XXV. Remarks upon Appendicularia and Doliolum, two genera of the Tunicata.

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(late of H.M.S. "Rattlesnake"). Communicated by Prof. Edward Forbes, F.R.S.

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79. THE genus Appendicularia was first formed by Chamisso from an animal found by him near Behring's Straits, and thus described: "Corpus gelatinosum, subovoideum, vix quartam pollicis partem æquans, punctis rubescentibus (interaneis) transparentibus. Appendix gelatinosa cestoidea, rubro marginata corpore duplo vel triplo longior. Motu flexuoso natationi inserviens. Motus animalis vividus." And he adds, "genus ultra recognoscendum, generi Cestum (Les.) forsitan affine." The specific name "flagellum" was conferred upon the animal, and it was figured (P. XXXI.), though very indifferently\*.

Ten years afterwards (in 1828) Mertens, voyaging in the same regions, rediscovered this animal, and he subsequently published a long account of it  $\uparrow$  under the name of Oikopleura Chamissonis.

The only other notice of the genus (so far as I am aware) is that given by MM. Quoy and Gaimard. It was observed in immense masses off Algoa Bay, South Africa, and was called by them *Fritillaria*, until they afterwards became acquainted with the descriptions of Chamisso and Mertens. Recognising as they do the priority of discovery of the former, they yet adopt the name conferred by the latter, and, without any very just reason, give to the specimens observed by themselves a new specific name, O. bifurcata.

Vast numbers of the species observed by myself were found on the coast of New Guinea and in the Southern Pacific. The differences separating this from the species observed by Mertens are not to my mind sufficient to form the basis of any specific distinction, and as the description given by MM. Quoy and Gaimard, and by Chamisso, are too imperfect to establish any certain distinguishing characters in their case either, I shall consider that only one species has been observed. And as I can see no reason for the construction of a new and by no means euphonious name by Mertens, I shall retain both the generic and specific names given by Chamisso, Appendicularia flagellum (Chamisso), Syn. Oikopleura Chamissonis (Mertens), Oikopleura bifurcata (Quoy and Gaimard).

- \* De Animalibus quibusdam et classe Vermium, Fasc. Secundus. Nova Acta Acad. Cur. tom. x. 1821.
- † In the Mémoires de l'Acad. Imp. de St. Pétersbourg, 1831.
- ‡ Zoology of the Astrolabe, vol. iv. p. 304.

80. The animal has an ovoid or flask like body, Plate XVIII. fig. 1, one-sixth to one-fourth of an inch in length, to which is attached a long curved lanceolate appendage or tail, by whose powerful vibratory motions it is rapidly propelled through the water.

The body frequently appears wrinkled and crumpled externally, and its upper, smaller extremity has rarely clear and well-defined edges. The lower part of the body is frequently separated from the upper by a slight cleft or constriction, fig. 4, and it is here that Mertens places the orifice of the mouth, supposing indeed that the upper part of the body plays the part of a maxilla!

81. The smaller extremity of the animal is perforated by a wide aperture (d) which leads into a chamber, which occupies the greater part of the body, and at the bottom of this chamber is the mouth. The chamber answers to the respiratory cavity of the Tunicata, and is lined by an inner tunic distinct from the outer; the space between these, as in the Salp x, being occupied by the sinus system.

On the side to which the caudal appendage is attached, an endostyle (c), altogether similar to that of the Salpæ, lies between the inner and outer tunics; and opposite to this, or on the ventral side, close to the respiratory aperture, there is a nervous ganglion, to which is attached a very distinct spherical auditory sac, containing a single, also spherical, otolithe. The sac is about  $\frac{1}{200}$ th of an inch in diameter. The otolithe about  $\frac{1}{800}$ th, figs. 1, 2, 4 a.

Anteriorly, a nerve is given off from the ganglion (a) which becomes lost about the parietes of the respiratory aperture; another large trunk passes backwards (b) over the left side of the esophagus, and between the lobes of the stomach, until it reaches the appendage, along the axis of which it runs, giving off filaments in its course, fig. 2. I did not observe anything resembling the "languet" of the Salpæ; but Mertens describes two leaf-like laminæ existing, one on each side of a "semicylindrical" body, which seems to be the nervous ganglion.

82. There is no proper branchia; but that organ seems to be represented by a richly ciliated band or fold (e) of the inner tunic, which extends from the opening of the mouth forwards, along the ventral surface of the respiratory cavity, to nearly as far as the ganglion; when it divides into two branches, one of which passes up on each side, so as to encircle the cavity (f). This circlet evidently represents the "ciliated band" of Salpa.

