

## THE SALPIDAE: A TAXONOMIC STUDY.

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In studying the interrelationships of the Salpidae, one finds the greatest significance attaching to three sets of organs—the gut, the nervous system, and the muscles, the symmetry or asymmetry of the body and its muscles being a somewhat distinct point worthy of considerable emphasis. Other features will occasionally be mentioned, but are of minor importance. In all of these particulars the solitary form is readily seen to be the more conservative, while the aggregated individuals diverge far more. This more plastic character of the aggregated form causes it to present a larger body of phenomena in which evidence of relationship may be seen. In studying the Salpidae we are fortunate in having in the life cycle of each species a conservative member, the solitary form, showing in larger measure ancestral traits, and a more divergent member, more sensitive to modern trends in the evolution of the family.

In most groups of animals the nervous system is found to be a conservative organ system, not liable to much modification from superficial influences. It is therefore, in general, one of the best sources of taxonomic evidence. In the Salpidae, on the other hand, some features of the nervous system are found to be quite inconstant. For instance, the number of the nerves radiating from the ganglion is found to be variable, the grouping of the fibers into nerves being different in different individuals, or even on the two sides, right and left, of the ganglion in the same individual. This inconstancy is probably connected with the fact that the nervous system of the Salpidae is secondarily simplified (“degenerate”). There are outgrowths from the ganglia of certain species, especially in the aggregated forms, and the character of these is constant within the species and of taxonomic significance.

<sup>1</sup> This paper is written by Maynard M. Metcalf. He has had the assistance of Miss Bell in studying the anatomy of the *Cyclosalpa*, and *Traustedia*, and all of the original drawings of these forms were made by her. Numerous other drawings, as noted in each instance, have been made by Mr. Hoyt S. Hopkins usually after careful independent study, and I wish to acknowledge my indebtedness to him not only for the drawings, but also for his observations, which have checked up and have supplemented my own.

The form of the horseshoe-shaped eye is much the same in the solitary individuals of all species, therefore little taxonomic data is found here. In the solitary forms of several species there are accessory eyes, or accessory portions of the horseshoe-shaped eye, and the character of these should be considered. But it is in the aggregated forms that the eyes furnish the chief taxonomic evidence. This evidence will be emphasized in the present paper. I have studied the eyes of the solitary and aggregated forms of all species of Salpidae except *Brooksia rostrata*, *Apsteinia magalhanica*, *Ritteria retracta*, *R. picteti*, *R. amboinensis*, *Thalia longicauda*, and *Traustedtia*, in none of which have the eyes of the aggregated forms been adequately studied for any profitable comparisons, except in the case of *Traustedtia multitentaculata*, for which Traustedt (1893) and Dober (1912) give meager data, which, however, will be seen to be significant. Göppert (1892) has made very accurate studies of the eyes of five species. Redikorzeff (1905) carefully reviews the structure of the eyes of three species, and Dober (1912) makes casual mention of the eyes of a number of species, figuring surface views with little detail. Citations will be made from all these sources.

Accessory, smaller eyes are present in the aggregated forms of a number of species. The number, form, position and histological condition of these accessory eyes, as well as the form, position and histological condition of the chief eye, will furnish usable evidence.

Divergent as are the eyes in the several subgenera and species of Salpidae, their structure is constant within the species, and so furnishes an abundance of taxonomic evidence. This evidence is of especial value, because the changes that have occurred in the phylogeny of these eyes have been so largely degenerative rather than adaptive. Adaptive divergence and convergence can be left out of consideration in connection with these degenerating organs. Such changes as have occurred in these eyes in their recent phylogeny probably have been due to trends within each species and not to adaptation to environment. The natural affinities of the species are therefore probably more clearly expressed than they could be were the freedom to change the structure of the eyes limited by relations of utility.

Reference to the chart on page 158 will show the classification of species which I have adopted, and it should be studied a few moments at this point, if my nomenclature is to be understood in the further reading of this paper. There seems little choice as to the purely academic question whether the subdivisions of the Salpidae given in this chart be taken as genera or subgenera. The argument from convenience would favor treating them as subgenera. Relationships are indicated with equal clearness according to either usage.

I have been fortunate in having for study, in addition to my own considerable collections, all the collections of Salpidae made by the

United States Bureau of Fisheries <sup>1</sup> since the year 1875, including extensive lots from the northern, the equatorial, and the southern Atlantic Ocean, from the Pacific Ocean off the South American and North American coasts, from the Hawaiian Islands, and from the Philippine Islands. In addition, I have received material of three species from the Naples Zoological Station. Through the courtesy of Prof. E. A. Andrews, of the Johns Hopkins University, I have received all of Prof. W. K. Brooks's collections of Salpidae, including the specimens of *Cyclosalpa floridana* from which he redescribed that rare species. Prof. W. E. Ritter, of the University of California, has also very kindly given me three good specimens of his *Cyclosalpa bakeri*, solitary individuals, one of which bears an old stolon, at the tip of which are well-formed individuals of the aggregated generation. From him I also received two wheels and a very large aggregated zoöid of *Cyclosalpa affinis* from the California coast. I wish to express my most hearty thanks for this material to Professor Ritter and Professor Andrews, to the United States Commissioner of Fisheries, and to the authorities of the United States National Museum, and I wish to acknowledge my indebtedness to the Naples Station for the privilege of purchasing their beautifully preserved material. I wish also to acknowledge with thanks the assistance given by the librarian of the United States National Museum in locating in the libraries of Washington and other cities some of the volumes in the literature of the Thaliidae which are not easy to obtain.

Subgenus CYCLOSALPA (de Blainville), 1827.

Five species of this subgenus have been described:

*Cyclosalpa pinnata* FORSKÅL, 1775, *type*.<sup>2</sup>

*C. affinis* CHAMISSO, 1819.

*C. floridana* APSTEIN, 1894, *b* (not 1906, *b*).

*C. bakeri* RITTER, 1905.

*C. virgula* VOGT, 1854.

Sigl (1912, *a* and *b*) has described as a distinct species *Cyclosalpa polae*, a form which so closely resembles *C. pinnata* that it can best be treated as a subspecies of *pinnata*, much as *Salpa aspera* is classed as a form of *S. fusiformis* and *S. bicaudata* as a subspecies of *Pegea confederata*.<sup>3</sup>

*Cyclosalpa pinnata* is the best known of the *Cyclosalpas*, especially through Brooks' extensive studies. *Cyclosalpa affinis*, which has been carefully studied by Ritter and Johnson (1911), is a closely related species. Very different from these are *C. floridana*, named

<sup>1</sup> Chiefly by the United States Bureau of Fisheries steamer *Albatross*.

<sup>2</sup> The author prefers the Latin form of this word, *typus*, when used in the strictly taxonomic sense, but he defers to the custom of the United States National Museum in its publications.

<sup>3</sup> The character of the eye, as well as the presence of appendages, justifies recognizing *bicaudata* as a somewhat distinct form.

by Apstein (1894, *b*), and *C. bakeri*, described by Ritter (1905). *Cyclosalpa virgula* is the sole representative of still a third division of the subgenus. Ritter's (1906, *b*) *Cyclosalpa retracta*, of which only the solitary form is known, seems very similar to Apstein's (1904) *Salpa amboinensis*, and with this species and with *S. picteti* of Apstein (1904) and *S. hexagona* of Quoy and Gaimard (1824) it forms a natural group intermediate in some respects between the Cyclosalpas and those Salpidae which have the gut compacted into a so-called "nucleus." This group I am naming *Ritteria* after Professor Ritter, who described the species *retracta*.<sup>1</sup>

The three species *punctata*, *asymmetrica*, and *magalhanica*, which I have named *Apsteinia*, after *Apstein*, who first described two of this group,<sup>2</sup> agree with the *Ritterias*, so far as known, and with *Cyclosalpa bakeri*, *C. virgula*, and *Brooksia rostrata* in the asymmetry of their muscles in the aggregated forms, all but *Apsteinia punctata* showing also asymmetry in the shape of the body. Asymmetry is somewhat less marked in the higher members of the family, especially in *Thalia*, *Thetys*, *Pegea*, and *Traustedia*.

The Cyclosalpas may be divided into two groups—the symmetrical forms, *Symmetricales*, including *C. pinnata*, *C. affinis*, and *C. floridana*, and the *Asymmetricales*, including *C. bakeri* and *C. virgula*. The asymmetry characterizes only the aggregated forms of these species and may be related to the manner of their arrangement upon the stolon. Well-developed stolons of *C. virgula* or *C. bakeri* have not been described. For *C. bakeri*, neither Ritter's (1905) description nor our specimens show any indication of the formation of whorls, though one of our stolons is very old with the zooids apparently ready to drop off. Ritter writes: "As to the whorls of zooids, it can only be said at present that the close similarity of this species to *Cyclosalpa affinis* and *C. pinnata* in the arrangement of the zooids in the chain makes it highly probable that the whorls are likewise much the same in the two." In the *Albatross* Philippines collections were three individuals of the aggregated form of this species which were 12 mm. in length, three times as long as Ritter's and our specimens from the California coast. These three delicate collapsed individuals are united together, but not in any way indicative of either the presence or absence of whorl formation. The three symmetrical species of *Cyclosalpa* are well known to form distal whorls upon their stolons. We have no evidence that the Cyclosalpas with asymmetrical aggregated individuals do form such whorls, and one suspects that they do not and that the asymmetry of their aggregated individuals is correlated with the conditions of crowding in a biserial<sup>3</sup> stolon.

<sup>1</sup> Ritter, 1906, *b*.

<sup>2</sup> Apstein (1894, *b*, and 1901).

<sup>3</sup> Of course pseudobiserial; really a uniserial chain with alternate links crowded out to opposite sides.

The Salpidae, other than the *Cyclosalpae*, none of them form whorls upon their stolons, and many of them show more or less marked asymmetry in the aggregated individuals. This asymmetry affects both the shape of the body and the arrangement of the muscles in the aggregated *Apsteinia asymmetrica* and *A. magalhancia*. It affects the arrangement of the muscles, but not the body form, in the globose *A. punctata*. It affects the shape of the body and somewhat the arrangement of the muscles, especially those of the base of the atrial siphon, in the aggregated forms of *Ritteria amboinensis* and *R. hexagona*, *Salpa maxima* and its variety *tuberculata*, *S. fusiformis* and its form *aspera*, and *Iasis zonaria*. The aggregated forms of *Salpa fusiformis* and *S. cylindrica* are really asymmetrical in the shape of the body and in the position of the atrial siphon and its sphincter muscles, though the asymmetry is less marked in these species. *Thalia*, *Thetys*, *Traustedia*, and *Pegea* show little asymmetry. Possibly a detailed study of the attachment of the individuals in the stolon might throw light upon the absence of asymmetry in these species, but we have not undertaken the study.

CYCLOSALPA PINNATA<sup>1</sup> (Forskål) (1775).

*Thalia* No. 1 and No. 2, No. 3 (?), BROWNE, 1756.

*Holothuria thalia* LINNAEUS, 1758 [=Browne, *Thalia* No. 1].

*H. caudata* LINNAEUS, 1758 [=Browne, *Thalia* No. 2].

*Salpa pinnata* FORSKÅL, 1775.

*S. cristata* CUVIER, 1804.

*S. caudata* LAMARCK, 1813.

*Dagysa* [species not named] HOME, 1814.

*Salpa thalia* LAMARCK, 1816.

*S. cyanea* DELLE CHIAJE, 1828.

*S. proboscidiialis* LESSON, 1830.

*Cyclosalpa pinnata* HERDMAN, 1888.

*Cyclosalpa pinnata* is in some regards the most primitive of the Salpidae. Its body muscles have a hoop-like arrangement in the solitary form (pl. 1, fig. 1), and are interrupted both dorsally and ventrally in the median plane. To those who believe with Brooks that the Salps are descended from Doliolum-like ancestors, the regular hoop-like arrangement of the muscles would seem primitive and their dorsal and ventral interruption secondary. Their regularity of arrangement seems almost surely primitive.

The bilateral symmetry of the aggregated zoöids in this species, and in the other *Cyclosalpae symmetricales*, might at first thought seem another archaic feature, but the accuracy of this suggestion depends perhaps upon whether the habit of forming whorls of zoöids upon the stolon is primitive or secondary, for, as already noted, the

<sup>1</sup> The identification of Browne's "*Thalia* No. 1" and "*Thalia* No. 2" as *Cyclosalpa pinnata*, solitary and aggregated forms, seems in all probability correct. However, as the identification is not beyond question, it does not seem best to displace the long established species name *pinnata*, substituting the name *thalia* which Linnaeus gave, following Browne.

asymmetry observed in so many of the Salpidae may be due to crowding in a biserial stolon. I see no sufficient evidence that the cyclic grouping of the zooids upon the stolon is more archaic than the biserial arrangement, except the fact that it occurs in those species which for other reasons we regard as the most primitive.

We have even in *Cyclosalpa pinnata* an interesting bit of asymmetry in the larger eyes of the aggregated individuals, which Metcalf<sup>1</sup> has mentioned. "Göppert<sup>2</sup> points out that in *Salpa maxima*, in individuals from the right side of the chain, the long axis of the eye is directed obliquely toward the right, while in individuals from the left side of the chain the eye points toward the left. This gives importance to a slight though constant peculiarity I have observed in the otherwise symmetrical eye of the chain *Cyclosalpa pinnata*, which serves to determine the relation of the animal to the stolon. In this group the individuals stand with both their antero-posterior and dorso-ventral axes at right angles to the [young] stolon. In the large dorsal eye of each individual, on the side distal from the former attached end of the stolon, there is a small unpigmented spot in the midst of the pigment area of the second region of the eye." This minute asymmetrical feature is related to the position of the zooid in the at first biserial stolon. Only when the individuals have reached their adult form do they assume the whorl grouping. Even in *Cyclosalpa pinnata*, therefore, we find a trace of asymmetry in the aggregated form, and this is found to be correlated with the position of the zooids in the stolon in its earlier stages, before the whorls are formed and while the arrangement is that of a double series of individuals, as in the stolons of all the Salpidae except the *Cyclosalpaes symmetricales*. This suggests that the habit of forming whorls at the tip of the stolon in the *Cyclosalpaes symmetricales* is secondary.

It is in the anatomy and development of the eyes in the aggregated form that we find the clearest evidence of the relatively archaic character of *Cyclosalpa pinnata*. One familiar with the condition of the eyes in the several species of Salpidae could hardly believe that they show an ascending series culminating in the elaborate and histologically perfect eye of *Cyclosalpa pinnata*, though in my first papers upon this subject I took this position, which now seems to me so untenable.<sup>3</sup> We seem clearly to be dealing with a series of increasingly degenerate forms, so far as the structure of the eyes is concerned. This degeneration goes so far that in its most extreme condition one doubts the functional value of the organs affected. Such an imperfect and possibly functionless eye as we find at its worst could hardly be regarded as the starting point of an ascending

<sup>1</sup> Metcalf (1893, c), p. 370.

<sup>2</sup> Göppert (1892).

<sup>3</sup> Lest it be thought that I may have been influenced in this former conclusion by my teacher, Prof. W. K. Brooks, I would say that at the time of my writing the former papers he demurred from this opinion.

series of increasingly developed eyes. The character of the rod cells in the imperfect eyes of the more aberrant Salpidae seems clearly to indicate degeneration. A typical rod cell from any well-developed Salpa eye would be about as shown in figure 1. Compare this with a group of rod cells from, say, *Pegea confederata* (fig. 2). In the former the glassy modification of the protoplasm, which constitutes the "rod" (represented in black in the figures), is regular and is found at one end of the cell, as is characteristic of the rod cells of the eyes of vertebrates, of Amphioxus, of the ascidian tadpole, and of most invertebrates. On the other hand, in those species of Salpidae whose eyes I would consider degenerate, the rod cells are very irregular in shape, are irregularly crowded into masses instead of being arranged as a regular epithelium, and each rod cell has the protoplasm usually of its whole periphery converted into the typical glassy substance, this glassy layer being of different thickness in different rod cells and in different portions of the same cell.

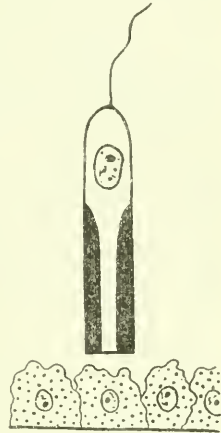


FIG. 1.—A SCHEMATIC REPRESENTATION OF A SINGLE ROD CELL AND FOUR PIGMENT CELLS FROM THE EYE OF A SALPA. FROM METCALF (1893, c).

Taking, then, as our starting point *Cyclosalpa pinnata*, which, from the arrangement of its muscles and the structure of its eyes, seems one of the two most primitive of the species of Salpidae, let us note its general structure, giving attention to a few new features we have discovered. Then let us briefly review the anatomy and development of its eyes, as already described by Metcalf (1893, c). Having refreshed our memories of the salient features in this species, we can proceed to comparisons with other species.

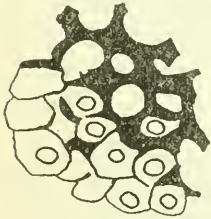


FIG. 2.—PEGEA CONFEDERATA, A GROUP OF ROD CELLS FROM THE DORSAL EYE OF THE AGGREGATED ZOÏD. OBSERVE THEIR IRREGULARITY OF FORM AND THE IRREGULARITY OF FORM AND THE UNEQUAL THICKENING OF THEIR CELL WALLS.  $\times 340$  DIAMETERS.

*Cyclosalpa pinnata* is represented in the collections of the United States National Museum by the following catalogue numbers:

Cat. No. 6460, U.S.N.M. (solitary form) from Naples Zoological Station; two specimens.

Cat. No. 6461, U. S. N. M. (aggregated form) from Naples Zoological Station; nine specimens, united.

Cat. No. 6553, U.S.N.M. (aggregated form), *Albatross* station D, 5456, east coast of Luzon, San Bernardino Strait, to San Miguel Bay, Philippine Islands; June 7, 1909; surface; surface temperature  $86^{\circ}$  F.; one specimen.

CYCLOSALPA PINNATA, solitary form.<sup>1</sup>

Plate 1, figs. 1 and 2; plate 2, fig. 6.

Referring to figure 1, which shows the solitary form of *Cyclosalpa pinnata* as seen from the right side, observe the general shape of the body, keg-shaped, with the anterior end rather abruptly narrowed and the posterior end more tapering. The test is delicate and thin, being thickest ventrally. The luminous organs are seen halfway up each side of the body, as a series of five spindle-shaped glands between the body muscles. In structure they resemble blood lacunae full of blood corpuscles, and such may have been their derivation, though now their cells are modified, each containing numerous yellow granules of a substance which by oxidation produces light. The luminous organs of *Pyrosoma* are very similar histologically.

The ribbon-shaped muscles are shown in figure 1. For convenience of description these may be divided, chiefly according to function, into body muscles (indicated by Roman numerals), oral muscles, and atrial muscles. There is also another muscle which in the more primitive Salpidae is associated with the body muscles but in the more modified species is more connected with the oral muscles. This is usually called by German zoölogists the "Bogenmuskel." We will refer to it as the intermediate muscle (*i. m.* in the figures).

Of the *body muscles* there are seven, as numbered in the figure. They are arranged like the hoops of a keg, but each is interrupted on the mid line both dorsally and ventrally. The intermediate muscle is continuous ventrally with its fellow of the other side, as are the lip muscles. It probably shares with the oral muscles the function of strengthening the lower lip which acts as a valve to close the mouth when the water is expelled through the atrial aperture by the contraction of the body muscles (fig. 6).

Most prominent of the oral muscles are the horizontal *oral retractors*, one on each side, running forward from the first body muscle to the angle of the mouth (fig. 1). Anteriorly each divides into two muscles, *oral sphincters*, which run around the lower lip, one near the edge (*l. 1*), the second a little farther back (*l. 2*). The anterior two sphincter muscles of the upper lip (*u. 1* and *u. 2*) are almost but not quite united to the retractor at their ventral ends. In addition to the oral retractor just described and the sphincters united to or acting in conjunction with it, there is on each side a more *ventral oral retractor*, running from lower down on the first body muscle diagonally forward and upward, passing outside of the intermediate muscle, to a point

<sup>1</sup> The drawings and descriptions are based on studies of abundant material of both solitary and aggregated forms of this species, chiefly from the central Mediterranean Sea and off the Atlantic coast of North America. Compare United States National Museum Collections, Cat. No. 6460.



a little posterior to the place of branching of the dorsal oral retractor. The ventral retractor is here internal to the dorsal retractor. At the point where the two retractors are at the same level, the ventral retractor divides, giving rise to a ventral branch, which forms the third sphincter of the lower lip (*l. 3*), and to a wider dorsal branch which after a very short course divides to form the third (*u. 3*) and fourth (*u. 4*) sphincters of the upper lip. We may describe the oral muscles as made up of two retractor systems, one consisting of the dorsal retractor and the anterior two sphincters of each lip, the second consisting of the ventral retractor, the third sphincter of the lower lip and the third and fourth sphincters of the dorsal lip. Well up on the side of the fourth sphincter of the dorsal lip there arises a muscle band, the dorsal horizontal muscle, which runs backward and dorsal-ward to unite with the dorsal end of the intermediate muscle, the fused muscle continuing its course postero-dorsally to a point at the side of the ganglion.

The *atrial muscles* in the solitary form of this species consist only of a series of sphincters which are complete hoops. The anterior atrial sphincter is a strong band and may function with the body muscles in expelling water from the body, but its position, well out on the base of the atrial siphon, and its complete hooplike character, make it natural to assign it to the atrial series. The adjacent sphincter is peculiar in the fact that its ventral portion bends forward, runs across the basal sphincter on the inside and crosses the ventral line well toward the last body muscle, at the level of the posterior ends of the two intestinal caeca. A higher development of a somewhat similar arrangement in the solitary form of *Cyclosalpa virgula* (pl. 11, fig. 26) gives the diagonal course of the ventral end of this muscle an atrial retractor effect. In *Cyclosalpa pinnata* this effect is hardly secured. The rest of the atrial sphincters are very delicate. They branch and the branches from one sphincter unite with other sphincters, forming a slight irregular network.

The relative strength of the several muscles is correlated with the amount of work they do. The strong body muscles, by vigorous contraction, expel the water from the pharyngo-atrial chamber within the body. Those who have observed living Salps, describe this contraction as ejecting water with considerable violence, throwing the whole Salpa forward a considerable distance. The oral sphincters have to resist the pressure of this water, preventing it from flowing out through the mouth. They are so much weaker than the combined strength of the whole series of body muscles that they would be unable successfully to resist the pressure of water caused by the contraction of the body muscles, were it not that the oral sphincters are

aided by a valve device, to be described in the next paragraph. The atrial sphincters are for the most part very delicate and able to perform little labor, but their function is merely to close the atrial aperture during diastole of the body. The enlarging of the body after contraction is due to the elasticity of the test, which in this species is very delicate. When once the atrial pore is closed, the suction due to the enlarging of the body will tend to keep it closed. Very slightly developed sphincters therefore are enough. It is important to have a series of sphincters instead of a single one at the edge of the atrial siphon. If only the edge of the aperture closed, leaving the rest of the siphon widely open, the tip would be introverted, and then even a strong sphincter at the edge of the aperture could hardly prevent water entering the body through the atrial pore. But the narrowing or complete closing of the whole atrial siphon avoids any danger of such introversion. The heavier sphincter muscle at the base of the atrial siphon probably aids in preventing the siphon as a whole from becoming introverted.

Reference was made in the previous paragraph to the *valve* action of the lower lip. The structural conditions bringing about this effect are shown in figure 6, plate 2, a dorso-lateral-anterior view of the mouth region of the solitary *Cyclosalpa pinnata*. The lower lip is turned inward, forming a deep rounded pouch. The edge of the lip is a thin irregular flap. At the base of the flap are the two admarginal sphincter muscles. Further ventral is the third sphincter, which serves to support the bulging middle portion of the pouch, while the admarginal sphincters cause a stronger contraction of the inturned portion of the lip, giving the pouch form to the whole lower lip. The backward pull of the dorsal oral retractor goes directly to the inturned portion of the lower lip, so that this is very strongly inturned. The contraction of the dorsal lip muscles, of the dorsal retractor system, brings the upper lip down into contact with the lower lip. The thin flap at the inturned edge of the lower lip lies against the inside of the contracted upper lip, serving effectively to prevent any egress of the water. The ventral retractor, with its two dorsal sphincters and one ventral sphincter, strengthen and support both lips. The actual closing effect, however, is due chiefly to the dorsal retractor system.

The positions of the gill, dorsal tubercle, endostyle, and peripharyngeal bands are sufficiently indicated in figure 1. The form of the aperture of the dorsal tubercle is shown in figure 2.

The *alimentary canal* consists of the huge pharynx (imperfectly demarcated by the gill from the atrium), the esophagus, intestine, and two caeca. No well-marked stomach is found. The flaring trumpet-shaped esophageal aperture lies at the ventral end of the

gill, the ciliated cells of the gill being continued into the esophagus into which they constantly carry a stream of mucus and entangled food particles. As in *Pyrosoma*, there is a line of cilia from the esophageal aperture to the posterior end of the endostyle, where it is continuous with the lateral ciliated bands of the endostyle. The direction of the currents caused by these cilia is not known. (For a drawing of this line of cilia in another species see figure 38, page 65.) The narrow esophagus curves to the right, then to the left, and is continued into the intestine. The curve of the gut is therefore a left-hand curve as in the Ascidians. The first portion of the intestine is somewhat enlarged, and might possibly be called the stomach, but in reality there is no demarcated stomach. The intestine is straight. It stretches along the dorsal side of the whole length of the gill, the anal opening leading into the atrium, just back of the ganglion. At the place where the esophagus joins the intestine two caeca arise. These turn backward, lying one on each side of the mid line. The position of the anal aperture in this species, far forward in the body, should not be seriously disadvantageous, for it is behind the gill, and there should be little danger of clogging the cilia currents of the gill with the fecal wastes.

The *heart* lies on the mid-ventral line a short distance in front of the esophageal aperture, between the fifth and sixth body muscles, in connection with a slight evagination of the mid-ventral surface of the mantle.

The *stolon* arises in front of the heart, on the mid-ventral line, and runs forward in the median plane. As shown by Brooks (1886), it is at first a single series of buds lying each with its ventral surface toward the free tip of the stolon. Later the alternate links of this chain become crowded out to opposite sides of the stolon, forming a pseudobiserial chain of buds. At the tip of the stolon, whorls of from  $5^1$  to  $15^2$  individuals are formed. None of our specimens show more than two whorls, one fully formed, the other beginning to assume the radial arrangement.

Opposite the intermediate muscles and near the median line are two languet-like protuberances of the mantle (*v. l.*, fig. 1), one on each side, extending into the test and nearly to its outer surface. Streiff (1908) has shown these in his figures. They are present also in *Cyclosalpa bakeri*. They suggest comparison with the more numerous and more developed mantle protuberances in *Thalia* and *Trustedtia*.

The spheroidal ganglion and nerves need no description here. Above the ganglion, and resting upon it, is a horseshoe-shaped *eye* with the

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<sup>1</sup> Sigl, 1912, *a* and *b*

<sup>2</sup> Our specimens from Naples.

ends of the horseshoe toward the front (fig. 3). Over the lateral and posterior portions of the eye runs the continuous layer of pigment cells (fig. 4). Dorsally these are just beneath the ectodermal epithelium; more ventrally they lie in the midst of the cells of the optic ridge: but in all regions they lie inside the continuous limiting mem-

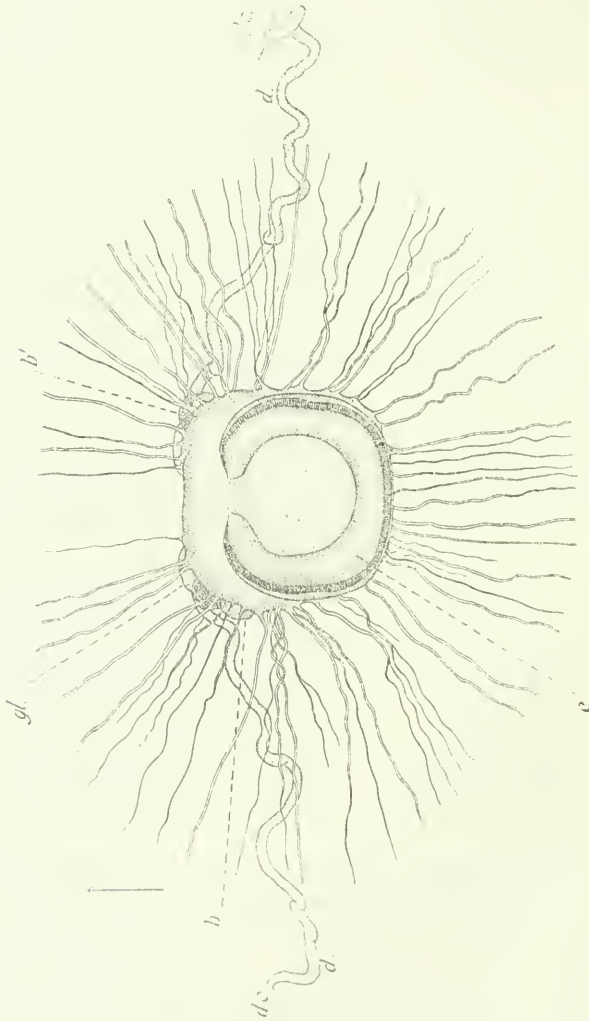


FIG. 3.—CYCLOSALPA PINNATA, SOLITARY FORM, DORSAL VIEW OF THE EYE, GANGLION, AND NERVES. THE DISKS OF THE NEURAL GLAND (*gl.*) SHOW A LITTLE BELOW THE GANGLION, AND THE LARGE-CELLED (*b'*) AND SMALL-CELLED (*b*) OUTGROWTHS FROM THE GANGLION CAN ALSO BE SEEN. X 107 DIAMETERS. FOR EXPLANATION OF THE INDEX LETTERS FOR THIS AND ALL OTHER TEXT FIGURES. SEE THE "EXPLANATION OF TEXT FIGURES AND PLATES" AT THE END OF THIS PAPER.

brane of the eye and ganglion. Along the whole inner side of the horseshoe are the elongated rod-cells with their thin-walled ends directed toward the center of the horseshoe, while their rods are directed toward the pigment layer. Between the rods and the pigment cells is a layer of intermediate cells. The innervation of the rod-cells has not been found by any observer in the solitary form of any species.

It is necessary to refer briefly to the embryonic development of this eye. Early in its development the central nervous system of the



FIG. 4.—CYCLOSALPA PINNATA, SOLITARY FORM. A TRANSVERSE SECTION OF THE GANGLION AND THE EYE.  $\times 150$  DIAMETERS. FROM METCALF (1893, c).

embryo is a short hollow tube opening in front through a funnel. Later the walls of the posterior portion of the tube thicken, first

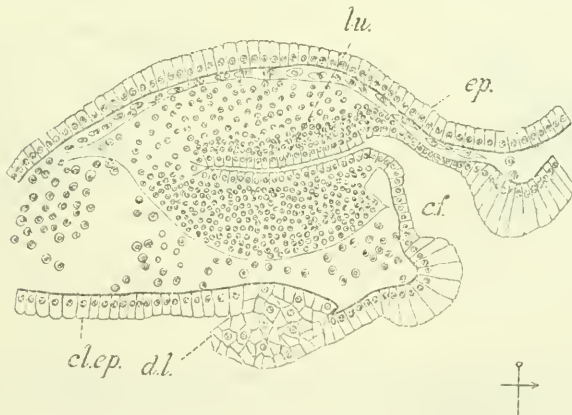


FIG. 5.—CYCLOSALPA PINNATA, EMBRYO, A SAGITTAL SECTION OF THE DEVELOPING GANGLION AND CILIATED FUNNEL.  $\times 180$  DIAMETERS. FROM METCALF (1893, c).

ventrally, then dorsally (fig. 5), to form the ganglion, the lumen of the tube becoming obliterated. At the same time the anterior por-

tion of the tube degenerates, the funnel becoming entirely separated from the ganglion. The funnel becomes the dorsal tubercle. The central cells of the ganglion degenerate and their place is taken by a feltwork of fibers, which in section has a punctate appearance. As the

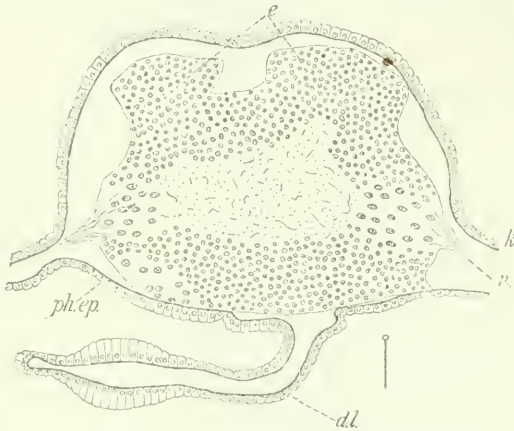


FIG. 6.—CYCLOSALPA PINNATA, EMBRYO, A TRANSVERSE SECTION OF THE DEVELOPING GANGLION AND EYE.  $\times 150$  DIAMETERS. FROM METCALF (1893, c).

central cells are degenerating, the dorsal cells of the ganglion are increasing in number, and some of them are pushing up to form a ridge, in the shape of a horse-shoe, in which later the histological differentiation occurs which gives the adult condition of the eye. The rudiment of the eye is, from the first, horseshoe-shaped and it continues in this form (fig. 6).

But one other set of structures needs mention in this description—the *neural glands* and the outgrowths from the ganglion which are connected with them. Ventral to the ganglion, on the right and on the left, is a flattened horizontal chamber opening to the atrium by

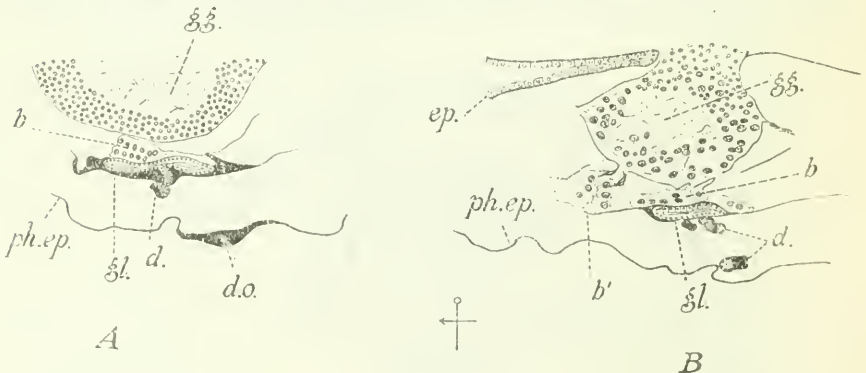


FIG. 7.—CYCLOSALPA PINNATA, AGGREGATED FORM, PARASAGITTAL SECTIONS THROUGH THE GANGLION, ONE NEURAL GLAND, AND THE OUTGROWTHS FROM THE GANGLION; FROM A DEVELOPING ZOÏD.  $\times 139$  DIAMETERS. FROM METCALF (1893, c).

a long slender and much coiled duct (figs. 7 and 8. See also fig. 71, which shows the similar, though larger, disks and ducts in the aggregated zoïds of *Salpa maxima*). The walls of the chamber and of its duct consist throughout of a single layer of epithelial cells. These are the structures which Dober (1912) and others have called otocysts. I know of no indication of otocystic function (Metcalf, 1893, c and

1899). In some other species they are clearly glandular, forming the secretion by proliferation of cells from the epithelium and their degeneration.

In the Salpidae the neural glands arise from the epithelium of the pharyngo-atrial chamber, in a manner described by Metcalf (1892, 1893, *b* and *c*). This is entirely different from the neural gland of Ascidians and Pyrosoma, which arises from the wall of the neural tube. The gland in Ascidians and Pyrosoma opens into the dorsal tubercle by a duct which is the persistent anterior end of the nerve tube. In the Salpidae the neural glands have never at any time any connection with the dorsal tubercle or the nerve tube, its ducts, like the glands themselves, coming from the epithelium of the pharyngo-

atrial cavity. There seems, at first thought, no ground for any homology between the neural glands in Salpidae and the neural glands of other Tunicates, and we have no fully convincing reason for believing their functions to be the same. But common function and true homology between the glands of Salpa and the gland of Ascidians is suggested by the conditions in *Ascidia mammillata* and some of its

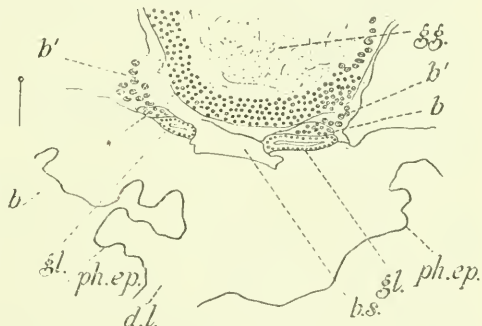


FIG. 8.—CYCLOSALPA PINNATA, AGGREGATED FORM, A TRANSVERSE SECTION THROUGH THE VENTRAL HALF OF THE GANGLION, THE NEURAL GLANDS, AND THE OUTGROWTHS FROM THE GANGLION.  $\times 130$  DIAMETERS. FROM METCALF (1893, *c*).

nearest relatives, in which the very slender and greatly elongated duct leading from the neural gland to the ciliated funnel<sup>1</sup> is much branched laterally, these branches connecting with the pharynx by small ciliated funnel-shaped pores. In these forms, the neural gland opens to the pharynx by the ciliated funnel proper and also by very numerous lateral pores.<sup>2</sup> In other Ascidians the neural gland opens only by way of the ciliated funnel. Embryonic Salpas and young buds have the neural tube opening forward into the ciliated funnel, but they have no neural gland. Later the neural tube closes and its connection with the ciliated funnel is lost. Then a new type of neural gland, as described, develops from the pharyngo-atrial epithelium. This may have arisen ancestrally from structures like the lateral ducts and pores of the neural gland in *Ascidia mammillata* and its relatives. In *Octacnemus*, which Herdman (1888) has placed among the Salpidae, I found the neural gland to be wholly of the Ascidian type. This is one of several features in its structure that have led me to count

<sup>1</sup> This is really the anterior end of the nerve tube.

<sup>2</sup> See Metcalf (1900), section I.

*Octacnemus* as an aberrant offshoot from the primitive Ascidiaceans, whose nearest extant relatives are the Clavelinidae.<sup>1</sup> To this classification Ritter (1906, *a*) has given his approval, and Herdman (1904) has recently expressed his agreement.

Above the neural gland, on each side, are two outgrowths from the ganglion, one of small cells continuous with the smaller cells of the ganglion itself (fig. 8, *b*), the other a mass of large cells (*b'*) like the larger cells of the ganglion. Both these masses of cells arise as outgrowths from the ganglion. The small-celled group retains its continuity with the ganglion. The large-celled group, on the other hand, is distinct from the ganglion, but is connected with it by numerous well-developed nerve fibres.

Many have studied the solitary form of *Cyclosalpa pinnata*. There are some discrepancies, for the most part slight, between our work and that of others, but it seems hardly well to burden this paper with a detailed discussion of these discrepancies. It is doubtful just how far the differences in description may be taken as indicating variation in structure in the species, and to what extent allowance must be made for the personal equation of the observers. In our observation of many specimens from the Atlantic Ocean and from the Mediterranean Sea we have found the structure uniform as we describe it. The very careful work of Streiff upon the muscles agrees with our observations, except in two minor regards. He does not show contact between the fourth oral sphincter muscle of the dorsal lip and the horizontal band which runs up and back to join the dorsal portion of the intermediate muscle. In other species we have found divergence in the near approach or actual connection of such accessory muscle bands, and we do not doubt the accuracy of Streiff's description. He does not show the diagonal second atrial sphincter which we have described as showing a rudimentary atrial retractor arrangement. We find no other authors' figures sufficiently accurate in detail for profitable comparison of this point. All our specimens show the condition which we figure.

CYCLOSALPA PINNATA, aggregated form.<sup>2</sup>

Plate 1, figs. 3 and 4; plate 2, figs. 5, 7, and 8.

The aggregated form of *Cyclosalpa pinnata* is shown in figure 3, which gives a view from the right side. One observes the presence of a stalk of attachment, or peduncle, by which the individual was joined with the other zooids into a whorl. Postero-ventrally the visceral region of the body is bulged out, the single intestinal caecum pushing out into a slight evagination of the mantle, suggesting comparison with the visceral protuberance ("post-abdomen" of Ritter) seen in *Cyclosalpa floridana* (pl. 5, fig. 15), *C. bakeri* (pl. 8, fig. 21),

<sup>1</sup> See Metcalf (1900), p. 579.

<sup>2</sup> United States National Museum Collection. Cat. No. 6461.



and *C. virgula* (pl. 12, fig. 29). The lower lip is inrolled to function as a valve, much as in the solitary form. This valvular action of the lower lip is characteristic of all species of Salpidae, both solitary and aggregated forms, and need not be mentioned in the reference to other species unless it shows some feature of special interest.

The *test* in the aggregated form is thicker than that of the solitary form, but is no less soft. The luminous organ is a single large gland on each side in the interval between the second and third body muscles.

There are four body *muscles* (I to IV). There is but a single oral retractor, with which are united the three sphincter muscles of the lower lip (*l. 1, l. 2, l. 3*). The first sphincter of the upper lip (*u. 1*) is almost, but not quite, continuous with the retractor. The second and third sphincters of the dorsal lip (*u. 2* and *u. 3*) are united to the intermediate muscle. There is no ventral oral retractor such as is found in the solitary form. The absence of this ventral retractor accounts probably for the difference in the insertion of the third sphincter of the lower lip (*l. 3*), which in the solitary individual belongs to the ventral retractor system, but in the aggregated individual is attached to the single retractor here present. The intermediate muscle (*i. m.*) bends backward at its dorsal end and unites with the upper portion of the first body muscle. There is an approach, but no union, of these muscles in the solitary form. The body muscles are much less regularly arranged in the aggregated form than in the solitary individuals. All are continuous dorsally across the mid line. Ventrally, as in the solitary form, the intermediate muscle is in contact with its fellow of the opposite side, but it is not continuous across the mid line. Each is continued ventrally into the peduncle. In young zoöids these anterior peduncle muscles are distinct except that they touch at their tips. In older zoöids they are closely appressed from their tips in the peduncle almost up to the mid-ventral line of the body. The intermediate muscles are therefore distinct, though at first glance in an older zoöid they appear united ventrally.

The aggregated individual differs from the solitary in having the last body muscle continuous ventrally with its fellow of the other side. The fused muscle (*v.*) turns forward on the mid line and runs a short distance toward, but not to, the gut. Figure 3 is slightly distorted, showing this part of the muscle as a flat band, rather than a line as it should appear in edge view.

We find in the aggregated form of this species a muscle not before described, lying on the mid-ventral line, beneath the intestine (*v.*) We have again distorted our figure to show this *visceral muscle* as a broad band instead of as a line which would be its true appearance in side view. Posteriorly the visceral muscle seems to be connected with the funnel-shaped group of connective tissue fibers whose apex

is near the ventral end of the last body muscle. These connective tissue fibers probably establish a functional connection between the ventral end of the last body muscle and the visceral muscle, so that their contraction probably produces much the same effect that would be secured if they were actually continuous. The last body muscle is similarly continued into the visceral region in *Cyclosalpa affinis* (pl. 3, fig. 10) *C. floridana* (pl. 5, fig. 15), and *C. bakeri* (pl. 8, fig. 22). None of these, however, shows a separate visceral muscle. There is nothing comparable in *C. virgula* (pls. 11, 12, and 13).

The intermediate muscles, which in older zooids are in contact ventrally, are continued as a strong double muscle through the peduncle almost to the stolon (or core of the whorl). On each side of the body the first body muscle unites with the third to form a broad band of muscle, which is similarly continued through the peduncle toward the core of the whorl, but it is not prolonged so far into the peduncle as are the intermediate muscles. There is one of these posterior peduncle muscles on each side. They are entirely independent of each other.

The sphincter muscles of the atrial siphon are unbranched. Each is a complete hoop. The first is a strong muscle and is connected with the last body muscle by a horizontal band which functions as an atrial retractor.

The gill is as in the solitary form. The outline of the aperture of the dorsal tubercle is shown in figure 4 (pl. 1). No comment is needed upon the endostyle and peripharyngeal bands.

The *gut* of the aggregated form differs from that of the solitary form in the presence of but one caecum and in the ventral position of the intestine, below the endostyle, the anus being well forward toward the front of the pharynx. It would seem that this position for the anus would be very disadvantageous, discharging feces in such a manner that they would become entangled in that current of mucus which by action of the cilia is constantly being carried forward on the endostyle, up on the peripharyngeal bands and back on the gill to the esophageal aperture.

The *heart* (*h.*) lies to the right of the intestine, a little higher up than in the solitary form.

The *ovary* is in front of the fourth body muscle, the oviduct leading forward almost to the third body muscle. The elongated *testis* lies between the endostyle and gut (pl. 2, fig. 5 *t.*). Its duct opens near the anus, as in other *Cyclosalpas*, but in this species the position of both apertures is further forward than in any other aggregated form in the Salpidae.

The ganglion is flattened on its dorsal surface where lies the large *eye* (pl. 2, figs. 7 and 8). The ganglion contains two pairs of minute hemispherical eyes, each of which is composed of about 25 rod cells (fig. 9, p. 23). The posterior pair lie one on side each of the middle point

of the posterior face of the ganglion (*ey*). These have no pigment. The thin-walled ends of the rod cells lie outward in the eye and toward the surface of the ganglion. The dorsal pair of minute eyes lie one below the base of each limb of the horseshoe-shaped larger eye, on the dorsal surface of the ganglion (*ex*). The rod ends of their rod cells are turned toward the surface of the ganglion, immediately below the pigment of the larger eye. No innervation has been found for any of the small eyes within the ganglion of this or other species of Salpidae. In some species pigment is found associated with them.

Projecting forward from the middle of the dorsal surface of the ganglion is a large horseshoe-shaped eye nearly equal in bulk to the whole ganglion (pl. 2, figs. 7-8). The middle of the curve of the

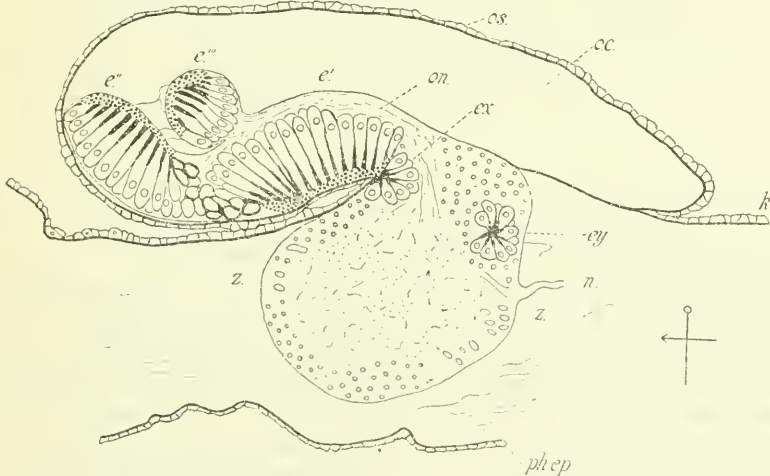


FIG. 9.—CYCLOSALPA PINNATA, AGGREGATED ZOÏD, A PARASAGITTAL SECTION THROUGH THE GANGLION, THE ACCESSORY EYES OF THE LEFT HALF OF THE GANGLION, AND THE LEFT LIMB OF THE DORSAL EYE. THE FIGURE REPRESENTS THREE SECTIONS COMBINED.  $\times 150$  DIAMETERS.

horseshoe and its two ends are thick; the sides are slender. Behind and a little above the curved portion of the eye is a laterally elongated plug of optic cells, lying above the space which intervenes between the two limbs of the horseshoe. The figures show, without much description, the structure of this large eye. Figure 8 (pl. 2) is a dorsal view and figure 7 (pl. 2) a view from the right side of the eye and ganglion. Figure 9, above, shows a parasagittal section and indicates also the position of the minute eyes in the ganglion. Figure 10, page 24, is from a transverse section of the posterior limbs of the horseshoe. Figure 1, page 11, is a diagrammatic drawing of one rod cell and a few pigment cells. One readily sees in figure 9, above, the innervation of the rod cells of the limbs of the horseshoe and of the plug, but no one has yet shown for the adult the innervation of the rod cells in the arch of the horseshoe. In the nearly mature eye, however, I have shown<sup>1</sup> nerve fibers passing down between the limbs of the horseshoe to innervate

<sup>1</sup> Metcalf, 1893, c. cf., plate 48, figure 9, o. n''.

the ventral thin-walled ends of the rod cells of the arch of the horseshoe. There are no intermediate cells between the rods and the pigment cells in the eyes of the aggregated *Cyclosalpa pinnata*. Such intermediate cells are present in the eye of the solitary form. In the aggregated zoöids of *C. pinnata*, as in those of all other species whose eyes have

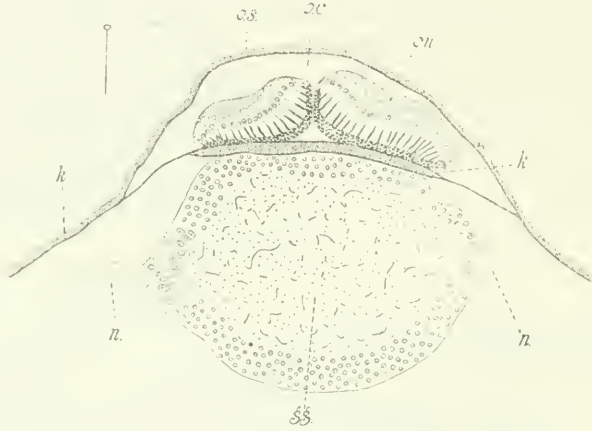


FIG. 10.—CYCLOSALPA PINNATA, AGGREGATED ZOÖID, A TRANSVERSE SECTION THROUGH THE GANGLION AND THE TWO POSTERIOR LIMBS OF THE DORSAL EYE.  $\times 150$  DIAMETERS. FROM METCALF (1893, c).

been studied, the pigment cells are superficial. In the solitary *C. pinnata* they lie deeper among the cells of the optic ridge.

Göppert (1892) has shown the presence of ovoid phacosphaeres in the rod cells of the large eyes of the aggregated forms of *Cyclosalpa pinnata* and *Pegea confederata*, also in the eye of the solitary *Salpa maxima*. I have not succeeded in demonstrating these, but doubtless careful work upon better preserved material would show them. One can not doubt the accuracy of Göppert's studies.

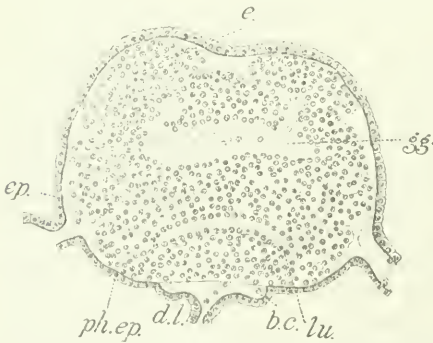


FIG. 11.—CYCLOSALPA PINNATA, AGGREGATED FORM, A TRANSVERSE SECTION OF THE DEVELOPING EYE. THE TWO ANTERIOR LIMBS (e) OF THE AT THIS STAGE HORSESHOE-SHAPED EYE ARE SHOWN.  $\times 200$  DIAMETERS. FROM METCALF (1893, c).

of the several species of Salpidae. When first discernible the rudiment of the eye is exactly similar to that in a young embryo of the solitary *Cyclosalpa pinnata*, a horseshoe-shaped ridge of cells, above the ganglion, with the ends of the horseshoe anterior (fig. 11). The simple horseshoe shape of the eye of the solitary

form is doubtless therefore primitive. This is also indicated by the fact that in the solitary forms of all Salpidae the eye has this horseshoe form.

In later stages of development of the aggregated zoöid, the arch of the horseshoe separates from the ganglion (fig. 12) and rises up, the whole rudiment of the eye swinging at first upward then forward and

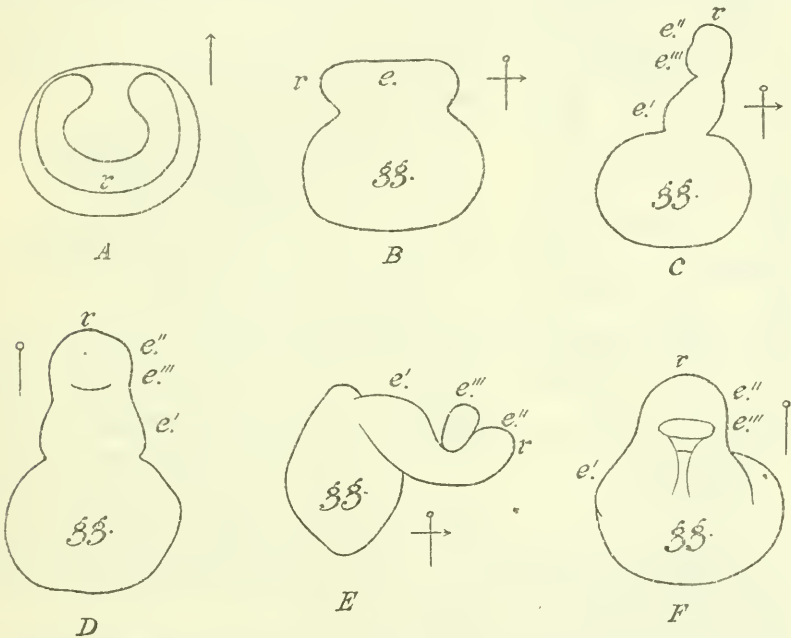


FIG. 12.—CYCLOSALPA PINNATA, AGGREGATED ZOÖID, DIAGRAMS SHOWING THE FORWARD ROTATION AND TRANSFORMATION IN SHAPE OF THE DORSAL EYE. FROM METCALF AND JOHNSON (1905); e, EYE; gg, GANGLION; r INDICATES IN EACH CASE THE SAME REGION OF THE EYE.

A, A DORSAL VIEW OF THE GANGLION AND THE EYE OF A SOLITARY SALPA. THE HORSESHOE-SHAPED EYE IS ABOVE THE GANGLION, WITH THE ENDS OF THE HORSESHOE POINTING FORWARD. THE DORSAL EYE OF THE VERY YOUNG AGGREGATED ZOÖID HAS THE SAME FORM.

B, THE SAME SEEN FROM THE RIGHT SIDE.

C, THE GANGLION AND THE EYE OF AN IMMATURE AGGREGATED ZOÖID. THE EYE HAS NOW ROTATED FORWARD AND UPWARD THROUGH AN ARC OF ABOUT 90°. THAT SURFACE OF THE EYE WHICH WAS DORSAL WHEN THE EYE WAS HORIZONTAL (B) IS NOW ANTERIOR.

D, THE SAME EYE AND GANGLION AS IN C, BUT VIEWED FROM BEHIND. THE EYE IS IN THE FORM OF A FLAT PLATE, THE HOLLOW OF THE HORSESHOE HAVING BECOME FILLED WITH CELLS.

E, THE EYE AND GANGLION OF AN ADULT SEEN FROM THE RIGHT SIDE. THE EYE HAS SHIFTED 90° STILL FURTHER FORWARD AND IS AGAIN HORIZONTAL, BUT WITH ITS FORMER POSTERIOR PORTION ANTERIOR AND ITS FORMER DORSAL SURFACE VENTRAL.

F, DORSAL VIEW OF THE SAME GANGLION AND EYE AS IN E. THE EYE IS NOW SPLIT POSTERIORLY INTO TWO LIMBS, RIGHT AND LEFT, BEING AGAIN HORSESHOE-SHAPED.

downward, the two ends of the horseshoe remaining attached to the dorsal surface of the ganglion and forming the pivots upon which the eye rotates. By this rotation the originally ventral surface of the rudiment of the eye becomes first posterior then dorsal. Three other changes occur in the developing eye during the gradual completion of this forward rotation. First the space between the limbs of the horseshoe-shaped optic ridge becomes nearly filled by proliferated

cells (fig. 12, *D*). Later these gather again into the limbs of the horseshoe, which become enlarged and entirely distinct from each other (*F*). The third change is the formation of the plug of optic cells,

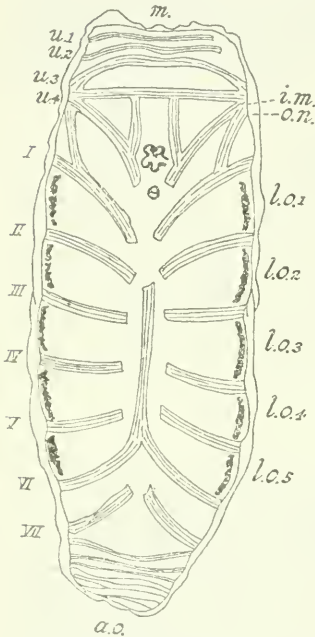


FIG. 13.—CYCLOSALPA PINNATA, SUBSPECIES POLAE, SOLITARY FORM, DORSAL VIEW. FROM SIGL (1912, *a*).

In the collections of the United States National Museum submitted to us are three specimens of the solitary *Cyclosalpa pinnata* which are of the subspecies *polae*. One is 17 mm. long; one is 7 mm. long; the third is an embryo 8 mm. long, in which the placenta is present. None of them show any peculiarity beyond the presence of the median dorsal extension of body muscles VI. In the same bottle, and of course from the same place of collection, is another solitary individual 24 mm. long, of the usual *pinnata* character. There are also 8 aggregated zooids 14 mm. long, four of them still attached together in a broken wheel, and 2 aggregated zooids 11 mm. long, not attached.

which arises by the tip of the arch of the horseshoe curling over backward (fig. 12, *C*) and later becoming the almost independent mass of cells figured (*E*, *F*, and pl. 2, figs. 7 and 8). For more adequate description of the structure and development of the ganglion and eyes of *Cyclosalpa pinnata* see Metcalf (1893, *c*).

The neural glands are similar in the solitary and aggregated forms.

**CYCLOSALPA PINNATA, subspecies POLAE (Sigl) (1912).**

*Cyclosalpa polae* SIGL (1912).

This subspecies is said by Sigl to be distinguished by two features: first, in the solitary individuals, the fusion of body muscles VI on the dorsal mid line and their continuance forward as a median muscle band reaching almost to the level of body muscles II (fig. 13); and, second, the long peduncle by which the aggregated zooids are united to form the wheel (fig. 14).

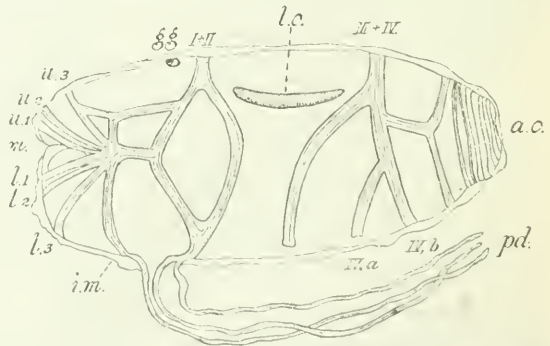


FIG. 14.—CYCLOSALPA PINNATA, SUBSPECIES POLAE, AGGREGATED ZOÏD VIEWED FROM THE SIDE. FROM SIGL (1912, *a*).

None of the aggregated zoöids show unusually long peduncles. In none of the solitary individuals is the stolon sufficiently developed to show buds, and the embryos in the aggregated zoöids are much too young to show muscles. These specimens bear the label Cat. No. 6432, U.S.N.M. (solitary form) *Albatross* station D 3901, Mokuhooniki Islet, Pailolo Channel between Maui and Molokai Islands, Hawaiian Islands, April 29, 1902; surface; surface temperature 74° F.; 10+ specimens.

CYCLOSALPA AFFINIS (Chamisso, 1819).

Plate 3 and plate 4, figs. 11 and 12.

*Salpa affinis* CHAMISSO, 1819 (*type*).

*C. affinis* de BLAINVILLE, 1827.

*C. affinis* HERDMAN, 1888.

*C. chamissonis* BROOKS, 1893.

The following specimens of *Cyclosalpa affinis* are in the collections of the United States National Museum:

Cat. No. 6450, U.S.N.M. (solitary form) *Albatross* station D 2585, off Cape May; Sept. 19, 1885; 542 fathoms; surface temperature 73° F.; one specimen.

Cat. No. 6451, U.S.N.M. (embryo) *Albatross* station 2749, south of Block Island, Sept. 19, 1887; 705 fathoms; surface temperature 67° F.; one specimen.

Cat. No. 2833 U.S.N.M. (aggregated form) *Albatross* station D 2587, off Cape May; Sept. 20, 1885; 326 fathoms; eight specimens.

*Cyclosalpa affinis* most resembles *C. pinnata* and is apparently its nearest relative. In the solitary form the resemblance in shape of body and character of test is close. *Cyclosalpa affinis* has no luminous organs in either the solitary or aggregated forms. Only in *Cyclosalpa pinnata* are luminous organs present in the aggregated form. They are found in the solitary forms of *C. pinnata*, *C. floridana*, *C. bakeri*, and *C. virgula*, that is, in all species of *Cyclosalpa* except *C. affinis*. One naturally guesses that the depths in the ocean to which the several species penetrate may be correlated with the presence or absence of luminous organs, but we have little data for testing this surmise. The greatest depths at which *Cyclosalpa*e are certainly known to have been taken are 55 meters (*C. pinnata* Ihle, 1910) and 500 meters (*C. pinnata*, subspecies *polae* Sigl 1912, *b*). Hauls with the vertical net, collecting everything from the greater depths to the surface, have sometimes contained *Cyclosalpas*, but we have no knowledge of the horizontal strata from which the examples were taken. Nor have we any data indicating that in *Cyclosalpa floridana*, *C. bakeri*, and *C. virgula* the solitary forms penetrate to greater depths than the aggregated forms. Observations upon the vertical distribution of the *Cyclosalpas* are to be desired. Since among the *Cyclosalpas*

luminous organs are found in the conservative solitary form of several species and in the aggregated form of only one species, we may judge that the possession of luminous organs was an ancestral character which most Salpidae have lost. The presence of luminous organs in *Pyrosoma* is in line with this suggestion.

In the solitary *Cyclosalpa affinis* there are seven hooplike body muscles, as in *C. pinnata* (pl. 3, fig. 9). The intermediate muscle is interrupted dorsally and complete ventrally (= *C. pinnata*). The first and second body muscles are interrupted both dorsally and ventrally (= *C. pinnata*). The rest of the body muscles are all interrupted ventrally (= *C. pinnata*), but they are continuous dorsally across the mid line.

The oral retractor muscle is divided horizontally to form two retractors, each continued forward into a sphincter muscle of the lower lip. The upper of these two sphincters is admarginal and aids in the incurving of the valve-like lower lip. The more ventral of the two sphincters supports the bulge of the pocket valve which the lower lip forms. There are but two sphincter muscles in the lower lip. The anterior two sphincters of the upper lip are as in the solitary *Cyclosalpa pinnata*. The third and fourth unite at their ventral ends and lie internal to the oral retractors, just in front of the point where the intermediate muscle passes inside them. The third and fourth sphincters of the upper lip are not in actual connection with either the retractors<sup>1</sup> or the intermediate muscle.<sup>2</sup> As in the solitary *C. pinnata*, there is in the solitary *C. affinis* a longitudinal band of muscle running diagonally upward from the fourth sphincter of the upper lip to the upper end of the intermediate muscle. It does not, however, come into as intimate union with either muscle as in *C. pinnata*. The atrial sphincters are quite similar to those in the solitary *C. pinnata*, but the atrial retractors are better developed, being connected posteriorly to two rather strong sphincters.

The gut resembles that of the solitary *Cyclosalpa pinnata* in position and form except that there is but one caecum, apparently median.

The heart lies below the esophagus, in a considerable evagination of the ventral wall of the body.

Our specimens of the solitary form of this species have the zooids on the stolon but slightly developed and do not show any whorls. After Ritter and Johnson's (1911) careful study of the stolon of this species there is no need of discussion of this structure from our material.

The outline of the aperture of the dorsal tubercle is shown in figure 12 of plate 4.

<sup>1</sup> In the solitary *Cyclosalpa pinnata* they connect with the ventral retractor.

<sup>2</sup> In the aggregated *C. pinnata* probably similar muscles connect with the intermediate muscle.



There are no languet-like protuberances opposite the ventral portions of the intermediate muscles, as in *Cyclosalpa pinnata*, but there are a pair of minute papillae, one on each side of the atrial opening. These were of larger size in the individual figured by Ritter and Johnson. Their internal structure suggests comparison with the tubular outgrowths of the mantle and test, which in *Thalia*, and especially in *Travstedtia*, are so much more developed.

The ganglion and its ventrolateral outgrowths, the neural glands and the eye resemble those of the solitary *Cyclosalpa pinnata* too closely to need description.

CYCLOSALPA AFFINIS, aggregated form.<sup>1</sup>

Plate 3, fig. 10; plate 4, figs. 11 and 12.

The aggregated form of *Cyclosalpa affinis* again presents evidence of close relationship between this species and *C. pinnata*, though there are some differences from the aggregated individuals of the latter species. The test is very much thicker, especially dorsally and ventrally, but it is as soft. The body muscles are the same in number, but in *C. affinis* the bands are more nearly parallel, i. e., body muscles I and II do not touch dorsally or ventrally and III and IV do not so closely approach dorsally. The body muscles in both species are continuous across the mid line dorsally, while ventrally all are interrupted except the posterior branch of the last.

The condition in the peduncle muscles, in the intermediate muscles, and in the last body muscles at their ventral ends need comparison with their condition in the aggregated *Cyclosalpa pinnata*. In *C. affinis* the ventral portions of the intermediate muscles approach and touch on the mid-ventral line of the body. They continue ventrally as full width bands closely appressed to each other for a short distance into the peduncle, their tips again separating slightly. It is therefore evident that the anterior peduncle muscle in this species is double, as in *C. pinnata*.

In *Cyclosalpa pinnata* the first and second body muscle on each side unite to form one of the pair of posterior peduncle muscles. In *C. affinis* the posterior peduncle muscles are distinct from all the body muscles. They do not closely approach either the first or second body muscle. They do bend back and approach near to the third body muscles on each side, somewhat above the mid line, but they do not unite. The slight protuberance from the front of the peduncle in figure 10 is probably without significance. It is not found in many individuals.

The ventral ends of the posterior branches of the fourth body muscle (IV, *a*) unite and continue into the visceral evagination (post-

<sup>1</sup> United States National Museum collections. Cat. No. 6449.

abdomen of Ritter) as a single broad band (*v.*) comparable probably to the slightly developed tip of the fused ends of the fourth body muscles in *Cyclosalpa pinnata* plus the visceral muscle which in *C. pinnata* is not continuous with this. The fourth body muscle on each side, near its ventral end, branches, giving rise to a small band which runs back into the visceral region (postabdomen).

The atrial retractor and sphincter systems, in the two species *Cyclosalpa affinis* and *C. pinnata*, are similar except in two minor points: first, in *C. affinis* the atrial retractor connects with the posterior branch of the fourth body muscle instead of connecting above its point of branching; and, second, the delicate sphincters branch form a slight network.

The gut differs in position and structure from that of the aggregated *Cyclosalpa pinnata*. It is in the form of a wide loop, the anal aperture being at the left of the esophagus, instead of far forward below the endostyle. There is a more marked stomach-like enlargement of the gut in this species. No caecum is present. The gut seems to be approaching the condition observed in the true *Salpae*, *sensu strictu*, in its curved form (though it is not yet a "nucleus"), in the absence of a caecum, and in the presence of a slight stomach enlargement. An intestinal gland is present, its duct stretching from its aperture into the stomach, across the empty space of the loop, the branches of the gland itself being along the distal half of the intestine. The crowded condition in *Cyclosalpa pinnata*, caused by the close approximation of the intestine, endostyle, and testis, makes the intestinal gland difficult to observe in that species.

The testis lies along the intestine as in *Cyclosalpa pinnata*, but the looped condition of the intestine allows it more space and it is a little more stocky. The vas deferens opens near the esophageal aperture. The ovary is in a position similar to that which it occupies in *Cyclosalpa pinnata*. The heart lies beneath the posterior end of the endostyle, in a slight ventral protuberance of the body.

The outline of the aperture of the dorsal tubercle is shown in figure 12, plate 4. The ganglion and its ventro-lateral outgrowths and the neural gland are so similar to those of the aggregated *Cyclosalpa pinnata* as to need no description. The large eye, on the other hand, shows a few significant divergencies from that of the aggregated *Cyclosalpa pinnata*. Its long axis points not horizontally forward as in *C. pinnata*, but forward and fifteen degrees upward (pl. 4, fig. 11). The rotation of the developing eye has not gone so far as in *C. pinnata*. The plug of optic cells is smaller than in the latter species and is less distinct from the arch of the horseshoe. The posterior portion of the eye is not divided into two swollen limbs, but is continuous from side to side and is thinner than are the limbs

of the eye in *C. pinnata* (fig. 15, this page). This recalls the condition of the developing eye of *C. pinnata* during the early part of its rotation (fig. 12, D, p. 25). The position of the eye and the undivided condition of its posterior portion, also the less developed state of the plug in the adult *Cyclosalpa affinis*, parallel features of the immature eye of *C. pinnata*. Shall we interpret this as indicating that *C. affinis* is more archaic than *C. pinnata*, or as showing it already to have begun those retrogressive changes which culminate in the decided degeneration of the eye in the more modified species of Salpidae? The approach in the condition of the intestine to that of the true *Salpae*, a secondary feature, makes one inclined to interpret the divergence in the eye as secondary, a slight degeneration, consisting of an inhibition of some of the later phases of the development. On the other hand, the more regular character of the muscles in the aggregated *Cyclosalpa affinis* is doubtless more archaic than the condition in *C. pinnata*.<sup>1</sup> The evidence from the muscles and that from the gut are therefore opposed. Our studies have inclined us to give weight to the latter and to interpret the comparative anatomy of the eyes accordingly.

