very gradually to the tips of the finest branches. The branches are arranged alternately. The largest one, which is the first formed, is at a point about two thirds the length of the arm from its base. From this point the branches decrease in size gradually toward the base of the arm, and more rapidly toward the 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. 34) 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, the *digitella*. These are covered by an epithelium containing nettle cells, and each has a gelatinous axis 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 (**'81**). The epithelium lining the tubes and funnels is ciliated.

There open also into the brachial canals the lumina of the oral vesicles (*v.*, Fig. 34). 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 Disc. — Although the eight oral arms seem to be placed at equal distances and to be alike, they are morphologically in pairs, each pair being homologous to one of the four lips of a semostomous medusa, — 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 disc, converge and unite into a single radial tube that is continued to the centre of the disc, where it unites with the other three. In this way the course of the tubes on the oral disc forms a pattern that resembles a Maltese cross. The larger *central vesicle* is attached at the centre of the cross. 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 radial canals near the junction of the brachial canals, and I have called them, therefore, the *radial vesicles*. In full-grown individuals there are eight more vesicles upon the oral disc, a little smaller than the last, one on each brachial canal distal to the junction. It is only near the periphery of the

disc that the canals are provided with oral funnels. For most of their course on the disc the canals give rise to the very small vesicles, finely speckled with a reddish brown pigment, that already have been mentioned. These have nettle batteries at their tips, and are so numerous as to cover completely the greater part of the disc and to hide the course of the canals. This mass of small vesicles, however, is not acquired 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. This replacement of the oscula on the oral disc by small vesicles has been observed to occur also on adult females of *Polyclonia frondosa*, but not in the males (Bigelow, '93). It is not improbable therefore that a similar difference between the sexes may be discovered in our species of Cassiopea.

The Subgenital Cavities and the Digestive Tract. — At each of the four points of junction of the brachial canals there is a slit-like passage, oesophageal canal, dipping vertically into the mesogloea of the disc, and opening into the stomach. The latter is a lens-shaped cavity, with a gently arched roof. Its floor consists chiefly of four lozenge-shaped areas, where the body wall is very thin and plaited in radial folds (Fig. 34). These thin parts of the body wall form the roofs of the subgenital cavities, which open to the exterior, each by an elliptical orifice, *osteum*, (*x*, Fig. 34) in the side of the oral disc near the subumbrella and in the angle between two pairs of arms (interradial). The gonad appears as a band which crosses this membrane tangentially at its greatest width. Just central to each gonad there is a multiple series of very many small gastric filaments forming a narrow band parallel to the ovary. These are ciliated, and provided with nettle and gland cells. The portion of the floor of the stomach not made up of these lozenge-shaped membranes is bounded by the firm mesogloea of the oral disc. 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.

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 canals in the radii of the rhopalia are larger and more nearly straight than the interrhopalial ones, and all are connected by a fine network of anastomosing branches, among which no distinct circular canal can be recognized. The meshes in the network of canals are connected by a plate of endodermal cells, the *endodermal lamella*. This lamella is also in contact with the subumbrellar ectoderm along a line encircling the umbrella a short distance from its mar-

gin, so that there is a complete sheet of endoderm separating the subumbrellar from the exumbrellar mesogloea.

Musculature. — The exumbrella is devoid of muscles, but on the opposite side there is a continuous sheet of muscle fibres, which is spread over the subumbrella, except a narrow zone at its margin, and is continued over the oral arms to their finest ramifications, and also into the subgenital cavities.

Most of the fibres on the subumbrella do not take an evenly circular course, but are undulating. They form in this way a series of double "arcades" like those found by Haeckel in other species of Cassiopea. There is one of these double arcades for each interrhopalial space. The surface of the mesogloea in this region is grooved. The sheet of muscle fibres lies directly upon it, and is therefore corrugated, the grooves being parallel with the fibres.

The muscular layer upon the oral arms is smooth, and its fibres take a longitudinal course, extending to the digitella and oral vesicles.

In the subgenital cavities the arrangement of the muscle fibres could not be made out; but their presence was revealed by the squirming movements of the thin membrane that separates the subgenital cavity and bears the gonads and gastric filaments.

Structure of the Marginal Sense Organs. — Each rhopalium has 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 those found in Pelagia. The rhopalium is the only organ in the sensory niche (Fig. 56). 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 the lumen of the rhopalium opens into the distal end of this canal. In the distal half of the rhopalium the lumen is nearly obliterated by the increase in thickness of its endodermal lining. Here the endoderm, instead of being a columnar epithelium as elsewhere, is a mass of parenchyma-like cells, each of which contains a large calcareous concretion, a so-called otolith. A thin, supporting membrane separates the endoderm 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 are found in Dactylometra (Bigelow, '90), and the 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, lying on the aboral side of the rhopalium immediately above the centre of the mass of concretions. This area is probably sensitive to light, but it 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 ('89) has found in Aurelia.

Habits.

The species of Cassiopea and the closely related genus Polyclonia find their habitat usually in quiet lagoons among the mangroves along the shores of the tropical seas. The mode of life of several species has been described by Brandt ('38) on the authority of Mertens, L. Agassiz ('62), Gray ('69), A. Agassiz ('81), Archer ('81), Fewkes ('82), Guppy ('82), and Agassiz and Mayer ('99). *Cassiopea xamachana* is no exception to the rule either in its habitat or its sedentary mode of life.

When the young medusa is set free from the strobila it is an active swimmer. It gradually becomes less active as the mouth parts acquire their adult structure, and by the time the animal has reached a diameter of two centimeters it has definitely taken up its abode upon the bottom. It lies there, as described in the Introduction, with the oral appendages upward, and seldom changes its position unless disturbed. The concavity of the exumbrella is an important aid in maintaining this posture against the action of waves and currents. The gelatinous tissue is firm and elastic, and causes the umbrella to assume its normal shape when the subumbrellar muscles are relaxed. The slight suction thus produced when the medusa comes to rest on a flat surface gives it such a hold that a certain amount of force is required to remove it.

Usually, however, the water in the lagoons is very quiet, and there is more danger from its stagnation than from its motion. A Cassiopea is enabled to avert this danger by the slight swimming movements of the thinner marginal part of the umbrella. By means of these rhythmic contractions the water is drawn in on all sides, and then is driven upward and away. A healthy specimen lying undisturbed on the bottom of an aquarium was observed during seven minutes to make on the average 19.7 contractions of the umbrella per minute. In this way the animal is enabled to draw to itself a fresh supply of oxygen and of its minute food material.

The oral arms and their branches are usually spread out so as to cover the subumbrella completely, but they are almost always in motion, bending to one side or the other, and they may be flexed aborally until the tips come within the umbrellar margin, or extended until they reach far beyond. Besides these general movements, the various appendages of the oral arms have movements of their own. Muscular contractions may be observed also in the thin membrane that separates the stomach from the subgenital cavities, and they probably serve to renew the water that bathes the gonads.

When the oral disc has been severed from the umbrella, both parts may remain alive for several days, and both retain their powers of spontaneous movement. The first effect of the operation is often to throw all of the parts into a strong tetanus, but shortly afterwards the pulsations of the umbrella may be renewed at a rate considerably more rapid than normal, — 32 to 34 per minute in one case. When the medusae have been for some time under unfavorable conditions, it frequently happens that the part of the body-wall surrounding the periphery of the stomach is ruptured, and thus the mouth parts as a whole become separated automatically from the umbrella.[1]

While at Bimini, Bahamas, in 1892, I observed that the food of *Polyclonia frondosa* consists chiefly of copepods and other small crustacea, and that these are caught by the combined action of the oral vesicles and the oscula ('93, p. 106). If a copepod strikes a vesicle, the vesicle bends quickly so as to cover the mouth of the adjoining osculum, and the copepod is thus enclosed in a trap. Artificial stimulation would cause the same reaction.

Experiments on *Cassiopea xamachana* made to determine whether or not this species obtains its food in the same way gave negative results. Stimulation of an oral vesicle causes only a slight bending on the side stimulated. Although these vesicles are provided with batteries of nettle cells near the tip, I was unable to see that they played any part in the taking of food. It may be that they are protective, but the sting is very feeble.

Examinations of the contents of the stomach were almost equally unsatisfactory. The contents of twenty-two stomachs were examined, and of these fourteen contained only a clear, very viscous fluid and, in some cases, a few apparently ripe eggs, more or less distorted, some small, colorless cells, probably sloughed off from the endodermal epithelium, and green cells identical with the "zoanthelae" found in the mesogloea. One or more copepods and other crustacea were found in five specimens. In one of these one small amphipod was found, and in another the cornea of an unknown crustacean.

[1] While this paper is passing through the press a paper has appeared by E. W. Berger (1900), in which he gives the results of experiments made by F. S. Conant upon Polyclonia and Cassiopea to test the effect of removing the rhopalia.

Diatoms and other algae, exclusive of the above-mentioned zoanthelae, were found in four cases out of the twenty-two. Almost always the first impression on opening a stomach was that it was empty; and it was only by careful examination that the contents of the stomach could be discovered. In two cases, however, a considerable amount of material was found in the stomach. In one of these the stomach contained, besides the usual eggs, zoanthelae, debris, etc., the remains of many copepods, some nematods, a zoea, and some diatoms. In the other one there was found a compact greenish mass, about one centimeter in diameter, composed of granular debris and diatoms of various species, together with some desmids, Oscillaria, foraminifera, infusoria, Vorticella, and some fine filaments with spirally arranged contents.

This species exhibits the power of regeneration of lost parts to a marked extent. Specimens were frequently met with in which branches of the oral arms, or even portions of the margin of the umbrella, had evidently been formed recently to replace parts that had been destroyed. Moreover, branches of the oral arms that had been cut off were observed to regenerate oscula and vesicles at the central end.

Ontogeny.

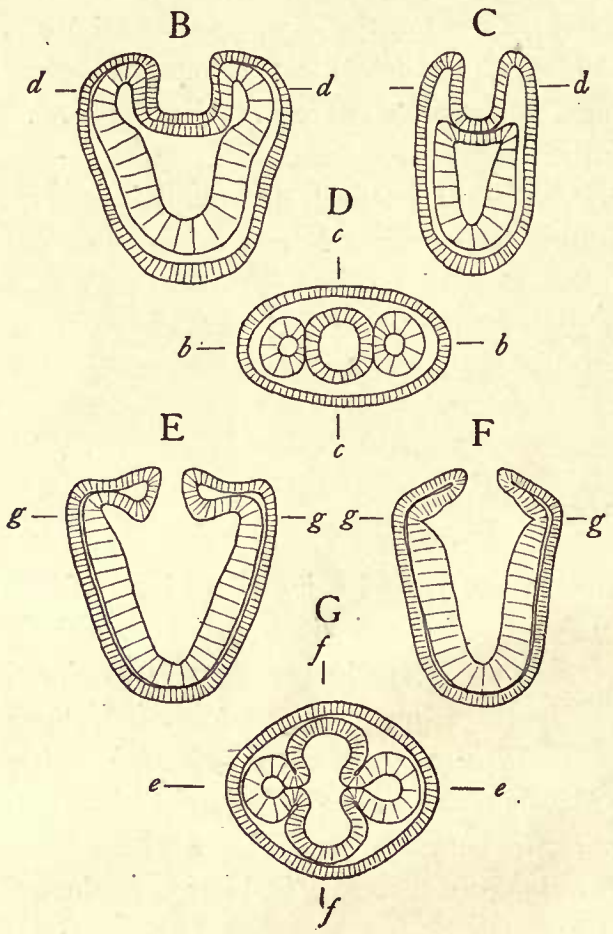
Historical Review. — Numerous studies upon the reproduction of various animals by budding have shown that the formation of organs in the bud may take an entirely different course from the development of homologous organs in the sexually produced embryo. As the observations to be described in the sequel were made entirely upon larvae that were observed, or supposed, to be asexually produced, they cannot settle any of the disputed points in regard to the development of sexually produced larvae. Nevertheless it will be of interest to compare the sexual with the asexual mode of ontogeny, especially as the development of a scyphistoma from a bud has never before been fully described.

The development of scyphomedusae from the egg has been studied in comparatively few forms. Several species of Aurelia have been studied by Sars, Haeckel, Schneider, Claus, Goette, Frank Smith, and Hyde. Two species of Cyanea have been studied by McMurrich and Hyde. A species of Chrysaora has been studied by Claus; and Kowalewsky, Metschnikoff, Krohn, and Goette have traced the very interesting abbreviated development of *Pelagia noctiluca.* The nearest ally of our species that has been studied with any degree of completeness is the Mediterranean rhyzostome *Cotylorhiza tuberculata,* which has been the subject of investigation by Claus and Goette.

From the description of the process of budding given in the next section, it will be

noted that the larvae produced by budding are set free in a form resembling planulae, and it is the planula stage in sexual reproduction which is the earliest that can be compared with any stage to be described in this paper.