The mouth (g) is wide, and situated at the posterior part of the ventral paries of the respiratory chamber. The  $ext{cosphagus}(h)$  short, and slightly curved, opens into a wide stomach (i) curved transversely, so as to present two lobes posteriorly.

Between the two lobes, posteriorly, the intestine (k) commences, and passing upwards (or forwards) terminates on the dorsal surface just in front of the insertion of the caudal appendage (l).

The heart lies behind, between the lobes of the stomach. I saw no corpuscles, and the incessant jerking motion of the attached end of the caudal appendage rendered it very difficult to make quite sure even of the heart's existence.

83. Merrens describes a vascular system, consisting of an aortic vessel, which runs forwards on the dorsal surface, and of a principal vein of a red colour, which passes to the ventral surface, and there divides into three branches, one of which runs forwards to the "semicylindrical body" (ganglion?), and the other two pass to the dorsal region.

A circular canal communicating with the aortic vessel exists, he says, on each side of the anus, and is connected with the ventral vessel by means of a vessel, through which no corpuscles were seen to pass.

I have seen nothing of this vascular system. The caudal appendage (A) is attached or rather inserted into the body on the dorsal surface just behind the anus. It consists of a long, apparently structureless, transparent, central axis (m), rounded at the attached, and pointed at the free end. This axis is enveloped in a layer (o) of longitudinal, striped, muscular fibres; which form the chief substance, in addition to a layer of polygonal epithelium cells, of the broad alary expansion on each side of the axis.

I did not observe the lateral canal containing air, described by Mertens.

84. The only unequivocal generative organ I found in *Appendicularia* was a testis (p), consisting of a mass of cells developed behind and below the stomach, enlarging so much in full-grown specimens as to press this completely out of place.

In young specimens the testis is greenish, and contains nothing but small pale circular cells; but in adults it assumes a deep orange red-colour, caused by presence of multitudes of spermatozoa, whose development from the circular cells may be readily traced.

This orange-red mass, or rather masses, for there are two in juxtaposition, is described by Mertens as the "Samen-behälter" or vesiculæ seminales. He describes them as making their exit, bodily, from the animal, and then becoming diffused in the surrounding water. This circumstance, indeed, appears to have furnished his principal reason for believing these bodies to be what the name indicates.

The spermatozoa have elongated and pointed heads about  $\frac{1}{5000}$ th of an inch in length, and excessively long and delicate filiform tails.

MERTENS describes as an ovary, two granulous masses, which he says lie close to the vesiculæ seminales, and have two ducts, which unite and open into this "ovisac."

This appears to me to be nothing more than the granulous greenish mass of cells and undeveloped spermatozoa, which exists in the testis at the same time as the orange-red mass of fully developed spermatozoa.

I saw nothing of any ducts, nor do I know what the "ovisac" can be, unless it be a further development of an organ which I found in two specimens (fig. 3q), consisting of two oval finely granulous masses, about  $\frac{1}{300}$ th of an inch in diameter, attached, one on each side of the middle line, to the dorsal parietes of the respiratory cavity, and projecting freely into it.

MERTENS' "ovisac" has about the same position as these bodies, and he says he MDCCCLI.

4 H

saw "living animals" proceed from it, the part being afterwards evidently collapsed.

Unfortunately, however, he does not appear to have noticed the endostyle, whence confusion might readily arise; nor does he give the slightest hint as to the nature of the "living animals" which he saw come forth.

85. Still less am I able to give any explanation of the extraordinary envelope or "House" to which, according to Merrens, each Appendicularia is attached in its normal condition. I have seen many hundred specimens of this animal, and have never observed any trace of this structure; and I have had them in vessels for some hours, but this organ has never been developed, although Merrens assures us that it is frequently re-formed, after being lost, in half an hour.

At the same time it is quite impossible to imagine, that an account so elaborate and detailed, can be otherwise than fundamentally true, and therefore, as Mertens' paper is not very accessible, I will add his account of the matter, trusting that further researches may clear up the point.

The formation of the envelope or "Haus" commences by the development of a lamina from the "semicylindrical organ" (ganglion?). This, as it grows, protrudes through the opening at the apex of the animal (respiratory aperture). Its corners then become bent backwards and inwards, and thus a sort of horn is formed on each side, the small end of which is turned towards the apex of the animal, while its mouth looks backwards, downwards and outwards.