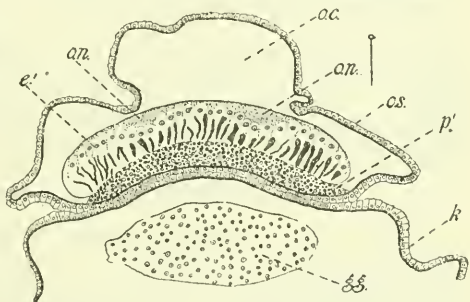


FIG. 15.—CYCLOSALPA AFFINIS, AGGREGATED ZOÏD, A CROSS SECTION OF THE POSTERIOR PORTION OF THE DORSAL EYE.  $\times 150$  DIAMETERS. FROM METCALF (1893, c).

The two pairs of smaller eyes in the ganglion of the aggregated *Cyclosalpa affinis* are similar to those in the chain form of *C. pinnata*.

Our figures and description of *Cyclosalpa affinis* are based upon the study of two specimens of the solitary form, one from an unnamed locality, the other from the Atlantic Ocean, off the mouth of Delaware Bay, in latitude  $38^{\circ} 24'$  north and longitude  $71^{\circ} 17'$  west [U. S. Bureau of Fisheries station 2717]; of three embryos 11 mm. and 14 mm. long, from the Atlantic Ocean, south of the eastern end of Long Island, in latitude  $39^{\circ} 42'$  north and longitude  $71^{\circ} 17'$  west [U. S. Bureau of Fisheries station 2749]; and of many specimens of the aggregated form from the Atlantic coast of North America, from Cape Hatteras to Cape Cod, and from the Pacific Ocean, off the California coast, the station not being more exactly stated. We

<sup>1</sup> I have not followed the development of the body muscles in embryos or buds of *Cyclosalpa affinis* or *Cyclosalpa pinnata*. In the development of the aggregated zooids of *Thalia democratica*, one sees that the body muscles arise first as regularly spaced hoops, and their dorsal approximation into two groups, as seen in the adult, occurs late in the development. This confirms the opinion that regular hoop-like arrangement of the body muscles is archaic.

have numerous others, embryos, but have not given them careful study.

The chief studies of *Cyclosalpa affinis* have been made by Ritter (1905) and by Ritter and Johnson (1911). A few minor discrepancies between their work and ours will be noticed as to the lip muscles, the branching of the atrial sphincters, and the presence of an atrial retractor; also they fail to describe the muscles of the peduncle. Brooks has shown the latter in his figures (Brooks, 1893, pl. 8), but not as we have indicated them. We find them as we show them in specimens from both the Atlantic and Pacific coasts of America.

**CYCLOSALPA FLORIDANA** (Apstein, 1894, b, not 1906, a).

*Cyclosalpa dolichosoma-virgula* TRAUSTEDT, 1893 (according to APSTEIN, 1894, b).

*Salpa floridana* APSTEIN, 1894, b, (type).

*Cyclosalpa floridana* IHLE, 1910.

This, the most aberrant of the *Cyclosalpae symmetricales*, has its nearest relative apparently in *C. bakeri*, one of the two species composing the *Cyclosalpae asymmetricales*, but we shall compare it first with the two species already discussed.

**CYCLOSALPA FLORIDANA, solitary form.**

Plate 4, figs. 13 and 14; plate 5, fig. 16.

Our figures and description are based on the study of three specimens 16 mm. long, the same upon which Brooks (1908) worked. These are from Nassau in the Bahama Islands and were collected in May and June, 1907. Specimens of this form are in the United States National Museum. Cat. No. 6452, U.S.N.M. (solitary form) *Albatross* station D 2585; off Cape May; Sept. 19, 1885; 542 fathoms; surface temperature, 73° F.; one specimen.

The form of the body, the thickness of the test, and the general arrangement of the viscera and muscles are seen in figure 13, a view from the left side. The luminous organs are a series of five weakly-developed glands similar to those of *Cyclosalpa pinnata*, but not composed of nearly so many cells. Their position is similar in the two species. The group of cells between body muscles I and II is but about a third as long as one of the next three groups. The fifth group, behind body muscle V, is so slightly developed as hardly to be discernible.

There are seven body muscles, as we group them. These are all interrupted dorsally, as in *Cyclosalpa pinnata*. Ventrally each is continuous with its fellow across the mid line, except muscle VI, which is interrupted. In the solitary form of both *C. pinnata* and *C. affinis* all of the body muscles are interrupted ventrally. The first, second, third, and fourth body muscles approach each other

ventrally, fusing into a common mass. The dorsal ends of the body muscles converge more than in the other *Cyclosalpae symmetricales*. The intermediate muscle is continuous ventrally but interrupted dorsally.

At first glance the oral muscles seem to show a pattern similar to that of *Cyclosalpa pinnata*, but closer observation shows the details of their relations to be quite different. The figure needs some description. The dorsal retractor is seen to divide into four bands, the lower or fourth of which passes forward into the lower lip to form what at first glance seems to be the first sphincter of the lip, but it is really the third sphincter. The lower lip is very strongly inturned, so that its first and second sphincter muscles appear in side view to lie behind the third sphincter. The upper branch of the dorsal retractor forms the first or admarginal sphincter of the strongly-incurled lower lip. The second branch of the retractor forms the second sphincter of the lower lip. The third branch of the retractor passes up outside the first and second branches to form the second sphincter of the upper lip. The first sphincter of the upper lip arises by one or two branches on each side from the second sphincter of the lower lip. (Compare with solitary and chain forms of *Cyclosalpa bakeri*.) The third and fourth sphincters of the upper lip unite below into the ventral retractor which, as in *C. pinnata*, passes inside the dorsal oral retractor and outside the intermediate muscle, diagonally downward and backward, to unite with the first body muscle, near its ventral end. The dorsal connection of the fourth sphincter of the upper lip with the intermediate muscle is as in *Cyclosalpa pinnata*, though the former is more prolonged postero-dorsally. Note that the third sphincter muscle of the lower lip in the solitary *C. floridana* is a branch of the dorsal oral retractor, as in the aggregated *C. pinnata*, *C. bakeri*, and *C. virgula*, while in the solitary *C. pinnata* and *C. bakeri* it is a branch of the ventral oral retractor.

The muscles of the atrial siphon differ slightly from those of either *Cyclosalpa pinnata* or *C. affinis*. There are fewer, but three, delicate sphincters, all of which are unbranched. There are two stronger basal sphincters, also unbranched, and there is a well-developed diagonal atrial retractor which continues ventrally as far forward as the last body muscle.

The gut (see also fig. 14) shows the usual trumpet-shaped esophageal opening and an excessively curved esophagus which opens into a small right caecum near its origin from the intestine. The straight intestine lies, as in the solitary forms of all the *Cyclosalpas*, along the dorsal side of the gill. The left caecum is noticeably larger than the right and lies further from the mid line.

The stolon in our specimens is curled to the right, differing from the straight ventral stolon of other *Cyclosalpas*. Our specimens do not show more than the beginnings of whorls. The position of the heart is indicated by a slight evagination in front of the intestinal caeca.

The form of the aperture of the dorsal tubercle is shown in figure 16. It is much simpler than in other solitary *Cyclosalpas* except the nearly related *C. bakeri*.

The horseshoe-shaped eye, the neural glands, and the outgrowths from the ganglion in connection with the neural glands agree so closely with the corresponding organs in the solitary *Cyclosalpa pinnata* and *C. affinis* as to need no description.

**CYCLOSALPA FLORIDANA, aggregated form.**

Plate 5, fig. 15; and plate 6.

Our figures and descriptions are based on the study of ten individuals from 6 to 9 mm. in length, collected in May and June, 1907, near Nassau, Bahama Islands. These are the specimens used by Brooks (1908) in the preparation of his paper upon this species. Some of Brooks' specimens have been deposited in this museum (U.S.N.M., Cat. No. 6676). We have also a poorly preserved specimen from the Gulf of Mexico, off Mobile Bay, United States National Museum, Cat. No. 6453 (aggregated form), *Albatross* station D 2402; off Cape San Blas, Gulf of Mexico; March 14, 1885; 111 fathoms; surface temperature 63° F.; one specimen.

The general form of the body is very different from that of the aggregated *Cyclosalpa pinnata* and *C. affinis*, being roughly triangular in side view, and the very noticeable postabdomen emphasizes the distinct appearance. In details of structure, however, the resemblance to the other *Cyclosalpas* is seen. The test is enlarged even more than in *C. affinis*. Luminous organs are entirely lacking.

Study of the body muscles shows but three. The intermediate muscle and the first body muscle are essentially similar to those of the aggregated *C. affinis*. The second body muscle of *C. affinis* and *C. pinnata* seems to be the one missing in *C. floridana*. It may be altogether lacking, but study of the aggregated *C. bakeri* suggests that its fibers may be fused with one of the other body muscles. The second and third body muscles of *C. floridana*, corresponding probably to the third and fourth of *C. affinis* and *C. pinnata*, are united in the manner shown in the figure. Noting a few details: observe that the intermediate body muscle passes outside the oral retractor, that ventrally it unites with its fellow of the opposite side, and that the common strand thus formed is continued back into the very slender

peduncle where it forms the anterior half of the single muscle. The third body muscle and its branches show a combination of characters which appear separately in *C. pinnata* and *C. affinis*, though nothing not found in one or the other of these species. From its upper part arises the atrial sphincter. (See last body muscle in *C. pinnata*.) The posterior branches of these muscles on the two sides of the body unite on the mid line below the base of the atrial siphon, and are continued on the mid line downward into the base of the postabdomen, stopping in the bend of the intestine, thus resembling *C. affinis*. From the lower end of the third muscle, on each side, arises a small strand, which curves backward and upward also into the postabdomen, as in *C. affinis*. This muscle on the left side is continued into the tubular portion of the postabdomen. On the right side its fellow ends near the enlargement referred to as a rudimentary stomach. Note that this third body muscle with its connections resembles not the third but the fourth body muscle of *C. pinnata* and *C. affinis*.

As in the solitary form, the atrial sphincters are few in number. The oral muscles are simpler than in the solitary form of this species or either form of *C. pinnata* or *C. affinis*. There is a single oral retractor running forward from the first body muscle. This divides anteriorly into three dorsal and three ventral branches forming the three sphincters of the dorsal and the ventral lips respectively.

The upper lip in both forms of this species is the larger externally, but the lower lip is enlarged internally and shows the same type of valve structure described for *Cyclosalpa pinnata*.

The gut is a little more curved than in *C. affinis*, the intestine crossing the esophagus so that the anus is behind and above the esophageal aperture. There is no caecum, but, as in the aggregated *Cyclosalpa affinis*, there is an enlargement of the intestine just behind its union with the esophagus. This stomachlike enlargement is greater than in *C. affinis*. The intestinal gland is present in the usual form, but to avoid the confusion of too many lines it is not shown in our figures.

The testis, instead of lying along the intestine as in *Cyclosalpa pinnata* and *C. affinis*, pushes out far behind the body, completely filling a long conoidal evagination of the mantle. Its duct passes above the intestine, through its loop, to open dorsal to the anus. The ovary lies just behind the last body muscle, instead of in front of it, as in *C. pinnata* and *C. affinis*. Its duct, however, passes forward, as in these latter species, to a point behind the next to the last body muscle. The heart has the usual position. The simple outline of the aperture

of the dorsal tubercle is shown in figure 16, plate 5. The ganglion and glands are as in *Cyclosalpa pinnata* and *C. affinis*. There are paired outgrowths from the ganglion toward the disks of the neural gland, as in other *Cyclosalpas*.

The large dorsal eye (fig. 16, this page) is much as in *Cyclosalpa affinis*, except that it is a little more compact. The transverse plug of optic cells ( $e'''$ ) behind and above the apical portion of the eye, is less distinct, being crowded against and into closer union with the rest of the eye, one common pigment layer serving the rod-cells of both the optic plug and the apical division of the eye.

*Cyclosalpa floridana* has been studied by Apstein (1894, *b*, not 1906, *b*), Brooks (1908), and Ihle (1910). Our studies result in considerable disagreement with the first two of these authors. Apstein's figures

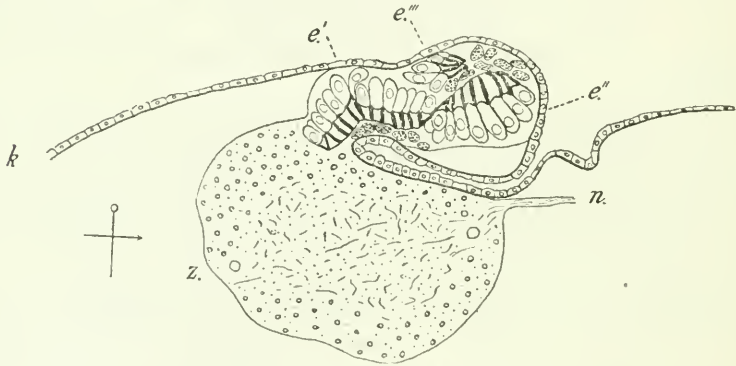


FIG. 16.—CYCLOSALPA FLORIDANA, AGGREGATED FORM, A SAGITTAL SECTION OF THE GANGLION AND DORSAL EYE.  $\times 300$  DIAMETERS.

lack details of the organs other than the muscles. The whole oral muscular system of the solitary forms he describes very differently, showing no dorsal oral retractor, two instead of three ventral lip sphincters, and different connections for all the oral sphincters. He does not show the atrial retractor. There is so little detail in his figures of the aggregated form that comparison with our results is difficult. No muscles are shown upon the ventral lip. He figures no connection between the third sphincter of the upper lip and the intermediate muscle. He shows but one muscle, the intermediate, continued into the peduncle. He unites the ventral ends of the first and second body muscles. He shows no branches from the third body muscle into the post-abdomen. He figures but one atrial sphincter.

Brooks, who studied the same specimens we used, gives a much fuller description than Apstein. In the solitary form we find one dorsal sphincter and two ventral sphincters in addition to those which he shows in the oral region of his adult specimens, but in his figure of a large embryo 4.5 mm. long he shows six instead of our four



dorsal sphincters and one instead of our three ventral sphincters. Brooks figures the dorsal and ventral oral retractors in this embryo, but gives them different relations with the oral sphincters. We have not had this embryo for study with Brooks' other specimens. Brooks does not figure the atrial retractor. We find the intermediate muscle and the first two body muscles approximated dorsally, but not actually united as Brooks figures and describes them in the adult. Part of the discrepancies between Brooks' results and ours may be due to the fact that he describes the appearance of the animal, in side view, and only for the embryo, while our studies are of adult individuals.

As to the structure of the aggregated form also, we find some discrepancies between Brooks' results and ours. He shows two fewer ventral oral sphincters than we. He prolongs the intermediate muscle and body muscle II, instead of the intermediate muscle and body muscle I, into the peduncle, carrying the ventral end of body muscle I back to join that of body muscle III. Observation of our figure 15 on plate 5 will explain the condition in this region, which might easily mislead if not studied under high magnification. Brooks shows no prolongation of any branches of body muscle III (as we number it) into the visceral protuberance.

Ihle's description of the solitary form is based upon Brooks' studies. He gives a good description of the aggregated form, and he shows very clearly Apstein's mistake in confusing *Cyclosalpa floridana* (Apstein, 1894), and *C. bakeri* which Apstein (1906) calls *C. floridana*. Ihle worked upon much younger zoöids of the aggregated form than we, and our slight differences from his results may be due to this fact. We show one more dorsal and two more ventral sphincters than he. Also he does not figure the posterior branch of the third body muscle (our number) as continued, after union with its fellow, into the visceral protuberance. It is interesting to note that he figures the large dorsal eye in his young zoöid as pointing postero-dorsally, while in our older individuals it is directed antero-dorsally. This indicates a forward rotation of this eye in its later development, similar to that which occurs in the aggregated *Cyclosalpa pinnata*.

CYCLOSALPA BAKERI Ritter, 1905.

*C. floridana* APSTEIN, 1906, *a*, not 1894, *b*.

*C. bakeri* IHLE, 1910.

This species, confused by Apstein (1906, *a*) with *C. floridana*, shows more than superficial resemblance to the latter species in both solitary and chain forms, but is a clearly distinct species, differing in many points of structure and form. Our figures and the descrip-

tion are based on studies of three specimens of the solitary form, most generously given by Professor Ritter, the discoverer of the species, and upon three specimens of the aggregated form collected in Philippine waters by the United States Bureau of Fisheries steamer *Albatross* (station D, 5437, between Bohol and Leyte, north of Minbanao). The specimens given by Professor Ritter came from off the California coast. Two of the three have stolons with well-formed zooids. Specimens of both the solitary and aggregated individuals are in the United States National Museum.

Cat. No. 6476, U.S.N.M. (solitary form), off San Pedro, California, (W. E. Ritter); 3 + specimens.

Cat. No. 6456, U.S.N.M. (aggregated form), *Albatross* station D 5437, Hermana Mayor Light, west coast of Luzon; May 8, 1909; 100-600 fathoms; surface temperature 86° F.; 3 + specimens.

CYCLOSALPA BAKERI, solitary form.

Plate 7.

This is very similar to the solitary *Cyclosalpa floridana*, but there are marked differences. The shape of the body, the test, and the luminous organs in the two are similar, though our specimens of *C. bakeri* show the latter more developed than they are in our specimens of *C. floridana*. All the body muscles are distinct in the solitary *C. bakeri* and none of them are continued across the mid-ventral line. The sixth body muscle on each side, in its dorsal portion, turns forward, passing the dorsal ends of the fifth and sixth body muscles. The dorsal oral retractor gives rise, strictly speaking, only to the first or admarginal sphincter of the lower lip. The second sphincter of the upper lip has its fibers inserted upon, but not a part of, the retractor. The first sphincter of the upper lip is continuous directly with the second sphincter of the lower lip, the two forming one continuous muscle. The third sphincter of the lower lip is a branch of the ventral retractor, as in the solitary *Cyclosalpa pinnata*. The basal three atrial sphincters are well developed and form something of a network, in which one can recognize ventrally the diagonal atrial retractor in its typical position. The delicate atrial sphincters are twice as numerous as in the solitary *Cyclosalpa floridana*.

For the gut, we need mention only the two caeca, which are of approximately equal size, and are larger than in the solitary form of any other species of *Cyclosalpa*.

Figure 20 shows the contour of the aperture of the dorsal tubercle, slightly more curved than in the solitary *Cyclosalpa floridana*. The stolon is straight, lying wholly on the mid-ventral line, instead of bending to the right as in our specimens of the solitary *C. floridana*.

Opposite the lower part of the intermediate muscle are a pair of languet-like processes of the mantle, one on each side. They resemble the corresponding structures in the solitary *Cyclosalpa pinnata*.

The ganglion, the neural glands, the outgrowths from the ganglion toward the neural glands, and the horseshoe-shaped dorsal eye are as in the solitary forms of the other *Cyclosalpas* already described.

**CYCLOSALPA BAKERI, aggregated form.**

Plates 8, 9, and 10.

In the aggregated form of this species we find again considerable resemblance to the aggregated *Cyclosalpa floridana*, in general shape and in the very flabby character of the animals, but they are sharply distinguished by many features, as Ritter and especially Ihle have shown. The younger zoöids, 4 mm. long, just detaching from the stolon, are different in shape from the larger Philippine specimens, 12 mm. long. The older individuals (pl. 8, fig. 21) have a longer atrial siphon and they seem to have lost the humpbacked form so noticeable in the younger zoöids, but our three older individuals are all so soft and flabby that it is difficult to be confident of the exact shape. It is, however, certain that the dorso-ventral diameter in front of the atrial siphon is relatively greater in the younger individuals. A marked difference between the older and younger zoöids in the arrangement of the oral muscles will be noted when we reach this part of the description.

The body muscles have a different arrangement on the right and left sides of the body, this species being one of the *Cyclosalpae asymmetricalae*. The intermediate muscles and their prolongation into the peduncle are as in the aggregated *Cyclosalpa floridana*. The first and second body muscles on the left side are fused dorsally and ventrally, but are distinct and widely separated through the middle part of their course. Both share in the formation of the posterior peduncle muscle. On the right side of the body there is a diagonal strand which we interpret as the second body muscle fused at its lower end with the first body muscle, and in its upper portion fused with the third body muscle. Comparison with the aggregated *Cyclosalpa floridana* suggests that, in the latter species, the muscle we have numbered I may in reality be equivalent to muscles I and II of *C. bakeri*. Its approach ventrally, in *C. floridana*, to touch muscle II and then passing on into the peduncle may be somewhat similar to the fact that muscle II in *Cyclosalpa bakeri*, if we correctly homologize it, connects with both muscle I and muscle III. On the left side of *C. bakeri*, muscles III and IV are united exactly as are the muscles numbered II and III in *Cyclosalpa floridana*. All their branchings are the same. This is true of the right side also, except

that the muscle we number II joins dorsally muscle III. The three muscles to the post-abdomen are closely similar to those in the aggregated *C. floridana*. The larger, median one, entering from above, terminates near the base of the post-abdomen, in the loop of the gut (pl. 10, fig. 25). Of the pair of more slender bands, arising from the lower part of the last body muscle, on each side, that on the left side is prolonged almost to the tip of the long slender testis, while that on the right side passes along the caecum and on nearly to the tip of the slender mass of degenerate (?) cells. This structure lying at the tip of the caecum is probably homologous with the cells at the tip of the caecum in the aggregated *Cyclosalpa virgula* and with the organ in the solitary forms of *Ritteria retracta*, *R. picteti*, and *R. amboinensis*, which Ihle regards as a blood-forming organ.

The peduncle muscles are, first, a fused anterior pair derived from the ventral ends of the intermediate muscles; second, a partially fused posterior pair derived from the ventral ends of the united first and second body muscles; and, third, a median strand arising at the ventral point of the united fourth pair of body muscles and running forward on the ventral mid line, past the third pair of body muscles from which it receives additional fibers, then passing forward, sometimes between the separated upper portions of the posterior pair of peduncle muscles, and bending down into the peduncle.

The muscles of the atrial siphon are as in the aggregated *Cyclosalpa floridana*, except that there are twice as many of the delicate sphincters. The oral muscles must receive separate description for the younger and the older zooids. In the younger zooids (fig. 22, pl. 8, and fig. 23, pl. 9) there is a well-developed oral retractor connected as usual with the first body muscle. Passing forward, this gives rise ventrally, first, to the third sphincter of the lower lip, then to a second ventral branch, the second sphincter of the lower lip, and finally passes into the first sphincter of the lower lip. The first sphincter of the upper lip arises on each side as a branch of the second sphincter of the lower lip. The second and third sphincters of the upper lip unite ventrally to form a common trunk which posteriorly joins with the ventral half of the intermediate muscle, not with the first body muscle. This arrangement of this muscle is comparable with what we find in the aggregated *Cyclosalpa pinnata* and *C. affinis*, except that the union of the diagonal strand with the intermediate muscle is further toward the ventral side. It seems hardly natural to call this a ventral oral retractor, for its attachments are different, but it functions in much the same way. The dorsal longitudinal muscle band does not extend quite far enough forward to come into contact with the fourth sphincter of the upper

lip, differing in this regard from the aggregated *Cyclosalpa floridana*. The relations in the older zooids are the same, except that the first sphincters of the dorsal and the ventral lips are continuous, forming one muscle, which has no connection with the oral retractor.

This divergence in the connection of the admarginal oral sphincters in the younger and older zooids makes one at first doubt the constancy of detail in the arrangement of the muscles in at least the aggregated Salps, but we have as yet no sufficient studies of variation in the Salpidae to determine this matter conclusively. In the aggregated zooids, as in the embryo, there are considerable changes during the process of establishing the adult condition of the muscles, but, once fully developed, these conditions so far as our studies indicate are constant.

The gut forms a long narrow loop, lying chiefly outside the body proper, in a long protuberance conveniently named by Ritter the post-abdomen. At the point of union of esophagus and intestine arises a long slender caecum, which passes out into a separate slender pouch of the post-abdomen. These relations are best shown in the dextrodorsal view drawn in figure 25, on plate 10. Observe the intestinal gland, opening into the intestine at the point of origin of the caecum and running across the space in the loop of the gut, to branch over the distal portion of the intestine.

The elongated testis (pl. 10, fig. 25, *t.*) fills nearly the whole of the larger of the two slender mantle pouches connected with the post-abdomen. Its duct passes over the bend of the intestine and dorsal to its distal end. In the younger zooids we can not trace it beyond this point, but in one of the three larger zooids, which we stained, we could trace a faint line of apparently degenerating duct forward on the right side until it joined the oviduct a little beyond the young embryo. The ovary lies on the right side, in front of the last body muscle, the oviduct extending forward nearly to the third body muscle.

At the tip of the caecum is an elongated, spindle-shaped group of cells of problematic nature (*q* in fig. 25, pl. 10). They resemble elaeoblast cells. The heart is in the usual position. Below it, in the younger zooids, is a vesicle subtended by a layer of cells whose appearance again suggests comparison with elaeoblast cells. There is little value in discussing the nature of either group of these elaeoblast-like cells until their development is known.

The outline of the aperture of the dorsal tubercle is shown in figure 24, plate 9.

The ganglion, the neural glands, and the outgrowths from the ganglion, near the glands, resemble these organs in the aggre-

gated *Cyclosalpa floridana*. The large dorsal eye (fig. 17, this page) also is very similar, the only notable difference being that the optic plug is still more intimately fused with the postero-dorsal face of the apical region of the eye. The presence or absence of accessory eyes in the ganglion can not be determined from sections of our poorly preserved formalin material of the young zoöids, and it does not seem best to sacrifice one of our two remaining older zoöids, the largest yet seen of this species.

*Cyclosalpa bakeri*, discovered by Ritter, has been carefully described by him. We modify his results but slightly and add little

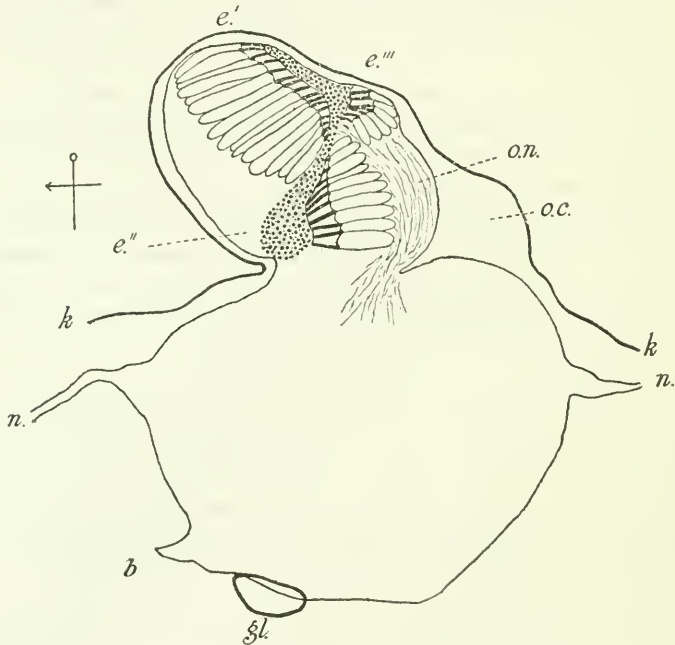


FIG. 17.—CYCLOSALPA BAKERI, AGGREGATED FORM, AN OPTICAL SECTION OF THE DORSAL EYE, WITH OUTLINE OF THE GANGLION AND ONE NEURAL GLAND.  $\times 175$  DIAMETERS.

to them except as to the anatomy of the eye of the aggregated form. In the solitary form we find a more complicated arrangement of the atrial sphincters which we find also more numerous than Ritter shows them. In our specimens, the oral retractor runs outside the intermediate muscle and the ventral oral retractor. Ritter shows it internal to them. He omits one sphincter of the lower lip (our first) and shows the connections of the other oral sphincters slightly differently from ourselves. (Ritter directs attention to considerable variation in the aggregated form.) There is an error in his drawings of the solitary form, doubtless inadvertent, though twice repeated,

for he shows the peripharyngeal bands connecting dorsally with the horns of the dorsal tubercle instead of with the anterior end of the gill. The latter is of course the arrangement not only in all the Salpidae, but in all Tunicata.

The results of our studies of the aggregated form agree with Ritter's, except for a few minor details. We show differently the visceral muscle prolonged into the base of the post-abdomen from the median line of the united posterior branches of body muscle IV. We show three more atrial sphincters than he. We show one more sphincter muscle in the lower lip and three instead of four sphincters in the upper lip, and slightly different connections for the sphincters of both lips. The zoöids Ritter describes are slightly younger than the youngest we studied and much smaller than our three larger specimens.

Ihle's careful review of this species showed the accuracy of Ritter's studies and the confusion in the work of Apstein, who refused recognition to *Cyclosalpa bakeri* as a species distinct from *C. floridana*.

CYCLOSALPA VIRGULA (Vogt 1854).

*Salpa virgula* VOGT, 1854.

*Salpa dolichosoma* TODARO 1883.

*Cyclosalpa dolichosoma-virgula* HERDMAN, 1888.

In the aggregated form of this species there is greater bilateral asymmetry than in any other species. Our studies of the species are based upon finely preserved material obtained from the Zoölogical Station in Naples. There are 11 individuals of the aggregated form and one large solitary individual. The solitary individual, and one of the aggregated zoöids are deposited in the United States National Museum: Cat. No. 6465, (aggregated form), from Naples Zoological Station; one specimen. Cat. No. 6475, (solitary form) from Naples Zoological Station; one specimen.

CYCLOSALPA VIRGULA, solitary form.

Plate 11, figs. 26 and 27.

The muscles of this form have been well described by Streiff (1908), and detailed description is hardly needed here. Observation of our figure will show the points of comparative interest. The intermediate muscle is continuous across the mid-ventral line, as in the solitary forms of all *Cyclosalpas*. All the body muscles are interrupted dorsally and ventrally. The forward prolongation of the dorsal ends of the sixth body muscles, seen in the solitary *C. bakeri*, is, in *C. virgula*, carried much further, the dorsal ends of the sixth and first muscles being thus united. Similarly the ventral ends of

the fifth body muscles are turned forward and the ventral ends of the first body muscles turned backward, until, in our specimen, they almost meet opposite body muscle III. In Streiff's specimens these ventral prolongations met and united into a continuous band. The arrangement of the oral retractors in our specimens recalls the aggregated *Cyclosalpa affinis*. Streiff found a different condition, the ventral oral retractor in his specimens being split posteriorly into an upper and a lower branch, both extending back to and inserted upon the first body muscle. The upper branch was in contact with the lower edge of the dorsal retractor. The lack of continuity of the third and fourth sphincters of the upper lip with any of the other muscles is again comparable to the condition in *C. affinis*. The atrial muscles show a very well-developed retractor continuous dorsally with four of the atrial sphincters and ventrally in contact with but not continued into five of the atrial sphincters. The two papillae, one on each side of the atral opening, recall the solitary *Cyclosalpa affinis*.

The gut is very similar to that of the solitary *Cyclosalpa pinnata*, there being two caeca. The tip of the intestine is curled further back than in other species. At its anterior end the stolon, in our specimens, curls up on the left side and terminates in a thin thread.

The neuro-glandular complex shows no noteworthy difference from the corresponding organs of the solitary forms of the other *Cyclosalpas*.

**CYCLOSALPA VIRGULA, aggregated form.**

Plate 11, fig. 28; plates 12 and 13.

This is the most asymmetrical member of the Salpa family,<sup>1</sup> yet point by point it shows fundamental resemblance to the other species of *Cyclosalpa*. All of our nine individuals show the same asymmetry, there being no distinction between dextral and laeval individuals. In general shape the zoëid somewhat resembles *C. bakeri*, but has an undivided post-abdomen more like *C. floridana*. The test is like that of *C. bakeri*. There is no stalk of attachment (peduncle), the zoëids being sessile upon the stolon, which is shown as a large tube on the ventral side of the animals we figure.

Four body muscles can be recognized, as in all other aggregated *Cyclosalpas* except *C. floridana* (in which the second is either wanting or is fused with muscle I), but in *C. virgula* the arrangement of these muscles is much modified, chiefly by partial fusion with one another, these fusions being very different on the two sides. The intermediate

<sup>1</sup> The aggregated zoëids of *Brooksia rostrata* are nearly as asymmetrical, so also are those of *Apsteinia asymmetrica*.



muscle and all the body muscles are interrupted ventrally (pl. 12, fig. 30). On the right side (pl. 11, fig. 28) the upper end of the intermediate muscle bends back in the usual *Cyclosalpa* manner and unites with the first body muscle, but this union is far down on the side, just above the oral retractor. In fact, the back-turned end of the intermediate muscle fuses with the posterior end of the oral retractor. On the left side (pl. 12, fig. 29) the upper end of the intermediate muscle does not quite reach to the first body muscle, but runs far up dorsally and stops before establishing the connection. It is as if the whole muscle system were so twisted over to the right side that the intermediate muscle on the left side, blocked by the ganglion, fails to reach its proper point of union with the first body muscle, while, on the right side, this attachment is present and by the same lateral twist is pushed ventralward.

On the right side the first body muscle, in its upper half, unites with both the intermediate muscle and the second body muscle, separating again further dorsally to pass over the actually (morphologically?) mid-dorsal line as a broad band whose breadth suggests that it contains some fibers properly referable to the intermediate muscle. On the left side, muscle I is distinct from both the intermediate muscle and body muscle II and does not even come into contact with the oral retractor.

On the right side, body muscle II joins the intermediate muscle and body muscle I above, as already noted, but a little further dorsally it parts company with them and, after a very short free course, unites with the fused muscles III and IV. This union is less perfect than in the case of some other muscles, for the line of demarcation between muscle II and the fused muscles III and IV can be traced through the whole course of their juxtaposition, across the mid-dorsal line, onto the left side. On the left side, muscle II joins the united muscles III and IV, but not the intermediate muscle or body muscle I. Here, again, the impression is that of a shifting of the muscles, over the dorsal surface, toward the right side.

On the right side, muscle III, in its upper half, is attached to muscle IV, but its fibers are not continued dorsally in union with the latter muscle. On the left side the union of III and IV is more intimate, their fibers passing together across the dorsal surface.

Muscle IV has its usual position, its ventral ends lying in front of the gut, while the posterior branch passes behind the gut, above the post-abdomen, to unite with its fellow from the opposite side. On the right side, the two parts of this muscle are separated so that the anterior branch does not quite touch the band which passes back above the

post-abdomen. On the left, the two branches are united. In the aggregated forms of other species of *Cyclosalpa* the posterior branches of muscle IV (or its homolog in *C. floridana*), at their point of union on the mid line, give rise to a band of muscle which runs on the mid line into the more or less developed post-abdomen. In the aggregated *C. virgula* the corresponding muscle arises well on the right side, but has a similar course into the base of the post-abdomen. Its position, on the right side rather than in the median plane, is another indication of the shifting of the whole muscular system toward the right. The dorsal view (fig. 33, pl. 13) gives the best impression of this great lateral distortion. Careful study of the origin and position of the zoöids upon the stolon might give the key to this distortion, but we have not material to undertake this.

The atrial muscles show a well-developed retractor on each side, whose position and connection with the atrial sphincters, when carefully compared, is seen to have some resemblance to what is found in the solitary form. The atrial retractor is not connected with the basal two sphincters on either side. These basal atrial sphincters are continuous on the right side, from the dorsal to the ventral surface. On the left side they are interrupted, and in front of the point of interruption the ends of the two are united into a common strand, which runs toward but not into contact with body muscle IV, suggesting comparison with the atrial retractors in the aggregated forms of other species of *Cyclosalpa*. Comparison with the solitary *C. virgula* indicates that that which corresponds to the continuous atrial retractor in the solitary form is, in the aggregated form, divided into two portions, proximal and distal, of which the distal portion, connected with the delicate sphincters, is present on both sides of the body, while the proximal portion, connected with the heavier basal two sphincters, is seen only on the left side, and even on this side is imperfectly developed.

The oral muscles are essentially alike on the two sides, but are less compact, and so more readily observed, on the right side. There is a single strong oral retractor which, on the right side, passes backward outside of and then joins the dorsal part of the intermediate muscle and runs with it to its insertion upon body muscle I. On the left the oral retractor passes over the intermediate muscle, but is not united to either this or body muscle I. Four sphincters of the lower lip and one sphincter of the upper lip are connected directly with the oral retractor on each side, as shown in the figures. The second sphincter of the upper lip is independent of all other muscles. This is seen more readily on the right side, where the oral muscles are not so crowded. The third (last) sphincter of the upper lip is a branch of the inter-

mediate muscle on each side of the body. The band of muscle, which, in the aggregated *Cyclosalpa symmetricales*, connects the dorsal portions of the last sphincter of the upper lip with the intermediate muscle, does not, in the aggregated *C. virgula*, make actual connection with the last oral sphincter on either side. This is also true of the other asymmetrical species, *C. bakeri*.

The gut resembles that of the aggregated *Cyclosalpa bakeri*, though its caecum is directed forward on the right side of the body (fig. 30, pl. 12) instead of protruding into a separate evagination of the mantle as in *C. bakeri*. This caecum arises from the left side of the intestine (fig. 28, pl. 11), but bends over to the right side of the enlarged base of the post-abdomen. It is really the morphological left caecum. There are a few loosely arranged degenerate (?) cells at the tip of the caecum, corresponding to the fusiform mass of such cells one finds in *C. bakeri*. There is a slightly developed right caecum. The position of the intestine in our figure 30, plate 12, a ventral view, is a little distorted by slight rotation, the large caecum being pulled a little to the right, so as to allow one to see the smaller, morphologically right caecum, which in ventral view is hidden by the base of the large caecum. The dorsal view (fig. 33, pl. 13) shows the true positions. The intestinal gland is seen from figures 28 and 29, plates 11 and 12, and figure 33, plate 13, to have the usual arrangement.

The testis lies in the distal portion of the great post-abdomen. Its duct has the usual course and opens into the atrial chamber, not far from the anus. The ovary is on the right side, in the usual position, between body muscles III and IV.

The outline of the aperture of the dorsal tubercle is shown in figure 32, plate 13.

The ganglion (fig. 31, pl. 13) shows no features of moment for our studies except the eyes and the outgrowths toward the neural glands. These glands are of the usual disk form with convoluted ducts leading from them (fig. 18, this page). There is a protuberance from the ganglion toward each glandular disk, the base of each protuberance containing small cells like the small cells of the ganglion, the distal portion of each protuberance containing a mass of larger cells, this group of cells being separated from the smaller cells by a distinct membrane.

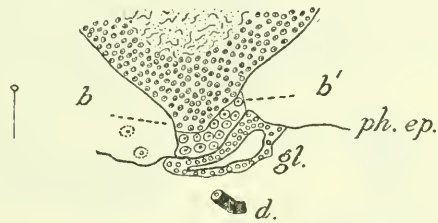


FIG. 18.—CYCLOSALPA VIRGULA, AGGREGATED FORM, AN OBLIQUE LONGITUDINAL SECTION THROUGH THE NEURAL GLAND AND THE OUTGROWTHS FROM THE GANGLION. FROM METCALF AND JOHNSON (1905).

The larger dorsal eye is seen in figure 31, plate 13, and figure 19, on this page (copied from Metcalf and Johnson, 1905). The section shows that

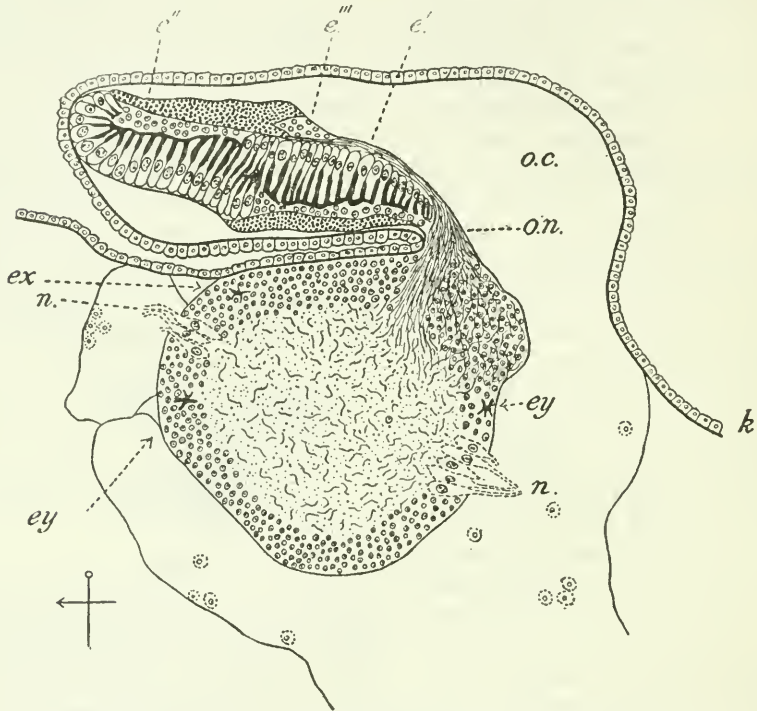


FIG. 19.—CYCLOSALPA VIRGULA, AGGREGATED FORM, A SAGITTAL SECTION OF THE GANGLION AND DORSAL EYE. FROM METCALF AND JOHNSON (1905).

the eye is divided into two main portions; a basal portion ( $e'$ ) in which the rod-cells are dorsal to the pigment, and a terminal portion ( $e''$ )

in which the rod cells are ventral to the pigment. A little behind the mid-dorsal point of this eye there is an area of thickened pigment partially surrounding a group of larger cells which are the remnant of the optic plug ( $e'''$ , see also fig. 20) which in *Cyclosalpa pinnata* and *C. affinis* is much better developed. In *C. floridana* and *C. bakeri* the optic plug becomes more closely united to the apical portion of the eye. In *C. virgula* there is but a vestige of this structure. The vestigial condition of its optic plug shows that, in the character of its large dorsal eye, *C. virgula* is intermediate between

the more archaic *Cyclosalpas* on the one hand and the *Apsteinias*, *Salpas*, and other subgenera on the other. The optic nerve enters the eye passing above the basal rod cells (fig. 19).

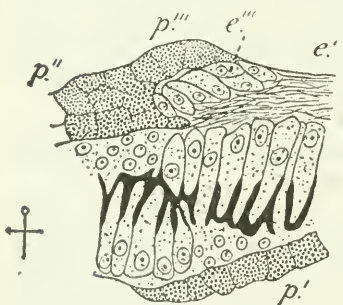


FIG. 20.—CYCLOSALPA VIRGULA, AGGREGATED FORM, THE MIDDLE PORTION OF THE SECTION OF THE DORSAL EYE SHOWN IN FIG. 19, MORE HIGHLY MAGNIFIED. FROM METCALF AND JOHNSON (1905).

In the ganglion, accessory smaller eyes are present (fig. 19, p. 48). These groups of imperfect rod-cells have no pigment associated with them. The groups vary in number and position, but have about the same structure, which is shown in figure 21. They are to be compared with the better developed accessory eyes of the other Cyclosalpas.

Just behind the optic nerve, at its origin, the ganglion is swollen to form a considerable protuberance whose cells, however, are not developed into rod-cells as they are in the corresponding part of the ganglia of some other species, as *Apsteinia punctata*, *Apsteinia asymmetrica*, *Salpa fusiformis*, *S. cylindrica*, and, as I interpret the relations, in the *Thalias*.

The musculature of *Cyclosalpa virgula* has been very carefully studied by Streiff (1908). For the solitary form he shows slightly different arrangement of the oral retractor muscles, the dorsal retractor being double and the ventral retractor uniting with the ventral division of the dorsal retractor. The ventral horizontal bands, connecting body muscles I and V, he shows as continuous. We find them interrupted. The dorsal longitudinal muscle band back of the upper lip he shows in contact with the last sphincter muscle of the dorsal lip. In our specimens these muscles are not in contact. Doubtless all these differences in our descriptions are due to differences in the specimens studied and indicate individual divergence within the species.

In the aggregated form, Streiff does not show the posterior branches of the last body muscle (our muscle IV, *b*) to be united above the post-abdomen (doubtless again divergence between his specimens and ours), nor does he describe any visceral muscle arising from the last body muscles and running into the base of the post-abdomen. We suspect that here Streiff failed to see a structure which was present, as he also fails to note the corresponding muscle in the aggregated *Cyclosalpa pinnata*.



FIG. 21.—CYCLOSALPA VIRGULA, AGGREGATED FORM, A SECTION THROUGH ONE OF THE ACCESSORY EYES IN THE GANGLION. FROM METCALF AND JOHNSON (1905).

#### THE CYCLOSALPAS IN GENERAL.

In our introductory remarks, and in the course of the descriptions of the several species, we have made numerous comparisons between the species of *Cyclosalpa*. The division of the subgenus into *Cyclosalpa symmetricales* and *Cyclosalpa asymmetricales*, while truly descriptive of the existing conditions, does not represent accurately degrees of relationship, for *Cyclosalpa bakeri*, an asymmetrical form, finds its nearest relative in *C. floridana*, an aberrant member of the group *symmetricales*. (Compare the chart on p. 158.) We have already noted that in the family Salpidae only the aggregated zooids

are asymmetrical, and that among *Cyclosalpa* only species which are not known to form whorls on the stolon show this asymmetry.

We can say that there is one type of muscular arrangement underlying the somewhat divergent conditions in the solitary forms of the whole subgenus *Cyclosalpa*, and another equally well-marked type underlying the various conditions seen in the aggregated zooids of all species of the subgenus. The evidence from the muscles points to the acceptance of the subgenus as a natural one. This conception of natural relationship is strongly borne out by the conditions in the eyes, in the outgrowths from the ganglion, and in the neural glands.

The gut is similar in position and structure in the solitary forms of all the species, except that in *Cyclosalpa floridana* the caeca are small and in *C. affinis* one is missing. The solitary *Cyclosalpa* are the only Salpidae which have the gut lying along the dorsal side of the gill. In the aggregated zooids, on the other hand, we find the more aberrant species of the subgenus approaching the true *Salpae*, the gut becoming bent into a loop, which however is not, in any species, compacted into what could be called a "nucleus."

Similarly, in the aggregated forms, the large eye of the asymmetrical species approaches the condition seen in *Ritteria*, *Apsteinia*, and the true *Salpae*.

#### BROOKSIA, new subgenus.

##### BROOKSIA ROSTRATA (Traustedt 1893).

*Salpa rostrata* TRAUSTEDT, 1893.

This subgenus I name after Prof. W. K. Brooks, who has so exhaustively studied the *Cyclosalpa* and whose studies of other members of the *Salpidae* have been extensive. Its only species, *rostrata*, resembles *Cyclosalpa virgula*, but differs from this species in having the gut, in both solitary and aggregated forms, in the shape of a rather close loop, much as is the case in the *Ritterias*. I have no specimens of this subgenus.

##### BROOKSIA ROSTRATA, solitary form.

This has been studied by Traustedt (1893), Apstein (1894, *b*), and Ihle (1910). The shape of the body is very peculiar for a solitary *Salpa* (figs. 22, and 23, p. 51). It has a great antero-ventral protuberance from below the mouth, equal in length to the whole of the rest of the body. In the aggregated zooids of *Salpa maxima*, *S. fusiformis* and *S. cylindrica* we find similar processes. They contain no musculature, but at least in some specimens, especially of *S. cylindrica*, one finds connective tissue fibers running lengthwise in the anterior protuberance. At the base of the protuberance they are continuous on each side with the ventral end of the intermediate muscle. These fibers in the anterior protuberance in the *Salpae* might function in

connection with the intermediate muscle to move the protuberance, much as the proboscis muscles in *Brooksia* must move the proboscis, were it not that the test in the *Salpae* (*sensu strictu*) seems too firm to allow much movement.

It is difficult, from the published descriptions and figures, to determine the number of body muscles, partly because the details of the oral region are not given for the adult form, so as to enable us to distinguish body muscles from oral muscles, and partly because there is disagreement between Apstein's figures of the embryo and Traustedt's and Ihle's figures of the adult. Traustedt and Ihle both show what seems to be an intermediate muscle and seven body muscles.

All the body muscles are continuous across the mid line dorsally and there is here, in some specimens, no union antero-posteriorly between adjacent muscles. In other individuals, body muscles I, II, and III are united dorsally, as are also muscles IV, V, VI, and VII. The muscles of the proboscis are unique among the Salpidae. Traustedt's and Apstein's descriptions of them do not

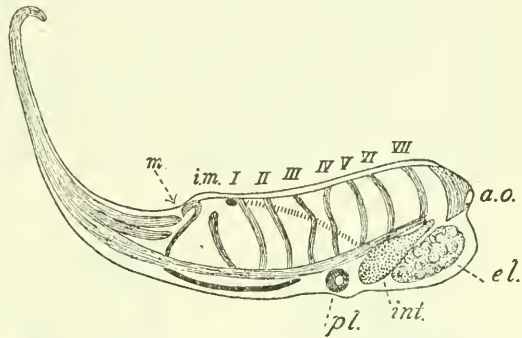


FIG. 22.—*BROOKSIA ROSTRATA*, SOLITARY FORM, VIEWED FROM THE LEFT SIDE. FROM TRAUSTEDT (1893).

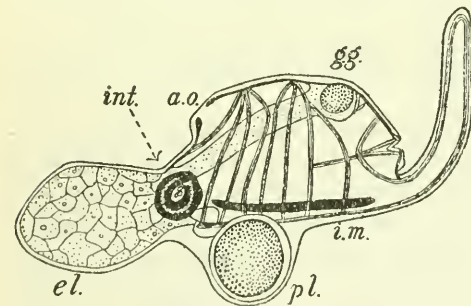


FIG. 23.—*BROOKSIA ROSTRATA*, EMBRYO, VIEWED FROM THE RIGHT SIDE.  $\times 50$  DIAMETERS. FROM APSTEIN (1894, b).

quite agree. In Apstein's figure of a side view of an embryo the dorsal bundle of muscles in the protuberance is continuous with the second sphincter of the lower lip. The ventral bundle of proboscis muscle fibers is prolonged on each side to nearly the posterior end of the body. It is doubtful if these bands are comparable to the less extensive ventral bands in the solitary *Cyclosalpa virgula* (pl. 11, fig. 26).

The oral muscles have been insufficiently described for use in detailed comparison. Apstein figures the presence of an oral retractor of the usual type and certain sphincters of the two lips. The atrial muscles are not described beyond Traustedt's figuring the presence of apparently very numerous delicate sphincters.

The gut is figured by Traustedt (1893) as apparently a compact "nucleus," but Apstein (1894, b) shows it in the embryo as a loop (fig. 23), but more compact than in any *Cyclosalpa*.

**BROOKSIA ROSTRATA, aggregated form.**

The aggregated form of *Brooksia rostrata* has been described only by Apstein (1894, b). It shows (fig. 24) about as much asymmetry as the aggregated *Cyclosalpa virgula*. The pattern of the asymmetry is constant, except that in some individuals it is exactly reversed. According to Apstein's description, in a dextral zoöid, there are four body muscles on the right side and three on the left, as is true of the aggregated *Cyclosalpa virgula*. On the right side the interme-

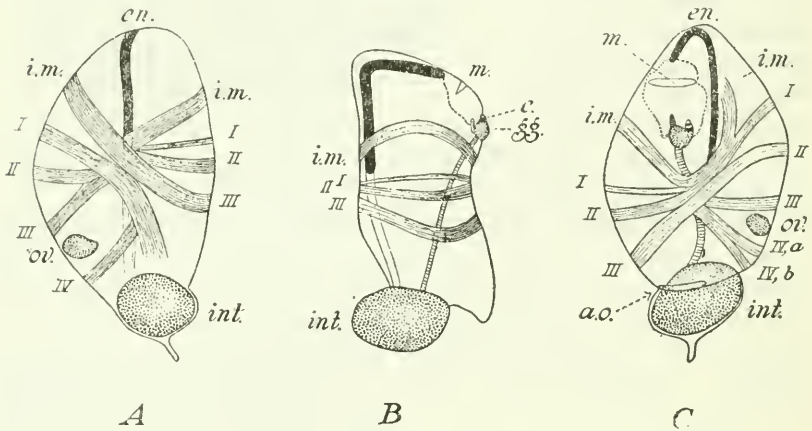


FIG. 24.—*BROOKSIA ROSTRATA*, AGGREGATED ZOOID: A, VENTRAL VIEW; B, VIEW FROM LEFT SIDE; C, DORSAL VIEW.  $\times 40$  DIAMETERS. FROM APSTEIN (1894, b).

diate muscle and body muscles I and II are united, or at least in contact, dorsally, as in *Cyclosalpa virgula*. Muscle III joins muscle II much as it would in *C. virgula* if the muscles were crowded toward the mid-dorsal point, as is the case in at least the young zoöids of *Brooksia rostrata*. Body muscle IV is similarly drawn forward, as contrasted with the condition in *Cyclosalpa virgula*. From muscle IV, on the right side, there is a branch (IV, b) running to near the base of the gut. On the left side of *Brooksia rostrata* there are three recognizable body muscles, as is the case on both sides of the aggregated *Cyclosalpa floridana*, in which species, as we have suggested, body muscles I and II may be fused. The body muscles of the aggregated *Brooksia rostrata* are thus seen to be of the *Cyclosalpa* type.

Apstein figures the eye, but not in sufficient detail to avail for comparisons. If he shows accurately the disposition of the pigment, the eye of the aggregated form of this species is different from that of any other known species.\*



## RITTERIA, new subgenus.

This subgenus includes the species *retracta*, *picteti*, *amboinensis*, and *hexagona*.

*Ritteria amboinensis* may be taken as the type of the genus, for it is nearer the norm of the genus than is *R. hexagona*, and these are the only two species in which the aggregated zoöid is well known.

This subgenus is characterized by having the gut ventral in the solitary form and less compacted into a nucleus than in the higher Salpidae, while in the aggregated zoöids of the only species whose aggregated forms are thoroughly known, *amboinensis* and *hexagona*, the gut is more closely coiled than in any aggregated *Cyclosalpa*. I have named the subgenus for Prof. W. E. Ritter, who described the species *retracta* and emphasized its resemblance to the *Cyclosalpas*. I have had for study specimens only of the species *amboinensis* and *hexagona* in this subgenus and base my conclusions as to classification largely on the studies of Apstein, Ritter, and Ihle.

## RITTERIA RETRACTA (Ritter, 1906, b).

*Cyclosalpa retracta* RITTER, 1906, b.

*Salpa amboinensis* APSTEIN, 1906, b, not 1904, b.

*Salpa retracta* IHLE, 1910.

In none of the species of this subgenus is the gut in the solitary form found dorsal to the gill, but in *Ritteria retracta* and *R. picteti* it is elongated.<sup>1</sup> The esophageal aperture is a widely flaring, trumpet-shaped opening at the base of the gill (fig. 25, p. 54). The esophagus bends forward, then backward, much as in the aggregated *Cyclosalpa virgula*. The intestine runs backward on the left of the esophagus, its tip being bent a little upward and to the right to open by the anus into the atrium, just inside of the atrial aperture. The caecum extends forward from the point of juncture of esophagus and intestine. The resemblance of the gut to that of the aggregated *Cyclosalpa virgula* is striking. The chief differences are the presence of a rudimentary second caecum in *Cyclosalpa virgula*, the greater forward bending of the distal portion of the intestine in *C. virgula*, and the flattened instead of cylindrical form of the caecum in *Ritteria retracta*.

But, observe, our comparison here is between the solitary *Ritteria* and the aggregated *Cyclosalpa*. The aggregated *Cyclosalpas*, in three species, *virgula*, *bakeri*, and *floridana*, show a more or less coiled intestine. The solitary *Ritteria* shows a similar condition—that is, the aggregated *Cyclosalpa* and the solitary *Ritteria* diverge from the more archaic *Cyclosalpa* character toward that of other Salpidae. The solitary *Ritteria retracta* is not greatly modified in the character of its gut, but the aggregated zoöids, if known, would probably show a still more curved and compacted gut.

<sup>1</sup> Ritter, 1906, b, fig. 2; Ihle, 1910, fig. 16, pl. 1.

The muscles of the solitary *Ritteria retracta* are numerous, the body muscles being 15 in number, as I would number them. Body muscles I to X are complete hoops, while body muscles XI to XV are interrupted ventrally, as is also the intermediate muscle. The oral muscles are distinctly of the *Cyclosalpa* type. There is a single oral retractor which passes outside the intermediate muscle. Apparently three sphincters are present in the lower lip, one of which ( $l_1$ ), very wide, seems to lie on the incurved portion of the lip. There is in Ritter's figure a delicate, imperfect, first sphincter at the edge of the upper lip, at the

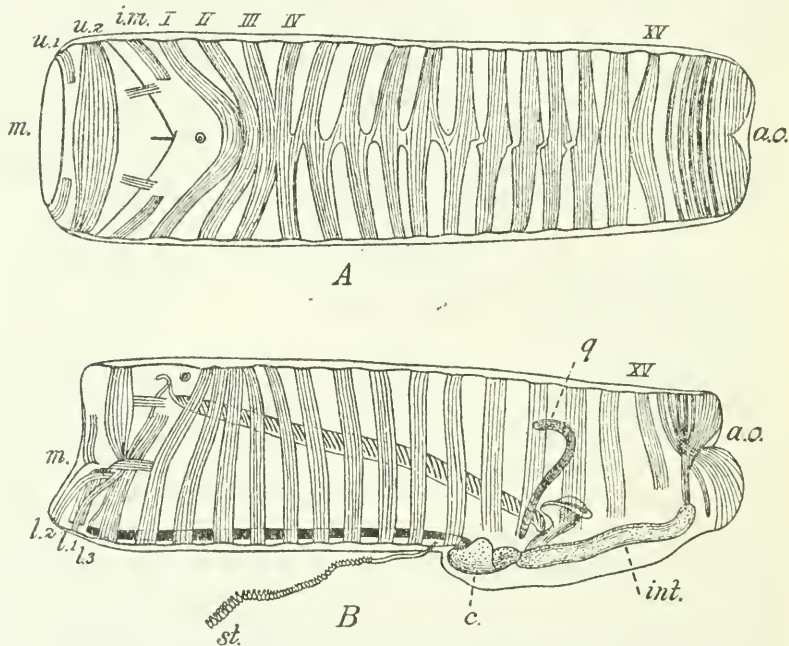


FIG. 25.—RITTERIA RETRACTA, SOLITARY FORM; A, DORSAL VIEW; B, VIEW FROM THE LEFT SIDE.  $\times 1\frac{1}{2}$  DIAMETERS. FROM RITTER (1906, b).

angles of the mouth, and a second, very broad sphincter in the upper lip, of whose connections ventrally I am not quite sure from Ritter's figure, though it seems to connect with the second and third sphincters of the lower lip. Dorsal, horizontal muscle bands lie, one on each side, between this broad sphincter and the upper ends of the intermediate muscle, but are not connected with the latter. Ritter's dorsal and side views disagree as to the union of this horizontal band with the sphincter. The atrial muscles, likewise, are distinctly of the *Cyclosalpa* type, most resembling those of the solitary *C. virgula* in the character, position, and connections of both retractor and sphincters, but there is resemblance also to the aggregated *C. virgula* in the fact that all the distal atrial sphincters are connected with the retractor.

In the elongation of the body and the large number of the body muscles, the Ritterias have passed distinctly away from the *Cyclo-salpa* condition.

The aggregated form of *Ritteria retracta* is unknown, except from one inadequate figure by Apstein (1906, *b*) of a small individual from the stolon of what he took to be "*Salpa amboinensis*," but which Ihle (1910) showed to be of the species *retracta*. No description of the aggregated zooid accompanies this figure, but it is sufficient to indicate close resemblance to the aggregated form of *Ritteria amboinensis*.

Apstein (1906, *b*) describes as *Salpa amboinensis* a form which, as Ihle (1910) has pointed out, is clearly Ritter's *retracta*.

RITTERIA PICTETI (Apstein, 1904).

*Salpa picteti* APSTEIN, 1904, *a*.

We have not as complete knowledge of this species as of *Ritteria retracta*, no description of the oral or atrial muscles, as seen in side view, being given. Apstein's figures (1904 and 1906, *a*) of dorsal and ventral views (figs. 26 and 27) show in one specimen 21 body muscles (Apstein, 1904), the presence of an incomplete intermediate muscle as in *R. retracta* not being quite certain from either the figures or descriptions. All are interrupted ventrally (fig. 27). In a second specimen, collected by the Deutsche Tiefsee-Expedition, Apstein (1906, *a*) shows 26 body muscles (fig. 27), there being here the same doubt as to the presence of an incomplete intermediate muscle. If I interpret him correctly, Ihle's description (1910) of his single specimen of this form indicates the presence of an incomplete intermediate muscle, which, like the body muscles, is interrupted ventrally. Ihle's specimen had 24 body muscles on the right side and 25 on the left.

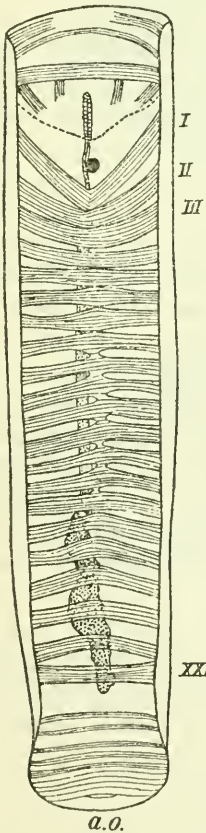


FIG. 26.—RITTERIA PICTETI, SOLITARY FORM, DORSAL VIEW.  $\times 2$  DIAMETERS. FROM APSTEIN (1904).

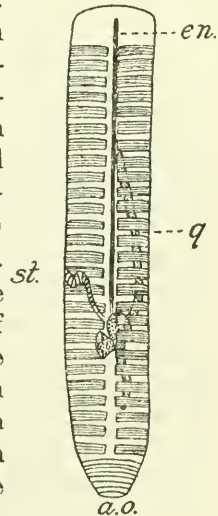


FIG. 27.—RITTERIA PICTETI, SOLITARY FORM, VENTRAL VIEW, NATURAL SIZE. FROM APSTEIN (1906, *b*).

specimen had 24 body muscles on the right side and 25 on the left.

Little can be said of the oral and atrial muscles except that, as figured by Apstein, there are three sphincters in the upper lip and that Ihle mentions the presence of an oral retractor stretching back to the first body muscle.

Ihle's figure (1910, fig. 16, pl. 1) of the gut (our fig. 28) shows conditions exactly paralleling what Ritter (1906, *b*) shows for *Ritteria retracta*, except that the caecum is apparently not flattened, as Ritter shows it for *R. retracta*. Apstein's best figure of the gut (1904, fig. 13, pl. 12), though not his description, while less clear, agrees with Ihle's description.

Ritter found in *Ritteria retracta* a problematic organ ("x") protruding on the left side of the body from near the junction of esophagus,

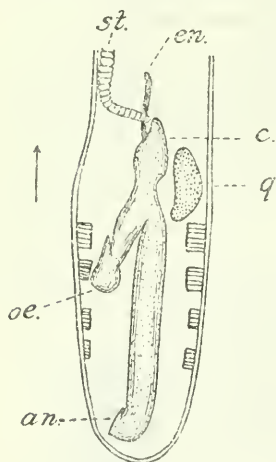


FIG. 28.—*RITTERIA PICTETI*, SOLITARY FORM, VENTRAL VIEW OF POSTERIOR END.  $\times 2$  DIAMETERS. FROM IHLE (1910).

intestine, and caecum (fig. 25 *B*, *q*, p. 54). He says: "A delicate strand seems to pass off from near its tip [base] toward the intestine." Apstein (1904 and 1906, *a*) shows for *Ritteria picteti* a probably similar organ, which he calls a glandular appendix of the intestine (fig. 27, *q*). Ihle finds a shorter, stockier body in a similar position, calling it a blood-forming organ (fig. 28, *q*). Its nature and function are in doubt, but its presence emphasizes the close resemblance between *Ritteria picteti* and *R. retracta*. This mass of cells, of problematic function, in these two species, is probably homologous with the more or less well-developed masses or groups of "eleoblast-like"<sup>1</sup> cells we have described in this paper for several species of *Cyclosalpa* (pl. 10, fig. 25, *q*; pl. 13, fig. 33, tip of caecum).

The function and interpretation of these cells can not well be discussed without knowing their embryonic origin.

The only noteworthy differences between *Ritteria picteti* and *R. retracta*, so far as our knowledge of them goes, are the larger number of body muscles in *R. picteti* and the interruption of all of them on the ventral side. These features, especially the latter, leave no doubt of the distinctness of the species.

The aggregated form of *Ritteria picteti* is unknown.

#### RITTERIA AMBOINENSIS (Apstein, 1904).

*Salpa amboinensis* APSTEIN, 1904, not 1906, *b*.

*S. amboinensis* IHLE, 1910.

Apstein (1904) and Ihle (1910) have studied this species. I have had 11 specimens of the solitary form, but no well-grown aggregated

<sup>1</sup>This resemblance to eleoblast tissue is in histological appearance only. It is not intended to suggest that there is any homology with eleoblast cells.

zoöids. Dober (1912) gives a figure of a form which he names *Salpa amboinensis*, but from the character of the intestine, only faintly delineated, it seems to be *Ritteria retracta*. Both solitary and chain forms of *R. amboinensis* are known. As Ihle has shown, it is clearly distinct from *R. retracta*, though the musculatures of the solitary forms of the two species are very much alike. The gut is very different in the two.

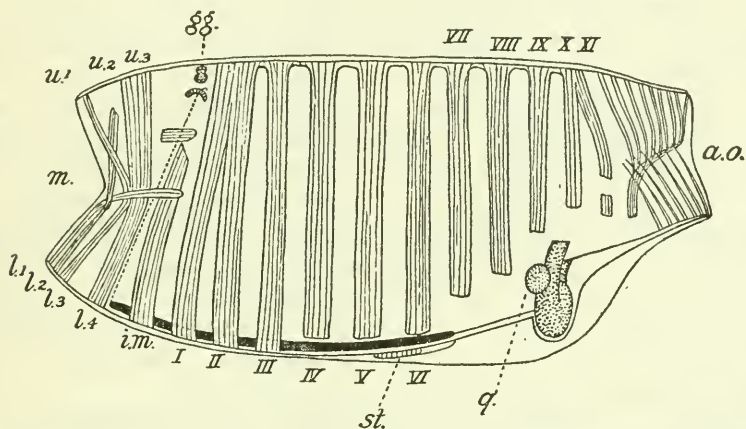


FIG. 29.—RITTERIA AMBOINENSIS, SOLITARY FORM, VIEWED FROM THE LEFT SIDE.  $\times 5$  DIAMETERS. FROM IHLE (1910). THE ORAL MUSCLES ARE SLIGHTLY CHANGED FROM IHLE'S DRAWING

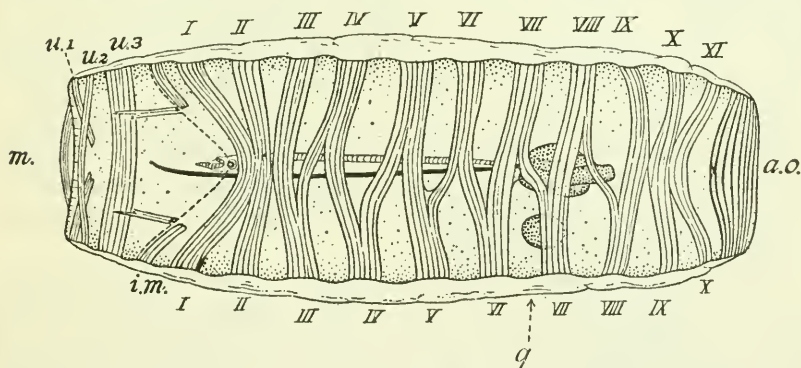


FIG. 30.—RITTERIA AMBOINENSIS, SOLITARY FORM, DORSAL VIEW.  $\times 4\frac{1}{2}$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

RITTERIA AMBOINENSIS, solitary form.

Ihle's figure of a left side view of this form (fig. 29) can best be used for comparison with the other Ritterias. Compare also our figure of a dorsal view (fig. 30).

There are 10 to 13 body muscles and a dorsally incomplete intermediate muscle. According to Apstein (1904), in the embryo the intermediate muscle is complete dorsally, being united to body

muscle I (see fig. 30, which shows a different condition in the adult). The intermediate muscle and the anterior three body muscles are continuous across the ventral mid line; the others are interrupted ventrally. The atrial retractor and its connected sphincters exactly resemble those of *Ritteria retracta*, but the strong basal sphincter of the latter species seems to be missing in *R. amboinensis*. There is close resemblance between these two species in the oral muscles also. The oral retractor lies external to all but the first of the muscles which it crosses. Ihle shows it external to this muscle also. It connects in front with the first sphincter of the lower lip and gives some fibers into the second lower lip sphincter also. Most of the fibers of this sphincter muscle pass on, outside the oral retractor, to form the first sphincter of the upper lip. The first sphincter of the upper lip and the second of the lower lip are thus connected, while the second sphincter and the very broad third sphincter of the upper lip continue below into the third and fourth sphincters of the lower lip. The oral retractor does not quite connect with body muscle I. The dorsal, horizontal band between the last sphincter of the upper lip and the intermediate muscle is as in *Ritteria retracta*, being connected with neither.