All agree that the planula of the Scyphomedusae is a more or less oval, ciliated larva, somewhat flattened on one side. It consists of two layers of cells surrounding a cavity which is completely shut off from the exterior. The first step toward the development of the scyphistoma is an invagination of the ectoderm at the posterior pole of the planula. According to Goette and Miss Hyde, the endoderm is invaginated at the same time in such a way that two endodermal pouches remain in the plane of the long diameter,—"Hauptebene," Goette,— (Fig. B, and *b–b* Fig. D), one on each side of the invagination, while the endoderm is pushed entirely away from the oral pole in the plane of the short diameter (Fig. C, and *c–c* Fig. D). The ectodermal invagination is the oesophagus (Schlund), its external opening is the mouth, and the endodermal evaginations are the first pair of gastric pouches. Soon an opening is formed (Schlundpforte) between the base of the oesophagus and the central stomach, and at the edge of the opening the ectoderm fuses with the endoderm. Then the second pair of gastric pouches is formed. According to Goette these are produced in Cotylorhiza and Pelagia entirely from the ectoderm of the lower part of the oesophagus (Fig. F). According to his view the lower edges of these evaginations coincide with the margin of the gastro-oesophageal opening (Schlundpforte), and are therefore at the level of the upper edges of the first pair of pouches. As these pouches extend out-



Figs. B–G. Two stages in the development of the mouth and gastric pouches in a sexually produced scyphistoma, according to Goette. Figs. B to D are sections in the three dimensions of space of a larva in which the oesophagus is invaginated and the first pair of gastric pouches are formed. Figs. E to G are similar sections of a larva in which the opening from the oesophagus into the stomach (Schlundpforte) has been established and the second pair of gastric pouches are in the process of formation. *b*, *c*, *d*, etc., indicate the plane of Figs. B, C, D, etc.

ward the ectoderm is pushed out until the principal radii) *e–e* and *f–f*, Fig. G) gradually become equal. This results in the formation of the flattened peristomal disc (Figs. E and F). At the same time the wall separating the oesophagus from the first pair of gastric pouches (Taschenvorhang) is split upward until the openings into the two pairs of pouches are upon the same level, and the " Taschenvorhang " is reduced to a low ridge, while the oesophagus is very much shortened. Portions of the original lining of the lower part of the oesophagus persist as the covering of the inner edges of the septa which separate the four gastric pouches. The larva is now in what Goette calls the scyphula stage. He regards this stage as of great phylogenetic importance, showing clearly, he thinks, a close genetic connection between the Scyphomedusae and the Anthozoa; so that these groups should be placed in a single class, Scyphozoa, to distinguish them, on the one hand, from the Hydrozoa, including the hydroids, hydromedusae, and, on the other, from the Siphonophorae.

This view, which is confirmed by Miss Hyde, is antagonized by Claus, and has given rise to a prolonged controversy. The parties to this dispute are practically in accord in regard to the facts of observation, as represented by the figures in their latest contributions. It is in the interpretation of these facts that they differ mainly. Claus ('90) admits that there is an ectodermal invagination previous to the formation of the mouth, and that the lining of the proboscis is ectodermal. He maintains, however, that the condition represented in Figs. B, C, and D, is due to a severe contraction of the animal, and is without morphological significance. He denies that there is any oesophagus, " Taschenvorhang," or " Schlundpforte," in the sense that Goette uses these terms; and with these he rejects the idea of a close affinity between the Anthozoa and scyphomedusae, with the correspondingly sharp distinction between the latter and the hydromedusae. He admits, however, that a distinction of importance between scyphistoma and hydropolyp is to be found in the possession by the former of an ectodermal lining of the proboscis, and in the presence of gastric pouches and septa.

Goette's position has been strengthened considerably by his latest contribution on this subject ('93), and his conclusions are confirmed in nearly every particular by Miss Hyde. Goette's figures appear to be camera drawings of serial sections, and are a great improvement over the rather diagrammatic illustrations in his earlier papers. They are not entirely convincing, however, for the ectoderm and the endoderm grade into each other so that it is impossible to determine the exact boundary; and the material is so subject to distortion during the preservation that it is often difficult to determine whether a given fold of the epithelium is of morphological value or is merely an artifact.

Miss Hyde fails to confirm the view that the whole of the second pair of gastric

pouches (and hence, according to Goette, five eighths of the peripheral digestive tract of the medusa) is of ectodermal origin. On page 550 of her paper she speaks of only the roof, i. e., the lining of the oral side, of these pouches as formed from oesophageal ectoderm, and her sections bear out this view.

The foregoing brief summary of the present state of knowledge regarding the early stages in the development of the sexually produced scyphistoma will serve as an introduction to what is to follow. Mention of the work of others upon the later stages will be made when we come to the corresponding periods in the development of *Cassiopea xamachana.*

The Formation of the Bud. — In 1841 Sars described the budding of scyphistomas that were supposed to belong to a species of either Aurelia or Cyanea. The buds, according to this account, may grow out directly 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 be formed, apparently in various positions on the scyphistoma at one time. The figures show the buds attached to the parent and provided with a well-developed crown of tentacles at the distal end. Agassiz ('60) found a similar process of budding to occur occasionally in Aurelia. Goette ('87) has confirmed these observations, and has found that the larvae of *Cotylorhiza tuberculata* also produce buds.

In Cotylorhiza the bud is formed as an outgrowth from the body of the scyphistoma; and as it grows it gradually approaches the shape of its parent, but its relative position is just the reverse of what Sars found; for the distal end forms the stem, and the proximal end begins to flatten out into a circumoral disc. In this condition the bud is set free, and swims about, rotating on its long axis, with its distal end forward. The mouth is formed at the point where the constriction finally separates the bud from its parent, and the larva fixes itself by the opposite end.

Claus ('92) has found that the scyphistomas of Cotylorhiza not only produce buds, but that they produce them in large numbers. Scyphistomas reared from eggs that had been laid in September, 1890, were kept alive in the aquaria at Trieste and Vienna throughout the following winter and spring. No change was observed after the larvae had reached the sixteen-tentacle stage, until the following July, when budding occurred. The process was not restricted to a few well-nourished individuals, but seemed to be a general and repeated phenomenon, and it resulted in a large increase in the number of larvae. Claus's brief description of the formation and fate of the bud, accompanied by three figures, corresponds perfectly with what I have to describe in the following pages. The strobilization, he says, took place in August, and was monodiscous.

Another case of rapid multiplication of scyphistomas by budding is described by Lacaze-Duthiers ('93). A colony of these larvae, of unknown origin, was discovered in

an aquarium at Banyuls in 1892. No strobila or ephyra was observed up to October, 1893, but in the meantime the number of scyphistomas had increased enormously. The buds appeared as elevations on the side of large individuals. The base of this elevation became elongated into a filamentous stolon carrying the bud at its tip. The bud fixed itself to the glass, gradually developed tentacles, and finally became independent by the disappearance of the stolon.

In *Cassiopea xamachana* the process of budding is an important, if not the chief, factor in the perpetuation of the species. On looking over collections of scyphistomas taken from the Great Salt Pond during May, June, and July, a considerable number was found with buds attached in various stages of development (Figs. 1, 2, and 26), and budding continued in the aquaria.

There is no stolon. The first visible rudiment of the bud is 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. 36). 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 mesogloea and apparently growing out from a thickened area of the ectoderm at the apex of the bud (*sm*, Figs. 38 and 39). This appearance seems to indicate that the septal muscles of the bud are formed, as in sexually produced scyphistomas, by an ingrowth of the ectoderm.

Careful study of serial sections through young buds shows, however, that the septal muscles of the bud are connected with septal muscles of the parent. In Fig. 37 the course of the septal muscles is reconstructed from a series of longitudinal sections. The muscle sm_1 passes around the base of the bud on the side away from the observer and gives rise to two branches, sm'_1 and sm'_3. These extend toward the apex of the bud, and each one divides dichotymously. Muscle sm_4 gives off a branch which fuses with sm_1, at the base of the bud. Sm_2 produces three branches which unite into a single branch. This branch extends into the base of the bud, but it was impossible to trace it further. It may be connected, perhaps, with the muscle sm'_2, which was traced for a short distance from the apex of the bud.

On account of the presence of the muscles, it is possible to study the relation of the plan of symmetry of even young buds with the symmetry of the parent. A series of sections made at right angles to the long axis of the bud shows that the vertical perradii of the bud lie in the plane of one of the perradii of the parent. But in transverse sections it is impossible to trace the muscles of the bud, except for short distances, owing to their extreme fineness.[1]

However, the study of longitudinal sections makes it reasonably certain that the sep-

[1] The position of the bud is always perradial, although in some preparations it appears to be interradial, owing to the obliquity of the sections, as in Fig. 36.

tal muscles of the bud are derived from outgrowths of one or both of the septal muscles of the parent which lie in the interradii adjoining the perradial area of bud formation. If this be true, then every part of the young bud is formed from the corresponding part of the parent, viz., — ectoderm from ectoderm, mesogloea from mesogloea, endoderm from endoderm, muscles from muscles, and digestive tract from digestive tract. There is no indication of any method of budding of the kind described by Lang ('92).

In the young bud the mesogloea is very thin, so that the ectoderm and endoderm are very nearly in contact. The evagination gradually increases in size, becoming first hemispherical and then more elongated. At the same time a constriction appears close to the body of the scyphistoma, which deepens until the bud becomes a spindle-shaped body attached to its parent by a short and narrow stem consisting of a film of mesogloea covered with ectoderm, the digestive cavity of the bud being entirely closed (Fig. 1).

Scyphistomas are never found with more than two buds attached. When two buds are present they are always of different ages, and the elder is always attached to the apex of the younger (Fig. 2).

The Planula-like Larva. — When finally constricted off, the bud is a simple, spindle-shaped, hollow body, without trace of mouth or tentacles. It is like a planula in form and habits. The whole surface is covered with cilia, and it swims about, rotating from right to left upon its long axis. In swimming, the distal end is directed forward. While swimming, the larva is constantly changing its shape, assuming in a few minutes various forms from an elongated spindle to a short heart-shape (Fig. 3, *A*, *B* and *C*). It swims near the bottom, hiding under any object that it may find there. When it strikes an obstacle, it may rest there quietly, or it may rotate slowly upon its long axis. In all its movements it reminds one very strongly of Agassiz's description of the planulae of Aurelia.

The larva is white, speckled with a few greenish brown spots. It is rather opaque, but much of the structure may be seen in a living specimen. A longitudinal section shows that the ectoderm consists of a deep layer of very narrow and closely-packed columnar cells (Fig. 39). The mesogloea contains a few green cells (producing the greenish brown spots), and some widely scattered colloblasts. The layer is thickest at the equator, diminishing gradually to a very thin layer at both ends. The four septal muscles (*sm*) are seen clearly at the distal end of the larva, embedded in the mesogloea and united with the ectoderm near the apex (Fig. 38). In one specimen, not yet detached from the parent, it was possible to trace one of the muscles all the way from the proximal to the distal end. The muscle fibres are already differentiated and line the tube of mesogloea, while the nuclei occupy a central position.

The endoderm is a columnar epithelium, rather thin, with the cells closely packed

together and coarsely granular at the proximal or posterior end of the larva. Toward the equator the cells become higher; and at the distal, or anterior, end they are large and clear. The character of the endoderm makes it possible to identify the anterior end of the swimming larva with the distal end of the bud.

The Formation of the Mouth. — The first change to be seen in the swimming larva is the formation of the mouth, which occurs two or three days after the larva has been set free. When writing my preliminary paper ('92 a), I was in doubt as to the relation between the poles of the bud and those of the larva. The better and more abundant material obtained during the second visit to Jamaica proved conclusively that the proximal end of the bud forms the oral end of the larva, just as it does in Cotylorhiza, according to Goette. The identification is made easy by the polar differentiation of the endoderm described in the previous section.

When first seen the mouth looks like a minute pin-hole in the posterior end of the larva (*m*, Fig. 4 *B*). In longitudinal sections at this stage the first indication of the formation of the mouth is the disappearance of the mesogloea from a small area at the posterior end, so that there is no longer a distinct boundary there between the ectoderm and endoderm (*m*, Fig. 40). At the same time a small dent appears in the outer surface. This deepens until it forms a minute tube connecting the endodermal cavity with the exterior (Fig. 41). The mouth thus formed gradually widens and becomes slightly funnel-shaped.

Further stages in the development of the mouth are represented in Figs. 5, 6, 7. In In Fig. 6 there is a distinct circular groove which outlines the base of the proboscis and separates it from a rudimentary peristome. In Fig. 7 the peristome is well developed, and the mouth is widely open.

There is no invagination of the ectoderm connected with the formation of the mouth, and there is no oesophagus, "Schlundpforte" or "Taschenvorhang." So, if Goette's account of the formation of the mouth in the sexually produced scyphistomas be accepted, we have here a case where an agamogenetic differs to a marked degree from the gamogenetic course of development.

The Scyphistoma. — With the elongation of the forward end, the formation of tentacles, and the development of four gastric pouches, the free-swimming larva becomes a typical scyphistoma.

By the end of the third or fourth day after the bud has been set free, the forward end of the larva has elongated to form a stem equal in length to the rest of the body (Figs. 7, 8, 9, and 11). The end of the stem becomes expanded, generally flattened, and the epithelium covering it becomes deeper than the rest (Fig. 42). This epithelium produces a secretion which serves to fasten the larva to some solid object. Fixation usually takes place during the fourth or fifth day, but the time varies greatly.

Development of the Tentacles. — During the third day the peristome appears as a minute ridge surrounding the posterior end of the larva, a short distance from the mouth. The first series of tentacles arises during the following twenty-four hours as four perradial angles in the margin of the peristome (Fig. 8). Four interradial tentacles appear almost simultaneously with these, or sometimes considerably later (Figs. 9, 10, 11, and 12). The elongation of the tentacles takes place rapidly, so that at about the end of the sixth day the peristome is surmounted by a crown of eight tentacles, which equal the proboscis in length.

With the broadening of the peristome the differentiation of the body of the scyphistoma into stem and calyx becomes apparent externally (Figs. 13 and 14). When the eight perradial and interradial tentacles have become long enough to reach some distance beyond the mouth, eight adradial tentacles appear in the angles between them. In Fig. 14 the adradial tentacles are distinctly developed, and two of the tentacles of the first series are bifurcated near the base. Figs. 15 and 16 represent the typical scyphistoma in the sixteen-tentacle stage. The tentacles are now long and graceful, and thickly dotted with batteries of nettle cells.