At the same time two other horns are developed upwards (the animal is supposed to have its small end downwards), one on each side. These are smaller and more convoluted than the others.

This four-horned structure consists of a very regular network of vessels, in which, at the time of the development of the organ, a very evident circulation is visible; the blood-corpuscles streaming from the attached end of the organ. "The clearness with which the circulation was perceptible, together with the great abundance of vessels and the large extent over which they were spread, were circumstances which led me (says Mertens) to believe this truly enigmatical structure to be an organ, whose function was the decarbonization of the blood. The ease with which the animal becomes separated from this organ is no objection to this view; the necessity there seems to exist for the reproduction of the latter rather confirming my opinion."

It is highly desirable that more information should be gained about this extraordinary respiratory organ, which, if it exist, will not only be quite sui generis in its class, but in all animated nature. And in a physiological point of view, the development of a vascular network, many times larger than the animal from which it proceeds, in the course of half an hour, will be a fact equally unique and startling.

86. As to the zoological relations of *Appendicularia*, its discoverer, as we have seen, considers that "it may possibly be allied to *Cestum*," a conjecture in which no one can possibly coincide.

MERTENS, on the other hand, says, "The relation of this animal with the *Pteropoda* is unmistakeable; if the *Oikopleura* possessed two tail-like appendages, every one would recognize in them the wings of the *Pteropoda*;" and he proceeds to draw, what seems to me, a very forced comparison between *Oikopleura* and *Clio*.

I do not think that any one who has read the preceding pages will be at all disposed to agree with Mertens either.

87. For my own part, I think there can be no doubt that the animal is one of the *Tunicata*. The whole organization of the creature, its wide respiratory sac, its nervous system, its endostyle, all lead to this view.

In two circumstances, however, it differs widely from all *Tunicata* hitherto known. The first of them is, that there is only one aperture, the respiratory, the anus opening on the dorsum; and secondly, that there is a long caudal appendage.

As to the first difference, it may be observed, that, in the genus *Pelonaia*, an undoubted Ascidian, there are indeed two apertures, but there is no separation into respiratory and cloacal chambers. Suppose that in *Pelonaia* the cloacal aperture ceased to exist, and that the rectum, instead of bending down to the ventral side of the animal, continued in its first direction and opened externally, we should have such an arrangement as exists in *Appendicularia*.

With regard to the second difference, I would remark, that it is just the existence of this caudal appendage which makes this form so exceedingly interesting.

It has been long known that all the Ascidians commence their existence as larvæ, swimming freely by the aid of a long caudate appendage; and as in all great natural groups some forms are found which typify, in their adult condition, the larval state of the higher forms of the group, so does *Appendicularia* typify, in its adult form, the larval state of the Ascidians.

Appendicularia, then, may be considered to be the lowest form of the Tunicata; connected, on the one hand, with the Salpæ, and on the other with Pelonaia, it forms another member of the hypothetical group so remarkably and prophetically indicated by Mr. MacLeay, and serves to complete the circle of the Tunicata.

88. Doliolum.—This name was given by Otto\* to a free-swimming gelatinous case, altogether structureless, of which a single example was found by him in the Gulf of Naples. Its nature is altogether unknown, for it is hardly justifiable, in the face of Otto's words, "Die Ränder sind aber völlig glatt ohne alle Spur von Zerreissung, nirgend sieht man inwendig Rauhigkeiten wo die Eingeweide angessessen haben könnten und die äussere Haut geht ohne Unterbrechung in die innere über," to assume with MM. Quoy and Gaimard, that it is only a Biphore whose intestines have been destroyed by a parasitic Phronima.

Furthermore, Otto states that the animal moved by a "worm-like contraction of its walls," which by no means describes the mode of contraction of the Salpæ, with which animals he was perfectly acquainted, and with a mutilated specimen of which,

<sup>\*</sup> Nova Acta Acad. Curiosorum, t. xi. pars secunda, pp. 313 and 314.

he expressly states he might, except for its peculiar motion, have confounded the form he describes\*.

MM. Quoy and Gaimard, altogether denying the existence of Otto's genus as a distinct form, appropriated his name for two species of tunicate animals observed by them at Amboyna and Vanikoro, and which they justly recognized as being very closely allied to the Salpæ.

Of these two species, *Doliolum denticulatum* and *Doliolum caudatum*;, the former is the only one with which I have met.

