

PYROSOMA.—A TAXONOMIC STUDY, BASED UPON THE
COLLECTIONS OF THE UNITED STATES BUREAU OF
FISHERIES AND THE UNITED STATES NATIONAL
MUSEUM.

By MAYNARD M. METCALF and HOYT S. HOPKINS,

Of Oberlin, Ohio.

INTRODUCTION.

The family Pyrosomidae is generally regarded as containing but one genus *Pyrosoma*. There are, however, two very distinct groups in the family, the *Pyrosomata ambulata* and the *Pyrosomata fixata*, which might as properly be regarded as two separate genera. In this paper we are treating them as subgenera, although it would be equally well to give each group its own generic name. The members of the family all have the form of free swimming, tubular colonies, and they all emit a strong phosphorescent light. They are said to be the most brilliantly luminous of all marine organisms.

Pyrosoma was first described by Peron (1804), and was later more thoroughly studied by Lesueur (1815). The earlier specimens known came from the Atlantic Ocean and Mediterranean Sea, but many have since been collected from all seas, with the exception of the Arctic Ocean. About sixteen species and varieties are now known, including the new forms described in this paper, whereas previous to the year 1895 only three had been described. In that year appeared Seeliger's memoir, "Die Pyrosomen der Plankton Expedition," and this was followed by important memoirs by Neumann and others upon collections made by different oceanographic expeditions. The anatomy, embryology, and budding have been well studied, but little is known of the behavior of the living animals or of their physiology.

Our studies are based upon the remarkably rich collections of the United States Fisheries Steamer *Albatross* in Philippine waters during the years 1908 and 1909 and upon the extensive collections in the United States National Museum, made almost wholly by vessels of the United States Bureau of Fisheries, chiefly the steamer *Albatross*, which since 1883 has been almost continuously engaged in oceanographic studies. The Plankton, the German Deep-Sea and the German South-Polar Expeditions all made important collections, but all of these combined do not equal in number of types the collections of the *Albatross* Philippine Expedition. We have had for study two hundred and thirteen colonies, comprising thirteen species and varieties, including all but four of the forms of *Pyrosoma* hitherto described,

and our collections contain six undescribed forms. The abundance of material is but little less important than the number of species and subspecies represented, for the genus is one in which many of the forms intergrade in a way that can only be made to appear from study of extensive collections. We wish to express to the United States Commissioner of Fish and Fisheries and to the authorities of the United States National Museum our hearty thanks for the privilege of working upon these great collections, among the most extensive and probably the most varied ever gathered.

At the same time that work upon these collections has been going forward, there have been under way studies by the senior author upon the United States Bureau of Fisheries and United States National Museum collections of Salpidae, gathered in general from the same waters as the collections of *Pyrosoma*. Among the Salpidae, species are sharply distinct: In the genus *Pyrosoma*, on the other hand, there is such intergradation that entirely confident demarcation of species and subspecies is not possible. Intercrossing between species is not indicated among the Salpidae. Among the *Pyrosomata* it is altogether probable, cross fertilization seeming to be universal, and different forms being known to be present together in the same waters. Under these conditions it is probable that some of the forms of *Pyrosoma* found are but transient forms, the genus being in flux, interbreeding causing new combinations of characters to appear from generation to generation.

How shall such a genus be treated from the taxonomic point of view? Upon a strictly scientific definition of species every mutation, however slight the divergence, if it be a true mutation, establishes a new species with a new species mean around which is clustered a whole group of conditions due to fluctuating variation. Whether mutation is now occurring often in *Pyrosoma* we do not know. It must have been frequent in the past, establishing a remarkable series of divergent conditions in regard to many of the characters of the organism, for we find such diversity today in these characters.

Does each combination of conditions of the several characters, which we find today, represent properly a species, or are such combinations, due to the mere shuffling of characters, not to be so regarded? The first appearance of a new character, or of a new condition of an old character, arising through mutation, must be said, strictly considered, to produce a new species. Any attempt at demarcation of species on any other basis, within a mutating and interbreeding group of organisms, introduces too much of the personal judgment of the student to be truly scientific.

If into a group like *Pyrosoma* there should be introduced some influence preventing interbreeding, of course each combination of characters now present would be persistent and would represent a true species, however similar some of these species might be to one another.

If some of these forms were to be exterminated, leaving the gaps between species more evident, the specific value of the remaining complexes of qualities would be more clearly seen, but no more real.

But the treatment of each of these complexes of characters as a true species to be described and illustrated compels us to almost endless labor and produces results intelligible only to special students who have the minutest details of structure clearly in mind. It is not a practical solution of the taxonomic problem. One must adopt a more conventional conception of species than this.

In the genus *Pyrosoma*, so far as now known, there is one major line of cleavage, apparently not obscured by intercrossing. This may be indicated by recognizing two subgenera, *Pyrosomata fixata* and *Pyrosomata ambulata*, and we find that these prove to be sharply distinct. Within each subgenus so recognized, there are divergent groups of forms, and between some of these groups intergradation is not observed or is far from complete. These groups may conveniently be classed as species. Minor divergencies within these groups, where intergradation is imperfect, may be given subspecific value. There remain still, especially in the group we name *atlanticum*, a number of forms which diverge considerably at the extremes, but completely intergrade through intermediate forms. What shall we do with these? We cannot describe each condition observed. This would mean a separate description for almost each colony. We compromise by describing as a "*forma*" *dipleurosoma*, one of the most interesting conditions, and grouping the rest under the convenient but not scientifically classificatory term "*intermedium*."

What is the meaning of the taxonomic conditions described for *Pyrosoma*? What has been the history of the genus? Were the lines of cleavage into "subgenera," "species" and "subspecies," which we find to-day, established long ago, to become partially obscured by a more recent period of mutation accompanied by interbreeding, or are the subdivisions of the genus becoming established in the midst of present conditions? I do not see that the data we possess can be so analyzed as to answer these questions for us. We do not even know whether mutation is continuing at present. Until we can answer this most fundamental question there seems little chance of even valuable conjecture as to the further questions that suggest themselves.

There are, of course, many parallels to the condition of flux seen in *Pyrosoma*, especially in the *atlanticum* group. Perhaps as striking an example as any is seen in *Neretina virginica* (Metcalf, 1904), whose color and color pattern show the greatest divergence in different individuals and the most complete intergradation between any two forms one may select. Similarly the silver spot butterflies (*Argynnis*), which have been analyzed into many species, show complete intergradation between the divergent forms. The con-

ditions here, as in *Pyrosoma*, suggest constant interbreeding between numerous forms originally established by divergent mutation. In all groups of this sort, which show such perfect intergrading, species as used in taxonomy, must be purely conventional. Only in groups where physiological, or other, isolation prevails can species distinctions of any considerable magnitude and of scientific value be made. In these groups taxonomic systems can be real, can express clearly observed natural conditions. In groups like *Pyrosoma atlanticum* the lines of demarcation into subdivisions must in part be artificial.

We have assumed in the foregoing that interbreeding between divergent forms is prevalent among the *Pyrosomas*. The conditions in the genus seem different from those in a genus which is merely given to great mutation without interbreeding. Such a genus is *Opalina* among the Protozoa *Ciliata*, a genus the senior author has been studying at the same time that these studies of *Pyrosoma* have been going forward. The species of *Opalina* are numerous and there are species which intergrade between more divergent species, but the distinctions here seem to be truly specific. For example in several cases, in species so similar that one is at first doubtful if they be distinct, the number of chromosomes in the nuclei of the two forms is found to be different. This seems a conclusive distinction. In other cases the form of the mitotic figure is different in species otherwise so similar as to be distinguished only with difficulty. The isolation of the several species of *Opalina* within their often distinctive hosts, for all are parasitic, makes the possibility of interbreeding seem slight. Among the *Opalinae* we have apparently numerous species¹ truly independent, which have arisen through a strong tendency to divergent mutation, and we do not seem to have in this group any reshuffling of unit characters through interbreeding.

Salpa, *Pyrosoma*, and *Opalina*, therefore, present taxonomic conditions very interesting to compare. *Salpa* shows very distinct species which do not intergrade and are not interbreeding. *Opalina* presents species which in some cases very perfectly intergrade but apparently do not interbreed, their intergrading being due to the completeness of the response to the influences tending to produce mutants. In *Pyrosoma* there has been abundant mutation in many of the characters, and the conditions strongly suggest that at least some of the different forms are freely interbreeding, causing a permutation of the several qualities into almost all possible combinations. It would be interesting to do for *Pyrosoma* what has been done for *Opalina* and to test for some of the more similar forms the

¹ These considerations are based upon the study of a number of as yet undescribed American forms, as well as upon the well-known species.

question of their specific distinctness by determining the chromosome number. Our material, however, is not suitable for such study.

This introductory discussion of the meaning of our taxonomic distinctions has seemed necessary before entering upon the description of the different forms of *Pyrosoma*. We trust it has given the reader an understanding of the difficulties that have confronted us and will make him more kindly disposed toward our conclusions as expressed in our classification. The results are unavoidably some-

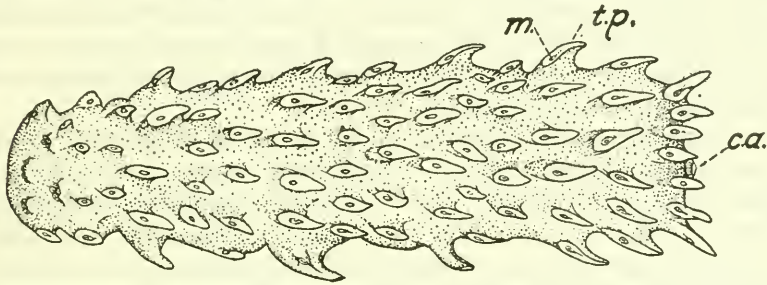


FIG. 1.—A COLONY OF *PYROSOMA ATLANTICUM ATLANTICUM*; TWICE NATURAL SIZE. AFTER RITTER (1905). FOR SIGNIFICANCE OF REFERENCE LETTERS SEE EXPLANATION OF PLATES, P. 265.

what vague and uncertain. The facts of structure of course are clear, but the digestion of these phenomena and their expression in a definitive classification is in considerable measure a matter of judgment.

GENERAL DESCRIPTION.

Pyrosoma has the form of a compact colony composed of numerous individuals or ascidiozooids imbedded in a gelatinous tube which is

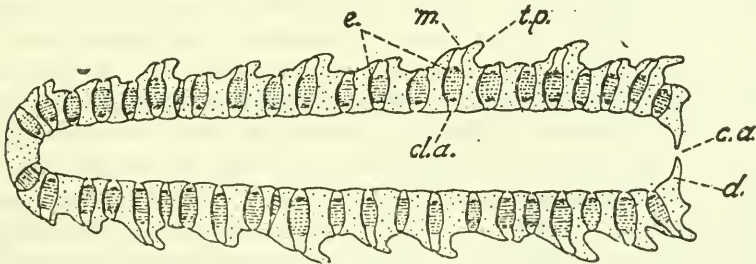


FIG. 2.—A DIAGRAMMATIC LONGITUDINAL SECTION OF A *PYROSOMA* COLONY; TWICE NATURAL SIZE.

generally rather long, of somewhat uniform diameter, closed at one end and open at the other (fig. 1). The zooids are placed with their oral apertures to the outer surface of this tube, the atriopores opening into the common axial colonial chamber. Thus the respiratory current passes from the outside, through the zooids, into the colonial tube, and thence to the exterior by way of the colonial aperture. A longitudinal section through the entire colony (fig. 2) reveals the form to best advantage. The cornus is nearly cylin-

drical, usually tapering somewhat toward the closed end. The zoöids are found to be arranged radially around the central axis. At the open end of the colony the aperture is bounded by a diaphragm, a shelflike continuation of the test, serving to narrow the aperture. This diaphragm contains numerous spindle cells, which for the most part are arranged in circles parallel with the free edge of the diaphragm, and have even been observed by Seeliger to form definite circular bands. Whether these are contractile or not is unknown. Seeliger thinks them merely elastic, but the similarity between these cells and those at the frayed-out ends of some of the muscles of the zoöids suggests strongly that they may be muscular, and effective in contracting the colonial aperture.

The thickness of the test walls is nearly uniform for each colony, and this corresponds roughly to the normal length of the zoöids; it ranges from about 0.2 cm. to 2.0 cm. This maximum thickness is reached only in large colonies of *P. spinosum*. Often the test is colorless and transparent, but in many preserved specimens it is slightly colored—yellowish, blue-green, grayish or flesh colored, the colony as a whole appearing darker because of the opacity of the zoöids.

The test may be soft and gelatinous or rigid and cartilaginous, in some forms even leathery. Usually it is fairly firm and gives to the colony some definite form, which may be characteristic of the species. It appears that in the subgenus *Pyrosomata fixata* the test is always flabby and gelatinous; even alcoholic specimens, which ordinarily are quite hard, in this subgenus are surprisingly limp.

The arrangement of the individual zoöids can be seen from a superficial examination of the entire colony. The zoöids, with only occasional exceptions, are disposed with their dorsal sides directed toward the open end of the colony. In some of the larger forms (*P. atlanticum gignatum*, *P. ovatum*) it is not uncommon to find some zoöids turned around, so that their ventral sides are directed toward the colonial aperture. Keferstein and Ehlers (1861) described this position of the zoöids as a diagnostic character of the species "*P. elegans*," but this seems unwarranted, since it is found, to a greater or less degree, in a number of species, and seems to be due merely to overcrowding of the zoöids. Seeliger thinks Keferstein and Ehlers may have been working on broken specimens, mistaking a broken end for the open end of a colony; or that perhaps they examined *P. aheriosum* colonies, which are sometimes larger at the closed than at the open end, and that they overlooked the position of the aperture. An orderly arrangement of the zoöids obtains in some species. In the young colonies of almost all types there is some degree of regularity (fig. 53, pl. 36). This may persist throughout life in the smaller, verticillate forms, but generally in a modified way (fig. 54, pl. 36); or it may become completely obliterated in others (*P.atlan-*

ticum and subspecies, pl. 34). *P. spinosum* acquires a degree of regularity in the arrangement of its zooids, but only after it becomes large and mature. It then contains longitudinal rows of zooids, those of one row alternating with those of the next. In *P. verticillatum* and a few related species the regularity arises with the earliest budding of the zooids, these coming to lie in both longitudinal and transverse rows (figs. 43 and 44, pl. 33). The longitudinal rows soon become obscured, but the transverse rows (verticils) persist.

The older distinction for dividing the genus into two groups (Savigny, 1816) according to the arrangement of the zooids in the colony, whether regular or irregular, appears not to have been well grounded. The form designated as "*P. elegans*," whose zooids were regularly arranged, was probably a young specimen of some form of the species we treat as *P. atlanticum*, since some of these forms are known to pass through a stage in which the zooids are arranged with a considerable degree of regularity. This original distinction should not be confused, however, with that which now holds good in separating the so-called verticillate forms from the others of the genus. These have all been discovered very recently (1909 and subsequently).

The test. The outer surface is never quite smooth and even. The embryo, at least in several species, when first released from the parent colony, develops spine-like outgrowths of the test, which apparently aid in suspending the young animal in the water. These are purely embryonic structures, however, which always disappear after the new colony has commenced active growth through budding. In many species of *Pyrosoma* true test processes are present on the adult colony. These processes are of two distinct types. Those characteristic of the group *Pyrosomata fixata* are small, quadrangular spines, located on the test surface, just ventral to the oral apertures of the zooids (fig. 6, pl. 18 and fig. 8, pl. 19). Originally they point slightly in the direction of the open end of the colony, thus giving one the impression that they slightly overarch the oral apertures of the zooids. The test processes of the other type, which are found in some species of *Pyrosomata ambulata*, always occur in connection with zooids; that is, each test process surmounts a zooid, whose oral siphon traverses the length of the test process to open by the mouth upon its truncated ventral surface, or at its distal end (fig. 45, pl. 34, and fig. 30, pl. 26). This relation often gives rise to long buccal siphons surrounded by the tubular outgrowths of the test (as in *P. ovatum*, *P. aherniosum*, and others. See fig. 26, pl. 25). There are no other definitive spines or processes found in any members of this sub-genus, which originate independently of the zooids. Irregularities and denticulations of the test are found, but they are, for the most part, unimportant. In some cases this roughened or denticulate condition

gives to the colony a peculiar opacity. It is occasionally of some taxonomic value, as will be noted later.

Certain other structures should be described here, on account of their relation to the colony as a unit, namely: the vessels of the tunic and the fibers connecting the cloacal muscles of adjacent zooids. Discussing the latter first, it is probably by means of these fibers that contractile movements among the individuals composing the colony are coordinated, and it may be that the simultaneous action of the cloacal muscles (and the fibers?) is effective to cause contraction of the colonial tube. In any case their action, whether contracting only the individual cloacal chambers, or contracting the whole colonial tube, must bring about locomotion by the expulsion of water from the colony through the aperture at its open end. The longitudinal fibers of the tunic vessels may share in this effect. In the performance of this function there must be some nervous coordination, some means by which the cloacal muscles in all the zooids are stimulated to contract simultaneously. Since these test fibers are the only connections between the zooids, they must be the carriers of nervous impulses from one individual to another.

The tunic vessels, above mentioned, appear in the earliest buds of the colony, as ectodermal outgrowths from their dorsal walls. Two are found in connection with each of the four primary ascidio zooids probably of all the species, and with the subsequently formed zooids of the *Pyrosomata fixata*. In the other subgenus, however, the secondarily developed buds send out but one vessel each. The tunic vessels are cylindrical tubes consisting of a single epithelial layer lined with longitudinal muscle fibers. They all end blindly in the diaphragm of the colony when this is present. They serve the purpose of a colonial circulatory system. In young colonies these vessels are well developed and functionally active, but in adult colonies they often undergo degeneration, especially the enormously elongated vessels which arose in connection with the oldest zooids.

The test is rich in test-cells. These originate in the mesoderm of the early formed buds and wander out through the ectoderm to their place in the test.

The zooids (fig. 1, pl. 15) are numerous and almost independent, being held together in a common matrix, the test. They may be examined most readily by cutting out thin sections of the wall of the colony, parallel to its long axis. The outer ectodermal sheath, the epidermis, is attached to the test only at the oral and atrial apertures. As in the other Tunicates, there are two principal body chambers, a pharynx, and an atrium with its two large peribranchial pouches. Between these two chambers, postero-ventrally and near the mid line, lie the viscera, namely, the digestive and reproductive organs and the heart. The muscles of the zooid (fig. 8, pl. 19) are only weakly developed.

All lie, in general, transverse to the long axis of the body. There are oral and atrial sphincter muscles in all species. A little behind the mouth and encircling the prebranchial chamber, are one to several fine bands or fibers, which we may call the circum-oral muscles (*c. m.*). In the *Pyrosomata fixata* there is a system of branching fibers not found in the other sub-genus, the so-called lateral muscular system. It consists of two transverse strands, a posterior one (*l. m.'*) crossing in front of the ganglion, and an anterior one (*l. m.*) in front of the endostyle, both sets branching somewhat on each side of the body. A pair of transverse, cloacal muscles (*cl. m.*) are found in all Pyrosomas. In the *Pyrosomata ambulata* these lie one on each side of the common cloaca (fig. 37, pl. 30); in the *Pyrosomata fixata* they lie over the middle of the peribranchial sacs (fig. 3, pl. 16). The cloacal muscles of one zoöid are connected with those of adjacent zoöids by means of the test-fibers already referred to.

The oral aperture leads directly into the pharynx. It is circular and is reinforced and held in position by a projecting shelf of the test. The inner epithelium inside the mouth is produced into a number of tentacle-like processes arranged in a ring. In the *Pyrosomata ambulata* only the median, ventral process can be regarded as a true tentacle (fig. 13, pl. 22); the others are really nothing more than thickened folds in the edge of the mouth, although in some species they are quite prominent. In the members of the other subgenus all of these processes are true tentacles (fig. 2, pl. 16). They are each supplied with nerve fibers and are probably sensory, for sensory cells have been discovered in the similarly placed tentacles of other Tunicates (as *Molgula*, Hunter, 1898).¹ The median, large, ventral tentacle is said by Ussow (1876) to contain otoliths in the expanded, vesicle-like portion at its base, but, on the basis of our own and other's observations, this report seems to be mistaken. Ussow's description, if it were accurate, would indicate that the tentacle functions as an organ of direction, through perception of gravity. Joliet (1888) and Salensky (1891) suggest that by distending its basal vesicle with blood the tentacle may be erected so as to close the mouth.

The pharynx shows two portions, the prebranchial chamber (buccal cavity) anterior to the peripharyngeal bands and behind this the branchial sac whose lateral walls form the so-called branchial basket, the respiratory area of the pharynx. The prebranchial chamber is sometimes very short, but in the majority of species it is more or less elongated to form an oral siphon. The water which passes through the mouth into the pharynx makes its way out through the stigmata into the right and left peribranchial sacs,

¹ Compare the less conclusive studies upon *Doliolum* by Keferstein and Ehlers (1861), Grobben (1882), and Utjanin (1884), and Neumann's discussion of the conditions in *Pyrosoma* (1909-13, p. 57).

thence into the common cloaca (fig. 3). On the ventral side of the pharynx is the endostyle, extending nearly the whole length of the branchial chamber. The endostyle in *Pyrosoma* does not differ materially from that of other Tunicates. Peripharyngeal bands, continuous with the ciliated ridges bordering the endostyle, pass around the pharynx, immediately in front of the stigmata, uniting

behind the ganglion. In the *Pyrosomata ambulata* they come together at a broad angle immediately under the ganglion (fig. 13, pl. 22), but in the *Pyrosomata fixata* they continue backward nearly parallel to each other, one-third to one-half of the distance from the ganglion to the esophageal aperture, where they come together at a very sharp angle (fig. 5, pl. 17). At the point where they unite the dorsal languets commence, the latest formed of these lying in front (fig. 7, pl. 18; fig. 17, pl. 23). The lateral ciliated cells of the endostyle are continued behind onto the postero-ventral wall of the pharynx as an indistinct ciliated band which runs to the opening of the esophagus.

In each of the branchial lamellae are a large number of stigmata which lie in rows. These originate from simple, elongated, transverse gill slits such as are seen in *Doliolum*. In *Pyrosoma* they are divided very early by the growth, across the inner surface of each branchial lamella, of longitudinal folds containing lymphatic liquid,

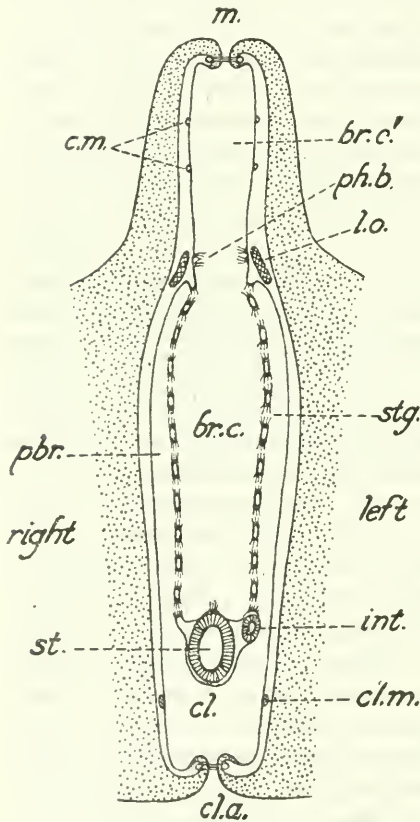


FIG. 3.—A DIAGRAMMATIC FRONTAL SECTION THROUGH A ZOÏD, OF THE ELONGATED TYPE, OF *PYROSOMA ATLANTICUM*. THE ACTUAL NUMBER OF STIGMATA IS MUCH GREATER THAN SHOWN. AFTER SEELIGER (1895).

but apparently no corpuscles (Burghause, 1914). Thus the primitive elongated slits are changed into a great number of secondary stigmata which are oblong in shape. The stigmatal rows thus formed do not always lie in a direction transverse (dorso-ventral) to the zooid, but in the *Pyrosomata fixata* they run obliquely from the postero-dorsal to the antero-ventral part of the pharynx (fig. 8, pl. 19). Each stigma is abundantly ciliated, as in other *Tunicata*. Ordinarily the branchial lamellae are oval, elongated in the axis of

the zooid; in a few species they are higher (dorso-ventrally) than long (as *P. agassizi*, fig. 3, pl. 16; *P. verticillatum*, fig. 12, pl. 21).

In *Pyrosoma* the organs of digestion resemble very closely those in other Tunicates. They are located centrally in that portion of the body wall which forms a partition between the pharynx and the cloaca. The long axis of this rather open "nucleus" is perpendicular to the antero-posterior axis of the zooid in most cases; in *P. spinosum*, however, it is distinctly oblique (fig. 8, pl. 19). The esophagus is a short, funnel-shaped tube in all species. It opens from the pharynx at its posterior end near the dorsal side, then curves downward, entering the stomach posteriorly (fig. 25, pl. 24; fig. 4, pl. 17). This latter organ is cylindrical, ovoid or triangular. It is sharply demarcated from the esophagus, but is not so distinct from the intestine. Between the stomach and the true intestine is a short, constricted portion, which may be called a pylorus (figs. 17 and 18, pl. 23). The intestinal tube runs ventrally, then curves forward and upward, and opens at the left side of the stomach into the cloacal chamber. The intestinal curve is a sharp loop in some species (fig. 17, pl. 23), while in others it is more evenly curved, or almost circular (fig. 34, pl. 28). In the *Pyrosomata fixata* the intestine curves sharply upward immediately after leaving the stomach (fig. 7, pl. 18; fig. 8, pl. 19). There is a digestive, or pyloric, gland as in other Tunicates. It lies over the distal limb of the intestinal loop as a branching system of tubules. These converge to form the common duct which enters the stomach on the left side near its ventral end (fig. 27, pl. 25).

The peribranchial chambers, one on each side of the pharynx, correspond pretty closely in contour with the branchial lamellae (fig. 3, p. 204.) They are flattened diverticula of the common atrium, extending forward just far enough to receive the exhalent water coming through the stigmata from the pharynx. The lateral walls between pharynx and atrium are very thin, consisting of endoderm, ectoderm, and but little mesoderm, abundant blood lacunae, however, being present. There are delicate trabeculae connecting the inner wall of the peribranchial chamber with the outer one.

The common cloaca, that is, that portion of the atrial chamber lying posterior to the pharynx, is of variable size, forming in most species a considerable cavity (pls. 30 and 31), but in some species it is but a shallow bay opening by a very wide cloacal aperture into the central, colonial chamber (fig. 3, pl. 16). Into the cloaca the sexual elements, the faeces, and the respiratory water are discharged; and it undoubtedly serves, in part at least, to conduct away the products of excretion, though there are no well defined renal organs in *Pyrosoma*. In this cavity, also, the embryo, in some species, continues its development for a period after becoming detached from the ovary. On account of its great diversity in size and structure, no condition of the

cloacal aperture can be described as typical. In the *Pyrosomata fixata* it is broad and of variable form (plate-figs. 3, 4, and 8); on its dorsal edge is a flattened, pointed tentacle, which will be referred to as the cloacal tentacle. In the other subgenus the aperture is usually a circular pore (pl. 29).

The small, ovoid ganglion is located dorsally, near the anterior end of the branchial basket. A pigmented layer in its ventral portion probably enables some of the adjacent ganglion cells to perceive not only the presence of light, but also its direction. From the sides of the ganglion the nerves arise, eight pairs in all (fig. 5, pl. 17; fig. 13, pl. 22). Their distribution is characteristically different in the two sub-genera. (See pp. 214 and 225.) Beneath the ganglion, closely applied to its ventral and posterior surfaces, is the subneural gland, and running forward between it and the ganglion is the duct which

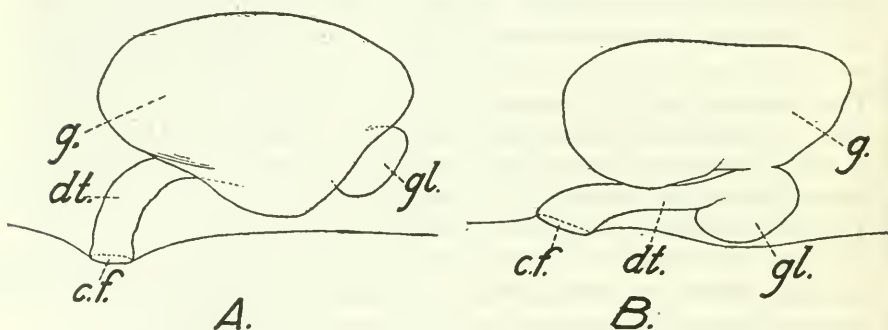


FIG. 4.—OUTLINE DRAWINGS OF THE GANGLION AND NEURAL GLAND: A, IN *PYROSOMA AGASSIZI*; B, IN *P. ATLANTICUM*. $\times 193$ DIAMETERS.

connects it with the pharynx (fig. 4). The duct in *Pyrosoma* is short and not prominent. Its aperture, the ciliated pit, is oval or round. It is directly beneath or often a little in front of the ganglion

Circulatory system (fig. 1, pl. 15). The heart (*h*) lies at the posterior end and a little to the right of the endostyle. As in other Tunicates, the heart lies within a delicate pericardium, from which it originated by dorsal, median invagination. The fold thus formed is closed along its inner side by the endodermal wall of the pharynx. Each end remains open, communicating with the blood sinuses. Of these sinuses there are three principle ones, and several of secondary importance. A median ventral sinus (*v. s.*), below the endostyle, is continuous in front with a pair of peri-pharyngeal vessels (*ph. s.*), one running along each of the peri-pharyngeal bands, and expanding laterally to contain the cells of the luminous organ (*l. o.*). These two sinuses unite around the ganglion and continue along the dorsal side of the pharynx as a median, dorsal sinus (*d. s.*). The dorsal and ventral sinuses are connected further by means of the transverse vessels of the branchial lamellae, one in each trabecula. This connection is not a direct one,

for the branchial vessels open both above and below into longitudinal vessels which lie parallel to the ventral and dorsal sinuses. There are two on each side, one above and one below, following the dorsal and ventral contours of the branchial basket. The two ventral, delimiting, branchial vessels (*v. l. s.*) are connected by numerous ducts with the median ventral sinus, and the two dorsal (*d. l. s.*) are similarly connected with the median dorsal sinus. In the region of the stomach the dorsal sinus breaks up into a ramifying system of branches, which originated in the bud from a large, undivided canal, the visceral sinus (*vc. s.*). One branch traverses the stomach and intestine before reaching the heart; others unite posteriorly to form a genital circuit, (*g. s.*), which goes to the gonads, and thence to the heart. The growing stolon is supplied with two vessels, one from each end of the heart. Two small branches of the ventral sinus, one to the oral region (*v. a. s.*) and one to the cloaca, receive blood from two corresponding branches from the dorsal sinus (*d. a. s.* and *d. p. s.*). The tunic vessel (*t. s.*) is supplied with blood from the dorsal sinus, but the blood does not circulate in it. It is through these tunic vessels that some of the mesenchyme elements pass into the cellulose test.