When fully developed, the scyphistoma is about one millimeter and a half in diameter; and it is provided typically with thirty-two tentacles.[1] But there is as much variation in the number of tentacles in the scyphistoma as there is in the number of sense organs and parameres in the adult. The number of tentacles is seldom less than thirty-two, often greater. The way in which this variation takes place is indicated in Figs. 21 and 14. All degrees of anomaly may be observed, from a bifurcated tentacle shown at x in Fig. 21, through the condition represented in Fig. 14, to two completely separated tentacles occupying the position of one typical one.

The tentacles of a well-developed scyphistoma, when fully expanded, exceed the length of the body several times. According to the position in which they are held, the tentacles may be divided into two series. Those of one series are held nearly erect, while those of the other series, consisting of the alternate tentacles, are bent backward until their tips nearly touch the ground upon which the animal rests. The action of the tentacles in capturing prey may be observed in a small aquarium, under the microscope. As soon as a tentacle comes into contact with a small floating body, such as a copepod, it is whipped quickly into the mouth, and at the same instant the side of the mouth toward the tentacle is opened more widely. On one occasion I saw two tentacles make captures at the same time, and the mouth expanded in both directions at once, showing a close co-ordination between the movements of the tentacles and of the mouth.

[1] Specimens have been found with twenty-four tentacles, but it is uncertain whether this is a regular stage in development between the sixteen- and thirty-two-tentacle stage, or a duplication of tentacles of the earlier stage.

Development of the Gastric Pouches. — While the final result is the same, the method of development of the gastric pouches differs entirely in our larva from the process as described by Goette. The free-swimming larva is somewhat flattened laterally (Fig. 4), and the long and short diameters are in the planes of the perradii. But there is no evidence that the gastric pouches in the long diameter are formed any earlier than those in the short diameter, and the ectoderm plays no part in their development. The formation of the gastric pouches is usually described as a process of evagination; but in this case, at least in the earliest stages, the delineation of the pouches seems to be due rather to the ingrowth of the septa.

These appear at the time of the formation of the first tentacles (Fig. 8) as four minute vertical folds of the endoderm (*sep*, Fig. 43), placed equidistantly in the angle formed by the peristomal fold (compare Fig. 42). The mesogloeal portion of the septum is at first very thin, and in the four-tentacle stage (Figs. 8 and 43) is no higher than the thickness of the endodermal layer of cells. The septal muscles do not penetrate the septa at this stage. While well-developed below, they can be traced upward only to within 35 or 41 μ[1] from the base of the septa.

In the eight-tentacle stage (Fig. 13) the septum is still very small, and the septal mesogloea near the margin of the peristome is very thin, hardly thicker than a cell wall. But at the central margin it has increased in thickness, and now the septal muscle may be traced from the stem upward through this thickened portion of the septal mesogloea to the peristomal ectoderm (*sm*, Figs. 44 and 47). It is impossible to determine whether the new portion of the septal muscles is formed by growth upward of the muscles already present in the stem, or whether it is the result of a proliferation of the peristomal ectoderm which may grow downward and fuse with the older portion of the septal muscles.

The four septa are now complete, and divide the digestive cavity into a large central stomach, extending into the stem, and four shallow marginal gastric pouches. The gastric pouches expand with the growth of the peristomal disc, so that the ectoderm and endoderm remain in close contact at the margin; while the central edges of the septa retain their original relative position. Thus the gastric pouches and the septa become deeper as the larva increases in size. This is evident in the sixteen-tentacle stage (Figs. 15 and 45 to 49). It will be shown later that the relation of the interradial tentacles to the septa is variable. In this stage, however, the distal part of the septal mesogloea has begun to disappear, so that immediately under the interradial tentacles the endoderm of adjacent pouches is fused (Figs. 45, 46, and 47). In the fully developed scyphistoma this area of fusion is perforated, so that there is a communication between adjacent pouches, forming the "Ringsinus" of German authors. In the specimen with

[1] 35 or 41 μ = about one seventh of the length of the larva.

forty-two tentacles, from which the section represented in Fig. 51 was taken, this perforation was very small. Figs. 52 and 53 represent a little later stage, in which the opening has become much wider.

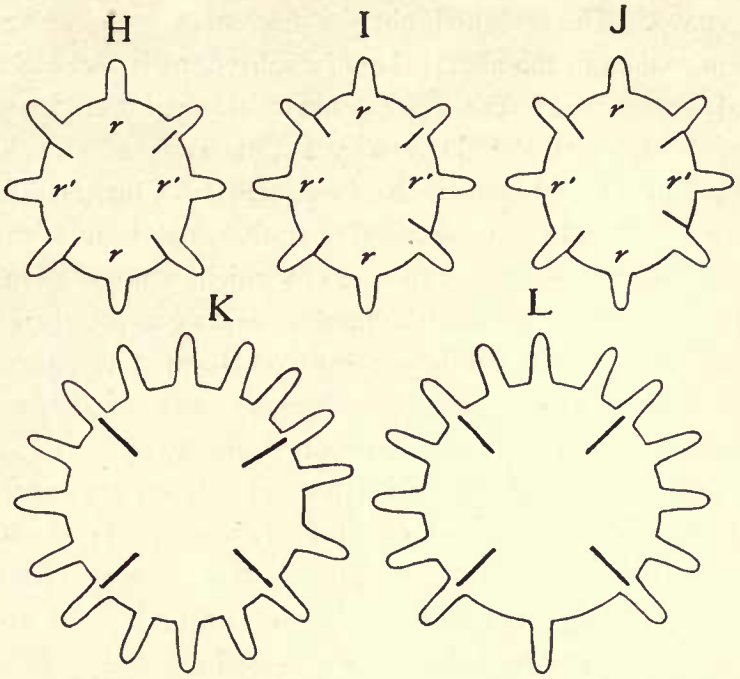
Each septal muscle is a solid cord of cells, with a single layer of longitudinal muscle fibres in its periphery. In the peristome the fibres of the septal muscles spread out in a fan-shaped arrangement toward the margin.

Four slight interradial depressions in the peristome may be observed as early as the four-tentacle stage. They are deeper in the eight- and sixteen-tentacle stages, and the septal muscles may be seen to join the ectoderm at their bottoms. These depressions may be homologous with the septal funnels of the Stauromedusae, or they may be merely the result of the contracted condition of the larva. The question is of no importance, for there can be no doubt about the homology of the muscles; and whether they are solid or hollow is merely a matter of detail. In later stages (Figs. 51 and 52) sections seem to show that the peristomal depressions have deepened centrally so as to leave the insertion of the septal muscles high up on the peripheral side. But here, again, before any morphological conclusions can be drawn, account must be taken of the growth of the perradial angles of the proboscis and of the effect of the contraction of the septal and peristomal muscles.

Relation of Septa to Interradial Tentacles. — According to Goette, the interradial tentacles are always interseptal in origin. That is, two of these tentacles are produced as diverticulae from each of the second pair of gastric pouches (ectodermal), and their subsequent position in the planes of the septa is due to a secondary shifting. He finds in this important evidence in favor of his theory of the close affinity between the Scyphomedusae and the Anthozoa, for the tentacles of the latter are also invariably interseptal. Claus, on the other hand, finds that the interradial tentacles of Aurelia and Cotylorhiza are variable in origin. According to his observations ('91 and '92), an interradial tentacle may be interseptal, that is, arise as a diverticulum of a single gastric pouch, the endoderm growing out and pushing the ectoderm before it; or it may arise in the plane of a septum by the union of two endodermal diverticulae, one from each of the adjacent pouches. He holds, therefore, that the origin of the tentacles cannot be used as evidence to uphold Goette's theory.

My observations on Cassiopea are in perfect accord with those of Claus. A number of series of transverse serial sections made from young scyphistomas in the eight- and sixteen-tentacle stages were studied carefully with the aid of camera sketches drawn on transparent paper. By this means the relations of the parts could be determined accurately; and the results are embodied in the series of diagrams, Figs. H to L. In the eight-tentacle stage, according to Goette, the gastric pouches in the long diameter, *r r*,

should each give rise to a single tentacle, while the pouches in the short diameter, r' r', should each produce three. From a glance at Figs. H and J it will be seen that this is not the case in Cassiopea. To be sure, most of the tentacles at this stage are interseptal in position, but the interradial tentacles arise as often from pouches in the long diameter, r r, as from those in the short diameter, r' r'; and in both Figs. H and I there is one interradial tentacle that is distinctly septal in position. The septa are still complete, so that there can hardly be any chance of a shifting of position. In the sixteen-tentacle stage, there is a tentacle in the plane of each septum (Figs. K and L); but here the perforation of the septa has commenced, and a shifting of relative position is possible. Even at this stage irregularities are common. For example, one of the septa in Fig. K is placed asymmetrically with relation to the tentacles, and two tentacles are wanting in Fig. L.



Figs. H–L. Diagrams illustrating the space relations between the septa and the tentacles, observed in five young scyphistomas of *Cassiopea xamachana*. r — radii of the long diameter, r′ — radii of the short diameter.

The Strobila, — Development of the Rhopalia. — When the scyphistoma has reached a diameter of about two millimeters, there appear the first characters 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 circumoral disc 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 (Figs. 17 and 18). The tentacles containing these will be called the rhopalial tentacles.

These concretions, or otoliths, increase in number until they form a conspicuous mass, while the basal cone begins to broaden laterally. This is now distinctly non-

contractile, and may be spoken of as a marginal lobe of the peristome (Figs. 19 and 20). In the specimen shown in Fig. 21 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 semicircular 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. 22). Fig. 23 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 bend from the distal portion, 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. 54 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 endoderm of the distal part of the tentacle, and opens toward the centre into a gastric pocket. The endodermal lining of the lumen is a columnar epithelium, the more distal cells being deeper and containing the concretions. Compare Fig. 54 with Fig. 53, which, being interradial, was certainly destined to be a rhopalial tentacle.

The growth of the marginal lobes, which were semicircular at the stage of Fig. 21, has continued, and each lobe has now produced 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. 54). The 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. 24, 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. 24, 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 disc. The tentacle at this stage is in a process of degeneration for about fifteen hundredths of a millimeter outward from the ocellus. In this area of degeneration (*t.* Fig. 55) the endodermal 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 may be seen many small and deeply stained nuclei. There are also a number 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 tentacle is brought about would seem to be as follows: The axial cells adjoining the cells that bear the concretions (Fig. 54) 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, however. The products of degeneration probably pass through the rhopalial canal into the digestive tract. As this process continues, the inward movement of the ectodermal 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. 25 and 55), it is a solid mass of small cells with small nuclei that stain dark. Some of these cells contain a large vacuole and have the nucleus pushed to one side. Scattered among the small cells, there are a number 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 (*oc.* Fig. 55).

At about this time the interrhopalial tentacles begin to be absorbed in their turn (Fig. 25). The umbrellar margin has in the mean time grown out beyond the insertion of each interrhopalial tentacle, on its aboral side, into two lobes with a hood between (Figs. 25 and 26). This structure, although smaller, corresponds exactly to the rhopalial lobes and hood, and is further evidence for the homology between the tentacles and the rhopalia. The drawing reproduced in Fig. 25 was made between the hours of eleven in the morning and two in the afternoon. At five o'clock of the same 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. The rhopalium (Fig. 56) 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.

These observations, then, confirm those of Claus ('83,) who, without going into the details of development, maintained that the rhopalia are modified basal portions of the tentacles of the scyphistoma; and they contradict Goette's statement that the rhopalia are developed independently of the tentacles.

Other Phenomena of Strobilization.— While the marginal structures are undergoing the metamorphosis that has just been described, important alterations are taking place in the general shape of the body. The horizontal constriction first noticed in Fig. 21 has deepened (Fig. 24), while the fold below it has heightened, and the upper portion has broadened and flattened, until the condition shown in Fig. 26 is reached. At this final stage the upper portion has all the characteristics of a free-swimming medusa (ephyrula), except that it is attached by a slender aboral stem to the centre of a goblet-shaped basal polyp. The four interradial depressions in the peristome of the earlier stages have become nearly flattened out, all that remains of them being the hollows between the projecting radial angles, or pillars, of the proboscis, which have now become very prominent.

At the stage of Fig. 21, there may be noticed on the proboscis eight patches of thickened ectoderm containing many nettle cells. These nettle batteries are arranged symmetrically, one on each side of each pillar of the proboscis. At a little later stage (Fig. 24) the batteries have become invaginated, forming cup-shaped depressions, thickly crowded with nettle cells in all stages of development.

During the time when the larva is being differentiated externally into an upper and a lower portion, internal changes are taking place in the former, which result in the disappearance of structures characteristic of the scyphistoma and the appearance of others distinctive of the medusa.

The orifices in the gastric septa have become relatively larger (*cs.* Fig. 52 and *rc.* Fig. 57) until the septa are reduced to columnar pillars, columellae, connecting the upper and lower walls of the body and pierced longitudinally by the septal muscles (*c.* Fig. 58). The columellae are called by German authors "Septalknoten," but they are not homologous with the so-called "Septalknoten," or areas of adhesion, in the Peromedusae. The columellae of the Peromedusae are the walls of the large septal funnels where they pass from the subumbrella to the exumbrella, and, according to Haeckel's figures, are separated by the gonads from the areas of adhesion.