The gut is a vertical loop, moderately compact, with the anus at the left of the esophageal opening. No caeca show, but the part of the intestine into which the esophagus opens is enlarged, seemingly something as in the aggregated zoïd of *Cyclosalpa floridana* (fig. 15, pl. 5). The problematic organ, named by Ihle a blood-forming organ, is present at the left of the intestine (*q*, fig. 29), in a position similar to that occupied by the base of the corresponding organ in the other Ritterias. This organ is elongated cylindrical in *Ritteria retracta*, shorter and approaching globular in Ihle's specimen of *R. picteti*, and nearly spherical in *R. amboinensis*. In our specimens it is slightly larger than in Ihle's.

The position of these problematic organs, near the intestine, and what we know of their histology (Ritter), suggests their homology with the structure at the tip of the caecum in the aggregated zoïds of *Cyclosalpa bakeri* (pl. 10, fig. 25, *q*) and *C. virgula* (pl. 12, fig. 30). We thus have an instance of the appearance in the solitary Ritterias of a feature found among the Cyclosalpas in the aggregated zoïds only. The most noteworthy feature in the solitary *Ritteria amboinensis* is the looped character of the intestine, which is approaching the "nucleus" condition.

There is in the National Museum one lot of specimens, Cat. No. 6457, U.S.N.M. (solitary form) *Albatross* station D 5530, Balicasag Island, between Siquijor and Bohol Islands; August 11, 1909; surface; surface temperature, 84° F.; 3+ specimens.

RITTERIA AMBOINENSIS, aggregated form.

The aggregated form of this species is known from the studies of Apstein (1904) and Ihle (1910). Ihle's figures and description are much the fuller and will be used here. The shape of the zoöids in side view (fig. 31) is very like that of the aggregated *Cyclosalpa*

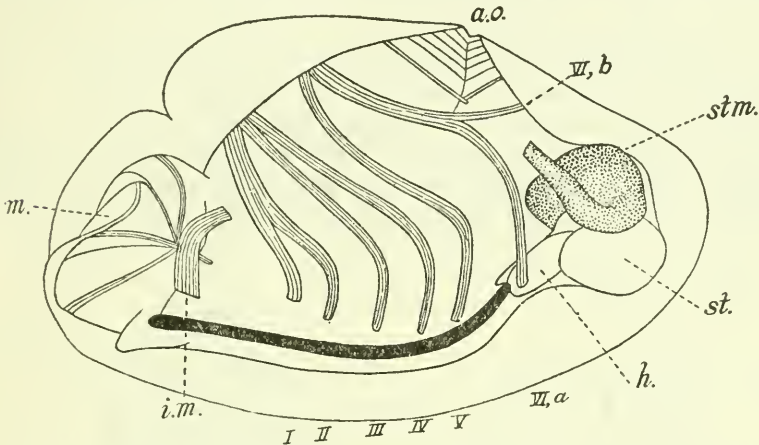


FIG. 31.—RITTERIA AMBOINENSIS, AGGREGATED ZOOID, VIEWED FROM THE LEFT SIDE.  $\times 11$  DIAMETERS FROM IHLE (1910).

*bakeri* (pl. 8). In dorsal view (fig. 33, B) or ventral view (figs. 32 and 33, A) it resembles *Salpa maxima* (fig. 67, p. 85). The aggregated *Apsteinia magalhanica* (fig. 63, p. 82) and *Ritteria hexagona* (fig. 41, p. 67) have somewhat the same shape in dorsal view.

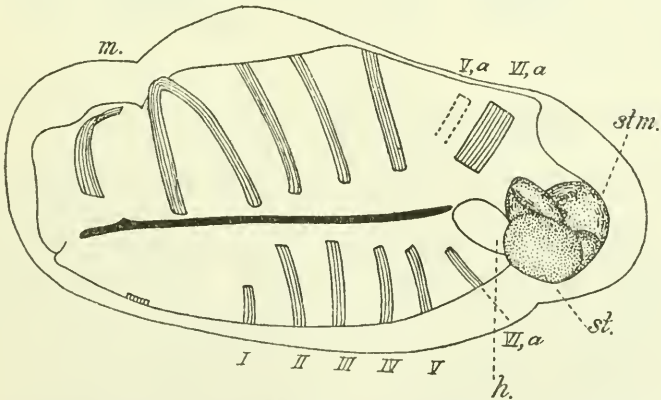


FIG. 32.—RITTERIA AMBOINENSIS, AGGREGATED FORM, VENTRAL VIEW.  $\times 11$  DIAMETERS. FROM IHLE (1910).

The body muscles are asymmetrical. There is a short, wide intermediate muscle, incomplete both ventrally and dorsally (fig. 31). It must function more in connection with the oral system than with the body muscles. Six body muscles are present, I and II united

throughout the dorsal half of their course, III and IV converging to meet them on the dorsal surface, making a broad common trunk. Similarly V and VI unite dorsally into one broad muscle. Muscle VI has an anterior branch in front of the gut and a posterior branch which joins its fellow of the other side at the base of the atrial siphon, giving rise here, on the midline, to a median muscle, which runs into the base of the postabdomen (fig. 33, *B*). This is clearly the homolog of the visceral muscle we have emphasized in our description of the aggregated *Cyclosalpa*. No muscles are described arising from the lower part of the anterior branch of body muscle VI and passing into the post abdomen, this agreeing with the aggregated *Cyclosalpa virgula*. Just above its point of branching, body muscle VI connects with the well-developed atrial retractor muscle. In an older zoöid

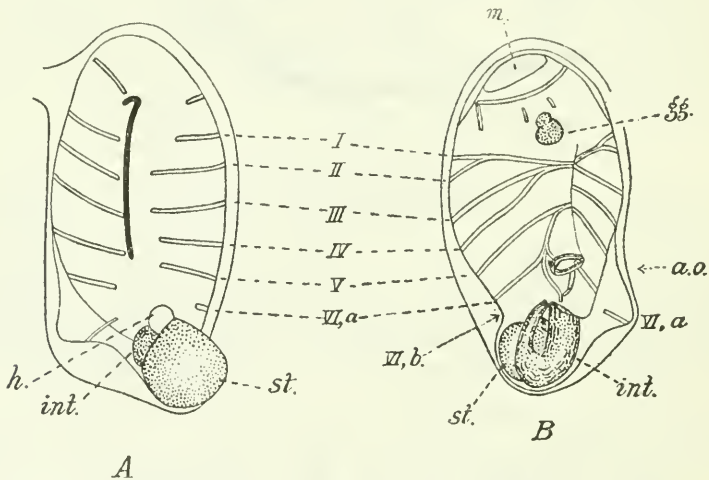


FIG. 33.—RITTERIA AMBOINENSIS, YOUNG AGGREGATED ZOÖID FROM THE STOLON: *A*, DORSAL VIEW; *B*, VENTRAL VIEW.  $\times 49$  DIAMETERS. FROM IHLE (1910).

Ihle shows the atrial sphincter distinct at its base from body muscle VI. Body muscle VI corresponds closely in its position, branches, and connections with body muscle III of *Cyclosalpa floridana* and body muscle IV of the other *Cyclosalpas*. In the solitary forms of the *Ritterias* there is an increase in the number of body muscles. The same is seen to be true of the aggregated zoöids in *R. amboinensis* and it is also true of the aggregated form of *R. hexagona* (fig. 41, p. 67), these being the only species of *Ritteria* whose aggregated zoöids are known.

On the right side the arrangement of the body muscles is slightly different (figs. 32 and 33 *A*), but their number is the same. There is considerable asymmetry, both at their dorsal and their ventral ends, between the body muscles of the right and left sides. At the base of



a postero-lateral protuberance<sup>1</sup> from the body is an unconnected broad muscle which probably should be included among the body muscles (fig. 32). No corresponding muscle is known in other Ritterias or in the Cyclosalpas.

The atrial muscles (fig. 31) resemble those of the aggregated *Cyclosalpa bakeri*, the distal delicate sphincters being connected (doubtless on each side) with a delicate retractor, a distinct stronger retractor being connected with the broad basal sphincter (fig. 33, *B*). In the aggregated *Cyclosalpa bakeri* this basal retractor is present only on the left side. The descriptions and figures of the aggregated *Ritteria amboinensis* do not include the atrial muscles of the right side.

The oral muscles (fig. 31) include a retractor and, in the upper and lower lips, two sphincters each, the details of whose connections are not figured or described. Ihle shows the oral retractor internal to the broad intermediate muscle (his "*Bogenmuskel*"). Such an arrangement is not known in other Salpidae except in the aggregated *Cyclosalpa floridana*.

The gut of the aggregated *Ritteria amboinensis* (fig. 31) is very similar to that of the solitary form. It is a loop with the wide esophageal aperture on the right and the anus above it on the left. At the point of union of esophagus and intestine there is a large rounded swelling on the left side (fig. 33, *B, st*), which Ihle calls the "stoloblast" or "eleoblast."<sup>2</sup> Its connections are not clearly shown and its nature is doubtful. It may correspond to the problematic organ "*q*" found in a similar position in the solitary form (fig. 29) or it may be a caecum, though, if it were either, Ihle, whose work is so uniformly accurate, would naturally have so described it. The gut is a little more compact in the aggregated zooid than in the solitary form. It could perhaps be called a "nucleus."

The eyes of the aggregated *Ritteria amboinensis* (fig. 34) are figured by Apstein (1904) with sufficient detail to allow some comparison with other species. The larger dorsal eye shows the anterior and posterior divisions characteristic of the true Salpas. In the posterior region the rod-cells are dorsal to the pigment; in the distal region they are ventral. One familiar with the eyes of other species must doubt the accuracy of Apstein's drawing, as to the arrangement of the rod-cells in the basal portion of the eye. They probably should lie with their long axes more nearly vertical. Behind the large dorsal

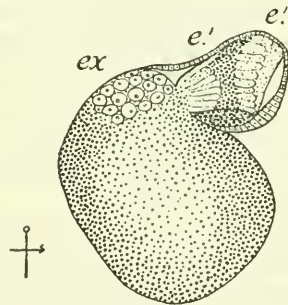


FIG. 34.—RITTERIA AMBOINENSIS, EYE AND GANGLION OF AN AGGREGATED ZOÏD.  $\times 150$  DIAMETERS. FROM APSTEIN (1904).

<sup>1</sup> Right or left according to the position on the stolon (Ihle).

<sup>2</sup> Of course the aggregated zooid has no stolon rudiment and no eleoblast.

eye, in the upper part of the ganglion, is an accessory mass of optic cells, very similar to that seen in the aggregated forms of *Salpa cylindrica* (figs. 87, p. 98, and 89, p. 99), *S. fusiformis* (fig. 79, p. 92), and *Apsteinia punctata* (figs. 56, p. 77, and 57, p. 78).

RITTERIA HEXAGONA (Quoy and Gaimard, 1824).

*Salpa hexagona* QUOY AND GAIMARD, 1824.

(?) *S. biennis* DE BLAINVILLE, 1827.

*Iasis hexagona* HERDMAN, 1891.

This species is somewhat unlike the other Ritterrias, and the appropriateness of its inclusion in the same subgenus is perhaps doubtful. The numerous wide irregularly united muscle bands and the loosely looped gut, in the solitary form, and the rather decided asymmetry of the aggregated zoöids have, however, seemed sufficient to justify such classification.

I have abundant material of both solitary and aggregated forms of this species which has been studied by a number of zoologists. Streiff, who has done such accurate work on the muscles of many species, has not observed this form. The drawings here given are after Traustedt (1885) and Apstein (1894, *b*) and from specimens in the collections of the United States Bureau of Fisheries and the United States National Museum, which include many individuals of both solitary and chain forms from Philippine waters and the northern Pacific Ocean off Alaska.

The following specimens are in the collection of the United States National Museum:

Cat. No. 6428, U.S.N.M. (solitary form), *Albatross* station D 5258, Juraojurao Island, off southern Panay; June 2, 1908; surface; surface temperature, 84° F.; surface density, 1.02587; one specimen.

Cat. No. 6458, U.S.N.M. (embryo), *Albatross* station D 5128, Nogas Island, Sulu Sea; February 4, 1908; surface; surface temperature, 80° F.; one specimen.

Cat. No. 6455, U.S.N.M. (aggregated form), *Albatross* station D 5196, Capitancillo Island, off northern Cebu Island; April 3, 1908; surface; surface temperature, 82° F.; surface density, 1.02518; three specimens.

Cat. No. 6516, U.S.N.M. (aggregated form), *Albatross* station D 5128, Sulu Sea, vicinity Southern Panay, Philippine Islands, February 4, 1908; surface; surface temperature, 80° F.; 60 plus specimens.

Cat. No. 6531, U.S.N.M. (solitary form), *Albatross* station D 5350, Palawan Passage, Philippine Islands; December 27, 1908; surface; surface temperature, 80° F.; surface density, 1.02381; one specimen.

Cat. No. 6539, U.S.N.M. (aggregated forms), *Albatross* station D 5128, Sulu Sea, vicinity southern Panay, Philippine Islands; February 4, 1908; surface; surface temperature, 80° F.; three specimens.

Cat. No. 6570, U.S.N.M. (aggregated form), *Albatross* station D 5175 Sulu Sea, Southeast of Cagayanes Islands, Philippine Islands; March 8, 1908; surface; surface temperature, 82° F.; 100 + specimens.

Cat. No. 6590, U.S.N.M. (solitary form), *Albatross* station D 5616, Molucca Passage, Philippine Islands; November 22, 1909; surface; surface temperature, 84° F.; one specimen.

Cat. No. 6591, U.S.N.M. (chain form), *Albatross* station D 5128, Sulu Sea, vicinity southern Panay, Philippine Islands; February 4, 1908; surface; surface temperature, 80° F.; 15 + specimens.

Cat. No. 6592, U.S.N.M. (aggregated form), *Albatross* station D 5186, between Panay and Negros, Philippine Islands; March 30, 1908; surface; surface temperature, 80° F.; surface density, 1.02530; 25 + specimens.

Cat. No. 6611, U.S.N.M. (aggregated form), *Albatross* station D 5234, between Bohol and Leyte, Philippine Islands; May 7, 1908; surface; surface temperature, 84° F.; surface density, 1.02531; 36 specimens.

Cat. No. 6621, U.S.N.M. (solitary form), *Albatross* station D 5601, Gulf of Tomini, Celebes; November 13, 1909; surface; surface temperature, 83° F.; two specimens.

Cat. No. 6623, U.S.N.M. (aggregated form), *Albatross* station D 5437, W. coast of Luzon, Manila Bay to Lingayen Gulf; May 8, 1909; surface; surface temperature, 86° F.; one specimen.

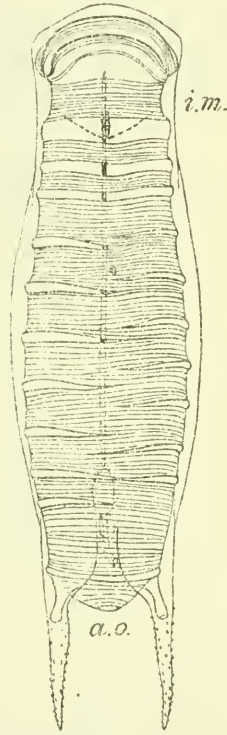


FIG. 35.—RITTERIA HEXAGONA, SOLITARY FORM, DORSAL VIEW. FROM TRAUSTEDT (1885).

RITTERIA HEXAGONA, solitary form.

The very broad body muscles are irregularly continuous across the mid-dorsal line, but are widely interrupted ventrally (fig. 35). Their disposition is not identical on the right and left sides. At the posterior end of the body the body muscles form an almost complete layer, the degree of antero-posterior fusion between the successive muscle bands differing in different individuals, so one can not say how many such bands are typically present. Among my specimens I find individuals showing 9 on one side and 10 on another; 10 on each side; 10 on one side and 11 on the other; 11 on each side; 11 on one side with 12 on the other; and, in one of the largest specimens, 12 on each side.

The intermediate muscle (*i. m.*) seems to be the very broad band which lies across the dorsal surface, in front of the ganglion (fig. 36).

The upper lip bears a broad third sphincter with a very delicate second sphincter branching from its base and a rather narrow admarginal sphincter attached at its base to both the oral retractor and the third dorsal sphincter. The lower lip has a rather narrow admarginal sphincter, continuous at each angle of the mouth with a rudimentary oral retractor muscle whose unconnected posterior end lies horizontally between the intermediate muscle and body muscle I. A broad second sphincter lies near the base of the incurved flap of the lower lip.

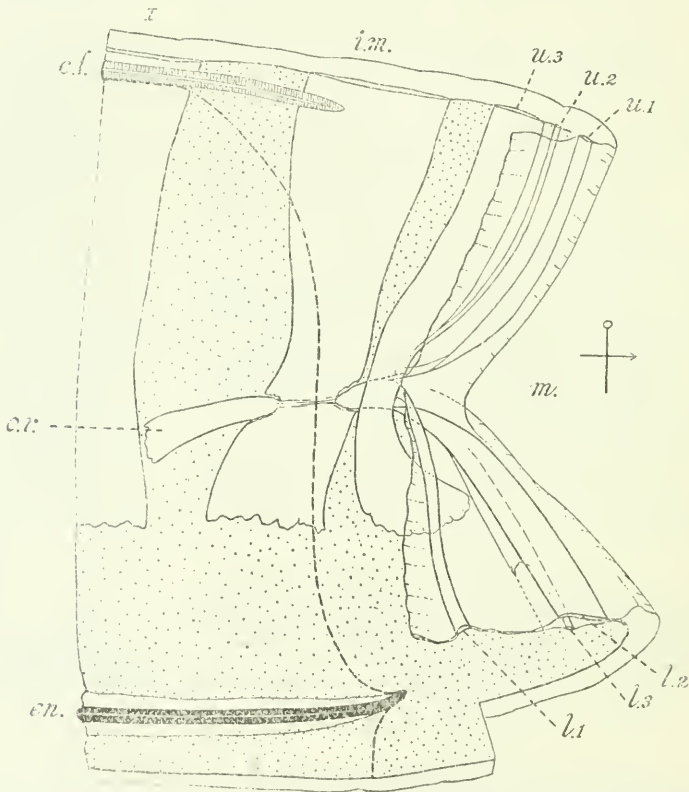


FIG. 36.—RITTERIA HEXAGONA, SOLITARY FORM, ORAL MUSCLES OF THE LEFT SIDE, SEEN FROM THE INSIDE  
 X 5 DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

A third sphincter arises from the oral retractor in front of the second. It is at first broad, but soon narrows to a thread, which lies just beneath the second sphincter, that is, on the endodermal side of the incurved flap. Both lips are seen to be incurved, the ventral more strongly than the dorsal. There are no horizontal muscles lying between the basal oral sphincter and body muscle I, as there are in most species.

On each side of the body, posteriorly, is a well-developed horizontal atrial retractor muscle (fig. 37) continuous with the very numerous

strands of the atrial sphincters, which are so close together that they seem to form a broad band continuous over both lips of the atrial aperture. The fibers of this atrial sphincter are less closely approxi-

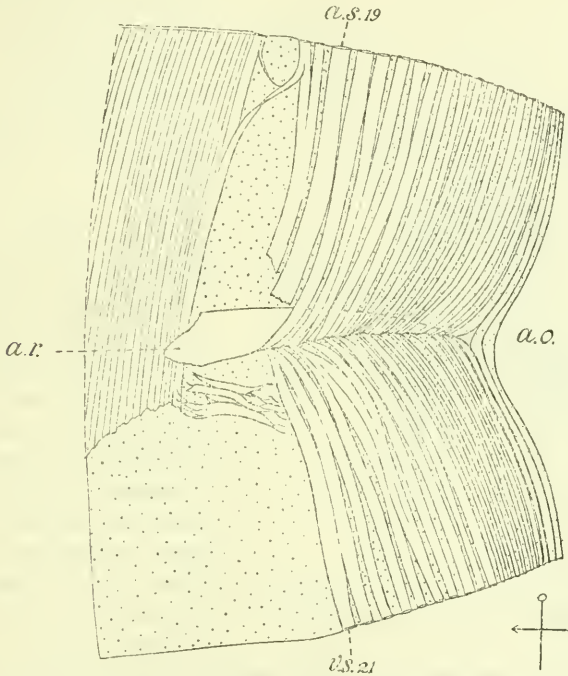


FIG. 37.—RITTERIA HEXAGONA, SOLITARY FORM, ATRIAL MUSCLES, VIEWED FROM THE LEFT SIDE.  $\times 5$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

mated than are those composing one of the body muscles, the fibers not actually touching side by side in the former while they do in the latter.

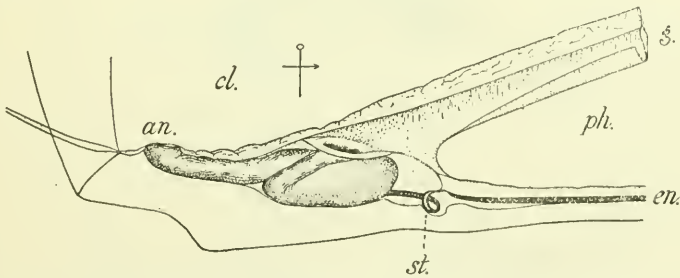


FIG. 38.—RITTERIA HEXAGONA, SOLITARY FORM, THE GUT VIEWED FROM THE RIGHT SIDE.  $\times 3\frac{1}{2}$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

Ventral to the base of the atrial retractor muscle are several branching muscle strands not observed in other species.

The gut (fig. 38), as in the other solitary Ritterias, is a simple loop. In *R. hexagona* there is a bend where the esophagus enters the intes-

tine, the first portion of the intestine lying along the esophagus. The distal, free end of the intestine extends back, as in *Ritteria retracta*, and *R. picteti*, to open a little in front of and below the atrial aperture.

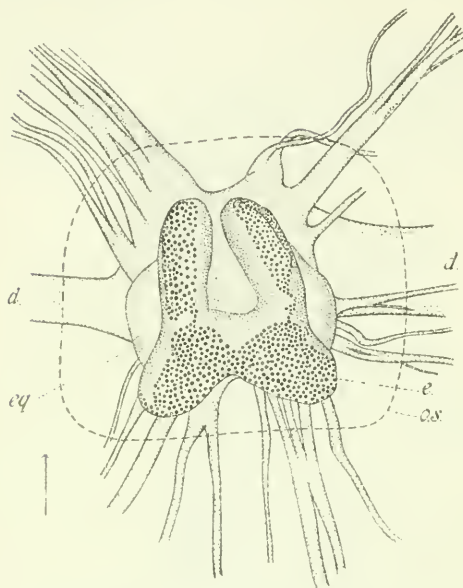


FIG. 39.—*RITTERIA HEXAGONA*, SOLITARY FORM, DORSAL VIEW OF EYE AND GANGLION;  $\times 58$  DIAMETER.

The condition of the neural glands and eye (fig. 39) in the solitary *Ritteria hexagona* has not heretofore been described. The disks of the gland are well developed (fig. 40). Their ducts (*d*) are peculiar. Instead of being a narrow coiled tube, as in other species, each duct is very wide, its diameter being nearly half as great as that of the discoidal gland itself, and its aperture to the pharyngocloacal chamber being of the same width as the duct. There are no distinct outgrowths from the ganglion in connection with the glands, though one sees a broad protuberance (*b*) of the ganglion where each gland touches it. The cells in these protuberances are like the ordinary smaller cells of the ganglion.

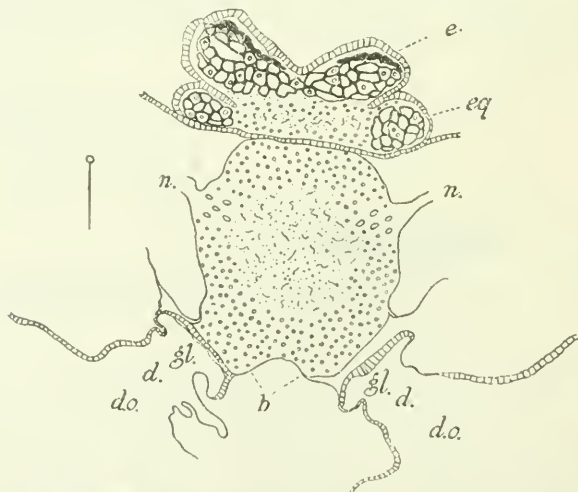


FIG. 40.—*RITTERIA HEXAGONA*, SOLITARY FORM, TRANSVERSE SECTION OF EYE, GANGLION AND NEURAL GLANDS.  $\times 47$  DIAMETERS.

The horseshoe form of the eye (fig. 39) is modified in this species, the postero-lateral regions of the horseshoe being drawn upward, making quite an angle, these regions being also enlarged.

The rod-cells (fig. 40) are degenerate angular cells with irregularly thickened walls, as in the solitary *Salpa fusiformis* (fig. 79, p. 92). Below the main mass of the horseshoe, on each side, is a secondary mass (*eq*) of similar irregular rod-cells with no associated pigment.

There are a pair of conical, denticulate protuberances (fig. 35) from the postero-lateral angles of the body, somewhat similar to those of *Thalia longicauda* (fig. 113, p. 120) and *Thetis vagina* (fig. 114, p. 122). Into the base of each runs a tube of mantle epithelium.

RITTERIA HEXAGONA, aggregated form.

The aggregated zooids of this species (fig. 41) are quite strongly asymmetrical, but the asymmetry affects chiefly the test, which has an angular protuberance at one side of the posterior end of the body.

As in the solitary form, the muscle bands are broad and strong, and the test very firm. There are six body muscles, continuous across the dorsal mid line, but widely interrupted ventrally. The intermediate muscle (*i. m.*, fig. 42) shows a condition which aids us in interpreting the relations in the solitary form. There is a broad band (*i. m.*) continuous across the mid-dorsal line, and branching obliquely backward from this on each side is a narrower band of muscle (*i. m.*<sub>2</sub>), whose posterior end approaches but does not touch the dorsal region of body muscle I. These oblique bands are apparently the intermediate muscles. The broader band, on the other hand, which is continuous across the dorsal mid line, is the apparent homolog of the muscle which in the solitary *Ritteria hexagona* we called the internerve muscle. Apparently, in the aggregated zooids of this species, the intermediate muscle is double, the posterior division being oblique and discontinuous dorsally, the anterior division lying more vertical and being continuous across the dorsal line. In a number of the more aberrant species of Salpidae the intermediate muscle is double.

The oral retractor muscle on each side is very short and broad (fig. 42). It bifurcates in front, the dorsal branch being continued into the first sphincter of the upper lip. In the upper lip are a second narrow sphincter and a third very broad. The lower end of the second sphincter abuts upon, but does not fuse with, the third sphincter; this third sphincter similarly abuts upon the oral retractor muscle without fusing with it. The ventral branch of the retractor muscle is continued into the very broad third sphincter of the lower lip. There are two other sphincter muscles in the lower

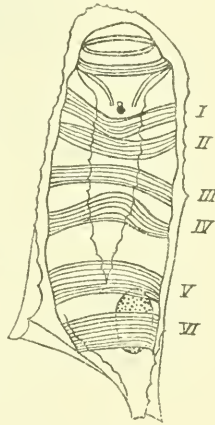


FIG. 41.—RITTERIA HEXAGONA, AGGREGATED ZOÏD, DORSAL VIEW.  $\times 2$  DIAMETERS. FROM APSTEIN (1894, b).

lip, attached to the ventral branch of the retractor. The first of these, the admarginal sphincter, is of moderate width. The second is still narrower. Distally it fuses with the third sphincter. The dorsal horizontal bands, which in most species lie between the basal oral sphincter and the first body muscle, are wanting in this species.

There is an atrial retractor muscle on each side (fig. 43), internal to the sphincters, of which there are fourteen in each of several individuals studied. The basal two sphincters are broad and strong; sphincters 6 to 12 (numbering from the aperture) are attached to the ventral edge of the retractor. In sphincters 7 or 8 to 12 only part

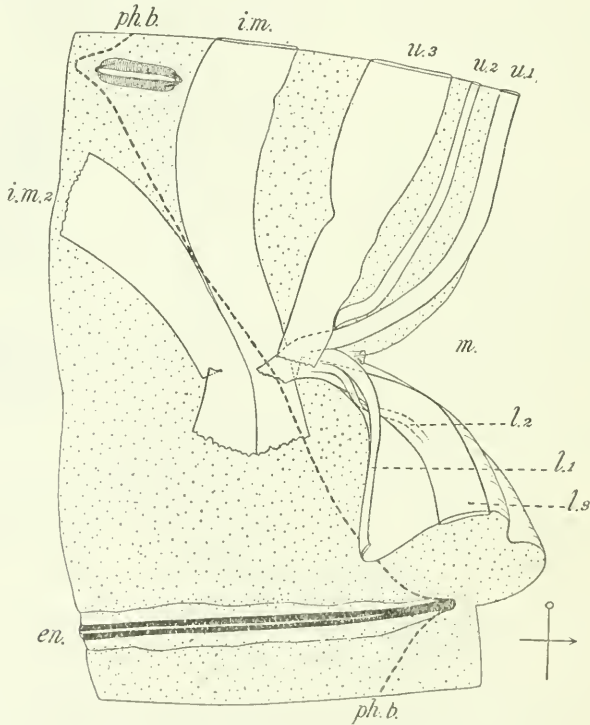


FIG. 42.—RITTERIA HEXAGONA, AGGREGATED FORM, ORAL MUSCLES OF THE LEFT SIDE SEEN FROM THE INSIDE. (DRAWN BY HOYT S. HOPKINS.)

of the fibers bend and run into the retractor; other fibers pass across the retractor, making complete hoops. The distal five sphincters are not connected with the retractor muscle. The terminal three are very delicate. The fibers of the sphincter muscles, like those of the body muscles, form an even single layer. The fibers are flat, and lie edge to edge, presenting a perfectly regular appearance. The fibers of the retractor, on the other hand, are elliptical, not flat, in cross section, and are more irregularly arranged.

In all the body muscles and in the wider atrial sphincters one fiber, or sometimes two or three fibers, at each edge of each muscle band



are much broader than the rest of the fibers of the band. The more distal sphincters have their fibers, 2 to 10 in number, uniformly narrow. All the inner fibers in all the muscles are narrow.

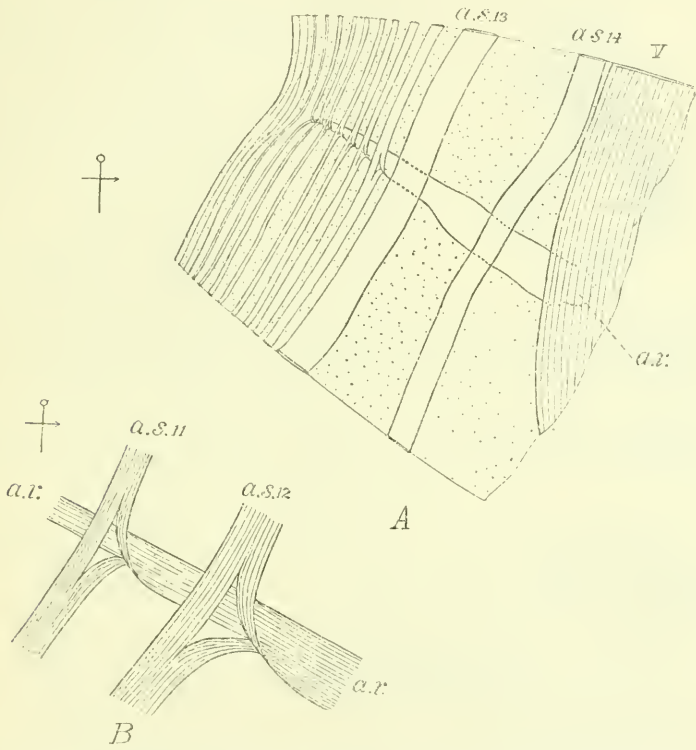


FIG. 43.—RITTERIA HEXAGONA, AGGREGATED FORM: A, ATRIAL MUSCLES VIEWED FROM THE RIGHT SIDE; B, DETAIL SHOWING ATTACHMENT OF THE SPHINCTERS TO THIS ATRIAL RETRACTOR MUSCLE. (DRAWN BY HOYT S. HOPKINS.)

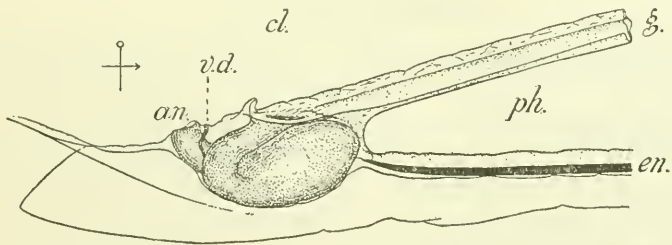


FIG. 44.—RITTERIA HEXAGONA, AGGREGATED FORM, GUT SEEN FROM THE RIGHT SIDE.  $\times 3$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

The gut (fig. 44) forms a somewhat compact “nucleus,” as in the aggregated zooids of *Ritteria amboinensis*, but the course of the intestine can be seen without dissection. Its condition is closely similar to that in the solitary form except that the intestine is shorter.

The large dorsal eye (figs. 45 and 46) resembles that of *Cyclosalpa virgula*, except for three points: First, the optic plug is wholly wanting, as is true of all species outside the subgenus *Cyclosalpa*; second, the rod-cells are very irregular and are evidently degenerate; third, the position of the eye with reference to the ganglion is different. In *Ritteria hexagona* the ganglion has rotated forward forty-five degrees, as is shown by the position of the zone of large cells from which the nerves arise (*z.* in fig. 46). The originally dorsal surface is dorso-anterior. The eye is connected with the originally anterior part of the originally dorsal surface [now the dorsal part of the anterior surface], as in all other species. A similar rotation is seen in *Apsteinia punctata* (fig. 57, p. 78), and is still more marked in *Thalia* (fig. 111, p. 117). The long axis of the eye in

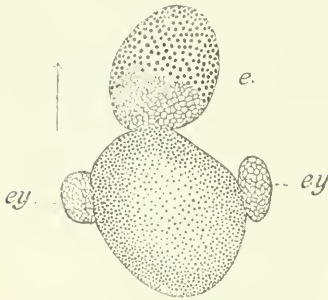


FIG. 45.—RITTERIA HEXAGONA, AGGREGATED FORM, DORSAL VIEW OF GANGLION, EYE AND ACCESSORY EYES.  $\times 100$  DIAMETERS. FROM METCALF (1893, c).

more marked in *Thalia* (fig. 111, p. 117). The long axis of the eye in



FIG. 46.—RITTERIA HEXAGONA, AGGREGATED FORM, SAGITTAL SECTION OF GANGLION AND EYE.  $\times 150$  DIAMETERS. FROM MELCALF (1893, c).

*Ritteria hexagona* stands at an angle of 45 degrees to the originally dorso-ventral axis of the ganglion. The same is true in *Salpa maxima* and *S. fusiformis* (fig. 79, p. 92). In the *Cyclosalpas*, on the other hand, the eye has bent forward until its long axis is nearly parallel to the antero-posterior axis of the ganglion. The *Cyclosalpas* retain the ganglion in its primitive position, but rotate the eye forward from  $160^\circ$  to  $180^\circ$  in different species. *Ritteria hexagona* and *Apsteinia punctata* (fig. 57) rotate the ganglion forward  $45^\circ$  and the eye rotates about  $140^\circ$  forward. *Thalia democratica* rotates the whole ganglion and eye forward nearly  $180^\circ$ . The position of the eye in relation to the body of the salpa is about the same in the aggregated zooids of all species except the *Thalias*, *Pegea*, and the *Traustedtias*, but it is effected in some by the rotation of the eye alone; in others by the rotation of both eye and ganglion.

There are no accessory eyes in the ganglion proper in the aggregated *Ritteria hexagona*, but there are a pair of outgrowths (*ey* in figs. 45 and 47), one on each side, near the dorsal surface of the ganglion, which contain cells closely resembling the degenerate rod-cells in the eyes of many species of Salpidae; as for instance, *Salpa fusiformis*, solitary, dorsal eye (fig. 76, p. 91), *S. fusiformis*, aggregated, accessory eye (fig. 79, p. 92), *Thetys vagina*, aggregated, dorsal and accessory eyes (fig. 118, p. 126), and *Pegaea confederata* (figs. 126 and 127, p. 136, and 132, p. 143). No pigment is associated with these masses of degenerate rod-cells in *Ritteria hexagona*. The position of these outgrowths, just above the disks of the neural gland, suggests their homology with the large-celled outgrowths in other species.

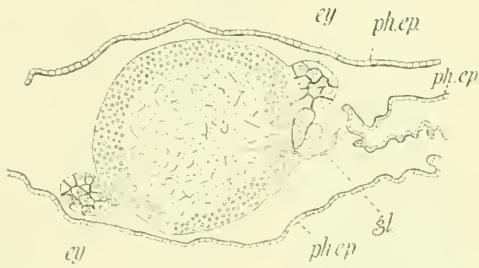


FIG. 47.—RITTERIA HEXAGONA, AGGREGATED ZOÏD, OBLIQUE SECTION OF GANGLION SHOWING A BIT OF ONE OF THE NEURAL GLANDS (*sl*) AND THE TWO LATERAL OUTGROWTHS (*ey*.) FROM THE GANGLION WITH THEIR CELLS DEVELOPED AS DEGENERATE ROD-CELLS.  $\times 150$  DIAMETERS. FROM METCALF (1893, c.).

The Ritterias show close similarity to one another in their muscular system, which is of the *Cyclosalpa* type, except that the body muscles are more numerous. In the character of the gut they are intermediate between the *Cyclosalpas* and the other Salpidae. In the asymmetry of the aggregated zoïd (in the three species in which the aggregated form is known) they resemble the *Cyclosalpae asymmetricales* and the *Apsteinias*. In fact some degree of asymmetry is observed in the aggregated zoïds of most species of Salpidae.

#### APSTEINIA, new subgenus.

It includes the species *punctata*, *asymmetrica*, and *magalhanica*.

The species *punctata* may be taken as the type of this subgenus, for it is the best known of the three species. We have had material of only *Apsteinia punctata*.<sup>1</sup> Other species have been studied by Apstein (1894, *b*), Fowler (1896), Dober (1912), and Streiff (1908).

This subgenus is characterized by the marked asymmetry of its aggregated zoïds, in which it agrees with the *Ritterias*, *Brooksia*, and some *Cyclosalpas*, and by the compact condition of the gut, which, in both solitary and aggregated forms of all species, forms a "nucleus," as in the higher Salpidae. The *Apteiniae* differ from the *Salpae*, *sensu strictu*, in having all the body muscles in the solitary forms in the condition of complete hoops, as in *Doliolum*.

<sup>1</sup> After this paper was in press material of *Apsteinia asymmetrica* was obtained. See Appendix, page 183.

## APSTEINIA PUNCTATA (Forskål, 1775).

*Salpa punctata* FORSKÅL, 1775.*S. punctata* VOGT, 1854.*S. musculosa* HERDMAN, 1888.

We have had for study four specimens of the solitary form of this species and five of the aggregated zooids, besides the well-developed zooids on the stolons of two of the solitary individuals. Specimens of both solitary and aggregated forms have been deposited in the United States National Museum.

Cat. No. 6463 U.S.N.M. (solitary form), from Naples Zoological Station; one specimen.

Cat. No. 6464, U.S.N.M. (aggregated form), from Naples Zoological Station; four specimens.

Careful comparison of our specimens has shown Streiff's work so accurate that for the musculature we use mostly his figures.

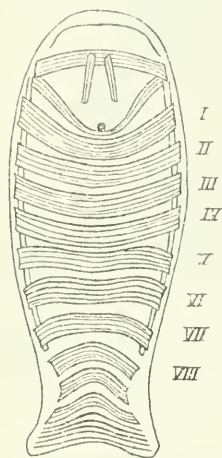


FIG. 48.—APSTEINIA PUNCTATA, SOLITARY FORM, DORSAL VIEW SHOWING MUSCLES. FROM STREIFF (1908).

## APSTEINIA PUNCTATA, solitary form.

There are eight body muscles (figs. 48 and 49), all broad complete bands except the eighth, which is interrupted ventrally at the sides of the gut, as the homologous muscle is in the Cyclosalpas and, of course, the Ritterias. The intermediate muscle and body muscles I and II are in contact dorsally. The edges of all the body muscles are composed of wide fibers (fig. 51). The central fibers are much narrower. The bands thus appear lighter on each edge.

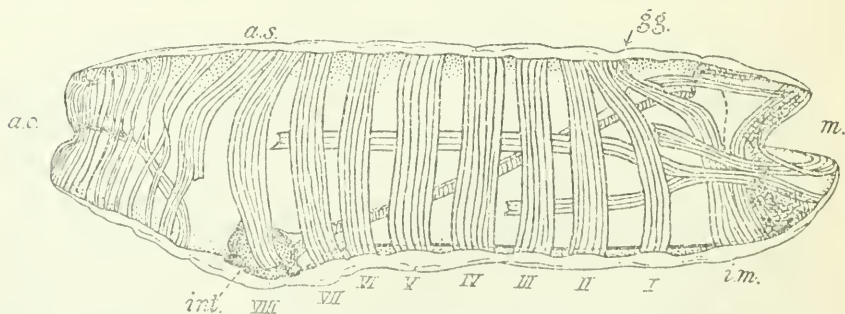


FIG. 49.—APSTEINIA PUNCTATA, SOLITARY FORM, VIEWED FROM THE RIGHT SIDE.  $\times 2$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

The oral muscles (fig. 51) include a dorsal retractor and a ventral retractor which posteriorly is bifurcated, its dorsal division running back along the side of the body in a horizontal plane, reaching beyond the posterior edge of the seventh body muscle (figs. 48 and 49). Its

ventral division runs backward and a little ventralward, to the posterior edge of the third body muscle (fig. 49). In the lower lip there is a very short unconnected band (*l. 1*) at the edge of the lip (fig. 51), not before described, and a second, broad, sphincter (*l. 2*) not split as in the embryo Streiff figures (fig. 50), and continuous with the dorsal retractor. There is a third sphincter, not so broad as the last, continuous dorsally with the first sphincter of the upper lip. The dorsal retractor shows broad fibers on its edges, as does the main trunk of the ventral retractor. The two elongated posterior divisions of the retractor, on the other hand, do not show their marginal fibers broader than their central ones. The fourth sphincter of the lower lip is broad. Posteriorly it is continuous with the ven-

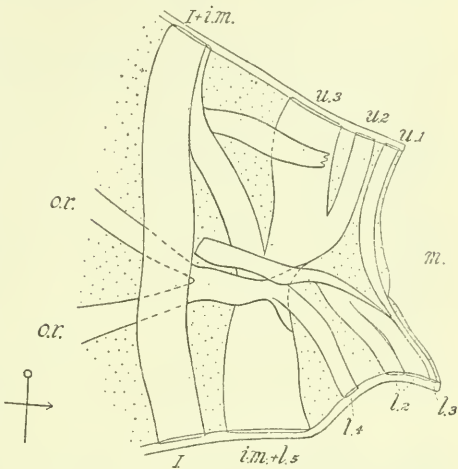


FIG. 50.—*APSTEINIA PUNCTATA*, EMBRYO, ORAL MUSCULATURE, VIEWED FROM THE RIGHT SIDE. FROM STREIFF (1908), MY LETTERING.

tral oral retractor. Just in front of the intermediate muscle lies a very broad fifth sphincter of the lower lip, with broad marginal fibers.

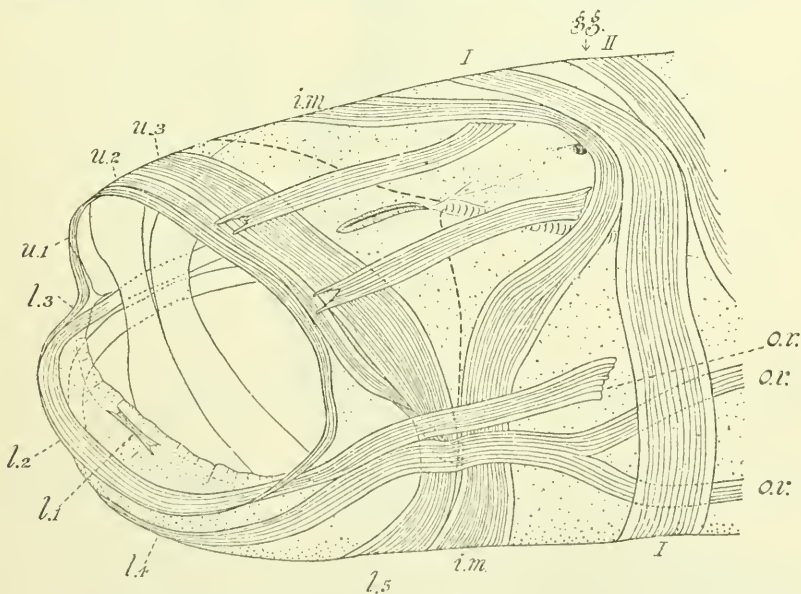


FIG. 51.—*APSTEINIA PUNCTATA*, SOLITARY FORM, ADULT. THE ORAL END OF THE BODY, ANTERO-LAEVO. DORSAL VIEW.  $\times 5$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

tral oral retractor. Just in front of the intermediate muscle lies a very broad fifth sphincter of the lower lip, with broad marginal fibers.

In the upper lip there are, in the embryo figured by Streiff (fig. 50) and in two of our adults, three sphincters, one, moderately broad, at the edge of the lip, continuous ventrally with the posterior edge of the second sphincter of the lower lip, a second slightly broader sphincter, and a third, very broad, the latter continuous ventrally with the broad fifth sphincter muscle of the lower lip. The second sphincter of the upper lip twists and bends back, attaching to the inside of the ventral oral retractor. In two others of our adult specimens, sphincters 2 and 3 of the upper lip are united throughout their course, forming a very broad band. The dorsal retractor is external to all the muscles it crosses. The ventral retractor is external to the intermediate muscle, but both its posterior extensions are internal to all the body muscles they cross.

Streiff, in describing and figuring the conditions in his embryo, apparently made one slight error, failing to note the incurling of the edge of the lower lip, so that the muscles of the incurled portion of the lip are incorrectly given. The minute rudimentary first sphincter muscle he doesn't show. His first sphincter should be number three. That is, he has exactly reversed the space relations.

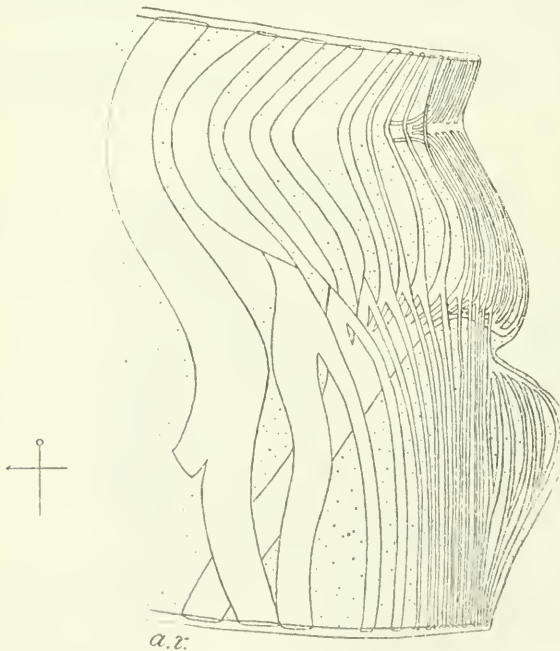


FIG. 52.—*APSTEINIA PUNCTATA*, SOLITARY FORM, ATRIAL MUSCULATURE, SEEN FROM THE LEFT SIDE. FROM STREIFF (1908).

The oral muscles of the solitary *Apsteinia punctata*, including the dorsal horizontal band between the intermediate muscle and the sphincters of the upper lip, are rather similar to those described for the *Cyclosalpa* and *Ritterias*, showing no important differences except the great posterior extension of the dorsal and ventral branches of the ventral oral retractor. This is a remarkable feature. Streiff, however, shows for the solitary form of *Cyclosalpa virgula* a ventral oral retractor which is split posteriorly into dorsal and ventral branches. These branches extend back only to the first body muscle. In our specimens of the solitary *Cyclosalpa virgula* the ventral oral retractor is undivided (pl. 11, fig. 26).

The atrial muscles, well shown by Streiff (fig. 52), conform to the condition seen in the solitary Ritterias and the solitary *Cyclosalpa virgula*, except that in the latter species the distal sphincters are not connected with the retractor (pl. 11, fig. 26) and in *Ritteria retracta* Ritter shows the atrial retractor external to the atrial sphincters (fig. 25, p. 54). Streiff describes, and our specimens show, a folding and interruption of the marginal sphincters dorsal to the atrial retractor.

Both lips of the solitary *Apsteinia punctata* bear the numerous delicate cylindrical branches of a gland (?) whose histological structure suggests that it may possibly be a phosphorescent organ (fig. 49). Its form, however, is very different from any known luminous organ in other species. Glands of similar appearance, though less developed, are on the lips of the aggregated zooids. Behind the gut, and on each side of it, are similar branching glands in the solitary form.

The eye is in the condition usual in the solitary Salpidae.

APSTEINIA PUNCTATA, aggregated form.

This zooid (fig. 53) is strongly asymmetrical, though not so much so as is the aggregated *Brooksia rostrata* (fig. 24, p. 52) or the aggregated

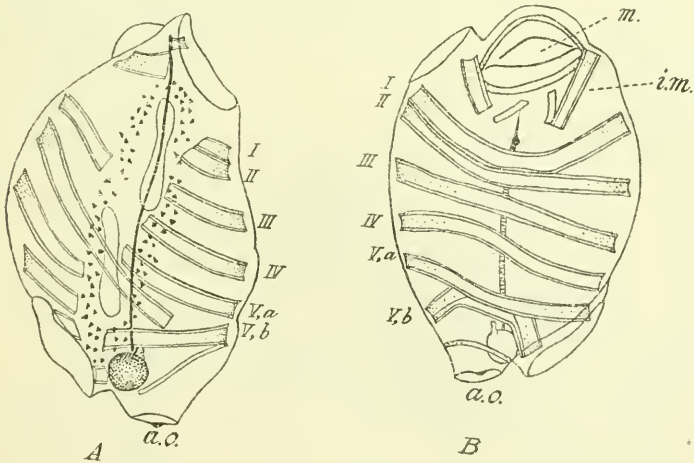


FIG. 53.—APSTEINIA PUNCTATA, AGGREGATED ZOÏD FROM THE LEFT SIDE OF THE STOLON: A, VENTRAL VIEW; B, DORSAL VIEW. FORM STREIFF (1908) WITH MODIFICATIONS.

*Cyclosalpa virgula* (pls. 11, 12, and 13). Its muscles are sufficiently indicated by the figures. In this species, as in *Brooksia rostrata*, there are dextral and laeval individuals.

The body muscles are five in number, the fifth being divided into the usual two branches seen in the aggregated zooids of other species. On one side only of the body, a delicate branch arises from body muscle V b and runs to the region of the gut (fig. 53 A). This reminds one of the delicate branch in the aggregated zooids of

*Cyclosalpa affinis* (pl. 3, fig. 10), *C. floridana* (pls. 4, 5, and 6), and *C. bakeri* (pls. 7, 8, 9, and 10), arising on each side of the body from

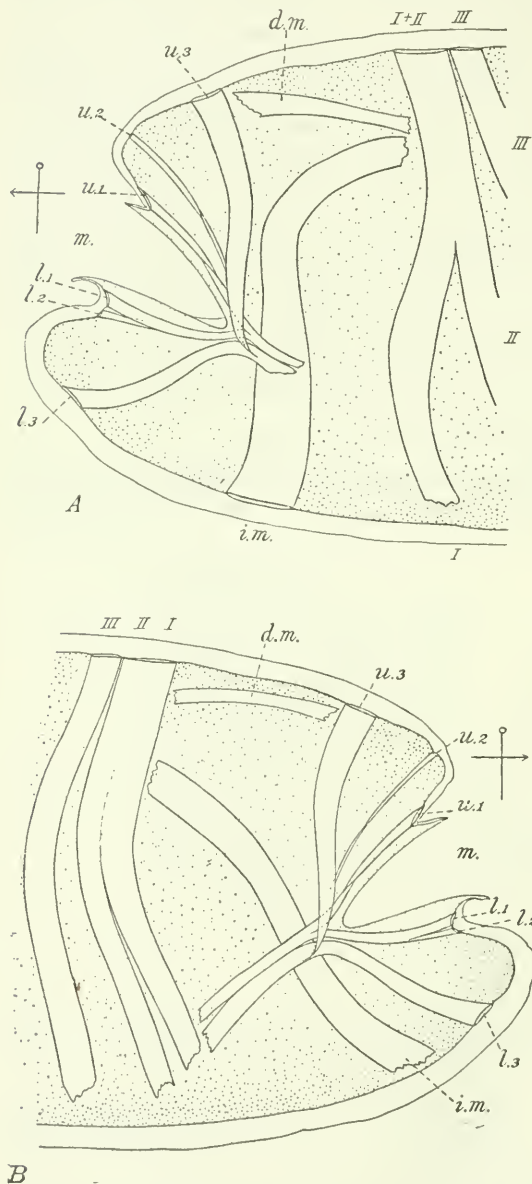


FIG. 54.—*APSTEINIA PUNCTATA*, AGGREGATED ZOÏD FROM THE LEFT SIDE OF THE STOLON, ORAL MUSCULATURE VIEWED FROM THE INSIDE: A, RIGHT SIDE OF THE BODY; B, LEFT SIDE OF THE BODY.  $\times 7$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

the last body muscle, and running to the viscera. Note, however, that in these *Cyclosalpas* this delicate strand arises from the anterior branch of the last body muscle while in *Apsteinia punctata* it arises from the posterior branch of this muscle. All the body muscles are interrupted ventrally. The intermediate muscle is present on each side as a broad band, much longer on one side than the other. The oral and atrial muscles are shown in figures 54 and 55, the latter copied from Streiff. Observe the asymmetry in the intermediate muscle of the two sides, and the greater length of the oral retractor muscle on one side.

The gut is a compact "nucleus" (fig. 53).

The eyes (figs. 56 and 57) have been described by Metcalf and Johnson (1905). They show definite departure from even the most modified *Cyclosalpa* type, that of *C. virgula*, and conform quite closely to that seen in

the true Salpas. That portion of the large dorsal eye which in the *Cyclosalpas* we called the plug, and which in *Cyclosalpa virgula*



is so greatly reduced ( $e'''$ , figs. 19 and 20, p. 48), is entirely wanting in *Apsteinia punctata*. At the place where it should lie is an intruding branch of the pigment layer (fig. 57, p. 78), which is probably a reminiscence of the former presence of the plug. The other features of the large eye are much as in *Cyclosalpa virgula*, except that it is much shorter, more like the eye of the aggregated *Salpa maxima*.

No pairs of minute eyes are found in the ganglion. In the less aberrant *Cyclosalpas* there are two pairs of these very small eyes. In *C. virgula* there are a varying number of still more minute groups of less developed rod-cells. In *Apsteinia punctata*, while the minute eyes are wanting, there is a large group of rod-cells ( $ex$ ) in two layers, one above the other, on the dorsal side of the ganglion, just in front of the origin of the optic nerve. Similar masses of rod-cells, in a corresponding position, are found in the aggregated

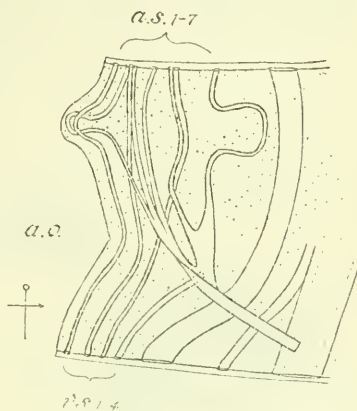


FIG. 55.—APSTEINIA PUNCTATA, AGGREGATED ZOÏD, ATRIAL MUSCULATURE OF THE LEFT SIDE, SEEN FROM WITHIN. FROM STREIFF (1905).

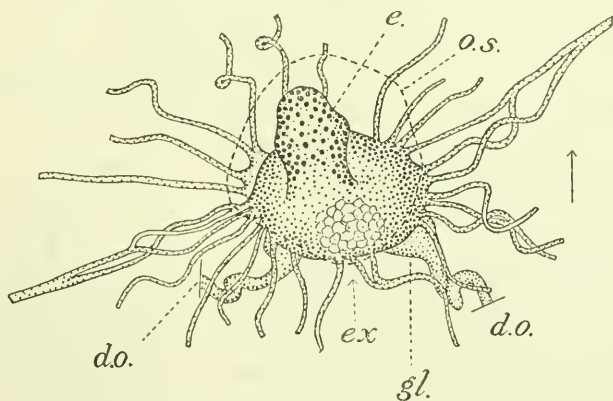


FIG. 56.—APSTEINIA PUNCTATA, AGGREGATED ZOÏD, DORSAL VIEW OF GANGLION, EYES AND NEURAL GLANDS. FROM METCALF AND JOHNSON (1905).

zooids of other species of the subgenus *Salpa* (fig. 79, p. 92). In *S. cylindrica* (figs. 87, p. 98, and 89, p. 99) the rod-cells form a single layer; in *S. fusiformis* and *S. maxima* they are irregularly arranged and degenerate. Homologous groups of rod-cells will be described later for *Thalia*.<sup>1</sup>

The neural glands show the usual character.

<sup>1</sup> And for *Apsteinia asymmetrica*, see Appendix, page 183.

## APSTEINIA ASYMMETRICA (Fowler, 1896).

*Salpa asymmetrica* FOWLER, 1896.

This species, described by Fowler, has been observed also by Apstein (1901). I have had no specimens.<sup>1</sup> Dober (1912) figures

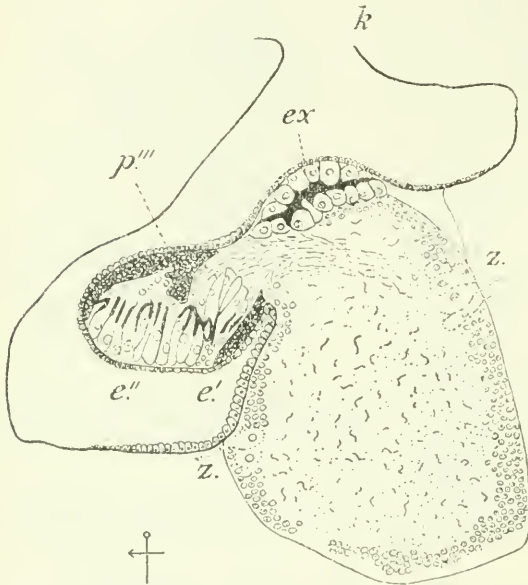


FIG. 57.—APSTEINIA PUNCTATA, AGGREGATED ZOÏD, SAGITTAL SECTION OF GANGLION AND EYES. FROM METCALF AND JOHNSON (1905).

belongs to the atrial series. The intermediate muscle and body muscles I and II are in contact dorsally, so also are body muscles III and IV and VIII and IX. The gut is described as a compact "nucleus."

One interesting feature of the oral musculature is observed in Fowler's figures. There is on each side a strong oral retractor muscle, which posteriorly is bifurcated, as in *Apsteinia punctata*, into dorsal and ventral portions. The ventral division extends back to the fifth body muscle; the dorsal division reaches past all the body muscles to the atrial sphincters. The resemblance to *Apsteinia punctata* is very marked and is a very clear indication of the affinity of the two species. Fowler's description and figures are ob-

the nervous system, but without detail in the eye, so no use can be made here of his work. Details of the structure of the oral and atrial muscles are not included in these descriptions, nor is the character of the eye sufficiently known for comparisons.

APSTEINIA ASYMMETRICA.  
solitary form.

Judging from Apstein's figure (fig. 58), interpreted with the aid of Fowler's side view of the embryo (fig. 59), there are apparently 10 body muscles, though the tenth very possibly

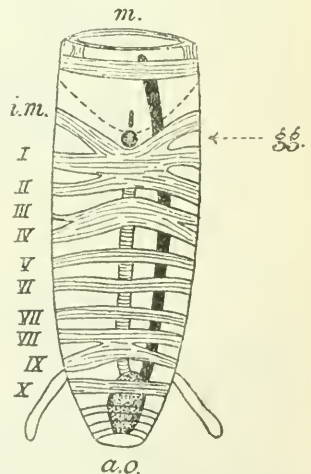


FIG. 58.—APSTEINIA ASYMMETRICA, EMBRYO, DORSAL VIEW.  $\times 22$  DIAMETERS. FROM APSTEIN (1901).

<sup>1</sup> Specimens obtained after this paper was in press are described in the Appendix, see page 183.

scure. He mentions "a right and left longitudinal slip of unequal length in connection with the two circumoral sphincters," evidently meaning that one "slip" is on the right and the other on the left. It seems evident, however, from his figures, and from the relations in other species between oral retractor and oral sphincter muscles, that we have in *Apsteinia asymmetrica* a dorsal and a ventral division of the oral retractor on each side of the body. The junction of the two "slips" and their connection with the oral sphincters, which Fowler figures, is not possible on any other interpretation. I have therefore modified an obscure portion of his "Figure 8" [fig. 59, B] to show the

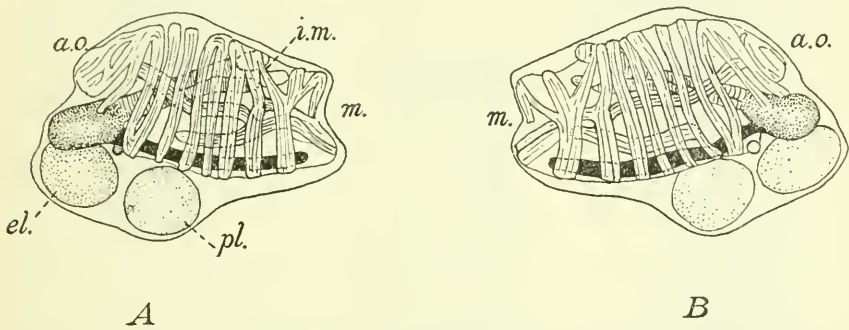


FIG. 59.—*APSTEINIA ASYMMETRICA* EMBRYO: A, FROM THE RIGHT SIDE; B, FROM THE LEFT SIDE  $\times 16$  DIAMETERS. FROM FOWLER (1896); B, SLIGHTLY MODIFIED.

dorsal division of the oral retractor passing *over* the gill. Fowler's "Figure 8," though obscure, seems to show the gill above the muscle band.

*APSTEINIA ASYMMETRICA*, aggregated form.

The atrial siphon is asymmetrically placed (figs. 60 and 61). The body muscles also are asymmetrical, their arrangement being rather like that seen in the aggregated *Apsteinia punctata*. There are five upon each side, muscles I, II, and III being asymmetrically in contact dorsally. Muscle V shows the usual anterior and posterior branches. Ventrally the intermediate muscle and all the body muscles are interrupted except the two branches of body muscle V. The ventral ends of the muscles of the right and left sides are very asymmetrical, as shown in the figures. The gut is described as a compact "nucleus." The condition of the eye and neural gland is unknown.

The resemblance between the aggregated forms of this species and *Apsteinia punctata*, in the asymmetry both of the body and of the body muscles, and the compact character of the gut in both solitary and aggregated forms of *Apsteinia asymmetrica*, indicate that this species should be placed among the *Apsteinias* rather than the

Ritterias. The oral retractor muscle so resembles that of *Apsteinia punctata* as to indicate close relationship between that species and

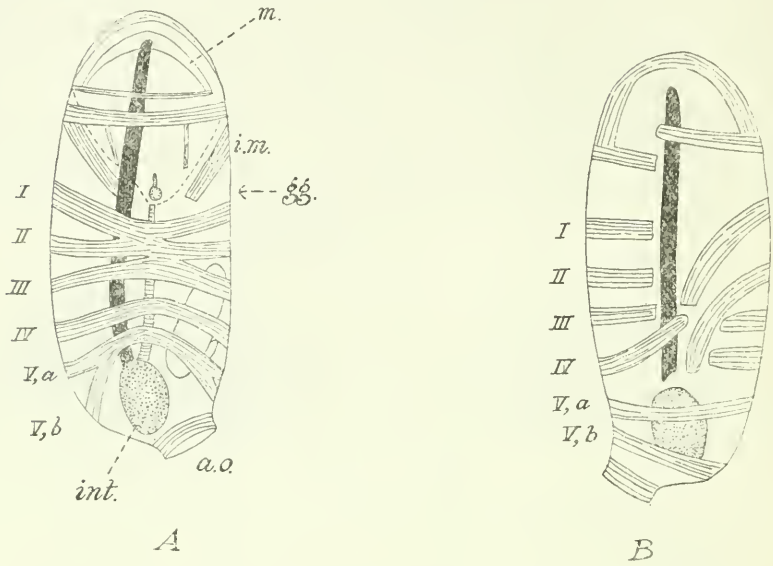


FIG. 60.—*APSTEINIA ASYMMETRICA*, AGGREGATED FORM: A, DORSAL VIEW; B, VENTRAL VIEW  $\times 22$  DIAMETERS. FROM APSTEIN (1901).

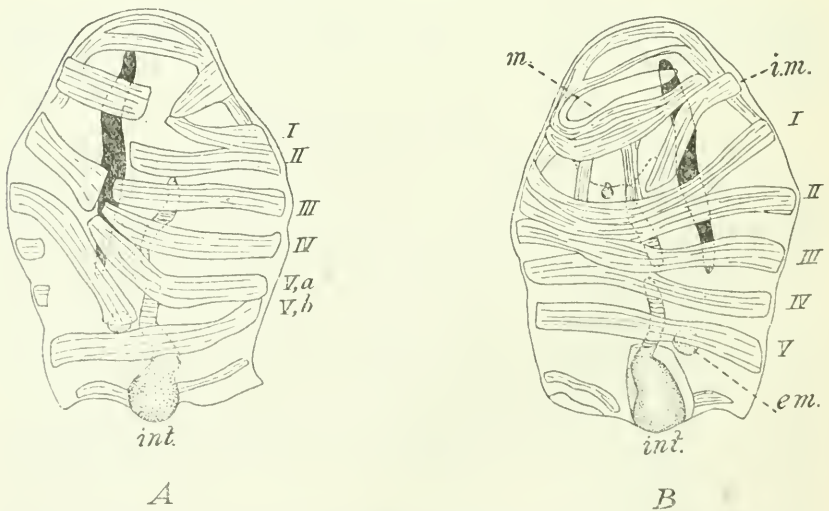


FIG. 61.—*APSTEINIA ASYMMETRICA*, AGGREGATED ZOÏD: A, VENTRAL VIEW; B, DORSAL VIEW  $\times 4\frac{1}{2}$  DIAMETERS. FROM FOWLER (1896).

*A. asymmetrica*. The very marked asymmetry of the aggregated zoïds separates this species from the true *Salpae, sensu strictu*.

## APSTEINIA MAGALHANICA (Apstein, 1894, b).

*Salpa magalhanica* APSTEIN, 1894, b.

This species has been studied by Apstein (1894, b) and Streiff (1908). I have had no specimens. Streiff, unfortunately, gives no figures. His descriptions do not fit Apstein's figures, but of course one can not correct Apstein's drawings from a verbal description. I am under the necessity, therefore, of copying Apstein's drawings, in spite of the fact that there is reason to believe them inaccurate in detail.

## APSTEINIA MAGALHANICA, solitary form.

The body muscles (fig. 62), seven in number, are broader than those of the solitary *Apsteinia asymmetrica*. Muscles I, II, III, and IV approach one another dorsally and also ventrally, but they are not fused. Muscles V and VI Apstein shows in contact dorsally. Muscles IV and V are in contact laterally. Streiff says that the first cloacal muscle is fused dorsally with the last body muscle. Apstein interprets both as body muscles.

The intermediate muscle and the dorsal horizontal bands in front of body muscle I are shown in figure 62.

From Streiff's description, the oral musculature seems to resemble that of the solitary *Apsteinia punctata*, except there are no elongated posterior branches of the oral retractor. The atrial muscles also seem, from Streiff's description, to show resemblance to those of *Apsteinia punctata*.

The gut is described as a compact "nucleus."

## APSTEINIA MAGALHANICA, aggregated form.

The zooids are strongly asymmetrical (fig. 63), as noted above. There are five body muscles on each side, whose arrangement is shown in the accompanying figures (from Apstein.) The intermediate muscle is present. It seems to be double. The dorsal horizontal band is also found.

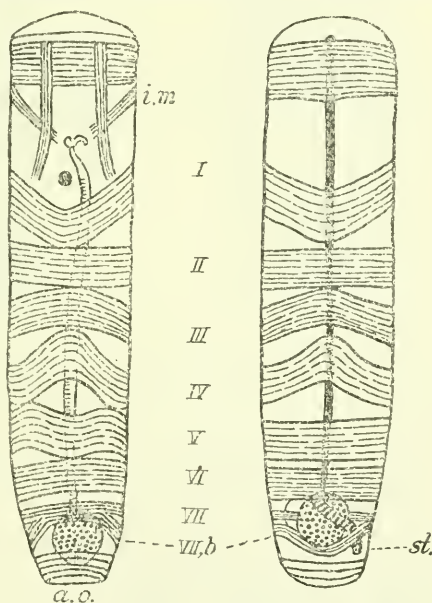


FIG. 62.—APSTEINIA MAGALHANICA, SOLITARY FORM: A, DORSAL VIEW; B, VENTRAL VIEW.  $\times 4$  DIAMETERS. FROM APSTEIN (1906, b).

Streiff describes the cloacal musculature as resembling the usual type for tubular cloacal siphons such as are seen in *Apsteinia punctata*.