Blood-forming organs. On the dorsal side of the zoöid, some distance in front of the esophageal aperture, there are two elongated masses of mesoderm cells which seem to be leucocytes, lying in an expanded portion of a blood sinus (pl. 15, *b. o.*). The function of these cell masses is uncertain. They were formerly thought to be glandular. Seeliger (1895) found them to contain many actively dividing blood corpuscles, and believes them to be organs for the formation of blood cells.

The luminous organs lie one on each side of the pharynx, just over the peripharyngeal bands (pl. 15, *l. o.*). They are flat, oval masses of mesodermal cells, contained within an enlargement of a blood sinus. They resemble the blood-forming organs in general appearance and structure and in their relation to the blood stream. Their method of producing light is not well understood, though it is probably by the oxidation of a yellowish granular substance within the cells, as seems to be the case in the luminous organs of *Salpa*. Light is also emitted from cells in the region of the intestine and gonads.

Gonads. *Pyrosoma* is hermaphrodite. The organs of reproduction are found in the ventral body wall, below the digestive tract. In the *Pyrosomata fixata* the testis is closely applied to the postero-ventral side of the digestive tract (pl. 19, fig. 8, *t.*), and the egg (*ov.*) lies considerably posterior to it. In the other *Pyrosomas* the testis is at some distance from the digestive tract, the egg developing at the right of the testis (fig. 31, pl. 27). In species with small colonies

(those which reach a definitive length of about 4 cm. or less) the majority of zoöids are protogynous. The larger forms, on the contrary, contain a large number of protandrous zoöids, especially during their period of active growth. This condition seems to result from the fact that, in actively budding zoöids, the nutriment demanded by the maturing sex cells is diverted for the formation of buds; hence the development of the egg, which requires a large amount of nutriment, is delayed. The testis is an aggregate of lobes

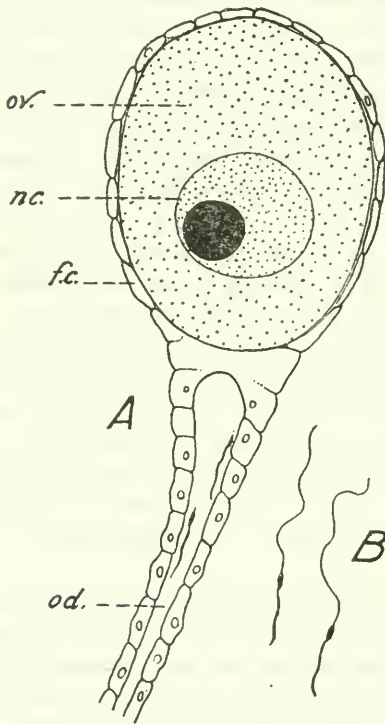


FIG. 5.—PYROSOMA ATLANTICUM PARADOXUM: A, OVARY AND OVIDUCT WITH TWO SPERMATOZOAN IN THE OVIDUCT, B, TWO SPERMATOZOAN.

forming an organ of somewhat hemispherical form, either quite compact (pl. 23, figs. 17 and 18), or, in other species, rather open (fig. 22, pl. 24), its lobes forming a sort of rosette. There are a variable number of lobes, from 12 to 20 in the majority of forms, but there may be as many as 77 in *P. spinosum*. These lobes converge on the ventral side (dorsal side in the *Pyrosomata fixata*) from which point the sperm duct arises and leads to the cloaca (fig. 22, pl. 24). The single egg lies in an ovarian vesicle formed by the outer and inner epithelia of the cloacal wall. It contains much yolk and is surrounded by a follicular membrane. In connection with the young egg is a so-called oviduct, a narrow duct dilated next to the egg, which runs forward and opens into the cloaca.

It serves as a sperm receptacle. After sperms have entered it, the aperture grows shut and the spermatozoa are retained until the egg is ready for fertilization (fig. 5).

The embryology of *Pyrosoma* is complicated, owing, first, to the large accumulation of yolk in the egg, which distorts the early stages of development; second, to the very early appearance of budding; and, third, to the fact that the cyathozoöid degenerates before reaching fully adult structure. Cleavage is incomplete and discoidal. There are formed by meridional division two, four, and then eight cells, which continue to divide more irregularly, leading to the formation of a flat germinal disk. The embryo develops from a central, thickened

portion of this disk (fig. 6). This definitive blastoderm gives rise to two thin layers, one of ectoderm cells, and another of mes-endo-dermal nature beneath it, both lying above the yolk. A cavity then forms in the mes-endo-dermal mass of cells, which corresponds probably to the archenteron. Certain cavities appearing in the axial mesoderm have been referred to as representing the notochord.

The organs of the embryo form very much as they do in other Tunicates (figs. 6 and 7). A neural rudiment (*n. r.*) is defined by the infolding of an ectodermal thickening. There is formed also a ciliated funnel (*c. f.*) communicating with the neural rudiment by a short duct. Two invaginations, one on each side of the neural rudiment, push forward for a considerable distance as peribranchial pouches (*pbr.*). Their apertures grow together later behind the ganglion, forming a

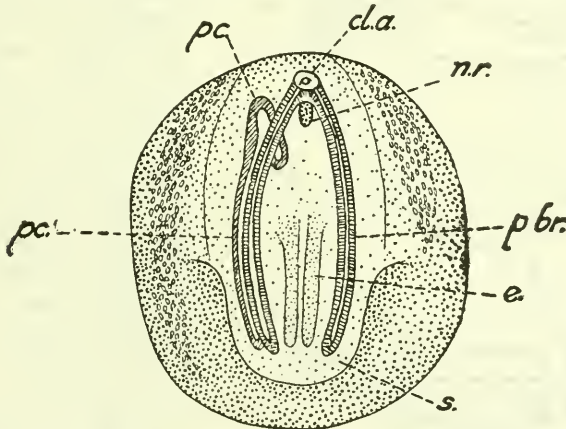


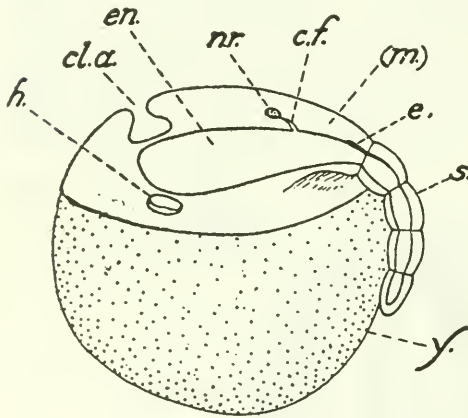
FIG. 6.—AN EMBRYO OF PYROSOMA GIGANTEUM (?). AFTER KOWALEVSKY (1875).

common cloacal aperture (*cl.a.*). The mesoderm gives rise anteriorly to a layer of cells inclosing a paired coelomic space, and this to a pair of lateral outgrowths. The right one of these, only, develops a lumen, the pericardial canal, which swells into a pouch distally. This swollen portion becomes separated off as the future pericardium, and the original canal degenerates.

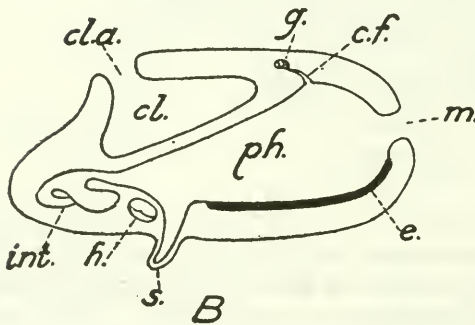
The embryo, at this stage of its development, contains an archenteron, undifferentiated mesoblast cells, a pericardium, a nerve ganglion and ciliated funnel, and peribranchial and cloacal chambers. The energy is now thrown into the formation of a proliferating stolon and the subsequent production of buds. The embryo, from this time on, ceases to become more differentiated, except in a few particulars. A functional circulatory system is evolved, by means of which the yolk nutriment of the embryo is transferred to the growing buds. This first individual, then, which develops from the egg,

the so-called cyathozooid, corresponds to the solitary form of *Doliolum* and of *Salpa* (fig. 7). In *Pyrosoma* the solitary generation is reduced to a transient, embryonic stage. This cyathozooid gives rise very early to four buds, or primary ascidiozooids, which in turn bud and form a great number of secondary ascidiozooids; and thus the colony is established.

The stolon of the cyathozooid develops very early as a prominent, sac-like outgrowth from that end of the embryo which lies opposite to



A



B

FIG. 7.—DIAGRAMS TO SHOW THE POSITION OF THE ORGANS IN A PYROSOMA CYATHOZOÏD (A) AND A SALPA (B), SOLITARY FORM. AFTER KORSCHULT AND HEIDER (1900).

the cloacal aperture (figs. 6 and 7). This outgrowth soon becomes marked off into four short segments, by partial constrictions. Each of these segments is destined to develop into a primary ascidiozooid. The stolon, originally straight, becomes curved to the left, so that by further growth it comes to encircle equatorially the yolk of the cyathozooid. The buds all lie with their ventral surfaces distal from the parent.

The earliest organs of the chain of buds originate for the most part as direct continuations of the corresponding organ rudiments in the cyathozooid. The ectoderm is directly continuous in the two. The enteric canal is a tubular outgrowth running throughout the chain.

There is found in the cyathozooid the rudiment of an endostyle-fold on the outer layer of endoderm, and this also is prolonged into the stolon. In addition to these, are a pair of peribranchial tubes, a transient pericardial tube on the right side of the body, and two strands of mesoblast cells. The nervous system has a new origin in each bud, forming as an invagination of the dorsal ectoderm.

During the growth of its buds the ectoderm of the cyathozooid secretes a layer of cellulose around itself and its buds, just within the

follicle membrane. Later, mesenchyme cells enter this secreted layer, forming the so-called test-cells. Kowalevsky thought that the atrium of the cyathozooid became the colonial cavity of the colony. According to Salensky, the cyathozooid degenerates and the colonial aperture has an independent origin. In our colonies we find embryos in which the atrium of the cyathozooid is completely overgrown by a layer of cellulose. After the four buds become more separated by the constrictions of the stolon each one enlarges through growth and then turns through an angle of 90° so as to take up a position with its dorsal side toward the cloaca of the cyathozooid. While the aperture of the colony is developing in this region each ascidiozooid sends out dorsally two ectodermal processes, the test vessels, into the test. At about this stage, or perhaps somewhat earlier, the little tetrazooid colony is set free from the cloaca of the parent zooid, passing out of the colony, and commences an independent existence. A mouth and atrial aperture form in connection with each zooid, the latter communicating with the exterior through the colony chamber. The primary ascidiozooids are now capable of growing independently and of producing buds for the further development of the colony.

We shall not enter into detail in describing the organogeny of the zooids. In the four primary ascidiozooids the processes are somewhat easier to interpret than are those in the later formed, secondary zooids. The peribranchial tubes of the stolon segment into four pairs of peribranchial pouches. These, growing together posteriorly in each zooid, form the atrium, the aperture of which appears later from an invagination of the outer ectoderm. The enteric tube likewise becomes constricted, but not completely so until quite late. From the enlarging pharynx cavity are formed several organs: the definitive endostyle, from an endostyle rudiment; a digestive tract, by evagination of the posterior (lower) side of the pharynx wall; the branchial chamber; and later the oral chamber and mouth, partly by the infolding of the outer ectoderm of this region. Gill-slits appear as elongated pores, always lying transverse to the endostyle; these are crossed by folds formed later across their inner surface (longitudinal bars). The nervous system arises from the ectoderm by invagination, as previously mentioned. The heart develops anew from a right, mesodermal cell strand very much as it does in the cyathozooid. The remaining mesoderm passes into the stolon to give rise to genital and eleoblast tissue.

In the secondary ascidiozooids the peribranchial pouches are derived, according to Seeliger, from the genital strand (mesoderm). According to this same author the neural rudiment also comes from mesoderm. But Neumann (1912) maintains that the peribranchial pouches and the nervous system arise from corresponding stolon-rudiments derived from the parent zooid, hence they are probably

ectodermal. In most other respects the development of the organs is similar in the primary and secondary ascidiozooids.

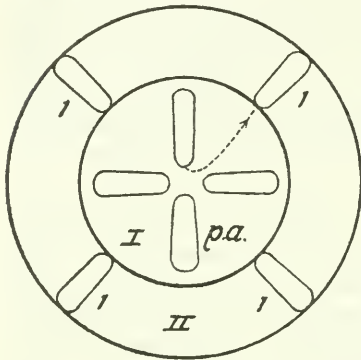


FIG. 8.—A DIAGRAM OF AN END VIEW OF A COLONY OF PYROSOMA AHERNIOSUM, WITH THE ZOÏDS PROJECTED ONTO ONE PLANE.

with the first formed four (No. 2, fig. 9). Thus far two rings, or tiers, of zooids are established; an older one of four primary ascidiozooids,

The growth and formation of the colony has been deciphered by Seeliger and Neumann for *Pyrosoma aherniosum*, and to some extent for other species, as *P. verticillatum*. Each primary ascidiozooid gives rise first to a single bud, and these buds move around to the left and occupy positions dorsal to the interspaces between the parent zooids (No. 1, fig. 8). The next set of buds produced by the primary ascidiozooids again move dorsally, this time occupying positions directly above the parent zooids, and in the same whorl

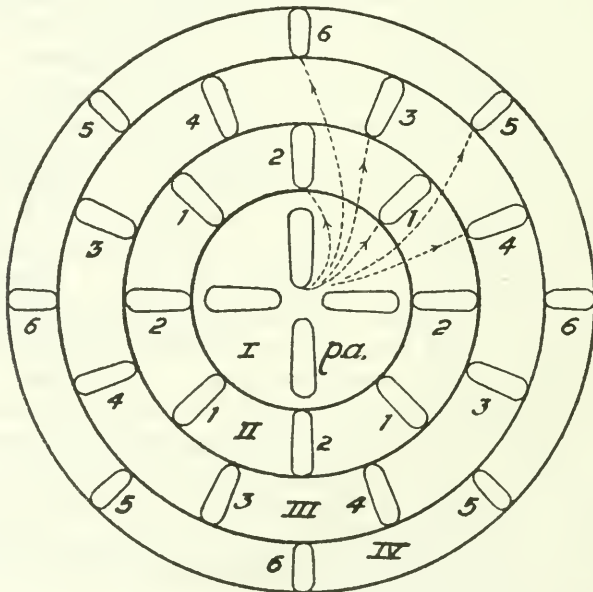


FIG. 9.—A DIAGRAM SIMILAR TO FIGURE 6, BUT ILLUSTRATING AN OLDER COLONY.

and a younger one of eight secondary ascidiozooids. Another set of four buds is again produced by the primary ascidiozooids, these occupying positions above the interspaces between the secondary zooids

of the second whorl, II (No. 3, fig. 9). In a similar manner a fourth set of four buds is produced (No 4, fig. 9), and the two sets (3 and 4) go to make up a third row (III). As many as seven or eight rows may thus be established, each row containing eight zoöids (*P. aherniosum*). At about this time, or sometimes earlier, the zoöids of the second row begin to bud, then those of the third and fourth rows, and so on. These later buds also migrate toward the open end of the colony and occupy the interspaces between the zoöids of the original transverse rows, establishing secondary rows. In this way the regularity of arrangement of the zoöids tends to be lost; in some species the transverse rows persist, but in others they disappear early.

The conditions of colony-formation thus far described, are those observed in the *Pyrosomata ambulata*. In the species *P. agassizi* and *P. spinosum*, on the other hand, the buds do not migrate freely through the test, so far as is known. Buds are produced in chains of three or four, or even as many as seven, individuals. These tend to move away from the parent zoöids and from each other, probably through the growth of the cellulose test separating them. From the first, the arrangement of the zoöids in these colonies is irregular. Large colonies of *P. spinosum* have been observed, however, in which the zoöids form longitudinal rows.

Subgenus PYROMOSOMATA FIXATA.

The *Pyrosomata fixata* are sufficiently distinct from the *Pyrosomata ambulata* to justify recognizing both as genera, but in this paper we have chosen arbitrarily to treat the two groups as subgenera.

The method of budding, so far as it is now known, is sharply distinct in the two subgenera. It has been taken by Neumann (1909-13) as a basis for naming the two groups. Among the *fixata* the buds form by the constriction of a proliferating stolon, produced at the posterior tip of the endostyle. As soon as one has been formed as a definite bud at the tip of the stolon, others form successively between it and the parent zoöids. There is formed thus a chain of several small buds of different sizes, as many as 7 having been observed in *P. spinosum*. The buds do not separate until comparatively late, and there has been observed no active shifting in their position, such as occurs in the *Pyrosomata ambulata*. Each takes its place ventral to the parent zoöids, so that in old colonies they show a semblance of regularity, lying apparently in longitudinal rows. It has not yet been determined just how the buds become distributed in the colony—whether the primary ascidiozoöids remain at the closed end of the colony, or around its aperture, all the buds taking positions ventral to them. Young colonies are needed for such study.

Each bud, when formed, sends out two tunic vessels from its dorsal side, which extend as far as the aperture of the colony. This is true of the secondary zoöids, but is true only of those which lie rather close to the aperture of the colony. The condition in the primary ascidiozoöids has not been determined.

Characteristics of the colony. The test is always of a soft and gelatinous nature, and ordinarily is transparent and colorless. The test processes are very characteristic of the group, being small, sharp, quadrangular spines, which always develop ventral to the zoöids and do not carry their oral apertures (fig. 6, pl. 18; fig. 3, pl. 16). There is no diaphragm at the colonial aperture, or only a rudiment of one. Some colonies bear four processes of the test projecting beyond and surrounding the colonial aperture (fig. 6, pl. 18).

The zoöids. The most striking feature in connection with the zoöids is the oblique position of the rows of stigmata in the branchial lamellae. This condition is very apparent in *P. spinosum*, (fig. 8, pl. 19), the stigmatal rows, instead of being vertical, having shifted over eighty degrees, until they lie almost parallel with the antero-posterior axis of the zoöid. In addition the branchial basket is broader in the direction of the stigmatal rows than at right angles to them.

The oral aperture bears several true tentacles (fig. 2, pl. 16), in addition to a median, ventral tentacle found in all *Pyrosomas* (fig. 13, pl. 22). The peripharyngeal bands come together at a sharp angle considerably posterior to the ganglion (fig. 5, pl. 17). Besides the luminous organs lying on each side of the pharynx, there are two other cell tracts, one on each side of the cloaca, near its ventral side (*l. ó.*, fig. 8, pl. 19), which probably have a similar function. There is no blood-forming organ on the dorsal side of the body, but Neumann (1909-13) believes that it is represented in this group by a mass of mesoderm cells lying around the digestive tract.¹ The endostyle is rather large in the members of this group, and shows histological features which, though characteristic, are not mentioned here, because they are of little taxonomic interest.²

In connection with the nervous system (pl. 16, fig. 2, and pl. 17, fig. 5) there should be noted the relatively large size of the ganglion, the slightly longer duct of the sub-neural gland (fig. 4, A), which opens directly beneath the ganglion, and the distribution of the nerves. This last is characteristically different in the two subgenera, as may be seen by comparison of figures 5 (pl. 17) and 13 (pl. 22). The first, second, fifth, and seventh nerves are the more prominent. Each of the peribranchial (cloacal) muscles is innervated by a prominent unbranched nerve, the seventh, while the fifth nerve goes to the

¹ Compare *Salpa virgula*, aggregated zoöid. (Metcalf and Bell, 1918.)

² For details of the structure of the endostyle, and figures of same, see Neumann (1909-13).

cloacal sphincter, and the eighth, reduced in size, goes to the stolon process of the bud. In other respects the distribution of the nerves is somewhat similar in the two subgenera.

The cloaca is diverse in size and shape (fig. 3, pl. 16; fig. 8, pl. 19). Its aperture is broad and bears on its dorsal edge a flat tapering languet (cloacal tentacle). The cloacal sphincter is incomplete, being broad and well developed on the dorsal edge, and lacking on the ventral edge (fig. 8, pl. 19).

The musculature is unique in some respects (figs. 2 and 3, pl. 16; fig. 8, pl. 19). The pair of muscles found one on each side of the cloaca in the *Pyrosomata ambulata*, are represented here by similar bands, but lying over the peribranchial spaces, near their middle. A variable number of branching and anastomosing muscle fibers surround the oral sphincter. Between the mouth and the ganglion, and between the mouth and the endostyle, are muscle fibers which branch on each side of the body. These constitute the lateral muscle system, which is peculiar to this group of the Pyrosomas.

Gonads. The testis forms between the stomach and the intestine (fig. 9, pl. 20; fig. 4, pl. 17), and consists of numerous, short lobes radiating toward the ventral side of the zoïd. The egg lies posterior to it. The large embryo is detached from the parent relatively early. Zoïds protandrous.

PYROSOMA AGASSIZI (Ritter and Byrbee, 1905).

Plates 16, 17, 18, and fig. 42, plate 33.

This species was first described from material taken from the Pacific Ocean. Subsequently it has been reported from the Atlantic and Indian Oceans. Our specimens come from the Pacific. We have seventeen in all, from ten different stations, and these agree very closely with the original description of the species. Some are preserved in alcohol, others in formalin.

The colony is rather long and slender, and is always limp because of the soft, gelatinous nature of the test. The test itself is very transparent, the zoïds being rather opaque. They are yellowish in the colonies preserved in alcohol, whitish in the formalin specimens. Usually there are present, at the open end of the colonial tube, four rather large processes of the test which are of variable length, and are quadrangular in cross section (fig. 6, pl. 18). One angle is toward the colonial aperture, one is on the opposite side, and two are lateral. The outer and the lateral of these ridges continue back onto the surface of the colony, which bears generally twelve ridges near its open end. Toward the closed end of the colony the arrangement of the ridges is less regular, instead of twelve, ten or less being found. Some of our colonies have the ridges less marked. The ridges at the closed end of the colony and those at the open end are for the most part not

directly continuous, the arrangement over the middle of the body being confused by the interruption of most of the ridges and the suppression of others. In some of the larger specimens the processes at the open end of the colony are entirely lacking. It may be that we have here a retrograde variety characterized by the absence of these processes. In addition to the ridges, there are always present on the test the small quadrangular spines so characteristic of members of this subgenus (fig. 6, pl. 18). If anything, they are a little less numerous than in *P. spinosum*. On some colonies they are rather inconspicuous; the largest reach 5 mm. in length (Ritter and Byxbee). The relative dimensions of the colony do not vary widely. Small colonies are more fusiform, or taper more toward the closed end, than do large ones. All our preserved specimens are flattened except for one or two very young colonies. We can not be at all certain whether this flattening is natural or due to collapsing in preservation because of the extreme softness of the test. The colony is described as cylindrical by Ritter and Byxbee, who state that the diameter of a 12 cm. colony is about 1 cm. Our larger specimens do not exceed 8-11 centimeters in length, and this seems to be the maximum length attained by the majority of specimens of this species, according to other writers (*see* Neumann, 1909-13, p. 13), but since no colonies of this species bearing sexually mature zoöids have been reported, larger specimens may be found. Possibly at the time of sexual reproduction this *Pyrosoma* lives customarily at considerable depth.

The zoöids are arranged in the test irregularly (fig. 42, pl. 33). It is possible that they assume a more regular arrangement in longitudinal rows in the oldest colonies, as this is the case in the nearly related species, *P. spinosum*. The dimensions of our largest zoöids, in each of which is visible a small mass of cells between stomach and intestine, probably the forerunner of the testis, are as follows: length, as measured from the mouth to the atrial aperture, 2.5 mm.-3.2 mm.; height, measured dorso-ventrally at right angles to the longitudinal axis, 2.5 mm.-3.5 mm. From these figures it will be seen that the zoöid is higher than long. This appearance is emphasized by the fact that the disproportionate height of the branchial basket is even more marked, it being elliptical with the greater axis vertical. The oral and cloacal chambers are very much reduced. The rectum opens almost directly into the common colonial chamber because of the shallowness of the cloaca.

The mantle is a thin, delicate lamella in which the cell layers, ectoderm, endoderm, and mesoderm can scarcely be distinguished, so intimately are these fused together. The muscles associated with the mantle may be roughly assigned to three systems more or less independent of each other. Those of the oral region consist of an oral sphincter, and outside of this a variable number, three or four,

of anastomosing circum-oral fibers. These latter are generally not present in young zoöids (fig. 7, pl. 18),¹ hence they seem to be of secondary development. In the lateral muscular system one finds ordinarily one ventral cross-strand in front of the endostyle (*l. m.*) and a dorsal set of about three strands just in front of the ganglion (*l. m'*). The ventral strand branches once on each side of the zoöid; the three dorsal strands may branch once or twice on each side. In many of the older zoöids there is but one transverse band on the dorsalside, and this does not branch greatly (fig. 3, pl. 16). The fact that in this species the lateral muscular system is less developed in many adult zoöids than in the buds, and the further fact that this system is always still more developed in *P. spinosum*, indicate that, as regards the lateral muscles, *P. agassizi* is secondarily simplified. The branches from the two sets of fibers do not unite distally, as in *P. spinosum*. There is often a connection, however, between the dorsal portion of the lateral musculature and the circum-oral rings, by means of two connecting fibers, one on each side of the zoöid (fig. 3, pl. 16). The cloacal muscles, one lying on each side of the pharynx, over the peribranchial chamber, are rather long and slender (fig. 3, pl. 16). The dorsal end of each is connected with the ganglion by a prominent unbranched nerve, the seventh (figs. 3, pl. 16, and 5, pl. 17). There is a cloacal sphincter which is developed rather strongly on the dorsal side of the aperture but scarcely at all on the ventral side (fig. 3, pl. 16).

The pharynx. The oral aperture opens almost directly into the branchial chamber proper. It is relatively wide and bears a prominent fringe of true tentacles, these being fairly constant in number. There is one median tentacle which is the longest, and 16 to 18 others, arranged in most cases with an appearance of bilateral symmetry (fig. 2, pl. 16). The branchial chamber proper is broad and elliptical. The endostyle curves strongly near its anteroventral end. The dorsal languets, about 5 or 6 in number, commence just at the posterior termination of the peripharyngeal bands and continue back to the esophagus (fig. 7, pl. 18). They are fairly long but never very prominent. There are about 16 branchial bars, occasionally as many as 17, and from 20 to 31 stigmatal rows, usually 26. The stigmata in this species, instead of lying at right angles to the longitudinal axis of the zoöid, are so placed as to form an angle of 50° to 70° with this axis; that is, the stigmatal rows run from the antero-ventral side of the animal upward obliquely toward the postero-dorsal side. In the following species (*P. spinosum*) this angle is even smaller, 5°-20°.

Luminous organs (*l. o.*). These are best seen in young, actively growing colonies. They are variable in size and shape, usually quadrangular or elliptical, and are not at all prominent. As the

¹ See to the contrary Neumann, 1909-1913, p. 92.

zooids grow older the cells composing them become scattered and in some instances disappear.

Nervous system (figs. 2, pl. 16, and 5, pl. 17). The ganglion is rather prominent. The distribution of the nerves connected with it is characteristic of the subgenus, as above described. The duct of the subneural gland bends downward strongly before opening into the pharynx (fig. 4 A, p. 206).

Digestive tract. The esophagus, a short funnel-shaped tube, enters the stomach posteriorly near its middle (figs. 3, pl. 16, and 4, pl. 17). In consequence of this peculiar juncture, the stomach has a cloven or bilobate appearance. The intestine is rather wide and forms an evenly curved loop, the oval anal opening lying opposite to the dorsal end of the stomach on the left side. The digestive gland is by no means conspicuous in this or in the following species (*P. spinosum*). Over the gut it presents a few small ridges, which converge to form the common duct of the gland.

As before mentioned, the cloaca is very broad and short. Its aperture is rather broad also, circular in outline, or broadly heart-shaped (fig. 4, pl. 17). There is a tentacle on its dorsal edge in large zooids; in the immature zooids this is represented by a small thickened prominence, or papilla, which shows the origin of the tentacle (see figs. 3, pl. 16, and 7, pl. 18). This tentacle is flat and triangular, and tapers to a narrow point when fully grown; its maximum length about equals the width of the atriopore.

Gonads have not previously been observed in *P. agassizi*. In the zooids of one of our colonies we find what we take to be the developing testis (fig. 4, pl. 17). It lies between the two limbs of the digestive tract, and consists of a number of indistinctly demarcated groups of cells, which give a vague appearance of radiating from the central mass. No duct could be discovered leading away from it. The egg was not found, hence we are led to believe that some of the zooids, at least, are protandrous.

Occurrence and distribution. *P. agassizi* is known to occur in the southern Atlantic, Indian, and Pacific Oceans. It seems to be most abundant in the Pacific.

Specimens of *Pyrosoma agassizi* were obtained at the following dredging stations during the *Albatross* Philippine Expedition, 1907-1910:

D. 5126, Nogas Islands, Sulu Sea, vicinity of southern Panay; Feb. 3, 1908; 742 fathoms; surface temperature 80° F.; one specimen, Cat. No. 6488, U.S.N.M.

D. 5233, Limasaua Island, between Bohol and Leyte; May 7, 1908; 15 fathoms; surface temperature 84° F.; surface density 1.02531; one specimen, Cat. No. 6422 U.S.N.M.

D. 5320, China Sea, vicinity of Formosa; Nov. 5, 1908; 1,804 fathoms; surface temperature 80° F.; one specimen, Cat. No. 6423 U.S.N.M.

D. 5378, Mompog Island; Mar. 4, 1909; 395 fathoms; one specimen.

D. 5458, Legaski Light, east coast of Luzon; June 7, 1909; 200 fathoms; surface temperature 85° F.; one specimen.

D. 5498, Bantigui Island, between Leyte and Mindanao; Aug. 3, 1909; 960 fathoms; surface temperature 82° F.; one specimen, dried out.

D. 5514, Camp Overton Light, vicinity northern Mindanao; Aug. 8, 1909; 697 fathoms: surface temperature, 83° F.; one specimen, Cat. No. 6489 U.S.N.M.

D. 5543, Tagolo Light, vicinity northern Mindanao; Aug. 20, 1909; 162 fathoms; surface temperature 84° F.; one specimen, Cat. No. 6424, U.S.N.M.

D. 5607, Binang Unang Island; Gulf of Tomini, Celebes; Nov. 18, 1909; 761 fathoms; surface temperature 83° F.; one specimen, Cat. No. 6512 U.S.N.M.

D. 5214, East of Masbate Island, Philippine Islands; April 21, 1908; surface; surface temperature, 81–82° F.; surface density 1.02475; two specimens, Cat. No. 6618, U.S.N.M. These specimens we have not had for study.

D. 5518, northern Mindanao and vicinity, Philippine Islands; Aug. 9, 1909; surface; surface temperature, 85° F.; one specimen, Cat. No. 6617, U.S.N.M. This specimen we have not had for study.