In the fully developed scyphistoma of Cassiopea, the septal muscles are solid throughout their length, and there is no cavity corresponding to the septal funnels, which, according to Goette, are well developed in Aurelia. But in the strobila there does appear a slight depression extending a very short distance into the end of each septal muscle. In Figs. 57 and 58, where this is well marked, much of the depression may be due to the strongly contracted condition of the specimens; but other specimens

not so contracted show at least the deeper part of the cavity, which therefore, may be truly a vestige of the septal funnel.

At an early stage of strobilization there may be noticed a short conical projection from the central edge of each columella. It extends also around the sides. These projections are probably the rudiments of the first four gastric filaments, which are distinctly developed at the time when the ephyrula is set free (*gf*, Fig. 58).

While the septa are shrinking to become the columellae, ridges appear opposite each other on the upper and lower walls of the peripheral part of the digestive tract between the bases of the tentacles. The epithelial membranes at the summits of opposite ridges unite, 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. The two discs of mesogloea never fuse along these lines of adhesion, but the endoderm remains between them as the endodermal lamella, or cathammal plate. At the stage of Fig. 24 the lines of adhesion occupy about half the space from the margin to the columellae.

The lower disc of the strobila remains simply an annular fold of the body wall until the metamorphosis of the upper disc is nearly complete. The septal muscles in this region bend outward with the rest of the body wall (Fig. 57). At length, however, the endoderm grows out toward the periphery as four shallow pouches, leaving septa between them which contain the longitudinal muscles. Very soon after this the septa are perforated so as to allow a fusion of the endoderm at their upper angles (Fig. 58). In the last stage of strobilization (Figs. 26 and 59) the longitudinal muscles may be traced from the peristome through the columellae and the mesogloea of the exumbrella to the narrow isthmus where the ephyrula disc joins the basal polyp. The latter has now a well-developed peristome (Fig. 59), and the mesogloea in this region is very thin. Just in the isthmus the muscles have disappeared, but they may be found again in the peristome of the basal polyp and traced for a distance close under the epithelium to the edges of the septa, where they bend abruptly downward, and continue through the septa into the stem.

Although seldom visible in the living specimen, sections show that the basal polyp at this stage possesses eight short tenacles (Fig. 59). It has also an annular fold of the ectoderm, closely surrounding the isthmus (Fig. 59 and *p*. Fig. 60). This fold is the rudiment of a new proboscis, which is without doubt entirely ectodermal in origin. But, as Goette has pointed out, it does not follow from this that the lining of the proboscis is ectodermal in scyphistomas developed from the egg. Pulsating contractions of the umbrella are first noticed at the time when the rhopalial tentacles begin to be absorbed (Fig. 24). They are then feeble and at long intervals. At the stage of Fig. 26 these

movements are rapid and violent. The rhythm is interrupted by few pauses, and these are short. The result of these movements is that the thin wall of the isthmus is ruptured, and the ephyrula is set free.

After this separation, the basal polyp has the appearance represented in Figs. 27 and 28. It is a scyphistoma with seventeen short tentacles and a rudimentary proboscis (Figs. 61 and 62). The proboscis and the tentacles grow rapidly, so that in a few days it is impossible to distinguish a regenerated basal polyp from a young scyphistoma in the sixteen-tentacle stage, except that the former has a somewhat thicker stem. It may be inferred from this complete regeneration of the basal polyp that it undergoes repeated strobilization, as Claus[1] has found to be the case in Aurelia.

The Ephyrula.— The ephyrula of Cassiopea is very different in appearance from the corresponding stage in ordinary scyphomedusae with eight 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 Figs. 29 and 30 in this paper, which are camera drawings of well-preserved ephyrulas of Cassiopea, mounted in balsam. Fig. 29 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. 64. The typical ephyrula of Aurelia or Cotylorhiza has eight marginal arms with two lobes at the end of each, and between each pair of lobes there is a rhopalium. In Cassiopea 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 on the umbrella, alternating with an equal number of ridges, which at an earlier stage bore the interrhopalial 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 peripheral end of each ridge the margin of the umbrella is produced into two lobes, those adjoining the rhopalia being well marked, the others small and inconspicuous (*il.* Fig. 30).

In Fig. 29 there are seventeen, and in Fig. 30, twenty-three, rhopalia. The latter 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, as described in the section on variations.

At this stage the rhophalia have come to lie, as in the adult, wholly within the margin of the umbrella, and project from its subumbrellar surface. The interrhopalial tentacles

[1] See foot-note, Claus ('92).

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 the four gastric filaments (Figs. 29 and 30). 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 the other two grooves, and that 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 the strobila. The margins of the lips are provided with numerous small processes, the digitella, which are arranged in a single continuous series.

Fig. 63 is a section of an ephyrula that has just become free. In this stage there is still an opening through the aboral wall of the stomach, and one may see the last vestige of the connection between the columella and the exumbrella, which contains also the degenerating remnants of the septal muscle.

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.

The Later Stages. — The later stages in the development of Cassiopea will be treated very briefly. While the umbrella remains at first unchanged, the metamorphosis of the mouth parts is inaugurated by the growth of the two outer angles of each of the more or less quadrate lips, so that they are soon drawn out into extended lobes (Fig. 31). At the same time the pillars of the proboscis thicken, and the mesogloea is continued outward along each of these lobes as a midrib. 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 ('79). 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.

Claus has described ('83) 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. But it appears to be merely the same thing expressed differently.

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 there are folds in the

margin. The deepest folds are the most distal, and they become progressively more shallow toward the base of the arm. The central mouth is still widely open. The subgenital cavities are well developed at this stage. Figs. 64, 65, and 66 show how the oral disc is formed, and how the subgenital cavities are produced by the great increase in thickness of the mesogloea at the pillars of the proboscis and the bases of the oral arms. By the growth of these structures, the subgenital cavities are necessarily produced. The only special adaptations are the subsequent growth and folding of the aboral 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 "vellar" lobe between two rhopalial ones.

At a little later stage, when there are three oral funnels at the tips of the arms (Fig. 33), the re-entrant angles between the pillars of the proboscis have grown inward, met at the centre, and fused. In this way the lumen of the oesophagus is divided into four tubes (Fig. 32), representing the grooves that were present in its angles in the earlier stages. In the figure 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 disc 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, has 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 four 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 ('81) states 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. 33). The fold deepens, and its edges are brought together on the ventral side and fuse, 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 disc, 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, grooves into oral funnels and brachial canal, together with the development of oral vesicles. 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 disc. 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 toward 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 about half the length of the arm, the distal funnels begin to subdivide. By this subdivision of the primary funnels new ones 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 dichotomous, but takes place in such a way as to produce alternate branches. The formation of a vesicle takes place at this stage in some way at about the time of the completion of the adjoining funnel. I have not been able to determine 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 funnel, as at first it seemed to me to be, and as Claus thinks it probably is.

According to Haeckel ('79), the genus Archirhiza represents a form that was the ancestor of all the rhizostomatous medusae. Of this genus there are two known species, *A. primordialis* 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 has been 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 the oral arm, in its distal half the vesicles are formed, and branches are in the process of formation.

The outline of the umbrellar 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.

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 gonads, all the organs of the adult are outlined. Here we must take leave of it.

Summary and Conclusions.

Cassiopea and Polyclonia are genera of rhizostomatous medusae peculiarly modified in adaptation to a sedentary mode of life in shallow water among the mangroves bordering tropical seas. A comparison of specimens of *Polyclonia frondosa* Ag. with *Cassiopea xamachana* shows that these two forms are specifically distinct, although in general appearance they are very similar and they have the same geographical range and habitat.

C. xamachana is remarkable for its variability. This is especially shown in the appendages to the mouth parts and in the structures at the margin of the umbrella. It will be noticed that the most frequent number of rhopalia, in the twenty-seven specimens examined, was sixteen, which is the typical number for the genus. But the variations are not arranged symmetrically on the two sides of this mode, for specimens having a greater number of rhopalia are more than twice as many as those having less. The species shows a strong tendency toward duplication of the rhopalia and associated structures of the umbrella; and at the same time the symmetrical relations of the parts tend to be preserved. The great majority of scyphomedusae have only eight rhopalia, and in Cassiopea with its sixteen rhopalia we have a beautiful illustration of Darwin's law that "A part developed in any species in an extraordinary degree or manner, in comparison with the same part in allied species, tends to be highly variable." Study of the color markings and measurements of the mouth parts indicates the division of the species into three varieties; and it was in one of these, var. *A*, that the duplication of marginal organs was especially prevalent.

The color of both larvae and adults is due to a great extent to the presence in the mesogloea of minute symbiotic algae. That these are plant cells was demonstrated by micro-chemical tests. Their presence undoubtedly enables the medusae to live in water that would be too poor in oxygen for most marine animals.

The search for developing eggs proved unsuccessful, but scyphistoma larvae were abundant, and it was found that they were multiplying rapidly by budding.

The bud arises as an evagination of the body wall of the scyphistoma. There is no evidence of any special gemminal epithelium. The bud, when set free, differs from a planula chiefly in the possession of a well-defined mesogloea and four septal muscles. The septal muscles are shown to be formed as branches of the two adjacent septal muscles of the parent. The mouth of the young scyphistoma is formed by a minute perforation at the former point of attachment, while the distal end of the bud becomes the stem. This remarkable orientation agrees with what Goette and Claus have found in Cotylorhiza. In

the formation of the mouth there is no evidence of any invagination of ectoderm Apparently the oesophagus, as well as the gastric pouches, is lined with endoderm. On the other hand, the oesophagus of the lower disc of the strobila is formed wholly of ectoderm.

The four radial tentacles are formed simultaneously, and the four interradial ones appear at the same time or slightly later. These are followed by eight adradial tentacles and sixteen more are added a little later, making thirty-two in all. It was found that the rudiments of the interradial tentacles are not at all constant in position with relation to the septa. Some were septal, others were interseptal, sometimes on one side of the septum, sometimes on the other, thus agreeing with the observations of Claus on Aurelia and Cotylorhiza.

The four gastric pouches are formed at the same time by the ingrowth of the septa. They are soon brought into communication at the periphery by the perforation of the septa, which become reduced to columellae surrounding the longitudinal muscles.

Contrary to Goette's opinion, it may be stated positively that the rhopalia are differentiated in the bases of alternate tentacles. After the rhopalium is fully developed, the distal part of the tentacle undergoes degeneration and is absorbed. The development was traced for the first time through all its stages, and the opinions of Agassiz, Claus, and Lendenfeld are fully confirmed.

The scyphomedusae are the only coelenterates, which possess four longitudinal muscles of ectodermal origin completely imbedded in the mesogloea between the points of insertion. The buds of Cassiopea have this distinctively medusoid characteristic long before they are detached. Moreover, the methods by which the mouth and the gastric pouches are formed differ entirely from what is said to take place in larvae that pass through an anthozoan stage. Therefore, whatever may be true of the larvae derived from eggs, this stage is certainly omitted in larvae produced by budding.

The first step toward the formation of the free-swimming medusa is the perforation of the gastric septa which takes place in the young scyphistoma before it is fully developed. Then follows a period of growth and reproduction by budding, and further metamorphosis begins finally with the process of strobilization. Besides the differentiation of the sense organs and the development of the marginal lobes of the umbrella, the most important events are the development of the angles of the mouth into quadrate lobes and the fusion of the two layers of endoderm along certain areas of adhesion so as to divide the periphery of the digestive tract into a series of radial canals. Only one medusa is formed; but, separated from this by a constriction, is a small basal segment which, a short time before the medusa becomes free, begins to develop gastric pouches, tentacles, and a proboscis. This becomes eventually a perfect scyphistoma, and after a period of growth probably undergoes strobilization again.

There has been considerable discussion in regard to the nature of strobilization; the question being whether the medusa is to be regarded as a metamorphosed scyphistoma, or as derived from the scyphistoma by a process of budding. In the monodiscous strobila of Cassiopea we have clearly a metamorphosis. The form of the medusa is the result of a series of changes which begin very early and involve all the essential organs of the scyphistoma. The portion not involved in these changes merely serves as a mechanical support. That this part is separated off and regenerates the lost parts, instead of being absorbed, may be regarded as merely an incidental fact.

If there be any question of budding it refers to this basal segment. And this suggests a striking analogy between the basal polyp and the peculiar planula-like buds. In the first place they have the same orientation relative to the upper disc. In both, the distal end forms the stem and the proximal end forms the mouth. In the second place, they have essentially the same structure. Each one consists of a simple sac with a wall made up of three layers, ectoderm, mesogloea and endoderm, and each is provided with four longitudinal muscles imbedded in the mesogloea. What differences appear in the subsequent development, may be attributed to the different ways in which the two become separated from the disc and to the greater size of the longitudinal muscles in the basal polyp. The production of supernumerary tentacles, rhopalia, and marginal lobes, is common in this species. Why may we not regard the buds as supernumerary basal polyps, and their subsequent development as a process of regeneration preserved and modified by natural selection for its obvious advantage?

The ephyrula of Cassiopea has the same number of rhopalia as the adult, and differs in shape from the corresponding stage of ordinary scyphomedusae with eight parameres.

The most important event in the later stages is the metamorphosis of the mouth parts. The angles of the four quadrate lips become extended to form eight oral arms somewhat similar to those found in the adult Aurosa. There is no Archirhiza stage, but there follows a stage with the oesophagus divided into four tubes, and with three oscula and an oral vesicle on each arm. A similar stage has been found in Pilema and Cotylorhiza, and it may have some phylogenetic significance.