MM. Quoy and GAIMARD give only the following short description:-

"Its form is nearly that of the vessel from which we have derived its generic name, that is to say, it is enlarged in the middle and narrowed at its two extremities where the openings are situated. The anterior opening is somewhat projecting and denticulated like a crown. Eight circles in relief surround the body at nearly equal distances. They have rather a polygonal than a circular form, and are probably vessels. In the interior the branchia is visible, divided into two portions, which have their oblique lamellæ upon a central vessel, as in the Pectinibranchiata. Near the union of the two divisions posteriorly is the heart, and between them (?) a vessel, the aorta, ascends; not far from the heart is a transparent nucleus. This is all that the vivacity of the mollusk, which bounded like an arrow through the water, allowed us to make out of its organization."

Although I cannot think that MM. Quoy and GAIMARD have done well in appropriating Otto's name to an animal confessedly different from that which he describes, it will perhaps cause least confusion to follow their example.

The specimens which I examined were taken in the South Pacific, a little to the northward of Sydney, N.S.W., between Sydney and New Zealand, and in considerable numbers just at the entrance of the Bay of Islands.

89. Doliolum denticulatum, figs. 5, 6.—A small transparent body, varying in length from one-sixth to one-third of an inch, and looking very much like a barrel open at each end, which swims by contracting its whole body, and forcing the water out at one or the other extremity.

The apertures are considerably less in diameter than the central cavity. The anterior (d) is produced into a sort of tube, with about twelve rounded dentations,

- \* Prof. E. Forbes informs me that a body answering precisely to Otto's description, was found by him, occurring in considerable numbers, on the coast of Scotland, and was eventually discovered to be nothing more than the detached siphonic tubes of Solenocurtis strigillatus.
  - † Voyage de l'Astrolabe. Zoologie, t. iii. part. 2. p. 599.
- ‡ Little more than a description of the outward form is given by MM. Quoy and Gaimard of the *Doliolum* caudatum, but it strikingly agrees in everything with what one of the associated forms of the singular genus Anchinaia might be supposed to become if set free; unfortunately, the description of the latter genus itself is very scanty. See note (60.)

Has the Doliolum denticulatum itself been ever an attached form? From certain appearances (90.) this appears very possible.

which are turned inwards. The base of the tube is surrounded by a thickened muscular rim.

The posterior extremity is similarly produced into a short tube with a thickened base, but the tube looks outwards, and its walls are very delicate, and consist of fine fibres like those of the fin of Sagitta.

90. The body of the animal consists of two tunics, an inner and an outer\*, which surround a wide central respiratory cavity.

Six muscular bands (t), pretty nearly equidistant, gird the inner tunic.

In some specimens a sort of shrivelled tubular process projects on the dorsal surface posteriorly between the two last muscular bands. Is this the remains of an earlier pedicle of attachment?

91. A tubular endostyle (c) lies in the dorsal sinus between the first and third muscular bands.

In the ventral sinus a round ganglion (a) lies just in front of the third muscular band. It gives off several long nerves, four of which are especially remarkable, and run diagonally to the anterior and posterior apertures. There is no auditory sac nor otolithes.

92. The branchiæ divide the respiratory cavity into an anterior and a posterior chamber. They are formed by the epipharyngeal and hypopharyngeal (x) bands which stretch aross the respiratory cavity, supporting on each side a number of tubular bars (y). In the upper and lower division of the branchiæ, these bars are adherent to the walls of the respiratory cavity, i. e. to the inner tunic, and there their canals open into the lateral sinuses; but in the middle part of the branchiæ their extremities unite and form loops without adhering to the inner tunic, merely lying against it. There is a free passage for the water between the bars, and on each side of the central supporting bands.

The edges of the bars are richly ciliated, and the cilia of their opposite sides move in opposite directions.

Although it appeared quite certain that the canals of the bars communicated with the sinus system, yet no blood-corpuscles could be traced into them.

The branchial bars did not extend so far forward above as below. In the former case they reach as far as the second muscular band only, in the latter, beyond the first; seen from above or below, the branchia appeared as an oval plate, with a clear space down its middle and transverse bars on each side.

93. The mouth (g) opens in the middle of the upper division of the gill, just anterior to the fourth muscular band; a narrow æsophagus (h) leads from it into a two-lobed stomach (i); from this a narrow intestine passes, and bending a little upwards and then downwards and to the left side, terminates in a papillary (l) anus. Just at its bend

<sup>\*</sup> The outer tunic, which I consider as homologous with the test and outer tunic of the Ascidian fused together, was found by MM. Löwig and Kölliker to contain cellulose, whence they concluded the Ascidian nature of the animal, a deduction strikingly confirmed by anatomical investigation.

the intestine gives attachment to three or four small cæca (s), which appear to represent a liver, and a system of transparent anastomosing tubules, similar to that described in Salpa, arises from the stomach and envelopes the intestine in a network.