The gut is said by Apstein to be a compact "nucleus." Apstein's description of the eye is too meager for use in our comparisons.

The Apsteinias, as I interpret their relationships, arose from forms which, like the *Cyclosalpa asymmetricales*, had aggregated zooids

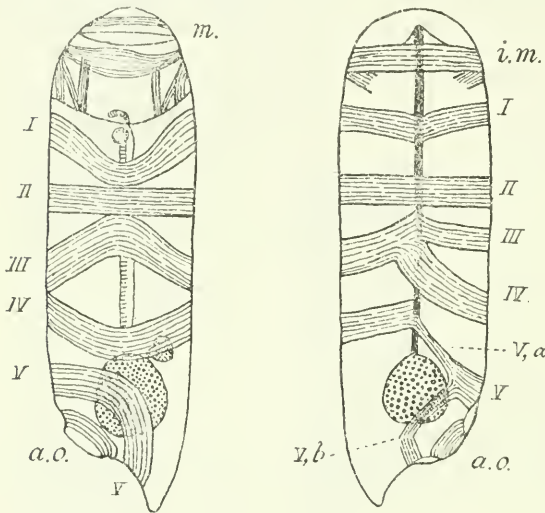


FIG. 63.—APSTEINIA MAGALHANICA, AGGREGATED FORM: A, DORSAL VIEW; B, VENTRAL VIEW.  $\times 4$  DIAMETERS. FROM APSTEIN (1906, b).

with great asymmetry. I have so grouped the species in the subgenus as to show decreasing asymmetry. (See chart on p. 158.) In the true Salpas this asymmetry is much more reduced, affecting none of the muscles except the atrial musculature, and observable in the body form chiefly in the asymmetrical position of the atrial siphon and the protuberances from the body.

The Apsteinias are distinguished from the Ritterias (also a subgenus with asymmetrical aggregated zooids) by the fact that in the former subgenus the gut of both solitary and aggregated forms is a compact "nucleus," while in the Ritterias the gut of the solitary form does not form a nucleus.

#### Subgenus SALPA (*sensu strictu*) (Forskål, 1775).

In this subgenus I include the species *maxima* and its variety *tuberculata*, *fusiformis* and its form *aspera*, and *cylindrica*. I have very abundant material of all these species. Herdman's description (1888) of the poorly preserved *Salpa mollis* is not sufficient to allow us to discuss its validity as a species, so no further reference will be made to it. The species *fusiformis* may be taken as the type.

The species of this subgenus are very similar to one another in form and musculature. They make a compact and well-demarcated group. The solitary forms of all have nine body muscles. The aggregated zooids all show more or less asymmetrical anterior and posterior protuberances from the body. In *Salpa maxima* the posterior

protuberance is strongly asymmetrical. In *S. fusiformis* both are large and somewhat asymmetrical. In both the type form and the form *aspera* the protuberances are often reduced in size, but are still asymmetrical. In *S. cylindrica* the processes are still more reduced and are nearly symmetrical. The gut in both forms of all species is a compact "nucleus."

SALPA MAXIMA Forskål, 1775.

*S. maxima* FORSKÅL, 1775.

*S. africana* FORSKÅL, 1775.

*S. birostrata* DE BLAINVILLE, 1827.

(?)*S. forskalii* LESSON, 1832.

*S. africana-maxima* KROHN, 1846.

*S. maxima* APSTEIN 1894, b.

This species has been studied by many students, among them Traustedt (1885), Herdman (1888), Brooks (1893), Göppert (1892), Metcalf (1893), and Streiff (1908).

The following specimens are in the collection of the United States National Museum:

Cat. No. 6448, U.S.N.M. (aggregated form), from Naples Zoological Station; 15+ specimens in a chain.

Cat. No. 6459, U.S.N.M. (solitary form), from Naples Zoological Station; one specimen.

Cat. No. 6520, U.S.N.M. (aggregated form), *Albatross* station D. 5458, east coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands; June 8, 1909; surface; surface temperature, 85° F.; two specimens.

Cat. No. 6525, U.S.N.M. (aggregated form), *Albatross* station D. 5669, Macassar Strait, Philippine Islands; December 29, 1909; surface; surface temperature, 84° F.; two specimens.

Cat. No. 6555, U.S.N.M. (solitary and aggregated forms), Jolo Anchorage, Jolo, Philippine Islands; March 5, 1908; surface; two specimens.

Cat. No. 6557, U.S.N.M. (solitary form), *Albatross* station D. 5539, between Negros and Siquijor, Philippine Islands; August 19, 1909; surface; surface temperature, 83° F.; one specimen.

Cat. No. 6612, U.S.N.M. (solitary form), *Albatross* station D. 5155, Sulu Archipelago, Tawi Tawi group; February 19, 1908; surface; surface temperature, 81° F.; surface density, 1.02437; 13 specimens.

Cat. No. 6614, U.S.N.M. (solitary form), *Albatross* station D. 5166, Sulu Archipelago, Tawi Tawi group; February 24, 1908; surface; surface temperature, 81° F.; surface density, 1.02644; one specimen.

Cat. No. 6616, U.S.N.M. (aggregated form), *Albatross* station D. 5186, between Panay and Negros, Philippine Islands; March 30, 1908; surface; surface temperature, 80° F.; surface density, 1.02530; 13 specimens.

Cat. No. 6627, U.S.N.M. (solitary form), *Albatross* station D. 5162, Sulú Archipelago, Tawi Tawi Island; February 22, 1908; surface; surface temperature, 80° F.; surface density, 1.02447; two specimens.

Cat. No. 6556, U.S.N.M. (aggregated form), Philippines; surface; one specimen.

SALPA MAXIMA, solitary form.

The characteristic shape of the body is well shown in figure 64. The ventral half of the test is comparatively thick and firm. The nine body muscles are limited to the dorsal half of the body. Each is entirely independent.

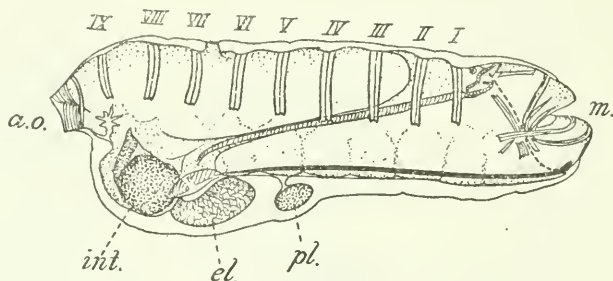


FIG. 64.—SALPA MAXIMA, SOLITARY FORM, SEEN FROM THE RIGHT SIDE. NATURAL SIZE. (DRAWN BY HOYT S. HOPKINS.)

Most of my specimens agree with Streiff's in the character of the oral musculature. (Fig. 65.) This shows the condition in my Medi-

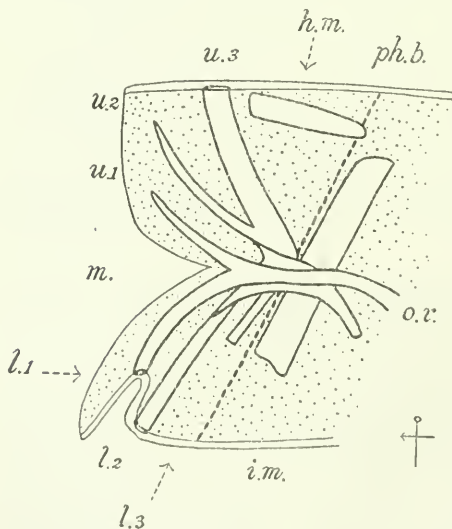


FIG. 65.—SALPA MAXIMA, SOLITARY FORM, ORAL MUSCLES SEEN FROM THE LEFT SIDE. FROM STREIFF (1908).

terranean and Atlantic specimens and in Streiff's material. In another of my specimens, from an unknown locality, the conditions are as in figure 64. In this individual the ventral end of the intermediate muscle is separated from the rest of the muscle. This specimen also has no ventral oral retractor, such as is shown by Streiff, connected anteriorly with dorsal sphincters 2 and 3 and ventral sphincter 2. None of this muscle is present except the postero-ventral end, which is entirely unconnected. It lies behind the ventral moiety of the intermediate muscle. The other oral muscles in this aberrant individual are about as shown by Streiff.



The atrial muscles are sufficiently shown in figures 64 and 66 without description.

SALPA MAXIMA, aggregated form.

The shape of the body and the character of the musculature is shown in figures 67 and 68. There are six body muscles, I and II being fused dorsally, also III and IV. Muscles V and VI approach dorsally and often touch, but do not unite. Muscles II and III touch but are not fused, though often they interlock as shown in figure 67. Muscle VI shows the usual anterior and posterior branches.

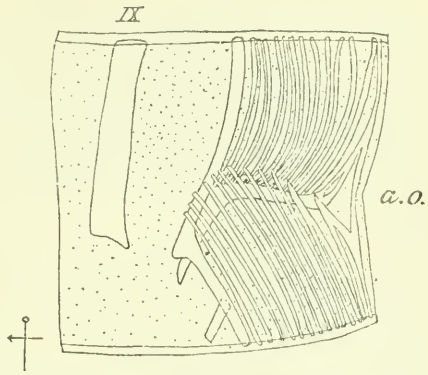


FIG. 66.—SALPA MAXIMA, SOLITARY FORM, ATRIAL MUSCULATURE SEEN FROM THE LEFT SIDE. FROM STREIFF (1908).

Both lips are incurled to act as valves, the lower lip more so than the upper. Streiff's figure of an inside view of the lips (fig. 69)

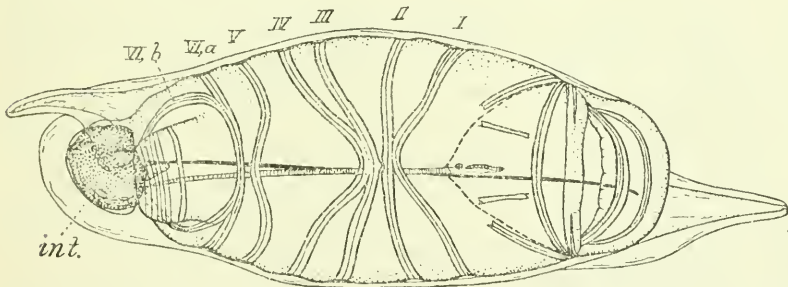


FIG. 67.—SALPA MAXIMA, AGGREGATED ZOÏD. DORSAL VIEW.  $\times 2$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

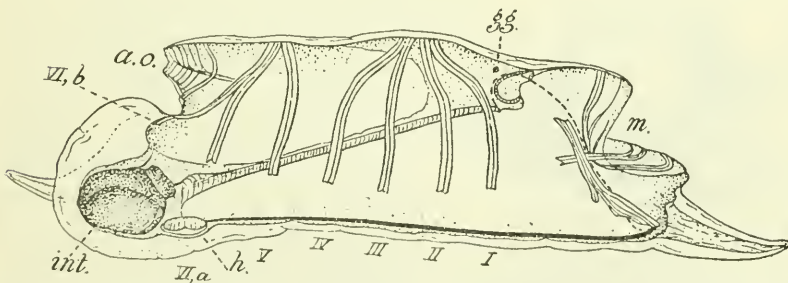


FIG. 68.—SALPA MAXIMA, AGGREGATED ZOÏD, SEEN FROM THE RIGHT SIDE.  $\times 2$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

shows well the way in which the muscles aid the lips in their valvular action. The cloacal musculature (fig. 70) is of the same general

type we have seen in the aggregated *Cyclosalpa virgula* (pl. 11, fig. 28 and pl. 12, fig 29) and *Apsteinia punctata* (fig. 55, p. 77).

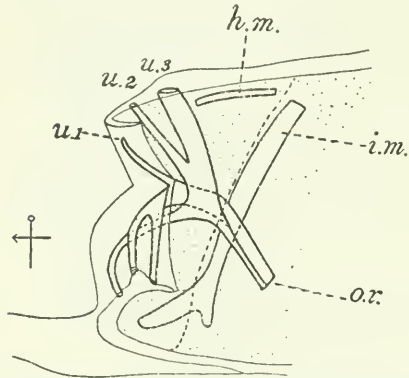


FIG. 69.—*SALPA MAXIMA*, AGGREGATED ZOÏD, ORAL MUSCLES OF THE RIGHT SIDE, SEEN FROM WITHIN. FROM STREIFF (1908).

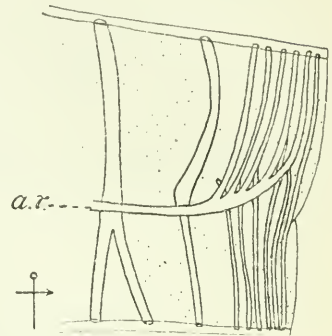


FIG. 70.—*SALPA MAXIMA*, AGGREGATED ZOÏD, CLOACAL MUSCLES OF THE RIGHT SIDE, VIEWED FROM THE INSIDE. FROM STREIFF (1908).

The eyes show resemblance to those of *Apsteinia punctata* (figs. 56, p. 77, and 57, p. 78) and almost exactly resemble those of *Salpa fusiformis* except that the large dorsal eye is shorter and more compact in *S. maxima*. Figure 79, page 92, a sagittal section of the upper part of the ganglion and the eye of *S. fusiformis* may be used in connection with this description of *S. maxima*. In the larger eye there is a group of rod-cells at the base of the eye, whose thin-walled, innervated ends are dorsal, and at the tip of the eye a group whose thin-walled ends are ventral. Intermediate cells are present between rod-cells and pigment cells in each of the two portions of the eye. The pigment cells are as figured. In the dorsal part of the ganglion there is a good-sized group of short rod-cells not associated with pigment. In *Apsteinia punctata* this group consists, as described, of two horizontal layers of rod-cells with their thick-walled ends contiguous.

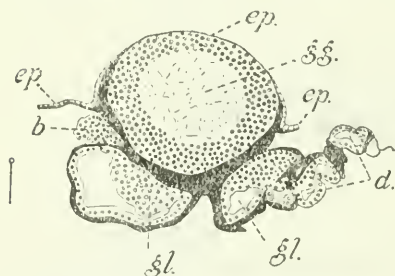


FIG. 71.—*SALPA MAXIMA*, AGGREGATED ZOÏD, CROSS SECTION OF THE GANGLION AND NEURAL GLANDS  $\times 145$  DIAMETERS. FROM METCALF (1893, c).

In *S. maxima* and *S. fusiformis* the rod-cells in the ganglion form an irregular group and the cells are very irregular in form. Degeneration has begun in this ganglionic group of rod-cells. *Apsteinia punctata* has a thickened mass of pigment cells in the position in which, in the Cyclosalpas, the optic plug is found. No such thickening

of the pigment layer is seen in *Salpa maxima*. *Salpa maxima* has departed from the archaic condition more than *Apsteinia*, since

there is no trace of the optic plug or its pigment, and the rod-cells in the ganglion are degenerate.

The neural glands are more developed than in any other species in the family (fig. 71), the disks and ducts both being larger, and the epithelium within the disks being greatly thickened on the side toward the ganglion. There are two pairs of well-developed outgrowths of cells from the ganglion, toward the disks, one pair (*b*) containing small cells, the other (not figured) containing large cells. The conditions are thus of the usual type, but the structures are unusually well developed.

**SALPA MAXIMA, variety TUBERCULATA (new variety), aggregated form.**

Only aggregated zooids of this variety are recognizable in the collections studied. They bear embryos indistinguishable from those of the species type. The collections contain about 50 specimens from station D. 5200, in the Mindanao Sea, Philippine Islands, United States National Museum. Cat. Nos. 6472 (Holotype) and 6454 (Paratypes) U. S. N. M. (aggregated form) *Albatross* station, D. 5200 Pamilacan Island, vicinity western Bohol; April 9, 1908; surface; surface temperature, 79° F.; surface density, 1.02468.

The musculature of the variety agrees with that of the species type; so also does the structure of all the internal organs.

Two characters distinguish the variety. The anterior and posterior protuberances from the body are as long as in any aggregated zooids of *Salpa fusiformis*, though they are of the distinctive *S. maxima* character, being more symmetrically placed and more ventral than in *S. fusiformis*. The second distinctive feature is the presence of two areas of tough and thickened test on the dorsal surface of the body on the right and left sides of the base of the atrial siphon. These thickened elevated areas bear numerous short triangular spines. The two spinose areas are of different sizes, the one above the embryo being about twice as large as the other.

The possibility has been considered that this tuberculate variety of *Salpa maxima* may be a hybrid between *S. maxima* proper and

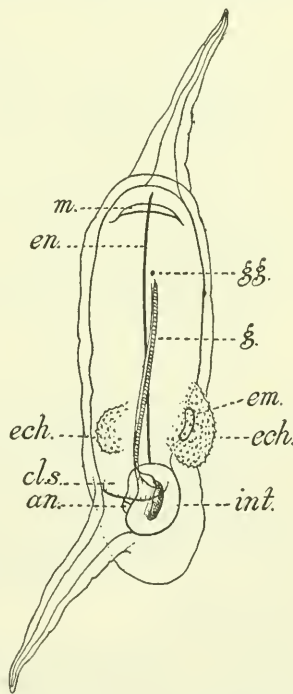


FIG. 72.—*SALPA MAXIMA*, VARIETY *TUBERCULATA*, AGGREGATED ZOÏD, DORSAL VIEW; *ech.* ECHINATE AREA OF THE TEST.  $\times 1\frac{1}{2}$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

*S. fusiformis*, form *aspera*, but no indication of this is found. The asperate *S. fusiformis* bears no special spinose thickenings near the base of the atrial siphon. The anterior and posterior protuberances in *S. maxima tuberculata* resemble those of *S. fusiformis aspera* only in their unusual length, not in form or exact position. The test on the ventral surface is thickened as in *S. maxima*, *S. fusiformis aspera* showing no such thickening. The ciliated funnel is curved as in *S. maxima*, not straight as in *S. fusiformis aspera*. The eye is of the short and compact *S. maxima* character, differing from the more elongated *S. fusiformis aspera* eye. The intestinal "nucleus" is a lateral mass in a thick semi-opaque spheroidal protuberance of the test as in *S. maxima* proper, while in *S. fusiformis* and its form *aspera* the intestinal mass protrudes very little and the test surrounding it shows little modification. There seems to be no indication of hybrid character in *S. maxima tuberculata*.

SALPA FUSIFORMIS Cuvier, 1804.

- S. maxima*, variety, FORSKÅL, 1775.  
*S. fusiformis* CUVIER, 1804.  
*S. runcinata* CHAMISSO, 1819.  
 (?) *S. moniliformis* MACCULLOCH, 1819.  
 (?) *S. dubia* CHAMISSO, 1819.  
*S. clostra* MILNE-EDWARDS, quoted by Cuvier, 1828.  
*S. maxima* MEYEN, 1832.  
*S. pyramidalis* LESSON, 1832.  
*S. runcinata-fusiformis* KROHN, 1846.  
*S. cymbiola* DALL, 1872.  
*S. fusiformis* APSTEIN, 1893, b.

This species, which is one the most abundant of the Salpidae, has been studied by many persons. I have had very abundant material from many localities.

In the collections of United States National Museum the following specimens are listed:

Cat. No. 3067, U.S.N.M. (solitary form), Carnegie Magnetic Expedition, Pacific Ocean between the Hawaiian Islands and California; one specimen.

Cat. No. 6444, U.S.N.M. (embryo), *Albatross* station D. 2029, south of Marthas Vineyard; May 25, 1883; 1,168 fathoms; surface temperature, 53° F.; one specimen.

Cat. No. 6445, U.S.N.M. (aggregated form), Carnegie Magnetic Expedition, Pacific Ocean between Hawaiian Islands and California; four specimens.

Cat. No. 6446, U.S.N.M. (embryo, old), *Albatross* station D. 2583, south of Block Island, September 19, 1885; 131 fathoms; surface temperature, 70° F.; one specimen.

Cat. No. 6522, U.S.N.M. (chain and embryo), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel

Bay, Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; 2 + specimens.

Cat. No. 6528, U.S.N.M. (solitary form), *Albatross* station D. 5128, Sulu Sea, vicinity southern Panay, Philippine Islands; February 4, 1908; surface; surface temperature, 80° F.; one specimen.

Cat. No. 6554, U.S.N.M. (solitary form), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; one specimen.

Cat. No. 6580, U.S.N.M. (solitary form), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; 10 + specimens.

Cat. No. 6581, U.S.N.M. (solitary and aggregated forms), *Albatross* station D. 5128, Sulu Sea, vicinity southern Panay; February 4, 1908; surface; surface temperature, 80° F.; 5 + specimens.

Cat. No. 6582, U.S.N.M. (solitary and aggregated forms), *Albatross* station D. 5128, Sulu Sea, vicinity southern Panay; February 4, 1908; surface; surface temperature, 80° F.; 6 + specimens.

**SALPA FUSIFORMIS, solitary form.**

The body muscles (fig. 73) are similar in number and arrangement to those of *S. maxima*, except that they extend more ventrally than in *S. maxima*, and muscles I, II, and III approach and usually touch dorsally, as do also muscles VIII and IX.

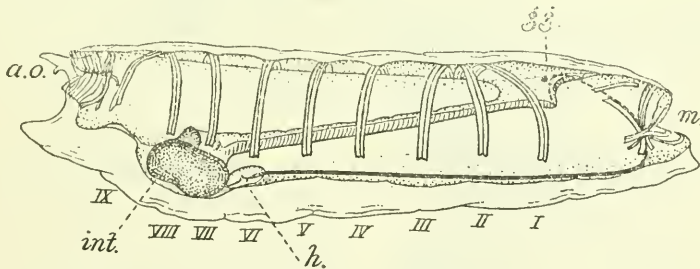


FIG. 73.—*SALPA FUSIFORMIS*, SOLITARY FORM, VIEWED FROM THE RIGHT SIDE.  $\times 4$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

The oral muscles are drawn in figure 74. The atrial muscles are well shown in Streiff's figure (fig. 75). Both sets of muscles are very similar to those of *Salpa maxima*. *S. fusiformis* shows an interruption of the delicate atrial sphincters, near the mid-dorsal line, as does *Apsteinia punctata* (fig. 52, p. 74).

The large dorsal eye (fig. 76) is very similar to that of *Ritteria hexagona* (figs. 39 and 40, p. 66) in histological condition and in form, except that the postero-lateral regions are not enlarged, and the

accessory masses of cells (*eq*) lie below the anterior ends of the horse-shoe, instead of below its sides.

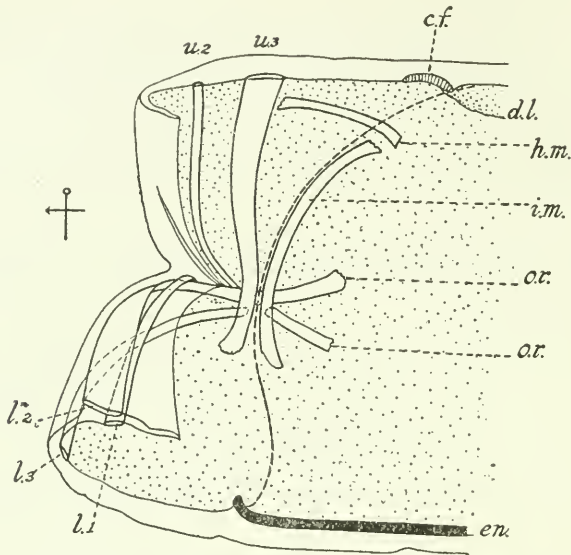


FIG. 74.—*SALPA FUSIFORMIS*, SOLITARY FORM, ORAL MUSCLES OF THE RIGHT SIDE, SEEN FROM THE INSIDE.  $\times 12$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

The ducts of the neural glands are larger than in most species. The disks are of the usual type.

There is a distinct outgrowth of large cells from the ganglion, on each side, lying close pressed between the ganglion and the disk of the gland. No small-celled outgrowth is distinguishable.

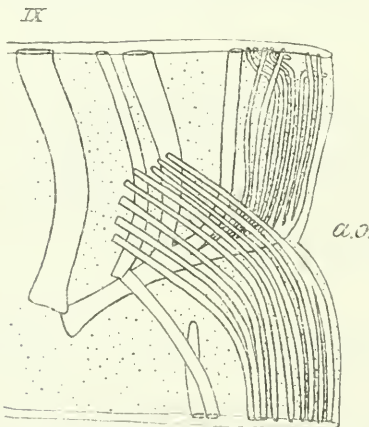


FIG. 75.—*SALPA FUSIFORMIS*, SOLITARY FORM, ATRIAL MUSCLES VIEWED FROM THE LEFT SIDE. FROM STREIFF (1908).

***SALPA FUSIFORMIS*, aggregated form.**

This closely resembles the aggregated *Salpa maxima*, except that both the anterior and posterior protuberances from the body are generally longer<sup>1</sup> and not so ventral (figs. 77 and 78), while the asymmetry of the posterior end is less noticeable. The body musculature is identical in the two species, except that in

*Salpa fusiformis* muscles IV and V always approach each other and often are in contact laterally. There is the closest resemblance also in the oral and atrial musculature.

<sup>1</sup> Not infrequently these protuberances are short, as shown in figure 81.

The eyes of the aggregated zoöids of *Salpa fusiformis* (fig. 79) and *S. maxima* are more nearly identical in structure than are the eyes of the aggregated forms of any other two species of *Salpa* whose eyes

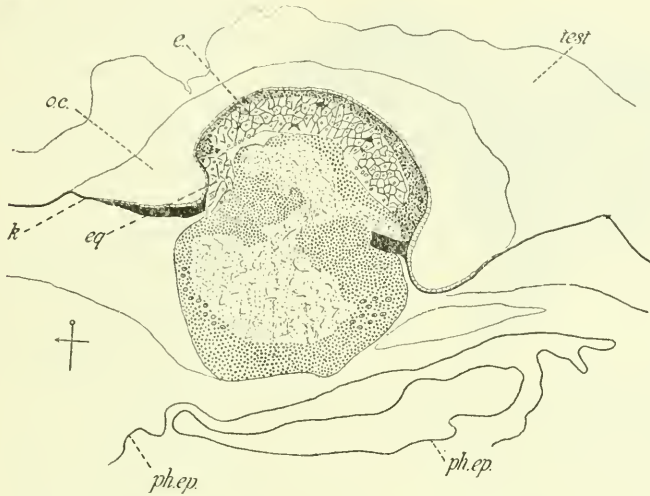


FIG. 76.—SALPA FUSIFORMIS, SOLITARY FORM, PARASAGITTAL SECTION THROUGH THE GANGLION AND ONE LIMB OF THE HORSESHOE-SHAPED EYE.  $\times 197$  DIAMETERS. FROM METCALF (1893, c).

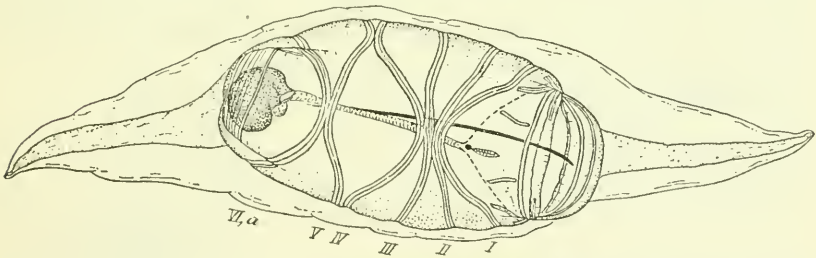


FIG. 77.—SALPA FUSIFORMIS, AGGREGATED ZOÖID, DORSAL VIEW.  $\times 2\frac{1}{2}$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

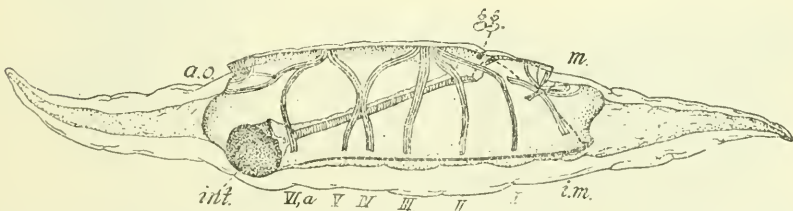


FIG. 78.—SALPA FUSIFORMIS, AGGREGATED ZOÖID, FROM THE RIGHT SIDE.  $\times 2\frac{1}{2}$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

have been studied. The large antero-dorsal eye is shorter and more compact in *Salpa maxima*, but this is the only observable difference. In the ganglion there is a large mass of irregular degenerate rod-cells, just posterior to the point of origin of the optic nerve. This is com-

parable to the mass of similar cells in the ganglion of *S. maxima* and to the masses of less modified cells in a similar position in *Apsteinia punctata* (figs. 56, p. 77, and 57, p. 78) and *Salpa cylindrica* (figs. 87, p. 98, and 89, p. 99).

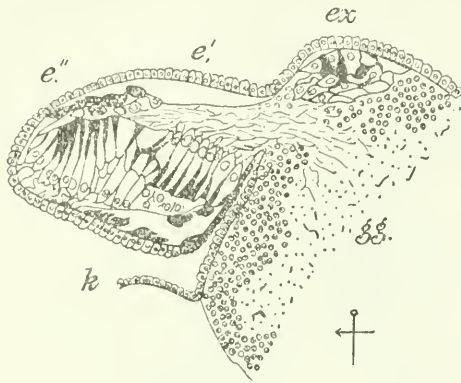


FIG. 79.—*SALPA FUSIFORMIS*, AGGREGATED ZOÏD, SAGITTAL SECTION OF THE EYES AND PART OF THE GANGLION.  $\times 155$  DIAMETERS. FROM METCALF (1903, c).

The pigment cells of the large eye in the aggregated form of *Salpa fusiformis* lie outside the limiting membrane of the eye, and so appear to be mesodermal. In all the aggregated Cyclo-salpas, as in all solitary forms, the pigment cells are inside the limiting membrane of the eye, which is continuous with that of the ganglion. They appear, therefore, to be ectodermal. There have not been sufficiently careful studies of the development of these cells to determine whether the discrepancy is real or only apparent.

The neural gland is of the usual character. There is a pair of large-celled outgrowths from the ganglion toward the disks of the gland.

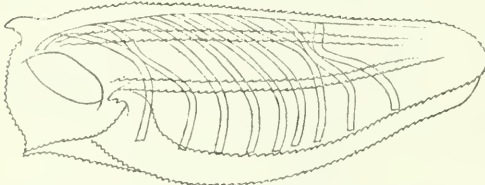


FIG. 80.—*SALPA FUSIFORMIS*, FORM ASPERA, SOLITARY INDIVIDUAL IN POSTERO-DEXTRO-DORSAL VIEW. AFTER RITTER (1905), MODIFIED.

***SALPA FUSIFORMIS*, Form ASPERA (Chamisso, 1819).**

- S. aspera* CHAMISSO, 1819.
- (?) *S. vaginata* CHAMISSO, 1819.
- S. echinata* HERDMAN, 1888.
- S. fusiformis*, var. *echinata* APSTEIN, 1894, a.
- S. fusiformis*, form *aspera* IHLE, 1911.

The form *aspera* (figs. 80 and 81) is very similar to *Salpa fusiformis* proper. The musculature and all the internal structure, including the character of the eyes, are practically identical in *S. fusiformis* and its form *aspera* in both solitary and aggregated individuals. The aggregated zooids of both the main species and the spinose form may

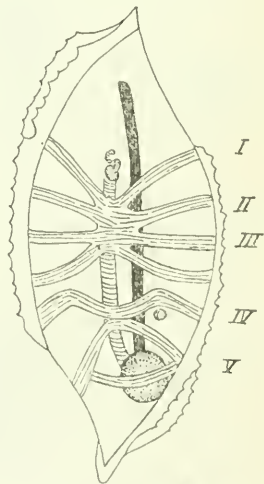


FIG. 81.—*SALPA FUSIFORMIS*, FORM ASPERA, AGGREGATED ZOÏD IN DORSAL VIEW.  $\times 6$  DIAMETERS. FROM APSTEIN (1906, b).



either be elongated, as in figures 77 and 78 of *fusiformis*, or be shorter, as in figure 81 of *aspera*. The only diagnostic feature of *aspera* is the ridged and spinose character of the test in both solitary and aggregated forms, and there is complete intergradation, even in these characters, in my collections, between the smooth form and the most spinose. For well-developed examples of *Salpa fusiformis* form *aspera* see United States National Museum collections, Cat. Nos. 6439 and 6440. For individuals showing a character intermediate between the form *aspera* and the smooth form see United States National Museum collections:

Cat. No. 145, U.S.N.M. (solitary and aggregated forms), *Fish Hawk* station 1027, off Marthas Vineyard; September 14, 1881; 93 fathoms; surface temperature, 65° F.; 10 ± specimens.

Cat. No. 617, U.S.N.M. (aggregated form), *Albatross* station D. 2575, off Cape Cod; September 3, 1885; 1710 fathoms; surface temperature, 71° F.; 10 specimens.

Cat. No. 6441, U.S.N.M. (solitary form), *Albatross* stations D. 5020–5021, off Maryland; May 21, 1883; 179 fathoms; surface temperature, 54° F.; 4 ± specimens.

Cat. No. 6442, U.S.N.M. (aggregated form), *Fish Hawk* station 925, off Marthas Vineyard; July 16, 1881; surface temperature, 71° F.; 6 + specimens.

Cat. No. 6613, U.S.N.M. (solitary form), *Albatross* station D. 5125, Sulu Sea, vicinity of southern Panay, Philippine Islands; February 3, 1908; surface; surface temperature, 80° F.; surface density, 1.02444; 1 + specimen.

Cat. No. 6583, U.S.N.M. (solitary form), *Albatross* station D. 5106, China Sea, off southern Luzon, Philippine Islands; November 7, 1909; surface; surface temperature, 78° F.; surface density, 1.02393; 2 + specimens.

#### SALPA CYLINDRICA Cuvler, 1804.

*Iasis cylindrica* SAVIGNY, 1816.

*S. coeruleascens* CHAMISSO, 1819.

This species, while less common than *Salpa fusiformis*, is fairly abundant and has been studied by a good many persons. Streiff, who has done such accurate work on the musculature of other species, has not studied this *Salpa*.

Specimens of this species in the collections of the United States National Museum are as follows:

Cat. No. 6447, U.S.N.M. (solitary form), *Albatross* station D. 2542, south of Block Island; August 7, 1885; 129 fathoms; surface temperature, 76° F.; 4 specimens.

Cat. No. 2687, U.S.N.M. (aggregated form), off Newport, Rhode Island; U. S. F. C., 1880; 75 + specimens.

Cat. No. 6526, U.S.N.M. (solitary form), *Albatross* station D. 5128, Sulu Sea, vicinity southern Panay, Philippine Islands; February 4 1908; surface; surface temperature, 80° F.; 2 specimens.

Cat. No. 6534, U.S.N.M. (solitary and aggregated forms), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; 15 + specimens.

Cat. No. 6558, U.S.N.M. (solitary form), *Albatross* station D. 5125, Sulu Sea, vicinity southern Panay, Philippine Islands; February 3, 1908; surface; surface temperature, 80° F.; surface density, 1.02444; 1 specimen.

Cat. No. 6559, U.S.N.M. (solitary form), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Island; June 7, 1909; surface; surface temperature, 86° F.; 10 + specimens.

Cat. No. 6560, U.S.N.M. (solitary form), *Albatross* station D. 5456, east Coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; 1 specimen.

Cat. No. 6561, U.S.N.M. (solitary form), *Albatross* station D. 5186, between Panay and Negros, Philippine Islands; March 30, 1908; surface; surface temperature, 80° F.; surface density, 1.02530; 2 specimens.

Cat. No. 6576, U.S.N.M. (solitary form), *Albatross* station D. 5128, Sulu Sea, vicinity southern Panay, Philippine Islands; February 4 1908; surface; surface temperature, 80° F., 2 + specimens.

Cat. No. 6577, U.S.N.M. (solitary and aggregated form), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; 10 + specimens.

Cat. No. 6578, U.S.N.M. (aggregated form), Kowloon, China; September 8, 1908; surface; 25 + specimens.

Cat. No. 6579, U.S.N.M. (solitary form), *Albatross* station D. 5616, Molucca Passage, Philippine Islands; November 22, 1909; surface; surface temperature, 84° F.; 1 + specimen.

Cat. No. 6584, U.S.N.M. (solitary form), *Albatross* station D. 5627, between Gillolo and Kayoa Islands, Philippine Islands, November 29, 1909; surface; surface temperature, 83° F.; 4 specimens.

Cat. No. 6588, U.S.N.M. (solitary form), *Albatross* station D. 5102, China Sea off southern Luzon, Philippine Islands; January 6, 1908; surface; surface temperature, 81° F.; surface density, 1.02447; 4 + specimens.

Cat. No. 6589, U.S.N.M. (aggregated form), Batangas Bay, Philippine Islands; July 22, 1908; surface; 25 + specimens.

Cat. No. 6624, U.S.N.M. (aggregated form), *Albatross* station D. 5155; Sulu Archipelago, Tawi Tawi Group; February 19, 1908; surface; surface temperature, 81° F.; 1 specimen.

**SALPA CYLINDRICA, solitary form.**

In the general shape of the body the solitary form of *Salpa cylindrica* (fig. 82) resembles that of other species of the true Salpas. The nine body muscles are all continuous dorsally across the mid line. Ventrally they all extend farther down than in *Salpa maxima* or *S. fusiformis*, but do not reach the mid-ventral line. Body muscles I to IV are in contact dorsally. As in the other true *Salpae*, the intermediate muscle is associated with the oral muscles rather than the body muscles.

There is a single oral retractor muscle, which gives rise directly to the two sphincters of the lower lip and is in contact with the basal ends of the admarginal sphincter of the dorsal lip. A second, broader sphincter of the upper lip passes inside the oral retractor muscle, just

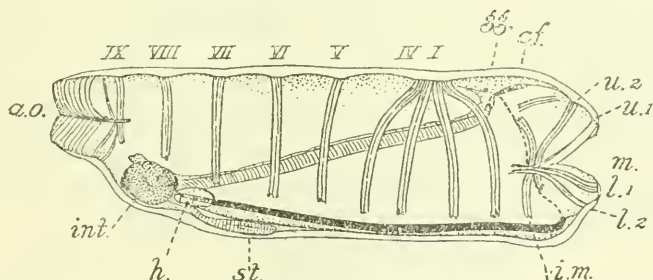


FIG. 82.—*SALPA CYLINDRICA*, SOLITARY FORM, VIEWED FROM THE RIGHT SIDE.  $\times 6$  DIAMETERS. FROM RITTER (1905) WITH MODIFICATIONS.

in front of the intermediate muscle. The short dorsal longitudinal muscle of the oral series is not in contact with the oral sphincters or the intermediate muscle, but is independent.

There is a well-developed atrial retractor muscle on each side, similar to the corresponding muscle of *Salpa maxima*. The arrangement of the atrial sphincters is also somewhat similar in the two species.

The gut is a compact "nucleus," as in the other true Salpas. The stolon is straight, lying below the endostyle. The eye is in the usual horse-shoe form. The neural glands and their ducts are in the usual condition, but there are no outgrowths from the ganglion

**SALPA CYLINDRICA, aggregated form.**

This form (figs. 83 and 84) has hollow conical anterior and posterior protuberances from the body, slightly asymmetrically arranged. Some specimens show irregular connective tissue fibers in the anterior protuberance, reaching to its tip. At the base of the protuber-

ance these connective tissue fibers lie just in front of and practically continuous with the ventral ends of the intermediate muscles. One is a little doubtful whether these conditions justify comparison functionally with the muscle bands in the anterior protuberance in the

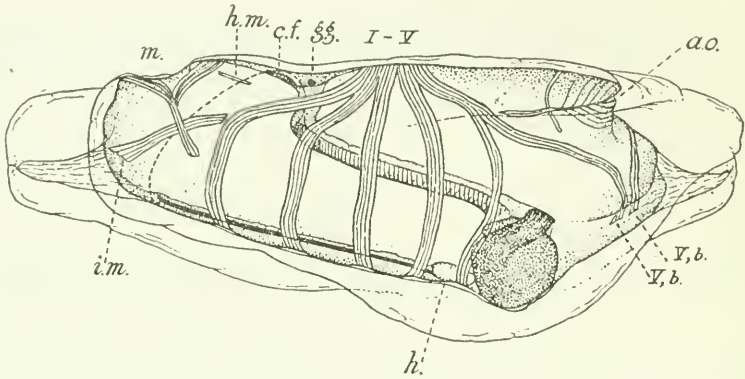


FIG. 83.—*SALPA CYLINDRICA*, AGGREGATED ZOÏD FROM THE LEFT SIDE OF THE STOLON, VIEWED FROM THE LEFT SIDE.  $\times 7$  DIAMETERS. THE SPECIMEN WAS COLLECTED OFF THE COAST OF CHINA. (DRAWN BY HOYT S. HOPKINS.)

solitary *Brooksia rostrata*. Similar fibers are seen in the posterior protuberance of the aggregated *Salpa cylindrica*, and in both the anterior and the posterior protuberances of the aggregated zoïds of *Salpa maxima* and *S. fusiformis*, but in all three species the test is too thick and firm to allow much if any movement.

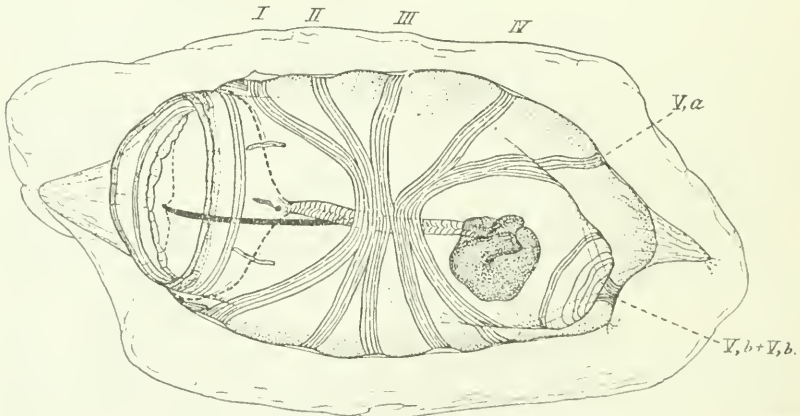


FIG. 84.—*SALPA CYLINDRICA*, AGGREGATED ZOÏD FROM THE LEFT SIDE OF THE STOLON, DORSAL VIEW.  $\times 7$  DIAMETERS. THE SPECIMEN WAS COLLECTED OFF THE COAST OF CHINA. (DRAWN BY HOYT S. HOPKINS.)

The five body muscles are continuous across the dorsal mid line and are arranged in two groups, I, II, and III in contact dorsally, as also are IV and V. Muscles III and IV are in contact in some specimens, while in others they are distinct. Body muscle V is branched in the

usual way, its posterior branch, on each side, passing to the base of the atrial siphon. Behind the siphon, at its base, these posterior branches are contiguous or may unite, forming a single band, which runs to one side of the broadly conical mantle tube that enters the asymmetrical posterior protuberance from the body. The united portion of these muscles doubtless corresponds to the visceral muscle of the *Cyclosalpas*.

The intermediate muscle is reduced (fig. 83), lying well down on the side of the body, at the base of the oral siphon. Its anterior end runs to the base of the anterior protuberance of the mantle. Its posterior end approaches, but does not unite with, the first body muscle. It is associated with the oral muscles, rather than the body muscles.

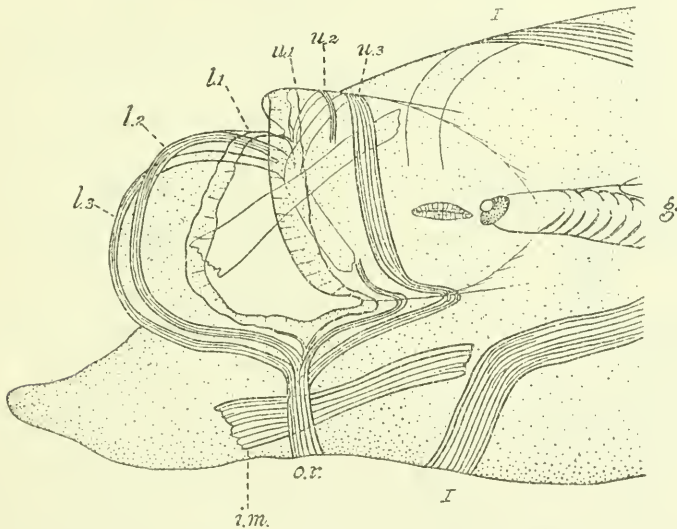


FIG. 85.—*SALPA CYLINDRICA*, AGGREGATED ZOÖID, ORAL MUSCLES, LAEVO-DORSAL VIEW. THE TEST IS OMITTED.

The oral muscles (fig. 85) consist of a well-developed oral retractor which gives rise antero-dorsally to three sphincter muscles on each lip, the arrangement of these muscles being a complicated one. A few postero-dorsal strands of the retractor are continued into the first and second sphincters of the upper lip and the first sphincter of the lower lip. The second sphincter of the upper lip is short, extending only a little beyond the angle of the mouth. The antero-ventral strands of the oral retractor divide into two sets of fibres, an internal set, which bend sharply back to form the broad third sphincter of the upper lip, and an external set, which immediately divide into two groups to form respectively the second and third sphincters of the lower lip.

The atrial system (fig. 83) shows a well-developed retractor muscle either united, or almost united, at its base, to body muscle V at its point of branching. This retractor muscle is connected distally with six or seven sphincter muscles, the basal one of which is considerably the stronger. The fibers of the sphincter muscles cross over one another where they join the retractor, as shown in the figure.

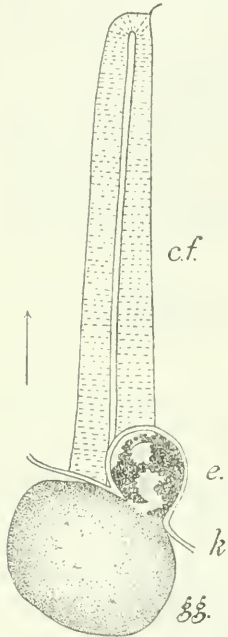


FIG. 86.—*SALPA CYLINDRICA*, AGGREGATED ZOÏD, DORSAL VIEW OF GANGLION, EYE AND CILIATED FUNNEL.  $\times 130$  DIAMETERS. FROM METCALF (1893, c).

The neural gland is reduced in the aggregated *Salpa cylindrica*. On the right side of laeval individuals and on the left side of dextral individuals the only remnant of the gland is a funnel-shaped pit in the wall of the branchial chamber, originally the mouth of the duct. The duct itself, with the disk, has wholly disappeared. On the other side the disk is wanting, but the distal portion of the duct is present, as is also its pharyngoatrial aperture. There is a pair of small-celled outgrowths from the ganglion at the points where the disks of the neural glands used to lie. (See Metcalf, 1903, c.)

The larger, dorsal eye (figs. 86, 87, and 88) is unique among the Salpidae. It has basal and terminal portions of the usual type, though very compactly arranged, as if by a shortening of the antero-posterior axis of the eye. At the point where these two portions join there is a small distinct group of optic cells (*a* in fig. 88, *A* and *B*) on each side, not shown in similar form in any other species studied. The thin-

walled ends of these rod-cells is toward the axis of the eye, and their thickened rods are just beneath the ectodermal epithelium of the optic chamber. The homologies of these two groups of rod-cells

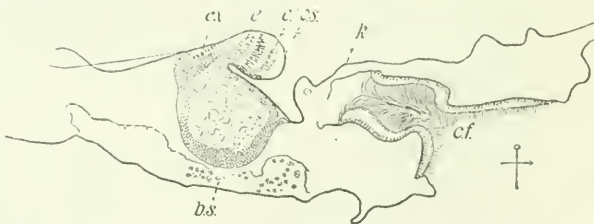


FIG. 87.—*SALPA CYLINDRICA*, AGGREGATED FORM. SAGITTAL SECTION OF THE GANGLION, EYES, AND THE BASAL PORTION OF THE CILIATED FUNNEL.  $\times 98$  DIAMETERS. FROM METCALF (1893, c).

can be determined only by a study of their origin in the developing zoïds, a study I have not yet undertaken.

In the ganglion there is one large accessory eye (figs. 87, *ex* and 89) in very much the same position it occupies in *Salpa runcinata* and

*Apsteinia punctata*. It consists of a single layer of rather short but well-developed rod cells, whose thick-walled ends ("rods") lie

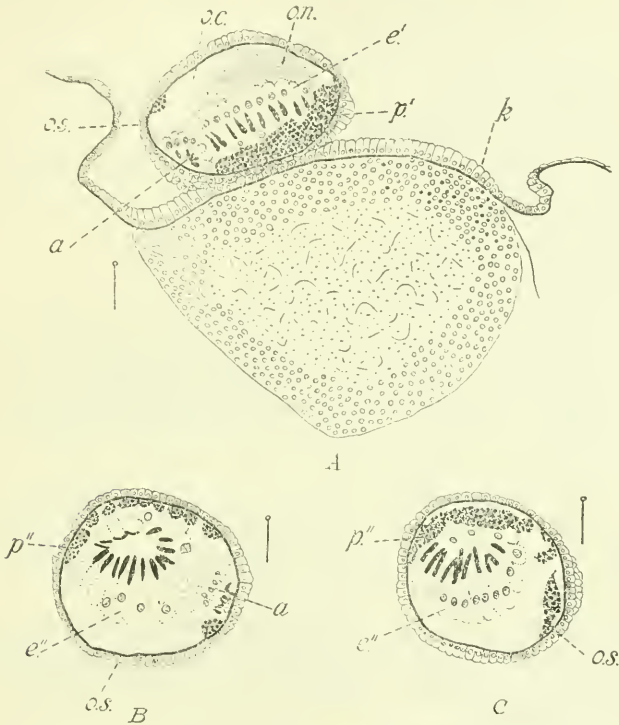


FIG. 88.—*SALPA CYLINDRICA*, AGGREGATED FORM, TRANSVERSE VERTICAL SECTIONS OF THE GANGLION AND DORSAL EYE: *A*, IS NEAR THE BASE OF THE EYE; *C*, NEAR THE TIP; AND *B*, INTERMEDIATE.  $\times 360$  DIAMETERS. FROM METCALF (1893, c).

external, just beneath the limiting membrane of the ganglion. The thin-walled ends of these rod cells are innervated directly from the large optic nerve which passes between the accessory eye and the large dorsal eye.

Close relationship of *Salpa cylindrica* to the other true Salpae seems to be indicated by the close resemblance of their solitary forms and by the resemblance in form and musculature between their aggregated zooids. The unique character of the eyes of the aggregated zooids is remarkable. They foreshadow, in some regards, the eyes of *Thalia*, as will be seen later.

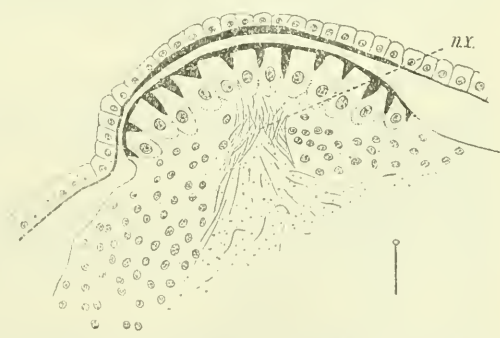


FIG. 89.—*SALPA CYLINDRICA*, AGGREGATED FORM, VERTICAL SECTION THROUGH THE ACCESSORY EYE AND PART OF THE GANGLION. FROM METCALF (1893, c).

## Subgenus JASIS (Herdman, 1891).

## IASIS ZONARIA (Pallas, 1774).

*Holothurium zonarium* PALLAS, 1774.

*Salpa polysericata* FORSKÅL, 1775.

*Holothuria zonaria* LINNAEUS, 1788-1791.

*Salpa zonaria* BRUGUIERE, 1789.

*S. cordiformis* QUOY AND GAIMARD, 1827.

*S. microstoma* QUOY AND GAIMARD, 1827.

*S. uvicuspudata* QUOY AND GAIMARD, reference by DE BLAINVILLE, 1827.

*S. tricuspida* LESSON, 1832.

*S. cordiformis-zonaria* KROHN, 1846.

*S. nitida* HERDMAN, 1888.

*Iasis cordiformis-zonaria* HERDMAN, 1891.

*Salpa zonaria* APSTEIN, 1894, *b*.

In this subgenus I include only one species, *zonaria*. Its relationships are doubtful. They will be discussed later. I have had abundant material of both solitary and aggregated forms.

Cat. No. 6431, U.S.N.M. (solitary form with chain), Fort Mansfield, Rhode Island; 2 specimens.

Cat. No. 6434, U.S.N.M. (aggregated form), Grampus, Gulf Stream (Prof. W. Libby); 12 specimens in a chain.

Cat. No. 6466, U.S.N.M. (aggregated form with embryos), from Naples Zoological Station; 1 specimen.

Cat. No. 6536, U.S.N.M. (aggregated form), *Albatross* station D. 5237, Pacific Ocean, east coast Mindanao, Philippine Islands; May 12, 1908; surface; surface temperature, 85° F.; surface density, 1.02477; 3 specimens.

Cat. No. 6537, U.S.N.M. (aggregated form), *Albatross* station D. 5402, between Leyte and Cebu, Philippine Islands; March 16, 1909; surface; surface temperature, 81° F.; 1 specimen.

Cat. No. 6538, U.S.N.M. (aggregated form), *Albatross* station D. 5196. Off northern Cebu Island, Philippine Islands; April 3, 1908; surface; surface temperature, 82°; surface density, 1.02518; 1 specimen.

Cat. No. 6540, U.S.N.M. (aggregated form), *Albatross* station D. 5186. Between Panay and Negros, Philippine Islands; March 30, 1908; surface; surface temperature, 80° F.; surface density, 1.02530; 2 specimens.

Cat. No. 6541, U.S.N.M. (aggregated form), *Albatross* station D. 5456. East coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands: June 7, 1909; surface; surface temperature, 86° F.; 10+ specimens.

Cat. No. 6542, U.S.N.M. (solitary and chain forms), *Albatross* station D. 5669, Macassar Strait, Philippine Islands; December 29, 1909; surface; surface temperature, 84° F.; 5+ specimens.

Cat. No. 6543, U.S.N.M. (aggregated form), *Albatross* station D. 5456. east coast of Luzon, San Bernardino Strait to San Miguel Bay,



Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; 1 specimen.

Cat. No. 6544, U.S.N.M. (aggregated form), *Albatross* station D. 5175, Sulu Sea, southeast of Cagayanes Islands, Philippine Islands; March 8, 1908; surface; surface temperature, 82° F.; 10+ specimens.

Cat. No. 6545, U.S.N.M. (solitary and chain forms), *Albatross* station D. 5186, between Panay and Negros, Philippine Islands; March 30, 1908; surface; surface temperature, 80° F.; surface density, 1.02530; 3 specimens.

Cat. No. 6546, U.S.N.M. (solitary and chain forms), *Albatross* station D. 5500, northern Mindanao and vicinity, Philippine Islands; August 4, 1909; surface; surface temperature, 84° F.; 6 specimens.

Cat. No. 6547, U.S.N.M. (solitary and chain forms); *Albatross* station D. 5672, Macassar Strait, Philippine Islands; December 30, 1909; surface; surface temperature, 83° F.; 15+ specimens.

Cat. No. 6548, U.S.N.M., *Albatross* station D. 5633, south of Patiente Strait, Philippine Islands; December 2, 1909; surface; surface temperature, 84° F.; 10+ specimens.

Cat. No. 6549, U.S.N.M. (solitary and chain forms), *Albatross* station D. 5500, northern Mindanao and vicinity, Philippine Islands; August 4, 1909; surface; surface temperature, 84° F.; 20+ specimens.

Cat. No. 6550, U.S.N.M. (aggregated form), *Albatross* station D. 5530, between Siquijor and Bohol Islands, Philippine Islands; August 11, 1909; surface; surface temperature, 84° F.; 4 specimens.

Cat. No. 6587, U.S.N.M. (aggregated form), *Albatross* station D. 5601, Gulf of Tomini, Celebes; November 13, 1909; surface; surface temperature, 83° F.; 2 specimens.

Cat. No. 6629, U.S.N.M. (aggregated form), *Albatross* station D. 5672, Macassar Strait, Philippine Islands; December 30, 1909; surface; surface temperature, 83° F.; 25+ specimens.

#### IASIS ZONARIA, solitary form.

There are apparently five broad body muscles (fig. 90) interrupted both dorsally and ventrally. The fifth extends only a short way down on the sides of the body. Possibly this should be accounted a basal atrial sphincter. What seems to be the intermediate muscle (*i. m.*) is of much the same appearance as the body muscles and evidently functions with them.

The oral musculature is unique among the Salpidae. Streiff (1908) describes it without figures, indicating that his figure of the oral muscles in the aggregated form shows also the condition in the solitary form. I find the oral musculature in the two forms very different. All of my many specimens of the solitary *Iasis zonaria*

agree and none correspond to Streiff's description in the character of the oral musculature. Streiff's work on other species is so very accurate that one can not think his observations so erroneous upon this form. His account, as it stands, does not agree with conditions in

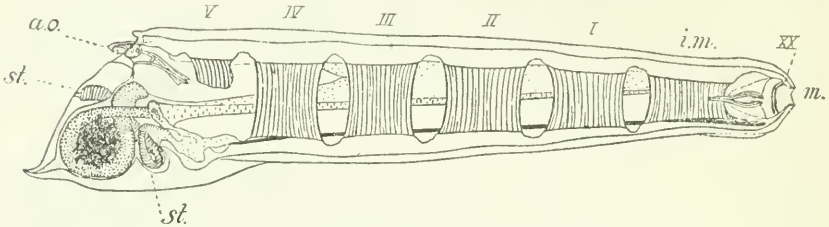


FIG. 90.—IASIS ZONARIA, SOLITARY FORM, SEEN FROM THE RIGHT SIDE. THE MANTLE IS SHRUNKEN AWAY FROM THE TEST ON BOTH DORSAL AND VENTRAL SURFACES.  $\times 1\frac{1}{2}$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

my specimens, but his accuracy as an observer must not be impugned. There is some confusion here. May it be that Streiff had specimens of Herdmann's "*Salpa nitida*," and this form thus proves a distinct subspecies? The body muscles of Streiff's specimens were much broader than those Herdmann figures.

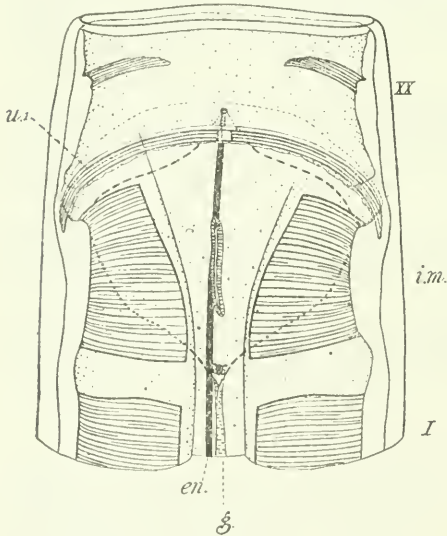


FIG. 91.—IASIS ZONARIA, SOLITARY FORM, DORSAL VIEW OF ANTERIOR END OF BODY.  $\times 3\frac{1}{2}$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

There is a single strong sphincter muscle in each lip (fig. 91). At the angles of the mouth their ends are united and run back a short way together, forming an oral retractor muscle. These sphincter muscles lie at the edges of the strongly inturned lips (fig. 92). Each is interrupted on the mid line. Further forward on the oral siphon, and separated by a considerable interval from the true sphincters, there is, on each side, a muscle (*xx*) of different histological appearance, opaque and browner in specimens preserved in either alcohol or formalin. These lie at the lateral angles of the flattened oral siphon and extend but a short distance onto the flat dorsal and ventral surfaces of the oral siphon. In a few of my older specimens, neither the largest nor the smallest, the muscle is interrupted at the angle of the siphon, making two half muscles instead of one continuous one. The second sphincter muscle

of the lower lip, described by Streiff, and his "Segelmuskel" ["A"] are not represented in any of my numerous specimens. In the character of its oral musculature in the solitary form, *Iasis zonaria* is the most aberrant of all the Salpidae, great reduction having occurred, and a new muscle (*xx*) being added. Both lips are strongly and

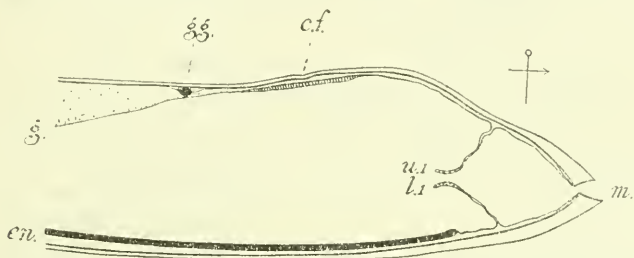


FIG. 92.—*IASIS ZONARIA*, SOLITARY FORM, A SAGITTAL SECTION OF THE ANTERIOR PART OF THE BODY.  $\times 4$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

equally inturned to serve as valves. The upper lip is somewhat inturned, though less than the lower lip, in some other species (see *Salpa maxima*, aggregated, fig. 69, p. 86, *Thalia democratica*, solitary and aggregated, fig. 104 B, p. 111, also figs. 105 and 108).

The musculature of the atrial siphon (fig. 93), in all my specimens agree, except for minor detail, with Streiff's description. There is a

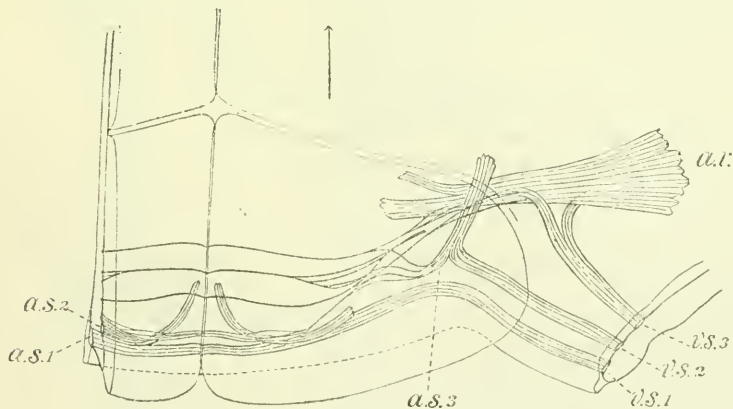


FIG. 93.—*IASIS ZONARIA*, SOLITARY FORM, DORSAL VIEW OF THE RIGHT SIDE AND A LITTLE OF THE LEFT SIDE OF THE ATRIAL MUSCULATURE, THE ATRIAL SIPHON BEING CUT LENGTHWISE ON THE VENTRAL MID LINE AND THE FLAPS SO FORMED SPREAD OUT Laterally.  $\times 13\frac{1}{2}$  DIAMETERS. MODIFIED FROM STREIFF (1908).

strong atrial retractor muscle (*a. r.*) on each side running to near the angle of the atrial opening. The ventral lip of the atrial opening bears three sphincters. The first of these (*v. s. 1*), admarginal, is continuous with the admarginal sphincter (*a. s. 1*) of the dorsal atrial lip. The second ventral sphincter (*v. s. 2*) extends forward, crossing the atrial retractor near its distal end. Near the angle of the atrial

opening, this second ventral sphincter is continuous with the third dorsal atrial sphincter (*a. s. 3*) which starts as a single band, but soon

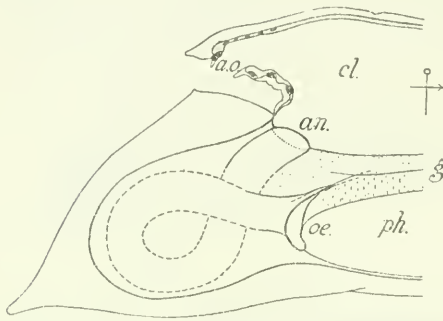


FIG. 94.—IASIS ZONARIA, SOLITARY FORM, SAGITTAL SECTION OF THE ATRIAL APERTURE AND THE ADJACENT TISSUES.  $\times 8$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

breaks up into fine strands that form something of a reticulum. Several strands from this reticulum run forward to join the atrial retractor. These are independent of the main trunk of the third dorsal sphincter, and may represent a fourth dorsal atrial sphincter. The third ventral atrial sphincter (*v. s. 3*) has no connection with muscles of the dorsal atrial lip, but is united by two branches to

the middle portion of the atrial retractor. The dorsal lip of the atrial aperture is in two parts. The first, a slightly developed flap, at a lower level, bears dorsal sphincter No. 1. Dorsal sphincter No. 2 is not connected with any other muscle. It lies in the upper division of the upper lip. It is interrupted on the mid line, its two ends being bent forward. The upper portion of the dorsal lip has its test developed to form two triangular stiffened areas, just beneath which lies the reticulum formed by the strands of the third and fourth (?) dorsal atrial sphincters. The vertical section of this region shown in figure 94 should help to make these structures clear.

The gut forms a rather close circular loop (figs. 90 and 94), but is much less compact than in *Apsteinia* and *Salpa* proper. It is much like Apstein's figure of the gut in *Brooksia rostrata* (fig. 23, p. 51).

The gut forms a rather close circular loop (figs. 90 and 94), but is much less compact than in *Apsteinia* and *Salpa* proper. It is much like Apstein's figure of the gut in *Brooksia rostrata* (fig. 23, p. 51).

In the character of its eye and the outgrowths from its ganglion (figs. 95 and 96), the solitary form of *Iasiszonaria* is one of the most aberrant of the solitary Salpidae. Indeed, with the exception of *Ritteria hexagona*, it is the only species in the solitary form of which these structures depart markedly from the usual type. The eye has

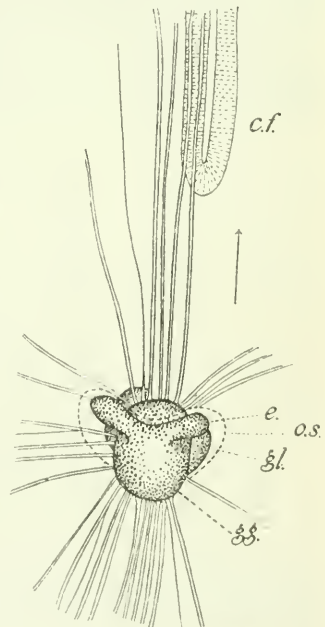


FIG. 95.—IASIS ZONARIA, SOLITARY FORM, DORSAL VIEW OF THE EYE, THE GANGLION, THE NERVES, THE LATERAL OUTGROWTHS FROM THE GANGLION, AND THE POSTERIOR PART OF THE CILIATED FUNNEL.  $\times 57$  DIAMETERS. FROM METCALF (1893, c).

its anterior ends elevated above the surface of the ganglion and not in contact with it. The ends are spread apart also, so that the typical horse-shoe shape is distorted to crescent shape.

At the lower edge of the ganglion, on each side, there is a wide rather thin outgrowth (*ey*) of very large irregular cells whose walls are in places thickened, resembling exactly the degenerate rod-cells of the other species of Salpidae. These outgrowths must be interpreted as accessory eyes. In only two other species of Salpidae (*Salpa fusiformis* and *Ritteria hexagona*) does the solitary form have accessory eyes, and these are mere ventral extensions of the mass of rod-cells in the anterior ends (*S. fusiformis*, fig. 76, p. 91), or on the side (*R. hexagona*, figs. 39 and 40, p. 66) of the horseshoe-shaped eye. The structures most similar to these optic lateral outgrowths in the solitary *Iasis zonaria* are the ovoid and somewhat smaller masses of degenerate rod-cells, seen as outgrowths from the sides of

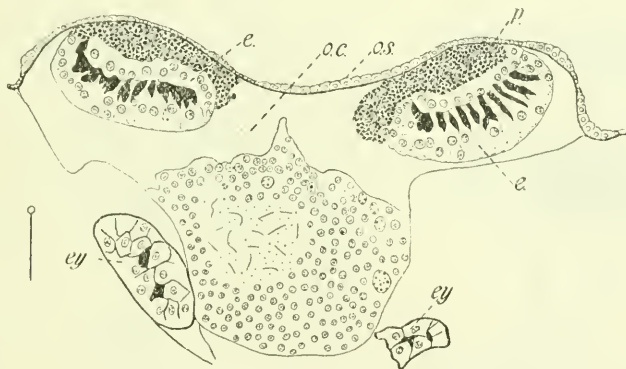


FIG. 96.—*IASIS ZONARIA*, SOLITARY FORM, CROSS SECTION THROUGH THE GANGLION, THE ANTERIOR LIMB OF THE DORSAL EYE, AND THE LATERAL OUTGROWTHS FROM THE GANGLION.  $\times 200$  DIAMETERS. FROM METCALF (1893, c).

the ganglion in the aggregated *Ritteria hexagona* (fig. 45, p. 70 and fig. 47, p. 71). The usually conservative solitary form has, in *Iasis*, departed widely from the general type in the character of the accessory eyes as well as in the form of the dorsal eye, and in the character of the musculature, including the reduction in the number of the body muscles and the peculiar character of the oral and atrial muscles.

#### *IASIS ZONARIA*, aggregated form.

This zoïd (figs. 97 and 98) is about as asymmetrical as is the aggregated *Salpa cylindrica* (fig. 84, p. 96), the asymmetry being shown in the lateral positions of the posterior protuberance and atrial siphon.

There are five broad body muscles, all but the first continuous across the mid-dorsal line and all widely interrupted ventrally. Body muscle 5 on the right side is divided into an anterior and a

posterior branch, the latter, though short, probably the homolog of the posterior branch of the last body muscle in the aggregated zooids of other species.