Three specimens Cat. No. 6499, U.S.N.M. were also obtained at *Albatross* station D. 3388, latitude 7° 06' N.; longitude 79° 48' W. off the Pacific coast of Panama; March 9, 1891; 1,168 fathoms; surface temperature 73° F.

Characteristic specimens of this species are found in the United States National Museum Collections, Cat. Nos. 6422, 6423, and 6424.

PYROSOMA SPINOSUM (Herdman, 1888).

Plates 19, 20, and fig. 11, plate 21.

This species was the first of its subgenus to be discovered. Its unique character seems to have been overlooked to some extent until later studies showed that it was organized upon a somewhat distinct plan. In fact, it has been proposed by some writers to place this species and *P. agassizi* together in a different genus from other Pyrosomas. The studies which have previously been made of this species were conducted chiefly upon Atlantic specimens, though Indian Ocean specimens have also been studied. We have two specimens from the Pacific, and one from the Atlantic Ocean, and in these we find a few new points of interest.

The colony. It is extremely difficult to secure material of this species suitable for describing the colony-form. Our specimens, like most of the others known, are fragmentary, in consequence of which

the proportions of the colony cannot be determined. The colonies appear to be cylindrical for the most part, and to taper but slightly toward the closed end; more than this we can not assert. The test is soft, gelatinous and extremely flabby. It is colorless in our specimens. On its outer surface there are numerous quadrangular, or triangular, spines such as we described for *P. agassizi*, each one placed ventral to, and overarching the oral aperture of a zoöid, (pl. 19). Organs corresponding to the four elongated "tentacles" surrounding the colonial aperture in *P. agassizi*, have not with certainty been found in this species. Krüger (1912) has described as *P. agassizi* an Atlantic *Pyrosoma* which apparently is no other than *P. spinosum*. As described and figured we would have no hesitation in assigning it to the latter species, for it has the characteristic form of zoöid, somewhat immature, and the complex musculature, numerous stigmata, etc., peculiar to this species. But some of the colonies are described as possessing four processes of the test, surrounding the colonial aperture. We are uncertain whether this remark is meant to apply to Krüger's specimens, or to *P. agassizi* in general, according to previous descriptions. If the former is the case, it would indicate that some colonies of *P. spinosum* do bear these four processes. Since they have been found to be so irregular in occurrence in *P. agassizi*, it seems likely that they may be so in *P. spinosum*; that is, present in some cases, absent in others, or perhaps large in young colonies and sometimes absorbed in older ones. Farran (1906) reports *P. spinosum* from the North Atlantic Ocean, figuring the colony with four test processes around the colonial aperture, but no adequate description of the zooids is given. There is no colonial diaphragm. The size of the colony is in a way rather distinctive; that is, the largest colonies of *Pyrosoma* reported belong to this species. Bonnier and Perez (1902) found specimens in the Indian ocean of enormous size, the largest 4 m. long; others $2\frac{1}{2}$ m. long, 20-30 cm. in diameter. The majority of the specimens collected, however, do not exceed 50 cm. in length.

Zoöids. An irregular arrangement of the zoöids in the test obtains in the younger colonies of *P. spinosum*. Large specimens have been found in which there is a fairly regular arrangement of the zoöids in longitudinal rows, those in one row occupying alternate positions to those in the adjacent rows (Herdman, 1888). Rather characteristic of this species is the thickness of the test wall, and coordinated with this, the extraordinary length of the zoöids. Mature individuals, from medium-sized colonies, measure 0.8 cm.—1 cm. in length from the mouth to the base of the cloacal tentacle. The largest ones known are fully 2 cm. long (see Neumann, 1909-'13). They are about 3 mm. to 4 mm. in width. We find in our specimens that the ventral side of the zooid is directed toward the closed end of the colony, as we might

expect, a point not definitely ascertained by other workers, on account of the poor condition of their material.

The mantle is thin and delicate.

The musculature is fundamentally similar to that in *P. agassizi*, but is much more highly developed (pl. 19). The fibers of the lateral muscular system are numerous and complexly interwoven. The dorsal portion, consisting of 8–10 long branches, is connected distally on each side of the animal, by two or three strands, with the ventral portion, which has about 4 branches. Some of the dorsal fibers are fused with the thick cloacal muscle. Around the oral aperture, outside of the sphincter, are an indefinite number of circum-oral fibers which are simple on the ventral side, but dorsally branch and anastomose freely with each other and with the oral sphincter. Their maximum number is 7 or 8. The cloacal muscle, over the peribranchial region, is short and thick. It runs nearly parallel with the long axis of the colony. An atrial sphincter is present on the dorsal edge of the cloacal aperture as a broad band. It does not extend more than halfway around on each side of the aperture.

In this species the prebranchial chamber is more prominent than in *P. agassizi*, but is never prolonged into a siphon. The oral aperture is a little sunken beneath the surface of the test. It bears a circle of long tentacles, about 15 in number, of variable size, the median ventral one longer than the rest.

The branchial chamber proper is a greatly elongated cavity, whose stigmatal rows lie at an angle of about 10° to the longitudinal axis of the zoöid. It is elliptical in contour and a trifle narrower at the anterior than at the posterior end. Each of the delicate branchial lamellæ bears about 55 narrow stigmatal rows and a large number of bars, 30–44, which in this species run nearly transverse to the principal axis of the zoöids. The anterior third of the endostyle is curved sharply around the front of the pharynx, so that this portion of it really bounds the anterior end of the zoöid. From its forward end the peripharyngeal bands pass diagonally toward the ganglion, continuing distinct posterior to it for quite a distance. At the point where they unite the dorsal languets commence. There may be as many as 22 of these (Neumann). We find in our Pacific specimens only 9 or 10, all rather long and slender and inconspicuous.

The luminous organ is a small indistinct group of cells, of oval form, lying over the peripharyngeal band and very near to the endostyle. Luminous organs also are found on each side of the cloaca, near the ventral end of its aperture (*l. o'*. in figs. 8 and 9). They are in the form of thin groups of loosely arranged cells.

The ganglion is egg-shaped. The duct to the ciliated funnel turns sharply backward before making connection with the wall of the pharynx.

Digestive tract. This "nucleus" of organs is so placed that its elongated axis is more nearly parallel to that of the zooid than in any other *Pyrosoma*. The rotated position of the pharynx seems to account for this. We find also that the intestine is greatly elongated, the anus being located considerably posterior to the stomach. The esophagus opens from the pharynx, between the posterior ends of the stigmatal rows, by a broadly funnel-like aperture. It enters the posterior side of the stomach, giving to this latter organ its broad, bilobed appearance (fig. 9, pl. 20).

In the region just anterior to the gut, the proliferating stolon develops (s., fig. 8). Between the base of the stolon and the endostyle one can sometimes observe an elongated tube, the pericardium, with a dorsal invagination, the heart.

The gonads can be found in the zooids of comparatively large colonies only. The testis, composed of a large number of radiating segments (we counted as many as 77 in one case), is a flatly hemispherical body lying posterior to, and between, the two limbs of the gut. A sperm duct takes its origin on the upper (inner) side of the testis and, passing back beneath the intestine as a dilated tube narrowed at its distal end, it opens into the cloaca. At the edge of the cloaca, and very near to the aperture of the sperm duct, the egg is attached (ov. fig. 8). This lies in a vesicle formed by the inner and outer layers of the cloacal wall. Embryos were found of rather large size, 1.5–2 mm. (fig. 11, pl. 21), but in only a few had the formation of the four primary ascidiozooids more than commenced. The embryos, whose stolons have segmented into four zooids, are much smaller (0.6 mm.), having the yolk mass greatly reduced. It would seem that this loss of volume of the yolk mass can not be due solely to its having been used as food, but that it must have lost bulk also by osmosis. All of these embryos were detached from the parental ovaries. From this fact, and because of their large size, it seems probable that they are customarily sent out of the colony at a very early period in their development. The species is strongly protandrous. In zooids in which the testis has developed into a very well-defined organ, with a duct, the egg has often just made its appearance; and in maturer zooids, in which the egg is ripe, the testis may be undergoing degeneration. This relation, of protandry in the zooid does not preclude the possibility of self-fertilization within the colony, for the various zooids mature at different periods.

In our material from the Pacific Ocean we find an organ of problematic function, which may possibly have something to do with reproduction. It is a reniform, vesiclelike organ attached by its end to the outer surface of the body near the ventral edge of the cloacal aperture (figs. 9 and 10, pl. 20).

The cloaca in *P. spinosum* is very greatly modified, perhaps in adaptation to the oblique position of the pharynx and digestive

tract. Its dorsal wall is greatly elongated, the ventral one much shorter, and as a result of this the aperture opens obliquely ventrally, that is, in the direction of the closed end of the colony. We find this to be true on examining the zoöids in place in the colony, although the test projects so far beyond the edges of the cloaca that it quite obscures the real direction of the opening. A long, sharp tentacle surmounts the dorsal rim of the cloacal opening. In length (2–3 mm.) it may exceed the breadth of the aperture.

Occurrence and distribution. The species is found in the Atlantic, Indian, and Pacific Oceans. Our specimens are the first ones reported from the Pacific Ocean; there are two of these, both from the vicinity of the Philippine Islands.

Specimens of *Pyrosoma spinosum* were obtained by the *Albatross* during the Philippine Expedition of 1907–1910, as follows:

D. 5613, Buka Buka Island, Gulf of Tomini, Celebes; November 20, 1909; 752 fathoms; surface temperature 84° F.; one specimen.

D. 5631, Dowarra Island, south of Patiente Strait; December 2, 1909; 809 fathoms; one specimen, Cat. No. 6407, U.S.N.M., also Cat. No. 6630, including 50 or more zooids from the same specimen as Cat. No. 6407.

One specimen, Cat. No. 6406, U.S.N.M., off the Massachusetts coast at station D. 2228, latitude 37° 25' N., longitude 73° 06' W.; September 11, 1884; 1,582 fathoms; surface temperature 77° F.

It seems probable that *P. spinosum* attains a larger size in the Atlantic than in the Pacific Ocean; and it seems certain that Pacific specimens come to sexual maturity earlier. Krüger (1914) found no gonads in the specimens which he describes as *P. agassizi*, but which we take to be *P. spinosum*. His largest colony was over a meter in length and about 10 cm. in diameter. Our largest Pacific specimen is not more than 5 cm. in diameter (dimension of a fragment), yet its zoöids contain mature gonads and well-developed embryos. According to other descriptions, there have been no embryos found in Atlantic specimens of this species, although colonies of over one meter in length have been reported. The very large colonies (4 m.) from the Indian Ocean (Bonnier and Perez, 1902) were not closely studied in this connection. It is natural to ask, is this difference in size due to environmental conditions affecting growth (temperature, abundance of food, and the like), or can it be that there are two races of this species.

Subgenus PYROSOMATA AMBULATA.

Budding. The production of buds is accomplished as in the *Pyrosomata fixata*, by means of a proliferating stolon formed at the

posterior end of the endostyle (fig. 30, pl. 26 and fig. 32, pl. 27). Only one bud is produced at a time, for as soon as one has formed it is set free and a new bud develops from the remainder of the stolon. After separating from the parent zoöid the young bud is moved dorsalward or toward the aperture of the colony, through the agency of special test cells given off from the dorsal side of the bud. These wandering buds take positions dorsal to the next older tier of zoöids. In young colonies they arrange themselves symmetrically,¹ coming to lie opposite the interspaces between the parent zoöids (figs. 50, 52, and 53, pl. 36). Some species preserve this regular arrangement (figs. 43 and 44, pl. 33); others lose it, usually rather early (pls. 34 and 35). A result of this manner of colony formation is that the four primary ascidiozoöids remain at the closed end of the colony, new buds continuing to form around the open end of the colony until a certain stage is reached (see p. 212).

There are two tunic vessels developed in connection with each primary ascidiozoöid, but only one from each of the subsequently formed buds.

The colony. The test is generally of rather firm, cartilaginous texture. It is transparent, usually colorless, but sometimes a little stained, probably from pigment contained in the zoöids. There are no "guarding" processes of the test surrounding the colonial aperture, but a diaphragm is generally present and well developed (fig. 46, pl. 34). Many species have test-processes over the general surface of the colony, in the form of conical protuberances, through which the oral siphons of the zooids project so as to open near their outer ends (pls. 34 and 35; fig. 24, pl. 24; fig. 26, pl. 25; fig. 30, pl. 26). Sometimes the general surface of the test is denticulate or roughened.

Zoöids. The rows of stigmata are not oblique, but run at right angles to the longitudinal axis of the zoöid. In most cases the branchial basket is elongated in the direction of this axis. The oral aperture bears a median, ventral tentacle, and a rather definite number of tentacle-like folds or swellings, forming a circle around its inner border (fig. 13, pl. 22). The prebranchial chamber may be short (pl. 23) or be elongated as an oral siphon (fig. 26, pl. 25). The peripharyngeal bands unite at a broad angle directly beneath the ganglion (fig. 13, pl. 22). A single pair of luminous organs, at the side of the peribranchial chamber, is always present. The blood-forming organ is present as a conspicuous, elongated mass of cells on the dorsal side of the zoöid.

Nervous system. In this subgenus the ganglion is smaller (fig. 13, pl. 22). The duct of the subneural gland runs obliquely forward from

¹ See Neumann, 1909, c and 1909-1913, for a fuller account.

the ganglion (fig. 4 B, p. 206), and is shorter than among the *Pyrosomata fixata*. An idea of the distribution of the nerves may be gained from figure 13. It will be seen that the fourth and sixth nerves are least prominent. The cloacal muscle is innervated by the fifth and, in part, by the eighth nerve, the atrial sphincter by the seventh, the last pair (eighth) being large and important.

The pigment cells, found to some extent in the zoöids of all *Pyrosomas*, are sometimes quite conspicuous in the members of this subgenus. In some species they occur in masses on the viscera; in others, as large, star-shaped cells scattered over the walls of the prebranchial or of the cloacal chamber (fig. 25, pl. 24).

The cloaca may be short and broad (fig. 17, pl. 23), but ordinarily it is elongated, and has a small, circular aperture (pl. 29).

Two cloacal muscles (*cl. m.*) lie one on each side of the common cloaca (pls. 30 and 31). There is no lateral muscle system, as in the *Pyrosomata fixata*, but there are two or three circumoral fibers, which do not branch and anastomose (pls. 26 and 27). Oral and cloacal sphincter muscles are present as simple, closed rings (fig. 36, pl. 29).

The gonads occupy positions ventral to the digestive tract, and generally quite distinct from it. The testis lies on the left side, the ovary on the right (fig. 31, pl. 27); both develop at about the same time, or one in advance of the other (protandry or protogyny). There are relatively few (12–30) lobes in the testis, and these project inward. The embryo is retained in the ovary until fairly late in its development. When released, it continues its growth in the cloaca, in those species in which the cloaca is large, or in the right peribranchial space, if the cloaca is short. The majority of the forms are rather small, hence mature their sexual products relatively early.

PYROSOMA VERTICILLATUM (Neumann, 1909, c).

Plate 21, fig. 12; plate 22, fig. 13.

This species was first taken from the Indian Ocean (Feb.–Mar., 1899, Deutsche Tiefsee-Expedition). Twenty-one colonies in all were collected, and have been described as representing a distinct type of *Pyrosoma*. They were characterized by their unique form, but more especially by the regular arrangement of zoöids which obtains, even in adult colonies.

Specimens taken by the *Albatross* in Philippine waters in 1908–1909, though undoubtedly belonging to this species, yet appear to differ from those described by Neumann. Since these points of difference are constant throughout the entire *Albatross* collection—of twenty specimens from five stations—it has seemed best to treat this new type as a variety of the present species. In variety *cylindricum*, as we name it, the colony is relatively longer—that is, more

slenderly cylindrical—and there are numerical distinctions—as regards number of stigmata, and the like—to be described later.

The colony of *P. verticillatum* is typically egg-shaped, occasionally somewhat elongated. The largest is but 3 cm. long, so that it is probable that this form reaches a definitive length seldom exceeding 2.5 cm. The zoöids are arranged in transverse, parallel rows, or verticils; the spaces between the zoöids and also between the rows are relatively great. Test-processes are completely lacking, and the test itself is firm, smooth, transparent, and colorless. The oral apertures are considerably sunken beneath the surface of the colony, so that there is a funnel-like depression in the test leading down to each.

Mature zoöids are 2.5–2.7 mm. long from mouth to cloacal aperture, 2.7–3 mm. high, i. e., in dorso-ventral measurement. They vary only slightly in size throughout the colony. The branchial basket in this form is quite short and is relatively simple in its make-up. There are about 21 dorso-ventral rows of stigmata on each side of the branchial chamber, and about 11 longitudinal bars. Dorsal languets, 4–5. There is only a very short cloacal chamber, the two peribranchial pouches opening almost directly into the colonial cavity by the very wide atrial opening. The cloacal muscle is long and narrow.

Gonads. The testis is described as consisting of from 12 to 15 lobes, lying rather more on the posterior than on the ventral wall of the body, and scarcely bulging beyond the general contour of the body. The egg is said by Neumann to mature earlier or sometimes later than the testis. This statement is based upon his own and upon Sceliger's observations, namely, that even in those species whose zoöids are ordinarily strongly protogynous, the four primary ascidiozoöids, and a few of the later formed zoöids, may ripen their spermatozoa first. Protogyny within the individuals of the colony seems to come about progressively from an original condition of protandry as new zoöids are formed by budding. Thus the possibility of self-fertilization in this species (considering the colony as the individual) is not precluded. Nevertheless it should be strongly emphasized that in this and some of its nearly allied forms, protogyny is the rule for most of the zoöids within the colony. In others, to be described later (as subspecies of *P. atlanticum*), there is even an approach to a condition of protandry in many zoöids. For the most part the male and female sex-cells in the zoöids of *P. atlanticum* and its several subspecies ripen at nearly the same period, although here also there is progressive maturing of the sex-cells from one end of the colony to the other.

The characteristics of *P. verticillatum* are given by Neumann as follows: the funnel-like oral depressions in the otherwise smooth surface of the test, the height (dorso-ventrally) of the zoöids, the

position of the testis on the posterior rather than the ventral body-wall, and especially the arrangement of the zoöids in regular transverse whorls.

P. verticillatum is found in the Indian Ocean, where it was collected first southwest of Ceylon, and again shortly afterwards west of the Chagos Archipelago. It is reported also from the Pacific Ocean, although it is probable that the Pacific specimens, if restudied, might have to be referred to the variety (*cylindricum*), which is found in these waters. The species is by no means abundant, to judge from the paucity of specimens obtained, hence it is not so well known as others.

PYROSOMA VERTICILLATUM CYLINDRICUM, new subspecies.

Plate 22, figs. 14 and 15; plate 33, fig. 43.

The form here considered is represented, as before mentioned, by 21 specimens taken during the Albatross Philippines Expedition (1908-1909).¹ As these differ in several particulars from the species just described, and since these distinctions are more or less constant, it seems quite possible that we have here a geographical race or subspecies confined to the Pacific Ocean.

The cylindrical form of the colony is in contrast to the more ovate form of *P. verticillatum*. As in *P. verticillatum*, a regular arrangement of zoöids obtains, even in the mature specimens. The largest colonies attain a length of 3.4 cm., the majority, however, about 2.5 cm. The width or thickness of the cylindrical trunk averages 1.2 cm. The test is very much like that of *P. verticillatum*—firm, colorless, transparent, and smooth except for the funnel-like depression over each oral aperture (fig. 15).

All the larger zoöids—those which have taken up a definitive position in the test—appear quite globular and short (fig. 15). In size these range between 2.2 and 2.4 mm. in length, averaging 2.4 mm. in height (dorso-ventrally). These vary little in size or form or in the character of their organs. There are always numerous small zoöids around the colonial aperture, those which have been formed most recently as a result of budding.

The atrium is very short and broad; the oral chamber—i. e., the portion of the pharynx in front of the stigmata—is almost lacking. On this account the zoöids, examined in side view, appear circular to quadrangular in outline. This appearance is emphasized by the height of the branchial basket, which is higher than long. In the better-known species, described below, the zoöid is elongated, often greatly so.

¹ United States National Museum. Cat. Nos. 6468 (type), 6412, 6413, and 6414. The authors much prefer the Latin form "*tyfus*" in taxonomic reference, but they conform to the editorial usage of the United States National Museum.

The mouth and its associated parts are simple, probably affording typical conditions for the subgenus, since there appear to be no muscles or nerve fibres which have become modified through overgrowth or atrophy. The inner border of the mouth is fringed with a variable number (usually 18) of small folds erroneously called tentacles; and on the ventral edge there is a median tentacle with a vesicle-like enlargement at its base. The whole constitutes what Huxley called the "tentacular fringe." Surrounding the mouth and fringe there is an oral sphincter muscle, and outside of this two delicate, circum-oral fibres. The nerves about the oral region are rather easily traced and identified.

The branchial basket shows about 14 longitudinal bars on each side, and from 27 to 28 rows of stigmata. This serves to distinguish this variety from *P. verticillatum* proper, in which the number of bars is about 11, and the stigmatal rows about 21. The number of the dorsal languets, five, seems to be constant in adult individuals. The endostyle is typical but short, making a strong, even curve along the ventral side of the pharynx. The digestive tract appears very narrow; the intestine makes a sharp bend upon itself instead of the wider, customary loop (see *P. atlanticum atlanticum*). The two dorsal leucocyte masses are distinct from each other. They are short and not very conspicuous. The luminous organs are usually oval and elongated dorso-ventrally.

The reproductive organs bear about the same relation to the zoöid as is characteristic of the species type. The testis causes the posterior wall of the body to bulge somewhat, often projecting considerably. Its lobes, about 15 in number, are directed nearly forward, or diagonally forward and upward; they rarely form a compact organ but lie rather open, and in the form of a rosette. As before mentioned, the cloaca is very short and broad. Its aperture is also broad, there being scarcely any diaphragm, so common in other Pyrosomas. Correspondingly we find the cloacal muscle long and narrow. The ovary lies to the right of the testis as usual, developing ordinarily much before the latter, so that the zoöids would be described as protogynous. In agreement with the observations of Neumann upon *P. verticillatum*, we find that in the variety *cylindricum* the primary ascidozoöids and the earlier formed buds may be protandrous; at least the testis makes its appearance first in the early zoöids of this variety.

Embryos in the four primary zoöid stage, tetrazoöid colonies, or "Viererkolonien," were found in the right peribranchial spaces of several zoöids. Some, less developed, were still fixed in the wall of the cloaca. Embryos with unsegmented stolons measure 0.6–0.9 mm. in diameter; those with the stolon dividing into four zoöids are about 0.6 mm. in diameter. There is therefore no rapid shrinking in this embryo such as occurs in those of *P. spinosum*.

All the known specimens of *P. verticillatum cylindricum* are from the northern Pacific Ocean in the vicinity of the Philippine Islands, and were taken by the steamer *Albatross* during the Philippine Expedition of 1907-1910 at the following stations:

D. 5120, Sombrero Island, Verde Island Passage; Jan. 20, 1908; 393 fathoms; surface temperature, 43.7° F.; surface density, 1.02386; one specimen, Cat. No. 6414 U.S.N.M.

D. 5125, Nogas Island, Sulu Sea, vicinity southern Panay; Feb. 3, 1908; 411 fathoms; surface temperature, 80° F.; surface density, 1.02444; seven specimens, Cat. Nos. 6468 (Holotype) and 6412 (Paratype) U.S.N.M.

D. 5320, China Sea, vicinity of Formosa, Nov. 5, 1908; 1,804 fathoms; surface temperature, 80° F.; one specimen.

D. 5437, Hermana Mayor Light, west coast of Luzon; Apr. 9, 1909; 100-600 fathoms; surface temperature 86° F.; two specimens.

D. 5456, Utara Point, Bongo Island.; May 22, 1908; 158 fathoms; surface temperature, 86° F.; surface density, 1.02262; ten specimens, Cat. No. 5456 U.S.N.M.

PYROSOMA HYBRIDUM, new species.

Plate 36, figs. 54 and 55; plate 23, figs. 16 and 17.

This is a fairly distinct form, representing to some extent a condition intermediate between the preceding species and *P. ellipticum*. It is not likely that it is a hybrid form, for there have been collected a considerable number of specimens, 16 in all, from four localities. Moreover, there are certain characters peculiar to this species which serve to distinguish it from all nearly related species. It seems not unlikely, however, that such varieties as the present one may have arisen originally as the outcome of hybridization. Its nearest relative is *P. verticillatum*, but it seems a little too divergent to be properly classed as a variety of this species, especially as no intergrading forms are known.

The colony is laterally flattened in all cases, and appears oval when viewed from the side (fig. 54). The relative dimensions are somewhat variable: An average specimen is 2.4 cm. long, 1.7 cm. wide, and 0.4 cm. thick. Larger specimens—the largest is 4.2 cm. long—are relatively more narrow. The ratio of the width to the thickness of the colony is about 4 to 1. All the zooids, and to some extent the test, are darkly stained bluish-gray, never yellow; the testes when mature appear as black bodies. A verticillate arrangement of zooids in transverse whorls obtains here, as in the preceding forms. In all but the older specimens they display a progression in size from one end to the other of the colony, those near the diaphragm being small and closely packed together, and those at the closed end largest.

There are no processes on the firm test, and its surface is quite free from denticulation. The oral apertures of the zoöids are only slightly sunken (fig. 17).

The zoöids are longer than high, averaging 3 mm. in length, 2.5 mm. in height. The oral chamber, while distinct, is very short; sometimes it is quite lacking. The cloaca is also short, never exceeding about one-fifth the length of the branchial basket.

In details of anatomy this form very much resembles the preceding one. The branchial basket, however, is longer than high, and contains more stigmata and supporting bars. On each side there are from 14 to 15 longitudinal bars (or rarely 16), and 27 to 30 rows of stigmata. The dorsal languets number from 5 to 7. As has previously been described for *P. verticillatum*, so in this form, the endostyle is rather strongly and evenly curved; but in this species it is, in addition, slightly shorter than the branchial chamber. In the species to be described next this shortening is even more marked. There is nothing peculiar in the organization of the digestive tract. It appears narrow; the intestine is sharply bent upon itself. Ordinarily the cloacal muscles lie opposite the stomach—one on either side of it.

This species also is protogynous, that is a preponderance of individuals in the colony show a protogynous condition. The testis is a rather compact and roughly hemispherical body, consisting of about 15 lobes. When mature it lies in a distinct evagination of the postero-ventral body wall, and it may at this time attain to a considerable size (0.7 mm. in diameter). The egg usually develops somewhat earlier than the testis; advanced embryos, after becoming detached from the body wall of the parent, complete their development in the right peribranchial space. Occasionally these may be found in the left peribranchial chamber, or in the cloaca.

Distribution. All of our specimens of *P. hybridum* were collected in the western Pacific Ocean, in Philippine waters, by the *Albatross* during the years 1907–1910, at the following stations:

D. 5238, Port Lambajon, east coast Mindanao; May 12, 1908; 380 fathoms; surface temperature 86° F.; surface density, 1.02453; two specimens; Cat. No. 6493 U.S.N.M.

D. 5320, China Sea, vicinity of Formosa; Nov. 5, 1908; 1,804 fathoms; surface temperature, 80° F.; 11 specimens; Cat. Nos. 6470 (Holotype) and 6408 (Paratypes) U.S.N.M.

D. 5457, Legaspi Light, east coast of Luzon; June 7, 1909; 146 fathoms; surface temperature, 85° F.; two specimens; Cat. No. 6484 U.S.N.M.

D. 5458, Legaspi Light, east coast of Luzon; June 7, 1909; 200 fathoms; surface temperature, 85° F.; one specimen; Cat. No. 6486 U.S.N.M.

PYROSOMA ELLIPTICUM, new species.

Plate 23, figs. 18-20; plate 33, fig. 44.

A single, small colony of *Pyrosoma*, which differs in certain fundamental points from all other known forms, was taken by the *Albatross* from the China Sea on November 5, 1908. In general appearance, however, it does not seem to represent a sharply demarcated species. One of the characters which distinguish it is the nearly complete flattening of the colony as a whole, so that in side view it is oblong with rounded corners and in edge view more nearly linear. (See the end view, fig. 20, pl. 23.)

Other characteristics are the regular, but not strictly verticillate, arrangement of the zoöids in the test; and certain differences in the organization of the zoöids. All these characters of the zoöids are rather uniform and constant, and all the zoöids show about the same size. The measurements of the specimen studied¹ are as follows: Length, 4.5 cm.; width, 2 cm.; and mean thickness about 0.7 cm. The open end is somewhat broader than the closed, as we might expect. In correlation with the flattened condition of the colony, the opening into its axial chamber is slit-like (fig. 20). At both ends of the colonial aperture there is a broad expansion of the diaphragm which effectually preserves the shape of the aperture. Any attempt to pull the test into cylindrical form must result in a tearing of this diaphragm at the ends of the ellipse. Hence, it is not probable that the flattened form of the colony in our preserved specimens of this species is due to any collapsing from mechanical causes.

A close and rather uniform arrangement of the zoöids obtains. They lie in rows transverse to the long axis of the colony, but the whorls thus formed appear more obscure than in any of the verticillate forms yet described. The zoöids in one whorl lie generally opposite interspaces between the zoöids of the adjacent whorls, thus forming somewhat obscure longitudinal rows. The arrangement, however, is not perfectly regular. The oral apertures of the zoöids open flush with the outer surface of the test; hence there are no funnel-like depressions in its surface such as are found in *P. verticillatum*. The zoöids also appear more collapsed or flattened laterally. There are no processes or denticles on the test. In color the colony in alcohol is yellowish-brown, the test itself being very clear and transparent. The color is probably due in part to the test absorbing color from the pigment cells on the esophagus of each zoöid. In our preserved specimens all the tissues of the zoöids appear brownish and the test is yellowish. There is no sediment or

¹ Other specimens, doubtfully of this species, were taken in September, 1899, at a station 600 miles northward of the Marquesas Islands. (Station 3783—*Albatross*.)

débris in the zoöids or any part of the colony to cause color. The viscera of the zoöids appear as dark-brown, opaque bodies, especially the testes, which are of large size in this species.

The form of the zoöids as seen in side view is best described as oval, some individuals being quadrangular or some elongated. In size they vary from 2 to 2.6 mm. in height and from 3.2 to 4 mm. in length, the average conditions being 2.4 mm. high and 3.7 mm. long. It should be emphasized in this connection that throughout the colony there is very great uniformity as to the size of the zoöids. This is strongly in contrast to conditions found in the three preceding forms (*P. verticillatum* and its variety *cylindricum* and *P. hybridum*). The atrium in this form is of moderate length, i. e., from one-third to one-half that of the branchial basket. The oral or prebranchial chamber is rather short but never entirely lacking (fig. 18).