The studies of numerous investigators upon the Ascidians have demonstrated that a knowledge of the gamogenetic development of an animal will not always enable one to predict how the organs will be formed in the agamogenetic process. So it may be objected that the results set forth in this paper do not afford a valid basis for the criticism of work done by others on larvae developed from the egg. On the other hand, the eight-tentacle stage of the bud larva of Cassiopea is so like the same stage of the sexually produced larva of its near relative Polyclonia that it would be impossible to tell them apart, and, in the absence of any evidence to the contrary, there seems to be no necessary reason

for supposing that their later history is different. At any rate, we have here the first fairly complete history of the development of a scyphomedusa from the bud; and when the sexual development of *Cassiopea xamachana* or an allied species is studied, this memoir will serve as a means of comparison, and will make it possible to determine whether or not the two modes of ontogeny are alike.

Literature.

Agassiz, A.

'65. North American Acalephae. Illustrated catalogue of the Museum of comp. zool. at Harvard College. No. 2, 1865, p. 41.

'81. Polyclonia frondosa. Nature, vol. 24, 1881, p. 509.

Agassiz, A., & Mayer, A. G.

'99. Acalephs from the Fiji Islands. Bull. mus. comp. zool., vol. 32, no. 9, 1899. (Description of *Cassiopea ndrosia*.)

Agassiz, L.

'60. Contributions to the natural history of the United States of America. Vols. 3 and 4. Boston, 1860.

Archer, H.

'81. Medusae. Nature, vol. 24, 1881, p. 307.

Berger, E. W.

1900. Physiology and histology of the Cubomedusae, including Dr. F. S. Conant's notes on physiology. Mem. biol. lab. Johns Hopkins Univ. vol. 4, no. 4.

Bigelow, R. P.

'90. The marginal sense organs in the Pelagidae. Johns Hopkins Univ. circ., vol. 9, 1890, no. 80, p. 65.

'92a. On reproduction by budding in the Discomedusae. J. H. U. circ., vol. 11, 1892, no. 97, p. 71.

'92b. On the development of the marginal sense organs of a rhizostomatous medusa. J. H. U. circ., vol. 11, 1892. no. 97, p. 84.

'92c. On a new species of Cassiopea from Jamaica. Zool. Anz., Jahrg. 15, 1892, no. 393, pp. 212–214.

'93. Some observations on Polyclonia frondosa. J. H. U. circ., vol. 12, 1893, no. 106, p. 106.

Brandt, J. F.

'38. Ausfürliche Beschreibung der von C. H. Martens auf seiner Weltumsegelung beobachteten Schirmquallen. Mem. Acad. imp. sci. St. Petersbourg, sci. math. phys. et nat., (6) vol. 4 (pt. 2, sci. nat., vol. 2), 1838, pp. 394–399.

Brooks, W. K.

'86. The life history of Hydromedusae, a discussion of the origin of medusae and the significance of metagenesis, Mem. Boston soc. nat. hist., vol. 3, no. 12, 1886; also Mem. biol. lab. Johns Hopkins Univ., vol. 1.

Claus, C.

'77. Studien über die Polypen und Quallen der Adria. Denkschr. d. math.-naturw. Classe d. k. Acad. d. Wissenschaften, Wien, Bd. 38, 1877.

'81. Ueber einige bislang noch unbekannte Larvenstadien von Rhizostoma. Zool. Anz., 1881, No. 76, p. 79.

'83. Untersuchungen über die Organisation und Entwicklung der Medusen. Prag and Leipzig, 1883, 96 pp., 20 pls.

'84. Die Ephyren von Cotylorhiza und Rhizostoma. Arb. zool. Inst. Wien, vol. 5, 1884, p. 169.

'90. Ueber die Entwicklung des Scyphostoma von Cotylorhiza, Aurelia, und Chrysaora, I. Arb. zool. Inst., Wien, vol 9, 1890, p. 29.

'92. Ueber die Entwicklung des Scyphostoma von Cotylorhiza, Aurelia und Chrysaora, sowie über die systematische Stellung der Scyphomedusen, II. Arb. a. d. zool. Inst. d. Univ. Wien, vol. 10, 1892, pp. 1–70.

du Plessis, G.

'81. Remarques sur les metamorphoses de la Cassiopée bourbonnienne. Bull. soc. vaudois, Lausanne, ser. 2, vol. 17, 1881, p. 633.

Fewkes, J. W.

'82. Notes on acalephs from the Tortugas, with description of new genera and species. Bull. mus. comp. Zool., vol. 9, no. 7, 1882.

Fischer, P.

'88. Note sur des scyphistomes de méduse acraspède. Bull. soc. zool. de France, vol. 13, 1888, p. 96.

Forskål, P.

1775. Descriptiones animalium .... quae in itinere orientali observavit. Hauniae, Möller, 1775, p. 107.

1776. Icones rerum naturalium, quas in itinere orientali depingi curavit. Hauniae, 1776, pl. 31.

Frantzius, A. v.

'53. Ueber die Jungen der Cephea (Cotylorhiza.). Zeitschr. f. wiss. Zool., Bd. 4, 1853, p. 118.

Goette, A.

'87. Entwicklungsgeschichte des Aurelia aurita und Cotylorhiza tuberculata. Hamburg and Leipzig, 1887.

'91. Claus und die Entwicklung der Scyphomedusen. Leipzig, 1891.

'93. Vergleichenden Entwicklungsgeschichte von Pelagia noctiluca Pér. Zeitschr. f. wiss. Zool. Bd. 55, 1893, pp. 645-695. [Die Larven von Cotylorhiza tuberculata L., pp. 645–659.]

Gray, J. E.

'69. Habits of the Medusae. Annals and mag. nat. hist., ser. 4, vol. 4, 1869, p. 295.

Guppy, H. B.

'82. Habits of Scyphomedusae. Nature, vol. 27, 1882, p. 31.

Haacke, W.

'85. Pseudorhiza Haeckelii spec. nov., der Endspross des Discomedusenstammes. Biol. Centralb., vol. 4, 1885, p. 291.

Haeckel, E.

'69. Crambessiden. Zeitschr. f. wiss. Zool., vol. 19, 1869, p. 509.

'79. Das System der Medusen. Jena, 1879.

'81a. Report on the deep sea medusae. Challenger reports, zool., vol. 4, 1881.

'81b. Metagenesis and Hypogenesis von Aurelia. Jena, 1881.

Hamann, O.

'81. Die Mundarme der Rhizostomen und ihre Anhangsorgane. Jenaische Zeitschr. f. Naturw., vol. 15, 1881, p. 243.

Hertwig, O. & R.

'78. Das Nervensystem und die Sinnesorgane der Medusen. Leipzig, 1878.

'79. Die Actinien. Jena, 1879.

Hesse, R.

'95. Ueber das Nervensystem und die Sinnesorgane von Rhizostoma cuvieri. Zeitschr. f. wiss. Zool., vol. 60, 1895, p. 411.

Hyde, Ida H.

'94. Entwicklungsgeschichte einiger Scyphomedusen. Zeitschr. f. wiss. Zool., vol. 58, 1894, p. 531–565.

Keller, C.

'83. Untersuchungen über neue Medusen aus dem Rothen Meere. Zeitschr. f. wiss. Zool., vol. 38, 1883, p. 621.

Lacaze-Duthiers, H. de.

'93. Scyphistome. Archives de zool. expér., ser. 3, vol. 1, 1893, notes et revues, p. xxx.

Lamarck, J. B. de

'37. Histoire naturelle des animaux sans vertébres. Ed 3. Paris, 1837, vol. 1, p. 457.

Lang, Albert.

'92. Ueber die Knospung bei Hydra und einigen Hydropolypen. Zeitschr. f. wiss. Zool., vol. 54, pp. 363–385.

Lendenfeld, R. v.

'82. Ueber eine Uebergangsform zwischen Semostomen und Rhizostomen (Pseudorhiza). Zool. Anz., Jahrg. 5, 1882, p. 380.

'84. Zur Metamorphose der Rhizostomen. Zool. Anz., Jahrg. 7, 1884, p. 429.

'88. Die australischen rhizostomen Medusen. Zeitschr. f. wiss. Zool., vol. 47, 1888, p. 201.

McMurrich, J. P.

'91. The Development of Cyanea arctica. Amer. nat., vol. 25, 1891, p. 287.

Metschnikoff, E.

'86. Embryologische Studien an Medusen. Wien, 1886.

Milne-Edwards, H.

'49. Les zoophytes. Cuvier, Regne animal illustré. Vol. 10, 1849, pl. 51.

Reid, J.

'48. Observations on the development of the medusae. Annals and mag. nat. hist., ser. 2, vol. 1, 1848, p. 25.

Sars, M.

'41. Ueber die Entwicklung der Medusa aureta und Cyanea capillata. Arch. f. Naturg., vol. 7, 1841, p. 9.

Schewiakoff, W.

'89. Beiträge zur Kenntnis der Acalephenauges. Morph. Jahrb., vol. 15, 1889, p. 25.

Schneider, A.

'70. Zur Entwicklungsgeschichte der Aurelia aurita. Arch, f. mik. Anat. vol. 6, 1870, p. 363.

Schultze, L. S.

'98. Rhizostomen von Ternate. Abh. senckenb. naturf. Ges., vol. 24, 1898, p. 153. [Occurrence of *Cassiopea*, sp.?]

Smith, Frank.

'91. The gastrulation of Aurelia flavidula Pér. & Les. Bull. mus. comp. zool., vol. 22, no. 2, 1891.

Tilesius, W. G. v.

'29. Zur Naturgeschichte der Medusen. Nova Acta Physico-Medica, N. C., vol. 15, 1829, p. 266.

Vanhöffen, E.

'88. Untersuchungen über semaeostome und rhizostome Medusen. Leuckart & Chun's Biblioth. Zool., Heft 3, 1888.

Explanation of Plates.

All the figures from 1 to 28, and Figs. 34 and 35, are freehand drawings made from the living animals. Figs. 29 to 33 are from well-preserved specimens mounted in balsam, and were outlined with the camera lucida. The remaining figures, except Fig. 37, are camera-lucida drawings of microtome sections. All the figures are reduced uniformly to slightly less than one half the diameter of the original drawings.

LETTERING COMMON TO ALL THE FIGURES.

b. — bud.
c. — columella.
c d. — circum-oral disc, or peristome.
c s. — circular sinus.
cx. — calyx.
d. — digitellum.
ect. — ectoderm.
e l. — endodermal lamella, or cathammal plate.
end. — endoderm.
e u. — exumbrella.
g. — stomach.
g f. — gastric filament.
g p. — gastric pouch.
h. — hood.
i l. — interrhopalial lobe.
i t. — interrhopalial tentacle.
l g. — labial groove.
m. — mouth.
mes. — mesogloea, or supporting membrane.
n f. — nerve fibres.
o a. — oral arm.
oc. — ocellus.
o d. — oral disc.
oe. — oesophagus.

oe. t. — oesophageal tube, or canal.
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.
za. — brownish green cells, symbiotic algae.

PLATE 31.

Fig. 1. Portion of the calyx and stem of a scyphistoma with a fully developed bud (*b*) attached. *A*, the outline of the same bud when contracted.

Fig. 2. Similar to the preceding, except for the formation of a second bud (*b'*) which bears the older one (*b*) upon its apex.

Fig. 3. The form of the planula-like bud during the first two days after becoming free. *A*, *B*, and *C*, are the successive changes in shape observed in one specimen during a few minutes. The arrows show the direction in which it swims.

Fig. 4. Larva of probably the third day. *A*, lateral aspect; *B*, oral aspect.

Fig. 5. A larva of about the same age, 48 hours or over.

Fig. 6. Another larva of 48 hours or over.

Fig. 7. Larva of the fourth day.

Fig. 8. Free scyphistoma of the fifth day, with rudiments of four tentacles. The arrows show the direction of progression and rotation.

Fig. 9. A scyphistoma of about the same age, with the rudiments of eight tentacles.

Fig. 10. Oral aspect of a similar larva, perhaps somewhat younger.

Fig. 11. A scyphistoma a little more advanced, probably in the fifth day.

Fig. 12. A still more advanced scyphistoma of the fifth day. The four tentacles first formed are much longer than the other four.

Fig. 13. Scyphistoma of the sixth day, attached, and with eight tentacles.

Fig. 14. Scyphistoma with rudiments of the second set of eight tentacles. Two tentacles of the first series are bifurcated.

Fig. 15. Scyphistoma with sixteen tentacles fully developed, in the attitude of feeding.

Fig. 16. Oral aspect of a similar specimen.

PLATE 32.

Fig. 17. Scyphistoma showing first traces of rhopalial structure.

Fig. 18. A small portion of the margin more highly magnified.

Fig. 19. Scyphistoma at a slightly older stage.

Fig. 20. Small part of the margin of a similar larva.

Fig. 21. An early stage in strobilization.

Fig. 22. A rhopalial tentacle of the same specimen seen from the side.

Fig. 23. An older rhopalial tentacle.

Fig. 24. Strobila in which the rhopalial tentacles have begun to degenerate.

PLATE 33.

Fig. 25. Strobila, in which the degeneration of the rhopalial tentacles is nearly completed, and the interrhopalial tentacles have begun to degenerate.

Fig. 26. A complete strobila. The basal polyp bears a bud which broke off and swam away while the drawing was being made. The ephyrula was detached during the following night. The rhopalia are visible through the umbrella. At *y*, is a pair of twin rhopalia ; compare *y*, Fig. 30.

Fig. 27. The basal polyp of the same specimen, a few hours after the separation of the ephyrula.

Fig. 28. Optical section of the same.

Fig. 29. An ephyrula recently set free. Oral aspect. The gastric filaments are visible through the mouth. × 31.

Fig. 30. A specimen of about the same age, showing variations of the margin at *u*, *w*, *x*, *y* and *z*. × 31.