The heart (r) lies above and in front of the mouth. In structure it resembles that of Salpa. There are no vessels of any kind, the blood-corpuscles making their way at random among the viscera. No reversal of the circulation was observed in this Ascidian.

94. All the specimens examined possessed only the male generative apparatus, in the shape of a long tubular \* testis (p), placed on the right side and below, and opening posteriorly into the respiratory chamber by a papillary elevation (p') just before the penultimate muscular band.

The testis lies quite freely in the sinus, and is bathed by the blood (fig. 7).

When most fully developed the testis nearly equals the body in length; but in young specimens it may be not more than one-half to one-third that size.

The young testis is a delicate sac, containing a mass of circular cells, about  $\frac{1}{3300}$ th of an inch in diameter, of a pale greenish colour, and flattened.

As development proceeds, these cells assume a redder tint, and become perfect spermatozoa, with elongated cylindrical heads  $\frac{1}{2500}$ th of an inch in length, and very delicate, long filiform tails.

95. There is a small cavity (u) resembling the ciliated fossa of the Salpw, seated upon the anterior face of the singular process of the ventral paries of the respiratory cavity.

This process lies anterior to the first muscular band; it is somewhat conical and excavated behind. The two lips of the excavation are thickened and ciliated, and the right lip is continuous on the left side with a ciliated band, which runs up parallel with the first muscular band, passes over to the right side, and running down, becomes eventually lost in the right portion of the base of the conical process.

This would seem to be a rudimentary languet. A number of small granular masses were always to be seen attached to the inner tunic close to the posterior aperture.

The structure of the branchiæ of this Ascidian, the position of the two orifices, and the structure of the testis, all indicate a position for *Doliolum* intermediate between Salpa and Pyrosoma.

Its apparent unisexuality very likely arises from the ova being developed, and leaving the parent in a younger state than any I examined. I have elsewhere mentioned the liability to deception in Salpa from a similar cause.

Note.—Since writing the above I have found a short notice of Appendicularia in Müller's Archiv for 1846, under the name of Vexilluria flabellum. The de-

<sup>\*</sup> Very similar to that of Salpa cristata, described as an hepatic organ by MEYEN.

<sup>†</sup> Bericht über einige neue Thierformen der Nordsee.

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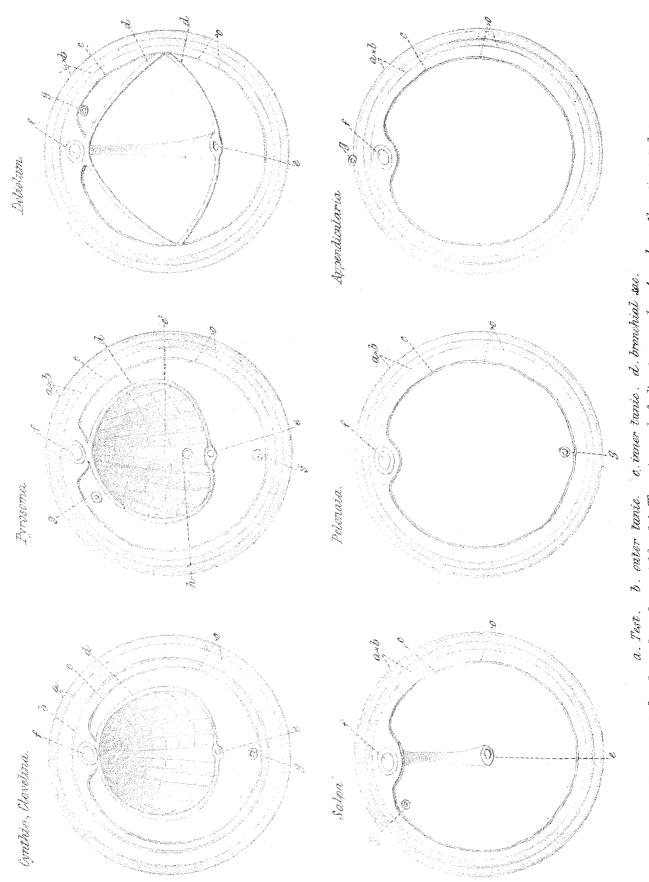
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Fig. 7.