The mantle is fairly firm in texture. Associated with it are the muscles usual in the subgenus. These are the customary pair of cloacal muscles—rather long and narrow—, oral and atrial sphincters, and two circum-oral ring fibers.

The short prebranchial zone never exceeds one-fourth of the length of the branchial basket. The mouth is small and shows the characteristic "fringe" and ventral tentacle. The branchial basket is nearly oval in side view, with slightly truncated posterior end. On each side there are 16 longitudinal bars, occasionally only 15, and 27 to 28 stigmatal rows. The endostyle is peculiar in being shorter than the branchial basket. Dorsal languets, 6 to 7. The luminous organs are mostly oval. Each of the dorsal leucocyte masses is small and distinct. A description of the digestive tract would correspond very closely to that given for *P. verticillatum cylindricum*. The stomach may be relatively larger, but is still rather narrow and rather square at the ends; the intestine is thicker and less sharply bent upon itself.

Gonads. In this species the zoöids are protogynous. The egg ripens early, and when considerably advanced in development, detaches itself from the cloacal wall and moves up into the right peribranchial space. The testis attains to a large size, and when mature is compact and globular, protruding strongly beyond the ventral body contour. It consists of about 18 finger-like lobes which are directed for the most part upward and slightly forward.

We see in this species, for the first time in this subgenus, an appreciable narrowing and likewise a lengthening of the cloaca. The reduced size of the atriopore is also characteristic, for although not so small as in some (*P. atlanticum* and its several subspecies) it is much more constricted than in the previously described members of this subgenus.

Distribution. This species is at present known only from the western Pacific Ocean, and was taken during the *Albatross* Philippine Expedition, 1907-1910, at the following stations:

D. 5319, China Sea, vicinity of Formosa; November 5, 1908; 20 fathoms; surface temperature 79° F.; one specimen (*Type*), Cat. No. 6416, U. S. N. M. Eastern Tropical Pacific Expedition.

H. 3788 (A.A. 15), latitude 4° 35' N.; longitude 136° 54' W.; 600 miles north of the Marquesas Islands; September 8, 1899, 2,583 fathoms; surface temperature 80° F., one specimen, Cat. No. 6425, U. S. N. M.

PYROSOMA OPERCULATUM (Neumann, 1908).

Plate 24, figs. 21-23.

Only one specimen of this interesting form has been collected. This was found in the Indian Ocean a little westward of the Chagos Archipelago (Deutsche Tiefsee-Expedition, Station 228). The colony is about 5½ cm. long and 3½ cm. broad. In form it is broad and cylindrical, roundly truncate at both ends, the closed end being somewhat broader than the open end, the shape of the colony being thus unique among the *Pyrosomas*. The surface of the test is quite smooth in this species.

The zoöids are closely and irregularly placed in the test. They attain a length of about 9 mm. The prebranchial chamber is of moderate length; it is encircled by two circum-oral muscle fibers. The branchial chamber in side view appears as a slightly prism-shaped box, narrowed behind, with straight sides, as the endostyle is not curved except at its extreme anterior end. There are about 40-45 rows of stigmata and 18-20 longitudinal branchial bars. Dorsal languets, about 16.

Gonads. The testis is composed of 15-17 tentacle-like lobes, and in their midst, a sperm duct with a dilated, spherical receptacle. It lies in an evagination of the body wall. This species is strongly protogynous. Growing zoöids, in which the embryo has reached the tetrazoöid stage of development, contain as yet only the rudiment of a testis.

The cloacal chamber is elongated and narrow, appearing three-cornered in cross-section. In young zoöids it may equal the length of the rest of the body, but in older ones it is relatively shorter—about one-half as long as the rest of the body. On the ventral border of the cloacal aperture there is a prominent, hood-like valve (figs. 22 and 23), which is found in no other species of *Pyrosoma*. The edges of the aperture are bordered by a narrow muscle band, probably identical with the cloacal sphincter in other forms. The function of this peculiar apparatus seems to be, as Neumann thinks, to prevent the water in the colonial chamber from flowing back into the pharynx

of the zoöid while water is at the same time entering it from the mouth.

PYROSOMA AHERNIOSUM (Seeliger, 1895).

Plate 24, figs. 24 and 25.

The German Plankton Expedition found this species of *Pyrosoma* in the tropical regions of the Atlantic, where it appears to be not at all uncommon. Forty-eight colonies were collected, from nine different stations, by this expedition, while others have been found subsequently in the Indian Ocean. The species is not represented in the collections made by the United States Bureau of Fisheries, hence we are dependent for our description upon Seeliger's original account and Neumann's later studies of the same form.

The form of the colony is stated as variable, being usually cylindrical or conical, the open end being broader than the closed end. In young colonies with but few whorls of zoöids the closed end may be considerably the broader. The maximum length is 3 cm., the width 14 mm., although it is possible, as Seeliger thinks, that larger specimens will be found. Since no specimens over 3 cm. long have been reported (Deutsche Südpolar, and Deutsche Tiefsee-Expedition), it seems very probable that this represents about the definitive colony length for the species, especially since the zoöids in colonies of this size are sexually mature. There is a regular arrangement of the zoöids in the young colonies with 1 to 3 whorls of zoöids, but in older colonies this is completely lost. The definitive test processes in this species resemble somewhat those of *P. ovatum*, except that they are much shorter (fig. 24). In form they are thick-walled tubes, which surround the oral siphons of the zoöids and stand out perpendicular to the surface of the colony. At their ends the oral apertures are sunken in crater-like depressions and usually face directly outward, sometimes a little ventrally.

The maximum length of the zoöid is 5 mm. The oral siphon is fairly long, almost equaling the rest of the body in some cases. Its great width is significant also, the anterior wall being broad and flat. On the inner (endodermal) wall of the oral siphon pigment cells have been found, extending as far forward as the mouth (Neumann, 1913, b). The branchial basket is broad (dorso-ventrally), about equally so at both its ends. The endostyle is only slightly curved. There are about 24 rows of broad stigmata, and ordinarily 14 longitudinal bars. The cloaca is a little narrower than the pharynx, the cloacal muscle rather long. Pigment cells are found on the outer epithelium of the cloaca (fig. 25), as well as on the follicle wall of the testis. The testis consists of about 12 large lobes which surround the intestinal loop. The organ does not lie in an evagination of the ventral body cavity, as is ordinarily the case in other *Pyrosomas*. The ovary occupies its usual position at the right side of the testis.

Gonads. The production of germ cells commences usually before the zoöid has reached its full development, and only after the embryo is set free does the parent zoöid complete its growth. Protogyny is the rule for this species, the egg in the majority of zoöids maturing before the testis. Neumann (1913, *b*) in working over this species found that the egg tends to ripen at about the same rate in all the zoöids. This is unlike the condition in *P. verticillatum*, where the egg comes tardily to maturity in the primary ascidiozoöids and develops more and more rapidly in each succeeding whorl of zoöids, "until a certain stage is reached." In *P. aherniosum* the primary ascidiozoöids ripen their eggs first in almost every case, then the succeeding whorls of zoöids ripen theirs, in the order of their proximity to the primary zoöids; that is, in the order of their age. After the embryo is set free from the ovary it completes its brood development in the right peribranchial sac.

Seeliger finds in a large number of his specimens that there are but three primary ascidiozoöids at the closed tip of the colony, in place of the usual four, a condition arising through the atrophy of one of these four original buds. He suggests that there may be a tendency here for a distinct variety to establish itself, one characterized by the presence of only three definitive, primary ascidiozoöids. Similar freaks have often been noted in other groups of animals, as pentamerous jellyfishes.

Distribution and occurrence.—This species, although rather recently discovered, has proven to be of rather common occurrence in the Atlantic Ocean, where it was first found. It has been reported since from the Indian Ocean from six stations. Herdman (1888) has described and figured a small *Pyrosoma* from the western Pacific Ocean which he took to be the "*P. elegans*" of Lesueur. It seems more probable that he was dealing with specimens of *P. aherniosum*; this is the opinion expressed by Seeliger and by Neumann, who have worked most on this form.

PYROSOMA OVATUM (Neumann, 1909, *b*).

Plate 25.

This species was described from 52 specimens collected in the South Atlantic Ocean (Deutsche Süd-polar Expedition). It is specially characterized by the egg-shaped or almost spherical colony, and by the long tubelike buccal processes standing out here and there from the surface of the test. The species is quite distinct from all other known *Pyrosomas*; its characters are well defined, and there appears to be no intergrading of this with other forms. The length of the colony is given as 1 to 5½ centimeters. The processes of the test show some resemblance to those in *P. atlanticum atlanticum*, but this resemblance is probably only superficial. The surface of

the colony is smooth, except for these long, slender processes. At the distal end of each process the surface of the test is raised into papilla-like elevations, or denticles, each one containing a test cell (fig. 29), and the oral aperture is surrounded by an overhanging wall of the test. In a longitudinal section (fig. 28) the test process is seen to be truncated obliquely so that the mouth opens somewhat ventrally.

A loose and irregular arrangement of zooids obtains. Occasionally a zooid will be found to be turned from its normal position, so that its ventral side is directed toward the aperture of the colony. The majority of individuals in the colony—that is, those lacking the oral processes—are about 5 to 7 mm. long (fig. 27). Those with the oral siphons well developed attain a maximum length of 19 mm., the siphon then measuring about 14 mm., or three-fourths of the total length of the entire zooid (fig. 26). The inner epithelium of the oral siphon is dotted with large, star-shaped and highly branching pigment cells of a reddish color. In addition to the pigment customarily found on the follicle of the testis there are scattered pigment cells on the inner ectodermal wall of the cloaca, in the region of the viscera. The occurrence of pigment cells in the cloacal region has been observed in no other forms except *P. aherniosum* and some varieties of *P. atlanticum*, and in the latter species they are not prominent.

The branchial chamber proper is oval or oblong, higher (dorso-ventrally) in front than at its posterior end. The endostyle is only slightly curved. In each branchial lamella there are 38 to 40 rows of stigmata and about 18 longitudinal bars. Dorsal languets, for the most part 9 to 10, sometimes as many as 12.

The luminous organs are small, elliptical bodies, lying equidistant from the dorsal and the ventral mid-lines of the zooid.

The digestive tract is rather large and prominent. The esophagus has a broadly funnel-shaped aperture; it enters the triangular stomach at its posterior side. In other respects the digestive tract is as usual. The cloaca is broad, and its two lateral muscles are long.

Gonads. The testis, consisting of about 30 lobes, causes only a very slight bulge in the ventral body wall. Consequently it extends upward so as to inclose the loop of the intestine. Just to the right of the testis and a little behind it is the ovary. This species is protandrous, but the degree of protandry which obtains is not so great as in other Pyrosomas (as *P. atlanticum giganteum*). In colonies 3 or 4 centimeters long, made up of numerous zooids, only a very few individuals can be found from which the embryos have been set free. Hence it seems probable that older colonies of this species will be found even larger than those already collected.

P. ovatum occurs in the Indian and South Atlantic Oceans.

PYROSOMA ATLANTICUM (Peron, 1804).

Plates 15, 34, and 35; plates 26-32; plate 36, figs. 50-53.

There is a large group of closely related forms which we are including in this species, classing as subspecies a number of forms previously described as species, and also several new types in our collections. To this group belong "*Pyrosoma atlanticum*" (Peron, 1804), "*P. giganteum*" (Lesueur, 1815), "*P. elegans*" (Lesueur, 1815), "*Dipleurosoma ellipticum*" (Brooks, 1906), "*P. triangulum*" (Neumann, 1909, *a*), and our new forms *hawaiiense*, *paradoxum*, and *echinatum*.

It is not possible to tell to which of our several subspecies belong the forms described by Peron and Lesueur. Those colonies of this group, collected in the Atlantic Ocean, which have been described in sufficient detail to allow exact identification, are all of the sort which we treat as the subspecies *giganteum*, and, from the large size often attained, they seem to be of the type which has long been called *P. giganteum*. The colonies which we take as the type and paratypes of the species *atlanticum* (subspecies *atlanticum*) are from the Pacific Ocean. They are distinct from the Atlantic forms generally classed as *giganteum*. They are probably the same as Huxley's southern Pacific specimens which he called *atlanticum* and are surely the same as Ritter's San Diego material named by him *giganteum*.

Somewhat intermediate between these *atlanticum* forms and the true *giganteum* are a number of colonies which we do not describe in detail, though we refer to them later under the name *intermedium*. Here would be placed the forms discussed by Seeliger and Neumann as *P. atlanticum* and its varieties *levatum* and *tuberculosum*. Peron's *P. atlanticum* probably should be placed here. *Pyrosoma minimum* we do not discuss.

The problem of nomenclature is intricate and confused. There are no descriptions of "*atlanticum*," not even Huxley's, which are clear enough for certain identification. The earliest description of colonies in this whole *atlanticum* group, which allow fairly confident identification, apply to large Atlantic specimens and are under the name *giganteum*. Under these circumstances it might seem natural to use the name *giganteum* for the species, holding the other forms as subspecies, though this would involve redefinition of *giganteum*, but, according to taxonomic conventions, we must retain the name first applied to a member of this major species, though it is not possible to tell to which of the several subspecies the individuals first described belonged.

In 1804, Peron described the first colony of these animals discovered, giving it the name *Pyrosoma atlanticum*. From his description, and the locality of its collection, we can say only that it is a *Pyrosoma*, probably of our larger *atlanticum* group. The fuller

descriptions of Lesueur (1813 and 1815) and Savigny (1816) materially advanced knowledge of the genus, and Huxley's studies (1851, 1860, *a*, 1860, *b*, and 1861) gave a still more adequate conception of its organization as well as of the reproduction. There has been much confusion between *P. atlanticum atlanticum* and the several other subspecific forms. We will make no attempt to follow through all these descriptions and resolve the confusion. The attempt would be tedious and at best only partly successful.

In our work on the extensive collections of *Pyrosoma*, made by the United States Bureau of Fisheries, we have been led to believe that no valid distinctions can be made among Atlantic forms of *Pyrosoma*, which would show the existence of the two nearly allied subspecies, *atlanticum* and *giganteum*, generally described. In the Pacific Ocean, however, there is found in comparative abundance a *Pyrosoma* which agrees with descriptions of *P. atlanticum* from the Pacific Ocean. It may occur in the Atlantic Ocean as well, but we do not find it among our 43 colonies from the Atlantic Ocean, 42 of which, collected at 30 stations, belong to the major *atlanticum* group, nor are there published descriptions which indicate the presence in the Atlantic Ocean of *P. atlanticum atlanticum*, as we define it. It seems best to recognize as *giganteum* the large colonies from the Atlantic Ocean so often described under that name.

We find, also, in the Atlantic Ocean less specialized forms of *Pyrosoma* than the typical *giganteum*, which appear to be intermediate between the Pacific type, *P. atlanticum atlanticum*, and the genuine *P. atlanticum giganteum*. These will occasionally be referred to for convenience as *P. atlanticum*, group *intermedium*, pending the study of further collections, which may indicate that some of these are distinct forms which have not reached full development.

The major species under consideration has been most often spoken of as the typical representative of the genus. It has ordinarily been described as having a conic-cylindrical colony, beset with truncated test processes or spines; the zoöids irregularly arranged in the test, and, for the most part, long; with other general data, in no way distinctive. This brief diagnosis, while accurate enough, serves only to set off a whole group of *Pyrosomas*, containing many diverse varieties. These, while easy to identify if characteristic specimens are at hand, show such intergradation one with another, and conform so closely with the fundamental plan for the group, that we are treating them as varieties or subspecies of a single species which we name *P. atlanticum*. Taking up, then, the several nearly allied subspecies, we treat first the form chosen as the species type, probably the same form Huxley (1851) described as *P. atlanticum*. The selection of this form as the species type seems natural, since, during the immature stages of the growth of the colony, some of the other subspecies

resemble closely the adult of the typical *P. atlanticum atlanticum*, diverging more and more from this central type as they mature.

PYROSOMA ATLANTICUM ATLANTICUM.

Plates 26 and 27; plate 28, fig. 33; plate 34, figs. 45 and 46; plate 36, fig. 53.

If we examine specimens of *P. atlanticum atlanticum*¹ from the Pacific Ocean, where the form seems to be most characteristically represented, we find remarkable variation among them in regard to size, color, and organization. The great range in size displayed here is in itself significant, when we contrast this with the species *verticillatum*, *hybridum*, *operculatum*, and *ellipticum* described previously, which are all small in comparison. The majority of specimens of *P. atlanticum atlanticum* in the Albatross Pacific collections do not exceed 8 cm. in length; the largest is only 12 cm. long.

Ritter (1905) has described as *P. giganteum* a type of *Pyrosoma*, found on the California coast, which agrees in almost all particulars except size with the one we here describe as *P. atlanticum atlanticum*. According to our distinction between these two forms, it would seem clear that he was dealing with material representing the latter. He was himself very uncertain about assigning his specimens to either one of the two species, as they were then treated. If his specimens were, as it seems, true *atlanticum*, it may be stated that this form is known to attain a length of 60 cm., for Ritter's largest specimen was of this size. He reports also several other exceptional specimens whose measurements are given as follows (Ritter, 1905): "Measurements of three largest preserved colonies: first, length, 25 cm., greatest thickness near open end 2.5 cm.; second, length, 25 cm., greatest thickness, 3.5 cm.; third, length, 19 cm., greatest thickness about middle of length, 3 cm.; largest colonies observed, measured in life, 60 cm. long, 40 cm. long, and 35 cm. long."

The form of the colony in the majority of specimens is conic-cylindrical, the open end of the colony being wider than the closed. There are numerous departures from this shape; some individuals are less conical, more truly cylindrical, than others; some are thickest in the middle and taper toward both ends; while in others there is the suggestion of natural flattening at the open end of the colony. That this flattening is not entirely due to artificial causes (shrinking or compression from poor preservation) is evident, for, if the diaphragm at the opening of the colony is examined, it will be found to be adapted to the form of the slit-like opening, as was shown for *P. ellipticum* (fig. 20, pl. 23). On the other hand, some quite mature colonies show no such flattening. From the data quoted above from Ritter it will be seen too that the ratio between length and thickness differs

¹ According to taxonomic conventions there seems no escape from the absurdity of naming these Pacific forms *atlanticum*.

greatly with individuals. This is apparent in smaller colonies as well. For example, the dimensions of certain of our specimens are as follows: Length, 8 cm., thickness at open end, 1.8 cm., at closed end, 1.1 cm.; length, 7.5 cm., thickness at open end, 1.5 cm., at closed end, 1.2 cm.; length, 10 cm., thickness at open end, 2.3 cm., at closed end, 1.5 cm.; length, 3.1 cm., greatest thickness, at open end, 0.9 cm.; etc. As already stated, some few individuals are thickest in the middle, some are almost uniformly cylindrical, but the majority are distinctly conical, that is, they taper toward the closed end (fig. 45, pl. 34).

The test is fairly rigid, retaining well the form of the colonial tube in preserved specimens. It is ordinarily colorless and transparent, but varies through pale yellowish to a distinct pinkish flesh-color. The color of the test may perhaps, as Herdman (1888) believes, be derived from the masses of pigment cells lying on the esophagus, intestine, and testis of the zoöid, though how they influence the color of the test is not clear. That these pigment cells may be the source of the test color is suggested by the fact that the colors of the two are about the same except for intensity, and that in the form *giganteum*, as described by Herdman, the inner zone of the test lying above these pigmented organs is deeper in shade than the outer layers. No specimens of the subspecies *atlanticum* have been reported in which there is any trace of blue or greenish color.

Characteristic of this whole group of forms is the presence of, and especially the shape of, the test processes (fig. 30, pl. 26). These are most characteristic as observed in rather young colonies (fig. 53, pl. 36). Here they arise each in connection with a zoöid. The process itself is a broad, obliquely truncated cone, the truncated surface of which faces slightly toward the closed end of the colony, i. e., in the same direction as do the ventral sides of the zoöids. Upon this truncated area the oral aperture of a zoöid is situated so that the mouth thus appears to open obliquely ventrally (fig. 30). In many younger zoöids of this type form (fig. 32) and occasionally in older zoöids of some of the other subspecies (fig. 36, pl. 29), this truncated area is depressed, forming more or less of a funnel leading to the mouth. In this particular form (*P. atlanticum atlanticum*) we have, appearing rather early, a characteristic denticulation along the lateral edges of the truncated area of the test process, and at its dorsal tip (figs. 30 and 33). This character almost serves in itself to distinguish this variety from the other varieties of the species, for it is of very constant occurrence, and, if at all well developed, seems to be one of the distinctive, though minor features indicating this race. In older colonies, test processes sometimes develop to great length, so that they give to the colony a bristling, spiny appearance (fig. 45, pl. 34). The oral processes of the corresponding zoöids lengthen themselves proportionately, so that

they still continue to open near the distal ends of the test processes. As illustrating the great degree of diversity in this form, we may add here that, in one of our specimens, almost all of the oral apertures were situated near the bases of the elongated spines.

When first formed the zoöids are arranged in the test with a semblance of regularity; that is, they lie in obscurely parallel transverse rows (fig. 53, pl. 36). This appearance is undoubtedly the basis of Lesueur's distinction between his "*P. elegans*" and the other two forms then recognized (*P. "atlanticum"* and *P. "giganteum"*). More recent students believe that Lesueur was dealing with a young colony of a form which we would now class as a subspecies of the species *P. atlanticum*, probably *giganteum*,¹ for, in the young stages of this variety, the zoöids show a tendency to arrange themselves in transverse rows. With further growth and budding within the colony, (2 cm. colonies and larger) new zoöids become interspersed between the old ones; but not all of these arise as do the former, that is, each zoöid in connection with a test process. In this way, in older colonies, all appearance of regularity in arrangement is lost, and the individuals of the colony become crowded.

In size the zoöids show great diversity. Those in small colonies (2 cm.) are of about uniform dimensions and shape (fig. 32); these are from 2.5 mm. to 3 mm. in height (dorso-ventrally), from 4 mm. to 4.2 mm. long when full sized. With growth, the oral-siphons become enormously elongated in some of the older zoöids (fig. 30), and the cloacal chambers moderately so (fig. 31). The total length often amounts to as much as 8 mm. The branchial sac, or basket, maintains a more uniform size, hence may be taken as a better criterion for comparing the size of the zoöids; it is found to range from 3 mm. to 3.5 mm. in length when fully developed. Ritter, in describing his specimens, which he called *P. giganteum*, gives 3 mm. for the usual length of the branchial sac, and for the total length, including both siphons, 5 mm. to 6 mm. The thickness of the test-wall of the colony averages 4.5 mm., but may be as great as 6 mm. in large specimens. The characteristic form of the zoöid can be studied to best advantage in the small or medium-sized specimens (6 cm. or less), for, as the colonies grow larger, the individuals become highly diversified. Figure 32 shows a zoöid from a 1.5 cm. colony, in which the contour of the body is circular to oblong, the oral and cloacal chambers forming slight prominences at the ends. This same figure shows also the usual relation which the zoöid bears to the test-process. Older zoöids (fig. 30, from a 9 cm. colony) have the branchial sac more elongated so as to appear oval or oblong.

The mantle, and consequently the branchial basket, is strongly

¹ Of this identification with *P. atlanticum giganteum* we can not be at all certain, so can not claim the relief such identification would give to the absurd nomenclature.

compressed in this form, perhaps owing to the crowding of the zoöids in the test.

The musculature of the zoöids is well developed, and shows little diversity of pattern. In addition to the oral sphincter there are two distinct circum-oral fibers or rings varying in position according as the oral chamber is long or short. When this is greatly elongated they lie near its distal end, somewhat widely separated from each other. The lateral muscles of the cloaca are quite prominent. They are usually short. They lie about at the level of the digestive tract; or they may be considerably posterior to the gut when the cloaca is long, as is often the case. The cloacal sphincter is a small thick ring which maintains an almost complete closure of the cloacal opening in preserved specimens.

The mouth differs very little from that of *P. verticillatum* subspecies *cylindricum*. If anything, it is a little more constricted; while the tentacular folds are even more pronounced. These number about 18 usually, not counting the true tentacle on the ventral border.

The pre-branchial chamber is narrower than the branchial sac; it is always present as a distinct cavity or siphon. It varies greatly in length, often equaling the length of the branchial sac, or even exceeding it (4 mm. or less).

The branchial chamber proper varies from oval or quadrangular to triangulate, narrowing toward the posterior end. Many times it will be found to be even harp-shaped owing to the strong curvature of the endostyle at its anterior end.

In each wall of the branchial basket there are 14 to 15, occasionally 16, longitudinal bars; 30 to 36 stigmal rows. Dorsal languets, from 6 to 10 in mature zoöids; in small colonies (1.5 cm.) the normal number is 4 to 5.

The dorsal masses of leucocytes form organs which are more prominent than usual, but they are not so distinctly separated.

The ganglion is small, or of moderate size. In number and arrangement, the nerves are as is typical for this subgenus (fig. 13, pl. 22). Two pairs extend forward from the ganglion, four out to the sides, and two backward. The third and fourth pairs of nerves are sometimes difficult to identify, because the third often tends to fuse for a distance with the second, and the fourth nerve is never very distinct at best.

The luminous bodies are comparatively large; in form they are oval or oblong, or sometimes circular as seen in side view.

Digestive tract. In this, as in the subsequent varieties of this species, the stomach is larger and more spherical in appearance than we have found it to be in the species we have thus far described; while the intestine is thick, and forms a round rather than a sharply bent loop. There have been demonstrated, for these forms also,

definite masses of reddish pigment cells lying on the esophagus and on the intestine, and occasionally some on the surface of the testis. These latter are very much in evidence in the yellowish colonies of *P. atlanticum giganteum*, where they can sometimes be seen with the unaided eye. It is this pigment which is thought to give the sand-yellow color to so many *Pyrosoma* colonies. The specimens of all forms of the species *atlanticum* collected by the *Albatross* in the Pacific are for the most part colorless or white.

The cloacal chamber is quite variable in form and size. It rarely exceeds half the length of the branchial sac; as typically developed it is much shorter than this. Its aperture is small. In good sized colonies young zooids, that is, independent buds, have long, neck-like oral and atrial siphons which seem to shorten somewhat (relatively) as these zooids mature. When the cloaca is long it is usually narrow, and its pair of muscles correspondingly short; when short it may be quite broad.

Gonads. The testis is a fairly compact, spherical body, consisting of 12 to 15 lobes. It protrudes strongly beyond the ventral body contour. Many of the well formed zooids of the colony are protandrous. According to our observations, in the majority of buds the egg ripens first, while in others the two come to maturity at about the same time. In other words, there is a strong tendency for a protandrous relation to establish itself in many individuals in the colony, probably, as Neumann thinks, as a result of the rapid rate at which budding occurs. This formation of buds by the early formed zooids, increasing the size of the colony, diverts nutriment from the growing germ cells, and the egg, which requires abundant nutrition for its growth, has its development retarded. The testis is thus enabled through its slow but steady growth to reach maturity first. The egg when fully grown is larger than the testis by one or two diameters. When it finally becomes detached from its position in the ovary, it completes its brood development in the cloaca of the zooid—not in one of the peribranchial pouches.

P. atlanticum atlanticum is one of the most abundant forms of *Pyrosoma* known. It is certainly the predominant form in the Pacific Ocean, where it is of common occurrence on both the east and west sides (California coast, vicinity of Philippine Islands, and the coast of Japan), and the Pacific Ocean is probably more prolific in *Pyrosomas* than is any other one of the great oceans. The largest number of species is reported from the Indian Ocean, but in number of colonies the collections from the Pacific probably surpass even those from the Indian Ocean. Its occurrence in the Atlantic Ocean as a form well demarcated from *giganteum* is a little doubtful. We find numerous specimens in the Atlantic Ocean, showing various intermediate conditions, but none which could be considered characteristic

atlanticum atlanticum. It is more likely that they are, in part, divergent individuals—in some cases immature specimens—of *giganteum*, and perhaps, to some extent, intermediate forms resulting from the intercrossing of *giganteum* with individuals of *atlanticum atlanticum* which had migrated from the Pacific. *Atlanticum atlanticum* is also reported as occurring in the Indian Ocean. Among the forms reported from the Atlantic Ocean, Seeliger's *P. atlanticum tuberculosum* approaches most nearly the specimens from the Pacific Ocean, which we here describe as *P. atlanticum atlanticum*. It seems absurd to apply the name *atlanticum* to forms known chiefly, and possibly only, from the Pacific Ocean, though others, especially Huxley (1851), have so named them. We therefore must ignore the absurdity of the name.

Specimens of *P. atlanticum atlanticum* were obtained during the cruise of the *Albatross*, as indicated below:

Albatross Philippine Expedition, 1907–1910:

D. 5120, Sombrero Island, Verdo Island Passage; January 20, 1908; 393 fathoms; surface temperature, 43.7° F.; surface density, 1.02386; 13 specimens, Cat. No. 6449 U.S.N.M.

D. 5125, Nogas Island, Sulu Sea, vicinity southern Panay; February 3, 1908; 411 fathoms; surface temperature, 80° F.; surface density, 1.02444; three specimens, Cat. No. 6505, U.S.N.M.

D. 5128, Nogas Island, Sulu Sea, vicinity southern Panay; February 4, 1908; surface; surface temperature, 80° F.; 13 specimens, Cat. No. 6439, U.S.N.M.

D. 5155, Bakun Point, Tawi Tawi Group, Sulu Archipelago; February 19, 1908; 12 fathoms; surface temperature, 81° F.; surface density, 1.02437; one specimen, Cat. No. 6506, U.S.N.M.

D. 5175, Manucan Island, Sulu Sea, southeast of Cagayanos Islands; March 8, 1908; surface; surface temperature, 82° F.; four specimens, Cat. No. 6403, U.S.N.M.

D. 5183, Lusaran Light, between Panay and Negros; March 30, 1908; 96 fathoms; surface temperature, 81° F.; surface density, 1.02489; one specimen, Cat. No. 6501, U.S.N.M.

D. 5195, Capitancillo Island Light, off northern Cebu Island; April 3, 1908; surface; surface temperature, 82° F.; surface density, 1.02518; one specimen, Cat. No. 6502, U.S.N.M.

D. 5223, Malabrigo Light, between Marinduque and Luzon; April 24, 1908; surface; surface temperature, 84° F.; one specimen, Cat. No. 6509, U.S.N.M.

D. 5263, Point Origen, off eastern Mindoro; June 4, 1908; 65 fathoms; surface temperature, 83° F.; one specimen, Cat. No. 6490, U.S.N.M.

D. 5299, China Sea, vicinity of southern Luzon; August 8, 1908; 524 fathoms; surface temperature, 83° F.; surface density, 1.02396; one specimen, Cat. No. 6507, U.S.N.M.

D. 5331, Hermana Menor Island, off western Luzon; Nov. 22, 1908; 178 fathoms; surface temperature 80° F.; surface density 1.02422; Cat. No. 6491 U.S.N.M.