PLATE 34.

Fig. 31. Mouth parts of a young medusa in the Aurosa stage. The gastric filaments may be seen through the central mouth opening. × 33.

Fig. 32. Oral disc of an older specimen. The oesophageal tubes appear as light areas, one at the junction of each pair of labial grooves.

Fig. 33. One of the oral arms from the same specimen as Fig. 32.

Fig. 34. 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 through the external orifice into this cavity, at *x*. The ultimate branches are represented on only one of the oral arms.

Fig. 35. Portion of the aboral surface of an adult. About half natural size.

PLATE 35.

Fig. 36. Section of a young bud. × Zeiss DD + oc. 2.[1]

Fig. 37. Diagram to show the branching of the septal muscles, sm_1, sm_2, sm_3 and sm_4, and the connections of the septal muscles of the bud, sm'_1, sm'_2, and sm'_3. Reconstructed from the series of sections of which Fig. 36 is one.

Fig. 38. Section through the distal apex of an older bud, showing the attachment of a septal muscle to the ectodermal epithelium. × Zeiss II + oc. 2.

Fig. 39. Longitudinal section of a planula-like larva. *D* was the distal, and *P* the proximal, end of the bud while attached. × Zeiss DD + oc. 2, dt. 160.

Fig. 40. Longitudinal section through the posterior end of a swimming larva, in which changes preparatory to the formation of the mouth are taking place. × B & L ⅛ + Zeiss oc. 2.

Fig. 41. Similar section of a slightly older larva, showing the mouth as a small opening not exceeding in width the thickness of the section. × B & L ⅛ + Zeiss oc. 2, dt. 160.

Fig. 42. Adradial section of a scyphistoma a little older than Fig. 9 (5th day). × Zeiss DD + oc. 2.

Fig. 43. Obliquely transverse section of a specimen of the same age, showing the greatest width of one septum. × B & L ⅛ + Zeiss oc. 2, dt. 160.

Fig. 44. A tangential section of an older larva, showing the connection of a septal muscle with the circum-oral disc. × Zeiss H + oc. 2.

PLATE 36.

Figs. 45 to 47 are consecutive transverse sections of one individual. Fig. 45 shows the continuity between the endoderm of adjacent gastric pouches at the base of an interradial tentacle. Fig. 47 is lower, and here the gelatinous septum completely separates the two pouches. × Zeiss II + oc. 2.

[1] Unless otherwise noted, the microscope was used with the draw tube not drawn out. Length of tube (dt.) = 137 mm.

Figs. 48 and 49 are from the same series. Fig. 48 is the second section below Fig. 47. It just clears the oesophagus. Fig. 49 is through the upper part of the stem. × Zeiss DD + oc. 2.

Fig. 50. Longitudinal section of a scyphistoma with sixteen tentacles, probably a little younger than Fig. 15. × Zeiss. DD + oc. 2, dt. 195.

Fig. 51. An obliquely transverse section of a fully developed scyphistoma, showing the relations of the septal muscles to the depressions in the circumoral disc. The mesogloea is shaded. × Zeiss B + oc. 2, dt. 160.

Fig. 52. Part of an interradial section from a scyphistoma a little older than the last. Owing to a slight obliquity of the section, the full extent of the circular sinus at the base of the tentacle is not shown. It extends to the point marked *x*. × Zeiss C + oc. 2.

PLATE 37.

Figs. 53 to 56 illustrate the development of the rhopalia.

Fig. 53. Median section of the interradial tentacle shown in Fig. 52 ; *x* marks a corresponding point in the two sections × Zeiss H + oc. 2.

Fig. 54. A radial section from the base of a rhopalial tentacle somewhat older than Fig. 23. × Zeiss H + oc. 2.

Fig. 55. Radial section of a rhopalium in the stage of Fig. 25. × Zeiss H + oc. 2.

Fig. 56. Radial section of a rhopalium in about the stage of Fig. 26. × Zeiss H + oc. 2.

Fig. 57. Radial section showing the course of a septal muscle in a strobila, at the stage of Fig. 24. × Zeiss DD + oc. 2.

Fig. 58. A similar section from a specimen a little older than Fig. 25 ; *x*, point of separation between the two discs. × Zeiss DD + oc. 2.

PLATE 38.

Fig. 59. Median vertical section of a strobila in the stage of Fig. 26; *x*, boundary between ephyrula and basal polyp. × Zeiss B + oc. 2.

Fig. 60. Portion of section from the same specimen, showing the proboscis of the basal polyp ; *x* marks same point as in preceding. × B & L $\frac{1}{8}$ + Zeiss oc. 2, dt. 160.

Fig. 61. Median vertical section of a basal polyp, stage of Fig. 27. × Zeiss B + oc. 2.

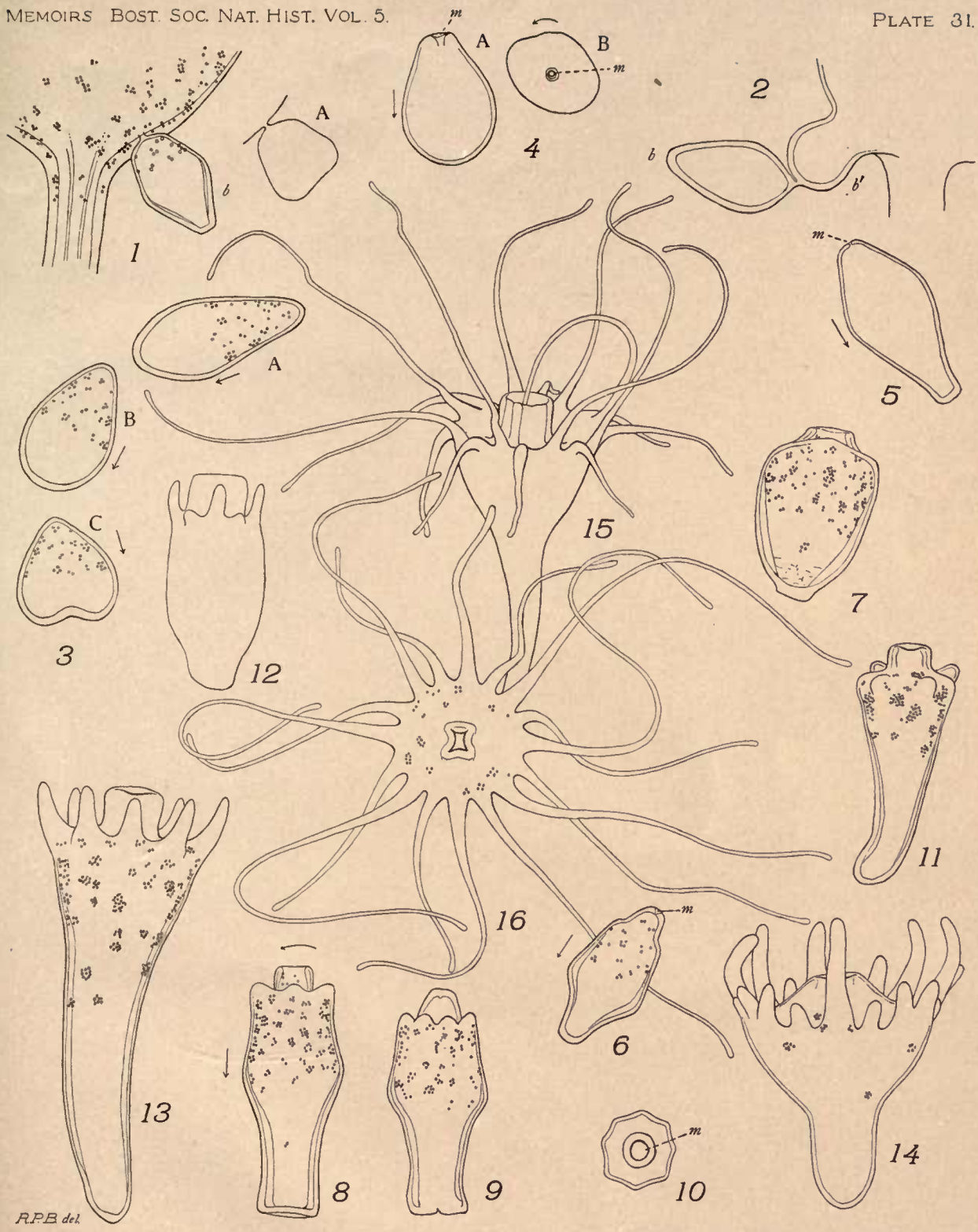
Fig. 62. Part of a section from the same specimen, showing the proboscis, p, and the vestige of the former connection with the ephyrula at *x*. × B & L $\frac{1}{8}$ + Zeiss oc. 2, dt. 160.

Fig. 63. Median vertical section of an ephyrula that has recently become free ; *x* is opposite the opening that formerly led into the cavity of the basal polyp. Cf. Fig. 29. × Zeiss DD + oc. 2.

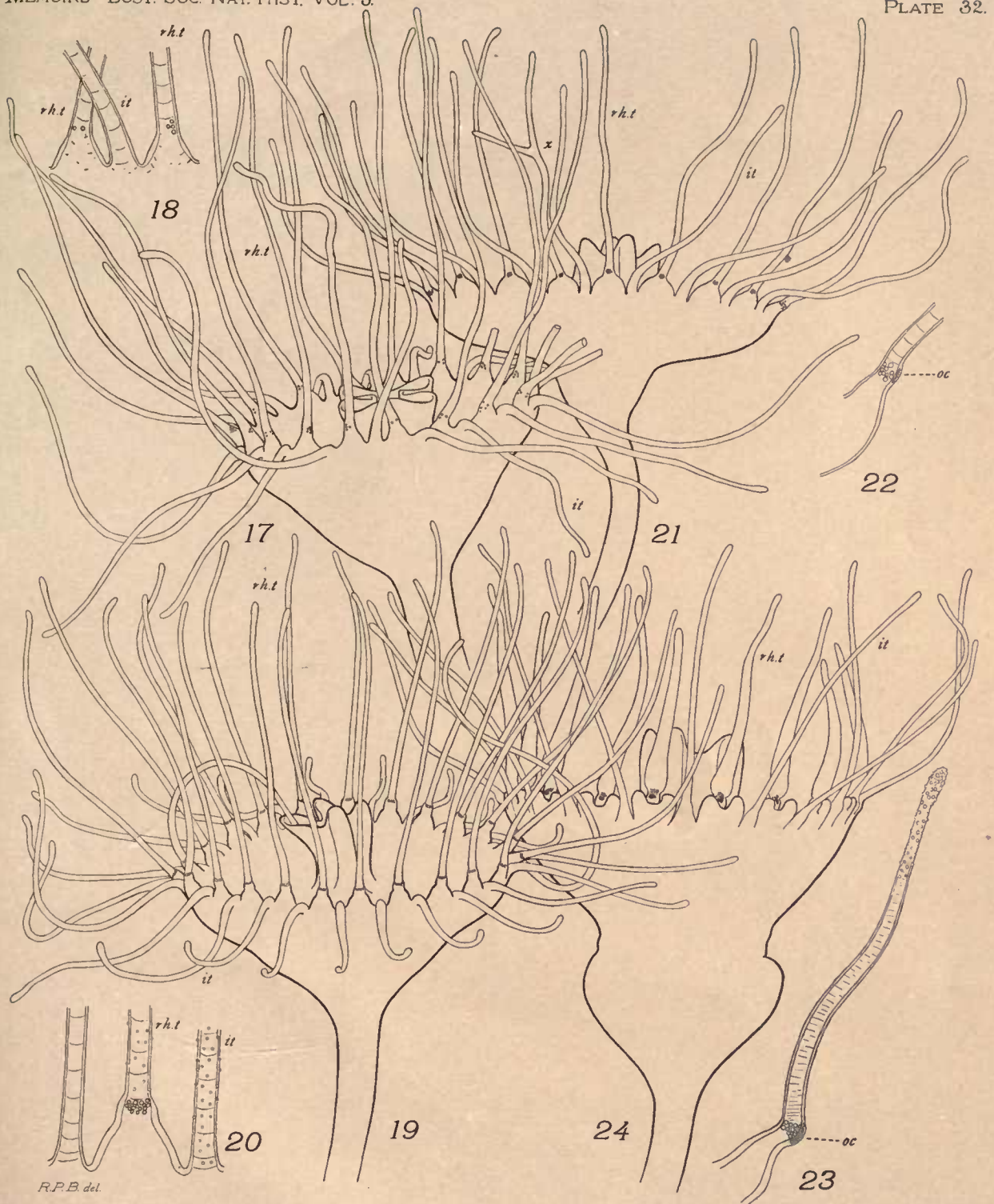
Fig. 64. Median vertical section from a young medusa intermediate in age between Figs. 31 and 32. The section is nearly interradial in position. × Zeiss AA + oc. 2, dt. 160.

Figs. 65 and 66. Tangential sections of the same specimen, parallel to the last, nearly at right angles to an interradius. Fig. 66 is the one nearer the periphery. × Zeiss AA + oc. 2, dt. 160.