The intermediate muscle is well developed ventrally, extending as near to the mid-ventral line as do the body muscles, but dorsally it passes but a little way beyond the angles of the mouth. Streiff interprets the intermediate muscle as double, an interpretation which seems to be borne out by comparison with some species still to be described.

The oral musculature (fig. 99) shows a short oral retractor, which gives rise, at the angle of the mouth, to a wide admarginal sphincter muscle in each strongly incurved lip. Across the angle of the oral siphon lies a band of dark-colored muscle, comparable to that seen in a similar position at the distal end of the oral siphon in the solitary form of this species. Comparisons, especially with the *Cyclosalpas*, will show how various are the interrelations of the intermediate muscle and the more basal sphincters of the lips, especially the upper lip. In several species the ventral portion of this

sphincter complex is reduced; *Iasis hexagona*, on the other hand, has the dorsal portion reduced.

The condition of the oral musculature, in the very numerous individuals among my material, is considerably different from that

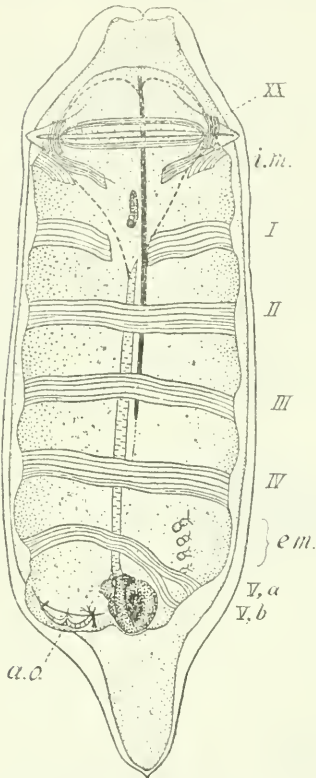


FIG. 97.—*IASIS ZONARIA*, AGGREGATED ZOÏD, DORSAL VIEW.  $\times 3$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

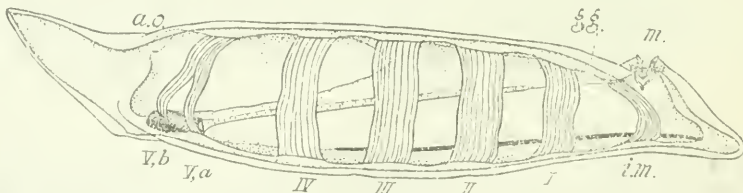


FIG. 98.—*IASIS ZONARIA*, AGGREGATED ZOÏD, SEEN FROM THE RIGHT SIDE.  $\times 3$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

figured and described by Streiff. I find no delicate second sphincter in the lower lip, such as he describes, and the dark-colored muscle at the angle of the mouth is situated more distally in my specimens.

The atrial siphon and its musculature (fig. 100) in the aggregated *Iasis zonaria* resembles, but is not identical with, that of the solitary form. Dorsally are similar triangular thickenings of the test. One sees a strong atrial retractor (*a. r.*), four ventral atrial sphincters

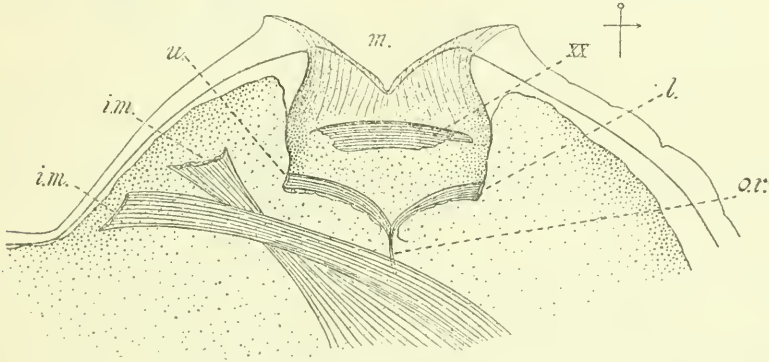


FIG. 99.—IASIS ZONARIA, AGGREGATED FORM, THE LEFT HALF OF THE ORAL SIPHON, SEEN FROM THE INNER SIDE. IT IS SHOWN SLIGHTLY STRETCHED OPEN.  $\times 18$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

(*v. s. 1-4*), the last three connected with the retractor and the first continuous with the admarginal dorsal sphincter. The second dorsal sphincter is not connected with the second ventral sphincter, differing in this regard from the corresponding muscle in the solitary form.

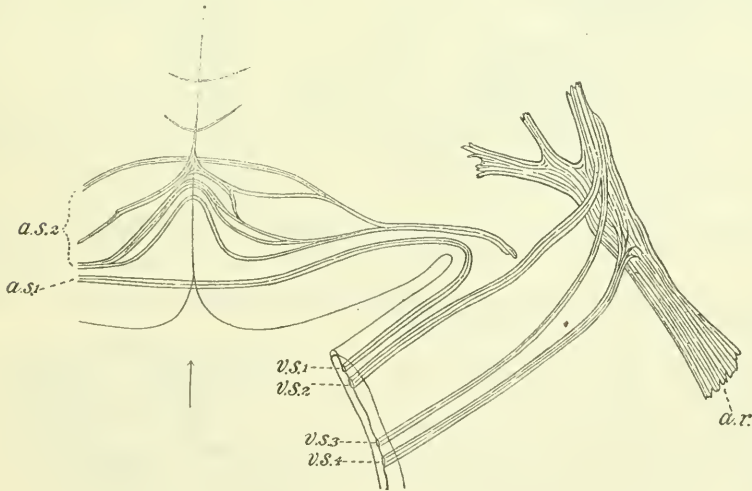


FIG. 100.—IASIS ZONARIA, AGGREGATED FORM, ATRIAL MUSCLES.

Like the third dorsal sphincter in the solitary form, the second dorsal sphincter breaks up distally into a number of fibres, forming a complex whose pattern differs in different individuals, and may even be different on the two sides of the same siphon. The atrial musculature in both solitary and aggregated forms of *Iasis* is very different from

that of most other Salpidae, *Thalia democratica* showing the most similar condition.

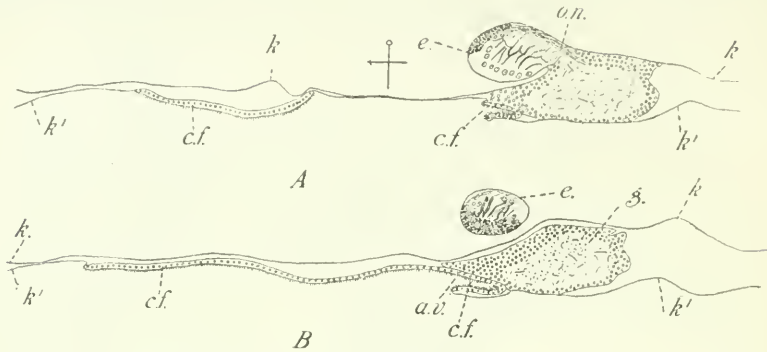


FIG. 101.—*IASIS ZONARIA*, AGGREGATED ZOÏD, LONGITUDINAL VERTICAL SECTIONS OF THE GANGLION, EYE, AND CILIATED FUNNEL.  $\times 97$  DIAMETERS. FROM METCALF (1893, c).

The gut (fig. 97) is a compact "nucleus," in which, however, the course of the intestine is readily seen without dissection.

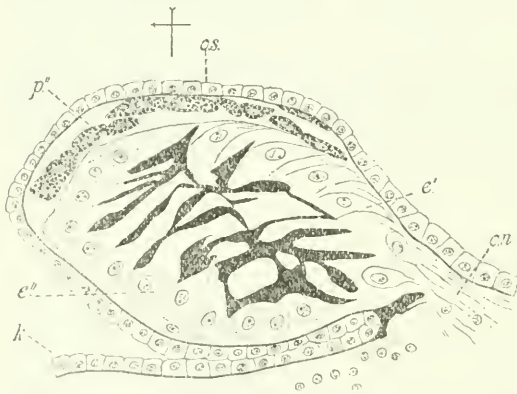


FIG. 102.—*IASIS ZONARIA*, AGGREGATED FORM, SAGITTAL SECTION OF THE EYE.  $\times 476$  DIAMETERS. FROM METCALF (1893, c).

gion of this species, but on each side of the ganglion there is a huge outgrowth (fig. 103 *ey*) composed of irregular cells with unevenly thickened walls, like degenerate rod-cells, as for instance, in the accessory eye of the aggregated *Salpa fusiformis* (fig. 79, p. 92). These outgrowths resemble those of the solitary *Iasis*. They are sessile upon the ganglion. They lie above the lateral pouches of the neural gland, in a position corresponding to that of the large-celled outgrowths from the ganglion in other species, with which they are probably homologous.

The large dorsal eye (figs. 101 and 102) is very compact, the typically distal portion being drawn back beneath the true basal portion, making the whole eye nearly spherical. The thick-walled ends of the rod-cells are somewhat irregular, but the cells can hardly be called degenerate.

There are no accessory eyes in the gan-

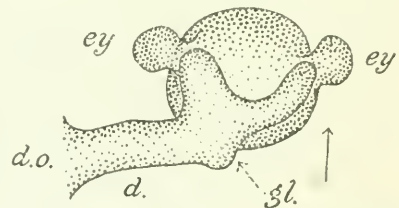


FIG. 103.—*IASIS ZONARIA*, AGGREGATED FORM, SCHEMATIC VENTRAL VIEW OF THE GANGLION, THE LATERAL OUTGROWTHS FROM THE GANGLION AND THE NEURAL GLAND.  $\times 40$  DIAMETERS. A RECONSTRUCTION FROM SECTIONS.

gion of this species, but on each side of the ganglion there is a huge outgrowth (fig. 103 *ey*) composed of irregular cells with unevenly thickened walls, like degenerate rod-cells, as for instance, in the accessory eye of the aggregated *Salpa fusiformis* (fig. 79, p. 92). These outgrowths resemble those of the solitary *Iasis*. They are sessile upon the ganglion. They lie above the lateral pouches of the neural gland, in a position corresponding to that of the large-celled outgrowths from the ganglion in other species, with which they are probably homologous.



The neural gland (fig. 103) consists of a postero-medial chamber, which pushes forward on both sides, beneath the ganglion, to form pouches in the usual positions of the hollow disks. There is but one lateral duct leading from the neural gland to the pharyngo-atrial chamber. This is very wide.

## RELATIONSHIPS OF THE SUB-GENUS IASIS.

*Iasis* is very distinct from all of the other subgenera. Like most of the species still to be discussed, it has a reduced number of body muscles. It has also a reduced oral musculature, as have also *Thetys*, *Pegea*, *Thalia*, and *Traustedtia*. Its atrial musculature is most like that of *Thalia*. The form of the body in the aggregated zooids is considerably like that in the aggregated forms of the true *Salpae*. The gut resembles that of *Ritteria* in being a loop in the solitary form and a fairly compact "nucleus" in the aggregated zooids. The eye of the solitary form is essentially of the ordinary horseshoe type, though distorted in form. In the aggregated zooids the larger eye, though very compact, shows the usual proximal and distal portions, as seen in the other species of the family thus far discussed. Its neural gland is peculiar. There are usually five embryos present in the aggregated zooids, showing different stages of development. It is difficult to draw confident conclusions as to the relationships of *Iasis*. I place it as an aberrant form, somewhat intermediate between *Ritteria* and the most divergent forms, *Thetys*, *Thalia*, *Pegea*, and *Traustedtia*.

Subgenus THALIA (Blumenback (?), 1810).

This subgenus includes the species *democratica* and *longicauda* (*flagellifera* of most authors). The former is the most widely distributed and most abundant of all the species of Salpidae. The latter is a rare species which has never been adequately studied. The species *democratica* may be taken as the type since it was the first described and is by far the best known.

## THALIA DEMOCRATICA (Forskål, 1775).

- Salpa democratica* FORSKÅL, 1775.  
*S. mucronata* FORSKÅL, 1775.  
 (?) *Thalia lingulata* BLUMENBLACH, 1810.  
*Salpa spinosa* OTTO, 1823.  
*S. pyramidalis* QUOY and GAIMARD, 1826-1834.  
*Biphora mucronata* COSTA.  
*B. democratica* COSTA.  
*Dubreullia cirrhosa* LESSON, 1830.  
*Salpa democratica-mucronata* KROHN, 1846.  
*S. cabotti* DESOR, 1851.  
*Thalia democratica-mucronata* HERDMAN, 1891.  
*Salpa mucronata* APSTEIN, 1894, b.  
*S. democratica* HEIDER, 1895.

Specimens of this species are found in the collections of the United States National Museum as follows:

Cat. No. 2809, U.S.N.M. (solitary form and aggregated forms), off Gay Head, Massachusetts; U. S. F. C., September 3, 1884; 100+ specimens.

Cat. No. 6429, U.S.N.M. (solitary form), off Castle Hill, Rhode Island, U. S. F. C. 1880; 20± specimens.

Cat. No. 132, U.S.N.M. (solitary and aggregated forms), *Fish Hawk*, off Newport, Rhode Island, 1880; 20+ specimens.

Cat. No. 6517, U.S.N.M. (solitary and chain forms), Nogas Point, Panay, Philippine Islands; surface; 100+ specimens.

Cat. No. 6521, U.S.N.M. (solitary form), *Albatross* station D 5196, off northern Cebu Island, Philippine Islands; April 3, 1908; surface; surface temperature, 82° F.; surface density, 1.02518; 10+ specimens.

Cat. No. 6524, U.S.N.M. (solitary and aggregated forms), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands, June 7, 1909; surface; surface temperature, 86° F.; 25+ specimens.

Cat. No. 6530, U.S.N.M. (aggregated form), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands, June 7, 1909; surface; surface temperature, 86° F.; 10+ specimens.

Cat. No. 6532, U.S.N.M. (solitary form), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands, June 7, 1909; surface; surface temperature, 86° F.; 25+ specimens.

Cat. No. 6551, U.S.N.M. (solitary form), *Albatross* station D. 5166, Sulu Archipelago, Tawi Tawi Group, Philippine Islands, February 24, 1908; surface; surface temperature, 81° F.; surface density, 1.02644; 1 specimen.

Cat. No. 6571, U.S.N.M. (solitary and aggregated forms), *Albatross* station D. 5128, Sulu Sea, vicinity southern Panay, Philippine Islands, February 4, 1908; surface; surface temperature, 80° F.; 100+ specimens.

Cat. No. 6575, U.S.N.M. (solitary and chain forms), *Albatross* station D. 5588, Sibuko Bay, Borneo, and vicinity, September 28, 1909; surface; surface temperature, 82° F.; 5+ specimens.

Cat. No. 6615, U.S.N.M. (solitary and chain forms), *Albatross* station D. 5196, off Northern Cebu Island, Philippine Islands, April 3, 1908; surface; surface temperature, 82° F.; surface density, 1.02518 100+specimens.

Cat. No. 6620, U.S.N.M. (solitary and chain forms), *Albatross* station D. 5128, Sulu Sea, vicinity southern Panay, Philippine Islands, February 4, 1908; surface; surface temperature, 80° F.; 1 specimen.

**THALIA DEMOCRATICA, solitary form.**

There are five body muscles (fig. 104), usually in two groups, I+II+III, and IV+V. In some individuals muscles IV and V do not touch on the dorsal mid line. All are continuous across the

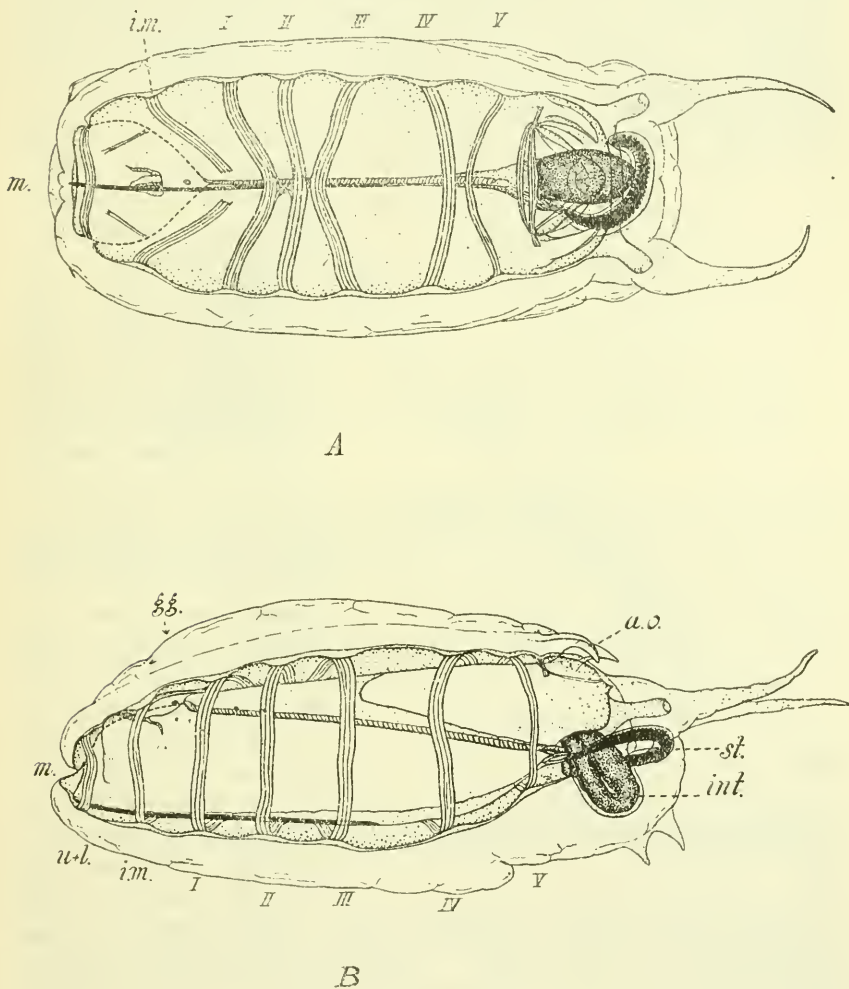


FIG. 104.—*Thalia democratica*, solitary form: *A*, dorsal view; *B*, seen from the left side.  $\times 7\frac{1}{2}$  diameters. From specimens collected off Newport, Rhode Island. (Drawn by Hoyt S. Hopkins.)

dorsal and ventral mid lines. The intermediate muscle is continuous ventrally, but interrupted dorsally.

The oral musculature is well shown by Streiff (1908), whose figure I copy (fig. 105). The well-developed retractor connects in front with three sphincters of the strongly incurved lower lip and one incomplete admarginal sphincter in the less incurved upper lip. A second

strong basal sphincter lies in the upper lip. This divides ventrally into two branches, an anterior, smaller, which gives rise to a fourth sphincter of the lower lip, and a broad posterior branch which Streiff regards as one of two divisions of the intermediate muscle (his "Bogenmuskel") but it seems rather to be comparable to such a ventral extension of the posterior dorsal lip sphincter as we see in *Cyclosalpa*. (See figures of both solitary and aggregated forms of *Cyclosalpa* on plates 1 to 13.) The dorsal horizontal bands are present in the usual position (fig. 104).

The atrial musculature (fig. 106) is a good deal like that of *Iasis zonaria*. Both species have a peculiar triangular area of modified

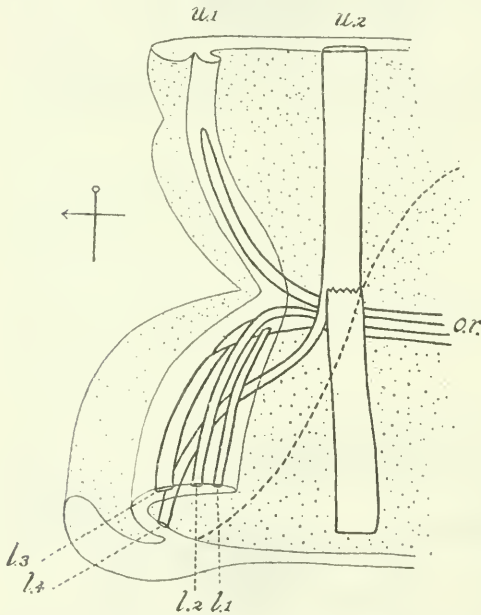


FIG. 105.—*Thalia democratica*, solitary form, ORAL MUSCLES OF THE RIGHT SIDE, VIEWED FROM WITHIN. FROM STREIFF (1908).

test, in a valve-like position on the dorsal side of the atrial siphon. There is a well developed atrial retractor muscle, which is connected at the angles of the atrial aperture with the broad third sphincter of the upper atrial lip and with a ventral branch which soon divides to form the first and third sphincters of the lower atrial lip. There is a strong continuous band of muscle which forms the broad (fourth) sphincter of the dorsal lip and the second sphincter of the ventral lip. The first and second sphincters of the upper lip are more delicate. They are united at their base, and distally make something of a network, seeming to correspond to the second sphincter of the upper atrial lip of *Iasis zonaria*. The first, admarginal, sphincter, which in *Iasis* is continuous through both atrial lips, is wanting in *Thalia*.

The gut forms an elongated loop (fig. 104, *B*), being bent upon itself in a vertical plane, much as in *Traustedia* (pl. 14). The two limbs of the loop are closely appressed in some individuals, but usually are separated by a slight space. The gut protrudes into a short, but well defined, postabdomen which it fills.

The eye is of the usual horseshoe shape, but shows three slight enlargements, one posteriorly, in the arch of the horseshoe, and one at the tip of each limb of the horseshoe.

test, in a valve-like position on the dorsal side of the atrial siphon. There is a well developed atrial retractor muscle, which is connected at the angles of the atrial aperture with the broad third sphincter of the upper atrial lip and with a ventral branch which soon divides to form the first and third sphincters of the lower atrial lip. There is a strong continuous band of muscle which forms the broad (fourth) sphincter of the dorsal lip and the second sphincter of the ventral lip. The first and second sphincters of the upper lip are more

There are no ganglionic outgrowths, but the gland shows the usual condition, consisting of a disk-shaped chamber on each side, connected by a convoluted tube with the pharyngeo-cloacal chamber.

The test protrudes to form several pairs of spines (fig. 104), a large postero-lateral pair containing a considerable tube of mantle epithelium, a smaller lateral pair dorsal to these, into the base of which there is a faint evagination of the mantle, and a weakly developed anterior pair, at the angles of the mouth, which show a distinct mantle evagination and but slight protrusion of the test. These structures are

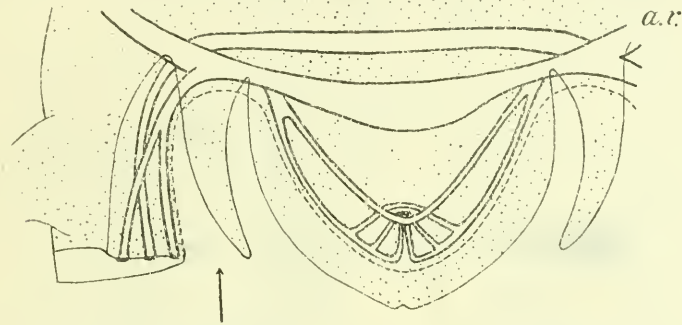


FIG. 106.—*Thalia democratica*, solitary form, dorsal view of atrial musculature. THE ATRIAL SIPHON WAS CUT ON THE VENTRAL MID LINE, AND THE LEFT FLAP THUS FORMED IS LAID OUT LATERALLY, THE RIGHT FLAP IS OMITTED. FROM STREIFF (1908).

doubtless comparable to the postero-lateral protrusions of *Thetys* (fig. 114, p. 122) and *Ritteria hexagona* (fig. 35, p. 63) and to the numerous "tentacles" of *Traustedtia* (pl. 14).

***Thalia democratica*, aggregated zoöid, Atlantic Ocean form.**

The asymmetry of the aggregated *Thalia democratica* is slight (fig. 107, *B*) being noticeable chiefly in the asymmetrical position of the cloacal aperture and the presence of a lateral protuberance of both test and mantle on one side of the posterior end of the body, much as in *Salpa maxima* (fig. 67, p. 85).

There are four body muscles, continuous across the dorsal mid line, but widely interrupted ventrally. I, II, and III are in contact on the dorsal mid line. Muscle IV is branched, as the last body muscle is in the aggregated zooids of other species. Its posterior branch is delicate. It passes by the base of the atrial siphon, but does not extend more than halfway around the latter. Of course, then, it does not meet its fellow of the opposite side or form any visceral muscle.

The intermediate muscle is well developed (figs. 107, *A*, and 108). It is divided into an anterior and a posterior division. The posterior of these arises a little at one side of the mid-ventral line, in front, and

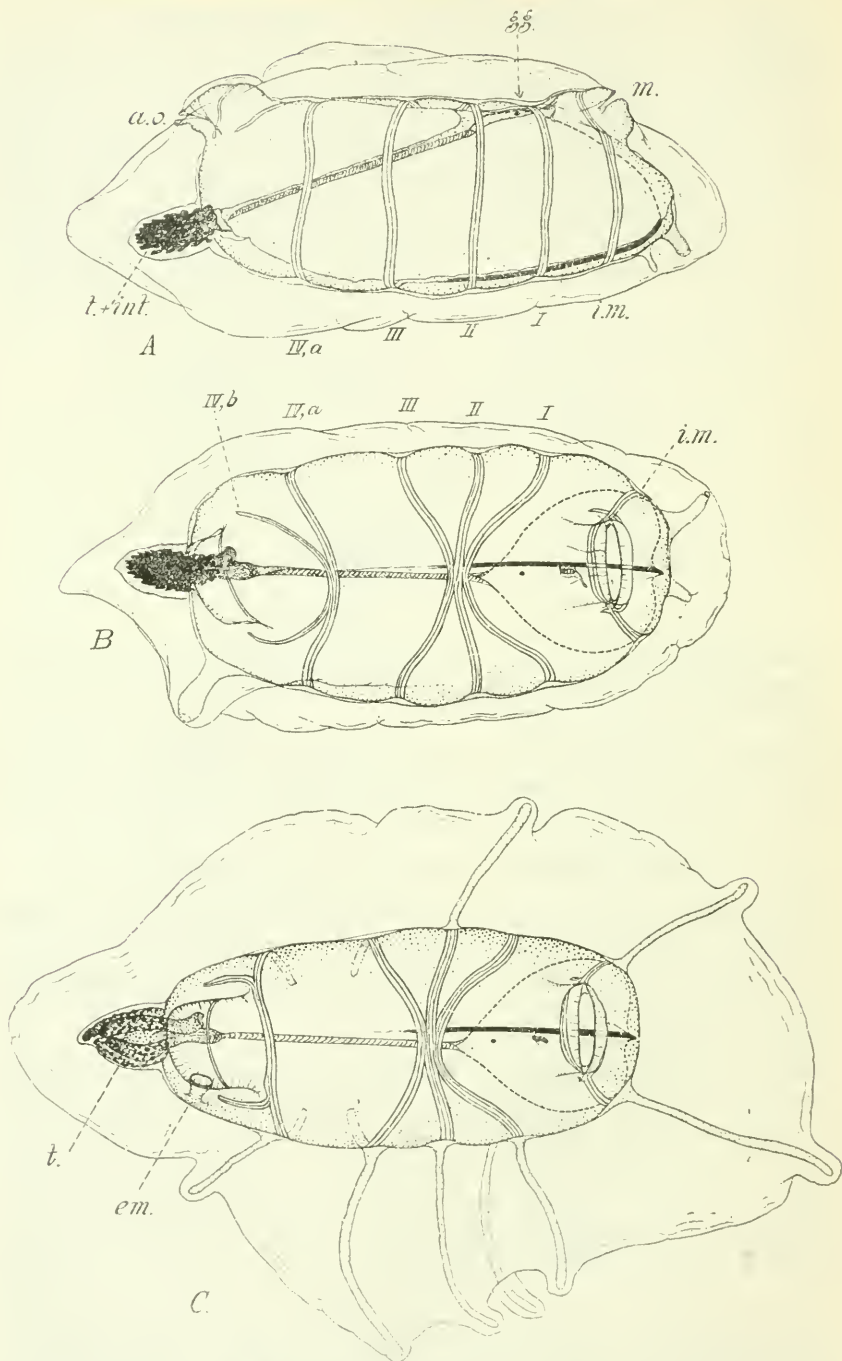


FIG. 107.—*Thalia democratica*, aggregated zooids.  $\times 3\frac{1}{2}$  diameters. *A*, an individual from the right side of the stolon, viewed from the right side; *B*, a dorsal view of an individual from the left side of the stolon; *C*, a dorsal view of a new western Pacific form of the same species. *A* and *B* represent the prevalent Atlantic form.

runs obliquely upward and backward, past the oral retractor muscle, and stops before reaching the dorsal surface. The anterior division follows the same course, but ends just short of the oral retractor muscle. The basal sphincter of the upper lip (*u. 3*) is a broad band which at first sight seems to be a continuation dorsally of the anterior division of the intermediate muscle. Closer inspection, however, shows it to be distinct from, though it abuts upon, the intermediate muscle. The short oral retractor muscle is continued forward into the first and second sphincters of the upper lip and the first and third sphincters of the lower lip. The second and fourth sphincters of the lower lip are united at the angle of the mouth, lying a little ventral to the oral retractor. They might be said to form a very short ventral division of the oral retractor muscle.

The cloacal musculature (fig. 109) differs in different individuals.

My specimens from the eastern and western Pacific Ocean (*A*) agree with Streiff's description (*D*), except as to the internal or external position of the overlapping muscles. Those from the Atlantic coast of New England (*B* and *C*) present slightly divergent conditions, none of which agrees exactly with the Pacific specimens, though some differ only minutely. For the Pacific type I copy Streiff's figure, modifying only the overlapping of the muscles, which I find not as Streiff shows. For the New England coast specimens I twice again modify Streiff's figure to show two of the several variants, one of which (*C*) most nearly approaches the Pacific type, and another (*B*) which is more unlike the Pacific specimens. In general the internal or external position of muscles which overlap is constant in other species of Salpidae. It is therefore a little surprising to find discrepancy in this regard between Streiff's specimens and mine. The divergence in the grouping and attachment of the muscles is no more than might be expected in this very widely distributed and very abundant species. It is of some interest that in my very abundant material from both the Atlantic and Pacific Oceans, the Atlantic animals should show considerable diversity in the cloacal muscles, while the Pacific animals show almost none.

The gut is more compact than in the solitary form. The endostyle, in both solitary and aggregated forms, is confined to the anterior

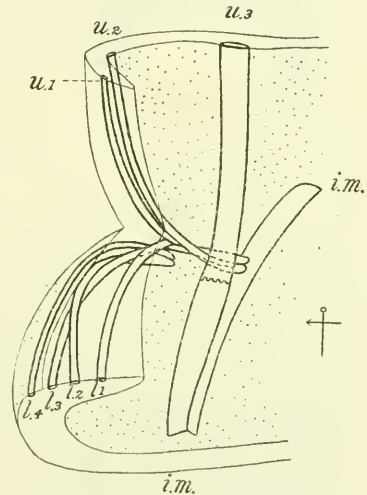


FIG. 108.—*Thalia democratica*, AGGREGATED FORM, ORAL MUSCLES OF THE RIGHT SIDE SEEN FROM WITHIN. STREIFF (1908).

half of the body, being shorter even than in *Thalia longicauda*. The aggregated *Iasis zonaria*, also, has the endostyle short and in the anterior part of the body. In all three of these species there is a considerable gap between the posterior end of the endostyle and the intestine. In *Pegea confederata* the endostyle is short and in the anterior part of the body, but the gap between the intestine and endostyle, especially in the solitary form, is less marked.

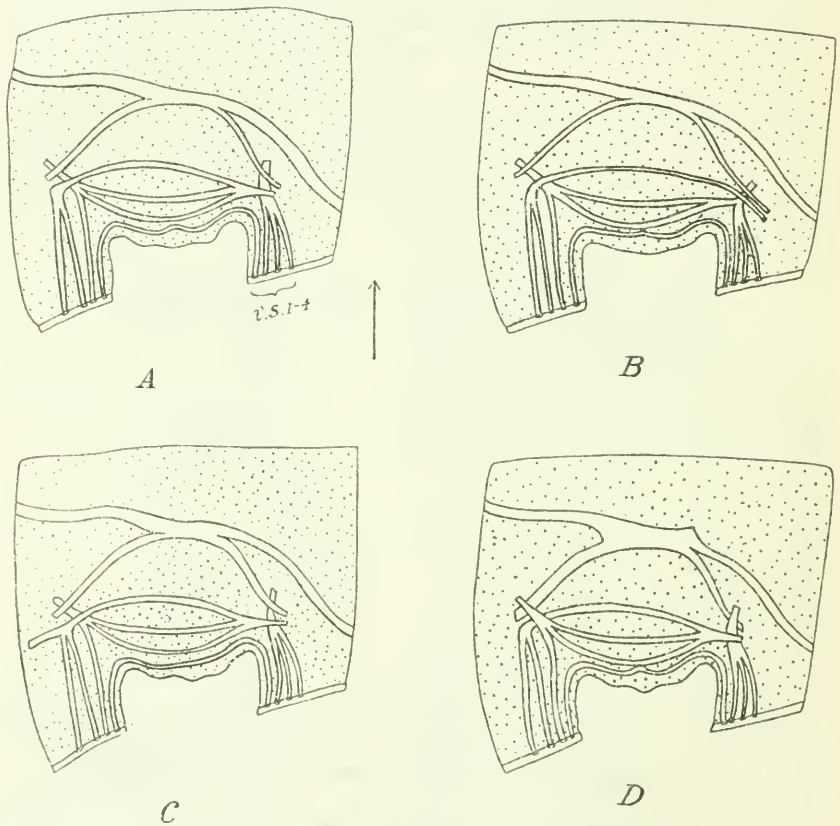


FIG. 109.—*Thalia democratica*, aggregated form, dorsal views of atrial siphons which have been cut open on the mid-ventral line and the flaps laid out laterally: A, from a Pacific Ocean specimen; B, from a New England coast form; C, from a specimen collected off Newport, Rhode Island; D, copied from Streiff (1908).

The eyes of the aggregated *Thalia democratica* (figs. 110, 111, and 112) are very different from those of the other subgenera, but the structural conditions and the development indicate the homologies. Three distinct portions of the eye are seen on the antero-ventral surface of the ganglion, an anterior, larger portion (*ex*), and two somewhat asymmetrical posterior portions (*e'1* and *e'2*). The



probable homologies appear when we realize that the anterior rotation of the eye, observed in the development of *Cyclosalpa pinnata* (fig. 12, p. 25) occurs in the same way in *Thalia democratica* but has gone about one hundred and twenty degrees further, the ganglion itself sharing in this rotation, as is clearly shown by the development of the eye and ganglion in the buds and by the arrangement in the adult of the ectodermal epithelium over the originally dorso-anterior face of the ganglion, which is now ventral. If, in imagination, we rotate the ganglion back one hundred and twenty degrees to a position comparable to that in, say, *Salpa fusiformis* (fig. 79, p. 92), we see that in position relative to the ganglion, and in the relative position of the rod and pigment cells, the anterior portion of the eye in *Thalia democratica* (*ex*) is comparable to the large accessory eye (*ex*) in the ganglion of *Salpa fusiformis*. Its pigment layer, present in *Thalia*, is wanting in *Salpa*. The two posterior portions of the *Thalia* eye (*e'1* and *e'2*) represent, then, the large dorsal eye of the true *Salpae*, or rather the proximal portion of this eye, as is shown by the position of rod-cells and pigment cells. The division of this eye into two parts, right and left, is a reversion to the condition seen in *Cyclosalpa pinnata* (figs. 7 and 8, pl. 2), in which the proximal portion of the large dorsal eye is divided into distinct right and left limbs. The innervation of the portions of the eye in *Thalia* agrees with this interpretation. The anterior portion (*e''*) of the large dorsal eye, found in *Cyclosalpa pinnata* and in the other species thus far described in this paper, is lacking in *Thalia*, as is also the optic plug (*e'''*). That portion of the eye which is marked *e'2* is seen to be oriented

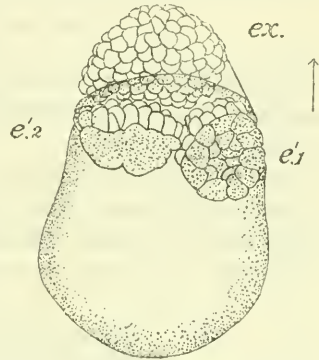


FIG. 110.—*Thalia democratica*, aggregated form, dorsal view of ganglion and eyes.  $\times 362$  diameters from Metcalf (1893, c).

slightly differently from the portion marked *e'1*. The meaning of this difference in orientation is not clear. It may have to do with the position of the zooid in the chain.

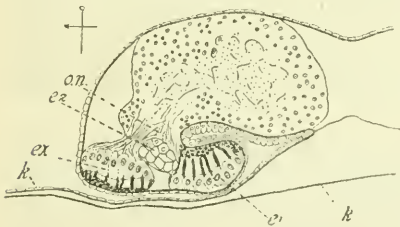


FIG. 111.—*Thalia democratica*, aggregated zooid; longitudinal vertical section through the ganglion and eyes.  $\times 300$  diameters. From Metcalf (1893, c).

Neither in the fully formed aggregated individuals of *Thalia democratica*, nor in the course of their development, are there any traces of outgrowths from the ganglion, or of either the chambers

or the ducts of the neural glands. The remarkable absence of these organs in this species may be associated with the great rotation of the ganglion. It is of interest as showing that these organs are not of indispensable physiological importance in the Salps, for this species, which lacks these organs, is the most abundant and widely distributed of all the species in the family.

**THALIA DEMOCRATICA, aggregated zooid: Philippine form.**

Characteristic specimens of the Philippine form of aggregated zooids of this species are in the collections of United States National Museum as follows:

Cat. Nos. 6473 (Holotype) and 6474 (Paratype) U. S. N. M. (Aggregated, Philippine form), *Albatross* station D. 5456; June 7, 1909; 142 fathoms; surface temperature, 86° F.; two specimens.

In the prevalent form of the aggregated zooids of *Thalia*

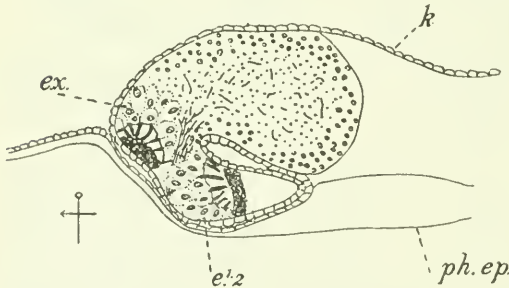


FIG. 112.—*THALIA DEMOCRATICA*, AGGREGATED FORM, LONGITUDINAL VERTICAL SECTION OF GANGLION AND EYES, SHOWING THE INNERVATION OF *e* 1,2. X 300 DIAMETERS. FROM METCALF (1893, c).

*democratica* from the Atlantic coast of the United States (fig. 107, A and B) there are but few tubular protuberances of the mantle into the test. At one of the postero-lateral angles of the body there is one which protrudes slightly beyond the general contour of the test. There are gener-

ally an unequal pair in front not protruding beyond the general contour of the test. If there are others they are generally weakly developed.

On the other hand, in the Philippine collections of this species, made by the Bureau of Fisheries steamer *Albatross*, there are very numerous specimens of a form of aggregated zooid, which show more numerous and much more developed mantle protuberances (fig. 107, C). This zooid strikingly resembles *Traustedtia radiata* in musculature, form of "nucleus," and "tentacles." This resemblance is so marked that one, at first glance, thinks these zooids to be the aggregated form of the latter species. The testis in these aberrant Philippine zooids is readily seen to be in the form of four lobes surrounding the intestine.

Among the Atlantic specimens are some which, in the number of mantle protuberances, approach the Philippine type, but I have found none with the protuberances so well developed as in the latter.

Our collections from the Philippines, on the other hand, contain numerous individuals of the prevalent Atlantic type, having the mantle protuberances few in number (though rather too long to be characteristic), having the lobes of the testis subdivided into numerous lobules, and having the test behind the intestinal "nucleus" pointed instead of rounded. There seems to be rather complete intergradation between the two types. It seems hardly worth while to give them distinct varietal names.

From study of the smallest (youngest) of the aggregated zooids of the Philippine type one point of interest in the development of the eye is seen. In an early stage of its development, those portions of the eye marked  $e_1$  and  $e_2$  in figures 110, 111, and 112, are united into one, and the eye is thus in two instead of three divisions. In *Cyclosalpa pinnata* buds the eye is at first horseshoe-shaped, the hollow of the horseshoe soon becoming filled; later the posterior portion of the inverted disk becomes again divided into two limbs. In *Thalia democratica* the latter two stages are the only ones I have found, the eye of the aggregated zooid appearing, in the earliest stage I have seen, as a disk not a horseshoe. In other species of Salpidae the final stage, involving splitting of the posterior part of the inverted disk into two limbs, is omitted.

**THALIA LONGICAUDA** (Quoy and Gaimard, 1824).

*Salpa longicauda* QUOY AND GAIMARD, 1824.

*S. democratica-mucronata*, var. *flagellifera* TRAUSTEDT, 1885.

*S. flagellifera* APSTEIN, 1894, *a*.

Of this species I have had no specimens. It is very similar to *Thalia democratica*, being distinguished by the presence of two unusually long and slender appendages from the posterior angles of the body in the solitary form (fig. 113); by having the body muscles not continuous across the ventral line in the solitary form; by the independence, in the solitary form, of all the body muscles, which are not united dorsally into two groups as in the solitary *Thalia democratica*; and by the fact that in the aggregated individuals the intermediate muscle and body muscles are composed of more fibers than they are in *Thalia democratica*. Apstein (1906, *a* and *b*) gives the numbers as follows (using my notation).

Body muscle:	<i>Thalia democratica</i> fibers.	<i>Thalia longicauda</i> fibers.
I.....	5	8-11
II.....	3-4	6-9
III.....	3	8-9
IV, a.....	3-4	5-7
IV, b.....	2	2

Apstein's body muscle V is here counted as the posterior branch of the body muscle IV.

The oral and atrial muscles of *Thalia longicauda* have not been studied, nor have the neural glands and the outgrowths from the ganglion. The eye of the aggregated form has not been observed. Dober (1912) gives a figure of the eye of the solitary form showing little detail, but apparently indicating that the pigment is in three divisions corresponding to the enlargements of the eye in the ordinary *Thalia democratica*.

The *Thalias* are a sharply demarcated subgenus. They grade into the other subgenera less even than do the *Cyclosalpas*. This is shown especially in the character of the eyes and the absence of neural

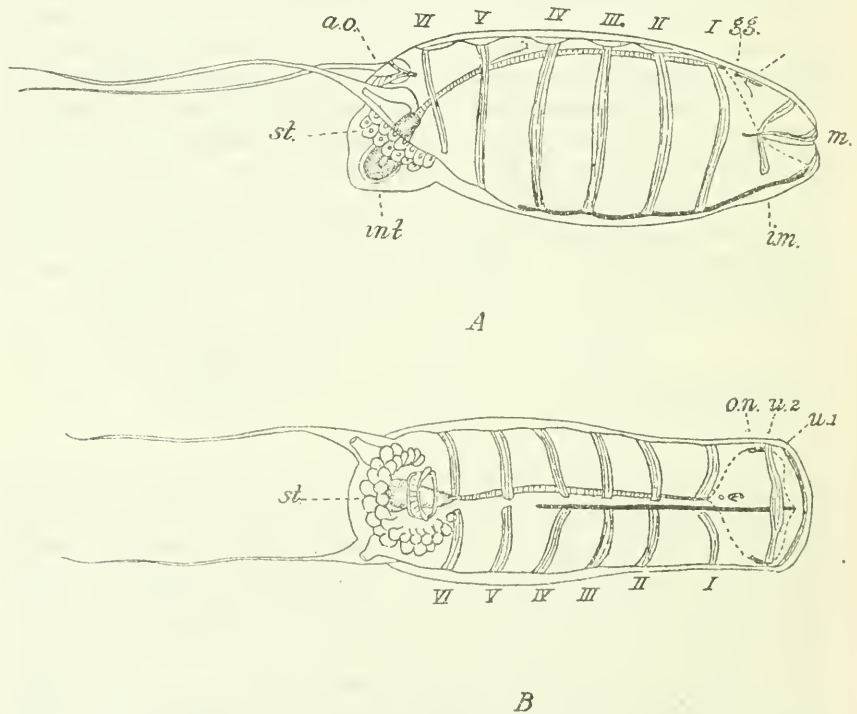


FIG. 113.—*Thalia longicauda*, SOLITARY FORM: A, VIEW FROM THE SIDE; B, VENTRAL VIEW. FROM TRAUSTEDT (1835).

glands and outgrowths from the ganglion in the aggregated zooids, but the subgenus is recognizably distinct also in the character of its appendages and of the tubular protuberances from the mantle into the test. In the latter two features it shows some general resemblance to *Traustedia*.

We have one bit of evidence that aids us in determining which of the two species of *Thalia* is the more archaic. In studying the development of the buds upon the stolon of *Thalia democratica*, one sees that the body muscle bands arise as regularly spaced loops and that only late in the development do they become approximated

dorsally into two groups of three and two respectively. This shows that, as one would naturally expect, the condition with dorsally approximated body muscles is secondary. If this is true for the aggregated zooids, it is doubtless true also for the solitary individuals. *Thalia longicauda*, with its regularly spaced body muscles in the solitary form, is therefore to be regarded as more archaic than *Thalia democratica* with its body muscles in the solitary form approximated dorsally into two groups.

## SUBGENUS THETYS Tilesius, 1802.

## THETYS VAGINA Tilesius, 1802.

*Salpa tilesii* CUVIER, 1804.

*Dagysa strumosa* HOME, 1814.

"Another species" HOME, 1814.

*Salpa costata* QUOY and GAIMARD, 1824.

*S. bigibbosa* QUOY and GAIMARD, 1824.

*S. gibbosa* QUOY and GAIMARD, 1824.

*S. herculea* DALL, 1872.

*S. infundibuliformis* QUOY and GAIMARD, 1824.

(?) *S. neapolitana* DELLE CHIAJE, 1841.

*S. costata-tilesii* KROHN, 1846, and more recent authors.

*Iasis costata-tilesii* HERDMAN, 1891.

*Salpa vagina* IHLE, 1911.

To the subgenus *Thetys* may be assigned the single species *vagina* (*Salpa tilesii* of most authors), the largest of the Salpidae. I have had two very good specimens of the solitary form besides several degenerate specimens. Of the aggregated form I have had about fifty specimens from six localities. Specimens of this species are found in the United States National Museum collections as follows:

Cat. No. 6438, U.S.N.M. (solitary form), *Albatross* station D. 5441, S. Fernando Point Light, west coast of Luzon; May 10, 1909; 186 fathoms; surface temperature, 87° F.; one specimen.

Cat. No. 6426, U.S.N.M. (aggregated form), *Albatross* station D. 3132, off Point Conception, California, March 14, 1890; 33 fathoms; surface temperature, 55° F.; one specimen.

Cat. No. 6427, U.S.N.M. (aggregated form), *Albatross* station D. 2402, Gulf of Mexico, March 14, 1885; 111 fathoms; one specimen.

Cat. No. 6515, U.S.N.M. (solitary form), *Albatross* station D. 5243, Pujada Bay and vicinity, Philippine Islands; May 15, 1908; surface; surface temperature, 84–85° F.; surface density 1.02453; eight specimens.

Cat. No. 6518, U.S.N.M. (tests of solitary and also aggregated form), *Albatross* station D. 5242, Pujada Bay and vicinity, Philippine Islands; May 14, 1908; surface; surface temperature, 85° F.; surface density, 1.02457; 44 specimens.

Cat. No. 6552, U.S.N.M. (test), *Albatross* station D. 5569, north of Tawi Tawi, Philippine Islands; September 22, 1909; surface; surface temperature, 83° F.; one specimen.

Cat. No. 6585, U.S.N.M. (test of solitary form), *Albatross* station D. 5244, Pujada Bay and vicinity, Philippine Islands; May 15, 1908; surface; surface temperature, 85° F.; surface density, 1.02497; 3 specimens.

Cat. No. 6609, U.S.N.M. (solitary form. Tests), *Albatross* station D. 5241, Pujada Bay and vicinity, Philippine Islands; May 14, 1908; surface; surface temperature, 85° F.; surface density, 1.02453; 10 specimens.

Cat. No. 6610, U.S.N.M. (aggregated form), *Albatross* station D. 5243, Pujada Bay and vicinity, Philippine Islands; May 15, 1908; surface; surface temperature, 84–85° F.; surface density, 1.02453; one specimen.

**THETYS VAGINA, solitary form.**

Like some of the *Ritterias*, the solitary form of this species has a variable number of body muscles (fig. 114). The number is about the same as in *Ritteria picteti*, 16 to 20, or more. All the muscles are interrupted on the dorsal mid line, and many of the anterior

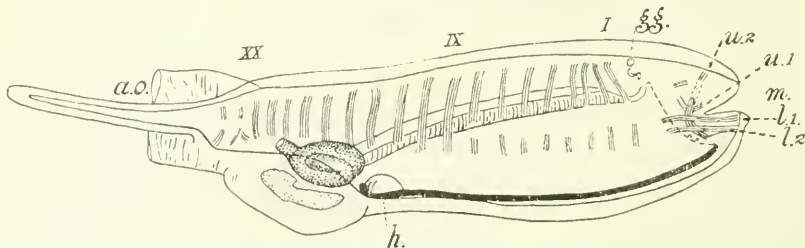


FIG. 114.—*THETYS VAGINA*, SOLITARY FORM, VIEWED FROM THE RIGHT SIDE, ONE-HALF NATURAL SIZE. MODIFIED FROM RITTER (1906).

and some of the posterior ones are also interrupted dorso-laterally. The muscles barely extend onto the ventral half of the body.

The intermediate muscle (fig. 115) is reduced to a mere vestige at the angle of the mouth.

The oral muscles are rather weakly developed for such a huge salpa. In two specimens I have had for study the conditions are somewhat different. The relations in the smaller individual are shown in figure 114. Those in the larger individual appear in figure 115. In the first figure the inverted portion of the lower lip is drawn forward to the outer surface. In the second figure the natural relations are shown. Two oral retractor muscles are present, each continued forward into a well-developed sphincter of the lower lip (*l. 2* and *3*). In the smaller specimen (fig. 114) these are distinct; in the larger specimen (fig. 115) they are united through the ventral half of their course. Another very delicate sphincter (*l. 4*) is present in both individuals. In the smaller specimen (fig. 114) it is continuous at its upper end with the ventral edge of the ventral oral retractor and

at its other end with the ventral edge of the second sphincter of the lower lip. In the larger specimen (fig. 115) the third sphincter is wholly independent, but its base is connected by a blood sinus with the ventral retractor. In the larger specimen there is an exceedingly delicate first sphincter of the lower lip (*l. 1*), admarginal, which arises from the dorsal edge of the dorsal oral retractor.

The muscles of the upper lip also differ in the two specimens. In the smaller there is a short, but fairly broad, first sphincter (*u. 1*). In the larger individual no corresponding muscle is found, but in its place is the muscle blood sinus (fig. 115). The second sphincter is

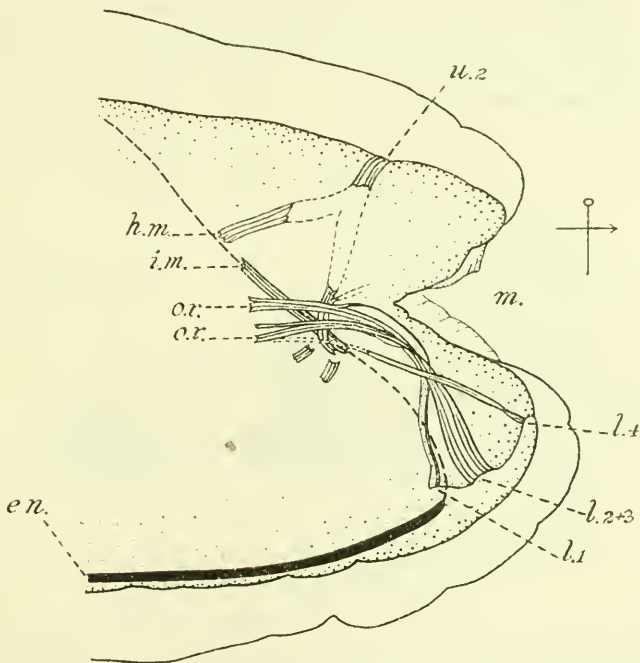


FIG. 115.—*Thetys vagina*, SOLITARY FORM, ORAL MUSCLES SEEN FROM THE RIGHT SIDE.  $\times 1\frac{1}{2}$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

broad. Like the body muscles, it is interrupted on each side, the interval showing the continuous blood sinus.

The dorsal horizontal band is short and independent of other muscles, though it is united to the second sphincter of the upper lip by a blood sinus. The intermediate muscle is short in both specimens. It is shorter in the smaller specimen (fig. 114) and is united to the base of the first sphincter of the upper lip. Postero-ventral to the lower end of the intermediate muscle one sees, in each specimen, two very short problematic muscles entirely disconnected. Comparison with the aggregated zoöid (fig. 117) seems to indicate that these minute muscles are isolated ventral fragments of the sphincters of the upper lip. Compare also the conditions in the solitary *Salpa*

*maxima* (figs. 64 and 65, p. 84), in which some specimens show isolated ventral moieties of the intermediate and ventral oral retractor muscles.

*Thetys vagina* shows very well a feature that often helps in determining the true relation of muscles. Each muscle in a *Salpa* is formed upon a blood sinus, and when a muscle is interrupted the sinus is generally continued across the interval, showing the real relations. In comparing embryos and adult solitary individuals, or younger and older aggregated zooids, one sometimes finds in one a muscle, while in a corresponding position in the other there is only the muscle blood sinus. The same difference may be observed between divergent adult individuals, as for instance, note the abortive first sphincter of the upper lip (*u. 1*) in figure 114 and the blood sinus in a similar position in figure 115.

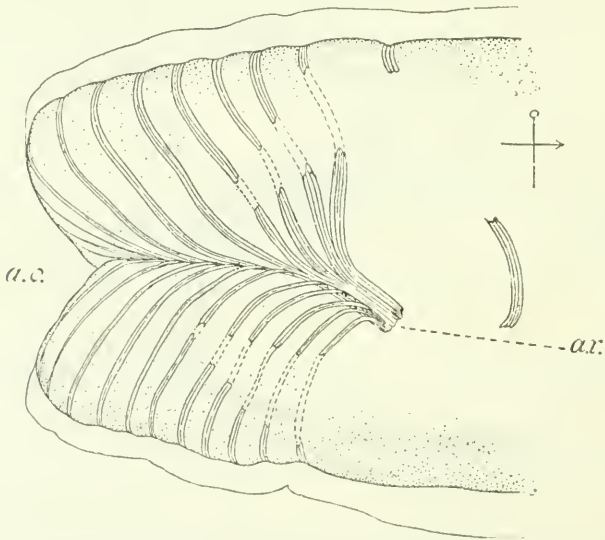


FIG. 116.—*THETYS VAGINA*, SOLITARY FORM, ATRIAL MUSCLES VIEWED FROM THE RIGHT SIDE.  $\times 3$  DIAMETERS. (DRAWN BY HOYT S. HOPKINS.)

The atrial siphon is a broad tube and bears 11 delicate sphincter muscles (fig. 116) on its upper and lower lips. These unite at each angle of the aperture to form a rather weakly developed short atrial retractor muscle. For so large an animal the whole musculature is very weak. There are lateral interruptions of several of the atrial sphincters, both above and below the retractor.

From near the posterior end of the body there protrudes, on each side, a cylindrical curved protuberance, generally from a fourth to a fifth as long as the whole body (fig. 114). This contains a tube whose epithelial walls are continuous with the mantle epithelium. These tubular protuberances closely resemble the "tentacles" of *Traustedtia*



(pl. 14), even in the peculiar appearance of the enlarged tips of the inner tubes. Protuberances of the test at the posterior angles of the body are found in numerous species, and in many of these species they contain tubes whose epithelial lining is continuous with the mantle.

The gut is a round coil which may be called a "nucleus," though it is less densely compacted than in the *Apsteinias* and *Salpas*. One can make out the course of the intestine without dissection.

I have not had sufficient material to study the histology of the neural organs and gland. Examination of total preparations shows the eye to be of the usual horseshoe form.

THETYS VAGINA, aggregated form.

There are five body muscles (fig. 117), all narrowly interrupted dorsally and extending laterally only to the sides of the body. The ventral half of the body has no muscles of any sort. The fifth body

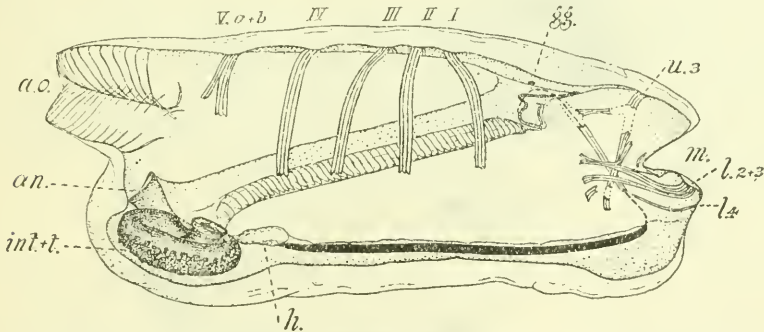


FIG. 117.—THETYS VAGINA, AGGREGATED ZOÏD VIEWED FROM THE RIGHT SIDE,  $\frac{2}{3}$  NATURAL SIZE. (DRAWN BY HOYT S. HOPKINS.)

muscle is divided on each side into an anterior and a posterior branch, as in the aggregated forms of other species, but the posterior branches are short and do not pass below the atrial siphon or give rise to any visceral muscle.

The intermediate muscle is as in the larger of my specimens of the solitary form of this species, not being fused with the rudimentary first sphincter of the upper lip. The oral musculature, including the horizontal dorsal band, is like that of the solitary form, except that there are three, instead of two, dorsal sphincters, the first very short and very slender, the second also very short. The musculature of the atrial siphon, also, is like that of the solitary form, except that there are 12 to 15, instead of 11, sphincters in my specimens. On the dorsal side the basal sphincter is widely interrupted in the middle, and ventrally its ends do not come into contact with the atrial retractor muscle.

The gut, in the aggregated as in the solitary form, is a close coil, but one can readily trace the course of the intestine, except that the overlying test is usually very dense and somewhat opaque.

In no species of Salpidae is the pocket valve structure of the lower lip clearer than in the aggregated *Thetys vagina*.

The aggregated form of *Thetys vagina* has a large dorsal eye and two large masses of optic cells in the ganglion (fig. 118), in all of which the rod cells are irregularly polyhedral in shape, not elongated, and their walls are unevenly thickened to form the rod-like materials. In the large dorsal eye, two portions may be distinguished, a basal portion with pigment ventral to the rod cells, and an apical portion whose pigment is dorsal to the rod cells, thus showing resemblance to the eye in the true *Salpae*, except for the degenerate condition of the

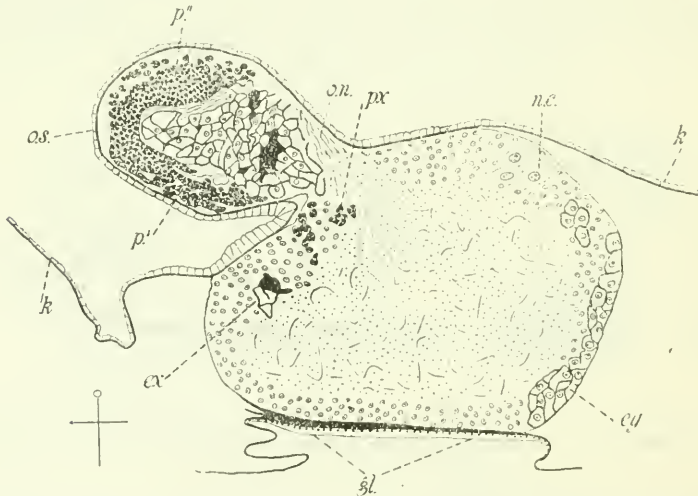


FIG. 118.—*THETYS VAGINA*, AGGREGATED FORM, SAGITTAL SECTION OF GANGLION, DORSAL EYE, AND NEURAL GLAND.  $\times 98$  DIAMETERS. FROM METCALF (1893, c).

rod cells in *Thetys*. The eye of *Thetys* is short and compact, as in *Iasis zonaria*, (figs. 101 and 102, p. 108), and the pigment layers of its basal and apical portions are continuous at the sides of the eye but not on the mid-ventral line. The section figured is parasagittal, not sagittal, and shows the pigment of the two regions continuous.

In the ganglion are two large masses of irregular rod cells, as indicated by the rod-like material of which their unevenly thickened wall are composed. The larger of these masses covers the whole postero-ventral face of the ganglion and is probably homologous with the posterior pair of smaller eyes in the ganglion of *Cyclosalpa pinnata*. In the interior of the ganglion, below its antero-dorsal surface, is a considerable mass of similar irregular rod cells and just dorsal to

them is a mass of pigment cells.<sup>1</sup> *Thetys* is noteworthy in having abundant pigment associated with the antero-dorsal eye within the ganglion.

The neural gland in the aggregated zoöids of *Thetys vagina* (fig. 118) is unique. Instead of two disks below the ganglion, each opening by a tube to the peripharyngeal chamber, there is a single huge evagination of this chamber, with a single wide median aperture. The epithelium of that part of the evagination which is in contact with the ganglion is thickened and resembles the dorsal portion of the epithelium of the glandular disks in other species. Remembering the origin of the typical disks in other species, as paired evaginations from the pharyngeo-cloacal epithelium, it is not so great a divergence from the usual conditions, which *Thetys* shows. Instead of two evaginations, one right and the other left, *Thetys* has a single huge median evagination, and this does not develop far enough to close off from the pharyngeo-cloacal chamber. In *Iasis zonaria* there is a single postero-median chamber in the neural gland (fig. 103, p. 108) but this shows paired anterior prolongations. There is also but one duct, but this is lateral, one duct being present and the other absent. [Cf. *Salpa cylindrica* Metcalf, 1893, c.] In *Thetys* the gland is further modified and it and its single aperture are median.

Like *Iasis*, the aggregated zoöid of *Thetys* bears several embryos.

Subgenus PEGEA, (Savigne 1816).

PEGEA CONFEDERATA, (Forskål 1775).

- Salpa confederata* FORSKÅL, 1775.  
*S. gibba* BOSCH, 1802.  
*S. scutigera* CUVIER, 1804.  
*S. octophora* CUVIER, 1804.  
*S. vivipara* PERON, 1807.  
*Pegea octophora* SAVIGNY, 1816.  
*Salpa ferruginea* CHAMISSO, 1819.  
*S. informis* QUOY AND GAIMARD, 1824.  
*Salpa femoralis* QUOY AND GAIMARD, 1826-1834.  
*S. quadrata* HERDMAN, 1888.  
*Pegea scutigera-confederata* HERDMAN, 1891.  
*S. confederata* APSTEIN, 1894, a.

In the collections of the United States National Museum there are the following specimens:

Cat. No. 6433 U.S.N.M. (solitary form), *Albatross* station D. 4037, Kawaihae Strait, Penguin Bank, south coast Oahu Island, Hawaiian Islands; July 10, 1902; surface; surface temperature 80° F.; 1 specimen.

<sup>1</sup> It is noteworthy to find these pigment cells *within* the ganglion instead of superficial as in the case of the eyes of the aggregated zoöids of all other species. In the eyes of some solitary *Salpae*, the pigment cells are within the optic ridge, instead of just beneath the epithelium, as in *Cyclosalpa pinnata* (fig. 4, p. 17). I am unable to say whether these internal pigment cells are mesodermal, as the superficial pigment cells in the eyes of aggregated zoöids seem to be.

Cat. No. 6435, U.S.N.M. (solitary form—i. e., large embryo), *Albatross* H. 543, south of Marthas Vineyard; surface; 1 specimen.

Cat. No. 6436, U.S.N.M. (embryo), *Albatross* (No. 127), 70 miles off Point Galera, Ecuador; 20+ specimens.

Cat. No. 6467, U.S.N.M. (aggregated form), *Albatross* collection, Jolo anchorage, February 8, 1908; 10+ specimens.

Cat. No. 6467, U.S.N.M. (aggregated form), Jolo Archipelago, Philippine Islands; February 8, 1908; surface; 30+ specimens.

Cat. No. 6514, U.S.N.M. (aggregated form and large embryo), *Albatross* station D. 5234, between Bohol and Leyte, Philippine Islands; May 7, 1908; surface; surface temperature, 84° F.; surface density, 1.02531; 20+ specimens.

Cat. No. 6523, U.S.N.M. (solitary form, rare), *Albatross* station D. 5144, vicinity of Jolo, Philippine Islands; February 15, 1908; surface; surface temperature 81° F.; surface density, 1.02514; 1+ specimen.

Cat. No. 6529, U.S.N.M. (embryo), *Albatross* station D. 5234, between Bohol and Leyte, Philippine Islands; May 7, 1908; surface; surface temperature, 84°; surface density, 1.02531; 3 specimens.

Cat. No. 6533, U.S.N.M. (aggregated form and embryo), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; 25+ specimens.

Cat. No. 6535, U.S.N.M. (solitary form, rare; also aggregated form), *Albatross* station D. 5553, Jolo Island and vicinity, Philippine Islands; September 17, 1909; surface; surface temperature, 83° F.; 2 specimens.

Cat. No. 6562, U.S.N.M. (embryo), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; 2 specimens.

Cat. No. 6563, U.S.N.M. (aggregated form), *Albatross* station D. 5196, off northern Cebu Island, Philippine Islands; April 3, 1908; surface; surface temperature, 82° F.; surface density, 1.02518; 1 specimen.

Cat. No. 6564, U.S.N.M. (aggregated form), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel Bay—Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; 1 specimen.

Cat. No. 6565, U.S.N.M. (solitary form, rare), *Albatross* station D. 5578, North of Tawi Tawi, Philippine Islands; September 23, 1909; surface; surface temperature, 82° F.; 1 specimen.

Cat. No. 6566, U.S.N.M. (aggregated form), *Albatross* station D. 5530. Between Siquijor and Bohol Islands, Philippine Islands; August 11, 1909; surface; surface temperature, 84° F.; 1 specimen.

Cat. No. 6567, U.S.N.M. (embryo), *Albatross* station D. 5456, East coast of Luzon, San Bernardino Strait, to San Miguel Bay, Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; 1 specimen.

Cat. No. 6572, U.S.N.M. (aggregated form and embryo), Labuan Blanda Island, Philippine Islands; December 13, 1909; surface; 28 specimens.

Cat. No. 6573, U.S.N.M. (aggregated form), Bubuan Island. Anchorage. Jolo, Philippine Islands; February 14, 1908; surface; 33 specimens.

Cat. No. 6586, U.S.N.M. (aggregated form), *Albatross* station D. 5561. Jolo Island and vicinity, Philippine Islands; September, 18 1909; surface; surface temperature, 82° F.; 2 specimens.

Cat. No. 6593, U.S.N.M. (aggregated form and embryo), *Albatross* station D. 5540. Between Negros and Siquijor, Philippine Islands; August 19, 1909; surface; surface temperature, 83° F.; 50 + specimens.

Cat. No. 6594, U.S.N.M. (aggregated form), *Albatross* station D. 5196. Off northern Cebu Island, Philippine Islands; April 3, 1908; surface; surface temperature, 82° F.; surface density, 1.02518; 13 specimens.

Cat. No. 6595, U.S.N.M. (aggregated form and embryo), *Albatross* station D. 5539. Between Negros and Siquijor, Philippine Islands; August 19, 1909; surface; surface temperature, 83° F.; 25 + specimens.

Cat. No. 6596, U.S.N.M. (aggregated form), Jolo, Philippine Islands; February 10, 1908; surface; 12 + specimens.

Cat. No. 6597, U.S.N.M. (aggregated form), *Albatross* station D. 5456. East coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; 30 + specimens.

Cat. No. 6598, U.S.N.M. (aggregated form), *Albatross* station D. 5604. Gulf of Tomini, Celebes; November 15, 1909; surface; surface temperature, 83° F.; 10 + specimens.

Cat. No. 6599, U.S.N.M. (aggregated form), *Albatross* station D. 5663. Macassar Strait, Philippine Islands; December 27, 1909; surface; surface temperature, 84° F.; 4 specimens.

Cat. No. 6600, U.S.N.M. (aggregated form), *Albatross* station D. 5616, Molucca Passage, Philippine Islands; November 22, 1909; surface; surface temperature, 84° F.; 5 + specimens.

Cat. No. 6601, U.S.N.M. (aggregated form), China Sea, vicinity southern Luzon; July 20, 1908; surface; 2 specimens.

Cat. No. 6602, U.S.N.M. (aggregated form), *Albatross* station D. 5540, between Negros and Siquijor, Philippine Islands; August 19, 1909; surface; surface temperature, 83° F.; 10 + specimens.

Cat. No. 6603, U.S.N.M. (aggregated form), *Albatross* station D. 5320, China Sea, vicinity Formosa; November 6, 1908; surface; surface temperature, 80° F.; 1 specimen.

Cat. No. 6604, U.S.N.M. (large embryo and small), *Albatross* station D. 5540, between Negros and Siquijor, Philippine Islands; August 19, 1909; surface; surface temperature, 83° F.; 25 + specimens.

Cat. No. 6605, U.S.N.M. (aggregated form), *Albatross* station D. 5140, vicinity of Jolo, Philippine Islands; February 14, 1908; surface; surface temperature, 80°–82° F.; surface density, 1.02477; 5 specimens.