D. 5366, Escareo Light, Batangas Bay, Luzon; Feb. 22, 1909; 240 fathoms, surface temperature 79° F.; one specimen, Cat. No. 6508 U.S.N.M.

D. 5409, Capitancillo Island Light, off northern Cebu Island; March 18, 1909; 189 fathoms; surface temperature 80° F.; five specimens, Cat. No. 6419 U.S.N.M.

D. 5410, Bagacay Point Light, between Cebu and Leyte; March 18, 1909; 385 fathoms; surface temperature 80° F.; three specimens, Cat. No. 6404 U.S.N.M.

D. 5437, Hermana Mayor Light, west coast of Luzon; May 8, 1909; 100–600 fathoms; surface temperature 86° F.; twelve specimens, Cat. No. 6494 U.S.N.M.

D. 5613, Buka Buka Island, Gulf of Tomini, Celebes; Nov. 20, 1909; 752 fathoms; surface temperature 84° F.; one specimen, Cat. No. 6504 U.S.N.M.

D. 5331, Hermana Menor Island, off western Luzon, Philippine Islands; Nov. 22, 1908; surface: surface temperature 80° F.; surface density 1.02422; three specimens, Cat. No. 6491, U.S.N.M. These specimens we have not studied.

Jolo anchorage, Electric Light, March 5, 1908; one specimen, Cat. No. 6503, U.S.N.M.

Albatross Northwestern Pacific Cruise 1906:

D. 5064, off Ose Saki, Suruga Gulf, Japan; Oct. 15, 1906; 575 fathoms; surface temperature 69° F.; twelve specimens, Cat. No. 6492 U.S.N.M.

Other specimens in the collection of the United States National Museum are as follows: Carnegie Magnetic Expedition between Hawaii and California (not more accurately located); one specimen, Cat. No. 6500 U.S.N.M.

Three specimens from an unnumbered station off La Jolla, California; July 23, 1904 (Ritter), two of these are Cat. No. 6485 U.S.N.M.

One specimen, from Ward's Natural Science Establishment, from the "South Pacific," Cat. No. 6511 U.S.N.M.

Two small specimens of doubtful identification taken by the *Albatross* at:

D. 3750, off Honshu Island, Japan; May 10, 1900; 83–140 fathoms; surface temperature 65° F.; one specimen.

D. 5124, Point Origon, off eastern Mindoro; Feb. 2, 1908; 281 fathoms; surface temperature 79° F.; surface density, 1.02468; one specimen, dried out.

One hybrid (?) and another specimen of doubtful subspecific rank were taken in the Philippines, as follows:

PYROSOMA ATLANTICUM ATLANTICUM × **P. ATLANTICUM DIPLEUROSOMA**.

Cat. No. 6471, U.S.N.M., (Type) *Albatross* station D. 5223, Malabrigo Light, between Marinduque and Luzon, April 24, 1908; surface; surface temperature 84° F.; one specimen.

PYROSOMA ATLANTICUM, *subspecies*.

Cat. No. 6625, U.S.N.M., *Albatross* station D. 5124, east coast of Mindoro, Philippine Islands; Feb. 2, 1908; surface; surface temperature, 79° F.; surface density, 1.02468; one specimen.

PYROSOMA ATLANTICUM HAWAIIENSE, *new subspecies*.

Plate 28, fig. 34; plate 35, fig. 49.

This is a form occurring in the northern Pacific Ocean, which, according to our present knowledge, is truly distinct. All of the specimens (six) were collected at one "catch," from a depth of five fathoms, at a station between the Hawaiian Islands and California. The characters by which this form is known make it so unique that it might well be considered a new species, but its relation to the species *atlanticum* is so evident that it seems well to class it as a subspecies of *atlanticum*. In dealing with these spinous forms the safer course has seemed to be to treat them all as nearly related, although perhaps distinct, subspecies, because of the manifest tendency on the part of some to intergrade with others.

The colony is long and quite cylindrical, tapering scarcely at all toward the closed end; some specimens are a little fusiform. The cornus is relatively more slender than in specimens of *P. atlanticum*. For example, the dimensions of the six specimens studied are as follows: length of first 11 cm., width (average) 1.7 cm.; second, length 12 cm., width 1.4 cm. (1.6 cm. at open end, 1.2 cm. at closed end); third, length 16 cm., width 2 cm.; fourth, length 16 cm., width 2.2 cm.; fifth, length 16 cm., width 2.4 cm.; sixth, length 17 cm., width 2.4 cm. From these figures it will be seen that there is remarkable uniformity in the size and the form of the colonies, with only slight differences in the relative width of each.

The test processes are low, rounded protuberances with extremely blunt ends. Over the entire outer surface of the colony there are minute rounded elevations, which are visible only under magnification, these giving to the test a granular opaqueness. It is worth remarking here that the test processes of the largest colonies are all proportionately more reduced in height and broader than those of the smaller colonies, a condition which would suggest that the ancestral form from which this variety was derived had longer and more pointed test processes. This is just what we should expect if the

form we are describing is a subspecies of *P. atlanticum*. The test walls of the colony are thick (about 6 mm.) and very rigid even in formalin specimens. The colonial aperture is a very small, round pore.

There are some points of taxonomic interest in connection with the zooids. Of these structural modifications there should be mentioned the shortening of the oral or prebranchial chamber—except in those zooids which open onto test processes; the displacement of the cloaca dorsally; a peculiar disposition of the digestive organs, giving a spheroidal appearance to the stomach, and a rotation of the esophagus so that it opens almost from the dorsal side of the pharynx. There are about 30 to 32 stigmatal rows, and 15 to 16 (occasionally 17) longitudinal bars in each of the branchial lamellae. The number of dorsal languets is pretty constantly 8 to 9. The length of the zooid varies with the colony from 4.5 mm. to 6 mm., the height from 2 mm. to 3 mm. (averaging 2.3 mm.). The cloaca is usually three-fourths as long as the branchial sac, but it may be much shorter than this, especially if the colony is small. It is rather uniformly 2 mm. to 2.4 mm., long in zooids from the larger colonies. The cloacal muscle lies at about its middle.

In this form the gonads are quite prominent, hence easy to observe. The ovary is a large hemispherical compartment, which, when full-sized, bulges out beyond the ventral contour of the body. In its cavity the single, large egg develops until it is set free by the rupturing of the inner cloacal epithelium. The embryo, thus loosed, continues its metamorphosis for a time in the cloaca of the zooid. There are about 14–17 lobes in the testis, which hold together as a fairly compact or rounded-hemispherical body. If a study is made of a small colony (the smallest one referred to above was used) it will be found that practically all the zooids are protandrous; but in the largest colonies the reverse condition obtains; that is, with hardly an exception in the developing zooids, the egg comes to maturity much before the testis has reached its definitive size (fig. 34). This seems to be in keeping with Neumann's hypothesis that it is the rapid budding within the colony which delays the development of the egg and results in a condition of protandry. In this particular variety, it is probable that the colony reaches a definitive size which corresponds roughly to that of our largest specimens, and probably in consequence of this, the rate of budding is somewhat slackened in older specimens and the primitive condition of protogyny is allowed to establish itself.

Distribution. As mentioned at the head of this description, only six specimens of this form are known. These were all collected in the north Pacific Ocean, somewhere between the Hawaiian Islands and California. Carnegie Magnetic Expedition, between Hawaii

and California, not more accurately located; six specimens, Cat. Nos. 6443 (Holotype) and 3069 (Paratypes) U.S.N.M.) It seems likely that this is a geographical subspecies, whose distribution is limited to the waters of the Pacific.

PYROSOMA ATLANTICUM PARADOXUM, new subspecies.

Plate 29, figure 35.

Among the specimens of *Pyrosoma* collected in the Pacific by the *Albatross*, was one which in general appearance closely resembled *P. atlanticum atlanticum*. On making a study of the zoöids, however, certain small but distinctive differences were found. In making this a subspecies, then, we describe conditions as they are found, not for the purpose of multiplying varieties indefinitely, but rather to point out and illustrate the great degree of divergence in this group.

As characteristic of the colony, should be mentioned its remarkable limp and gelatinous condition (formalin preservation), which is exceptional in this major species; also the weak development of the colonial diaphragm, and the consequent large size and irregular contour of its aperture. The test-vessels running into the diaphragm appear to have degenerated completely. In other respects the colony resembles that of *P. atlanticum atlanticum*; the test is very transparent, the zoöids whitish; test-processes fairly long and tapering, with oblique areas of truncation which are a little denticulate on their edges. The dimensions of the colony are, length 8.6 cm., width, at open end 2.4 cm., at closed end 1.3 cm.; from which it will be seen that the colony tapers rather strongly. There is a suggestion of flattening, but this may not be natural. The zoöids are irregularly arranged in the test.

But the features which most strongly characterize this subspecies are found in the zoöid. The mantle, and in fact all the tissues of the body, are quite delicate. The branchial components are more numerous than in the subspecies *atlanticum*: of longitudinal branchial bars there are 16-17, only rarely 15; the rows of stigmata are 33-37. There are about 9 dorsal languets. Other differences more difficult to describe may be noticed on contrasting this with its related forms. The luminous organs have a compact epithelium-like structure, because the cells of which they consist are polyhedral and fit together closely, whereas these cells are separated or even scattered in other *Pyrosomas*. The stomach wall has a similar thin, epithelial texture. In addition, the shape of the stomach is somewhat peculiar, being cylindrical, long, and with squarish ends. The branchial sac presents a characteristic oval contour as seen in side view, its ventral wall bulging strongly so as to give to the endostyle a strong even curvature. This latter organ, it should be noted, is shorter than the branchial region proper, a feature not found in other forms of the

species *P. atlanticum*. The dorsal masses of leucocytes are reduced to small size. Dimensions of the zooids: average length 4.6 mm. (4.2 mm.—5 mm.); average height 2.5 mm. (2.2 mm.—2.8 mm.). The oral and cloacal chambers are both short. Cloacal muscles rather narrow and short.

Gonads. The testis is a compact body, consisting of about 14 lobes. In form it is narrowly hemispherical to globose. It was relatively small in the specimen studied, which was perhaps not mature. In the colony, no eggs were found which had progressed beyond the one-cell stage. Since these were all very small and the testes relatively large, it seems that the zooids are protandrous. On dissection, mature spermatozoa were found in the testis of one individual. The ovum in this same zooid was nearly mature, but did not appear to have been fertilized. In the flasklike receptacle connected with it sperms were found (fig. 5, p. 208).

Occurrence and distribution. The only known specimen of this form was found in the Pacific Ocean, being collected northwest of the Hawaiian Islands, during the *Albatross* Philippine Expedition, 1907–1910: latitude 25° 10' N.; longitude 166° 20' W., Nov. 3, 1907; one specimen, Cat. No. 6409 (Type) U.S.N.M.

PYROSOMA ATLANTICUM, form DIPLEUROSOMA Brooks, 1906.

Plate 32, figs. 39–41; plate 34, fig. 47.

This *Pyrosoma*, which we here treat as a form of *P. atlanticum*, has already been described by Brooks under the generic name *Dipleurosoma*. That it is not so distinct as to be made the type of a separate genus is very evident to one who has had the privilege of observing large collections. In fact, except for the one feature so prominent, namely the flattening of the colony, it would be rather impracticable to draw any lines of distinction between this form and the typical *P. atlanticum atlanticum*, which also sometimes shows more or less flattening of its colonies, especially near the open end. It may well be that we do not have a distinct race represented here, but merely an interesting phase, exhibiting itself in various individuals of the *P. atlanticum* group, both in the Atlantic and in the Pacific Oceans. This is further indicated by the fact that there are many intergrading forms which are flattened only slightly (see description of *P. atlanticum atlanticum*). The form *dipleurosoma* appears to be not uncommon.

The characteristic shape of the colony is represented in figures 39 to 41, which are copied from Brooks's drawings of a *Dipleurosoma* taken in the Gulf Stream. We have material from the vicinity of the Philippine Islands in which the form of the colony corresponds almost exactly with that shown in the above figures. The test wall forms a permanently flattened tube, and, as was shown for *P. ellip-*

ticum (fig. 20, pl. 23), this flattening must be natural, and not the result of mechanical pressure, for the diaphragm is so formed at the ends of the elliptical aperture that any attempt to bring the colony to a cylindrical form would rupture the diaphragm at these points. The proportions of different colonies are various. They are as follows for several of our specimens: length, 12 cm., width, 2.8 cm.; length, 12 cm., width at open end, 4 cm., at closed end, 2.5 cm.; length, 12.4 cm., width at open end, 3.5 cm., at closed end, 2.5 cm.; length, 9.8 cm., width, 3.2 cm.; length, 4.3 cm., width, 1.4 cm., etc. That is, some colonies are relatively broader than others; some taper strongly, others scarcely at all. The larger of these colonies measure from 7 mm. to 10mm. in thickness. The test is either transparent and colorless or more often it is somewhat flesh-colored or yellowish. The test processes also show various degrees of development. They may be quite absent—except for a few slight elevations—or they may be large and numerous. The processes are rarely long or tapering, but almost all show the characteristic truncation at their ends.

The zoöids do not differ in essentials from those of the subspecies *atlanticum*. They vary greatly in shape and in size: length of average individuals about 4 mm.; height, from 1.2 mm. to 2.2 mm. The oral processes are for the most part relatively short; the cloacal cavities longer, but rarely exceeding the length of the pharynx. Owing to the subsequent crowding of the buds in the older colonies, the resulting zoöids tend to become narrow and often quadrangular. In the majority of the zoöids the egg appears to mature after the testis has developed. Hence we probably have here a strong tendency toward protandry within those zoöids which are rapidly budding, as already mentioned in connection with preceding forms.

Our knowledge of the distribution of the form *dipleurosoma* is probably quite incomplete. It was first found in the Gulf Stream off the coast of North Carolina. We have 14 specimens from the vicinity of the Philippine Islands, North Pacific Ocean, and one from the South Pacific Ocean, as follows:

Albatross Philippine Expedition, 1907–1910:

D. 5196, Capitancillo Island Light, off northern Cebu Island; April 3, 1908; surface; surface temperature, 82° F.; surface density, 1.02518; two specimens, Cat. Nos. 6469 (Holotype) and 6420 (Paratype), U.S.N.M.

D. 5262, Point Origan, off eastern Mindoro; June 4, 1908; surface; surface temperature, 83° F.; surface density, 1.02448; three specimens, Cat. No. 6411, U.S.N.M.

D. 5398, Gigantangan Island, between Masbate and Leyte; March 15, 1909; 114 fathoms; surface temperature, 80° F.; two specimens, Cat. No. 6483, U.S.N.M.

D. 5403, Capitancillo Island Light, off northern Cebu Island; March 16, 1909; 182 fathoms; surface temperature, 81° F.; two specimens, Cat. No. 6410, U.S.N.M.

D. 5408, Capitancillo Island Light, off northern Cebu Island; March 18, 1908; 159 fathoms; surface temperature, 80° F.; surface density, 1.02462; five specimens, Cat. No. 6440, U.S.N.M.

One specimen, from Ward's Natural Science Establishment; from the "South Pacific," Cat. No. 3182, U.S.N.M.

Six specimens from the Southern Californian coast, 1 mile south of Catalina Island, U.S.N.M., "acc. 397, T. 127. 3-30-16."

One hybrid of *Pyrosoma atlanticum dipleurosoma* × *P. atlanticum paradoxum*.

D. 5196, Capitancillo Island, off northern Cebu Island, Philippine Islands; April 3, 1908; surface; surface temperature, 82° F.; surface density, 1.02518; one specimen, Cat. No. 6420, U.S.N.M.

PYROSOMA ATLANTICUM, subspecies GIGANTEUM (P. GIGANTEUM, Lesueur, 1815).

Plate 30, fig. 37.

This is the best-known form of *Pyrosoma*, as it was one of the first to be described and occurs in relative abundance in the North Atlantic Ocean. But in the several attempts to work out its distribution there has been great confusion and misunderstanding. As *P. atlanticum giganteum* we recognize a form which reaches its typical development in the Atlantic Ocean—a *Pyrosoma* which ordinarily attains a large size and is recognized by certain characteristics which, if taken together, make it rather distinct. It seems to intercross, however, with other less specialized races of the major species *atlanticum*, so that its identification is not at all certain unless typical specimens are at hand. Consequently, if we are to continue the use of this name *giganteum* it ought to designate a particular, well-defined subspecies or variety. The application of this name to all *Pyrosomas* of large size leads to misunderstanding as to the identity of the one in question; for size alone, unless shown through extensive collections to be distinctive, is at best a poor criterion by which to identify a *Pyrosoma*.

We have 16 *Pyrosoma* colonies, from 15 different stations in the Atlantic Ocean, which truly correspond to the published descriptions of "*P. giganteum*." Fully 13 other *Pyrosomas* were collected in the same waters, from 11 stations, which might very well be referred to the same subspecies. We have chosen, however, to treat these latter apart from the more typical 16, not because we believe they are a distinct race, but in order to avoid confusion in describing the subspecific character. As mentioned above in connection with *P. atlanticum atlanticum*, it is possible that these various aberrant specimens found in the Atlantic result from the intercrossing, perhaps

some generations ago, of individuals of the two nearly allied races, *giganteum* and *atlanticum*.

[We have adopted the term "group *intermedium*" as a convenience to include all these doubtful forms. It is not at all a distinct subspecies and needs no extended description. Our specimens are very diverse in form and in color. Some colonies are long, slender, and cylindrical, others short and thick. For the most part the elevations on the surface of the test suggest papillae rather than processes or spines. The outer surface of the colony is often finely denticulate or wrinkled, a thing rather characteristic of most Atlantic forms. The test is usually yellowish or pinkish flesh-color. One colony contains zoöids which are quadrangular in side view and have the dorsal leucocyte masses thick, broad, and merged together along the mid-dorsal line. Other specimens resemble typical *atlanticum atlanticum* in the character of their zoöids. So that at best we can say only that there is great diversity within the group. Specimens representing this "*intermedium*" group were obtained by the *Albatross* off the east coast of North America at the following stations:

D. 2039, off Maryland; July 28, 1883; 2369 fathoms; surface temperature 81° F.; one specimen, Cat. No. 6497, U.S.N.M.

D. 2058, off Nantucket; Aug. 30, 1883; 35 fathoms; surface temperature 58° F.; two specimens.

D. 2092, south of Block Island; Sept. 21, 1883; 197 fathoms; surface temperature 67.5° F.; one specimen.

D. 2396, off Cape San Blas, Fla. Gulf of Mexico; Mar. 13, 1885; 335 fathoms; surface temperature 66° F.; one specimen, Cat. No. 440, U.S.N.M.

D. 2602, off Cape Lookout; Oct. 18, 1885; 124 fathoms, surface temperature 78°; one specimen, Cat. No. 2729, U.S.N.M.

D. 2626, off Charleston, S. C.; Oct. 21, 1885; 353 fathoms; surface temperature 76° F.; two specimens, Cat. No. 2737, U.S.N.M.

D. 2667, off Fernandina, Fla.; May 5, 1886; 273 fathoms; surface temperature 75° F.; one specimen, Cat. No. 794, U.S.N.M.

D. 2669, off Fernandina, Fla.; May 5, 1886; 352 fathoms; surface temperature 77° F.; one specimen, Cat. No. 797, U.S.N.M.

D. 2673, off Charleston, S. C.; May 6, 1886; 240 fathoms; surface temperature 77° F.; one specimen, Cat. No. 804, U.S.N.M.

D. 2675, off Charleston, S. C.; May 6, 1886; 327 fathoms; surface temperature 75° F.; one specimen, Cat. No. 6496, U.S.N.M.

An unnumbered station "off Pensacola," Fla.; one specimen, Cat. No. 2761, U.S.N.M.]

Colony. *P. atlanticum giganteum* is of increased interest because it has been extensively studied by European workers. The colony undergoes considerable change in passing from the young condition to extreme development. Small colonies are conic-cylindrical, semi-

transparent, and are not deeply colored. The test processes then show the characteristic oblique truncation at their ends. These soon lose their typical form, becoming long and irregular in shape, or reduced in size and nodular. Among our largest specimens we find exhibited all those color phases described by Savigny (1816, *b*) for *P. giganteum*, as then named. Some are strongly bluish, but not diaphanous as Savigny has described his. (This opacity may result only from preservation.) Some are greenish; the majority, however, are brownish or tan-yellow. But we fail to find the same correlation between the color of the colony and the shape of the test processes, which Savigny reports. The test processes for the most part, even in specimens differing greatly in color, are thick, rounded papillae, while, scattered here and there, are long, fingerlike tentacles. An occasional specimen is completely covered with these longer processes, which are sharply pointed and flattened at their tips as a result of the extremely oblique truncation. The surface of the colony usually presents a finely denticulate or wrinkled appearance under magnification. The test wall, as seen in preserved specimens, is rigid and cartilaginous. Its average thickness is about 7.5 mm. (from 6 to 8 mm.), varying of course with different colonies. A diaphragm is always present, although sometimes reduced. It is relatively narrow in large colonies, where its width equals one-third to one-half the radius of a section through this end of the colony. Hence the aperture is relatively large.

The dimensions of certain of our specimens are as follows: first, length 19.5 cm., width at open end 3.6 cm., at middle 3.9 cm., at closed end 2.5 cm.; second, length 31 cm., width at open end 4 cm., at middle 4 cm., at closed end 2.6 cm.; third, length 40 cm., width at open end 3.5 cm., at closed end 1.6 cm. The colony does not taper greatly, and may well be said to be more cylindrical than *P. atlanticum atlanticum*, but this one feature has little taxonomic value. Herdman (1888) gives the dimensions of a specimen captured south of Australia, which is probably of this subspecies, to judge from the description appended. They are as follows: length 36 cm., breadth at open end 3 cm., at widest point 4.5 cm., at closed end 1.5 cm.; the diameter of the common cloacal aperture 1 cm.; thickness of the test 0.4 cm. He reports also a fragment from a colony which is 7 cm. in breadth, with an aperture 4.5 cm. in diameter. The total length of such a specimen would probably exceed 55 cm., to judge from calculations based on the relative dimensions given above.

An irregular arrangement of the zooids establishes itself very early. These then become crowded and as a result assume various abnormal positions in the test. Sometimes a group of them are inclined or bent over *en masse*; or individuals may become completely reversed, that is, may be with their ventral side directed toward the aperture

of the colony, but this is rather unusual. For the most part the zoöids are long and slender, owing to the extreme elongation of the cloacal processes. The total length, corresponding roughly to the thickness of the test, approximates 7.4 mm. (large colonies). The height of the zoöids is 2.4 mm. to 3 mm. The cloaca is ordinarily 3 mm. long, ranging between 2.6 mm. and 3.6 mm. The elongated branchial basket is best defined as oblong. At the anterior end the tip of the endostyle causes an elbowlike protrusion in the body wall, best understood by reference to the figure. In each branchial lamella there are about 36 stigmatal rows, and 17-18 longitudinal bars (occasionally only 16, or as many 20).

These numerical distinctions, according to our experience, serve better than any others in demarcating this form from *P. atlanticum atlanticum* for in none of the Pacific specimens of *P. atlanticum* which we have examined could we find more than 16 longitudinal bars in each gill-lamella. Ritter found 15 to be the maximum number of these branchial bars, in the specimens which he describes as *P. giganteum*, but which we have regarded as of the subspecies *atlanticum*. In the Atlantic Ocean, however, there is a rather similar form, our *giganteum*, with nearly cylindrical colony, of yellow or bluish color, with greatly elongated zoöids, and whose branchial bars usually number 17 or 18, sometimes as many as 20. Here seems to be the clearest distinction between these two forms so long confused.

As before noted, there are often masses of reddish pigment lying on the viscera. These have been found on the esophagus and the intestine, and in some cases on the testis. Often they are so distinct as to be readily seen without a lens, after the wall of the colony has been cut. We do not find these pigment masses in the zoöids of any but the yellowish colonies. In the blue ones the viscera are densely opaque, and of dull bluish or gray color. The red pigment may have something to do with the yellow color of the test, but it is hard to see how any such connection could exist. The color of the test, at least in some of the greenish colonies, is most dense in the outer, peripheral zone.¹ In this region also the test-cells are most numerous, which may indicate that these cells have something to do with the color of the test.

Rather characteristic of this form, is the great length of the cloaca. It tapers regularly toward its distal end. The cloacal muscle occupies a position about midway of its length.

Gonads. This is another of those forms in which protandry is common among the zoöids of growing colonies. The testis is a large hemispherical organ consisting of a variable number of lobes (18 in one instance). The embryo finishes its brood-development in the cloaca of the parent zoöid.

1. See Herdman (1888, p. 28) to the contrary.

Occurrence and distribution. This is the commonest Pyrosoma in the Atlantic Ocean. It seems to be the only one thus far reported from the Mediterranean Sea. The *Challenger* took specimens in the Antarctic Ocean, south of Australia, in latitude 47° 25' S. From the Antarctic Ocean it would be easy for this form to be carried into the Indian and Pacific Oceans. In the Indian Ocean its occurrence has been pretty well established, but reports of *P. atlanticum giganteum* occurring in the Pacific are not so clear. The published descriptions of Pacific forms which could be classed in the *atlanticum* group apply only to what we have been calling the subspecies *atlanticum*.

Specimens of *P. atlanticum giganteum* in the United States National Museum collection are as follows:

Taken by the *Albatross* on the east coast of North America at station—

D. 2088, south of Marthas Vineyard, Sept. 20, 1883; 143 fathoms; surface temperature 68° F.; one specimen, Cat. No. 200 U.S.N.M.

D. 2089, south of Marthas Vineyard; Sept. 20, 1883; 168 fathoms; surface temperature 69° F.; one specimen, Cat. No. 6402 U.S.N.M.

D. 2091, south of Block Island; Sept. 21, 1883; 117 fathoms; surface temperature, 69° F.; one specimen, Cat. No. 6487 U.S.N.M.

D. 2094, south of Block Island; Sept. 21, 1883; 1,022 fathoms; surface temperature 68° F.; one specimen.

D. 2171, off Maryland, July 20, 1884; 444 fathoms; surface temperature 75° F.; one specimen.

D. 2381, off New Orleans, Gulf of Mexico; March 2, 1885; 1,330 fathoms; surface temperature 69° F.; one specimen, Cat. No. 428, U.S.N.M.

D. 2642, Straits of Florida; April 9, 1886; 217 fathoms; surface temperature 74° F.; two specimens, Cat. No. 790, U.S.N.M.

D. 2655, north of Great Bahama Island; May 2, 1886; 338 fathoms; surface temperature 76° F.; one specimen, Cat. No. 791 U.S.N.M.

D. 2668, off Fernandina, Florida; May 5, 1886; 294 fathoms; surface temperature 76° F.; one specimen, Cat. No. 792, U.S.N.M.

D. 2674, off Charleston, South Carolina; May 6, 1886; 316 fathoms; surface temperature 76° F.; one specimen, Cat. No. 799 U.S.N.M.

D. 2714, off Cape Henry; Sept. 17, 1886; 1,825 fathoms; one specimen, Cat. No. 874 U.S.N.M.

An unnumbered station south of Block Island (240 miles east of Cape Cod); one specimen, Cat. No. 6405, U.S.N.M.

Taken by the *Fish Hawk*, while dredging in Gulf Stream, during the year 1903:

Sta. 7518, off Cape Florida; March 30, 1903; 156 fathoms; surface density 1.024; one specimen, Cat. No. 6510, U.S.N.M.

Sta. 7519, off Cape Florida; March 30, 1903; 186 fathoms; surface density, 1.024; one specimen, Cat. No. 6498 U.S.N.M.

PYROSOMA ATLANTICUM, subspecies TRIANGULUM.

(P. TRIANGULUM, Neumann, 1909, a).

Plate 29, fig. 36.

This form was first discovered in the Indian Ocean (Deutsche Tiefsee Expedition). From the careful description given by Neumann of the single specimen captured, there can be no doubt as to its relationships. During the *Albatross* Philippine Expedition two *Pyrosoma* colonies were collected, which agree in about all particulars with Neumann's *P. triangulum*; that is, the colony is conic-cylindrical, yellowish, and resembles closely the smaller specimens of *giganteum*. The zoöids have somewhat triangular pharyngeal chambers, and are further characterized by a short, broad cloaca, a small number of branchial bars and stigmatal rows, and by certain other minor features.

Among Pacific specimens of the species *atlanticum* we find so many which approach this one in the triangular character of the branchial basket that we deem it unwise to treat this as other than a subspecies.

Our two colonies of this subspecies, one 8 cm., the other 9 cm. long, differ from other *Pyrosomas* collected near the Philippines in being more deeply colored (yellowish). They show greater affinity with Atlantic forms in this respect, and also in the fact that the test processes are weakly developed, short, and for the most part sharply tipped.

The zoöids are irregularly arranged and closely placed. They attain a length of 6 mm. (Neumann); in our specimen they are smaller, from 4 mm. to 5 mm., or averaging 4.5 mm. long; average height about 2.3 mm. As characterizing the subspecies, their blunt, triangular form is noteworthy. This is due to the extreme shortness of the branchial basket, relative to its height, and to the sharp bend which the endostyle makes near its anterior end. This effect is increased because the cloaca, and the viscera lying anterior to it (the gut and testis), are displaced somewhat toward the dorsal side of the animal. In each branchial lamella the number of longitudinal bars is pretty constantly 13-14, of stigmatal rows 25-27. There are from 6 to 8 dorsal languets. The cloaca is rather broad, the cloacal muscle long. The testis, consisting of about 15 lobes, shows no unusual conditions.

One of our specimens presents a characteristic condition of progression in the manner in which the sex cells mature in different parts of the colony. At the middle, and near the closed end of the colony, the majority of the zoöids are protandrous; around the open end of the colony practically all are protogynous. So we have here another of those forms which are referred to as protandrous—meaning, of course, that there is a preponderance of protandrous zoöids within the growing colony.

Distribution: *P. atlanticum triangulum* occurs in the Indian and Pacific Oceans. In the Indian Ocean one specimen was taken by the *Valdivia* in 1899 off the Somali coast (Deutsche Tiefsee Expedition station 263). The following specimens were taken by the *Albatross* during the Philippine Expedition of 1907–1910, and off Japan in 1910:

D. 5402, Capitancillo Island Light, off Northern Cebu Island; March 16, 1909; 188 fathoms; surface temperature, 81° F.; one specimen; Cat. No. 6495, U.S.N.M.

D. 5410, Bagacay Point Light, between Cebu and Leyte; March 18, 1909; 385 fathoms; surface temperature, 80° F.; one specimen; Cat. No. 6415, U.S.N.M.

An unnumbered station off Honshu, Japan, 1910, one specimen.

PYROSOMA ATLANTICUM ECHINATUM, new subspecies.

Plate 35, fig. 48; plate 31, fig. 35.