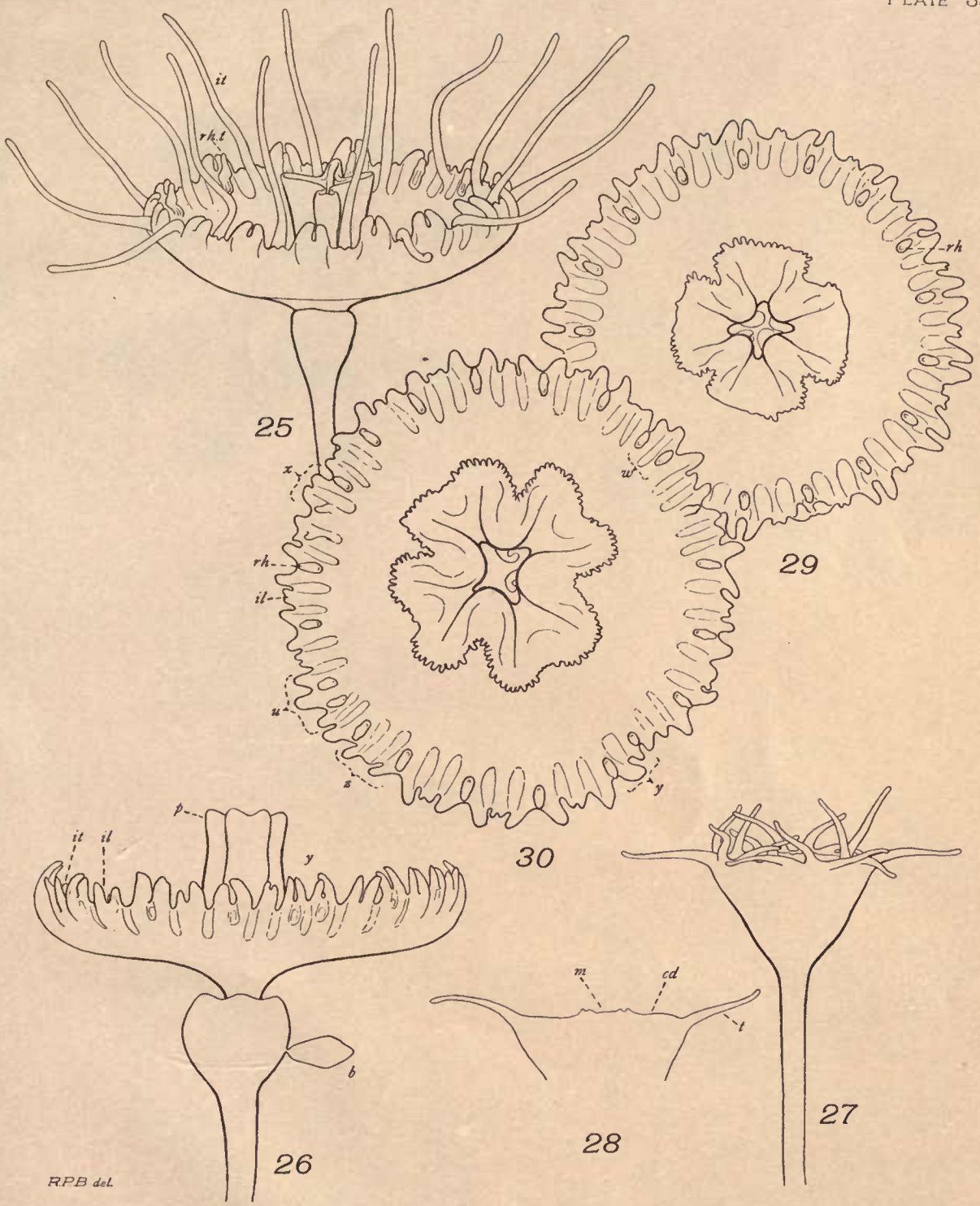
Printed, August, 1900.



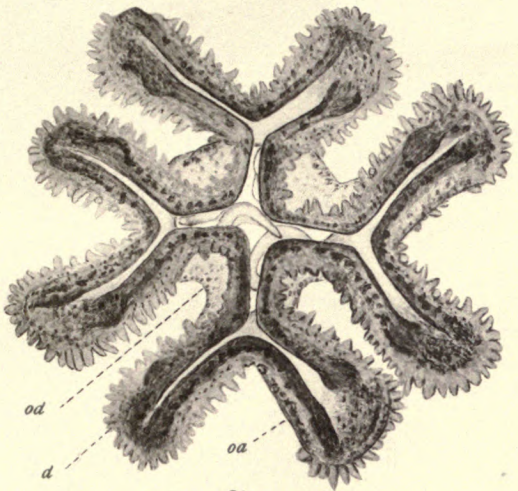
BIGELOW, CASSIOPEA XAMACHANA.



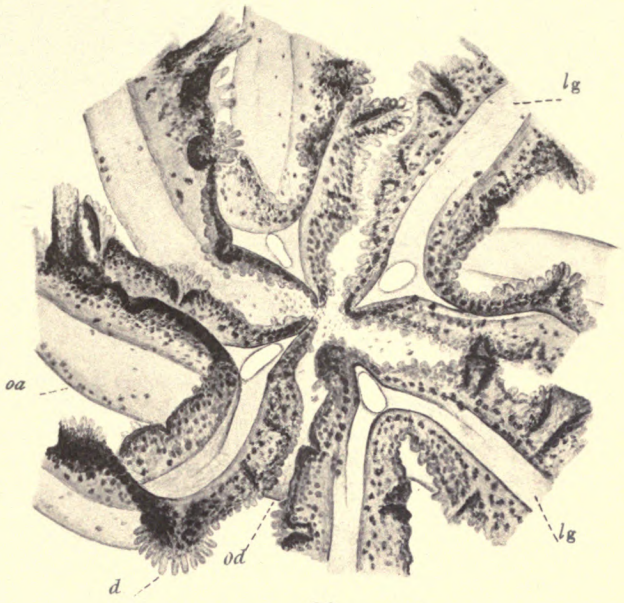
BIGELOW, CASSIOPEA XAMACHANA.



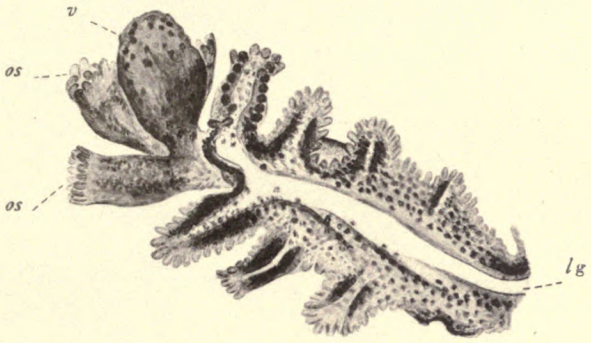
BIGELOW, CASSIOPEA XAMACHANA.



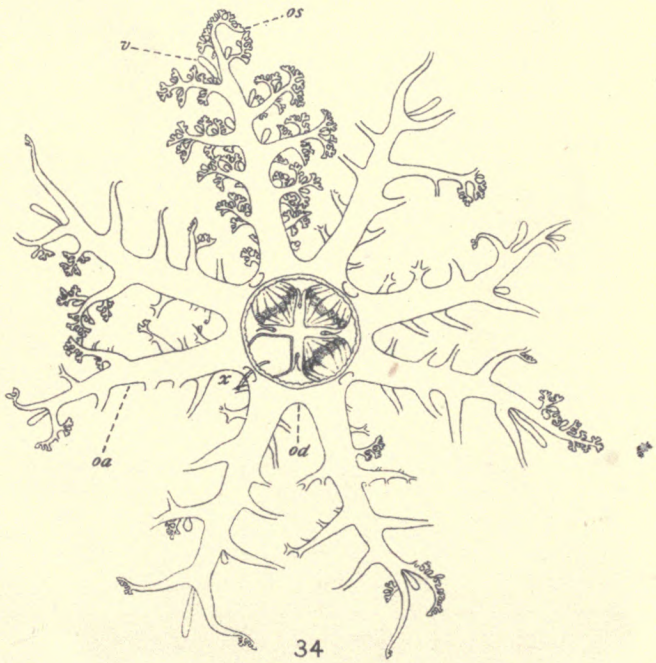
31



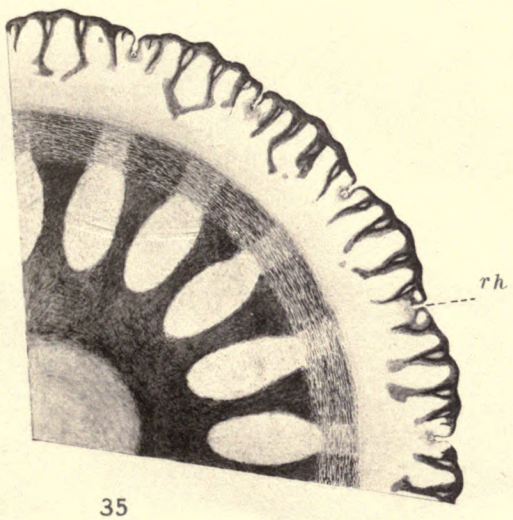
32



33.



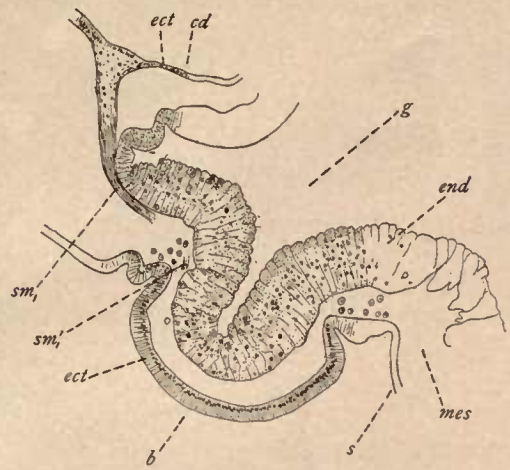
34



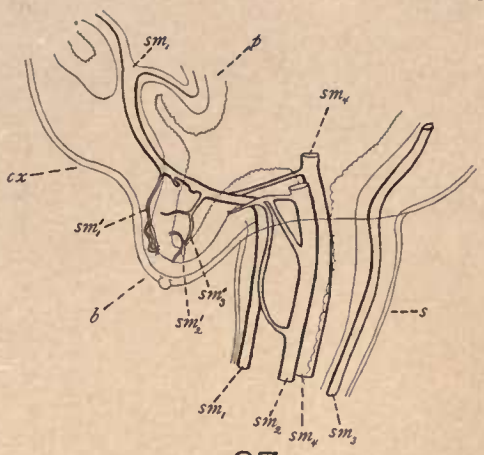
35

RPB del.

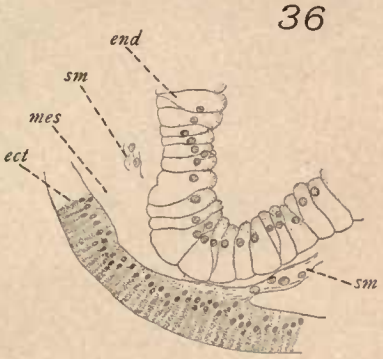
BIGELOW, CASSIOPEA XAMACHANA.



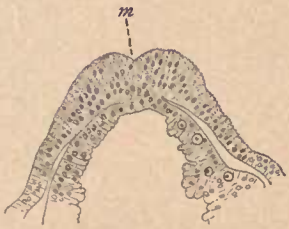
36



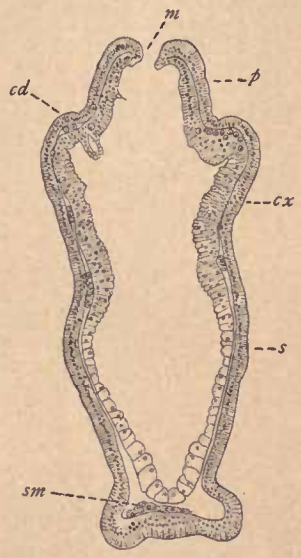
37



38

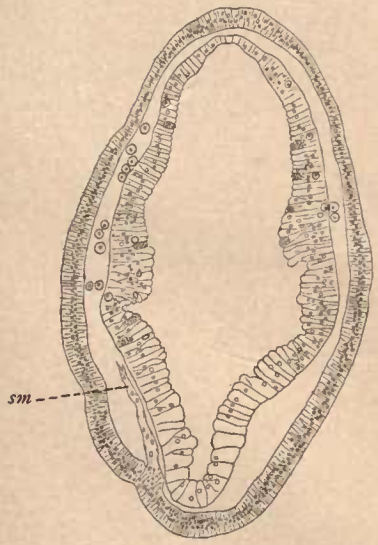


40



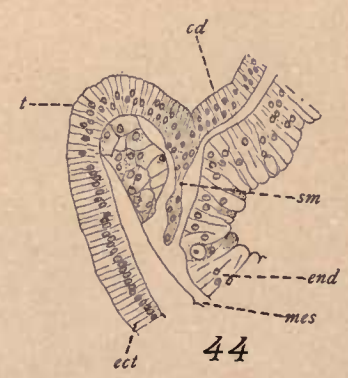
42

P



41

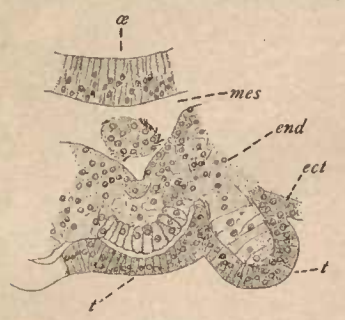
43



44

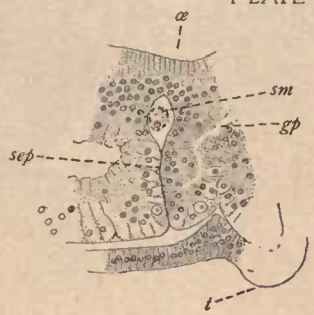
R.P.B. del. D 39

BIGELOW, CASSIOPEA XAMACHANA.