Cat. No. 6606, U.S.N.M. (aggregated form), *Albatross* station D. 5232, between Bohol and Leyte, Philippine Islands; May 7, 1908; surface; surface temperature, 84° F.; surface density, 1.02531; 3 specimens.

Cat. No. 6607, U.S.N.M. (aggregated form), *Albatross* station D. 5456, east coast of Luzon, San Bernardino Strait to San Miguel Bay, Philippine Islands; June 7, 1909; surface; surface temperature, 86° F.; 10 + specimens.

Cat. No. 6608, U.S.N.M. (aggregated form and one large embryo), Bubuan Island anchorage, Philippine Islands; February 14, 1908; surface; 47 + specimens.

The musculature of this species is less developed than in any other of the Salpidae except *Traustedia*.

PEGEA CONFEDERATA, solitary form.

In the solitary form there are four muscles which should be classed as body muscles, two in front and two posterior, arranged as shown in figure 119. The fifth muscle on the dorsal surface is probably the homolog of the basal atrial sphincter in other species. All these muscles are confined to the dorsal surface. They do not reach even well onto the sides of the body. There is an intermediate muscle (fig. 120) which, as in *Thetys vagina* (fig. 115, p. 123), functions in connection with the oral muscles rather than the body muscles. It is divided lengthwise into an anterior and a posterior band, which are parallel. The dorsal horizontal band on each side is continuous posteriorly with the anterior band of the intermediate muscle. In front it is near to but not in contact with the broad sphincter of the dorsal lip.

The oral musculature (fig. 120) shows a retractor muscle which is divided into dorsal and ventral divisions, the dorsal division having two branches anteriorly. The ventral retractor connects anteriorly with the broad sphincter of the upper lip, the only complete sphincter in this lip. It connects also with the third sphincter of the lower

lip. The ventral branch of the dorsal oral retractor is continuous only with the second sphincter of the lower lip.

The dorsal branch of the dorsal oral retractor is continued forward into the first sphincter of the lower lip and also gives rise to a short muscle on each side, which runs up onto the upper lip, as if to form a first admarginal sphincter, but this is incomplete.

The musculature of the atrial siphon is shown in part in figure 121, which is a drawing of the siphon of an embryo cut open on the mid-

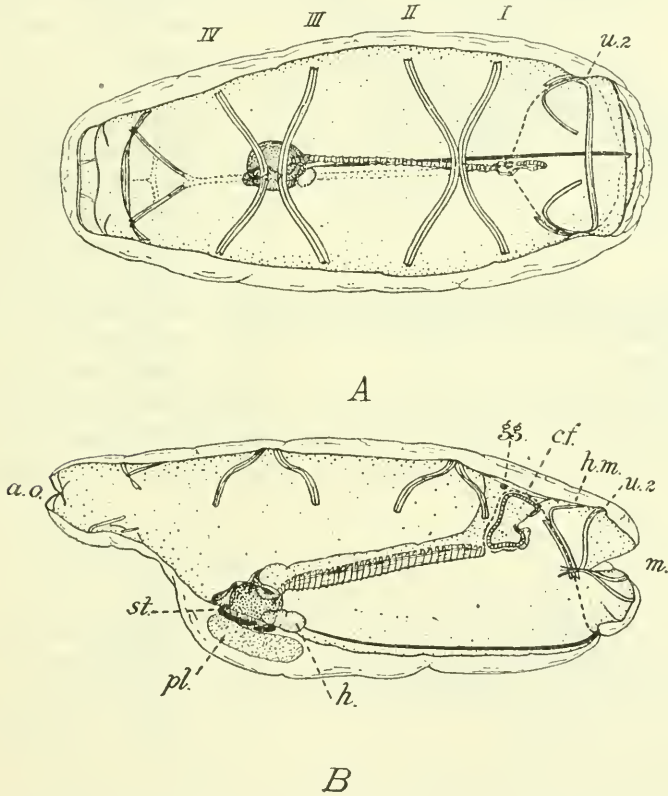


FIG. 119.—*PEGEA CONFEDERATA*, SOLITARY FORM: *A*, DORSAL VIEW; *B*, VIEW FROM THE RIGHT SIDE.  $\times 2$  DIAMETERS. FROM SPECIMENS COLLECTED IN PHILIPPINE WATERS AND OTHERS FROM THE ALASKA COAST. (DRAWN BY HOYT S. HOPKINS.)

dorsal line and spread out flat, the drawing showing an exterior (ventral) view of the preparation. Figure 122 shows a similar preparation of the cloacal siphon of an adult, in similar view.

Figure 119, *A* and *B*, show additional muscles on the dorsal side at the base of the atrial siphon. These do not appear in figures 121 and 122. There is a slightly developed atrial retractor muscle, continuous, in the embryo, with the second dorsal sphincter, in the

adult, with both first and second dorsal sphincters. There are two complete dorsal sphincters and two incomplete, the fourth much reduced in the adult. There are two ventral sphincters, the second

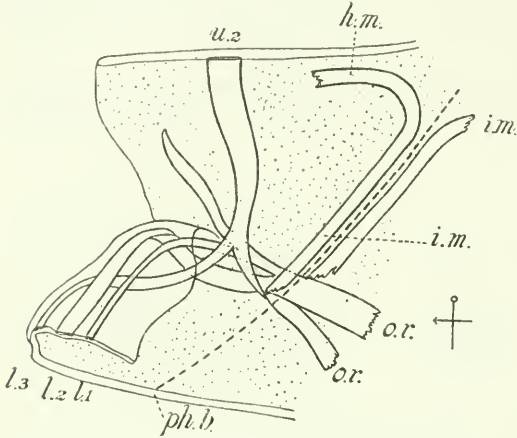


FIG. 120.—*PEGEA CONFEDERATA*, SOLITARY FORM, ORAL MUSCULATURE OF THE RIGHT SIDE VIEWED FROM WITHIN. MODIFIED FROM STRIEFF (1908). THE ORAL MUSCULATURE OF THE AGGREGATED ZOÏD IS SIMILAR.

being double along the middle portion in the embryo. In the adult the posterior division of the second ventral sphincter separates and lies independent behind the main trunk of the sphincter. There is a weakly developed group of longitudinal fibers at the mid-ventral line, running back from the posterior division of the second ventral sphincter. Across the dorsal surface of the

base of the atrial siphon there runs a well-developed muscle band (fig. 119, A). This connects on each side with a band which runs forward and toward the median line, reaching about halfway to

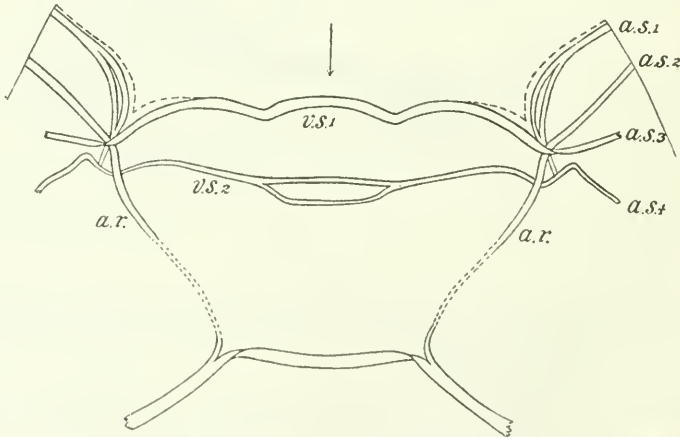


FIG. 121.—*PEGEA CONFEDERATA*, EMBRYO, ATRIAL MUSCULATURE IN VENTRAL VIEW. THE ATRIAL SIPHON WAS CUT OPEN ALONG THE DORSAL MID LINE AND THE FLAPS LAID OUT LATERALLY.  $\times 150$  DIAMETERS.

body muscle IV. These basal atrial muscles of the dorsal surface are not represented in figures 121 and 122. Across the ventral surface of the base of the siphon there is a well-developed muscle band (figs. 119, B, 121, 122), a small branch from which on each side



runs toward the atrial retractor. The end of this branch and the tip of the atrial retractor are connected by a blood lacuna.

The gut, as in the *Thalias* (fig. 104, p. 111), is a close loop, almost as compact as in the true *Salpae*. The course of the wide intestine can however be made out without dissection.

The eye shows the customary horseshoe form. Its rod-cells are irregularly polyhedral, with unevenly thickened walls, that is, they are degenerate. The neural glands are of the usual type. There are large-celled and small-celled pairs of outgrowths from the ganglion, just above and in front of the disks of the glands.

**PEGEA CONFEDERATA, aggregated form.**

The muscles of the aggregated *Pegea confederata* (fig. 123) show a closer resemblance to those of the solitary form than is the case in any other species of Salpidae. There are four body muscles, in two groups, on the dorsal surface, often hardly reaching to the sides of the body. The intermediate muscle and the oral musculature (fig. 124) are as in the solitary form, except for minor details which comparison of the figures will show.

The atrial musculature in my very numerous specimens is as shown in figure 125. There is a well-developed atrial retractor giving rise above to the broad third dorsal sphenster muscle, which,

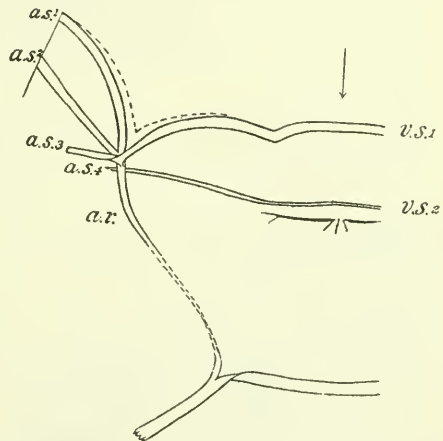
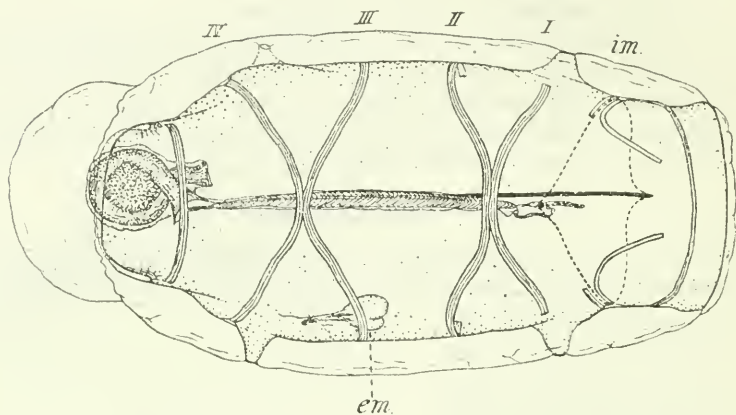


FIG. 122.—PEGEA CONFEDERATA, ADULT SOLITARY FORM  
ATRIAL MUSCULATURE OF THE LEFT HALF OF THE BODY,  
FROM A PREPARATION SIMILAR TO THAT FROM WHICH  
TEXT FIGURE 122 WAS DRAWN.  $\times 12$  DIAMETERS.

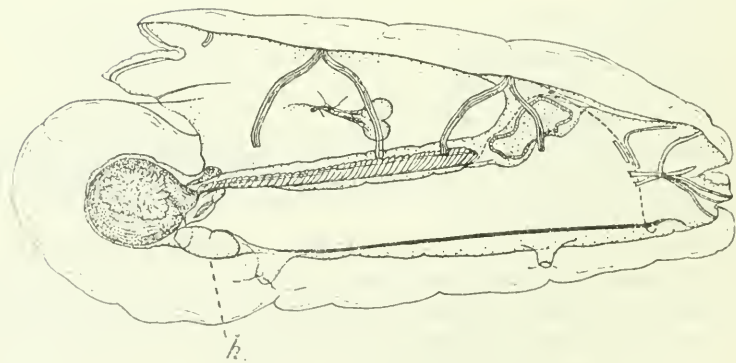
by the way, is interrupted on each side. There is a delicate admarginal dorsal sphenster, also interrupted on each side, and a second dorsal sphenster, which is very incomplete, being represented only by a short branch on each side. The first and second dorsal sphensters are united below into a broad band which lies external to the third dorsal sphenster and atrial retractor. The admarginal ventral sphenster arises by two roots, one from the posterior edge of the third dorsal sphenster, at its junction with the atrial retractor, the other from the ventral edge of the common portion of the first and second dorsal sphensters. These two roots soon unite to form the single admarginal ventral sphenster. A second ventral sphenster muscle (*v. s. 2*) corresponds to the basal atrial sphenster of other species, only its ventral half being present in *Pegea* (see fig. 3, pl. 1,

of *Cyclosalpa pinnata*). It is connected with the fourth body muscle, as shown in the figure.

In front of this basal sphincter lies another, broader muscle which is morphologically the posterior branch of the fourth body muscle,



A



B

FIG. 123.—*PEGAEA CONFEDERATA*, AGGREGATED ZOÏD: A, DORSAL VIEW; B, VIEW FROM RIGHT SIDE.  $\times 1\frac{1}{3}$  DIAMETERS. FROM SPECIMENS COLLECTED IN PHILIPPINE WATERS. (DRAWN BY HOYT S. HOPKINS.)

though it is, in *Pegaea*, actually distinct from the latter. It runs toward, but does not reach, the mid-ventral line of the base of the atrial siphon, its ventral end turning slightly forward toward the gut, suggesting the origin of the visceral muscle (*v*) in other forms (see fig. 3, pl. 1, *Cyclosalpa pinnata*, and fig. 13, pl. 4, *Cyclosalpa floridana*).

The gut in the aggregated zooids is similar to that in the solitary form. It is more or less covered by the fine brown branches of the intestinal gland. In the loop of the gut lies the well-developed greenish yellow testis. Surrounding the viscera in the post abdomen is a large blood sinus from which vessels or lacunae pass into the visceral mass, usually between the testis and the gut. The open ends of these vessels in surface view look like perforations such as would be made by a dissecting needle.

The neural gland shows the usual two disks, each with a convoluted duct. There are a pair of elongated, large-celled outgrowths from the ganglion, one on each side.

The eyes (figs. 126 and 127) are of interest. The large dorsal eye is in two parts, a posterior portion ( $e''$ ) with the pigment below the rod-cells, and an anterior portion ( $e'$ ) with its pigment above the rod-cells. The optic nerve runs between the two, giving fibers to each portion.

The rod-cells are irregular in shape with irregularly thickened walls; that is, they are degenerate.

Comparison with the eyes of any other subgenus except *Traustedia*, say with those of *Cyclosalpa pinnata* (figs. 9, p. 23, and 12, p. 25), shows that in *Pegea* there has been no reversal of the dorsal eye such as has occurred in other Salpidæ. In *Cyclosalpa pinnata* the optic nerve leaves the ganglion, passes above the basal portions of the eye ( $e'$ ), some of the fibers going on to the middle of the eye where they pass through the arch of the horseshoe to reach the rod-cells of the apical portion of the eye ( $e''$ ), some fibers being given off first to innervate the optic plug ( $e'''$ ) (see Metcalf, 1893, c. pl. 48). In *Pegea* the optic plug is wanting. The crucial point is that the optic nerve passes directly to the rod-cells of the anterior portion of the eye, not up and over this part of the eye. In *Cyclosalpa* the basal portion

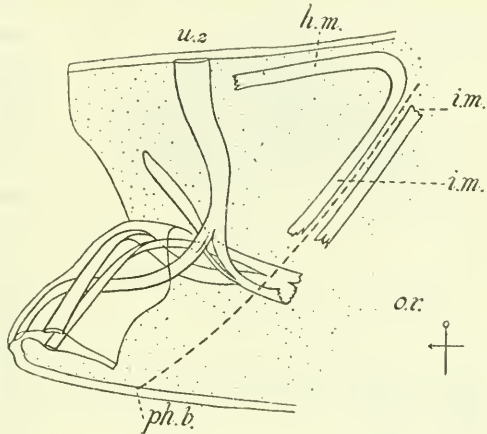


FIG. 124.—PEGEA CONFEDERATA, AGGREGATED FORM, ORAL MUSCULATURE OF THE RIGHT SIDE, SEEN FROM THE INSIDE. FROM SPECIMENS COLLECTED IN PHILIPPINE WATERS.

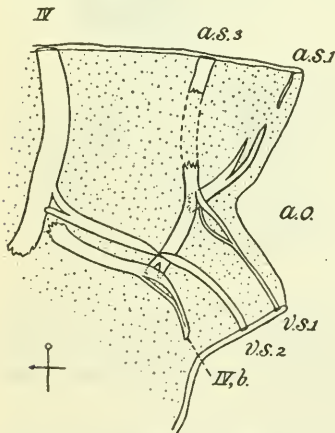


FIG. 125.—PEGEA CONFEDERATA, AGGREGATED FORM, ATRIAL MUSCULATURE OF THE RIGHT SIDE, VIEWED FROM WITHIN.

cells of the apical portion of the eye ( $e''$ ), some fibers being given off first to innervate the optic plug ( $e'''$ ) (see Metcalf, 1893, c. pl. 48). In *Pegea* the optic plug is wanting. The crucial point is that the optic nerve passes directly to the rod-cells of the anterior portion of the eye, not up and over this part of the eye. In *Cyclosalpa* the basal portion

of the eye (posterior limbs) has its pigment ventral and its rod-cells dorsal and the optic nerve passes up over the limbs of the eye to reach its dorsally lying rod-cells. In *Pegea* these relations are exactly

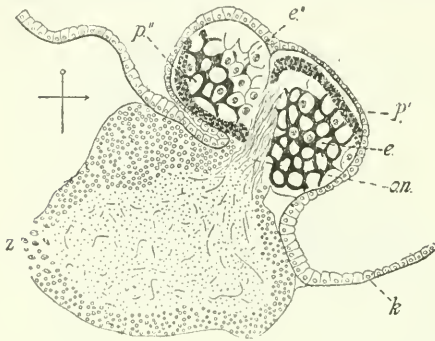


FIG. 126.—*PEGEA CONFEDERATA*, AGGREGATED FORM, SOMEWHAT OBLIQUE VERTICAL SECTION OF THE GANGLION AND DORSAL EYES.  $\times 170$  DIAMETERS. FROM METCALF (1893, c).

reversed in the corresponding portions of the eye ( $e'$ ). The pigment is dorsal and the nerve fibers reach the rod-cells directly from the ganglion. Of course, if no inversion has occurred in the eye of this species, that portion of the eye ( $e''$ ), which in *Cyclosalpa* lies anterior to the basal portion, must in *Pegea* lie behind the basal division. These are the relations observed in *Pegea*. Posterior to that portion of the eye which we have labelled

$e'$  lies a second division ( $e''$ ) whose rod-cells are dorsal and whose pigment is ventral. The optic nerve passes between the two portions of the eye to reach the rod-cells of the second portion ( $e''$ ). This lack of inversion of the dorsal eye in the aggregated zoïd of *Pegea* marks this subgenus off sharply from all the other subgenera except probably *Traustedtia*, which we will soon discuss.

In the ganglion of *Pegea confederata* are two accessory eyes (fig. 127), which I have before described as follows (Metcalf, 1893, c):

Two masses of similar, thick-walled cells are present in the ganglion, one on the right, the other on the left, a little above the midpoint, of the lateral faces of the ganglion. These cells exactly resemble the peculiar rod-cells of the large dorsal eye in size, shape, character of nuclei, thickness of cell walls, in manner

of staining and in their general appearance. The arrangement of chromatin in their nuclei and in the nuclei of the rod-cells of the dorsal eye is very different from that seen in the other cells of similar size found in the periphery of the ganglion. In the former, the nuclei contain many small chromatin granules, and no very large nucleolus. The other cells of the ganglion are of two sorts, the one sort small, with small nuclei. These are utterly different from the cells we are discussing. The other kind of ganglion cells is larger, about equal in size to the rod-cells of the eye. They have the same sized nuclei, but in these the chromatin is nearly all collected into a large nucleolus, giving a decidedly different appearance from the nuclei of the rod-cells. Besides this their

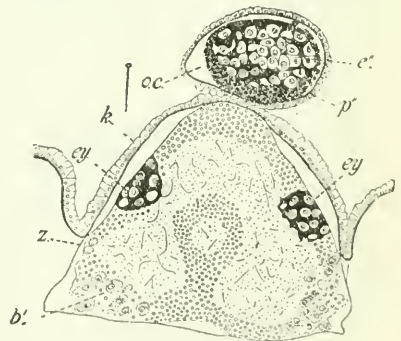


FIG. 127.—*PEGEA CONFEDERATA*, AGGREGATED FORM, CROSS SECTION OF DORSAL EYES AND OF GANGLION, SHOWING ALSO THE PAIR OF ACCESSORY EYES IN THE GANGLION.  $\times 170$  DIAMETERS. FROM METCALF (1893, c).

protoplasm reacts much more strongly with hæmatoxylin, giving a deep stain, while the protoplasm of the rod-cells stains very weakly. These characters, and especially the great thickness of their cell walls, distinguish the rod-cells of the eye, and of the two lateral masses in the ganglion, from any others of the nerve cells. We must, then, regard these two lateral masses of rod-like cells that are found in the ganglion as imperfect or degenerate eyes, bearing the same relation to the larger eye of this species as the smaller dorsal eyes of the chain *Cyclosalpa pinnata* do to the large, unpaired eye of that species. These structures just described form a connecting link between the smaller eyes found in *Cyclosalpa pinnata* [see fig. 9, p. 23] and *Salpa cylindrica* [see figs. 87, p. 98, and 89], which are undoubted optic organs, and other structures found in *Salpa hexagona* [see figs. 45, p. 70, and 47], *Salpa costata-tilseii* [see fig. 118, p. 126], and *Salpa cordiformis-zonaria* [see fig. 103, p. 108], which are so different from the typical eye that one would not readily recognize their true character.

#### OCCURRENCE OF *PEGEA CONFEDERATA*.

The aggregated form of *Pegea confederata* is one of the most abundant of the Salpa group. In the collections made by the United States Bureau of Fisheries steamer *Albatross* in the Philippine waters, it was the most abundant of all the Salpas, and in the United States National Museum collections made since 1875 it is very abundant. In all these collections there are, on the other hand, very few representatives of the solitary form of this species except numerous embryos from 5 mm. to 35 mm. long. There are five individuals, one 38 mm. long, two 40 mm. long, and two 42 mm. long, in which the cleoblast is absorbed. All the other specimens of the solitary form, even the few which are of large size (2-3½ cm. in length), show the cleoblast large and prominent and are evidently embryos recently set free. The larger individuals mentioned above may well be called adult, for all five of them show stolons, two of these showing the aggregated zooids 1½ mm. in length. These five solitary individuals were collected at the surface by the steamer *Albatross*, one in July at station 4037, Hawaiian Islands, three from Philippine waters in February and in September, and one from station 1098, off the coast of New England.

This scarcity of the solitary form of *Pegea confederata* is a general condition in collections of Salpidæ.

The *Challenger* Expedition (Herdman, 1888) found five aggregated zooids of the form *bicaudata* in one haul in Philippine waters, and no solitary specimens. They also found, in the south Pacific, the test of one large individual so degenerate that it was impossible to distinguish whether it belonged to a solitary or an aggregated individual.

The Plankton Expedition (Apstein, 1894, *b*) found, in the West Indies and the Gulf Stream, in the late summer and fall, 793 individuals of *Pegea confederata*, of which 437 were aggregated zooids and 356 were solitary forms including embryos. No indication is given in Apstein's report of the number of adult solitary individuals, if any such were present.

Apstein's report (1906, *a*) of the occurrence of *Pegea confederata* in the Südpolar collections may best be shown in tabular form:

Number of hauls.	Month.	Depth in meters.	Number of solitary form, including embryos.	Number of aggregated form.
6.....	August.....	0	2	1,022
1.....	do.....	0	( <sup>1</sup> )	( <sup>1</sup> )
1.....	September.	20	2	10
1.....	do.....	0	1	0
2.....	do.....	10	9	12
1.....	November.	0	0	6
1.....	April.....	(?)	3	6
1.....	May.....	20	1	24
2.....	do.....	0	1	4
Total.....			19+	1,084+

<sup>1</sup> Number and forms not stated.

Apstein reports from the Tiefsee Expedition (1906, *b*) the occurrence of *Pegea* as follows:

Station.	Depth in meters.	Number of solitary form, including embryos.	Number of aggregated form.
172.....	0	0	2
	0	0	1
173.....	0-2500	0	100
	30	0	( <sup>1</sup> )
182.....	0-2400	0	2
200.....	30	0	( <sup>1</sup> )
201.....	0	0	4
236.....	0-2000	0	( <sup>1</sup> )
237.....	0-2000	0	( <sup>1</sup> )
238.....	0-3000	0	1
250.....	0	2	0
258.....	0	4	0
261.....	0	1	107
262.....	0	0	35
263.....	(?)	5	( <sup>1</sup> )
	0-830	0	1
Total.....		12	256+5

<sup>1</sup> Number not stated.

Ihle reports (1910), from the *Siboga* Expedition, that the aggregated form of *Pegea confederata* was found at five stations, twice in great numbers, and that one specimen of the solitary form, 43 mm. long, was found at another station.

Ritter says, in his *Pelagic Tunicata*, of the San Diego region:

The aggregate generation is not rare in the area, but not a single zoöid of the solitary generation has thus far been observed. The species has been taken on the California coast from Monterey Bay southward, and in the months of January, February, March, May, June, July, and August.

Under date of March 10, Professor Ritter writes me:

Curiously enough, although the aggregated form of this species is one of the most abundant in this region, I have seen only two specimens of the solitary form.

In a later letter, referring to his paper on the Pelagic Tunicata of the San Diego region, he writes:

At the time I had seen but one specimen of the form. Since then the number has been increased to two by the handling of thousands of specimens.

It will be seen, therefore, how abundant the aggregated form of this species is, and how rare are full grown adults in collections thus far made. What may be the explanation of this condition? *Thalia democratica*, the most abundant and the most widely distributed of the Salpidae, shows conditions of vertical distribution that are suggestive in this connection. The solitary individuals lie at considerable depth during winter, spring, and early summer, coming to the surface with the aggregated zooids in the fall. It seems not unlikely that the solitary *Pegea confederata* lies generally in deep water the year round, a few wholly adult individuals coming to the surface only occasionally, the great majority probably never coming to the surface except more or less by accident. The Plankton Expedition reports 51 solitary individuals (including embryos) collected in four hauls of the vertical net. These may have been lying at any depth. In the Südpolar Expedition collections, three solitary individuals are reported from the surface, nine from a depth of 10 meters, three from a depth of 20 meters, and three from an unknown depth. How many of these were embryos was not stated. The Tiefsee Expedition reports seven of the solitary form from the surface and five from unknown depths. In this case again it is not stated whether the individuals were fully formed adults or embryos. More data as to the vertical distribution of *Pegea* are much to be desired. Such data as we have support the suggestion that the solitary individuals seldom reach the surface, but may be much more abundant at some depth.

**PEGEA CONFEDERATA, subspecies BICAUDATA (Quoy and Gaimard, 1826).**

*S. nephodea* LESSON, 1830.

*Salpa bicaudata* QUOY AND GAIMARD, 1826.

The solitary form of this salp has not been clearly distinguished. In fact, most recent authors deny to *bicaudata* any consideration even as a distinct variety. The aggregated zooids of the *Pegea* which Streiff studied and described as *P. confederata* belonged to the form *bicaudata*, and the presumption is that the solitary individuals were of the same subspecies to which the aggregated zooids belonged, but of course this is not certain. His specimens of the solitary form were very different from mine, in the character of their atrial musculature, and were somewhat different in the character of the oral

musculature. His specimens of the aggregated zoöids were clearly of the *bicaudata* character, as is shown by his "Fig. 25, Taf. 3" (my fig. 131, page 142), and they show considerable divergence from my specimens in oral and atrial muscles.

*PEGEA CONFEDERATA*, subspecies *BICAUDATA*, solitary form.

I have had two specimens which may be of this form. One is 5 mm. long. This was given me long ago by Prof. W. K. Brooks. Its source I do not know, nor do I know the authority for the label *bicaudata*. The other embryo is 25 mm. long, but shows the eleoblast still large. Both of these embryos agree in oral musculature with Streiff's figures (*bicaudata*?), but not in atrial musculature, in which they agree with *confederata*. Assuming that Streiff's specimens, though described as *P. confederata*, were really specimens of the subspecies *bicaudata*, I am copying his figures, giving merely enough description to call attention to the differences from *Pegea confederata*.

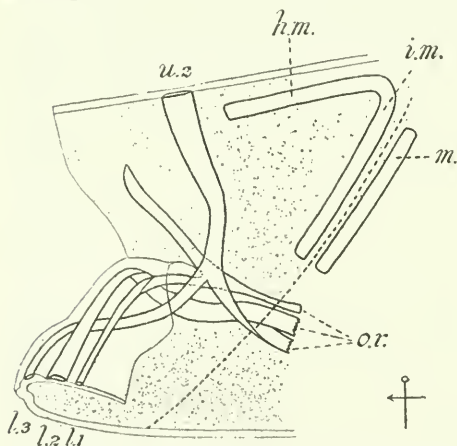


FIG. 128.—*PEGEA CONFEDERATA*, SUBSPECIES *BICAUDATA*, ORAL MUSCLES OF EITHER SOLITARY OR AGGREGATED FORM, SEEN FROM WITHIN. FROM STREIFF (1908).

Streiff describes the body muscles as agreeing exactly with those he describes and figures for the aggregated zoöids (fig. 130, p. 142). Their condition agrees also with what I find in the body muscles of *Pegea confederata*.

The intermediate muscle (fig. 128) is as in my specimens of *Pegea confederata* (fig. 120, p. 132), except that both its divisions are shorter ventrally, ending some distance above the oral retractor muscles.

Streiff says the oral musculature agrees exactly with that he describes for the aggregated zoöid (fig. 128). The divergence from my specimens of the solitary *Pegea confederata* is slight but is noticeable (fig. 120, p. 132). The oral retractor of *bicaudata* instead of being divided into two, a dorsal retractor and a ventral retractor, is divided into three horizontal bands, as in *Thalia* (fig. 105, p. 112). The oral sphincters connected with them are as in my specimens of *Pegea confederata*.

The atrial musculature described and figured by Streiff (fig. 129) is decidedly different from what I find in all of my specimens. I will not attempt even to indicate the homologies between the muscles in



the two forms, except in the case of the atrial retractor and the fourth body muscle, which I label in his figure, to aid in orienting it in comparison with my figure 122. The differences here would seem almost to deserve emphasis as of specific value. It seems probable that Streiff's specimens were *bicaudata* and that both of my possible *bicaudata* embryos are really *confederata*, though one bears the label *bicaudata* and the other is in a phial with two aggregated *bicaudata* and one aggregated *confederata*. The solitary form of *bicaudata* needs further study.

**PEGEA CONFEDERATA, subspecies BICAUDATA, aggregated form.**

I have had nine lots of alcoholic specimens of the aggregated zooids of this subspecies, collected by the United States Bureau of Fisheries, steamer *Albatross*, off the eastern coast of the United States between Cape Hatteras and Cape Cod, also three specimens from the Naples Zoological Station (U. S. National Museum, Cat. No. 6462). They show the appendages, and the eyes are of the *bicaudata* type. Their musculature also agrees with Streiff's description. The description here given is based chiefly on Streiff's results, confirmed, however, from my material.

The aggregated zooid (fig. 130) is very similar to that of the typical *Pegea confederata* but can be distinguished by several features: first, by the presence of a pair of long postero-lateral tubular appendages; second, by slight features in the character of the muscles of the oral region; third by more marked divergences from the species proper in its atrial musculature; and fourth, by the stalked character of its large dorsal eye.

The body muscles are as in the aggregated *Pegea confederata* proper. The intermediate muscle (fig. 128) is "as in the solitary" *bicaudata* and the aggregated *confederata* (fig. 124), differing from that of the solitary *confederata* (fig. 120) in being shorter, ending some distance above the oral retractor. The dorsal horizontal band with which it is continuous dorsally is as in the aggregated *confederata*, being longer than in the solitary *confederata*, reaching more

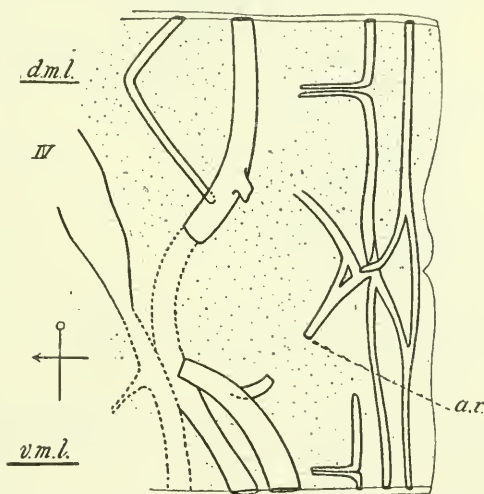


FIG. 129.—PEGEA CONFEDERATA, SUBSPECIES BICAUDATA, SOLITARY FORM, CLOACAL MUSCLES: *d. m. l.*, DORSAL MID LINE; *v. m. l.*, VENTRAL MID LINE. FROM STREIFF (1908).

nearly to the broad sphincter muscle of the upper lip. The oral muscles proper differ from those of the aggregated *confederata* only in the divisions of the oral retractor and in the position of the first sphincter of the ventral lip, which is just below the second sphincter in contact with the epithelium of its inner surface. The atrial muscles (fig. 131) differ more from those of the aggregated *confederata* (fig. 125). Each muscle in one is present in the other, but their conditions and connections are different.

The dorsal eye (fig. 132) differs from that of *confederata* (fig. 126) only in being raised on a stalk of considerable length, formed by the optic nerve, whose fibers in both *bicaudata* and *confederata* enter the eye between its two divisions.

The accessory eyes in the ganglion are similar in the species and in the subspecies.

With any strictly scientific definition of spe-

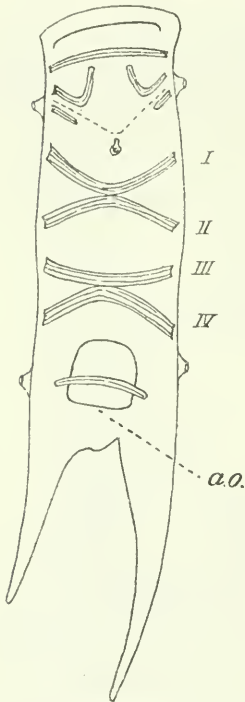


FIG. 130.—*PEGERA CONFEDERATA*, SUBSPECIES *BICAUDATA*. AGGREGATED ZOÏD, DORSAL VIEW. FROM STREIFF (1903).

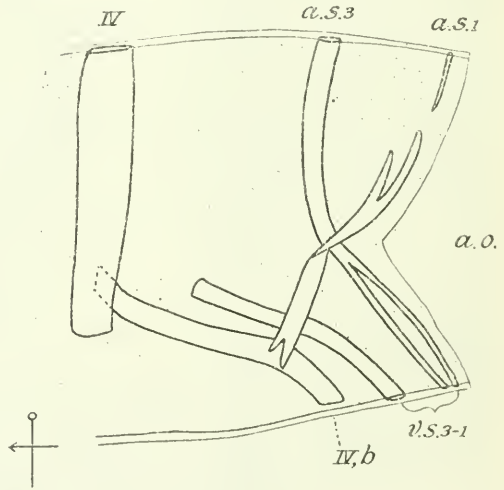


FIG. 131.—*PEGERA CONFEDERATA*, SUBSPECIES *BICAUDATA*, AGGREGATED FORM, ATRIAL MUSCULATURE VIEWED FROM THE LEFT SIDE. FROM STREIFF (1908).

cies, and species among the Salpidae are clearly demarcated and real, one would have to recognize *bicaudata* as a true species, but the resemblance to *confederata* is so close that it is probably preferable to rank *bicaudata* as a subspecies of *confederata*. This classification emphasizes the evident close relationship between the two forms.

*Pegera* is a highly modified subgenus. It is noteworthy that the solitary form, which in most species is in all respects more conservative than the aggregated zoïd, has, in this species, diverged from the ancient character almost as much as the aggregated zoïds.

This is seen in the muscles, which are equally reduced in the two phases of the life history. The gut also is in the same condition in the two.

In both forms of *Pegea*, as in *Thetys vagina* and *Iasis zonaria*, all the rod-cells in all the eyes of the aggregated zooids are irregular and degenerate.

TRAUSTEDTIA, new subgenus.

This subgenus includes the most highly modified members of the family. It has been studied by Quoy and Gaimard (1826-1834), Traustedt (1893), Apstein (1894, *b*, 1904, 1906, *b*) and Dober (1912). Ihle (1911) discusses briefly the nomenclature. In Apstein's several accounts two species seem to be confused. Our specimen aids little in clearing up this confusion. All the material previously known should be restudied. The Traustedtias are rare forms and new material is not likely often to be found or to be abundant when found. Assuming the general accuracy of the descriptions that have been published, I am tentatively recognizing two species—*multitentaculata* and *radiata*. We have had only a single specimen of the solitary form of the species *multitentaculata*. This will first be described. It is different enough from Apstein's specimen to be placed in a distinct subspecies. The species *multitentaculata* may be taken as the type of the subgenus since it was the first described and its aggregated form is known.

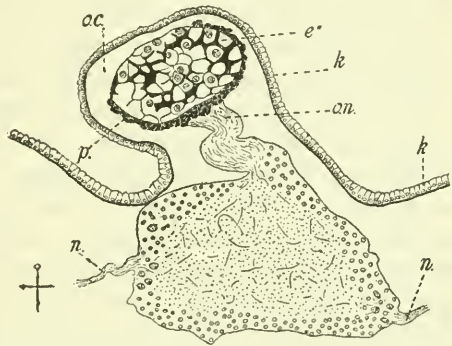


FIG. 132.—PEGEA CONFEDERATA, SUBSPECIES BICADATA, AGGREGATED FORM, OBLIQUE VERTICAL SECTION OF THE GANGLION, OPTIC NERVE AND ONE HALF OF THE DORSAL EYE. X 180 DIAMETERS. FROM METCALF (1893, c).

TRAUSTEDTIA MULTITENTACULATA, new subspecies BICRISTATA, solitary form.

Plate 14.

The United States National Museum collections contain a single example of the solitary form of this very rare salpa. Cat. No. 6430 (Type) U.S.N.M.; (solitary form), *Albatross* station D. 2585, off Marthas Vineyard; September 19, 1885; 542 fathoms; surface temperature, 73° F. It was collected at the surface of the ocean, along with very many solitary and aggregated zooids of *Thalia democratica*, among which we found it, in a large bottle containing several thousand *Thalias*. The specimen, 7.5 mm. long, is in perfect condition, being excellently preserved in picric acid and alcohol. We have

had no specimens of the aggregated zooids, nor is the stolon in our specimen sufficiently developed to tell anything of their character.

Of all described Salpas, the solitary form of the crested subspecies of *Traustedia multitentaculata* is by far the strangest and most bizarre in form. A complete verbal description is useless. The figures need, however, some description, if the peculiar crests and protuberances from the surface of the test are to be clearly understood.

The body is, in general, elongated ovoid,  $7\frac{1}{2}$  mm. long, the posterior end a little broader and considerably deeper than the anterior end. The test is much thickened below and considerably thickened on the sides of the body, but along the mid-dorsal line is a rather narrow area of thinner test. On each side of this thinner mid-dorsal strip the thickened test of the sides rises up into a huge longitudinal crest with a coarsely toothed dorsal margin. These structures may be called the dorso-lateral crests. The anterior edges of the crests are continuous below with the anterior edges of the thickened lateral areas of test. Similarly the posterior edges of the dorso-lateral crests are continuous below with the posterior and dorsal edges of the lateral and ventral area of thickened test. It is as if an envelope of greatly thickened test were laid under the ventral surface of the body and bent up around the sides, its upper edges not meeting on the dorsal surface but being elevated into two independent dorso-lateral crests, the anterior end of the body and the atrial siphon, covered only with thin test, protruding in front and postero-dorsally from the thickened envelope.

The test over the lower lip is somewhat thickened and is coarsely and irregularly papillate, the individual papillae resembling the irregular teeth upon the edges of the dorso-lateral crests. The mid-dorsal line of the upper lip bears a row of similar irregular papillae; so also do the mid-dorsal and the mid-ventral lines of the atrial siphon. Over the sides of the body, especially along the mid-lateral region, are similar papillae.

The great ventral thickening of the test is even more strongly emphasized posteriorly, where it forms a great pouch containing the viscera. This postero-ventral thickening is broad from side to side, its postero-dorsal edge showing two strongly toothed ridges running from side to side. The lower is the smaller of the two; the upper forms a sort of transverse crest behind and below the atrial siphon. Observation of the figures should, with this description, make the form clear.

As noticeable as the crests and ridges are the 13 "tentacles." These are of essentially the same character as the postero-lateral tubular protuberances in *Thalía* (fig. 104, p. 111) and *Thetys* (fig. 114, p. 122). Their positions are shown in the figures: a ventro-lateral

pair in front (1); two lateral pairs, one below the anterior group of body muscles (2), and another below the anterior one of the posterior group of muscles (3); a pair in the posterior edges of the dorso-lateral crests (4); a pair at the sides of the atrial siphon (5); a posterior pair near the mid line, ventral to the horizontal crest below the atrial siphon (6); and a single median posterior one (7) which does not actually protrude beyond the contour of the crests but lies in the lesser posterior ridge at the posterior end of the body. Each of these "tentacles" contains a tube of mantle epithelium, which at its tip is slightly enlarged.

The muscles are confined to the dorsal half of the body. They are but slightly developed. The intermediate muscle functions in connection with the oral muscles, as in *Thetys* and *Pegea*, and will be described in connection with these muscles. There are four, or perhaps five, muscles which should be accounted body muscles. The anterior three of these are united across the dorsal line into a single band, the group much resembling the anterior group in *Thakia democratica* (fig. 104, p. 111), although the latter merely touch without fusing. Body muscle IV is longer and stretches farther down on the side of the body, bending forward at its lower end. Body muscle IV is branched, its narrower posterior branch running on each side to the base of the atrial siphon where it again branches into two, the upper of which gives off a minute branch which runs up to connect with the delicate atrial sphincter, while its larger portion passes below the atrial siphon to fuse with its fellow from the other side. The more ventral of the two branches formed by the second dichotomy of muscle IV turns downward and forward toward the visceral mass, which however it does not reach.

This arrangement of the branches of the fourth body muscle reminds one of the conditions in the aggregated zooids of different species of *Cyclosalpa*, in which a posterior branch of the last body muscle passes beneath the atrial siphon, giving rise there to what we have described as the "visceral muscle," which in some cases is double (*Cyclosalpa affinis*, *C. floridana*) and in other cases is single (*C. bakeri*, *C. pinnata*, *C. virgula*). Even in *C. affinis* and *C. floridana* the visceral muscle is double only at its base, at its distal end the right and left halves being fused into one. But observe that the above comparison is between the solitary form in *Traustedia* and the aggregated zooids in the *Cyclosalpas*. In the very highly modified subgenus *Traustedia*, the solitary form shows a feature which, in the more archaic *Cyclosalpas*, appears only in the aggregated zooids. Even the conservative member of the life cycle, the solitary form, has in this divergent subgenus become much modified. Another modification of the solitary form is seen in *Traustedia* and in *Pegea* in the reduction of the number of the body muscles.

At the base of the atrial siphon is another muscle nearly as well developed as body muscle IV and seeming to belong to the body-muscle series, but its position at the base of the siphon, and the fact that body muscle IV in its branching resembles the last body muscle of the aggregated zoöids of numerous species, suggest that the muscle in question may better be interpreted as a basal atrial muscle. Compare the conditions in the *Cyclosalpas*, both solitary and aggregated forms. Without insisting upon its homologies I label it in the figures as body muscle V.<sup>1</sup> This muscle is branched, a small band arising from its upper portion, on each side, and running back to unite with the delicate sphincter of the atrial siphon near its point of union with the very delicate uppermost branch of the posterior division of body muscle IV.

Between body muscles IV and V there is a minute oblique muscle on each side of the dorsal mid line not attached at either end to any other muscle.

There are two atrial sphincter muscles, an admarginal one and a very delicate submarginal one, which, on each side, is fused for a very short distance with the admarginal muscle. There is a short portion of a third sphincter across the ventral surface of the siphon below, anterior to, the delicate sphincter. The axial tube of the lateral "tentacle" (5) of the atrial siphon arises from the mantle exactly at the level of the admarginal atrial sphincter muscle (fig. 35), but there is no continuation of the muscle into the "tentacle" as the figures seem to indicate.

The oral musculature, like that in *Pegea*, is weakly developed. The intermediate muscle is present as a short band running obliquely internal to the two oral retractors. The two oral retractor muscles are horizontal or nearly so. The more ventral divides into two short branches which form abortive sphincter muscles, one at the base of the upper lip and the other at the base of the lower lip. The dorsal oral retractor muscle divides into three branches the upper of which forms a similar abortive first sphincter of the upper lip, while the more ventral two form the narrower and the wider complete sphincters of the incurved lower lip. There are no dorsal horizontal bands between the oral and body muscles.

The gut is in the form of a vertically placed elongated loop, much more compact than in *Cyclosalpa affinis* (pl. 3, fig. 10), less compact than in *Thalía* (fig. 104, p. 111).

The stolon is curved around the base of the intestinal loop, making about two-thirds of a circle, the two ends, however, being at widely different levels, thus forming a partial spiral.

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<sup>1</sup> The distinction between posterior body muscles and basal atrial muscles is doubtless not a fundamental one. The conditions, especially in *Traustedia* and *Pegea*, seem to indicate that they are all serially homologous. The same muscle which in one species is developed as a body muscle may, in another species, serve as a basal atrial muscle.

The eye shows the usual horseshoe shape. Its histology has not been studied, since we were unwilling to sacrifice our sole specimen of the subspecies. For the same reason the neural glands and the outgrowths from the ganglion have not been observed.

**TRANSTEDTIA MULTITENTACULATA (Quoy and Gaimard, 1826-1834).**

*Salpa multitentaculata* QUOY AND GAIMARD, 1826-1834.

*S. verrucosa* APSTEIN, 1894, *b*.

*S. multitentaculata* IHLE, 1911, in part.

SOLITARY FORM.

In his report upon the Thaliacea of the Plankton Expedition, Apstein (1894, *b*) describes a single specimen (fig. 133) which he took to be an aggregated zoöid, but which proves to be a solitary salpa.

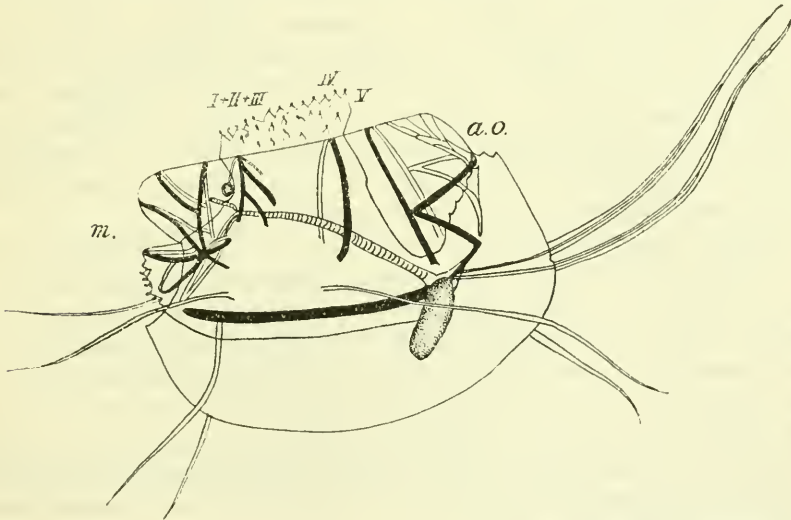


FIG. 133.—TRANSTEDTIA MULTITENTACULATA, SOLITARY FORM, VIEWED FROM THE LEFT SIDE.  $\times$  DIAMETERS. FROM APSTEIN (1894, *b*).

It differs markedly from our specimen but still seems to belong to the same species. He describes a single dorsal crest, but his only specimen was strongly laterally compressed, so the two crests, if present, may have appeared as one. The test was greatly thickened ventrally and his figure shows lines connecting the anterior and posterior edges of the crest with the thickened area of ventral test, just as we have shown them for our specimen. The form of the body is evidently quite similar in Apstein's specimen and ours. Apstein describes and figures four pairs of "tentacles" corresponding to the larger four pairs in our specimen. He does not describe the other five similar but less developed structures which we show in our form. He may have overlooked them, for they are not prominent.

The mass of the gut is of the same form and has a similar position in the two specimens.

One would without hesitation assign both specimens to the same species were it not for the different condition of the muscles. Body muscles I, II, and III (our notation) are very similar in the two specimens. Body muscle IV is unbranched in Apstein's specimen and branched in ours. The muscle next posterior is very different in the two specimens. The discrepancy would, however, be removed if we were to add to Apstein's figure a posterior branch of body muscle IV extending across the next posterior muscle and itself giving rise to the two oblique bands which Apstein figures between the gut and the atrial siphon. This would leave the fifth muscle unbranched below, as in our specimen, and it should then possibly be considered the basal muscle of the atrial siphon, as comparison with the *Cyclosalpas* suggests. Comparison of Dober's (1912) and Apstein's (1906, *a*) figures of *Traustedia radiata* (figs. 138 and 139) shows that the posterior branches of body muscle IV may be interrupted in some specimens and complete in others. In similar cases in other species, the potential position of an omitted or interrupted muscle is indicated by the presence of a muscle blood vessel along the course the muscle would take if present.

There is such disagreement in the oral and intermediate muscles as Apstein and we describe them as to necessitate treating his specimen and ours as representing distinct subspecies. The intermediate muscle (Apstein's first body muscle) is described and figured as complete across the dorsal mid line, being continuous with its fellow of the other side. In our specimens it extends but a little way above the angle of the mouth. Apstein says there is one sphincter muscle in each lip, but he figures two in each, all four complete from the angle of the mouth on one side, across the mid line, to the angle of the mouth on the other side.

In our specimens the two sphincters of the ventral lip are complete, but the two in the dorsal lip are very rudimentary, extending but a very short distance above the angle of the mouth. The distinctive features of Apstein's form, as compared with our specimen, are, first, the smaller number and greater length of the "tentacles," and the complete and conspicuous muscles crossing the dorsal surface of the anterior end of the body, that is, the first and second sphincters of the upper lip and the intermediate muscle, very different from the vestigial corresponding muscles in our specimen. These two subspecies, though apparently distinct, are very similar, as much alike as are the solitary forms of *Salpa maxima* and *S. fusiformis*, not so closely similar as *S. fusiformis* and its form *aspera*, which differ only in the character of the test.



Quoy and Gaimard's *Salpa multitentaculata* (fig. 134) seems to be the same as Apstein's *S. verrucosa*, though their figure and description are not sufficiently complete to make one entirely certain. Yet the general form of the body and the position of the four pairs of "tentacles" seem to indicate probable identity. Quoy and Gaimard's description and figure are given for comparison. Quoy and Gaimard's form seems clearly a *Transtedtia*, and of the probably two species now known it must belong to *multitentaculata*. It is either this species or one not as yet rediscovered. The elongation of the posterior "tentacles" in Quoy and Gaimard's and Apstein's specimens is greater than in our form. I therefore assign Apstein's specimen to the main species and our specimen to the subspecies.

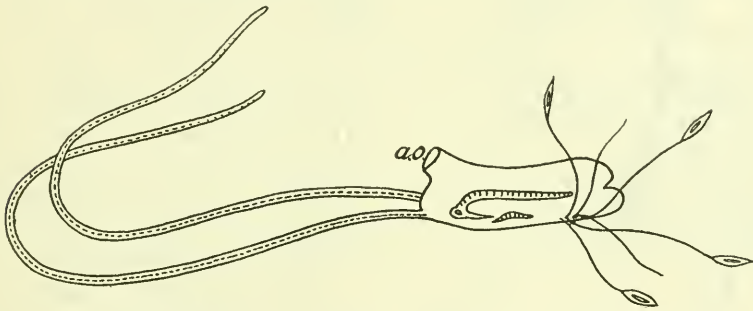


FIG. 134.—TRANSTEDTIA MULTITENTACULATA. QUOY AND GAIMARD (1826-1834).

Quoy and Gaimard's description is as follows:

15. BIPHORE MULTITENTACULÉ. SALPA MULTITENTACULATA, NOB.

Planche 89, figure 19.

Salpa, parva, cylindrica, postice longissime bicaudata, antice capillata; appendicibus gracilibus ápice tuberculosus; oribus terminalibus.

Cette espèce est une des plus singulières que nous ayons rencontrées, par les filaments qu'elle porte en avant. Elle est cylindrique, obtuse aux deux extrémités. L'antérieure, arrondie, a son ouverture terminale entre deux lèvres épaisses; la postérieure, un peu gibbeuse, a également son ouverture presque à la pointe portée sur un petit prolongement. De la gibbosité partent deux très-longs filaments déliés, marqués d'une ligne rouge dans toute leur étendue. Au-dessus de la partie antérieure sont fixes six appendices filamenteux, renflés, pointus à leur extrémité, qui est rouge. Ils sont presque aussi longs que le corps. Le nucléus est orangé; le reste de l'animal, blanc. Au-dessus des organes digestifs on aperçoit un petit corps contourné, qui est sans doute une chaîne d'œufs.

*Dimensions.*

	Pouces.
Longueur du corps environ.....	1
Longueur des filaments postérieurs.....	3 ou 4
Habite les mers de la Nouvelle-Irlande.	

TRAUSTEDTIA MULTITENTACULATA, aggregated form.

Traustedt (1893) first described the aggregated form of this species from specimens in the collections of the Plankton Expedition, from the

Atlantic Ocean off Rio Janeiro. He does not indicate the number of specimens he had. The individuals were 20 mm. long.

Apstein (1894, *b* and 1904) describes well-developed zooids, 1.5 mm. and 3 mm. long, still attached to the stolon of the parent, so that the connection between the solitary and aggregated forms is established. He reports (1906, *b*) numerous specimens from the

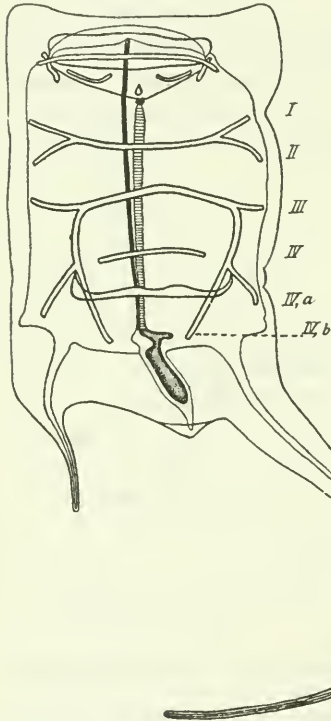


FIG. 135.—TRANSTEDTIA MULTITENTACULATA, AGGREGATED ZOÏD, DORSAL VIEW.  $\times 4\frac{3}{4}$  DIAMETERS. FROM DOBER (1912).

collections of the Tiefsee Expedition, agreeing exactly with those from the Plankton Expedition. Dober (1912) figures an individual from the Tiefsee collections which is clearly the same as Traustedt's original form. Traustedt and Dober both figure the ganglion and eye as seen in surface view. Our knowledge of the aggregated zooid of the species *multitentaculata* is thus considerable, though not complete as to the oral and atrial musculature.

Dober's figure is here copied (fig. 135) and also Apstein's (1904) side view of a much younger individual (fig. 136). The index letters and figures are mine and show the homologies with other species. I would call attention to the fact that there are but two well developed body muscles. The first of these is evidently

double. The second is branched in the same way as is body muscle IV in the solitary forms of this species and *Traustedtia multitentaculata*, form *bicristata*. We seem, therefore, to have four body muscles in the solitary form and three in the aggregated zooids. The next posterior muscle corresponds to the one which in the solitary individuals we interpreted as either a fifth body muscle or a basal atrial sphincter.

Neither Dober's nor Apstein's figure shows other atrial muscles clearly enough for us to discuss them.

Apstein shows a well developed intermediate muscle complete across the dorsal surface. Dober shows what appears to be a double intermediate muscle, the posterior portion reduced to a vestige at the angle of the mouth, the anterior portion lying more dorsal and

bending forward at its upper end to form what appears to be the homolog of the dorsal horizontal band of other species.

Apstein shows an oral retractor continued in front to form a single complete sphincter in each lip. Dober shows an oral retractor continuous with a complete sphincter in one lip (dorsal or ventral?), but no sphincter in the other lip.

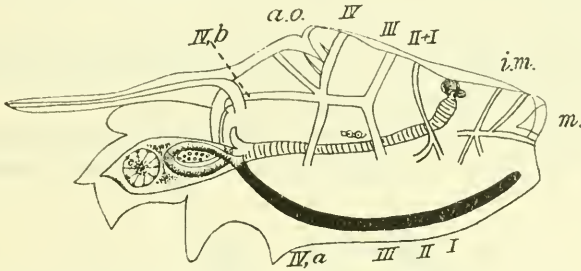


FIG. 136.—TRANSTEDTIA MULTITENTACULATA, AGGREGATED ZOÏD, VIEWED FROM THE RIGHT SIDE.  $\times 2$  DIAMETERS. FROM APSTEIN (1904).

Two embryos are said by Apstein to be borne by the aggregated zooids in all cases; Traustedt observed but one, this very young.

Traustedt describes the ganglion and eye, and Dober gives a still clearer figure which is here copied (fig. 137). The eye apparently is very similar to that of *Pegea*, the homologies of whose parts I have already discussed.

Beneath the ganglion are a pair of lateral disks forming the sub-neural gland. Dober does not describe their ducts, but these are doubtless present. Dober refers to the disks as auditory organs. Of course there is no ground for attributing any such function to them (see Metcalf, 1893, c).

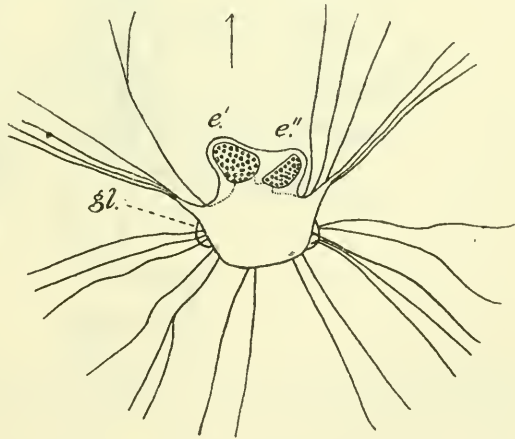


FIG. 137.—TRANSTEDTIA MULTITENTACULATA, AGGREGATED FORM, DORSAL VIEW OF THE GANGLION AND EYE. THE DISKS OF THE SUBNEURAL GLAND ALSO SHOW IN PART. FROM DOBER (1912).

All the aggregated Traustedtias hitherto described seem to belong to the species *multitentaculata*. Quite possibly some belong to its subspecies *bicristata*. The collections need to be restudied to determine this point, which is suggested by the discrepancy between the several descriptions. If both subspecies are represented, those with more rudimentary oral muscles probably should be assigned

to the subspecies *bicristata*, for the solitary form of this species has its oral muscles much less developed than do the solitary individuals of the species type which Apstein describes.

**TRAUSTEDTIA RADIATA, new name, solitary form.**

*Salpa henseni* APSTEIN, 1906, *b*. (This seems to be a homonym.)

*S. multitentaculata* IHLE, 1911 (part).

Apstein (1906, *a* and *b*) describes and figures this form and Dober (1912) gives a figure of it. As Dober's and Apstein's figures do not agree, both are included here (figs. 138 and 139).

Apstein (1906, *a*) says the form of the body is a short oval. It is rather flat and has a very thick test. No mention is made of any

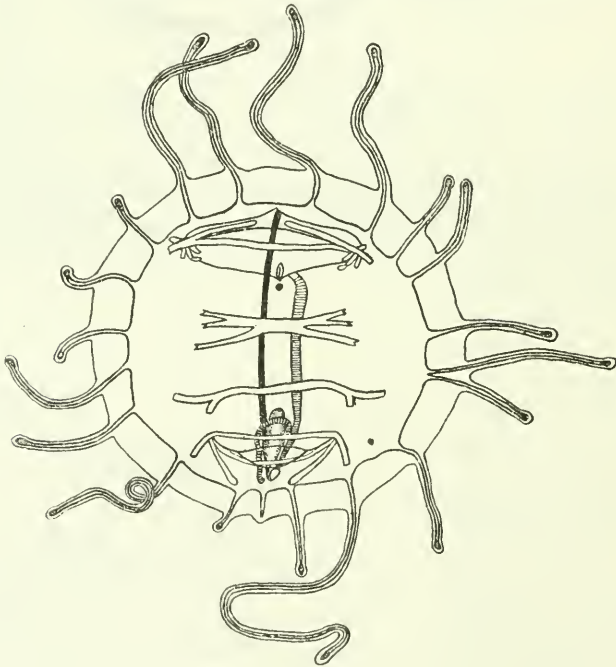


FIG. 138.—*TRANSTEDTIA RADIATA*, SOLITARY FORM, DORSAL VIEW.  $\times 3\frac{1}{2}$  DIAMETERS. FROM DOBER (1912).

crests or ridges such as Apstein (1894, *b*) had already figured for *Traustedtia multitentaculata*, in his Plankton Expedition report.

Body muscles I, II, and III are either fused dorsally (fig. 136, Dober) or approximated (fig. 139, Apstein). Body muscle IV, according to Apstein, is branched as in the subspecies *bicristata*. Dober shows the posterior branch interrupted. Probably there was in his specimens a continuance of the muscle blood vessel bridging the space between the tip of this short branch and the point a little farther back where three bands meet.

The posterior branch of body muscle IV is crossed by a band which may be a fifth body muscle, or perhaps a basal atrial sphincter lying across the dorsal side of the base of the atrial siphon. Just beyond this band, body muscle IV, *b* divides into two branches as in the form *cristata*, one branch passing behind the visceral mass, the other running below the atrial siphon, where it meets its fellow from the opposite side, thus forming a basal atrial sphincter on the lower side of the siphon. The other atrial muscles are not well shown by Apstein, and I am not quite sure of them in Dober's figure.

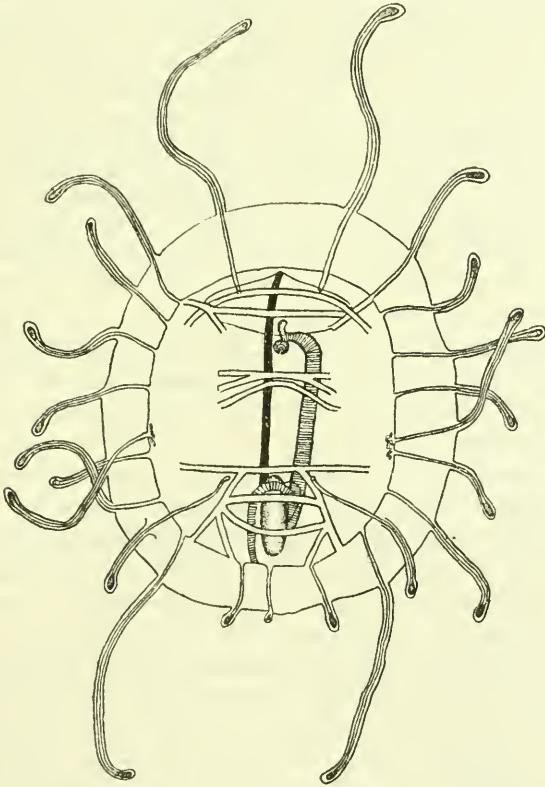


FIG. 139.—*TRANSTIDTIA RADIATA*, SOLITARY FORM, DORSAL VIEW.  $\times 3\frac{1}{2}$  DIAMETERS. FROM APSTEIN (1906, b).

The intermediate and oral muscles are quite differently figured by Apstein and Dober. The former shows what seems to be a very short intermediate muscle, a short oral retractor, and one complete sphincter in each lip. Dober's figure is not clear. It shows more muscles than Apstein depicts. Among them are a short intermediate muscle, an oral retractor, a delicate admarginal sphincter, which is complete, and a broader incomplete second sphincter, both in the lower lip, a broad complete first sphincter and an aborted very short second sphincter in the upper lip. This musculature is considerably

different from that of either *Traustedtia multitentaculata* or its subspecies *bicristata*.

The gut differs from that of the other species of *Traustedtia* in lying in a more horizontal position. The stolon has a position similar to that in the form *bicristata*. The eye (Dober) is of the usual horse-shoe form.

The characteristic thing in this species is the presence of 20 (Dober) to 23 (Apstein) "tentacles," which Apstein describes as follows:

Von der Leibeshöhle durchdringen den Mantel [test] eine Reihe Kanäle, von denen ich 23 zählte. Diese Kanäle setzen sich röhrenartig über die äussere Mantelfläche fort und werden vom Mantel mit dicken Wänden versehen. Gegen das Ende schwellen die Fortsätze an, auch der Hohlraum erweitert sich, ist aber geschlossen. Während die Salpe farblos war, sah ich in und an diesen Fortsätzen im Leben ein orange bis braunes und gelbes Pigment. Da, wo die Fortsätze die äussere Mantelfläche verlassen, wird der Hohlraum von einem orange Pigment umgeben. Oft fanden sich in der Mitte des Fortsatzes Querfalten und dann ebenfalls das orange Pigment in der dicken Wand des Fortsatzes. Der erweiterte Hohlraum am Ende war orange mit braun gefärbt, während die Wand in zartem Gelb schimmerte. Der Hohlraum schien meist leer zu sein, stellenweise fand sich eine feinkörnige Masse, deren Natur nicht erkennbar war. Am Vorder- und Hinterende fanden sich je 2 längere Fortsätze.

The shape of the body, the large number of "tentacles," the absence of crests and toothed ridges, the arrangement of the muscles,<sup>1</sup> and the position of the visceral mass, demarcate the solitary form of this species from that of either *Traustedtia multitentaculata* or its subspecies *bicristata*.

Apstein classed the radiate specimens in the collections of the German Deep-Sea Expedition in the same species, "*henseni*," as those he studied in the collections of the Plankton Expedition, making no mention of the absence of crests and toothed ridges in the "Deep-sea" specimens, and ignoring the presence of a much greater number of "tentacles." His and Dober's drawings of the radiate forms can not represent *multitentaculata*, for the shape of the body and the shape and sculpturing of the test are very different in the latter species. It seems necessary to recognize these radiate individuals as a distinct species, which for obvious reasons I name *radiata*. This disposition of the matter must be regarded as tentative, pending restudy of the "Deep-sea" specimens.

#### THE TRAUSTEDITAS IN GENERAL.

Let me again suggest that reexamination of the solitary forms of *Traustedtia* in the collections of the Tiefsee and Plankton Expeditions may show the two tentative subspecies I have recognized, to

<sup>1</sup> Apstein (1906, b) in his discussion of the Tiefsee-Expedition specimens says "Die Muskulatur stimmt mit der früher beschriebenen überein." By this he must refer to his description of the single specimen in the collections of the Plankton Expedition, which he at first named *Salpa verrucosa*, and which I have assigned, from his description to the species *multitentaculata*. The musculature in the two forms, according to Apstein's figures, is really considerably different. Dober and Apstein both worked upon specimens collected by the Tiefsee-Expedition.

be one. In that case Quoy and Gaimard's name *multitentaculata* will be retained for this species. But, as the published descriptions now stand, we must recognize two subspecies. It seems hardly possible that such restudy will show the form I have named *radiata* to be the same as *multitentaculata*, as Apstein thought, for both Apstein's and Dober's figures show a character quite divergent from the latter species.

The arrangement of its muscles, and especially the character of its eyes, show that *Traustedtia* is more nearly related to *Pegea* than to any other subgenus.

The feature of the *Traustedti*as, which at first glance is most noticeable, is the presence of numerous tentacle-like processes in the solitary individuals. These all correspond in structure to the hollow protuberances found in its aggregated zoöids and in other species at the postero-lateral angles of the body. The *Thalias* show similar but less developed tubes at other points on the body. Some aggregated zoöids of *Thalia democratica*, especially those collected by the *Albatross* in Philippine waters, have numerous well developed tentacle-like processes, which very closely resemble those of *Traustedtia* (fig. 107, *C*, p. 114). In this connection we may remember that among the Ascidians—as among the Botryllidae—there are numerous tubular protuberances of the mantle into the test. The structures in the Salpidae seem essentially of the same character, though far more definite. The postero-lateral protuberances are symmetrically developed in the solitary forms of those species which bear them. In the aggregated zoöids, on the other hand, they are unequally developed on the two sides of the body, as in *Pegea confederata bicaudata* and *Traustedtia multitentaculata*. It is quite possible that the single postero-lateral protuberance seen in the aggregated zoöids of the several species of the subgenus *Salpa* may be homologous with one of the pair present in *Pegea* or *Traustedtia*. It is doubtful how far this comparison may be carried, whether it may include the divisions of the postabdomen in the *Cyclosalpe* and the asymmetrical posterior processes in the other subgenera. The strict homology of these structures throughout the aggregated Salpidae is doubtful, but they are all in the same region of the body, are all protrusions of the test, which, so far as described, contain an inner tube of mantle tissue, the lumen of the tube being continuous with the spaces of the mantle.