A single, large *Pyrosoma* specimen in our possession, procured from the Naples Zoological Station and labeled by them *P. elegans*, seems to merit a separate treatment in this rather detailed study of the entire group. It is possible that this is nothing more than a colony of *P. atlanticum giganteum*; but, if so, it is the only specimen of this form which we have studied which is so perfectly transparent and colorless,¹ and which bears such extremely long and numerous test processes. It is probable, but not definitely known, that this specimen was taken from the Mediterranean Sea. Apparently this form is identical with the Naples species referred to by Krüger (1912, p. 6) as *P. elegans*, which he says is characterized by extremely long oral siphons. There is no indication that this is the form to which Lesueur originally gave the name *elegans*. To avoid confusion, it seems best not to use this name. Krüger's reference is insufficient for certain identification of the form he had.

The colony is a thick, cylindrical tube, and tapers but slightly toward the closed end; its widest part is near the middle. The dimensions are: length 12.5 cm., width at open end 2.8 cm., at middle 3 cm., at closed end 2 cm. The test is transparent, the whitish zooids giving to the whole colony a white appearance. Nearly all the test processes are long and fingerlike, and bend in the direction of the colonial aperture. At their ends they are not sharply pointed, but are narrow, and in edge view for the most part emarginate, being narrowed on the outward side. They average about 8 mm. in length, the largest of them attaining 1.3 cm.

Each of the more mature zooids has an extended oral-siphon, opening onto a test-process, near its tip. These zooids are narrow and tube-like, reaching a length of 0.9 cm.–1.9 cm. The less mature individuals average 0.6 cm. long; they appear slender and ovoid,

¹ Our specimen is preserved in alcohol.

width 1.8 mm. to 2.5 mm. The cloaca is long, in this form, usually about two-thirds the length of the branchial sac, which is 3 mm. to 3.5 mm. long. The cloaca is often found to be quadrangular in cross-section. There is extreme diversity as to the size and shape of the oral chamber, but it takes the form of a long, slender siphon in the majority of cases. Two circum-oral fibres can be seen, not always reaching completely around the oral chamber; the anterior one is sometimes abortive or very much constricted.

The luminous organs in this form are large and distinct. They are circular or quadrangular, but vary greatly in size, even those on the two sides of the same zoöid being of different sizes in some instances. In each branchial wall, which is long and elliptical, there are 16-17 longitudinal bars and 30-36 stigmatal rows. The endostyle never describes a very strong curve. The dorsal languets number from 8 to 9. The digestive tract is small, but in other respects is as usual for the species *atlanticum*.

The testis consists of a large number of lobes, 20-26, some of which may again be partially divided into secondary lobes or pouches. The entire organ becomes large and prominent when mature. We find the condition of protogyny almost universal among the zoöids of this one colony. Perhaps smaller ones would be found to contain a greater proportion of protandrous individuals.

Our knowledge of the occurrence of this form is based upon the single specimen obtained from the Naples Zoological Station. It is probable that it was secured in the Bay of Naples, or in the Mediterranean Sea, but its label bears no statement of the place of collection. This specimen has been deposited in the United States National Museum, and bears Cat. No. 6437 (Type) U.S.N.M.

GENERAL CONSIDERATIONS.

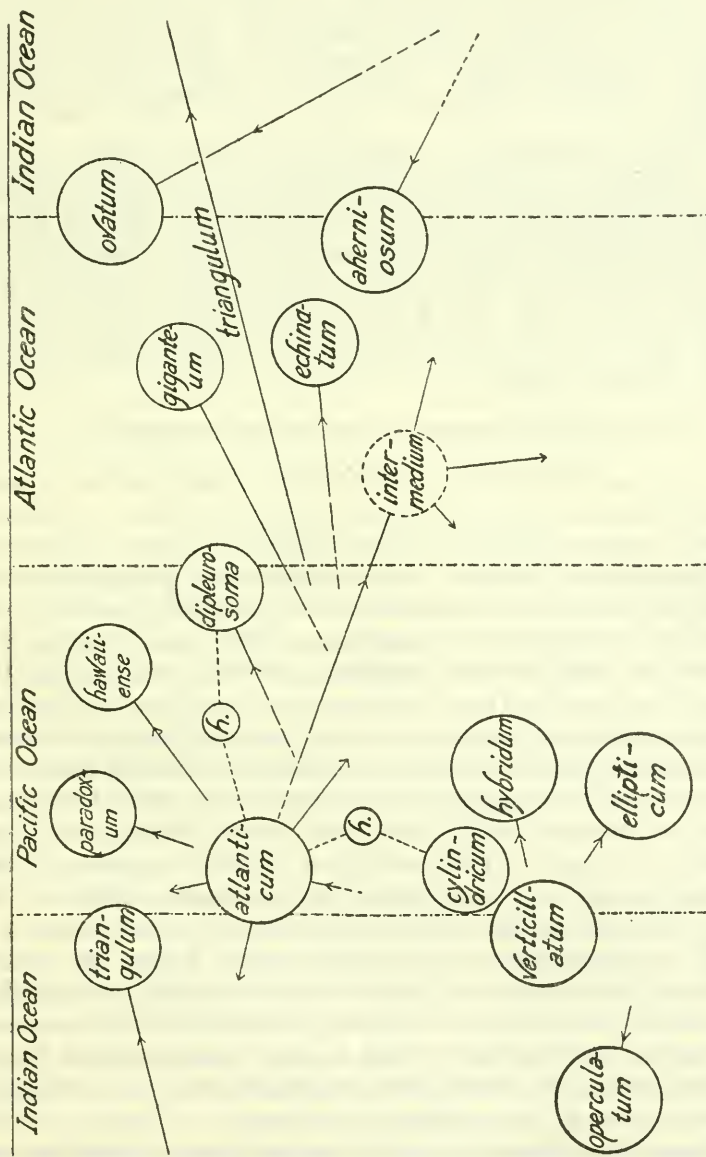
RELATIONSHIPS WITHIN THE FAMILY.

The accompanying chart indicates some possible relationships among the *Pyrosomata ambulata*, and also their apparent centers of distribution. The subspecies *atlanticum*, seems to be the parent form for the whole *atlanticum* group. Its home is apparently the Pacific Ocean. The smooth forms are shown as a distinct group, some members of which, however, interbreed with the *atlanticum* group; thus, we have four colonies which seem to be hybrids between *P. atlanticum atlanticum* and *P. verticillatum*, subspecies *cylindricum*.¹ If the form *dipleurosoma* is to be regarded as a distinct subspecies of *atlanticum*, we would have to say, from the evidence in our collections, that this subspecies interbreeds with *atlanticum atlanticum*.²

¹ United States National Museum, Cat. Nos. 6418 (*type*) and 6417.

² *Idem*, Cat. Nos. 6471 (*type*) and 6421.

and probably with its subspecies *paradoxum*,¹ as well as with members of the group "*intermedium*"; but a better expression of the conditions seems to be to say that any of these forms mentioned may be



SCHEME OF PROBABLE ORIGIN AND DISTRIBUTION OF THE PYROSOMATA FIXATA.

flattened, that is, may take on the *dipleurosoma* condition. In the chart, the small circles containing the letter "h" indicate forms in our collection interpreted as hybrids.

¹ United States National Museum, Cat. Nos. 6469 (*type*) and 6420.

The probable derivation of the *atlanticum* group from the group of smooth species, *verticillatum*, *hybridum*, *ellipticum*, and *operculatum*, is indicated by the fact that the young colonies of *atlanticum* and its subspecies are for a time smooth; that is, their test processes, at least in some colonies, develop rather late. The zoöids in young *atlanticum* colonies are short and more nearly round, as they are in the smooth species, excepting of course the considerably aberrant *operculatum*.

The subspecies *triangulum* resembles some of the Atlantic specimens of *atlanticum*, notably certain colonies of the group *intermedium*, more nearly than it does the Pacific forms. Like the former it has a considerably roughened test surface and its zoöids are short and angular. Because of these indications of nearer relationship to the Atlantic forms, the line of derivation for the subspecies *triangulum*, in the chart, is carried through the Atlantic Ocean into the Indian and Pacific Oceans.

ORIGIN AND RELATIONSHIPS OF THE FAMILY PYROSOMIDAE.

The origin and relationships of *Pyrosoma* should receive a word of discussion in any taxonomic paper upon the group. *Pyrosoma*, in its adult anatomy, shows no clear indication of close relationship to the Doliolidae or Salpidae, and classing these pelagic forms all in one major group, as is sometimes done, is hardly justified. On the other hand *Coelocormus* (Herdmann, 1886) and *Cyathocormus* (Oka, 1913), in their structure, suggest a probable origin of the free swimming Pyrosomidae from the Compound Ascidiaceans. Indeed, if a detached cylinder of *Cyathocormus* had happened to be discovered before the whole attached colony was known, it would have been classed with the Pyrosomidae, rather than with other Compound Ascidiaceans, on account both of the form of the colony and of the structure of the zoöid. The anatomical evidence in favor of this relationship seems very convincing, but thorough studies of the processes of budding and colony formation in *Coelocormus*, and especially in *Cyathocormus*, are greatly needed before we can be certain that *Cyathocormus* and *Pyrosoma* have reached their peculiar form in similar ways and are truly comparable in their structure.

Cyathocormus is regarded by Oka as most nearly related to the Distomidae among the Compound Ascidiaceans, and this conclusion appears borne out by the comparative anatomy.

The Pyrosomidae should, therefore, pending study of budding and colony formation in *Cyathocormus*, be classed as a divergent group of the Compound Ascidiaceans.¹

¹ For fuller discussion of the relationships among the *Tunicata* see Metcalf and Bell (1918).

SPECIATION.

As noted in the introduction to this paper, one of the features of *Pyrosoma*, of chief interest, is the remarkable intergradation shown between its different forms, and this is the more impressive when one compares this family with the family Salpidae, whose species are sharply distinct from one another. The conditions among the *Pyrosomas* suggest hybridization as a factor cooperating with mutation to produce the results observed. In the *atlanticum* group, at least, hybridization seems probably to be continuing to-day.

The differences between species are far greater among the Salpidae than among the *Pyrosomidae*. Lack of physiological isolation within the latter group has probably aided to prevent extreme divergence, but the inherent tendencies to divergence were doubtless also less. *Pyrosoma* is a remarkably stable form, its several species and subspecies differing from one another but slightly, and this chiefly in size of colony and in the character of the test processes, in the relative proportions of the series of three respiratory chambers in the zooids, and in the number of stigmata and of branchial bars.

INDIVIDUALITY AND FORM CONTROL.

Another keenly interesting feature in *Pyrosoma* is the way it presents the universal problems of form control and of individuality, two very closely related conceptions. *Pyrosoma*, like all other colonial organisms, has three grades of individuality, that of the cell, that of the zooid and that of the colony, but it is peculiarly interesting in that the individuality of the cell is not only subordinated to that of the zooid, but is also, in the case of some cells, directly subordinated to the colony as a whole, without reference to the zooids. This feature is best seen in connection with the form and sculpturing of the colonial test.

Note first a feature characterizing the oral test processes in *Pyrosoma atlanticum atlanticum* (fig. 30, pl. 26, and fig. 33, pl. 28), or in *P. ovatum* (fig. 29, pl. 25). Each elongated test process is obliquely truncated distally, the area of truncation being smooth and nearly flat, and containing the oral aperture. Outside the truncate surface, the tip of the oral test process bears numerous minute denticles, at the base of each of which lies a test cell, which doubtless either secretes the test material of which the denticle is composed, or so influences its arrangement that it takes the form of a denticle. These test cells are mesenchyme cells, which have wandered outside the zooids in which they arose, have migrated to a distance, and have each taken up a definite position in the test at a distance from the zooids, there to form or control the formation of a denticle, a minute protruding bit of test substance. They take their position, not on the area of

truncation, but at rather regular intervals around its edge and over the tip of the oral test process. These test cells are not connected with any nerve fibrils, and they are not in contact with any zoöid or any other cells, yet each produces, or causes to be produced, at the proper place on the surface of the test, the particular bit of sculpturing for which it is responsible.

Other similar denticles are found over the surface of the test, not in relation to oral processes or the zoöids. The cells which form these scattered denticles are acting in relation, not to the zoöids, but to the colony as a whole. It is the "soul" of the colony, and not of any zoöid, to which in their activity they are each subservient.

But we find more remarkable illustration of form control, in the case of the four quadrangular tentacle-like processes at the open end of the colony in *Pyrosoma agassizi* (fig. 6, pl. 18). These are not connected with any particular zoöids or groups of zoöids. They are composed of the cellulose test material with a few scattered test cells within them. Like the rest of the test, their material is nonliving substance. The test is secreted chiefly, or it may be wholly, by the ectodermal epithelium, the share of the test cells in this function being doubtful. How can these quadrangular test "tentacles", which apparently must elongate by growth at their bases, be so controlled that they assume their very definite quadrangular tapering form and lie in their four appointed places at the open end of the colonies, their outer and lateral angles being continued as ridges back over the surface of the colony, well toward its closed end?

Assuming for the moment that the formation of the four test "tentacles" is controlled by test cells, we find again an illustration of subservience of isolated cells to the colony as a whole and not to the zoöids from which they arose. The "sense of form" (!) which these cells possess has reference not to themselves, nor to the zoöids of which they were constituent parts, but to the colony as a whole, although they are isolated cells, lying at an appreciable distance from other cells or tissues, and not connected with any nerve fibrillae.

Or, choosing the other possibility and disregarding the doubtful activity of the test cells, we may say that the test substance composing these test "tentacles" is secreted by a number of small, discrete areas of ectoderm, the ectoderm of the several zoöids. The characteristic features of form of these "tentacles" are superficial and therefore separated by an appreciable distance, the thickness of the test, say 1-2 cm., from the secreting cells. How can the behavior of the test material, after it is formed, be so controlled that it assumes the proper relations of form and position, so that "tentacles" of the characteristic type and in the characteristic position, result? The test material is not alive, yet, at a distance from the cells which secrete it, it molds itself into particular form and takes a definite posi-

tion in the colony. This seems an even more remarkable instance of the "feeling for form" permeating the whole colony and affecting even the nonliving, secreted material of which the colony is in large part composed. Of course, this figurative manner of expressing the point is false in its implications. The thing of moment is, that if the test cells be not active in secreting the test substance or in controlling its modeling, then there is some type of control which affects not only the living cells of the ectodermal epithelia of the zooids, but the secreted test substance as well, and the reaction has relation to the form of the colony as a whole and not to its constituent zooids.

There is a further point of some interest. On the hypothesis of the direct response of the secreted test substance to controlling influences, causing it to take the definite form and positions characteristic of the four test "tentacles," we must say that these controlling influences are in the nature of tropisms and the response is a nonvital one. Of course, it is wholly probable that these tropisms themselves are established through the vital activities of the living constituents of the colony, but the response of the secreted material, which causes it to take definite form and position, is a nonvital response. If a structure so definite in form and position as one of these test "tentacles" is formed under the control of stimuli external to itself, by a response evidently nonvital, it suggests how intimate and how intimately controlling may be the influence of such tropisms upon living substance in this and other organisms.

Whether the test cells be active (first hypothesis) or inactive (second hypothesis) in the secretion of test material, *Pyrosoma* presents peculiarly interesting conditions. The behavior of the isolated test cells in *Pyrosoma atlanticum* and the formation of the test sculpturings, especially the ridges and "tentacles" of *Pyrosoma agassizi*, are even more mysterious than the behavior of migrating cells and tissues in the embryonic development of organisms, for there is in the former less of organic contact. We do not see that we are as yet in possession of data that enable us to make any suggestion as to the nature of the control over these phenomena. The problem, however, is presented in *Pyrosoma* in a most striking way that challenges attention.

GEOGRAPHICAL DISTRIBUTION.

The distribution of each species and subspecies of *Pyrosoma* has been stated in connection with our description of its structure, but it is well to bring the data together. The accompanying table shows the localities from which each form has been reported, and the authority for the statement. Where no authority is mentioned, the statement is based upon the collections of the United States Bureau of Fisheries and the United States National Museum, discussed in this paper. The question marks are explained each in a foot note.

Name.	Indian Ocean.	North Pacific Ocean.	South Pacific Ocean.	South Atlantic Ocean.	North Atlantic Ocean.	Mediterranean Sea.	Antarctic Ocean.
<i>P. agassizi</i>	× Neumann	×	× Ritter & B.	× Neumann			
<i>P. spinosum</i>	× Bonnier & P.	×		× Herdman	×		
<i>P. verticillatum</i>	× Neumann	21 Neumann					
<i>P. verticillatum cylindricum</i>		×					
<i>P. hybridum</i>		×					
<i>P. ellipticum</i>		×					
<i>P. operculatum</i>	× Neumann						
<i>P. ahcrnosum</i>	× Neumann	?2 Herdman		× Neumann	× Seeliger		
<i>P. ovatum</i>	× Neumann			× Neumann			
<i>P. atlanticum</i>	× Neumann	× Ritter	×	?3	?4 Seeliger	?5	
<i>P. atlanticum hawaiiense</i>		×					
<i>P. atlanticum paradoxum</i>		×					
<i>P. atlanticum diplevrosoma</i>		×			× Brooks		
<i>P. atlanticum giganteum</i>				×	×	?6	× Herdman
<i>P. atlanticum echinatum</i>						×7	
<i>P. atlanticum triangulum</i>	× Neumann	×					

¹ This may have been of the sub-species *cylindricum*, which is the Pacific form in our collections.

² The identification of this small specimen is a little doubtful.

³⁻⁵ The descriptions of these Atlantic forms do not show clearly the features we have taken as distinctive of *P. atlanticum atlanticum*. This species may very likely occur in the Atlantic Ocean, but it is equally likely that the Atlantic forms are of the sorts which we have grouped under the name *intermedium*, which does not represent a single, true subspecies.

⁶ The sub-species *gigantum* occurs in the Atlantic Ocean, and it is probable that the reports of "*gigantum*" from the Mediterranean Sea apply properly to this subspecies.

⁷ Our colony of this form, obtained from the Naples Zoological Station, was probably collected in the western Mediterranean Sea, but it bears no locality label.

A complete statement of the stations represented in our collections, arranged by species and subspecies, follows. When more than a single specimen was found, the number of specimens is given in brackets (as [4]) after the station.

PYROSOMA AGASSIZI.

Nine dredging stations from the *Albatross* Philippine Expedition, 1907-1910, as follows: 5126, 5233, 5320, 5378, 5458, 5498, 5514, 5543, 5607, all from among or near the Philippine Islands, and from off the Pacific coast of Panama, at station 3388 (*Albatross*) [3].

PYROSOMA SPINOSUM.

Albatross Philippine dredging stations 5613 and 5631, and station 2228 (*Albatross*), in Vineyard Sound, off the Massachusetts coast.

PYROSOMA VERTICILLATUM, subspecies CYLINDRICUM.

Albatross Philippine dredging stations 5120, 5125 [7], 5320, 5456[10], 5437 [2], all among or near the Philippine Islands.

PYROSOMA HYBRIDUM.

Albatross Philippine dredging stations 5238 [2], 5320 [11], 5457 [2], 5458, all among the Philippine Islands.

PYROSOMA ELLIPTICUM.

Albatross Philippine dredging station 5319, in the northern China Sea; and three small colonies of doubtful identification from station 3788, AA 15 (*Albatross*), latitude $4^{\circ} 35' N.$; longitude $136^{\circ} 54' W.$, 600 miles north of the Marquesas Islands.

PYROSOMA ATLANTICUM ATLANTICUM.

Albatross Philippine Expedition, 17 dredging stations among and near the Philippine Islands (5120 [13], 5125[3], 5128[13], 5155, 5175[4], 5183, 5195, 5223, 5263, 5299, 5331[4], 5366, 5409[5], 5410[3], 5437[12], 5613, and an unnumbered station "Jolo anchorage"); *Albatross* station 5064[12]; an unnumbered station off La Jolla, California, [3] (Ritter); a station of the Carnegie Magnetic Expedition, between Hawaii and California, not more accurately located; a specimen bearing a label of Ward's Natural Science Establishment, giving the locality merely as "South Pacific"; and two small specimens, of doubtful identification, from *Albatross* stations D 5124, in the Philippine Islands, and 3750, off Honshu, Japan.

PYROSOMA ATLANTICUM, subspecies HAWAIIENSE.

A station of the Carnegie Magnetic Expedition, between Hawaii and the California coast, not more accurately stated [6].

PYROSOMA ATLANTICUM, subspecies PARADOXUM.

An unnumbered station of the *Albatross* Philippine Expedition, Lat. $25^{\circ} 10' N.$, Long. $166^{\circ} 20' W.$

PYROSOMA ATLANTICUM, form DIPLEUROSOMA.

Five dredging stations of the *Albatross* Philippine Exhibition, all among the Philippine Islands, 5196[2], 5262[3], 5398[2], 5403[2], 5408[5], and a specimen bearing a label of Ward's Natural Science Establishment, naming the locality merely as "South Pacific."

PYROSOMA ATLANTICUM, subspecies GIGANTEUM.

Eleven dredging stations in the western north Atlantic Ocean, from the Bahamas to Cape Cod (*Albatross*, 2088, 2089, 2091, 2094, 2171,

2381, 2655, 2668, 2674, 2714, and an unnumbered station 240 miles east of Cape Cod); a station in the Gulf of Mexico, 2381 (*Albatross*) and one in the Straits of Florida, 2642 (*Albatross*) [2]; and two stations, probably in the western north Atlantic Ocean, 7518 and 7519 (*Fish Hawk*).

PYROSOMA ATLANTICUM, group INTERMEDIUM.

Nine *Albatross* stations in the western north Atlantic Ocean, from Florida to Cape Cod (2039, 2058[2], 2092, 2602, 2626[2], 2667, 2669, 2673, 2675), and two stations in the Gulf of Mexico, off the Florida coast (2396. *Albatross*, and an unnumbered station "off Pensacola").

PYROSOMA ATLANTICUM, subspecies ECHINATUM.

A colony from the Naples Zoological Station, labeled "*Pyrosoma elegans*," probably from the western Mediterranean Sea.

PYROSOMA ATLANTICUM, subspecies TRIANGULUM.

Albatross Philippine Stations D 5402 and D 5410, in Philippine waters, and an unnumbered station off Honshu, Japan.

At several stations more than one species was collected. This is of some interest as showing the possibility of hybridization. A list of these stations, with the species collected from each, is as follows: *Albatross* dredging stations in Philippine waters—5120, *Pyrosoma atlanticum atlanticum* and *P. verticillatum cylindricum*; 5125, the same forms; 5320, *P. agassizi* and *P. hybridum*; 5410, *P. atlanticum atlanticum* and *P. atlanticum triangulum*; 5437, *P. atlanticum atlanticum* and *P. verticillatum cylindricum*; 2458, *P. agassizi* and *P. hybridum*; 5613, *P. atlanticum atlanticum* and *P. spinosum*; Carnegie Magnetic Expedition, unnumbered station, between Hawaii and California, *P. atlanticum atlanticum*, and *P. atlanticum hawaiiense*; and an unnumbered station in the "south Pacific" Ocean, *P. atlanticum atlanticum* and *P. atlanticum*, form *dipleurosoma*.

LITERATURE CITED.

- BONNIER AND PEREZ (1902). Sur un nouveau Pyrosome gigantesque. Comp. rend. Acad. Sci., vol. 134.
- BROOKS (1906). *Dipleurosoma*, a new genus of *Pyrosoma*. Johns Hopkins Univ. Circ., vol. 26, p. 5.
- (1906). The affinities of the pelagic Tunicates. No. 1. On a new *Pyrosoma* (*Dipleurosoma elliptica*). Mem. National Acad. Sci., vol. 10.
- BURGHAUSE (1914). Kreislauf und Herzschlag bei *Pyrosoma giganteum* nebst Bemerkungen zum Leuchtvermögen. Zeitschr. f. w. Zoologie, vol. 108, p. 430.
- FARRAN (1906). On the distribution of the Thaliacea and *Pyrosoma* in Irish waters. Report of the Sea and Inland Fisheries of Ireland for 1896, pt. 2, Appendix I.
- GROBEN (1882). Doliothum und sein Generations wechsel. Arb. zool. Inst. zu Wien., vol. 4, p. 2.

- HERDMAN (1886). Report on the Tunicata collected during the voyage of H. M. S. *Challenger*, during the years 1873-76. II Ascidiæ compositæ. *Zool. Challenger Exped.*, vol. 14, pt. 38.
- (1888). Report upon the Tunicata collected during the voyage of H. M. S. *Challenger*, during the years 1873-76. III Ascidiæ Salpæiformes, Thaliacea, Larvacea, etc. *Zool. Challenger Exped.*, vol. 27, pt. 76.
- HUNTER (1898). Notes on the peripheral nervous system of *Molgula manhattensis*. *Journ. Comp. Neurology*, vol. 8.
- HUXLEY (1851). Observations upon the anatomy and physiology of *Salpa* and *Pyrosoma*. *Philos. Trans. Roy. Soc.*, 1851.
- (1860*a*). On the anatomy and development of *Pyrosoma*. *Trans. Linn. Soc. Lond.*, vol. 24 (1862), p. 1.
- (1860*b*). On the development of *Pyrosoma*. *Ann. Nat. Hist.* (3) vol. 5.
- (1861). On the nature of the earliest stages of the development of animals, *Proc. Roy. Inst.*, vol. 3 (1862).
- JOLIET (1888). Etudes anatomiques et embryogeniques sur le *Pyrosoma giganteum*, suivies de recherches sur la faune de Bryozoaires de Roscoff et de Menton. Paris, 1888.
- JULIN (1912). Recherches sur le developpement embryonnaire de *Pyrosoma giganteum*. *Les. Zool. Jahrbücher. Supplement XV*, 2 vols.
- KEFERSTEIN AND EHLERS (1861). Zoologische Beiträge gesammelt im Winter 1859-60 in Neapel und Messina. III Ueber die Anatomie und Entwicklung von *Doliolum*: IV, Bemerkungen über die Anatomie von *Pyrosoma*. Leipzig, 1861.
- KORSCHOLT AND HEIDER (1900). Textbook of the Embryology of Invertebrates *Trans. by Bernard and Woodward*, vol. 4.
- KOWALEVSKY (1875). Ueber die Entwicklungsgeschichte der *Pyrosoma*. *Archiv. f. mikrosk. Anat.*, vol. 11.
- KRÜGER (1912). *Pyrosomes et Appendiculaires* provenant des campagnes de *l'Hirondelle* et de la *Princesse-Alice* (1885-1910). Resultats des campagnes scientifiques accomplies sur son yacht par Albert Ier, Prince Soverain de Monaco. Fasc. 39. Monaco, 1912.
- LESUEUR (1813). Memoire sur quelques nouvelles especis d'Animaux mollusques et radiaires recueillis dans la Mediterranee pres de Nice. *Nouv. Bull. Soc. Philom.* vol. 3; also *Journ. Physique*, vol. 77.
- (1815). Memoire sur l'organisation des *Pyrosomes*. *Bull. Soc. Philom.*, 1815; also *Journ. Physique*, vol. 80.
- METCALF (1904). *Neritina virginea*, variety minor. *Amer. Naturalist*, vol. 38.
- METCALF AND BELL (1918). The *Salpidae*, a Taxonomic Study. The second paper of this volume.
- NEUMANN (1908). Mitteilungen über eine neue *Pyrosomen*-Art der Deutschen Tiefsee-Expedition (*Pyrosoma operculatum*). *Zool. Anzeig.*, vol. 33.
- (1909-1913). Die *Pyrosomen*, Bronn's Klassen und Ordnungen des Tier-Reichs. Vol. 3, Suppl. 2, Abth. 2.
- (1909*a*). Mitteilung über eine neue *Pyrosomen*-Art der Deutschen Tiefsee-Expedition (*P. triangulum*). *Zool. Anzeig.*, vol. 33.
- (1909*b*). Mitteilung über eine neue *Pyrosomen*-und *Doliolum*-Art der Deutschen Südpolar-Expedition. *Zool. Anzeig.*, vol. 33.
- (1909*c*). Mitteilung über eine neue *Pyrosomen*-Art der Deutschen Tiefsee-Expedition (*P. verticillatum*), nebst Bemerkungen über die Stockbildung und des Wandern der Knospen bei *Pyrosomen*. *Zool. Anzeig.*, vol. 34.
- (1912). Über Bau und Entwicklung des Stolo prolifer der *Pyrosomen*. *Zool. Anzeig.*, vol. 39.
- (1913*a*). Die *Pyrosomen* der Deutschen Tiefsee-Expedition. *Wissensch. Ergebn. der Deutschen Tiefsee-Expedition*, vol. 12, p. 4.

- NEUMANN (1913*b*). Die Pyrosomen der Deutschen Südpolar-Expedition. Deutsche Südpolar-Expedition, vol. 14, p. 1.
- OKA (1912). Eine neue phylogenetisch interessante Synascidie (*Cyathocormus mirabilis*, n. g., n. sp.). Zool. Anzeig., vol. 40, 10/11, Oct., 1912.
- (1913). On *Cyathocormus mirabilis*, nov. gen., nov. sp., The Type of a New Family of Compound Ascidiaceans, from Japan. Journ. of Coll. of Science. Imperial Univ., of Tokyo, vol. 32, art. 12.
- PERON (1804). Memoire sur le nouveau genre Pyrosoma. Ann. Mus. Hist. nat. vol. 4, and Journ. Physique, vol. 61.
- RITTER (1905). The Pelagic Tunicata of the San Diego Region, excepting the Larvacea. Univ. of California Publ., Zool., vol. 2, p. 3.
- RITTER AND BYXBEE (1905). Reports on the scientific results of the Expedition to the Tropical Pacific in charge of Alexander Agassiz, in the United States Fish Commission steamer *Albatross*, VIII. The Pelagic Tunicata. Mem. Mus. Comp. Zool., vol. 26, p. 5.
- SALENSKY (1891). Beiträge zur embryonalentwicklung der Pyrosomen. Zool. Jahrb. Anat., vol. 5, p. 1.
- DE SAVIGNY (1816*a*). Memoires sur les Animaux sans Vertebres. Paris, 1816.
- (1816*b*). Description de l'Egypte. Histoire Naturelle, I, 2. Tableau systematique des Ascidiées, tant simples que composées, etc. Paris, 1816 (dated 1809).
- SEELIGER (1895). Die Pyrosomen der Plankton-Expedition. Ergebn. der Plankton-Expedition der Humboldt-Stiftung, vol. 2, E, b. Kiel and Leipsig, 1895.
- ULJANIN (1884). Die Arten der Gattung *Doliolum* im Golfe von Neapel und den angrenzenden Meeresabschnitten. Fauna und Flora des Golfes von Neapel, vol. 10. Leipsig, 1884.
- USSOW (1876). Contributions to the knowledge of the organization of the Tunicata [Russian]. Trans. Nat. Soc. Moscow, vol. 18, p. 2.

EXPLANATION OF PLATES.

Reference letters used on plates and text figures.