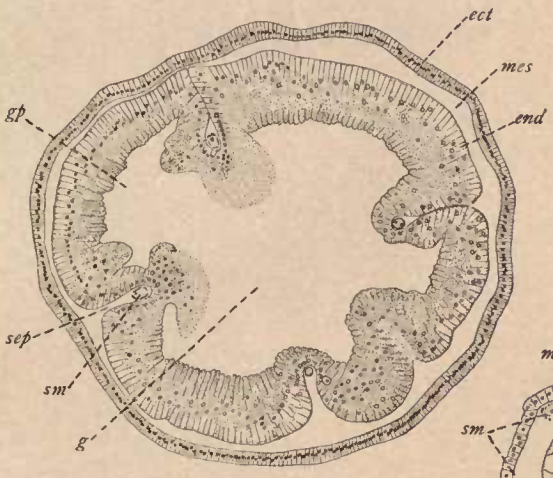


45

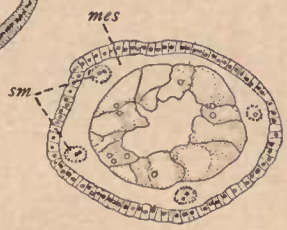
46



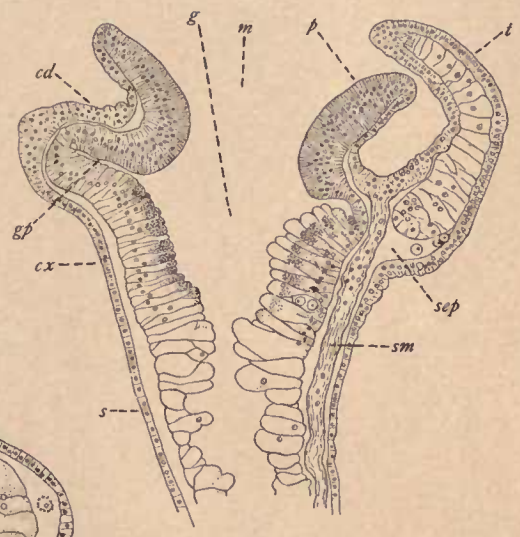
47



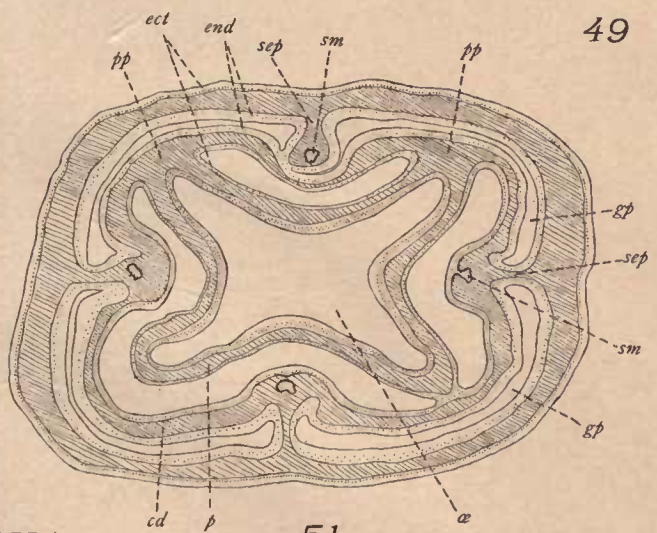
48



49

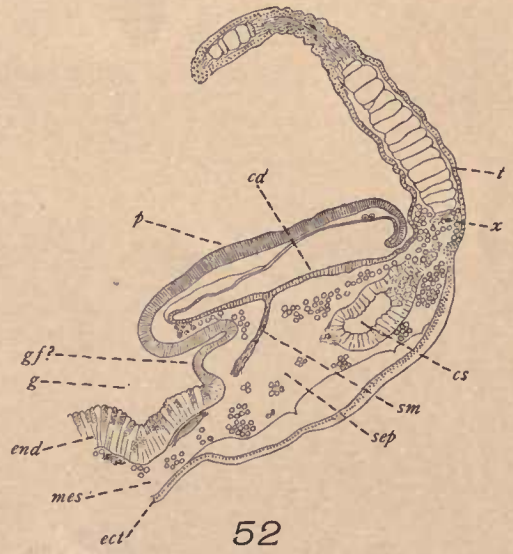


50



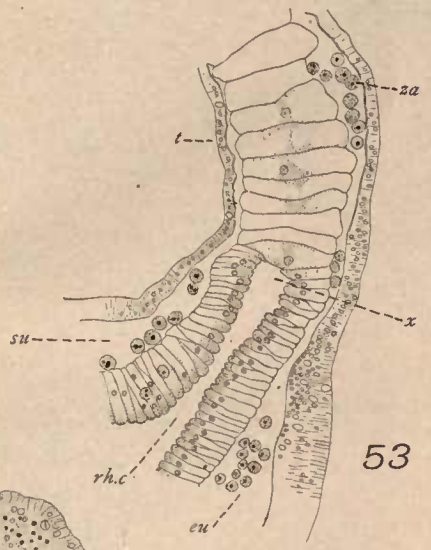
R.P.B. del.

51

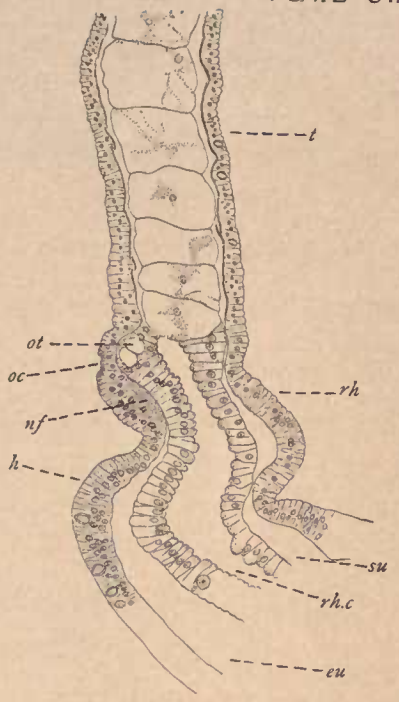


52

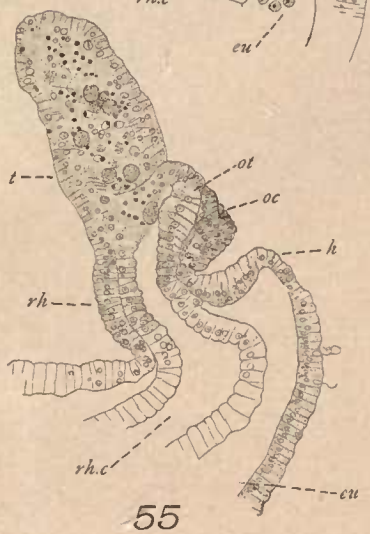
BIGELOW, CASSIOPEA XAMACHANA.



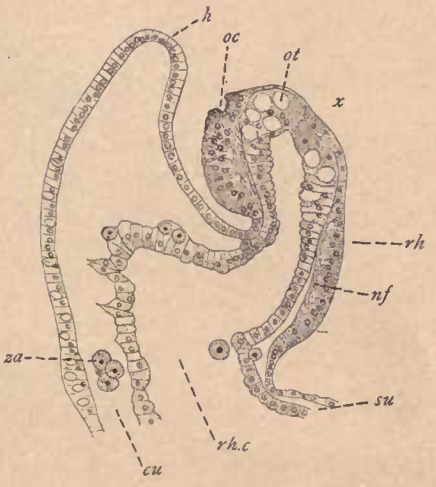
53



54

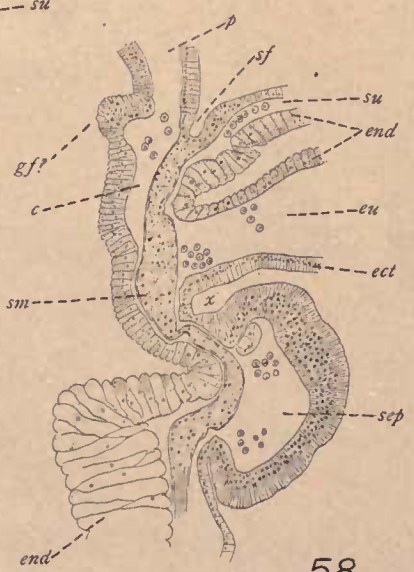


55



56

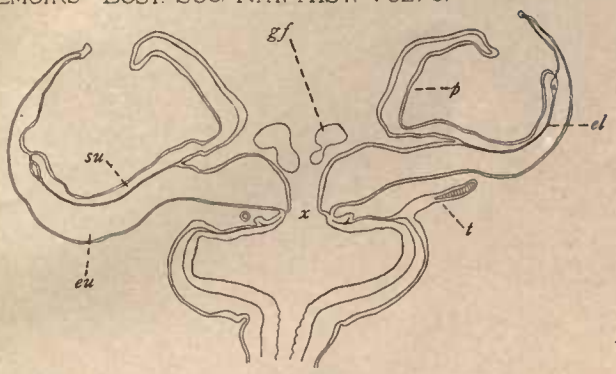
57



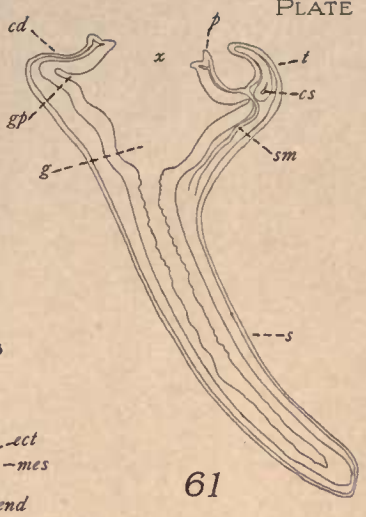
58

R.P.B. del.

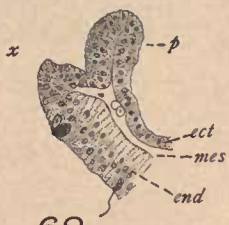
BIGELOW, CASSIOPEA XAMACHANA.



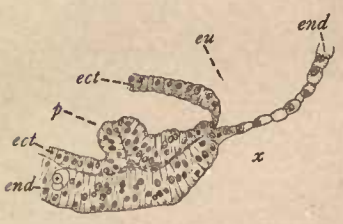
59



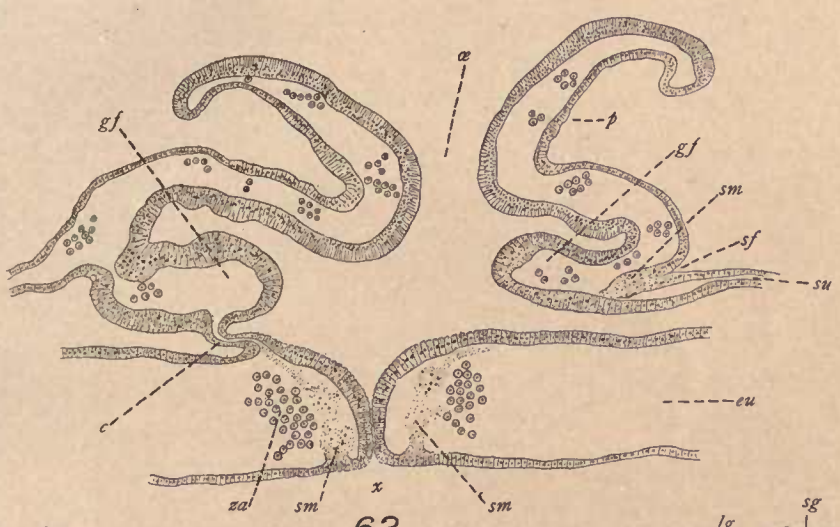
61



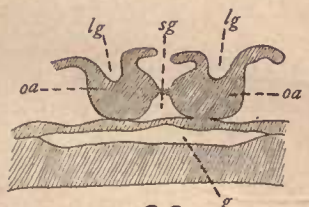
62



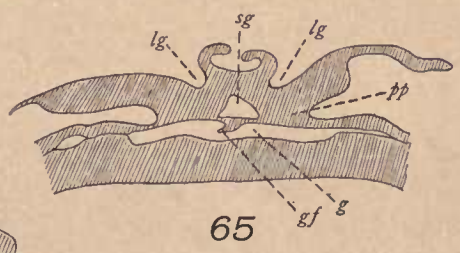
60



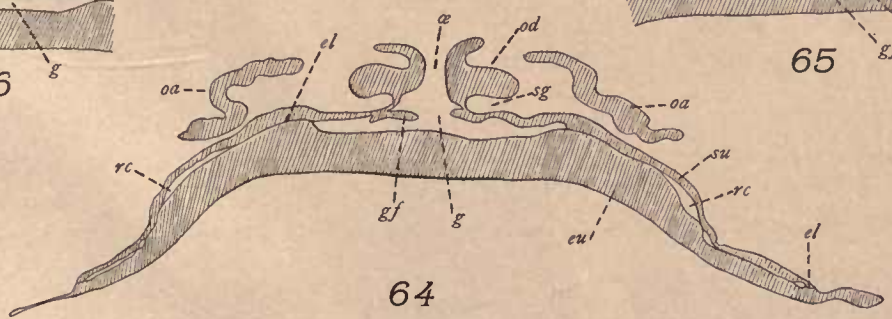
63



66



65



64

RPB del.

BIGELOW, CASSIOPEA XAMACHANA.

Bigelow,R.P. 299231 QL377
Anatomy and development of H9B5
Cassiopea xamachana. BIOLOGY
LIBRARY
G

299231 QL377
Bigelow H9B5
BIOLOGY
LIBRARY
G

UNIVERSITY OF CALIFORNIA LIBRARY