#### THE SALPIDAE IN GENERAL.

##### STRUCTURE AND RELATIONSHIPS WITHIN THE FAMILY.

Such a review of the species of Salpidae, as we have made, brings out the falseness of the distinction usually used in taxonomic keys to separate the Salpidae from the Doliolidae. The muscle bands in

the Doliolidae form complete rings, while in the Salpidae they are said to form incomplete rings: the animals of the former group being called *Cyclomyaria* (Gegenbaur), those of the latter group *Hemimyaria* (Herdman). Of course in many species of Salpidae, as Brooks (1893) long ago clearly showed, the muscle bands are complete. I suggest as preferable terms *Multistigmosa* for the Doliolidae, in which the pharyngo-cloacal partition contains numerous stigmata, and *Astigmosa* for the Salpidae, in which this partition has been reduced to a single axial rod, no stigmata being present.

Probably ancestrally the form and musculature of *Salpa* resembled somewhat that of *Doliolum* which, in the character of the stigmata and the relations in the nervous system, is more primitive than *Salpa*. Probably the primitive muscle schema consisted of a series of strong hoop-like bands around the body (the body muscles), and a series of more delicate sphincters at both the oral and atrial apertures. The body muscles in some of the Salpidae are still much in this condition, especially in the solitary individuals.

In the more aberrant subgenera of the Salpidae we observe a reduction in the musculature. In most species the aggregated zooids show fewer body muscles than do the solitary zooids of the corresponding species. Four is the usual number of the body muscles in the aggregated zooids of the Cyclosalpas (three in *C. floridana*), five the number in the aggregated zooids of all other species except *Ritteria hexagona* (six), the *Thalias* (four), *Pegea* (four), and *Traustedia* (three or four, according to interpretation). The intermediate muscle is somewhat reduced in the *Thalias*, and is greatly reduced in *Thetys*, *Pegea*, and *Traustedia*. In the solitary forms, reduction of the muscles is less usual, but in its extreme, in *Pegea*, is very marked. In the Cyclosalpas the solitary individuals show seven body muscles. In the Ritterias the number is large, being variable in at least some of the species. In the Apsteinias and the Salpas the number is eight or more. In *Iasis* the number is five. *Thetys* shows a very large number, confined however to the dorsal half of the body. *Thalia* has five, while *Traustedia* and *Pegea* have but four developed as body muscles and these very short, especially in *Pegea*.

The atrial musculature in the Cyclosalpas conforms to the supposed ancestral schema and there is great departure from this schema among the Salpidae only in the subgenera which have modified the atrial siphon into a strongly two-lipped structure in which the upper lip is developed as an overhanging valve, that is, in *Iasis* and *Thalia*. The atrial retractor muscle is not readily recognized in some species with cylindrical atrial siphon (*Cyclosalpa pinnata*, pl. I, fig. 1, a. r.) though in others it is well developed (*C. virgula*, pl. 11, fig. 26). In more modified species the atrial



siphon becomes two-lipped and in all these the atrial retractor is well developed.

The oral siphon in all forms is decidedly two-lipped and the oral musculature does not in any species show a simple series of regular circular sphincters.

Apparently the oral muscles, intermediate muscles, body muscles, and atrial muscles, should be regarded as serially homologous with one another, as *Doliolum* suggests. The intermediate muscle is developed in some species, in general the more primitive, to function with the body muscles. In the more modified species, especially those in which the musculature is reduced, the intermediate muscle functions with the oral muscles. Similarly between the body muscles and the definitive atrial sphincter muscles are one or often two bands which are intermediate in character between body muscles and atrial sphincters. A sharp line of demarcation between the two series of muscles does not generally exist.

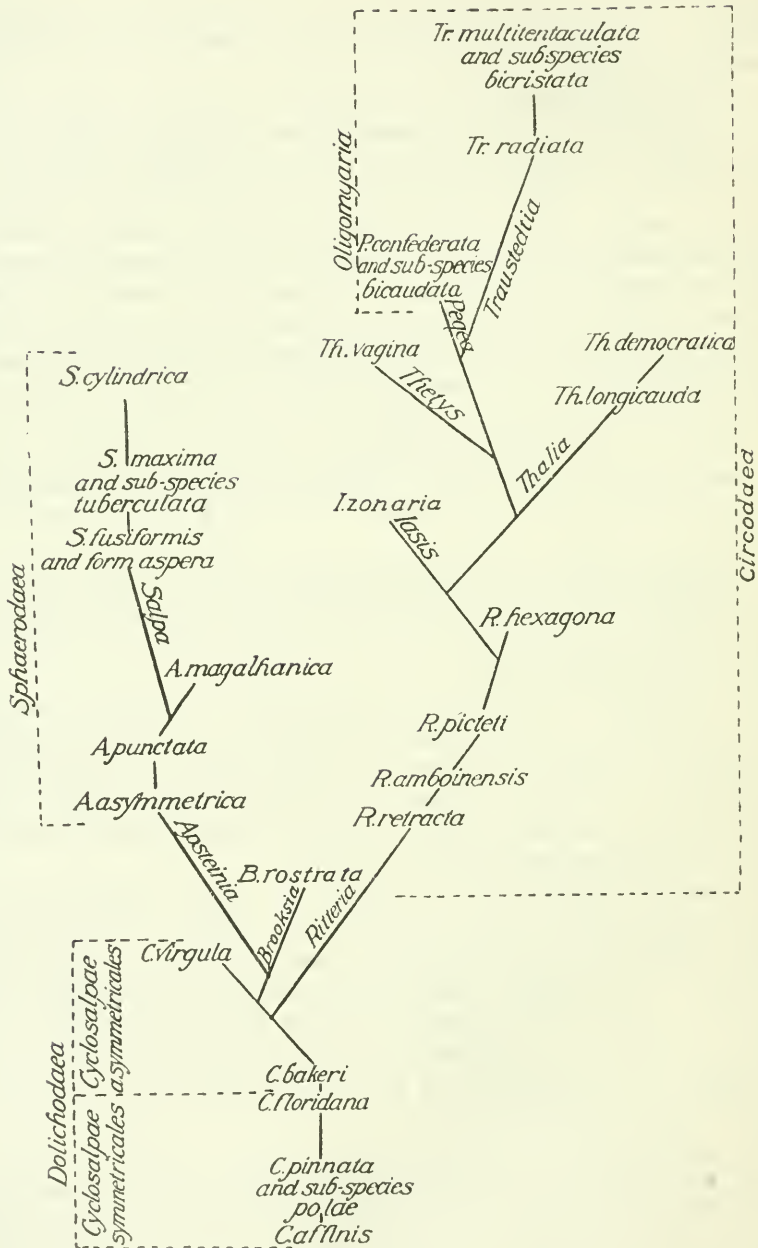
There is a reduction in the eyes of the aggregated zooids in one of the more highly modified of the Salpidae, the anterior portion of the large dorsal eye seen in all other species, being wholly wanting in *Thalia*.

In *Thetys* the basal and terminal portions of the large dorsal eye are less distinct from each other than in most species, the eye being very compact, but both portions are recognizable in the arrangement of the rod and pigment cells.

The histological condition of the rod-cells of the large dorsal eye of the aggregated zooids shows degeneration in the more modified sub-genera, as *Thetys* and *Pegea*. Their condition in *Traustedia* is not known. The eyes within the ganglia of some species show similar histological degeneration, as *Pegea*, *Thetys*, *Ritteria hexagona*, and even *Salpa fusiformis* and *S. maxima*.

The neural glands, also, depart from the usual condition, in the more modified species, being united into one below the ganglion in *Iasis* and *Thetys*, and being wholly absent in *Thalia*. Even in *Salpa cylindrica*, not a highly modified species in general, the disks of the gland are absent and the ducts are only slightly developed. The outgrowths from the ganglion in connection with the neural glands are reduced to a single pair or are even unrecognizable in some of the more modified subgenera.

The conclusions as to relationships among the Salpidae, which I have reached from a study chiefly of the muscles, gut, and eyes, are shown graphically, though too definitely, in the accompanying chart. Upon the exact points of origin of the divergent lines of descent I would by no means insist, but the vividness of the graphic method of presentation outweighs the overemphasis upon some of the details which is necessarily involved in such a chart.



The name *Cyclosalpa*, based upon the arrangement of the zooids in the stolon in whorls, probably does not appropriately apply to the *Cyclosalpae asymmetricales*, and it would seem more natural to place these two species in a distinct subgenus, but the very close relationship between the species *bakeri* (asymmetrical) and *floridana* (symmetrical) is an obstacle to such division of the subgenus.

The scheme of relationship figured shows the *Cyclosalpas* as the primitive members of the family, from which two major divisions have descended. The more primitive species, with elongated intestine at least in the solitary forms, may be called the DOLICHODAEA. These are the *Cyclosalpae*. The species with a very compact gut forming a spheroidal mass in both solitary and aggregated forms may be named the SPHAERODAEA. This group includes *Apsteinia* and *Salpa*. The species with a curved gut, which, however, at least in the solitary individual, does not form a close "nucleus," may be called the CIRCODAEA. This group includes *Brooksia*, *Ritteria*, *Iasis*, *Thetys*, *Thalia*, *Pegea*, and *Traustedia*. It is a much less compact group than either the Dolichodaea or the Sphaerodaea. This division, on the basis of the condition of the gut, seems accurately to express true relationship, but practically it is not so convenient as might be wished, for those of the Circodaea, which have a more compact gut, approach rather too closely for casual discrimination the condition of the Sphaerodaea.

*Iasis* and *Thalia* agree in the valvular character of the dorsal lip of the atrial siphon and the development of the dorsal atrial sphincters as a plexus. They also agree in the reduction of the neural gland in their aggregated zooids. In *Iasis* (fig. 103, p. 108) it is a median chamber with right and left lobes and a single lateral duct, while in *Thalia* it is wholly absent. In *Thetys* the neural gland is a single median chamber (fig. 118, p. 126). Because of the resemblance in their neural glands and larger eyes in the aggregated zooids, *Iasis* and *Thetys* seem to be somewhat near relatives, in spite of the great difference in their muscles. *Thalia* seems much more nearly related to *Iasis* than to *Thetys*.

Among the Circodaea there is greater instability of the muscular system, the eyes, and the neural glands. The musculature is over-emphasized in the *Ritterias*, the more primitive members of this division, while in the more aberrant forms, *Pegea* and *Traustedia*, it becomes much reduced. The term OLIGOMYARIA might well be limited to these two subgenera.

The eyes of the aggregated zooids become increasingly degenerate in the more aberrant forms. The aggregated *Iasis* and *Thetys* show the dorsal eye very compact. Degeneration of the rod-cells begins in *Iasis* and goes far in *Thetys*. In the aggregated *Thalia* the apical

portion of the large eye is missing, while in the aggregated *Pegea* and *Traustedtia* no inversion of the eye occurs. *Brooksia*, in its affinities, leans perhaps toward the Sphaerodaea, the aggregated zoöid being very asymmetrical, more so than in *Ritteria*, though its gut is described as less compact than is the gut in *Apsteinia* or *Salpa*. Its aggregated zoöids show marked resemblance to those of the most highly modified of the *Cyclosalpa*, *C. virgula*. The remarkable anterior protuberance in the solitary *Brooksia* seems to resemble in a general way the anterior protuberances seen in the aggregated zoöids of all the subgenus *Salpa*.

The most primitive of the Salpidae—the *Cyclosalpa symmetricales*—I suggest, may owe the absence of symmetry in their aggregated zoöids to their arrangement in the form of a wheel. The presence in the eye of *Cyclosalpa pinnata* of a slight though constant asymmetry (see p. 10) suggests that even the symmetrical *Cyclosalpas* may have been at one time more asymmetrical. The wheel-like grouping of their aggregated zoöids is probably a secondary character. The higher *Cyclosalpas* have very asymmetrical aggregated zoöids, so also do the more primitive members of the two major divisions derived from the *Cyclosalpas*, but the most aberrant members of the family Salpidae show decreasing asymmetry in the aggregated forms. All, however, show some asymmetry, however disguised. The position of the large eye in the aggregated zoöids is asymmetrical in all of these aberrant species.

In the group Salpidae, hybridization is not known. Each species is clearly demarcated. The two subspecies, *Cyclosalpa pinnata polae*, and *Pegea confederata bicaudata*, are definite. *Salpa fusiformis*, form *aspera*, seems hardly to be worthy of rank as a subspecies, for it completely intergrades with the species proper. On the other hand the tuberculate variety of *Salpa maxima* is not known to intergrade with the species itself.

The question of treatment of genera and subgenera, species, and subspecies is one a little troublesome to decide. If we are to define and use the term species with strict scientific accuracy I suppose every persistent mutant, however slightly it diverges, must be classed as a distinct species. Any other classification would be purely subjective, dependent upon the judgment of the student as to the importance or nonimportance of the diversities observed. Species and genera, as they are employed in classification, are largely conventional. They must be so, for the recognition in our taxonomic systems of every distinct mutant would be utterly impossible, and there is no criterion for genera which removes the personal equation of the observer. The question then, in its practical aspects, is one of convenience and of the best expression of probable relationship. I have chosen to treat as subgenera rather than genera the groups

*Cyclosalpa*, *Brooksia*, *Apsteinia*, *Salpa* (proper), *Ritteria*, *Iasis*, *Thetys*, *Thalia*, *Pegea*, and *Traustedtia*. This seems more convenient, in view of the long established use of the genus name *Salpa*. These groups are far more worthy of emphasis as genera than are many groups, in other families, which are recognized as genera. It has not seemed worth while to place the species *hexagona* in a distinct subgenus, though it diverges considerably from the other *Ritterias*. The resemblance is probably more deserving of emphasis than the divergence. Similarly the resemblance of the species *virgula* to the other *Cyclosalpas* seems more worthy of emphasis than its considerable divergence.

Treating as subspecies varieties and formae the forms *polae*, *tuberculata*, *aspera*, *bicaudata*, and *bicristata* seems reasonable, for their close similarity, respectively, to the species *pinnata*, *maxima*, *fusiformis*, *confederata*, and *multitentaculata* seems much more worth emphasizing than does their divergence each from its respective species.

*Bicaudata* and *polae* are clearly good subspecies. The tuberculate variety of *Salpa maxima* is, so far as known, a sharply distinct variety, but the form *aspera*, as noted, completely intergrades with *S. fusiformis*. Of course it would be of interest to know from observed breeding, in each of these cases, if the species ever "throws" the subspecies as a sport. This, apparently, we are likely never to know. There is no sufficient reason for supposing that this does occur. We must take the forms as we find them and endeavor in our taxonomy to make the clearest expression of probable relationship.

#### SPECIATION.

The very considerable diversity of the species within the family Salpidae is correlated with the great specialization of the family for its pelagic life. The two sets of phenomena are but different phases of the fundamental physiological quality of plasticity. This plasticity, as indicated in the later stages of the evolution of the family, during the time of formation of the diverse species, seems due not to sensitiveness in response to environmental influences, but more probably to an inherent instability working itself out in many directions, without special relation to environmental influence. The external conditions under which the several species live are remarkably uniform. Their divergence has not been in the nature of fitting into different types of environment. It must have resulted almost wholly from inherent qualities.

One naturally asks if there is evidence that hybridization has had a part in this trend toward divergent speciation in the family. Of course, in the complete absence of paleontological evidence, we can not say what may have been in the past, but there is no evidence of

hybridization to-day in the family. In this regard the Salpidae are sharply contrasted with the Pyrosomidae which show such intergradation between species as strongly to suggest hybridization.

Frequent reference has been made in this paper to the comparative stability of the solitary form and the greater divergence of the aggregated zooids. The life cycle of a salp begins with the egg and includes first the solitary form, then its buds. The fully formed aggregated zooid is the final stage of the ontogeny. It is, of course, in line with the conditions in other groups of animals to have the later stages of the ontogeny more divergent among the several species than are earlier stages, provided environmental conditions are uniform throughout the life cycle.

#### ORIGIN OF THE SALPIDAE.

In any taxonomic discussion of the Salpidae, reference should be made to the origin of the family and its relationships to other groups of the Tunicata.

In their adult structure there seems no clear evidence of near relationship between *Pyrosoma* and the true Thaliacea (*Doliolum*, *Anchinia*, and *Salpa*), nor does there appear evidence of closer relationship of the Thaliacea to any of the compound Ascidiaceans. The evidence from the manner of budding will be discussed a little later.

Among the attached Ascidiaceans, both simple and compound, the most archaic seem to be the Clavelinidae. Budding was probably acquired as a means of reproduction soon after the habit of attachment was formed, sedentary life among both plants and animals apparently tending toward asexual reproduction. In all families, in the Tunicata, in which budding occurs, it is by means of a proliferous stolon of the same general type, which is a prolongation of the epicardial tube, with associated mesodermal strands, into a cylindrical outgrowth of the epidermal epithelium. Outgrowths from the atrium may or may not be included in the stolon.

The Simple Ascidiaceans other than the Clavelinidae—that is, the Ascidiidae, the Cynthiidae, and the Molgulidae—have no proliferous stolon, though they show an epicardial tube. We have no evidence to determine if this absence of a stolon is primitive or secondary in these three families. At any rate, their adult structure is more complex than that of the Clavelinidae, which seem the most archaic sedentary members of the phylum now living.

The Larvacea are in many features much more archaic still. They have an elongated form with locomotor tail, a hollow dorsal nervous axis, a notochord lying in part at least between the nervous and alimentary tubes, and lateral skeletal muscles are present in the tail. There is a typical chordate endostyle, and there are gill slits opening into atrial pouches which may or may not be homologous to the

atrium of *Amphioxus* and the "atrial" furrows of *Balanoglossus*. The Larvacea show in their structure no indication of having had in their ancestry Ascidianlike forms. All their structure may well have been evolved during pelagic life. This is especially true of their remarkable test ("house") which is their most specialized feature.

The adoption of sedentary life led to change of form, accompanied by loss of the tail with its axial skeleton, its elongated nerve tube and its skeletal muscles, and to special development of the food collecting organ, the pharynx with its gill basket. Increased size also followed, and concomitantly the remnant of the nerve tube enlarged into the cerebral ganglion. As is so usual with sedentary forms, asexual reproduction was emphasized. *Clavelina* gives us our best picture of this stage of evolution in the phylum.

From some such early sedentary Ascidians apparently diverged several lines of descent. By one or more of these the nonbudding simple Ascidians arose, or they may have arisen before the budding habit was developed. By another line *Octacnemus* arose. Still another line, or possibly several independent lines, gave us the compound Ascidians, from which in time arose the secondarily pelagic *Pyrosoma*. The origin of *Pyrosoma* from compound Ascidians seems indicated by the remarkable Distomid, *Cyathocosmus mirabilis*. (See Oka, 1912 and 1913, also Metcalf and Hopkins, 1918). A final line, of doubtful origin, which early branched dichotomously, developed, on the one hand, into the Doliolidae, on the other, into the Salpidae.

The presence of a sedentary stage in the ancestry of *Doliolum* and *Salpa* is indicated by the possession by these two forms of features first acquired as an adaptation to sedentary life, that is, the large size, the short compact nervous system, the extensively developed branchial basket, and the great development of asexual reproduction.

*Doliolum* and *Anchinia*, returning to pelagic life, take with them their large size, their compact ganglion, their complex pharynx and highly developed atrium, all acquired under sedentary conditions. They adopt the barrel-shaped form of body, moving the mouth and atrial aperture to opposite ends of the body, modifying the sphincter muscles of their two siphons into a series of hoop-like muscles, whose contractions narrow the whole body, causing expulsion of water from the atrial opening and this propelling the body forward. The branchial basket moves backward from the two sides of the pharynx to form a transverse lattice-work between the pharynx in front and the atrium behind, which now has lost its peribranchial outgrowths.

The structural modification of the Doliolidae from the Ascidian condition is considerable, but their chief feature of specialization is the great development and the unique character of their asexual reproduction with migrating polymorphic buds.

The Salpidae have passed a little beyond the Doliolidae in structural development. Their muscle bands are less regular; the branchial basket is lost by the fusion of all the stigmata on each side of the raphe into a single large opening, the pharyngo-atrial partition being reduced to a mere rod; the dorsal part of the ganglion has developed into an eye of a type new to the Tunicata; and the old type of neural gland, derived from the central nerve tube, is lost, and one of a new sort, developed from the pharyngo-atrial epithelium, is substituted. In its structural features *Salpa* is the most modified of all Tunicata. Its processes of budding, however, are far simpler than those of the Doliolidae, and there is in *Salpa* no indication that it ever had and has lost a very complicated series of bud forms such as the Doliolidae show. *Doliolum* is clearly *Salpa*'s nearest relative, but the two must have diverged before the acquirement of polymorphism in the buds upon the stolon. *Salpa* passed on to higher structural modification, retaining a comparatively simple series of buds. *Doliolum*, remaining less modified in structure, has evolved a most complicated process of budding with decided polymorphism among the buds. Structurally *Salpa* is the most highly evolved of the Tunicata. In their life history the Doliolidae are the most elaborate.

It has generally been thought that the Doliolidae, structurally the more primitive branch of this last line, arose from *Pyrosoma*-like forms, the evidence usually cited being the simple character of the branchial basket in the two groups and the position in both of the oral and atrial apertures at opposite ends of the body. The latter seems a point of little weight, for it is a simple adaptation to environmental conditions, and might readily be independently acquired in the two families. After such change in the siphons, the condition of the branchial basket would be as readily derived from that of the Clavelinidae as from that of *Pyrosoma*.

A comparative study of the methods of budding, however, gives some indication that the Doliolidae and Salpidae probably arose from somewhat *Pyrosoma*-like forms. In *Pyrosoma*, *Doliolum*, and *Salpa* the stolon is more complex in structure than in the Ascidiaceae, but is more primitive in the relations of the several organs to the germ layers. In the Ascidiaceae all the internal organs of the bud are derived from the epicardial tube of the stolon, which is of course endodermal. Even the atrium and nervous system arise from this endodermal tissue. This of course is a very secondary condition.

The *Pyrosoma* cyathozooid has a more primitive stolon in two regards. The lateral tubes of the stolon, which give rise to the atrial chambers of the buds (ascidiozooids), arise from the atrial chamber of the parent, very near its aperture. These are therefore ectodermal, as is natural. The nervous systems of the buds arise from rods and



tubes of cells which are formed by proliferation from cells of the ectodermal sheath of the stolon. These nervous systems are therefore ectodermal.

In *Salpa* the atrial tubes of the stolon, which form the atrial chambers of the buds, arise from the atrium of the parent, thus resembling *Pyrosoma*. In *Doliolum* the conditions need further study. Atrial tubes are present, and from them arise the atrial chambers of the buds, but it is not known from what source in the parent, or in the stolon, these atrial tubes arise. In *Salpa* the nervous systems of the buds are derived from a neural rod and tube in the stolon, and this arises by proliferation from the ectodermal sheath, at the base of the stolon. The conditions are therefore as in *Pyrosoma*. In *Doliolum* the nervous rudiments of the buds are at first double, one coming from each atrial tube; later they unite. *Doliolum* is therefore aberrant in having the nervous systems of the buds arise from the atrial tubes while in *Pyrosoma* and *Salpa* they arise from the ectoderm at the base of the stolon. The distinction is probably not fundamental, as at first it appears, for in *Pyrosoma* the atrial tubes of the stolon arise from the ectoderm of the atrium, near where it opens out to the surface ectoderm.

*Pyrosoma*, *Doliolum*, and *Salpa* have well-developed mesodermal strands in the stolon which give rise to the gonads and the muscles (*Pyrosoma*?) of the buds.

In complexity of structure of the stolon, and in the relations of the organs in the buds to the germ layers, *Pyrosoma*, *Doliolum*, and *Salpa* agree, and are in sharp contrast to the Ascidians. The former three agree also in having the buds on the stolon, at least when they first appear, arranged in a linear series, all with their ventral surfaces toward the distal end of the stolon. These resemblances between these three forms in their manner of budding seem fundamental and not due to secondary convergence. We must therefore believe that the *Doliolum-Salpa* line of descent arose from forms which had already acquired the *Pyrosoma* type of stolon.

*Pyrosoma* shows two types of colony formation—one by means of migrating buds, the other by means of permanently attached buds. *Doliolum* shows the migrating type of buds. The origin of this migration in a definitively *Doliolum*-like form is very difficult to imagine. It seems more probable therefore that *Doliolum* has come from a colonial animal like *Pyrosoma*, which had already, in its colony formation, developed migrating buds. It is worth noting that in both the *Pyrosomata ambulata* and in *Doliolum* the buds, when formed, detach from the stolon and migrate to the dorsal side of their parent, there to take a position definitely oriented with reference to the parent, though their orientation is different in the two groups. (See Metcalf and Hopkins (1918), p. 017).

We see, therefore, that while the comparative anatomy of the adult Tunicata tells us little of the origin of the Doliolidae and Salpidae, the comparative study of the manner of budding gives us reason for believing that *Doliolum* arose from *Pyrosoma*-like ancestors, by giving up the compact colonial form, and that from *Doliolum*-like ancestors arose the Salpidae.

DISTRIBUTION OF THE SALPIDAE.

The distribution of the Salpidae has been studied chiefly by Traustedt (1893), Apstein (1894, *b*, 1901, 1904, 1906, *a* and *b*), and Ihle (1910).

*Apsteinia asymmetrica* is known from the equatorial Atlantic Ocean off Africa (Apstein, 1906, *b*) and from the North Atlantic Ocean east of Iceland (Fowler, 1896).

*Apsteinia magalhanica* is known from the Straits of Magellan (Apstein, 1894) and off the Cape of Good Hope (Apstein, 1906, *b*). We have not studied this species.

*Apsteinia punctata* is known from the western Atlantic Ocean off Bermuda (Traustedt, 1893), from the central equatorial Atlantic Ocean (Apstein, 1906, *b*), from the East Indies (Ihle, 1910), and it is more frequently found in the western Mediterranean Sea. Our material is from Naples, probably collected in the western Mediterranean Sea.

*Brooksia rostrata* is known from the western (Apstein, 1906, *b*) and central (Traustedt, 1893) north Atlantic Ocean, from the western and central equatorial Atlantic Ocean (Apstein, 1906, *b*), from the southern Indian Ocean (Apstein, 1906, *b*), and from the East Indies (Ihle, 1910). We have had no specimens of this rare salpa.

*Cyclosalpa affinis* was one of the earliest forms discovered and has been often collected. It has been reported from the eastern and central North Atlantic Ocean, also from east of Bermuda, from the eastern and central equatorial Atlantic Ocean, from the western Mediterranean Sea, from the northeastern and the northwestern Indian Ocean, from off the east coast of Australia, from the eastern Pacific Ocean from southern California to Hawaii and southward. We add from our collections a station in the northwestern Atlantic Ocean off Marthas Vineyard, and stations in the northern Pacific Ocean off the California and Alaska coasts and in Bering Sea.

*Cyclosalpa bakeri* has been reported from the coast of southern California (Ritter, 1905), and from the southern East Indies (Ihle, 1910). Apstein (1906, *a*) describes and figures as *Cyclosalpa floridana* a form which is really *C. bakeri*, failing to distinguish between the two species. In this paper he gives the following localities for "*C. floridana*:" Off the west coast of Africa from the Equator to the Cape of Good Hope, the northeastern Indian Ocean, and off the Somali coast of Africa. Some of the salpas so reported were *Cyclosalpa*

*bakeri*; some may have been *C. floridana*. The distribution of these two species is therefore uncertain. The collections of the Tiefsee Expedition should be restudied in reference to the distribution of these two species. Our collections show *Cyclosalpa bakeri* present in Philippine waters, 1,200 miles north of the East Indian region, in which it was found by the *Siboga* Expedition.

*Cyclosalpa floridana* has been reported from the northwestern Atlantic Ocean, 400 miles south of Newfoundland and southward (Apstein, 1904, *b*). Apstein may have included among the specimens reported some *Cyclosalpa bakeri*, which later he confused with *C. floridana*. The collections of the Plankton Expedition, as well as those of the German Deep-Sea Expedition, should be restudied with reference to the distribution of these two *Cyclosalpas*. Some of the specimens collected by the latter expedition and reported by Apstein (1906, *b*) as *Cyclosalpa floridana* were *C. bakeri*; others may have been *C. floridana*. The localities given by Apstein include the western Atlantic Ocean east of Bahama and the West Indian Islands; off Cape Verde; the central equatorial Atlantic Ocean; the west coast of Africa at the Equator and near the Cape of Good Hope; also the eastern, central and western Indian Ocean. Our collections add no new localities except to show the species present in the Gulf of Mexico and in the Gulf Stream off the coast of Florida and off the New England coast, and so nearer to the American coast than previous records show.

*Cyclosalpa pinnata*, the first discovered and probably the best known of the Salpidae, has been reported from the West Indies and the whole of the North Atlantic Ocean, both east and west, as far north as 56° north latitude, from the western Mediterranean Sea, from the equatorial and southern Atlantic Ocean, both east and west, to 23½° south latitude (off Rio de Janeiro), from the eastern and western Indian Ocean, from the Malay Archipelago, from southeast of Formosa, and from the eastern Pacific Ocean west of Panama. Our collections add localities in Philippine waters, and in the northern Pacific Ocean in Hawaiian waters and off the coasts of Lower California, Oregon, and Alaska as far north as 53° 6' 3" north latitude.

*Cyclosalpa pinnata*, subspecies *polae*, has been known only from the eastern Mediterranean Sea (Sigl, 1912, *a* and *b*). It is represented in our collections by three specimens of the solitary form from the Hawaiian Islands.

*Cyclosalpa virgula*, has long been known from the western Mediterranean Sea. It has been reported more recently from the eastern equatorial Atlantic Ocean (Apstein, 1906, *b*) and from the central Indian Ocean (Apstein, 1906, *b*). Our specimens were obtained from the Naples Zoological Station, and were doubtless collected in the western Mediterranean Sea.

*Iasis zonaria*, a very widely distributed and rather abundant species, has been reported from the whole Atlantic Ocean from 40° south latitude to Iceland and the coast of Greenland, the westernmost stations in the north Atlantic Ocean being east of the Bahama Islands and the eastern end of Cuba. It has been reported also from the western and central Mediterranean Sea, from all parts of the Indian Ocean, from the East Indies and Australasia north to Japan, and from the eastern Pacific Ocean from the Straits of Magellan to southern California. Our collections add stations along the east coast of North America from the mouth of Chesapeake Bay to Halifax, Nova Scotia, and numerous localities in the northern Pacific Ocean off the California and Alaska coasts to 56° north latitude.

*Thetys vagina*, the largest of the Salpidae, has been reported from the eastern Atlantic Ocean from 30° south latitude to the English Channel, from the western Atlantic Ocean east of the Bahama Islands, from the western Mediterranean Sea, from the southern and western Indian Ocean, from the western Pacific Ocean from New Zealand to Japan and eastward (but not from the East Indies), from the central south Pacific Ocean and from off the southern California coast. Our collections add a northwestern Atlantic Ocean station in the Bay of Funday, stations in Philippine waters, and stations in the eastern Pacific Ocean from the California coast to Behring Sea.

*Pegea confederata*, the most abundant species in the Philippine collections, is a widely distributed form and is apparently abundant throughout its range. Most students have failed to distinguish between this form and its subspecies *bicaudata*. The reports of its occurrence are therefore probably based in part upon collections of the form *bicaudata*. Ignoring this source of error, we may give the reported localities for *P. confederata* as follows: the eastern Atlantic Ocean from the Cape of Good Hope to the English Channel, the eastern and western Mediterranean Sea, the western south Atlantic a thousand miles east of Argentina, all regions of the Indian Ocean, the East Indies and the China Sea, and the southern, equatorial, and northern Pacific Ocean from 35° south latitude to the coast of southern California. Our collections add many stations in Philippine waters, and many along the whole eastern coast of America from the Florida Straits to New England (Marthas Vineyard Island). The absence of records of occurrence in northern Californian and Alaskan waters confirms the indication from the distribution in the Atlantic Ocean and shows this species to be a warm-water form.

*Pegea confederata*, subspecies *bicaudata*, has been reported from the Mediterranean Sea (Quoy and Gaimard, 1827, Krohn, 1846, and others), from the Indian Ocean (Lesson, 1832), from the southern Pacific Ocean (Apstein, 1894), and from the East Indies (Apstein, 1894). Probably some of the reports of *Pegea confederata* are based

upon specimens of the subspecies *bicaudata*. Our collections contain specimens from numerous stations along the Atlantic coast of America from Cape Hatteras to Cape Cod. Probably, when this subspecies shall be recognized as distinct from the tailless form, it will be reported from some at least of the other regions included in the reports of *Pegea confederata*. In our Atlantic Ocean collections *bicaudata* is found at fewer stations than *confederata*, and in our collections from the eastern Pacific Ocean it does not occur at all. It is surely rare in Philippine waters, if it occurs there. It must also be rare or absent off the southern California coast or Ritter would have reported it ere now.

*Ritteria amboinensis* has been reported by Apstein (1906, *b*, and 1904) from the equatorial and southern Atlantic Ocean off the coast of Africa, from the western and the northeastern Indian Ocean, and from the southern East Indies. Ihle (1910) also reports it from the East Indies. It is represented in our collections by a dozen specimens of the solitary form from the central Philippine waters.

*Ritteria hexagona* is a warm water species. It has been reported from the eastern Atlantic Ocean (Madeira Islands), from east of the Cape of Good Hope, from the northern Indian Ocean, from the southern East Indies, and from between New Zealand and Australia. Our collections add numerous stations in Philippine waters.

*Ritteria picteti*. This rare form has been reported by Apstein (1904) and by Ihle (1910) from the East Indies, and by Apstein (1906, *b*) from off the Somali coast of Africa. It is not represented in our collections.

*Ritteria retracta*. The first specimen of this species was collected in Suruga Bay, Japan (Ritter, 1906, *b*). The Tiefsee Expedition found other specimens. Apstein (1906, *b*) confused these with "*Salpa amboinensis*," so that the data as to distribution is not usable.

*Salpa cylindrica*, a species long known, has been reported from the northwestern, central, and southeastern north Atlantic Ocean, from the whole equatorial Atlantic Ocean, from the southern Atlantic Ocean west of the Cape of Good Hope, from the northwestern, the northeastern, and the southern Indian Ocean, from many stations throughout the East Indies, from off Formosa, from the eastern Pacific Ocean off the coast of Chile, and off southern California. Our collections add stations in the West Indies, numerous stations in the eastern Pacific Ocean near the Hawaiian Islands, and off the California and Alaska coasts and in the Bering Sea. Numerous stations in Philippine waters are also represented.

*Salpa fusiformis*, one of the earliest known and most abundant of the Salpidae, has been reported from the whole Atlantic Ocean from 55° south latitude to 60° north latitude, from the whole Mediterranean Sea, from the whole Indian Ocean and Antarctic waters to 65° south latitude, from the East Indies and the east coast of Australia, from

the east coast of Japan north to  $50^{\circ}$  north latitude, from the central equatorial Pacific Ocean, from the eastern Pacific Ocean between  $40^{\circ}$  south latitude and  $30^{\circ}$  north latitude. Our collections give additional localities—the West Indies and the Pacific coast of North America from California into Bering Sea.

*Salpa fusiformis*, form *aspera*. This form, which in our collections is more abundant than the smooth form, has been reported from the eastern Atlantic Ocean from  $50^{\circ}$  south latitude to  $20^{\circ}$  north latitude, from the northeastern, the northwestern, and the extreme southern Indian Ocean, from the East Indies, from between Japan and Kamchatka, from the Straits of Magellan, and the eastern Pacific Ocean from  $40^{\circ}$  south latitude to  $15^{\circ}$  north latitude, and from the southern California coast. Our collections add localities off the eastern coast of North America from Cape Hatteras to Halifax, Nova Scotia, and in the eastern Pacific Ocean from Hawaii to the central California coast and north to Puget Sound. Our collections also include many specimens intermediate between the smooth form and the fully developed asperate type. These are from the eastern and western coasts of the United States.

*Salpa maxima*, one of the earlier known species, has been reported from the whole eastern and southern Atlantic Ocean, from the whole Mediterranean Sea, from the southern Indian Ocean both east and west, from Cape Horn, and off the coast of Chile. Our collections add localities as follows: the western north Atlantic Ocean, off South Carolina and off Chesapeake Bay, the eastern Pacific Ocean between Hawaii and California and along the coast from San Francisco to Bering Sea, and the western Pacific Ocean (Philippine waters).

*Salpa maxima*, variety *tuberculata*, is a new variety collected by the Bureau of Fisheries' steamer *Albatross* in Philippine waters.

*Thalia democratica*, the most abundant of the Salpidae, is also very widely distributed, having been reported from all tropical and temperate seas except the eastern Mediterranean Sea, West Indian waters and the northern Pacific Ocean north of  $30^{\circ}$  north latitude. Our collections add the Gulf of Mexico (west coast of Florida), the Caribbean coast of the Isthmus of Panama, the Atlantic coast of the southern United States (off Cape Hatteras), and the Hawaiian Islands. The prevalent Atlantic form differs from the more common Philippine type.

*Thalia longicauda*, though known since Quoy and Gaimard's description (1826–1834), and though sometimes very abundant when found, has been reported but seldom and from but few stations. Traustedt (1885) reports it from the southeastern Atlantic Ocean and from the southwestern Indian Ocean. Apstein (1906, *b*) reports it from the southeastern Atlantic Ocean, from the southwestern and central Indian Ocean, and from the east coast of Australia. The species is not found in our collections.

*Traustedia multitentaculata* is a very rare species, first reported by Quoy and Gaimard (1826–1834) from the East Indies (New Ireland). It has since been reported from the southern Brazilian coast (Traustedt, 1893), from south of the Equator off the west coast of Africa (Dober, 1912), from the north Atlantic Ocean near Madeira (Apstein, 1906, *b*) and near the Azores (Apstein, 1894, *b*), and again from the East Indies (Amboina, by Apstein, 1904).

*Traustedia multitentaculata*, subspecies *bicristata*, is represented by a single specimen of the solitary form from the north Atlantic Ocean, off the New England coast.

*Traustedia radiata*, another very rare species, was first reported by Apstein (1906, *b*) from the eastern and western Indian Ocean (Tiefsee Expedition, station 182, north of Cocos Island, and station 235, north of Madagascar). This species is not represented in our collections. Its validity as a species is doubtful, pending the reexamination of the material.

#### UNIDENTIFIABLE SPECIES OF SALPIDÆ AND SPECIES OF DOUBTFUL VALIDITY.

Unidentifiable species of Salpidæ and species of doubtful validity are named below alphabetically with a word of comment. In the preparation of this list I am much indebted to Traustedt's (1885) detailed bibliographic studies. Identified species are named in the synonymy lists under each species.

*Biphora depressa* Sars, 1829, is said by Traustedt (1885) to be *S. fusiformis*. I have not succeeded in finding in this country this paper of Sars's.

*Holothuria denudata* LINNÆUS, 1758 [=Browne's (1756) *Thalia* no. 3].

*Pterolyra beroides* LESSON, 1832, not a salpa.

*Salpa amphoraformis* LESSON, 1832, apparently not a salpa.

*S. antarctica* MEYEN, 1832, can not be identified.

*S. antheliphora* PERON and LESUEUR, 1807, (*antheliophora*, MEYEN, 1832) can not be identified.

*S. bicornis* CHAMISSO, 1819, can not be identified.

*S. biennis* DE BLAINVILLE, 1827, may have been *Ritteria hexagona*.

*S. bipartita* BORY DE ST. VINCENT, 1804, not a salpa.

*S. clostra* MILNE-EDWARDS, quoted by Cuvier (1828), is said by Traustedt (1885) to be *S. fusiformis*. I have not found Milne-Edwards' reference to this species.

*S. cyanea* DELLE CHIAJE, 1828, may have been *Cyclosalpa pinnata*.

*S. cyanogaster* PERON, 1807, Traustedt thinks this may have been *Thalia democratica*. I do not see that it can be identified.

*S. cymbiola* DALL, 1872, apparently *S. fusiformis*, aggregated zoöid. This is indicated both by the published description and by the unpublished drawings which Dr. Dall has kindly shown me.

*S. dolium* QUOY and GAIMARD, 1826–1834, can not be identified with certainty. It may have been *Pegea confederata*.

*S. dubia* CHAMISSO, 1819, probably *S. africana*, aggregated zoöid.

*S. dubia* LESSON, 1832, apparently not a salpa.

*S. elongata* QUOY and GAIMARD, reference in de Blainville (1827), is said by Traustedt (1885) to be *S. cylindrica*. I have not found Quoy and Gaimard's

- description of this species. De Blainville's reference is insufficient for identification.
- S. emarginata* QUOY and GAIMARD, 1824, can not be identified.
- S. fasciata* FORSKÅL, 1775 (quoted by Bruguiere, 1789, Lamarck, 1816, and de Blainville, 1827), Traustedt (1885) thinks this may have been *S. fusiformis*.
- S. forskalii* LESSON, 1832, is said by Traustedt (1885) to be *S. maxima*, and the identification seems probable because of the size of the animal.
- S. fusiformis* CUVIER, 1804. There is confusion in Cuvier's paper. An aggregated zoöid of *S. fusiformis* is called *S. cylindrica* and a solitary *Pegea confederata* is named *S. fusiformis*. Strictly the reference "*S. fusiformis*, Cuv., 1804," is mistaken and one can not be wholly certain of Cuvier's intention. It is best, however, to let the reference stand, interpreting the discrepancy as mere confusion.
- S. garnotii* LESSON, 1832, shows a general resemblance to *S. cylindrica*, but can not be identified.
- S. gibba* Bosc, 1802, is said by Traustedt (1885) to be *Pegea confederata*, but the identification seems to me doubtful.
- S. herculea* DALL, 1872, is apparently *Thetys vagina*, as is shown by Dall's unpublished drawings, which he kindly showed me.
- S. iniformis* QUOY and GAIMARD, 1824, probably *Pegea confederata*, as is indicated by the two sets of body muscles.
- S. laevis* LESSON, 1832, can not be identified.
- S. lineata* LESSON, 1832, can not be identified.
- S. mollis* HERDMAN, 1888, a doubtful form based on a single imperfectly preserved specimen. Possibly it may be a somewhat aberrant solitary individual of *S. fusiformis*, subspecies *aspera*.
- S. moniliformis* MACCULLOCH, 1819, is said by Traustedt (1885) to be *S. fusiformis*. Hopkinson (1913) questions its being a salpa at all. I have not found the reference in Macculloch's paper. Fleming (1842), referring to Macculloch's description, says, "At each extremity of the back [the dorsal and ventral sides were generally reversed in early descriptions of Salpas] there is a conical longitudinal process nearly equal to the body in length." If this be a salpa at all it must be *S. fusiformis*, aggregated zoöid, unless, indeed, it is *S. maxima*, variety *tuberculata*, which seems altogether improbable.
- S. neapolitana* DELLE CHIAJE, 1841, probably *Thetys vagina*.
- S. nitida* HERDMAN, 1888, probably not distinct from *Iasis zonaria*, but merely a delicate form. The aggregated zoöids show a dorsal eye and a remarkable pair of lateral outgrowths from the ganglion, containing irregular rod-cells, all of which seem from Herdman's figures to be identical with the corresponding structures in *Iasis zonaria*.
- S. pelagica* Bosc, 1802, is said by Traustedt (1885) to be *Cyclosalpa pinnata*, but the identification seems to me very doubtful.
- S. polymorpha* QUOY and GAIMARD, 1824, not a salpa.
- S. pyramidalis* QUOY and GAIMARD, 1826-1834, probably *Thalia democratica*.
- S. pyramidalis* LESSON, 1832, probably *Salpa fusiformis*.
- S. quadrangularis* LESSON, 1832, possibly *Iasis zonaria*.
- S. quadrata* HERDMAN, 1888, seems to be an embryo of *Pegea confederata*.
- S. rhomboides* QUOY and GAIMARD, 1824 (*rhomboidalis* MEYEN, 1832) can not be identified, apparently not a salpa.
- S. rubrolineata* LESSON, 1832, can not be identified.
- S. siphon* FORSKÅL, 1775, not a salpa.
- S. socia* Bosc, 1802, is said by Traustedt (1885) to be *Pegea confederata*, but the identification seems to me very doubtful.
- S. solitaria* FORSKÅL, 1775, not a salpa.



- S. suborbicularis* QUOY and GAIMARD, 1824, not a salpa.  
*S. triangularis* QUOY and GAIMARD, 1824, apparently not a salpa.  
*S. tricuspida* LESSON, 1832, apparently *Iasis zonaria*, solitary.  
*S. tricuspida* QUOY and GAIMARD, 1824, can not be identified.  
*S. tricuspida* SARS, 1829, is said by Traustedt (1885) to be *S. fusiformis*. I have not succeeded in finding in this country this paper of Sars.  
*S. vaginata* CHAMISSE, 1819, can not be identified with certainty; it may be *S. fusiformis*, subspecies *aspera*, solitary form.  
*Thalia lingulata* BLUMENBACH, 1910. Traustedt regards this as *Thalia democratica*. The identification seems probable.

GENERIC AND SUBGENERIC NAMES.

The following list shows the first use of the several generic and subgeneric names applied to Salpidae:

- Apsteinia*, METCALF, in this paper.  
*Biphora* BRUGUIERE, 1789.  
*Brooksia*, METCALF, in this paper.  
*Cyclosalpa* DE BLAINVILLE, 1827.  
*Dagysa* BANKS and SOLANDER, 1773.  
*Dubreullia* LESSON, 1832.  
*Holothuria* LINNEUS, 1758.  
*Holothurium* PALLAS, 1774.  
*Iasis* SAVIGNY, 1816.  
*Pegea* SAVIGNY, 1816.  
*Pyrosomopsis* [= *Cyclosalpa*] MACDONALD, 1863.  
*Ritteria* METCALF, in this paper.  
*Salpa* FORSKÅL, 1775.  
*Thalia* BROWNE, 1756.  
*Thetys* TILESUS, 1802.  
*Traustedtia* METCALF, in this paper.  
*Pterolyra* LESSON, 1832, is not a salpa.

KEY TO THE SUBGENERA AND SPECIES OF SALPIDAE.

A. Intestine in the solitary forms a straight tube dorsal to the gill. In the aggregated zoöids it is either a straight tube or is bent into an open loop.

DOLICHODAEAE. One genus, *Cyclosalpa*.

$\alpha$ , 1 Aggregated zoöids bilaterally symmetrical. Terminal zoöids of stolon detached in the form of a whorl. *Cyclosalpa symmetricales*.

$\alpha$ , 1 Luminous organs 5 pairs in solitary form, 1 pair in aggregated form; body muscles in solitary form all interrupted dorsally; intestine in aggregated zoöid a straight tube below the endostyle.

(type<sup>1</sup>) *pinnata*.

$\alpha$ , 2 Luminous organs wanting in both solitary and aggregated forms: posterior 5 body muscles in solitary forms complete dorsally; intestine in aggregated zoöid an open vertical loop in the median plane, anus in front of esophageal aperture. *affinis*.

$\alpha$ , 3 Luminous organs in solitary form 5 pairs, the first and last slightly developed or almost wanting; luminous organs altogether absent in aggregated zoöids; caeca, 2 in solitary form, 1 in aggregated form, globular; body muscles in solitary form all interrupted dorsally; testis in the aggregated zoöid occupying a large conical postabdomen within a swollen mass of test. *floridana*.

The author prefers the latin form *typus* in strictly taxonomic use of this word.

- a, 2* Aggregated zooids bilaterally asymmetrical, terminal zooids of stolon not known to be detached in whorls..... *Cyclosalpae asymmetricales*.
- α, 1* Body muscles in solitary form not forming any ventral horizontal bands: postabdomen of aggregated zooid long and unequally bifurcate, the larger division occupied by the intestine proximally and the slender testis distally, the smaller division occupied proximally by the single caecum and distally by a cell mass superficially resembling the testis.  
*bakeri*.
- α, 2* Certain of the body muscles of the solitary form elongated to form a dorsal and a ventral pair of horizontal bands: aggregated zooid with undivided postabdomen containing intestine and testis..... *virgula*.
- B.* Gut in solitary forms not making a very compact nucleus. The course of the intestine can be traced without dissection. In the aggregated zooids the gut forms a "nucleus" in which, in most species, the course of the intestine can hardly be detected by superficial observation.

## CIRCODEA.

- b, 1* Solitary form with a long anterior protuberance below the mouth, containing wide muscle bands. Aggregated zooids very asymmetrical..... *Brooksia*.
- β, 1* One species..... *rostrata*.
- b, 2* Body muscles in the solitary form more than 10, asymmetrically continuous across the dorsal mid line..... *Ritteria*.
- β, 1* Body muscles 15: aggregated zooids inadequately known, asymmetrical..... *retracta*.
- β, 2* Body muscles in the solitary form 21 or more: aggregated zooids unknown..... *picteti*.
- β, 3* Body muscles in the solitary form 11, not so wide as to form an almost continuous layer; gut a transverse vertical loop: aggregated zooid asymmetrical, its gut a close loop but with the course of the intestine visible..... (type) *amboinensis*.
- β, 4* Body muscles in the solitary form very broad forming an almost continuous layer, especially posteriorly; a pair of postero-lateral appendages present: aggregated zooid showing 6 well-marked longitudinal ridges; it has 6 broad body muscles..... *hexagona*.
- b, 3* Solitary form with 5 pairs of very broad muscle bands and a narrower shorter 6th on the dorsal surface behind them, body terminating behind in a sharp point whose enlarged base contains the gut; atrial aperture a horizontal slit. Aggregated zooid with similar atrial aperture, 3-5 embryos, 5 strong body muscles, nearly parallel, all but the first continuous across the mid-dorsal line, body pointed behind and narrowing to a truncated point in front..... *Iasis*.
- β, 1* One species..... *zonaria*.
- b, 4* Solitary form with a pair of well-developed postero-lateral appendages.
- bb, 1* Atrial siphon in both solitary and aggregated forms tubular; body muscles in both forms confined to the dorsal half of the body, numerous in the solitary form, most of them interrupted both dorsally and laterally; body muscles 5 in aggregated zooid..... *Ihlea*.
- β, 1* One species..... *vagina*.
- bb, 2* Atrial aperture in both solitary and aggregated forms a slit... *Thalia*.
- β, 1* Appendages in solitary form about as long as body, body muscles nearly parallel, interrupted ventrally. Body muscles of aggregated zooid with from 5-11 fibers each..... *longicauda*

- $\beta$ , 2 Appendages in solitary form less than half as long as the body, body muscles forming complete uninterrupted loops: body muscles in aggregated zoïd with from 3-5 fibers each .....(type) *democratica*.
- b, 5 Body muscles in both solitary and aggregated forms 4, confined to the dorsal half of the body, forming an anterior and a posterior X-shaped group.....*Pegea*.
- $\beta$ , 1 Aggregated zoïd with a pair of postero-lateral appendages, usually of unequal length, eye somewhat stalked.  
*confederata*, subspecies *bicaudata*
- $\beta$ , 2 Without the characteristics specified under  $\beta$ , 1.....*confederata*.
- b, 6 Solitary form with numerous tubular appendages from different parts of the body.....*Traustedia*.
- bb, 1 Appendages in solitary form 20 or more, gut forming a horizontal spindle-shaped mass: aggregated zoïd probably not known.  
*radiata*.
- bb, 2 Appendages in solitary form not more than 13, gut forming a vertical spindle-shaped mass. Aggregated form with a single unequal pair of postero-lateral appendages.
- $\beta$ , 1 Appendages of the solitary form 8, the posterior pair about as long as the body. Oral muscles continuous across the mid-dorsal line.....(type) *multitentaculata*.
- $\beta$ , 2 Appendages of the solitary form 13. Oral muscles very short dorsally, hardly extending above the angles of the mouth.....*multitentaculata*, subspecies *bicristata*.
- C. Gut in both solitary and aggregated forms making a compact "nucleus," in which the course of the intestine can not be clearly seen without dissection.
- SPHAERODAEA.
- c, 1 Body muscles in solitary form widely interrupted ventrally: aggregated zoïds asymmetrically more or less pointed in front and behind, body muscles not very asymmetrical.....*Salpa*.
- cc, 1 Body muscles in solitary form all about parallel. Gut nucleus in aggregated zoïd on mid-line, pushing the posterior protuberance to one side; body muscles IV and V not in contact laterally.
- $\kappa$ , 1 Anterior and posterior appendages in aggregated zoïd about  $\frac{1}{4}$  as long as body, no swollen spinose areas at base of atrial siphon.....*maxima*.
- $\kappa$ , 2 Anterior and posterior appendages in aggregated zoïd about  $\frac{1}{2}$  as long as body, 2 unequal spinose thickenings of the test dorsally near the base of the atrial siphon.  
*maxima*, variety *tuberculata*.
- cc, 2. Body muscles I to III in the solitary form in contact dorsally, the rest parallel; body muscles IV and V in the aggregated zoïd in contact laterally.
- $\kappa$ , 1. Neither solitary nor aggregated forms bearing spinose ridges.....(type) *fusiformis*.
- $\kappa$ , 2. Both solitary and aggregated forms bearing spinose ridges.  
*fusiformis*, form *aspera*.
- cc, 3. Body muscles I to IV in the solitary form in contact dorsally. In aggregated zoïd body muscles I to III and IV and V are fused dorsally to form 2 broad bands. These 2 bands are in contact dorsally and may be united.....*cylindrica*.

- cc, 2. Body muscles in solitary form complete uninterrupted loops; in aggregated form decidedly asymmetrical. . . . . *Apsteinia*.
- κ, 1. Body muscles 7 in solitary form, 5 in aggregated form, continuous in both forms across mid-dorsal and mid-ventral lines; oral retractor muscle not continued far backward as 2 horizontal bands on each side. . . . . *maghalanica*.
- κ, 2. Oral retractor muscles in solitary form continued far backward as two horizontal bands on each side, the dorsal one much the longer; body muscles in aggregated form interrupted ventrally.
- κκ, 1. In solitary form lips and postero-ventral region near gut bearing many fine branching lines of pigment; aggregated zoöid punctate with pigment spots along mid-ventral line. . . . . (type) *punctata*.
- κκ, 2. No pigmented lines or spots on lips or mid-ventral area in either form. . . . . *asymmetrica*.

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


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#### EXPLANATION OF TEXT FIGURES AND PLATES.

Interpretation of index letters, numbers, and signs. These are the same in text figures and plates.

-  The ball is dorsal, the pointed end of the rod is ventral.
-  The arrow points anteriorly.
-  The previous two signs combined.

The endostyle in the text figures is generally shown in solid black, the peripharyngeal band as a dashed line.

- a* = lateral portion of the dorsal eye in *Salpa cylindrica*.
- an.* = anus.
- a. o.* = atrial opening.
- a. r.* = atrial retractor.
- a. s.* = atrial sphincter. The atrial sphincters are often numbered *a. s. 1*; *a. s. 2*, etc.
- a. v.* = antero-ventral prolongation of ganglion.
- b* = small-celled outgrowth from the ganglion.
- b'* = large-celled outgrowth from the ganglion.
- b. c.* = blood corpuscle.
- b. s.* = blood sinus.
- c.* = caecum.
- c'* = caecum of right side.
- c''* = caecum of left side.
- c. f.* = ciliated funnel, dorsal tubercle.
- cl.* = cloaca.
- cl. ep.* = cloacal epithelium.
- cl. s.* = cloacal siphon.
- d.* = duct of neural gland.
- d. l.* = dorsal lamina.
- d. m. l.* = dorsal mid line.
- d. o.* = aperture of duct of neural gland into the pharyngo-atrial chamber.
- dor.* = dorsal.
- e.* = eye, usually meaning the dorsal eye.

- e.1, e.2, e.3*, etc.=parts of dorsal eye labeled with no indication of homologies.  
*e'*.=basal portion of dorsal eye.  
*e''*.=apical portion of dorsal eye.  
*e'''*.=optic plug of *Cyclosalpa pinnata* or its homolog in other species.  
*ech*.=spinose area of the test in *Salpa maxima*, variety *tuberculata*.  
*el*.=cleoblast.  
*em*.=embryo.  
*en*.=endostyle.  
*ep*.=ectodermal epithelium.  
*eq*=accessory eye or accessory portion of eye in solitary form.  
*ex*=accessory eye in ganglion, dorsal.  
*ey*=accessory eye in ganglion, posterior, anterior, or lateral.  
*g*.=gill.  
*gg*=ganglion.  
*gl*.=gland.  
*h*.=heart.  
*h. m.*=dorsal horizontal muscle.  
*I, II, III*, etc.=body muscles.  
*i. c.*=intermediate cells.  
*i. m.*=intermediate muscle.  
*int.*=intestine.  
*k*=ectodermal epithelium.  
*k'*=pharyngeal epithelium.  
*l.*=oral sphincter muscle of lower lip. These are often numbered *l.1*,  
*l.2, l.3*, etc.  
*l. o.*=luminous organ.  
*lu.*=lumen of nerve tube.  
*m.*=mouth.  
*n.*=nerve.  
*n. c.*=nerve cell in ganglion in zone of origin of the nerves.  
*n. x.*=nerve to dorsal accessory eye in ganglion.  
*o.*=ovary.  
*o. c.*=optic chamber, a lymph space.  
*od.*=oviduct.  
*oe.*=esophagus or its aperture.  
*o. r.*=oral retractor.  
*o. s.*=optic sheath, of ectodermal epithelium.  
*p.*=pigment.  
*p'*.=pigment of basal portion of eye.  
*p''*.=pigment of apical portion of eye.  
*p'''*.=pigment of optic plug in *Cyclosalpa pinnata*, or its homolog in other  
species.  
*p. a.*=post-abdomen.  
*pd.*=peduncle.  
*ph.*=pharynx.  
*ph. b.*=peripharyngeal band of cilia.  
*ph. ep.*=pharyngeal epithelium.  
*pl.*=placenta.  
*p. x.*=pigment of dorsal accessory eye in ganglion.  
*q*=problematic organ (or cells) near intestine.  
*r*=primitively mid-posterior point of the eye. Used only in  
figure 12.  
*st.*=stolon. (In figs. 31-33, pp. 59 and 60, it indicates what Ihle calls  
the "stoloblast" or "cleoblast".)



- stm.* = stomach.  
*t.* = testis.  
*test* = test.  
*u.* = oral sphincter muscle of upper lip; often numbered *u.1*, *u.2*, *u.3*, etc.  
*v.* = dorsal visceral muscle.  
*v.'* = ventral portion of dorsal visceral muscle.  
*v.{'* = ventral visceral muscle.  
*v. d.* = vas deferens.  
*ven.* = ventral.  
*v. l.* = ventral languet.  
*v. m. l.* = ventral mid line.  
*v. s.* = ventral atrial sphincter, or ventral portion of atrial sphincter.  
*xx* = brown muscle of oral siphon in *Iasis*.  
*z.* = zone of large cells in the ganglion, from which the nerves arise.

PLATE 1.

*Cyclosalpa pinnata*.

- FIG. 1.—Solitary form seen from the right side.  $\times$ , 2.  
 2.—Ventral view of the ciliated funnel (dorsal tubercle) and adjacent structures in the solitary form.  
 3.—Aggregated zooid, seen from the right side.  $\times$ , 3.  
 4.—Ventral view of the ciliated funnel and adjacent structures in the aggregated zooid.

PLATE 2.

*Cyclosalpa pinnata*.

- FIG. 5.—Testis and adjacent structures. The endostyle is placed more dorsally than is normal so as to show the testis more clearly.  
 6.—An antero-dextro-dorsal view of the oral end of the solitary form.  
 7.—The ganglion and dorsal eye of the aggregated zooid seen from the right side.  
 8.—Dorsal view of the same structures, including also one neural gland and the ducts of both glands.

PLATE 3.

*Cyclosalpa affinis*.

- FIG. 9.—Solitary form viewed from the left side. Natural size.  
 10.—Aggregated zooid, seen from the left side. Natural size.

PLATE 4.

- FIG. 11.—*Cyclosalpa affinis*, aggregated form; ganglion and eye from right side.  
 12.—*Cyclosalpa affinis*, solitary and aggregated form, ciliated funnel and adjacent organs. Ventral view.  
 13.—*Cyclosalpa floridana*, solitary form, seen from the left side.  $\times$ , 9.  
 14.—*Cyclosalpa floridana*, outline drawing of the esophagus, caecum, and beginning of the intestine, from fig. 13.

PLATE 5.

*Cyclosalpa floridana*.

- FIG. 15.—Aggregated zooid, seen from the left side.  $\times$ , 14.  
 16.—Solitary and aggregated forms, ciliated funnel and adjacent organs. Ventral view.

## PLATE 6.

*Cyclosalpa floridana*, aggregated zooid.FIG. 17.—Ventral view.  $\times$ , 14.18.—Dorsal view.  $\times$ , 14.

## PLATE 7.

*Cyclosalpa bakeri*, solitary form.FIG. 19.—View from the left side.  $\times$ , 8.

20.—Ciliated funnel and adjacent structures. Ventral view.

## PLATE 8.

*Cyclosalpa bakeri*, aggregated zooid.FIG. 21.—Large zooid, seen from the right side.  $\times$ , 8.22.—Small zooid, seen from the left side.  $\times$ , 25.

## PLATE 9.

*Cyclosalpa bakeri*, aggregated zooid.FIG. 23.—Young zooid, seen from the right side.  $\times$ , 25.

24.—Ciliated funnel and adjacent structures. Ventral view.

## PLATE 10.

*Cyclosalpa bakeri*, aggregated zooid.

FIG. 25.—Older zooid, a more magnified dextro-dorsal view of the posterior end of the body.

## PLATE 11.

*Cyclosalpa virgula*.

FIG. 26.—Solitary form, seen from the right side. One-half natural size.

27.—Solitary form, ciliated funnel and adjacent organs. Ventral view.

28.—Aggregated zooid, seen from the right side.  $\times$ , 4.

## PLATE 12.

*Cyclosalpa virgula*, aggregated zooid.FIG. 29.—A view from the left side.  $\times$ , 4.30.—A ventral view.  $\times$ , 4.

## PLATE 13.

*Cyclosalpa virgula*, aggregated zooid.

FIG. 31.—Ganglion, eye and neural glands, in dorsal view.

32.—Ciliated funnel and adjacent structures. Ventral view.

33.—A zooid in dorsal view.  $\times$ , 4.

## PLATE 14.

*Transtedia multitentaculata*, subspecies *bicristata*, solitary form.FIG. 34.—Dorsal view.  $\times$ , 11.35.—View from the right side.  $\times$ , 11.

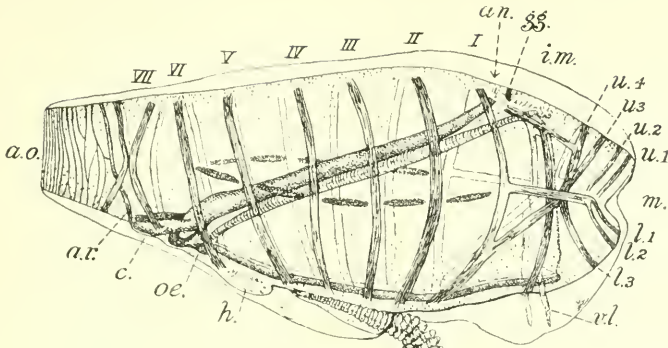


Fig. 1.

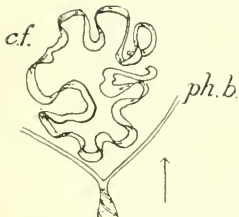


Fig. 2. s.

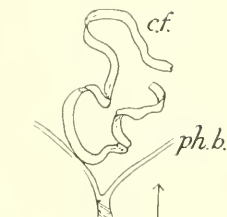


Fig. 4. g.

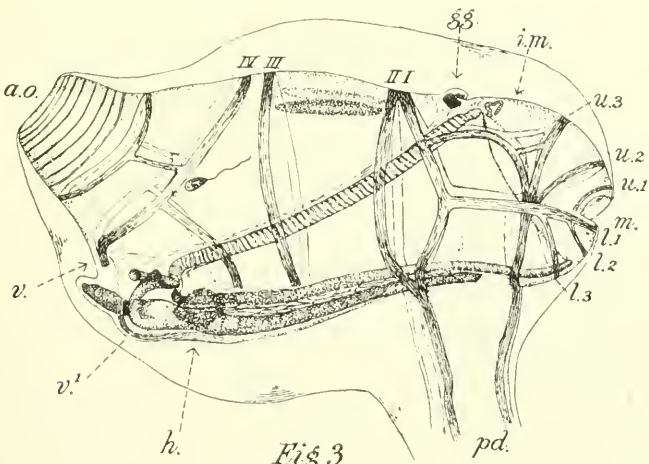


Fig. 3.

CYCLOSALPA PINNATA. 1, SOLITARY FORM, X 2; 2, SOLITARY FORM, THE APERTURE OF THE CILIATED FUNNEL; 3, AGGREGATED FORM, X 3; 4, AGGREGATED FORM. THE APERTURE OF THE CILIATED FUNNEL.

FOR EXPLANATION OF PLATE SEE PAGE 181.



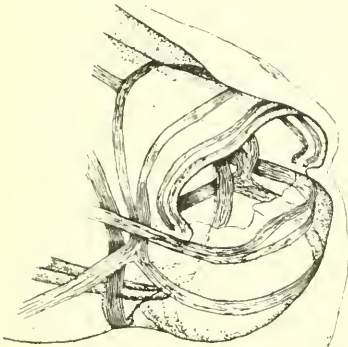


Fig. 6.

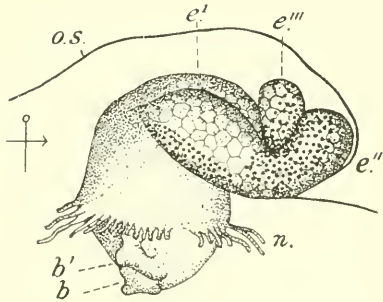


Fig. 7.

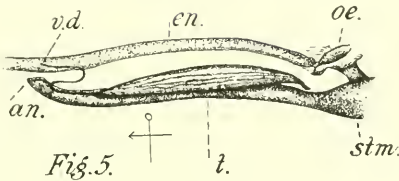


Fig. 5.

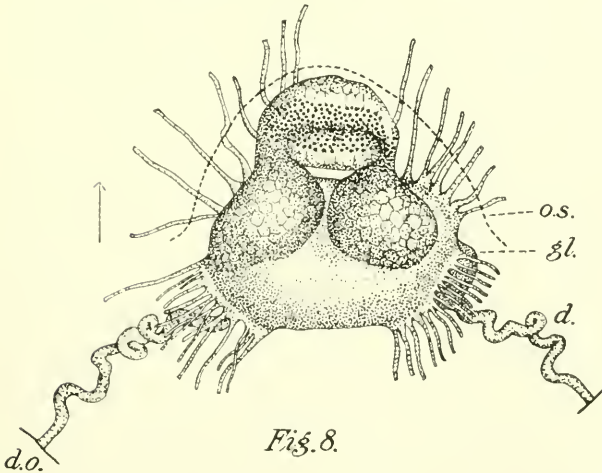


Fig. 8.

CYCLOSALPA PINNATA. 5, AGGREGATED FORM, TESTIS, PART OF THE GUT, AND THE ENDOSTYLE; 6, SOLITARY FORM, ORAL REGION; 7, AGGREGATED FORM, GANGLION AND EYE FROM THE RIGHT SIDE; 8, AGGREGATED FORM, GANGLION AND EYE FROM ABOVE.



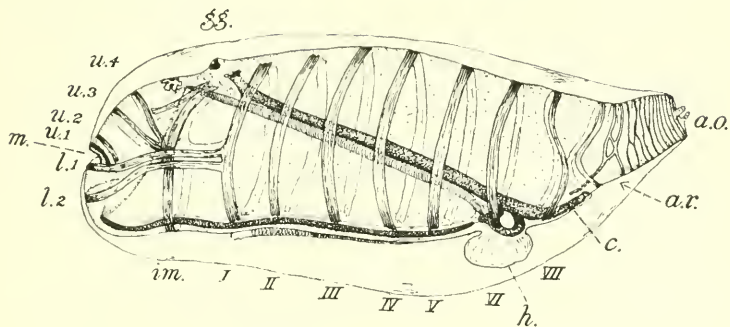


Fig. 9.

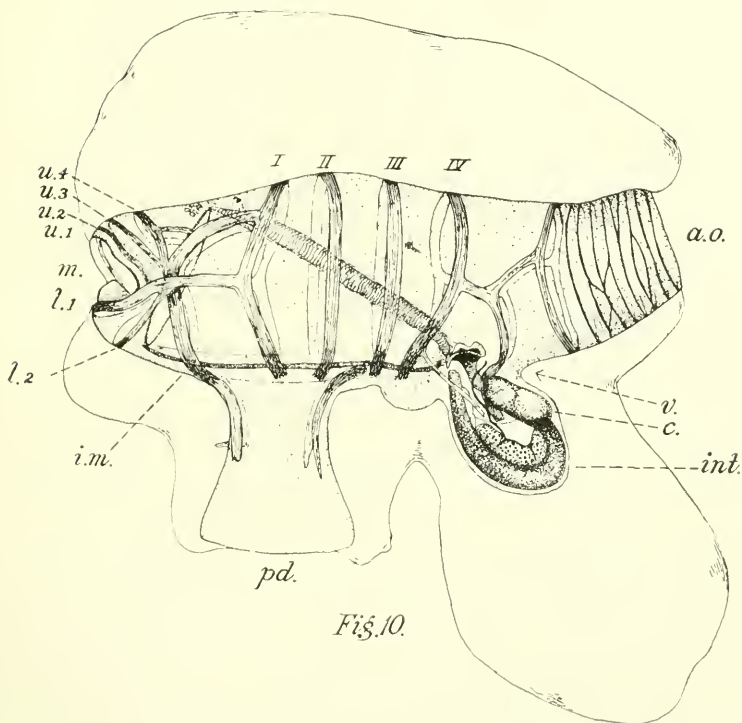


Fig. 10.