- 1-8* = nerves.
a. = anus.
b. = bud.
b. o. = blood-forming organ.
br. b. = branchial bars.
br. c. = branchial chamber.
br. c'. = prebranchial chamber.
c. a. = colonial aperture.
c. f. = ciliated funnel.
cl. = cloaca.
cl. a. = cloacal aperture.
cl. m. = cloacal muscle.
cl. tn. = cloacal tentacle.
c. m. = circum-oral muscle.
d. = diaphragm.
d. a. s. = dorsal anterior blood sinus.
d. l. = dorsal languet.
d. l. s. = dorso-lateral blood sinus.
d. p. s. = dorsal posterior blood sinus.
d. s. = dorsal blood sinus.
dt. = duct of neural gland.
e. = endostyle.

- en.* = enteron.
f. c. = follicle cell.
g. = ganglion.
gl. = neural gland.
g. s. = posterior gonadial sinus.
h. = heart.
int. = intestine.
l. m. = ventral lateral muscular system.
l. m'. = dorsal lateral muscular system.
l. o. = luminous organ.
l. o'. = cloacal luminous organ.
m. = mouth.
n. = nerve.
n. 1-n. 8 = nerves.
nc. = nucleus.
n. r. = neural rudiment.
o. = ovary.
od. = oviduct.
oc. = esophagus.
oc. a. = esophageal aperture.
op. = operculum.
ov. = ovum.
p. = pigment.
p. a. = primary ascidiozoöid.
pbr. = peribranchial chamber.
pc. = pericardium.
pc'. = pericardial tube.
ph. = pharynx.
ph. b. = peripharyngeal band of cilia.
ph. s. = peripharyngeal blood sinus.
py. = pylorus.
r. v. = reniform vesicle.
s. = stolon.
s'. = stolon process.
s. s. = stolon blood sinus.
st. = stomach.
stg. = stigma.
t. = testis.
t. f. = test fibre.
tn. = tentacle.
t. p. = test process.
t. s. = blood sinus to tunic.
v. a. s. = ventral anterior blood sinus.
vc. s. = visceral sinus.
v. d. = vas deferens.
v. l. s. = ventro-lateral blood sinus.
v. s. = ventral blood sinus.
y. = yolk.

PLATE 15.

Pyrosoma atlanticum.

FIG. 1.—A schematic figure of a zoöid, showing internal organization. After Burghause (1914).

PLATE 16.

Pyrosoma agassizi.

FIG. 2.—An oral view of the mouth region of a zoöid, showing tentacles, sphincter muscles, lateral muscles, nervous system, peripharyngeal bands and tip of endostyle. After Neumann (1909-1913).

3.—A nearly adult zoöid, seen from the left side. $\times 25$.

PLATE 17.

Pyrosoma agassizi.

FIG. 4.—A posterior view of a nearly adult zoöid. $\times 25$.

5.—The nervous system, exclusive of the oral region. After Neumann (1909-1913).

PLATE 18.

Pyrosoma agassizi.

FIG. 6.—The open end of a colony. After Ritter and Byxbee (1905).

7.—A young zoöid, seen from the left side. $\times 42$.

PLATE 19.

Pyrosoma spinosum.

FIG. 8.—An adult zoöid, seen from the left side. $\times 17$.

PLATE 20.

Pyrosoma spinosum.

FIG. 9.—A postero-ventral view of the posterior end of an adult zoöid. $\times 21$.

10.—The reniform vesicle and adjacent organs, seen from the left side. $\times 28$.

PLATE 21.

FIG. 11.—*Pyrosoma spinosum*: A, an embryo with unsegmented stolon. $\times 18$
B, an embryo with the four primary ascidiozoöids appearing as buds upon the stolon
 $\times 56$.

12.—*P. verticillatum*: An adult zoöid, seen from the left side. $\times 21$. After Neumann (1909c).

PLATE 22.

FIG. 13.—*Pyrosoma verticillatum*: The oral region of a zoöid, showing chiefly the nervous system. After Neumann (1909-1913).

14.—*P. verticillatum cylindricum*: Colony. $\times 2$.

15. *P. verticillatum cylindricum*: An adult zoöid, seen from the left side. $\times 21$.

PLATE 23.

FIG. 16.—*Pyrosoma hybridum*: Colony. $\times 2$.

17.—*P. hybridum*: An adult zoöid, seen from the left side. $\times 21$.

18.—*P. ellipticum*: An adult zoöid seen from the left side. $\times 21$.

19.—*P. ellipticum*: Colony. Natural size.

20.—*P. ellipticum*: The same colony as that shown in figure 19, seen from the open end. Natural size.

PLATE 24.

- FIG. 21.—*Pyrosoma operculatum*: Colony. $\frac{2}{3}$ natural size. After Neumann (1908).
 22.—*P. operculatum*: A nearly adult zoöid, seen from the left side. $\times 13$. After Neumann (1908).
 23.—*P. operculatum*: The end of the cloacal siphon, showing the opercular fold partly closed. $\times 15$. After Neumann (1908).
 24.—*P. aherniosum*: An adult zoöid, seen from the right side. $\times 25$. After Seeliger (1895).
 25.—*P. aherniosum*: The viscera of a young zoöid (testis immature), seen from the left side. $\times 52$. After Seeliger (1895).

PLATE 25.

Pyrosoma ovatum.

- FIG. 26.—The oral end of an adult zoöid of the elongated sort, seen from the left side. After Neumann (1913 b).
 27.—An adult zoöid of the shorter sort, seen from the left side. $\times 11$. Modified from Neumann (1909 b).
 28.—A sagittal section through the distal end of the oral siphon of a zoöid of the elongated sort. $\times 11$. After Neumann (1909 b).
 29.—A somewhat ventral view of the distal end of an oral siphon of a zoöid of the elongated sort. $\times 24$. After Neumann (1913 b).

PLATE 26.

Pyrosoma atlanticum atlanticum.

- FIG. 30.—An adult zoöid, seen from the left side. $\times 21$.

PLATE 27.

Pyrosoma atlanticum atlanticum.

- FIG. 31.—The posterior end of an immature zoöid, from a large colony, seen from the left side. $\times 32$.
 32.—A young zoöid from a small colony, seen from the left side. This was the most nearly mature zoöid in the colony. $\times 21$.

PLATE 28.

- FIG. 33.—*Pyrosoma atlanticum atlanticum*: An outline drawing of a ventral view of an oral process of an adult zoöid.
 34.—*P. atlanticum hawaiiense*: A nearly adult zoöid, seen from the left side. $\times 15$.

PLATE 29.

- FIG. 35.—*P. atlanticum paradoxum*: An adult zoöid, seen from the left side. $\times 21$.
 36.—*P. atlanticum triangulum*: An adult zoöid, seen from the left side. \times about 11. After Neumann (1909 a).

PLATE 30.

Pyrosoma atlanticum giganteum.

- FIG. 37.—An adult zoöid from a large colony, seen from the left side. $\times 19$.

PLATE 31.

Pyrosoma atlanticum echinatum.

- FIG. 38.—A mature zoöid of the sort without an elongated oral siphon. $\times 21$.

PLATE 32.

Pyrosoma atlanticum, form *dipleurosoma*.

- FIG. 39.—A colony, seen from the flattened face. $\times \frac{3}{2}$. After Brooks (1906).
 40.—An edge view of a colony. $\times \frac{3}{2}$. After Brooks (1906).
 41.—The open end of a colony. $\times \frac{3}{2}$. After Brooks (1906).

PLATE 33.

- FIG. 42.—*Pyrosoma agassizi*: An unretouched photograph of a colony. $\times 1\frac{1}{2}$.
 43.—*P. verticillatum cylindricum*: An unretouched photograph of a colony. $\times 2$.
 44.—*P. ellipticum*: An unretouched photograph of a colony. $\times 1\frac{1}{2}$.

PLATE 34.

- FIG. 45.—*Pyrosoma atlanticum atlanticum*: An unretouched photograph of a colony. About natural size.
 46.—An unretouched photograph of the open end of the colony shown in figure 45. Slightly enlarged.
 47.—*P. atlanticum*, form *dipleurosoma*: An unretouched photograph of a twisted colony, partly in edge view, partly in face view. About natural size.

PLATE 35.

- FIG. 48.—*Pyrosoma atlanticum echinatum*: An unretouched photograph of a colony. About natural size.
 49.—*P. atlanticum hawaiiense*: An unretouched photograph of a colony. About natural size.

PLATE 36.

- FIGS. 50-53.—*Pyrosoma atlanticum*, subspecies doubtful, figure 53 shows a form resembling the type of the species: Retouched photographs of young colonies. The open ends of the colonies are toward the top of the plate except in figure 51, which is a view of the closed end of the same colony that is shown in figure 50. \times about $1\frac{1}{2}$.
 54.—*P. hybridum*, a retouched photograph, showing the flattened face of the colony $\times 1\frac{1}{2}$.
 55.—A retouched photograph, in edge view, of the same colony as that shown in figure 54. $\times 1\frac{1}{2}$.

This manuscript was completed for the United States Bureau of Fisheries on July 10, 1915, and received for publication by the United States National Museum on February 21, 1917.

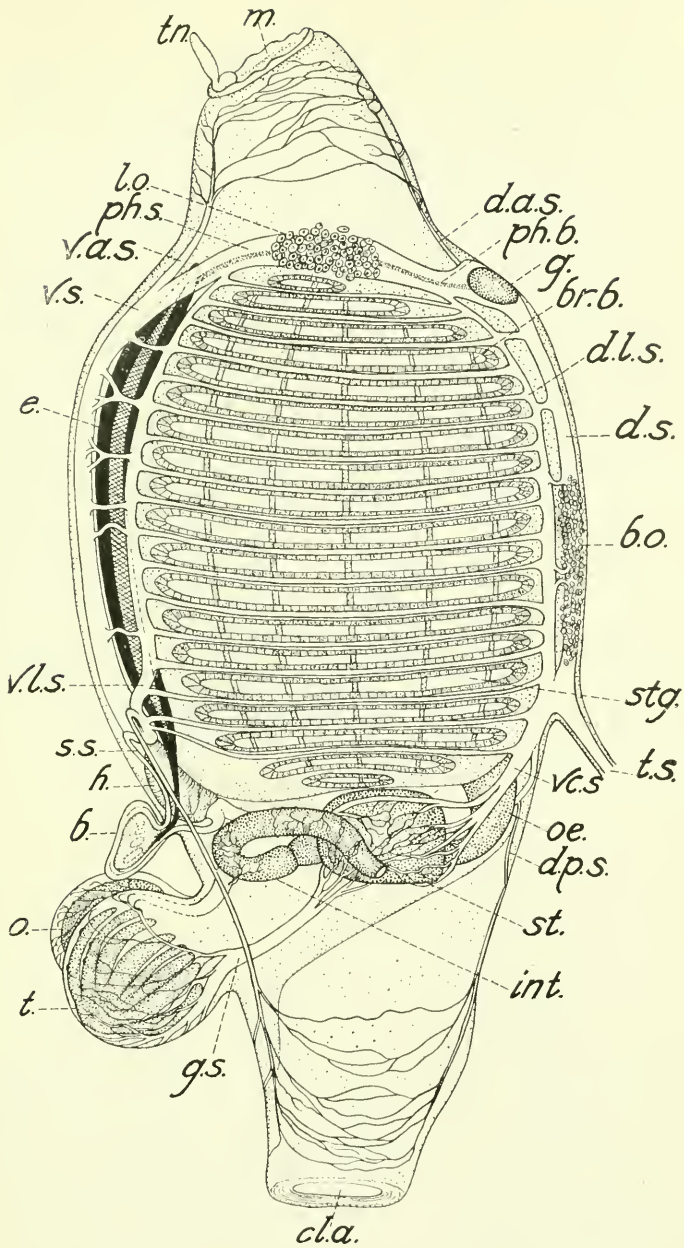


Fig. 1.

PYROSOMA ATLANTICUM.

FOR EXPLANATION OF PLATE SEE PAGE 270.



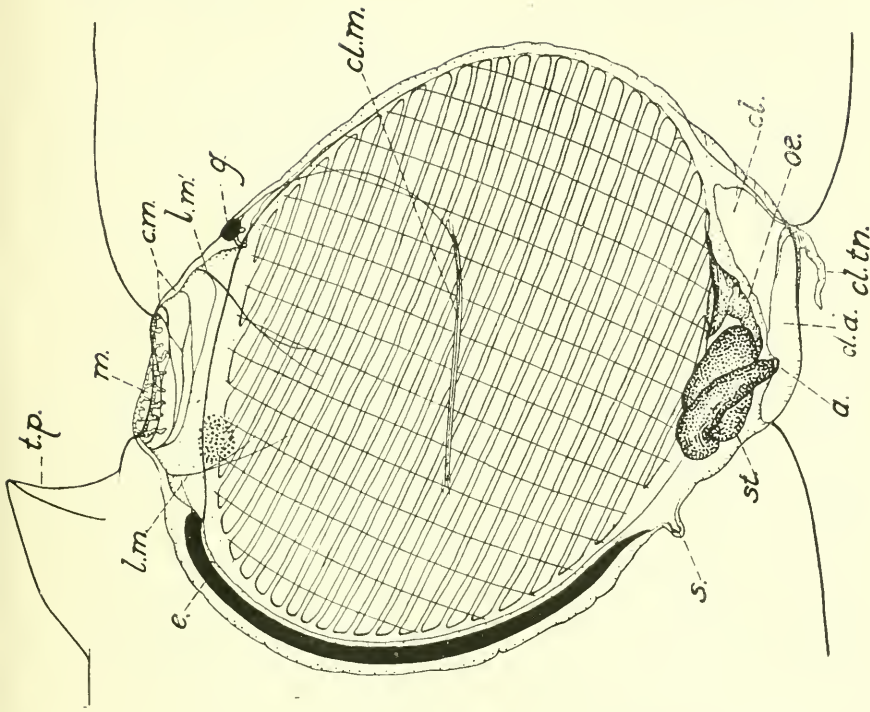


Fig. 3

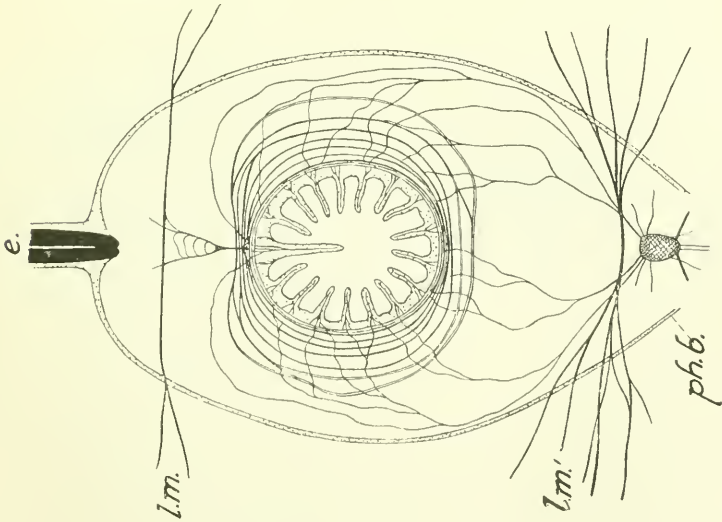


Fig. 2.

PYROSOMA AGASSIZI.

FOR EXPLANATION OF PLATE SEE PAGE 270.

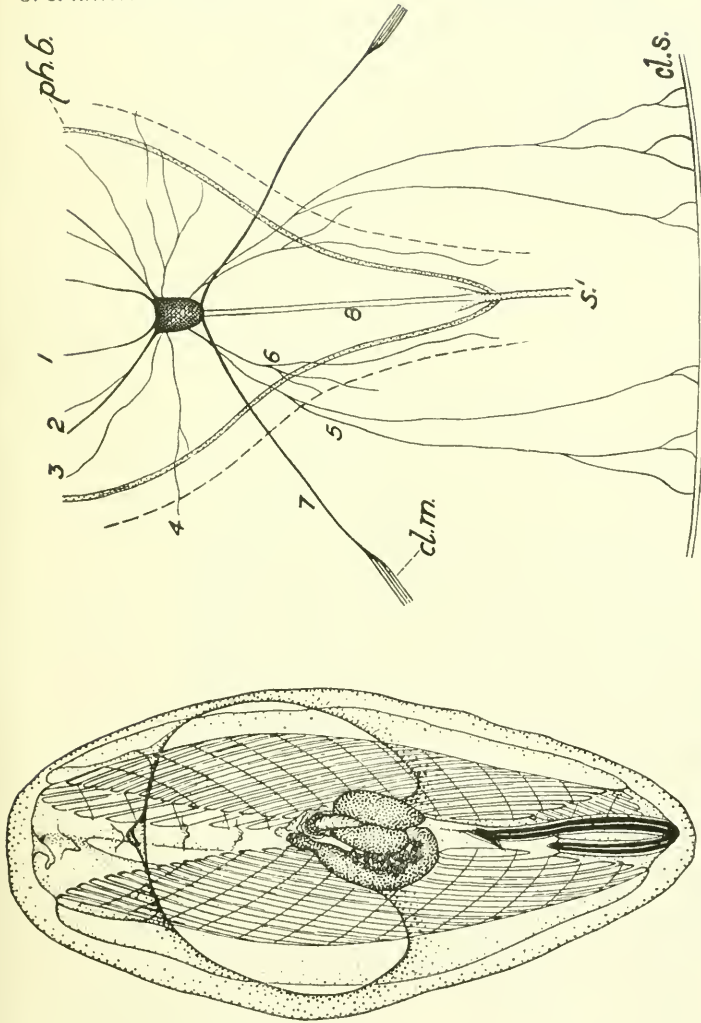


Fig. 5.

PYROSOMA AGASSIZI.

FOR EXPLANATION OF PLATE SEE PAGE 270.

Fig. 4.

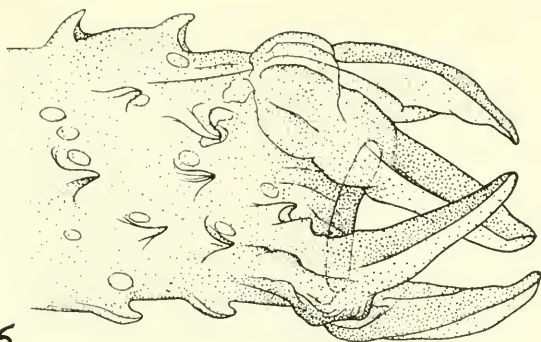


Fig. 6.

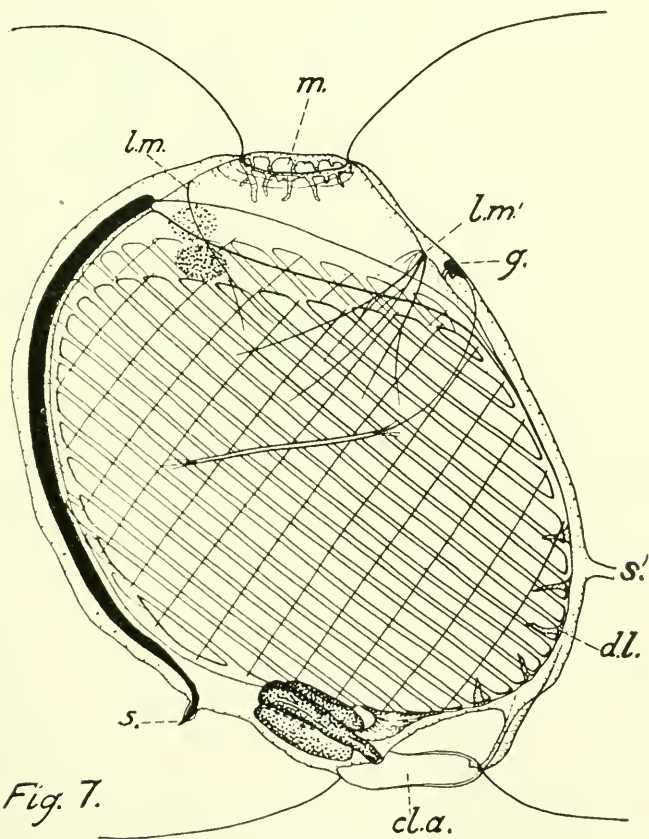


Fig. 7.

PYROSOMA AGASSIZI.

FOR EXPLANATION OF PLATE SEE PAGE 270.

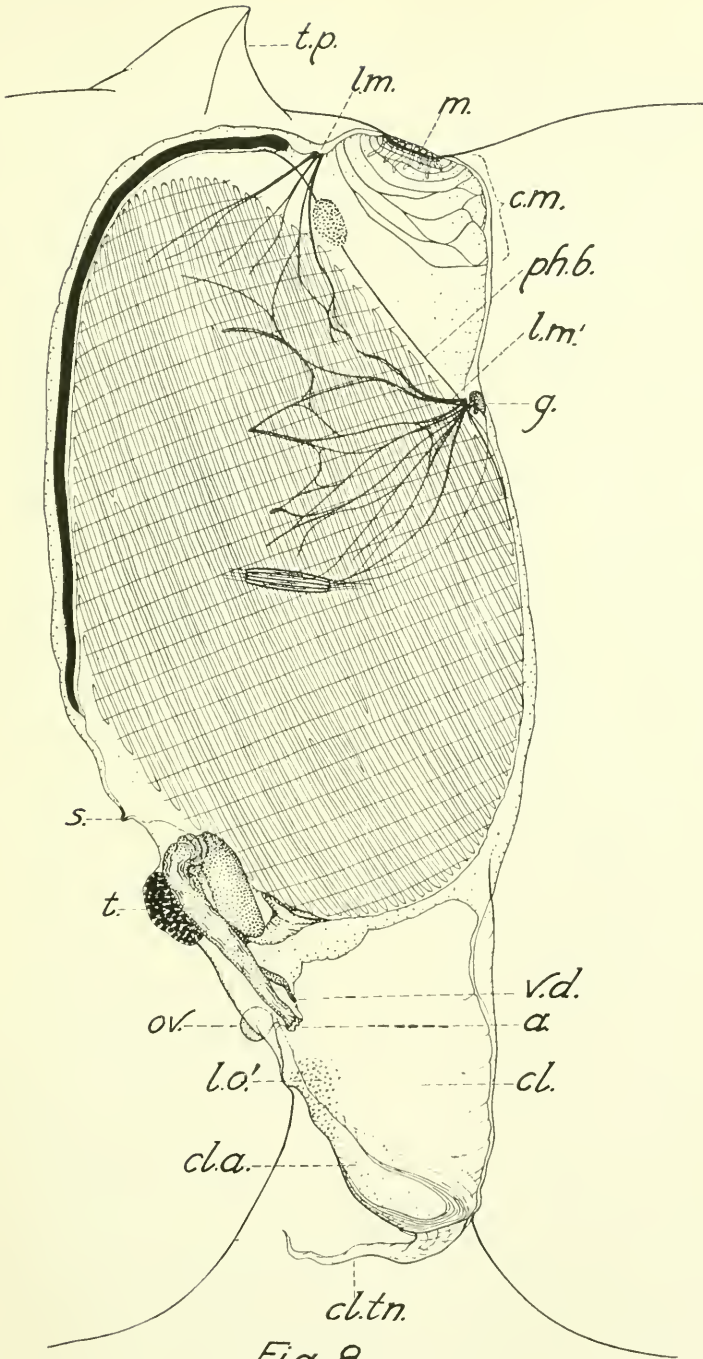


Fig. 8.

PYROSOMA SPINOSUM.

FOR EXPLANATION OF PLATE SEE PAGE 270.

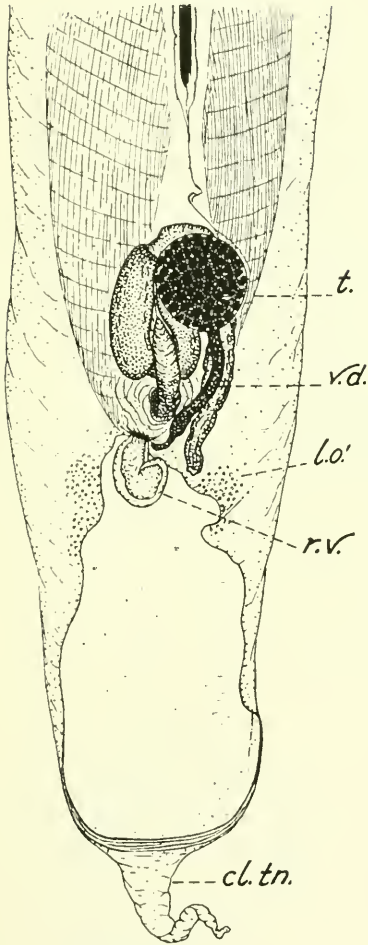


Fig. 9.

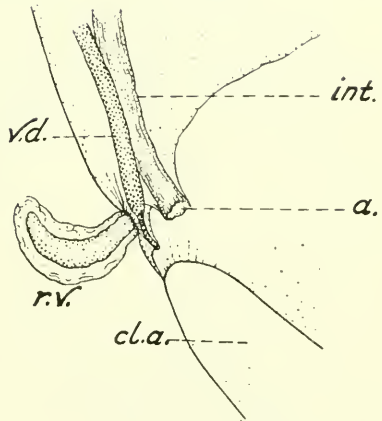
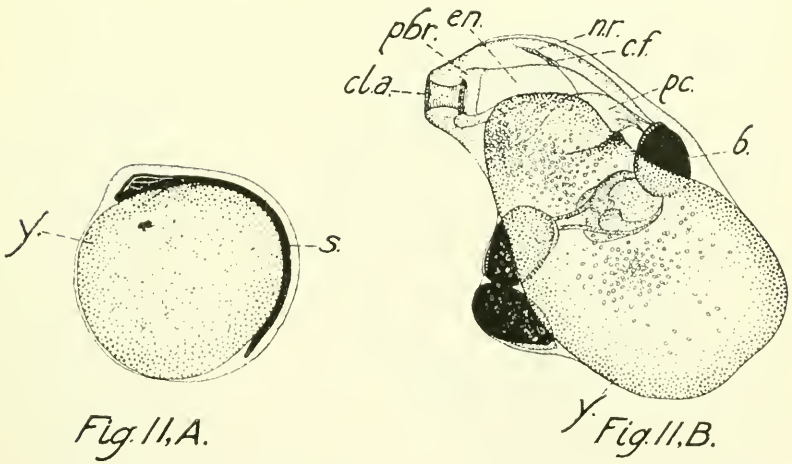
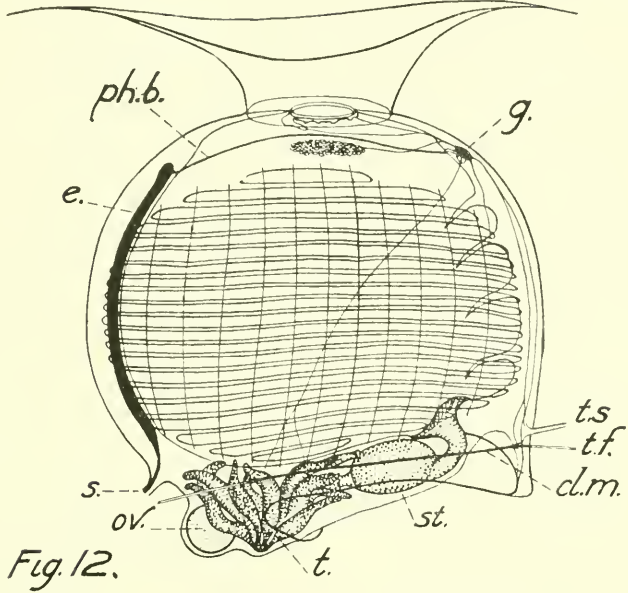


Fig. 10.

PYROSONA SPINOSUM.

FOR EXPLANATION OF PLATE SEE PAGE 270



PYROSOMA SPINOSUM (FIGS. 11, A AND B) AND P. VERTICILLATUM (FIG. 12).

FOR EXPLANATION OF PLATE SEE PAGE 270.

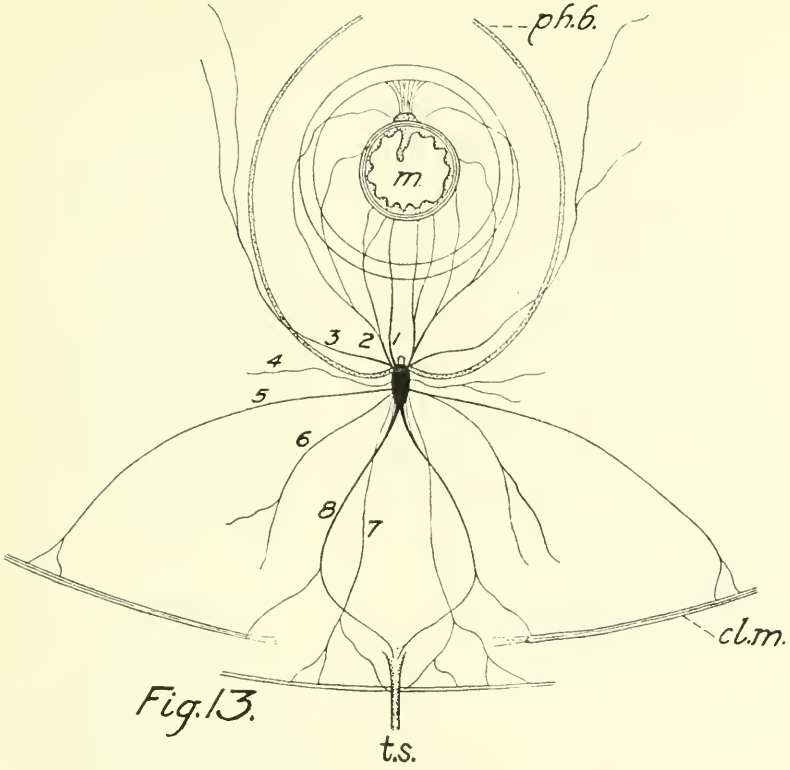


Fig. 13.

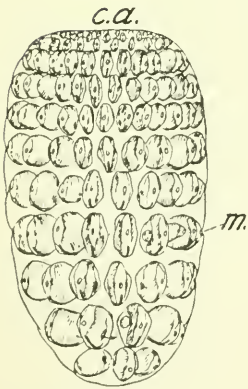


Fig. 14.

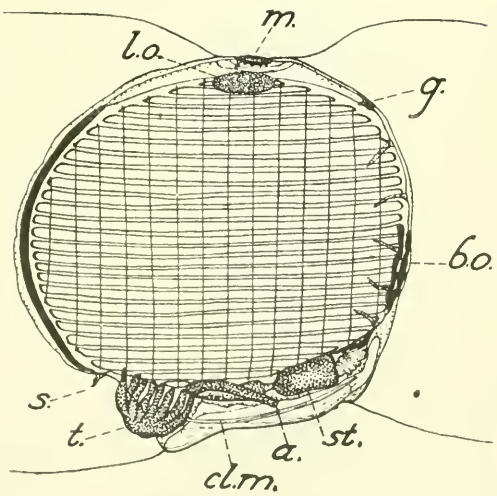


Fig. 15.