CYCLOSALPA AFFINIS. 9, SOLITARY FORM, FROM LEFT SIDE, NATURAL SIZE;  
10, AGGREGATED FORM, FROM LEFT SIDE, NATURAL SIZE.

FOR EXPLANATION OF PLATE SEE PAGE 181.





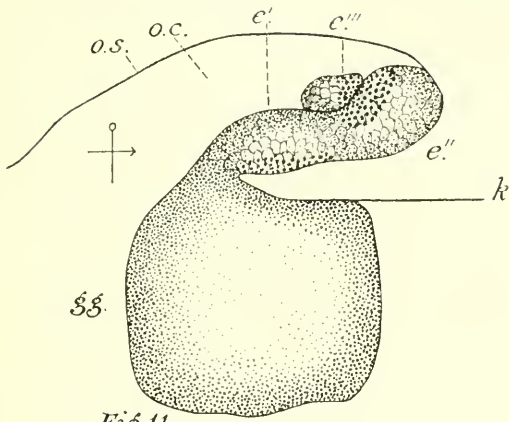


Fig. 11.

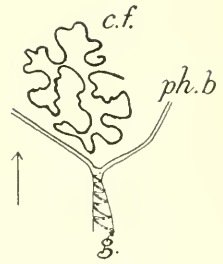


Fig. 12.

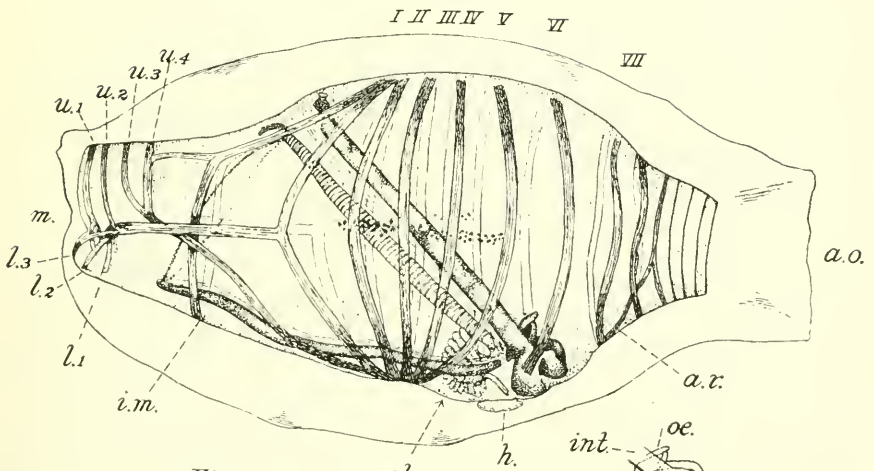


Fig. 13.

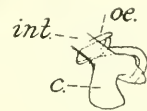


Fig. 14.

11, *CYCLOSALPA AFFINIS*, AGGREGATED FORM, GANGLION AND EYE FROM RIGHT SIDE; 12, *C. AFFINIS*, AGGREGATED FORM, APERTURE OF CILIATED FUNNEL; 13, *C. FLORIDANA*, SOLITARY FORM, FROM LEFT SIDE,  $\times 9$ ; 14, *C. FLORIDANA*, SOLITARY FORM, THE GUT DRAWN IN OUTLINE.



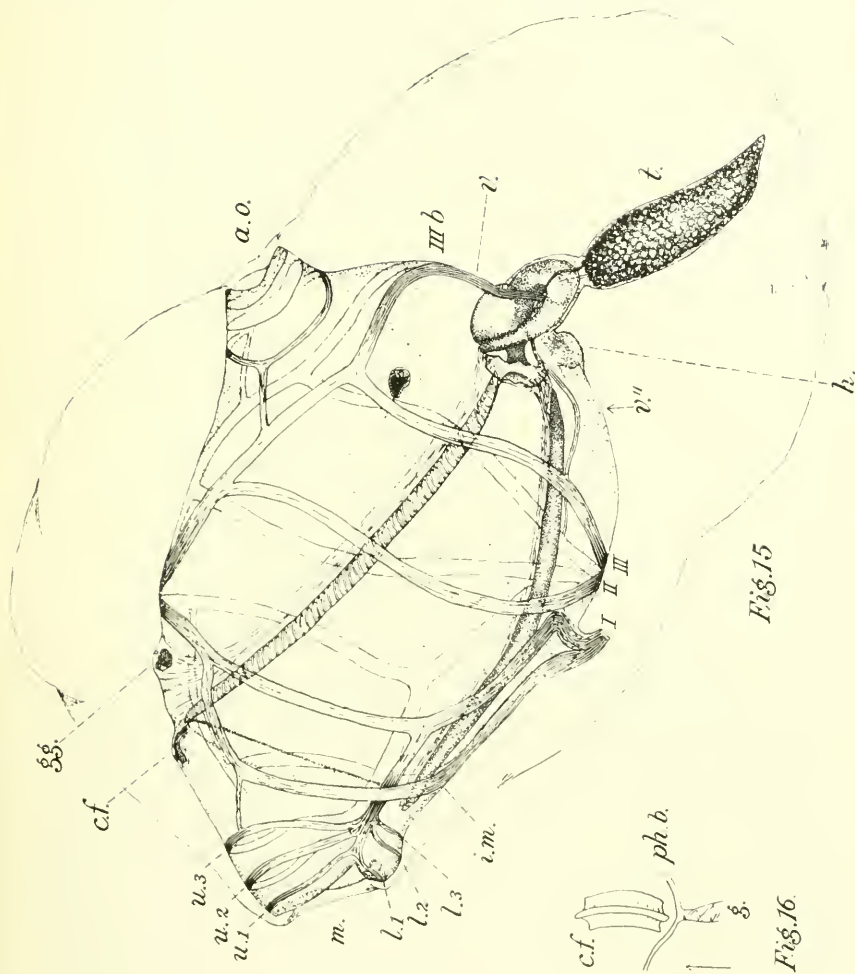


Fig. 15

Fig. 16

CYCLOSALPA FLORIDANA. 15, AGGREGATED ZOOID FROM LEFT SIDE, 14; 16, SOLITARY FORM, CILIATED FUNNEL.

FOR EXPLANATION OF PLATE SEE PAGE 181.



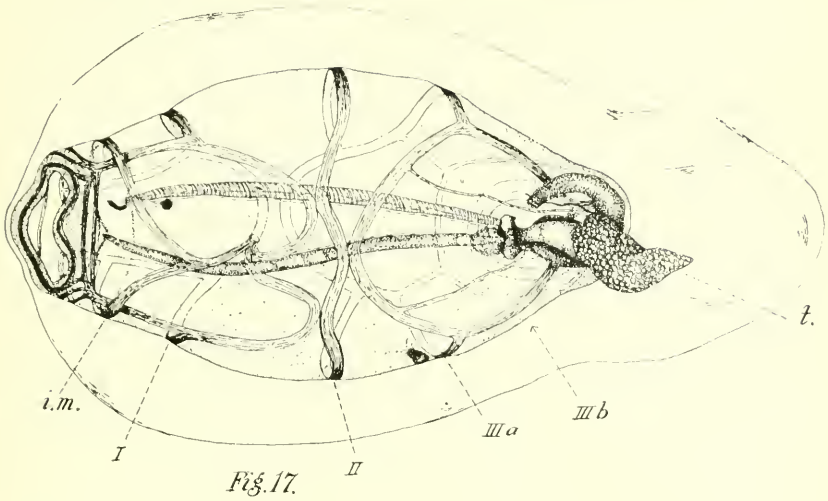


Fig. 17.

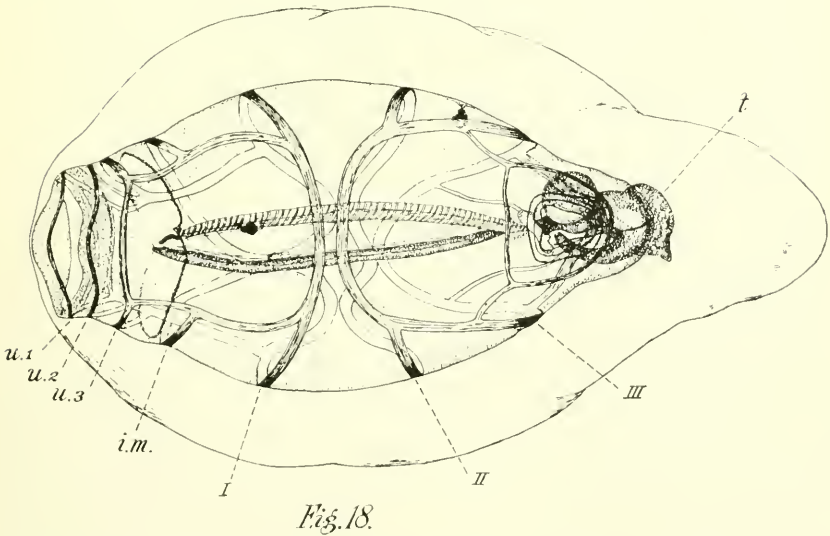


Fig. 18.

CYCLOSALPA FLORIDANA. AGGREGATED ZOOID. 17, VENTRAL VIEW,  $\times 12$ ; 18, DORSAL VIEW,  $\times 12$ .

FOR EXPLANATION OF PLATE SEE PAGE 182.



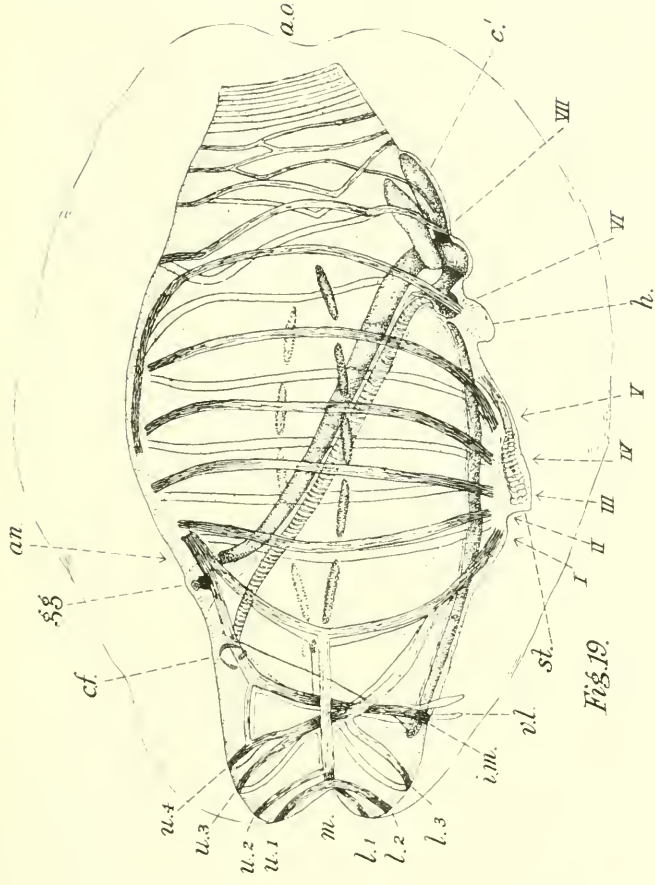


Fig. 19.

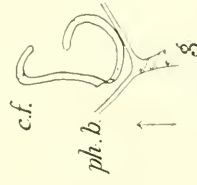


Fig. 20.

CYCLOSALPA BAKERI. SOLITARY FORM. 19, VIEW FROM THE LEFT SIDE, 8; 20, CILIATED FUNNEL.

FOR EXPLANATION OF PLATE SEE PAGE 182





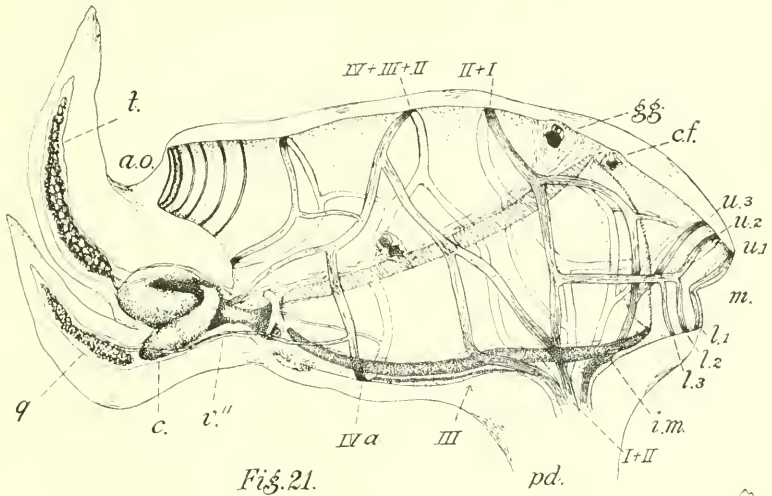


Fig. 21.

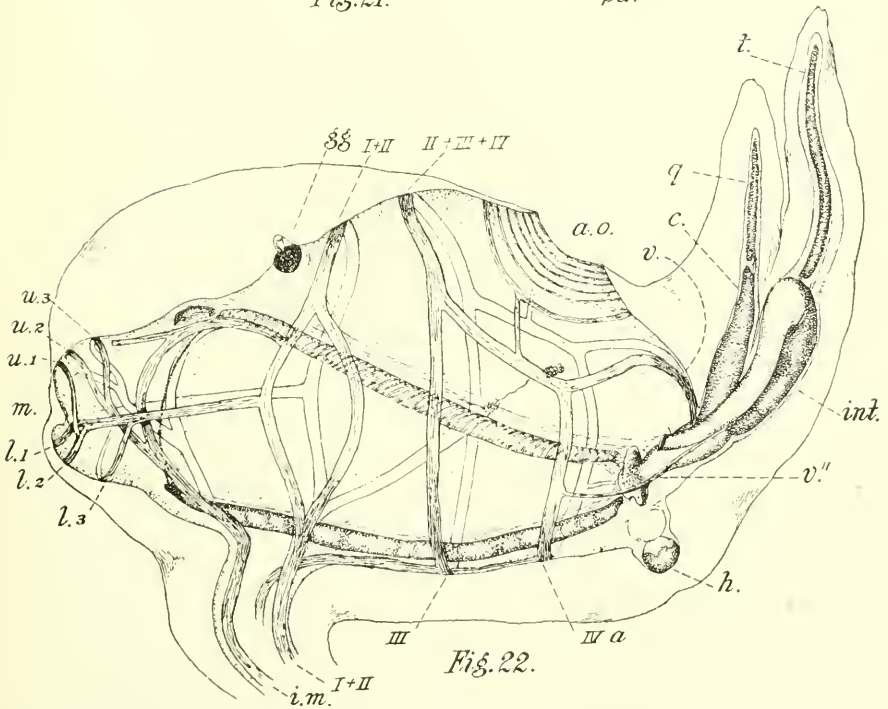


Fig. 22.

CYCLOSALPA BAKERI. AGGREGATED ZOOID. 21, VIEW FROM THE RIGHT SIDE,  $\times 8$ ; 22, YOUNGER ZOOID, FROM THE LEFT SIDE,  $\times 25$ . J



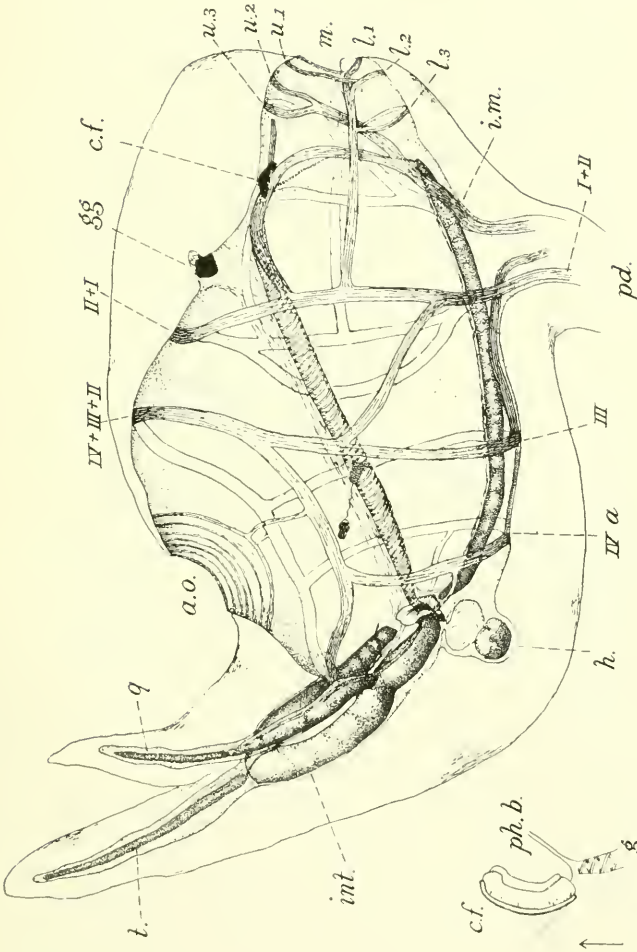


Fig. 23.

Fig. 24.

CYCLOSALPA BAKERI. AGGREGATED ZOOID. 23, YOUNG ZOOID VIEWED FROM THE RIGHT SIDE.  
 X 25; 24, CILIATE FUNNEL.

FOR EXPLANATION OF PLATE SEE PAGE 182.



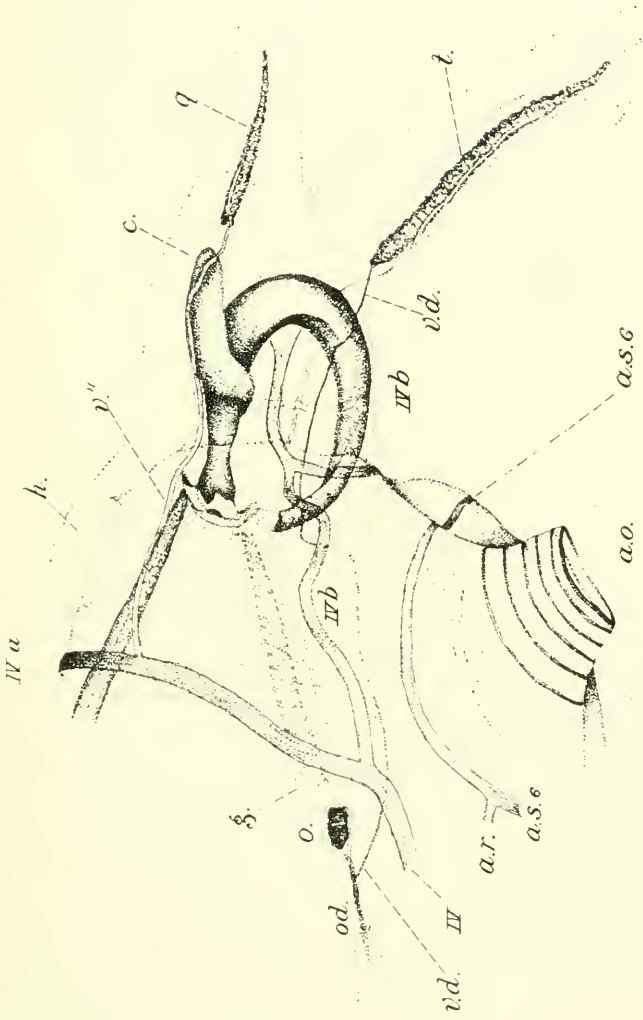


Fig. 25

CYCLOSALPA BAKERI. AGGREGATED ZOID; POSTERIOR END, MORE HIGHLY MAGNIFIED, DEXTROVENTRAL VIEW.

FOR EXPLANATION OF PLATE SEE PAGE 182.



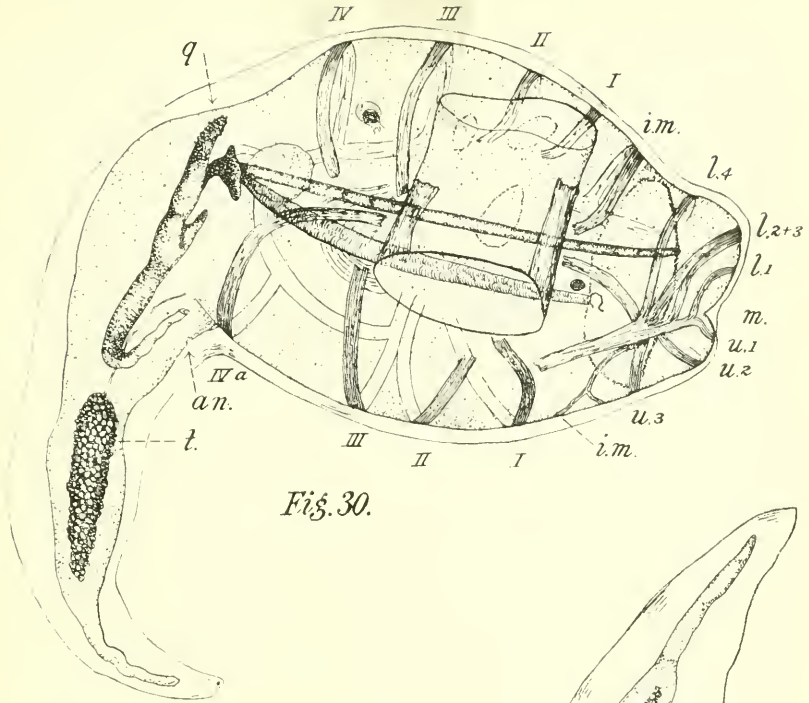


Fig. 30.

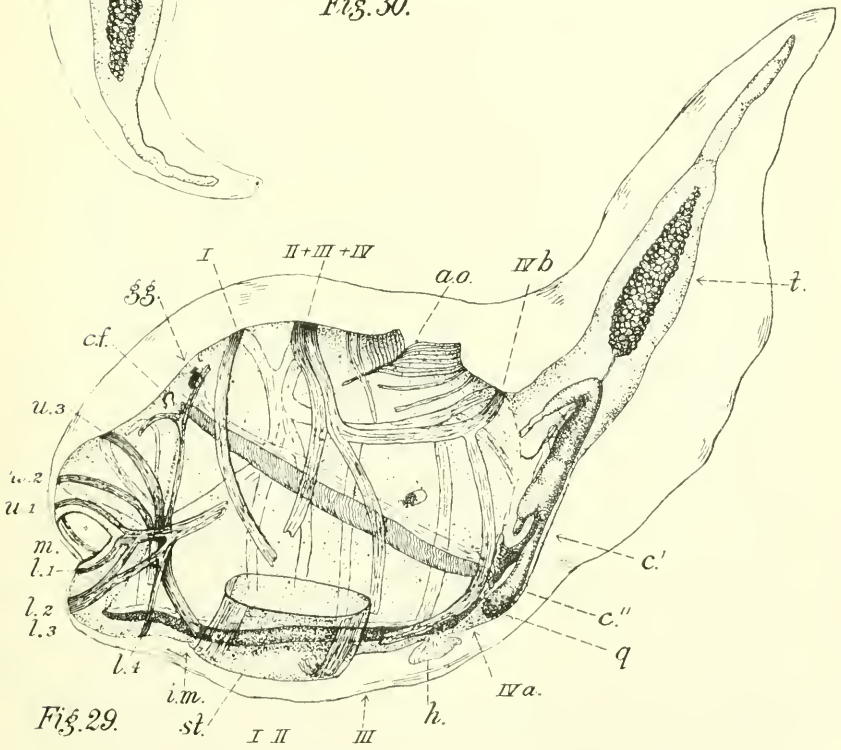


Fig. 29.

CYCLOSALPA VIRGULA. AGGREGATED ZOOID. 29, FROM LEFT SIDE,  $\times 4$ ;  
30, VENTRAL VIEW,  $\times 4$ .





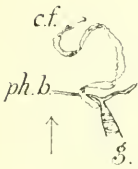


Fig. 32.

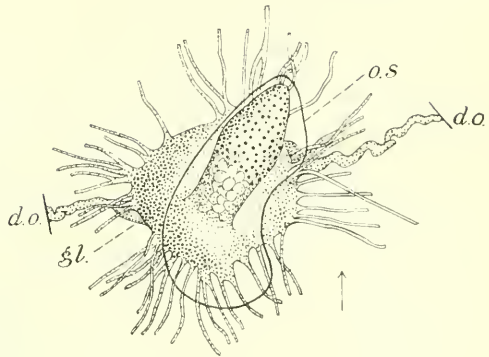


Fig. 31.

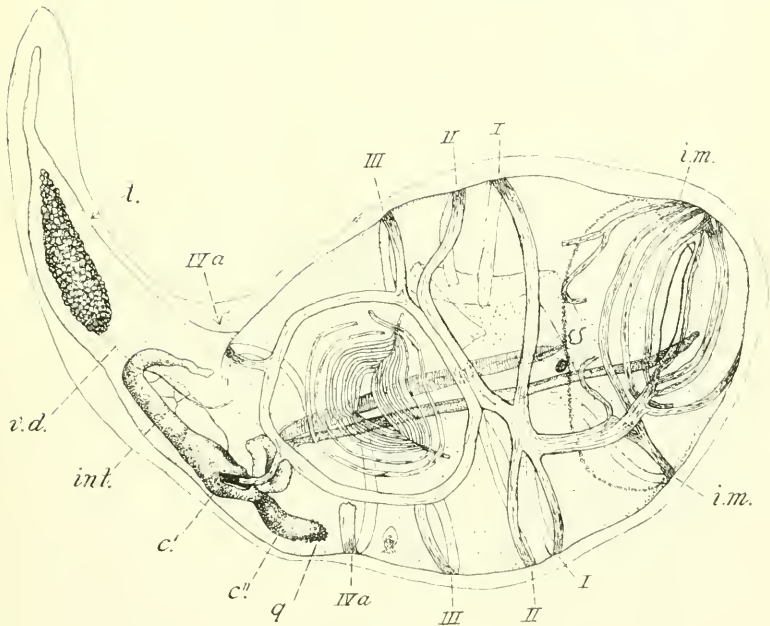


Fig. 33.

CYCLOSALPA VIRGULA. AGGREGATED ZOOID. 31, DORSAL VIEW OF GANGLION, EYE, AND NEURAL GLANDS; 32, CILIATED FUNNEL; 33, ZOOID IN DORSAL VIEW,  $\times 4$ .



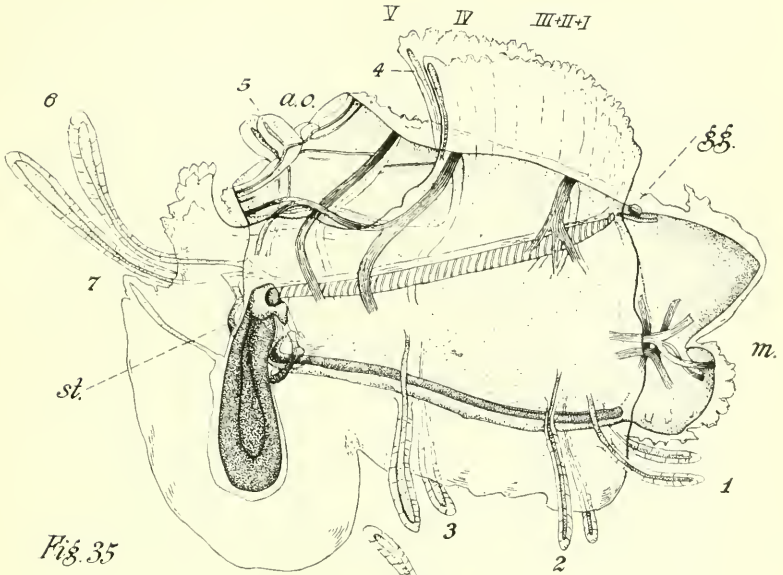


Fig. 35

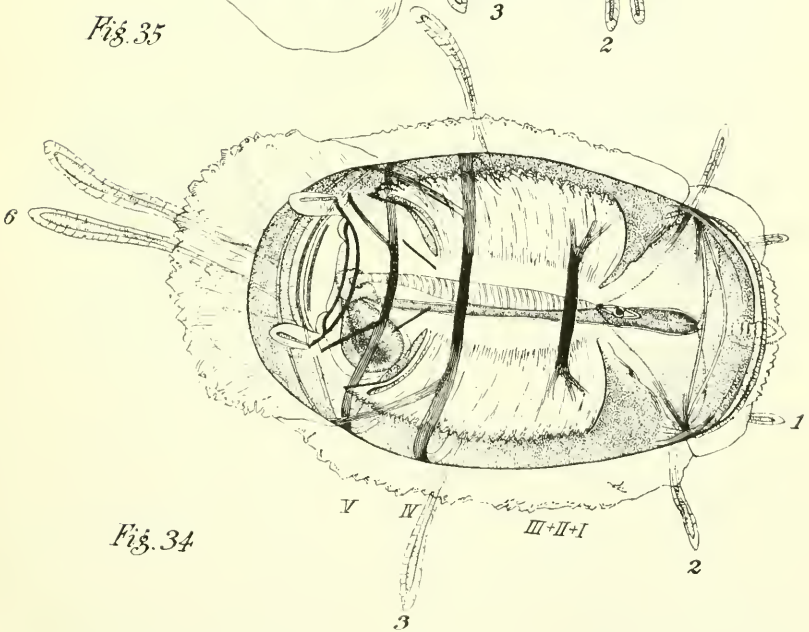


Fig. 34

TRAUSTEDTIA MULTITENLACULATA, SUBSPECIES BICRISTATA, SOLITARY FORM.  
34, DORSAL VIEW,  $\times 11$ ; 35, VIEW FROM RIGHT SIDE,  $\times 11$ .

FOR EXPLANATION OF PLATE SEE PAGE 182.



APPENDIX.

Since the foregoing paper was written the United States National Museum has obtained specimens of *Apsteinia asymmetrica* by exchange with Prof. Max Weber, of Amsterdam.<sup>1</sup> The author wishes to express his cordial thanks to Prof. J. E. W. Ihle, of Amsterdam, for arranging this exchange.

The adult individuals of both solitary and aggregated forms are so flabby and collapsed as to be difficult to study, but there is among them a beautifully preserved embryo 2½ millimeters long. As this embryo shows the muscles in essentially adult condition,

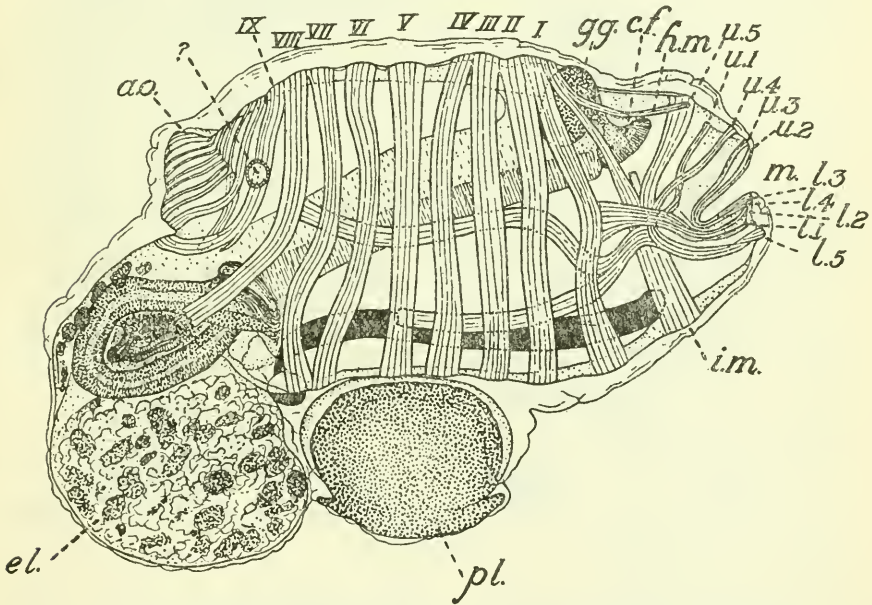


FIG. 140.—*APSTEINIA ASYMMETRICA*, AN EMBRYO 2½ MM. LONG, VIEWED FROM THE RIGHT SIDE. X 44 DIAMETERS.

it is used chiefly in the following description of the structure of the solitary individual.

*APSTEINIA ASYMMETRICA*, solitary form.

The body muscles (fig. 140) grade off behind into the cloacal sphincters in such a way that there is no sharp distinction between the two sets. Using the same notation as in *Apsteinia punctata*

NOTE.—The lettering of the figures in this appendix is the same as in the main paper. See the Explanation of Text Figures and Plates on p. 179.

<sup>1</sup> Cat. No. 6733, U. S. N. M. (immature aggregated zooids from chain). Cat. No. 6734, U. S. N. M. (solitary and aggregated forms). Cat. No. 6735, U. S. N. M. (embryo), 1 specimen.

(fig. 49, p. 72) and the *Cyclosalpas* (pl. 1, fig. 1; pl. 3, fig. 9; pl. 7, fig. 19; pl. 11, fig. 26), we might assign eight or perhaps nine to the body muscle series, preferably nine. In any case the two species closely agree in musculature, body muscle IX (or the basal cloacal muscle, if one prefers so to name it) being the same in the two, showing the same abortive anterior branch below and the same well developed posterior branch passing around the body between the cloacal siphon and the gut evagination.

The intermediate muscle is large and the horizontal muscle well developed. There are five oral sphincters in each lip. The first and

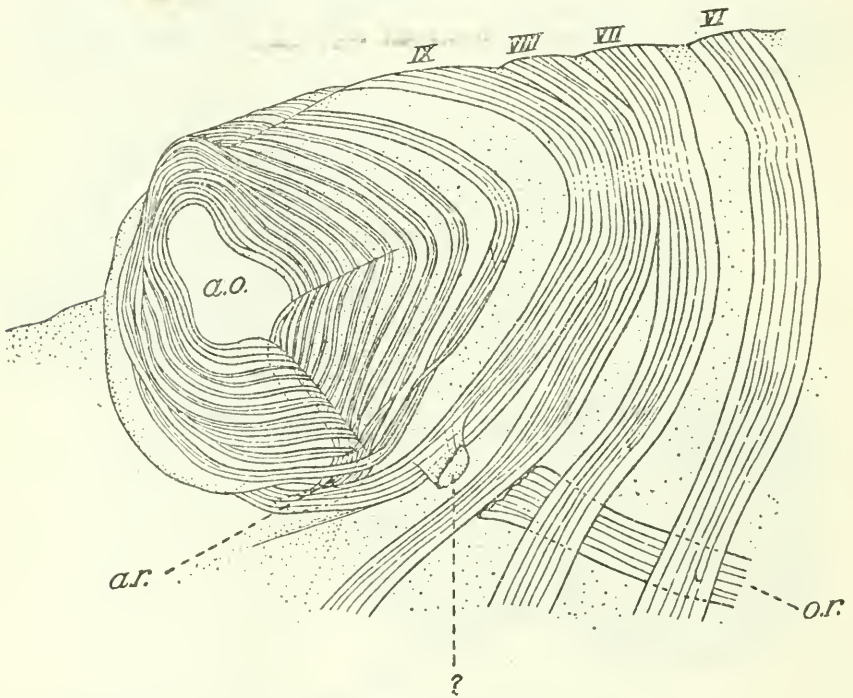


FIG. 141.—*APSTEINIA ASYMMETRICA*, EMBRYO. A DORSO-LATERAL VIEW OF THE ATRIAL SIPHON AND THE ADJACENT PARTS.  $\times 102$  DIAMETERS.

second sphincters of the lower lip lie upon the incurved portion of the lip. Posteriorly they unite to form the dorsal oral retractor muscle, which is continuous with them alone. As in *Apsteinia punctata* (figs. 49, p. 72; and 50), the posterior end of the dorsal oral retractor abuts upon the front edge of the first body muscle. Also the ventral oral retractor divides posteriorly into dorsal and ventral branches, the dorsal one of which runs back as far as the eighth body muscle, the ventral branch being shorter. In *A. asymmetrica* it reaches to the middle of the fifth body muscle, being a little longer than in *A. punctata*. The ventral oral retractor muscle divides anteriorly to form muscle 5 of the lower lip and muscle 4

of the upper lip. Muscle 5 of the upper lip is a branch of the intermediate muscle. Muscle 1 of the upper lip lies at its incurved edge. Posteriorly it is in contact with the dorsal retractor muscle and functions with it, though the fibers of the two muscles are not continuous. Muscles 2 and 3 of the upper lip are continuous, respectively, with muscles 3 and 4 of the lower lip and are not connected with either oral retractor muscle. The little blunt protuberance in figure 140, in the angle between the intermediate muscle and the fifth sphincter of the upper lip, is not a muscle, but a blood vessel.

The atrial muscles (figs. 140 and 141) form a graduated series, as in *Apsteinia punctata* (figs. 49 and 52, pp. 72 and 74), and show a similar atrial retractor.

Over body muscle IX, on each side, in the embryo, is a small, very short epithelial tube with collapsed, but not open, end. It is indicated by a question mark on figures 140 and 141. The function of these structures is doubtful, but one suspects they may serve as

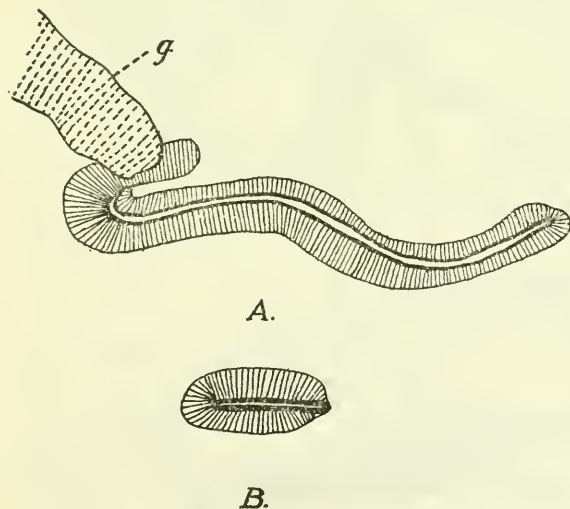


FIG. 143.—*APSTEINIA ASYMMETRICA*. DORSAL VIEWS: *A* OF THE CILIATED FUNNEL AND ANTERIOR END OF THE GILL OF AN ADULT SOLITARY INDIVIDUAL  $\times 50$  DIAMETERS; *B* OF THE CILIATED FUNNEL OF AN ADULT AGGREGATED ZOÏD.

In the adult the gut is more compact (fig. 142), really forming a so-called intestinal nucleus, though the elongated character of the stomach makes this "nucleus" less spherical than in the true *Salpae*.

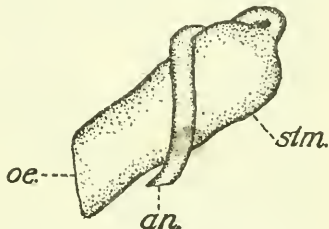


FIG. 142.—*APSTEINIA ASYMMETRICA*, SOLITARY FORM. VENTRAL VIEW OF THE OESOPHAGUS, STOMACH, AND INTESTINES FROM AN INDIVIDUAL 18 MM. LONG, SHOWING ADULT CHARACTER.

aids in attaching the embryo to its nurse. These organs are not present in our adult specimens. The much longer postero-lateral languets, shown by Apstein in the embryo of this species which he figures (fig. 58, p. 78), are probably the same structure.

The placenta and cleoblast are in the usual condition. The gut in the embryo forms an open loop around the intestinal gland.

The eye is not fully formed in the embryo we have. In the adult solitary individuals (fig. 144) it has the usual horseshoe form, except that the horns of the horseshoe are parallel and straight instead of curved.

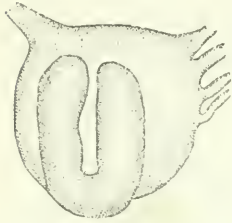


FIG. 144.—APSTEINIA ASYMMETRICA, SOLITARY FORM. DORSAL VIEW OF THE GANGLION AND EYE OF AN ADULT.  $\times 117$  DIAMETERS.

In the adult solitary individual the eloblast has disappeared with the placenta, and the intestinal "nucleus" drops down, allowing the atrical siphon to extend more backward instead of upward, the form of the body resembling that of *Apsteinia punctata* (fig. 49, p. 72).

APSTEINIA ASYMMETRICA, aggregated form.

The adult aggregated zooids in our material are so soft and collapsed that one can not determine the normal form of the body. Therefore no drawings of

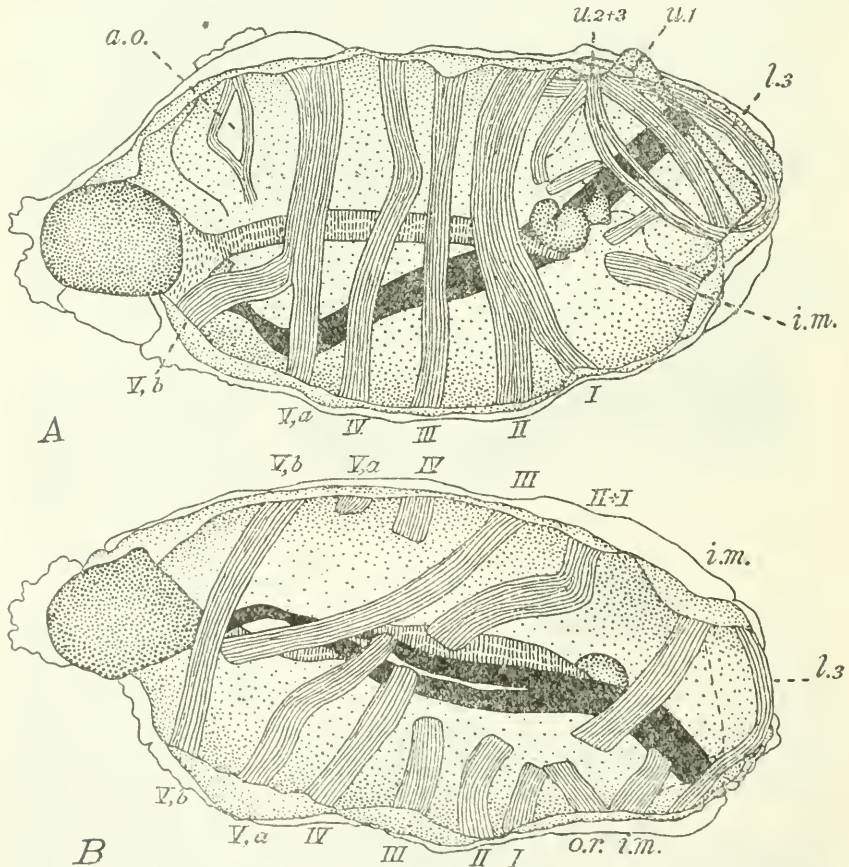


FIG. 145.—APSTEINIA ASYMMETRICA, aggregated form. IMMATURE ZOÏD STILL ATTACHED TO THE STOLON: A: DORSAL VIEW; B: VENTRAL VIEW.  $\times 63\frac{1}{2}$  DIAMETERS.

the adult are here included. There are, however, some excellently preserved young zooids still attached to the stolon. All of the



organs seem to be fully formed, except that the atrial aperture has not yet opened. The general structure, including the musculature, will be described from these small zoöids.

In dorsal view (fig. 145A) one sees that the mouth and atrial siphon are decidedly asymmetrical, right or left according to the position of the zoöid in the chain. The muscles in dorsal view show some asymmetry, and in ventral view their asymmetry is seen to be very great (fig. 145B).

*Musculature.*—There are five body muscles. I and II are fused over most of the dorsal surface. II, III, and IV are in contact, or nearly so, in the region which corresponds apparently to the mid-dorsal line. Muscles I–V, *a* are interrupted ventrally, their ventral ends being very asymmetrically placed, as shown in figure 145B. Body muscle V is branched, as is usual with the last body muscle. Its anterior branches, V, *a*, are interrupted and very asymmetrical ventrally. The posterior branches, V, *b*, are continuous across the ventral surface in front of the intestinal nucleus.

The oral muscles are best seen in side view (fig. 146). The intermediate muscles are not alike on the two sides. On the left side of a larval zoöid this muscle arises below near the endostyle, running up and back,

passing outside the oral retractor, and reaches the anterior edge of body muscle I. On the right side it rises below well to the left of the endostyle (fig. 145A), and curves up to about the level of the ganglion but does not reach body muscle I. The dorsal horizontal muscle is present on each side, stretching from the third sphincter of the upper lip to near the upper end of the intermediate muscle. There is a well-developed oral retractor muscle and three sphincters in each lip, the two sides being nearly alike. The first sphincter in each lip is submarginal and delicate. The second is wider, and the third is still broader. In dorsal view, sphincters 2 and 3 of the upper lip seem almost to form one band, but this is due to a foreshortened view of these muscles as they lie on the inclined dorsal surface of the oral siphon. In side view the true relations appear.

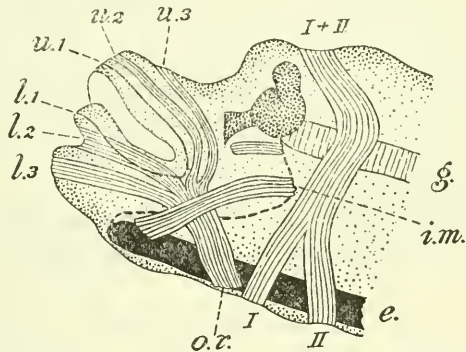


FIG. 146.—*APSTEINIA ASYMMETRICA*, AGGREGATED FORM. ORAL MUSCULATURE OF AN IMMATURE ZOÖID, VIEWED FROM THE LEFT SIDE.  $\times 63\frac{1}{2}$  DIAMETERS.

The atrial muscles in the young zoöids are as shown in figure 147, the condition evidently being one of immaturity. Over the future atrial pore lies an enlarged blood sinus, and further atrial sphincters will doubtless form in this region. There is a well-defined atrial retractor muscle on each side. There are two circular basal sphincters independent of the retractors, and three delicate distal branches of the retractors functioning as sphincter muscles. The retractor muscles are continued into the tip of the atrial siphon into the region overlaid by the blood sinus, where apparently further sphincter fibers are to be formed.

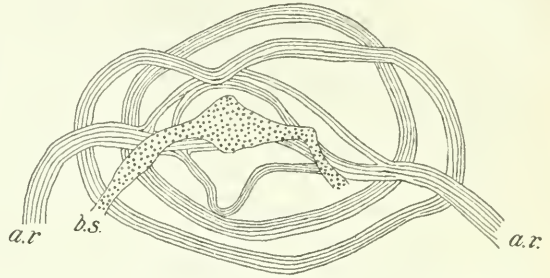


FIG. 147.—*APSTEINIA ASYMMETRICA*, AGGREGATED FORM. DORSAL VIEW OF THE ATRIAL MUSCULATURE OF AN IMMATURE ZOÖID.  $\times 184$  DIAMETERS.

The gut is a compact "nucleus." The endostyle is asymmetrical, its anterior end in a laeval zoöid bending to the left, its posterior end bending to the right.

The eyes almost exactly resemble those of *Apsteinia punctata*, as is shown by a comparison of figure 148 with figure 57 (p. 78).

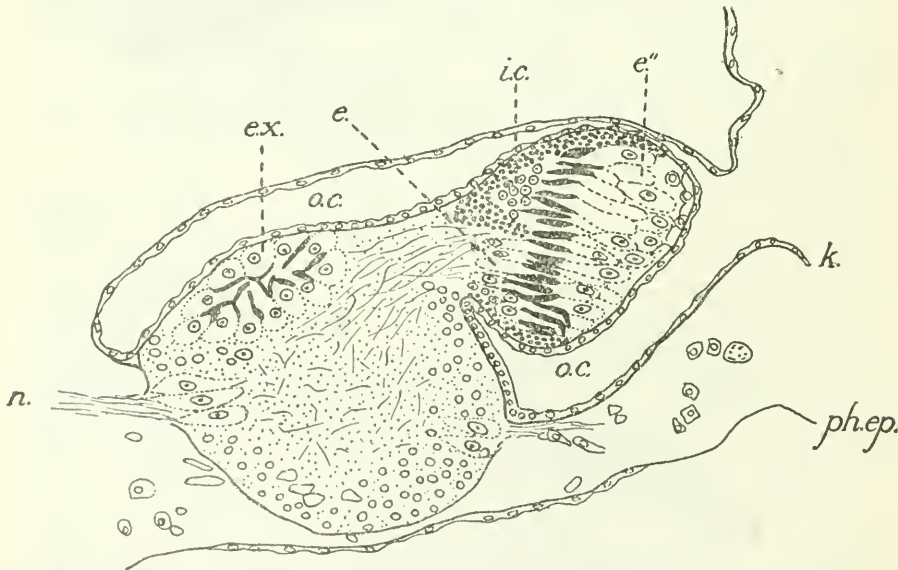


FIG. 48.—*APSTEINIA ASYMMETRICA*, ADULT AGGREGATED FORM; A SAGITTAL SECTION THROUGH THE GANGLION AND DORSAL EYE.  $\times 345$  DIAMETERS.

Observe that the zone of origin of the nerves from the ganglion (*n* in fig. 148 and *zz* in fig. 57, p. 78) is horizontal in *A. asymmetrica* and inclined  $45^\circ$  in *A. punctata*, showing that in the latter species the ganglion has rotated forward  $40^\circ$  more than it has in *A. asymmetrica*.

The neural glands (fig. 149) are about as in *Apsteinia punctata*, but the ducts and their apertures are very wide. On the posterior face of the ganglion on each side, there is a large outgrowth from the ganglion (fig. 150) containing chiefly large cells like those in the ganglion in the zone of origin of the nerves. Nerve fibers from the ganglion run into these outgrowths, and from the outgrowths



FIG. 149.—*APSTEINIA ASYMMETRICA*, ADULT AGGREGATED FORM. AN OBLIQUE VERTICAL SECTION THROUGH ONE OF THE TWO NEURAL GLANDS AND ITS DUCT.  $\times 345$  DIAMETERS.

arise some of the nerves. These postero-lateral outgrowths recall the lateral outgrowths from the ganglion of *Ritteria hexagona* (fig. 47, p. 71), but they do not contain rod cells as in the latter species. They suggest comparison also with the large-celled outgrowths from the ganglion of *Cyclosalpa* (*b'* in fig. 7, *B*, p. 18), and like the latter are not in contact with the neural glands.

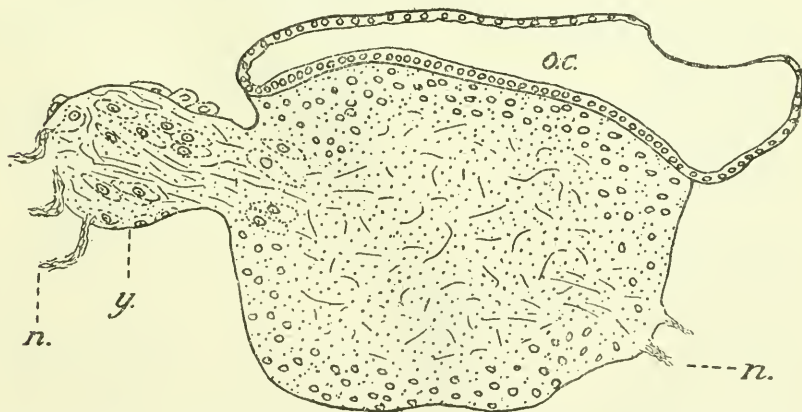


FIG. 150.—*APSTEINIA ASYMMETRICA*, AGGREGATED ZOÏD, AN OBLIQUE VERTICAL SECTION THROUGH THE GANGLION.  $\times 345$  DIAMETERS. AT *y* IS SHOWN ONE OF THE TWO LATERAL OUTGROWTHS FROM THE POSTERIOR FACE OF THE GANGLION.

It is evident that *Apsteinia asymmetrica* and *A. punctata* are very closely related. The somewhat more elongated form of the intestinal "nucleus" in the former suggests that it is probably the more primitive. The greater asymmetry of its aggregated zooid points in the same direction. (See the chart of relationships on page 158.)

The manuscript of this appendix was completed in October, 1917.



# INDEX.

	Page.
<i>affinis</i> ( <i>Cyclosalpa</i> )	7, 8,
	22, 27, 166, 173; plates 3 and 4
" <i>africana</i> " ("Salpa")	83
aggregated zoëid divergent	5, 50, 53, 142, 162
Albatross	8, 11,
	27, 32, 34, 38, 58, 62, 63, 83, 84, 87, 88, 89, 93, 94, 95,
	100, 101, 110, 118, 121, 127-130, 137, 143
alimentary canal (see gut)	
<i>amboinensis</i> ( <i>Ritteria</i> )	6, 8, 40, 53, 56, 58, 169, 174
" <i>amboinensis</i> " ("Salpa")	57
<i>Amphozus</i>	163
" <i>amphoraeformis</i> " ("Salpa")	171
<i>Anchinia</i>	162, 163
Andrews	7
" <i>antarctica</i> " ("Salpa")	171
" <i>antheliphora</i> " ("Salpa")	171
" <i>antheliphora</i> " ("Salpa")	171
Apstein	8, 32,
	36, 37, 43, 50, 51, 52, 53, 55, 56, 57, 59, 70, 78, 81, 82,
	83, 88, 92, 100, 109, 119, 127, 134, 138, 143, 147, 150,
	151, 152, 153, 154, 155, 166, 167, 168, 169, 170, 171
<i>Apsteinia</i>	8, 50, 71, 159, 173, 175, 183
<i>asymmetrica</i>	8, 9, 78, 166, 175, 183
<i>magathanica</i>	6, 8, 81, 166, 175
<i>punctata</i>	8, 71, 72, 166, 175
Ascidians	19, 162, 163, 165
<i>Ascidia mamillata</i>	19
<i>aspera</i> ( <i>Salpa fusiformis</i> )	7, 92,
	160, 161, 170, 172, 173, 175
<i>Astigma</i>	156
<i>asymmetrica</i> ( <i>Apsteinia</i> )	8, 9, 78, 166, 175
Asymmetricales	8, 49, 159, 174
Atlantic Ocean	7, 27,
	32, 34, 88, 95, 100, 110, 113, 118, 121, 128, 137, 141,
	143, 149, 166-171
<i>bakeri</i> ( <i>Cyclosalpa</i> )	7, 8,
	20, 22, 27, 37, 43, 49, 58, 166, 174; plates 7-10
<i>Balanoglossus</i>	163
Banks	173
Bell	5
" <i>beroides</i> " ("Pterolyra")	171
<i>bicaudata</i> ( <i>Pegea confederata</i> )	7, 137,
	139, 160, 161, 168, 175
" <i>bicornis</i> " ("Salpa")	171
<i>bicristata</i> ( <i>Traustedia multidenticulata</i> )	148, 171,
	175; plate 14
" <i>biennis</i> " ("Salpa")	171
" <i>bigibbosa</i> " ("Salpa")	121
" <i>bipartita</i> " ("Salpa")	171
" <i>Biphora</i> "	109, 171, 173
" <i>birostrata</i> " ("Salpa")	83
de Blainville	27, 62, 83, 109, 171, 172, 173
'blood-forming organ'	40, 56, 58
Blumenbach	109, 173
Bory de St. Vincent	171
Bosc	127, 172
Brooks	7, 9, 10, 27, 32, 34, 36, 37, 50, 83, 140, 156
<i>Brooksia</i>	71, 159, 160, 173, 174
<i>rostrata</i>	6, 50, 96, 166, 174
Browne	9, 171, 173
Bruguiere	100, 172, 173
" <i>cabotti</i> " ("Salpa")	109
California	7, 8, 38, 121, 138, 139, 166-171
" <i>caudata</i> " ("Salpa")	9
"Challenger" Expedition	137
Chamisso	27, 88, 92, 127, 171, 173
Circodæa	159, 174
" <i>cirrrosa</i> " ("Dubreullia")	109
Clavelinidæ	162, 163, 164
" <i>clostra</i> " ("Salpa")	171
" <i>coerulescens</i> " ("Salpa")	93
<i>confederata</i> ( <i>Pegea</i> )	11, 24, 127, 168, 172, 175
" <i>cordiformis</i> " ("Salpa")	100
Costa	109
" <i>costata</i> " ("Salpa")	121
" <i>cristata</i> " ("Salpa")	9
Cuvier	9, 88, 93, 121, 127, 171, 172
" <i>cyanea</i> " ("Salpa")	9, 171
" <i>cyanogaster</i> " ("Salpa")	171
<i>Cyathocormus</i>	163
" <i>Cyclomyaria</i> "	156
<i>Cyclosalpa</i>	5, 7, 8, 9, 49, 53, 70, 71, 106, 156, 159, 160, 173
<i>affinis</i>	7, 8, 22, 27, 166, 173; plates 3 and 4
<i>bakeri</i>	7, 8,
	20, 22, 27, 37, 43, 49, 58,
	166, 174; plates 7-10
<i>floridana</i>	7, 8, 20, 22, 27, 32, 37, 38,
	43, 49, 167, 173; plates 4-6
<i>pinnata</i>	7, 8, 9, 27, 167, 171,
	173; plates 1 and 2
<i>polae</i>	8, 26, 27, 160, 161, 167
<i>ringula</i>	7, 8,
	13, 21, 22, 27, 40, 43, 58,
	74, 167, 174; plates 11-13
<i>cylindrica</i> ( <i>Salpa</i> )	50, 93, 96, 169, 171, 172, 175
" <i>cymbiola</i> " ("Salpa")	171
" <i>Dagysa</i> "	9, 121, 173
Dall	88, 121, 171, 172
Delle Chiaje	9, 121, 171, 172
<i>democratica</i> ( <i>Thalia</i> )	70, 109,
	120, 139, 170, 171, 172, 173, 175
<i>Philippine form</i>	118
" <i>denudata</i> " ("Holothuria")	171
" <i>depressa</i> " ("Biphora")	171
Desor	109
Deutsche Tiefsee Expedition	55
divergence of aggregated zoëids	5, 142, 162
Dober	6, 57, 71, 78, 143, 150, 151, 152, 153, 154, 155, 171
Doliichodæa	159
" <i>dolichosoma</i> " ("Salpa")	43
Doliolidæ	155, 163, 164, 6
<i>Doliolum</i>	9, 156, 162, 163, 165, 16

	Page.		Page.
" <i>alium</i> " ("Salpa")	171	Larvacea	162, 163
" <i>ambia</i> " ("Salpa")	171	Leueur	171
" <i>Dubreullia</i> "	101	Lesson	9, 83, 88, 100, 109, 139, 168, 171, 172, 173
" <i>echinata</i> " ("Salpa")	92	" <i>lineata</i> " ("Salpa")	172
" <i>elongata</i> " ("Salpa")	171	" <i>lingulata</i> " ("Salpa")	109, 173
" <i>marginata</i> " ("Salpa")	172	Linnaeus	9, 100, 171, 173
Explanation of plates and figures	179	literature cited	7
eye	6, 10, 15+, 22+, 50, 109, 135, 157, 159;	locomotion	13, 14
also descriptions under each species		<i>longicauda</i> ( <i>Thalia</i> )	6, 109, 119, 170, 174
accessory	6, 20,	luminous organs	12, 21, 27, 32, 34
degeneration of	31, 42, 49, 62, 71, 77, 90, 98,	Macculloch	88, 172
development of	105, 108, 117, 120, 136, 142	MacDonald	173
rotation of	6, 10, 11	<i>magalhantica</i> ( <i>Apsteinia</i> )	6, 8, 81, 165, 175
" <i>fasciata</i> " ("Salpa")	172	material studied	6;
" <i>femorialis</i> " ("Salpa")	127	and data under each species	
" <i>ferruginea</i> " ("Salpa")	127	<i>maxima</i> ( <i>Salpa</i> )	10, 24, 50, 82, 83, 96, 160, 170, 172, 175
Fish Hawk	93, 110	" <i>maxima</i> " ("Salpa")	88
" <i>flagellifera</i> " ("Thalia")	109	Mediterranean Sea	166-171
Fleming	172	Metcalf	10, 11, 19, 26, 83, 98, 127, 135, 136, 165, 173
<i>floridana</i> ( <i>Cyclosalpa</i> )	7, 8,	Meyen	88, 171, 172
20, 22, 27, 32, 37, 38, 43,		" <i>microstoma</i> " ("Salpa")	100
49, 167, 173; plates 4-6		Milne-Edwards	88, 171
Forskål	9, 72, 83, 88, 100, 109, 127, 172, 173	" <i>mollis</i> " ("Salpa")	82, 172
" <i>forskalii</i> " ("Salpa")	83	" <i>moniliformis</i> " ("Salpa")	172
Fowler	70, 78, 166	" <i>mucronata</i> " ("Salpa")	109
<i>fusiformis</i> ( <i>Salpa</i> )	7, 50, 82, 83, 88, 96, 169, 171, 172, 175	Multi-stigmose	156
Gaimard	62, 100,	<i>multientaculata</i> ( <i>Traustedia</i> )	6, 143, 147, 171, 175
109, 119, 121, 127, 139, 143, 147,		muscles	5, 12+,
149, 155, 168, 171, 172, 173		21+, 50, 71, 82, 109, 120, 143, 155, 158, 157, 159,	
" <i>garnotii</i> " ("Salpa")	172	163, 164; also descriptions under each species	
Gegenbaur	156	Naples Zoological Station	7, 11, 43, 72, 83, 87, 100, 141
genera and subgenera	6, 160, 173	" <i>neapolitana</i> " ("Salpa")	121, 172
" <i>gibba</i> " ("Salpa")	127, 172	" <i>nepheoda</i> " ("Salpa")	139
" <i>gibbosa</i> " ("Salpa")	121	nerves	5
Göppert	6, 10, 24, 83	nervous system	5, 164;
Grampus	100	also notes under each species	
gut	5, 14, 50, 53, 71, 82, 109, 143; also	degeneration of	5, 6, 17
descriptions under each species		neural gland	19, 109, 157, 159;
Hawaffian Islands	7, 27, 127, 166-171	also description under each species	
Heider	109	" <i>nitida</i> " ("Salpa")	100, 172
" <i>Hemimyaria</i> "	156	<i>Octacnemus</i>	19, 20, 163
" <i>henseni</i> " ("Salpa")	152	Ola	163
" <i>herculea</i> " ("Salpa")	121, 172	Oligomyaria	159
Herdman	9, 19,	Otto	109
20, 27, 43, 62, 72, 82, 83, 92, 100,		outgrowths from gannion	20, 118,
102, 109, 121, 127, 137, 156, 172		157; and notes under most species	
<i>heragona</i> ( <i>Ritteria</i> )	8, 53, 62, 169, 174	ovary	22, 35, 41, 47
" <i>Holothuria</i> "	9, 171, 173	Pacific Ocean	7, 11,
" <i>Holothurium</i> "	173	38, 58, 62, 63, 83, 84, 87, 88, 93, 94, 100, 101, 110,	
Home	9, 121	115, 118, 121, 122, 127-130, 137, 138, 139, 166-171	
Hopkins	5, 165	Pallas	100, 173
Hopkinson	172	<i>Pegea</i>	8, 127, 142, 156, 159, 169, 175
hybridization	160, 161	<i>Pegea confederata</i>	11, 24, 127, 168, 172, 175
<i>Iasis</i>	100, 109, 150, 168, 173, 174	<i>bicaudata</i>	7, 137,
<i>zonaria</i>	100, 168, 172, 173, 174	139, 100, 161, 168, 175	
Ihle	32, 36,	" <i>pelagica</i> " ("Salpa")	172
37, 39, 40, 43, 50, 51, 53, 55, 56, 57,		Peron	127
58, 69, 92, 121, 138, 143, 147, 166, 169, 183		Philippine form of <i>Thalia democratica</i>	118
Indian Ocean	166-171	Philippine Islands	7, 8, 11
" <i>informis</i> " ("Salpa")	127, 172	38, 39, 58, 62, 63, 83, 84, 87, 88, 89, 92, 93, 94, 95,	
" <i>infundibuliformis</i> " ("Salpa")	121	100, 101, 119, 118, 121, 122, 128-130, 137, 166-171	
Johnson	7, 28, 32	<i>pieteti</i> ( <i>Ritteria</i> )	6, 40, 53, 55, 56, 58, 169, 174
Krohn	83, 88, 100, 108, 121, 168	<i>pinnata</i> ( <i>Cyclosalpa</i> )	7, 8,
" <i>laevis</i> " ("Salpa")	172	9, 27, 167, 171, 173; plates 1 and 2	
Lamarck	9, 172	Plankton Expedition	137, 139, 147, 149, 150, 154
		<i>polae</i> ( <i>Cyclosalpa pinnata</i> )	8, 26, 27, 160, 161, 167
		" <i>polyserica</i> " ("Salpa")	100

	Page.		Page.
"polymorpha" ("Salpa")	172	stolon	8, 9
"proboscidialis" ("Salpa")	9	15, 28, 34, 38, 50, 95, 146, 159, 162, 163, 164, 165	
"Pterolyra"	173	Sureiff	20, 49, 71-76, 81-85, 101-103, 106, 111, 139-141
"beroides"	171	"strumosa" ("Dagysa")	121
pulsation of body	14	"suborbicularis" ("Salpa")	173
punctata ( <i>Apostemia</i> )	8, 71, 72, 166, 175	Südpolar Expedition	138, 139
"pyramidalis" ("Salpa")	109, 172	Symmetricals	8, 9, 49, 160, 173
Pyrosoma	12, 15, 19, 162, 163, 164, 165, 166	symmetry	5, 8-10, 43, 49, 71, 82, 93, 113, 160
"Pyrosomopsis"	173	testis	22, 30, 41, 47
"quadrata" ("Salpa")	127, 172	<i>Thalia</i>	8, 29, 70, 109, 120, 159, 173, 174
"quadrangularis" ("Salpa")	172	"Thalia"	156, 171, 173
Quoy	62,	Thaliacea	162
100, 109, 119, 121, 127, 139, 143,		<i>Thalia democratica</i>	70, 109, 139, 170-173, 175
147, 149, 155, 168, 171, 172, 173		Philippine form	118
radiata ( <i>Traustedia</i> )	143, 152, 171, 175	longicauda	6, 109, 119, 170, 174
Redikorzeff	6	<i>Thetys</i>	8, 121, 156, 173, 174
retracta ( <i>Ritteria</i> )	6, 8, 40, 53, 56, 58, 169, 174	vagina	121, 168, 172, 174
"rhomboidca" ("Salpa")	172	"tilesii" ("Salpa")	121
"rhomboidalis" ("Salpa")	172	Tilesius	121
Ritter	7, 8,	Todaro	43
20, 28, 32, 37, 38, 39, 42, 43,		Traustedt	6, 32,
53, 55, 56, 58, 138, 139, 166, 169		50-52, 53, 119, 143, 150, 151, 166, 170-173	
Ritteria	8, 50, 53, 91, 80, 82, 156, 159, 160, 173, 174	<i>Traustedia</i>	5, 6,
amboinensis	6, 8, 40, 53, 56, 58, 169, 174	8, 29, 143, 149, 154, 156, 159, 160, 173, 175	
hexagona	8, 53, 62, 169, 174	multitenticulata	6, 143, 147, 171, 175
picteti	6, 49, 53, 55, 56, 58, 169, 174	bicristata	143, 171
retracta	6, 8, 40, 53, 56, 58, 169, 174	175; plate 14	
rod-cell	11, 157	radiata	143, 152, 171, 175
rostrata ( <i>Brooksia</i> )	6, 50, 96, 166, 174	"triangularis" ("Salpa")	173
"rubrolincata" ("Salpa")	172	"tricuspidata" ("Salpa")	100, 173
Salpa	50, 80, 82, 150, 173, 175	tuberculata ( <i>Salpa maxima</i> )	87, 161, 170, 172, 175
cylindrica	50, 93, 96, 169, 171, 172, 175	"unicuspidata" ("Salpa")	100
fusiformis	7, 50, 82, 83, 88, 96, 169, 171, 172, 175	United States Bureau of Fisheries	7, 31,
aspera	7, 92,	38, 110, 118, 137, 141, 179	
100, 161, 170, 172, 173, 175		United States National Museum	7, 11,
maxima	10, 24, 50, 82, 83, 96, 160, 170, 172, 175	27, 32, 34, 38, 43, 58, 62, 63, 72, 83,	
tuberculata	87, 161, 170, 172, 175	84, 87-89, 93-95, 100, 101, 110, 118,	
Salpidae	155	121, 122, 127-130, 137, 141, 143, 179	
distribution of	166	<i>vagina</i> ( <i>Thetys</i> )	121, 168, 172, 174
genera and subgenera	173	"vaginata" ("Salpa")	92, 173
key for identification	173	valve, oral	14, 21, 126
origin of	162	valve, atrial	14
speciation	162	"verrucosa" ("Salpa")	147
structure and relationships	155	vertical distribution of Salpas	27, 138, 139
unidentifiable species	171	<i>virgula</i> ( <i>Cyclosalpa</i> )	7, 8, 13,
Sars	171, 173	21, 22, 27, 33, 40, 43, 50, 52, 53, 58, 60, 70,	
Savigny	127, 173	74, 76, 77, 156, 158, 167, 174; plates 11-13	
"scutigera" ("Salpa")	127	visceral evagination ("post-abdomen")	29-34,
"Siboga" Expedition	138	40, 41, 46, 60, 112, 135	
Sigl	7	visceral muscle	21, 30, 35, 40, 49
"sipto" ("Salpa")	172	"vivipara" ("Salpa")	127
"socia" ("Salpa")	172	Vogt	7, 43, 74
Solander	173	Weber	183
"solitaria" ("Salpa")	172	zonaria ("Holothuria")	100
solitary form conservative	5, 105, 142	( <i>Iasis</i> )	9, 100, 174
speciation	161	("Salpa")	100
Sphaerodaea	159, 175	"zonarium" ("Holothurium")	100
"spinosa" ("Salpa")	109		