PYROSOMA VERTICILLATUM (FIG. 13) AND ITS SUBSPECIES CYLINDRICUM (FIGS. 14, 15).

FOR EXPLANATION OF PLATE SEE PAGE 270.



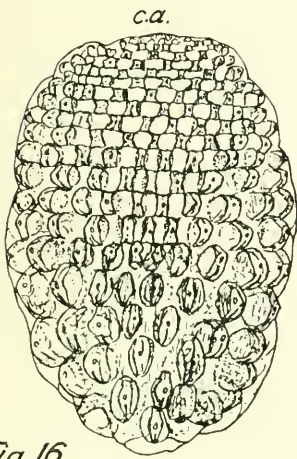


Fig. 16.

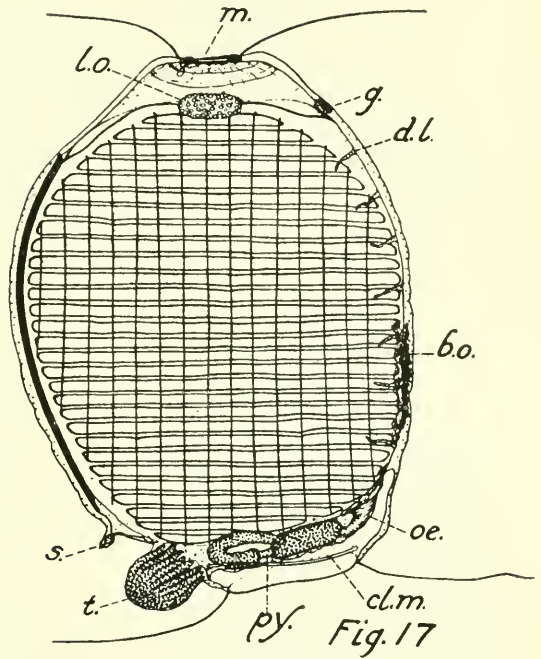


Fig. 17

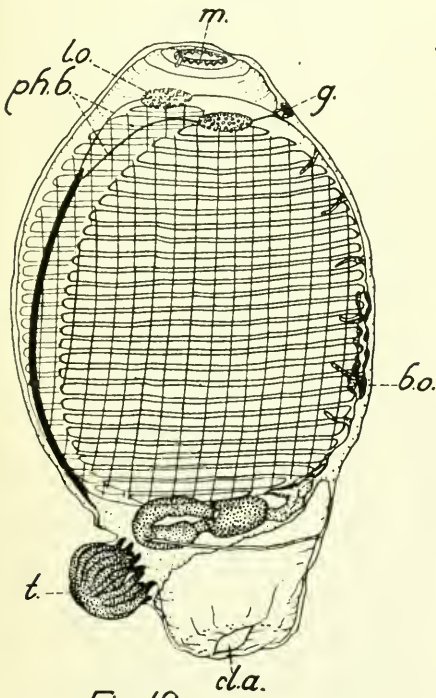


Fig. 18

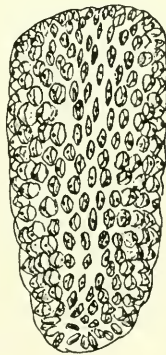


Fig. 19.



Fig. 20.

PYROSOMA HYBRIDUM (FIGS. 16, 17) AND P. ELLIPTICUM (FIGS. 18-20).

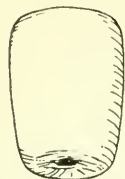


Fig. 21.

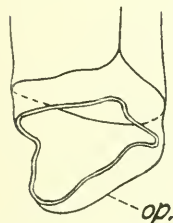


Fig. 23.

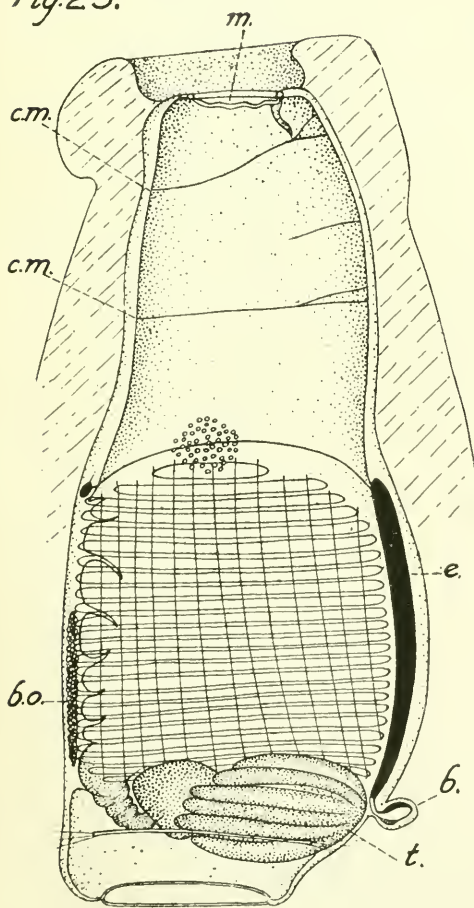


Fig. 24.

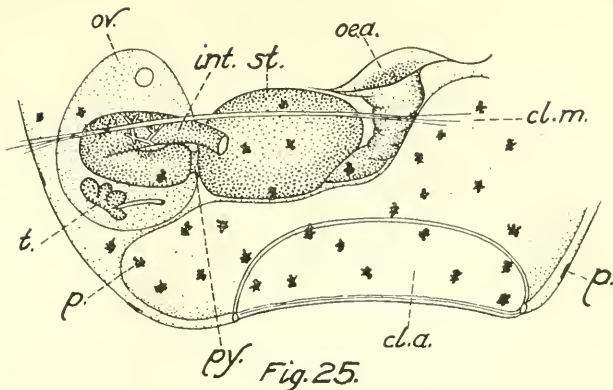


Fig. 25.

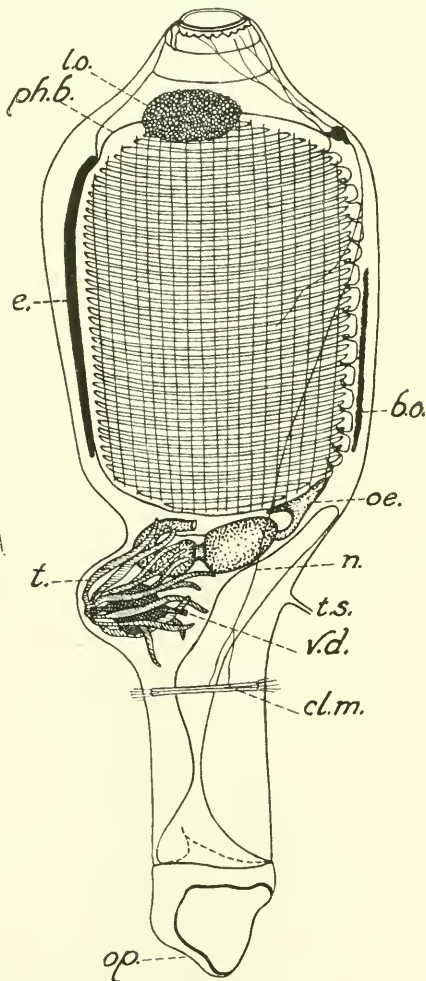


Fig. 22.

PYROSOMA OPERCULATUM (FIGS. 21-23) AND P. AHERNOSUM (FIGS. 24 AND 25).

FOR EXPLANATION OF PLATE SEE PAGE 271.

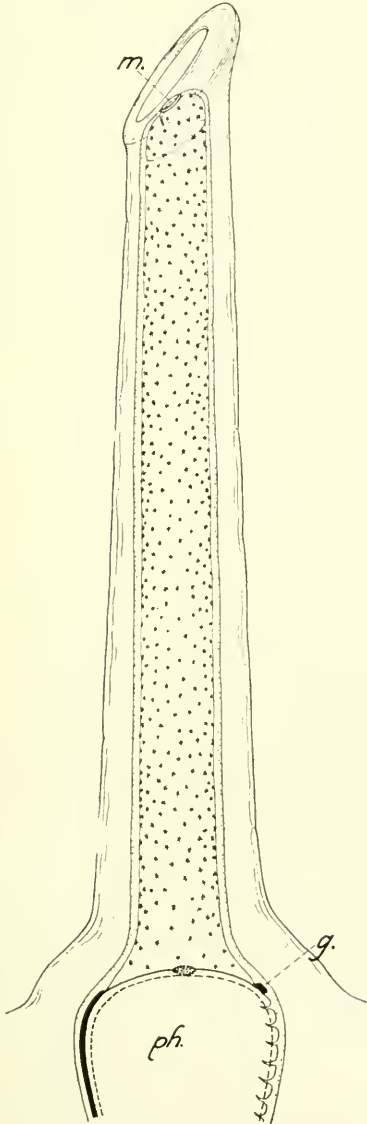


Fig. 26.

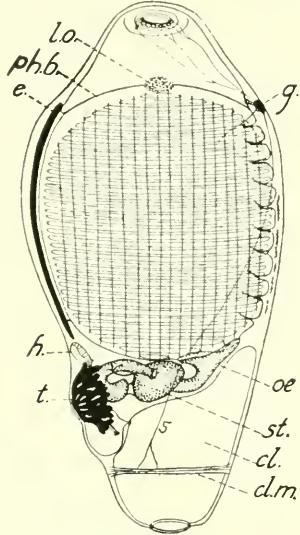


Fig. 27.

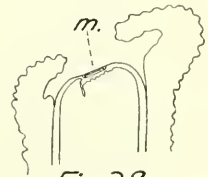


Fig. 28.

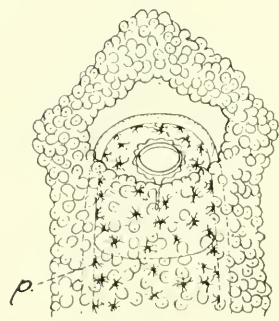


Fig. 29.

PYROSOMA OVATUM.

FOR EXPLANATION OF PLATE SEE PAGE 271.

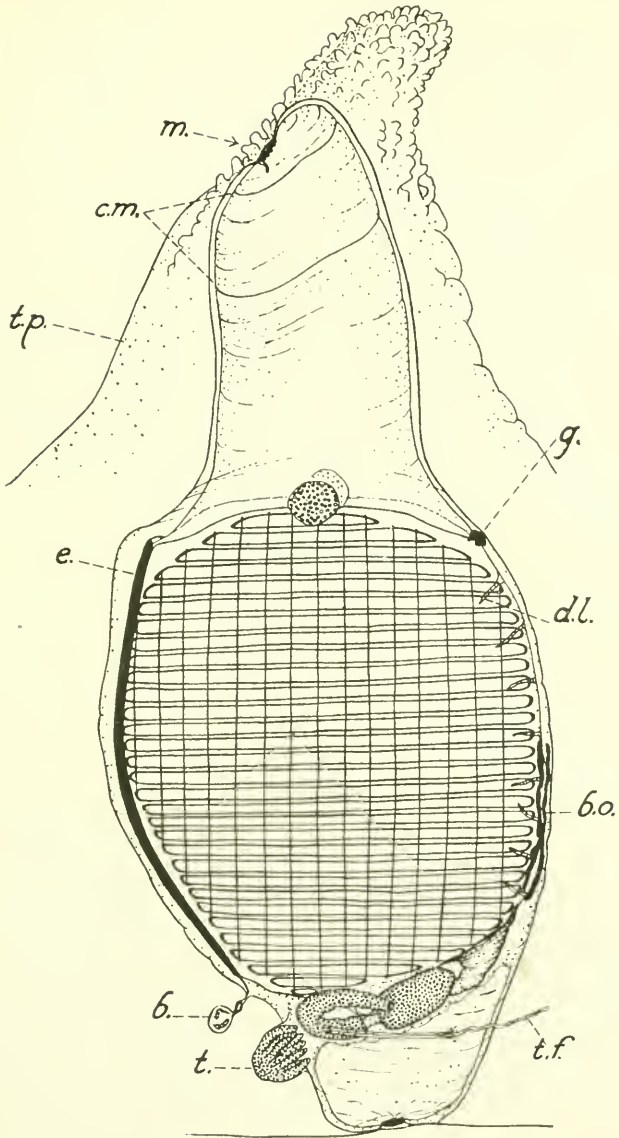


Fig. 30.

PYROSOMA ATLANTICUM ATLANTICUM.

FOR EXPLANATION OF PLATE SEE PAGE 271.

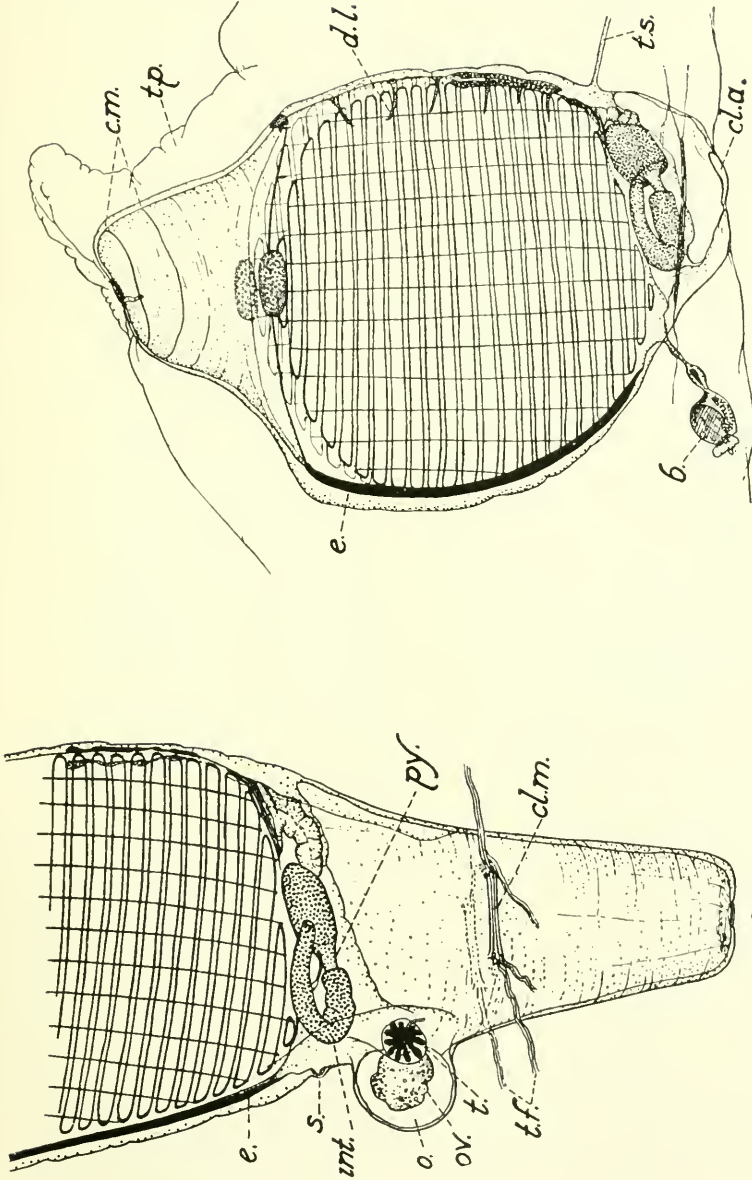


Fig. 32.

cl.a.
Fig. 31

PYROSOMA ATLANTICUM ATLANTICUM.

FOR EXPLANATION OF PLATE SEE PAGE 271.

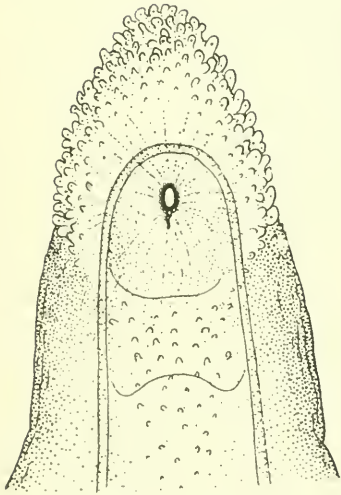
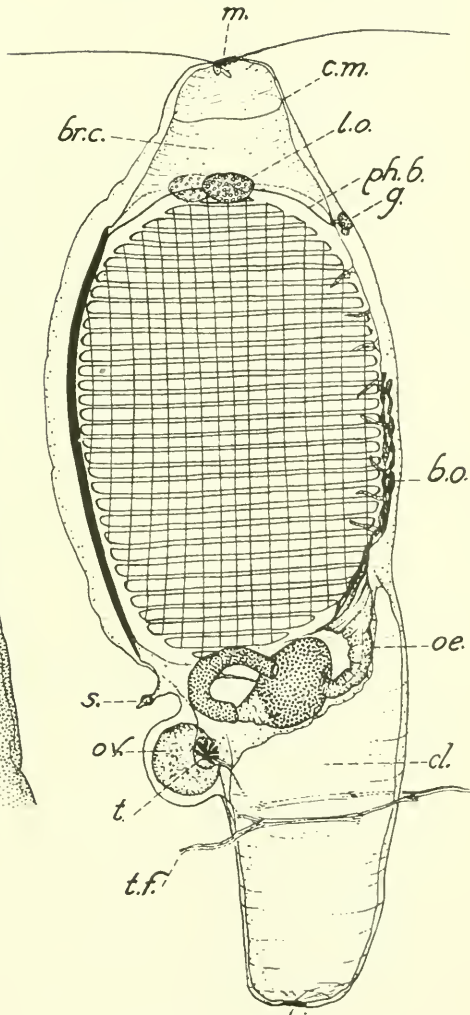


Fig. 33.



cl.a.
Fig. 34.

PYROSOMA ATLANTICUM ATLANTICUM (FIG. 33) AND P. ATLANTICUM HAWAIIENSE (FIG. 34).

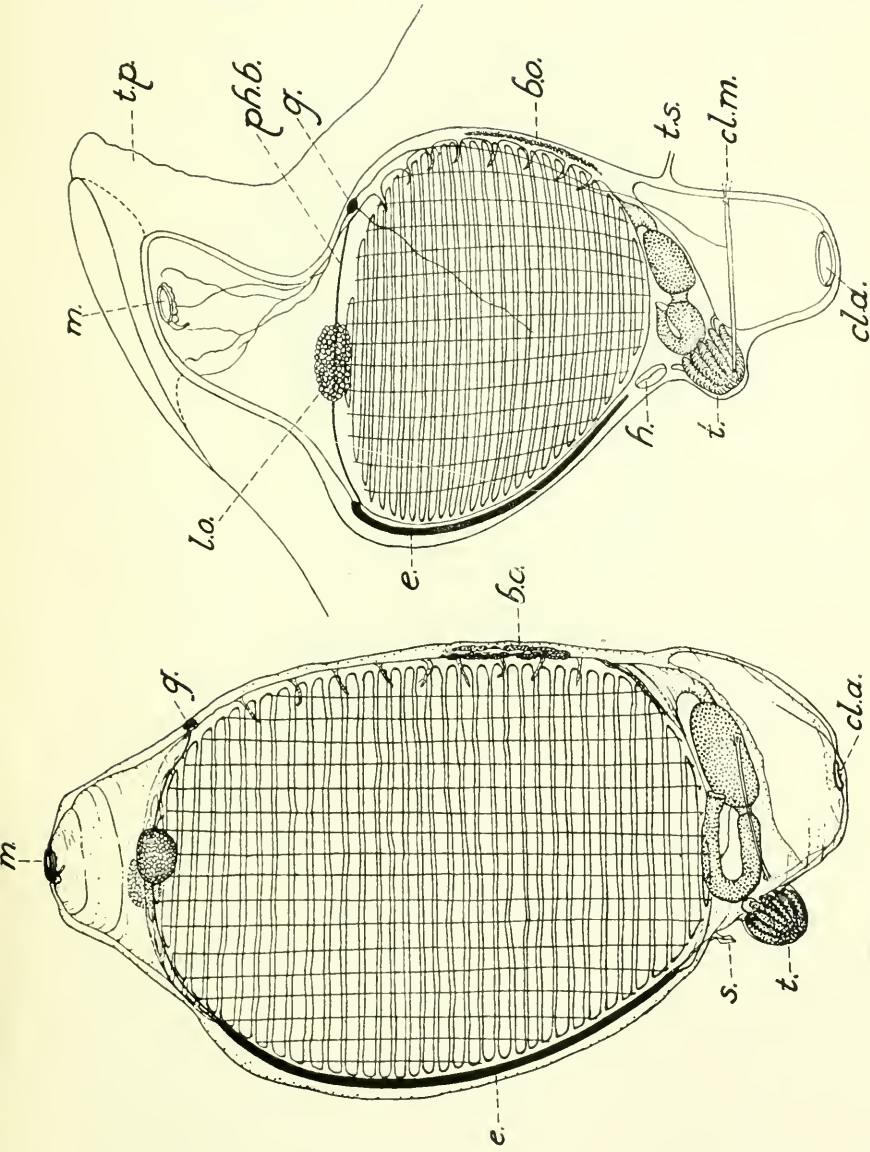
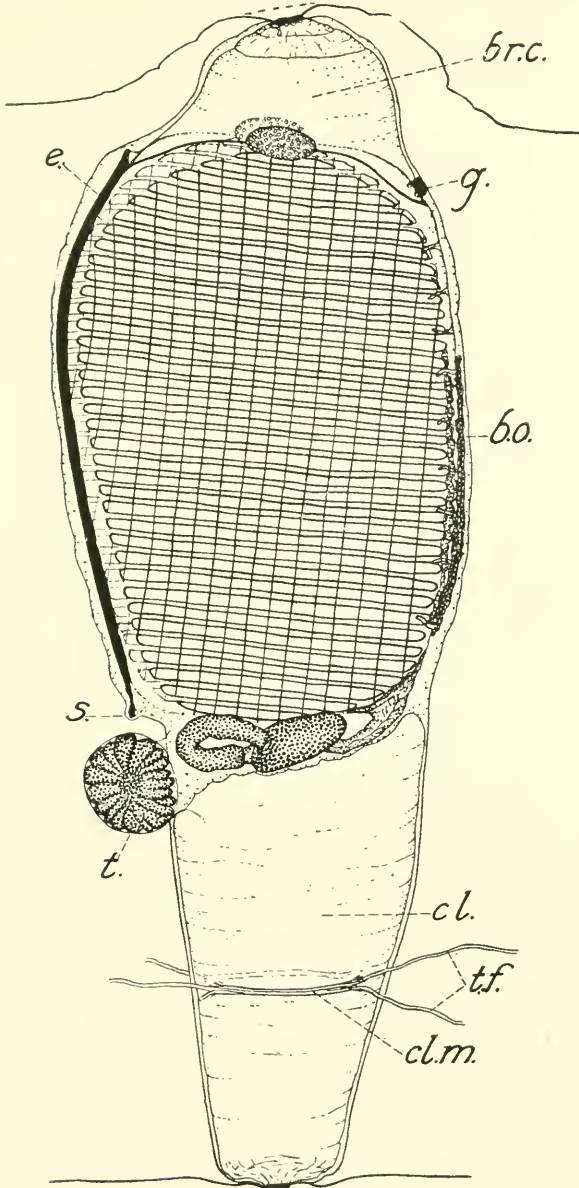


Fig. 36.

Fig. 35.

PYROSOMA ATLANTICUM PARADOXUM (FIG. 35) AND P. ATLANTICUM TRIANGULUM (FIG. 36).

FOR EXPLANATION OF PLATE SEE PAGE 271.



cl.a.
Fig. 37.

PYROSOMA ATLANTICUM GIGANTEUM.

FOR EXPLANATION OF PLATE SEE PAGE 571

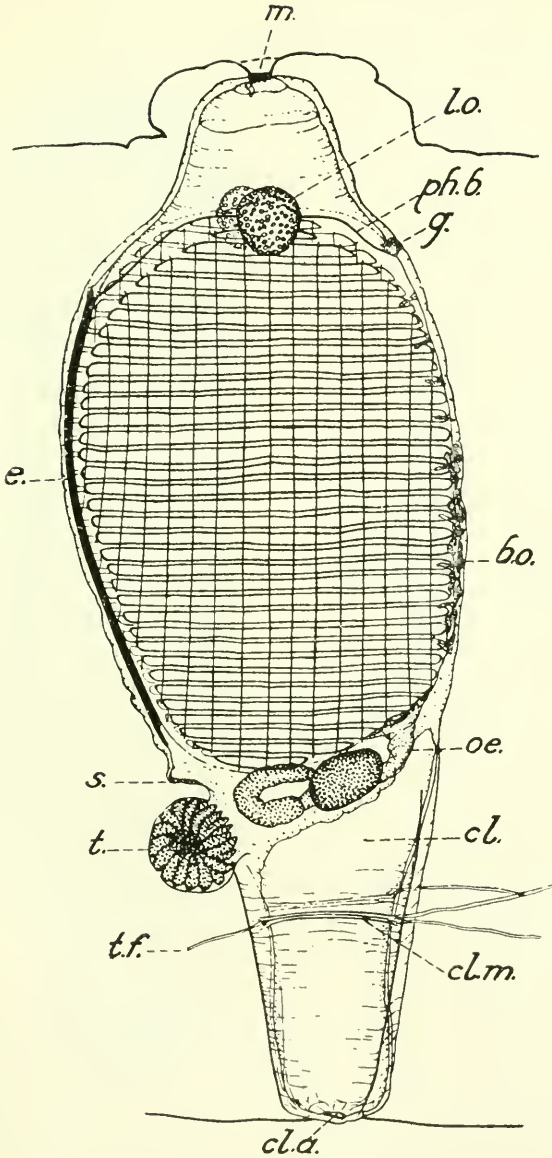


Fig. 38.

PYROSOMA ATLANTICUM ECHINATUM.

FOR EXPLANATION OF PLATE SEE PAGE 271.

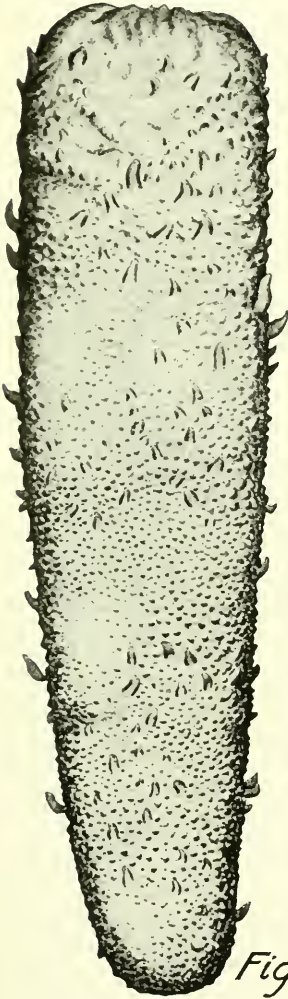


Fig. 39



Fig. 40



Fig. 41

PYROSOMA ATLANTICUM, FORM DIPLEUROSOMA.

FOR EXPLANATION OF PLATE SEE PAGE 272.



Fig. 42



Fig. 44



Fig. 43

PYROSOMA AGASSIZI (FIG. 42); P. VERTICILLATUM CYLINDRICUM (FIG. 43); P. ELLIPTICUM (FIG. 44).

FOR EXPLANATION OF PLATE SEE PAGE 272.

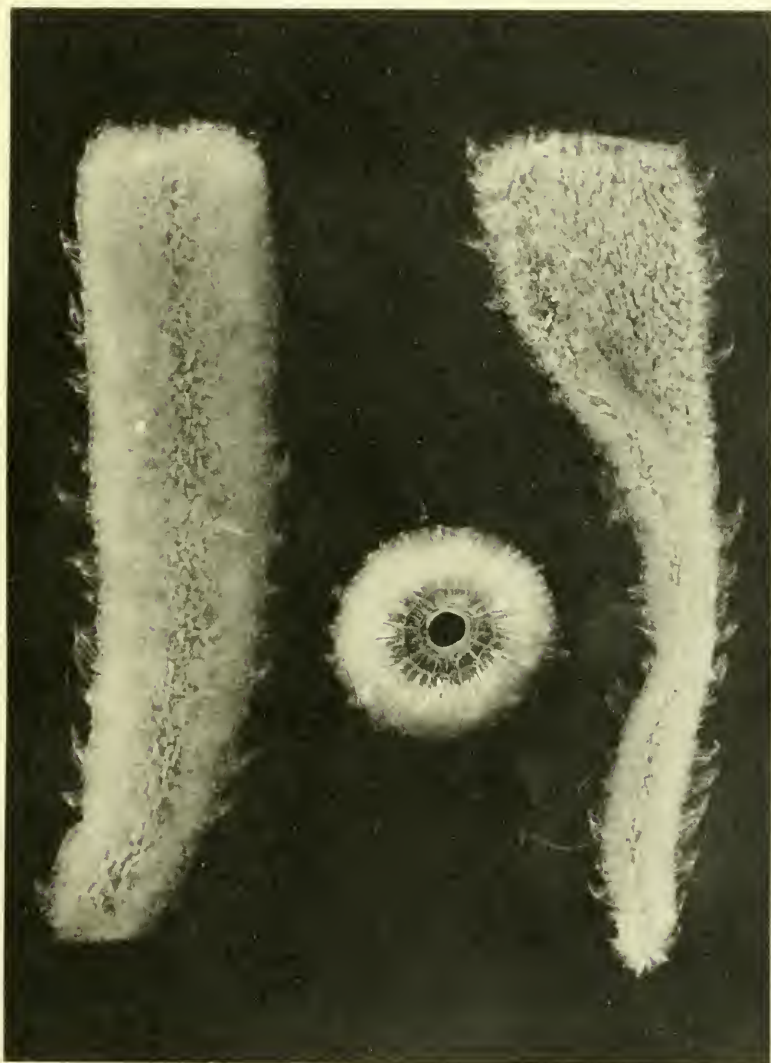


Fig. 45

Fig. 46

Fig. 47

PYROSOMA ATLANTICUM ATLANTICUM (FIGS. 45 AND 46); P. ATLANTICUM FORM DIPLEUROSOMA (FIG. 47).

FOR EXPLANATION OF PLATE SEE PAGE 272.





Fig. 48

Fig. 49

PYROSOMA ATLANTICUM ECHINATUM (FIG. 48); P. ATLANTICUM HAWAIIENSE (FIG. 49).

FOR EXPLANATION OF PLATE SEE PAGE 272.



Fig. 50



Fig. 51



Fig. 53



Fig. 52



Fig. 54

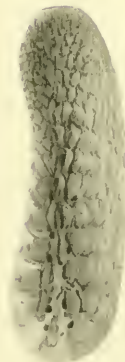


Fig. 55

PYROSOMA ATLANTICUM, SUBSPECIES DOUBTFUL (FIGS. 50 AND 52); P. ATLANTICUM ATLANTICUM (FIG. 53); P. HYBRIDUM (FIGS. 54 AND 55).