Frg. 2.

Fig.l

Fig. 2.a.



e. Poppophargrigial band. S. Moracic vessel. f. altinostary canal. g. Anus. h. mouth., c. sirus system. Sectional Diagrams of Tunicata. e. epipharyngeal band,

The section supposed to be made perpendientarty to the axis of the branchial cavity.

scriber, Prof. MÜLLER, confesses that he does not know in what division of the animal kingdom to place this creature; and his account of its structure is not a little vague, including little more than its mere external appearance. He does not seem to have observed anything corresponding to the "Haus" of Otto.

#### DESCRIPTION OF THE PLATES.

## PLATE XV. Salpa.

- Fig. 1. Salpa A.
- Fig. 2. Salpa B.
- Fig. 3. Dorsal view of Salpa A, the muscular bands being omitted.
- Fig. 4. Dorsal view of Salpa B, the muscular bands being omitted.
- Fig. 5. Intestinal canal of Salpa A.
- Fig. 6. Intestinal canal of Salpa B.
- Fig. 7. Dorsal view of extremity of Salpa B.
- Fig. 8. Part of the respiratory chamber of Salpa B, showing the fœtus suspended. View from above.
- Fig. 9. Connection of the gemmiferous tube with the heart.

### PLATE XVI. Salpa.

- Fig. 1. Young gemmæ (Salpa B) attached to the gemmiferous tube.
- Fig. 2. Nuclear end of one of these, showing the ovum and its pedicle or gubernaculum.
- Fig. 3. Nuclear end of a very young Salpa A, just detached.
- Fig. 3a. Placenta and gemmiferous tube of this enlarged.
- Fig. 4. Heart, placenta and gemmiferous tube of a young Salpa A, showing the rudimentary condition of the last structure.
- Fig. 5. Ganglion, otolithic sac and languet.
- Fig. 6. Young Salpa A, still attached by its placenta in the interior of Salpa B.

# PLATE XVII. Pyrosoma.

- Fig. 1. A single "zoöid," viewed from the right side.
- Fig. 2. A single "zoöid," viewed from above.
- Fig. 3. Part of the branchial network.
- Fig. 4. The ovum with its pedicle in situ.
- Fig. 5. Testis and ovisac in situ, both emptied of their contents.

- Fig. 6. Ovum and pedicle.
- Fig. 7. A young zoöid developed by gemmation.
- Fig. 8. A young zoöid separated and enlarged. Viewed from the ventral side.
- Fig. 9. Youngest form of gemma observed.
- Fig. 10. "Ciliated fossa," with the ganglion and otolithes.
  - a. Anterior extremity.
  - b. Posterior extremity.
  - c. Endostyle.
  - d. Ganglion and otolithes.
  - e. Gill band.
  - f. Languet.
  - g. Heart.
  - h. Gemmiferous tube (single gemma in Pyrosoma).
  - i. Nucleus.
  - k. Muscular bands.
  - l. Solitary fœtus, or young Salpa A.
  - m. Placenta.
  - n. Sinus running specially to the placenta.
  - o. Dorsal sinus.

- p. Testis.
- q. Ovary, or rather ovum.
- q'. Pedicle.
- r. Buccal orifice.
- s. Anal orifice.
- t. Lobe of the stomach.
- u. Tubular system.
- v. Branchial bars.
- w. "Ciliated sac."
- x. "Ciliated band."
- æ. Eleoblast.
- a. External tunic.
- β. Internal tunic.
- y. Partition of gemmiferous tube.
- δ. Cell masses in Pyrosoma.

### PLATE XVIII.

- Fig. 1. Appendicularia flagellum. Much magnified.
- Fig. 2. Still more magnified.
- Fig.  $2^a$ . Extremity of the caudal appendage.
- Fig. 3. Body of Appendicularia from behind.
- Fig. 4. Individual in which the testis is much enlarged.
- Fig. 5. Doliolum denticulatum, from the right side.
- Fig. 6. Doliolum denticulatum, from below.
- Fig. 7. A portion of the right wall to show the testis in situ.
- Fig. 8. The "ciliated sac" and the origin of the "ciliated bands" in Doliolum.
- Fig. 9. The intestine and heart, with the commencement of the branchiæ.

The letters have throughout the same signification.

- a. Ganglion with the auditory vesicle.
- e, f. Ciliated bands.

b. Nerve.

g. Mouth.

c. Endostyle.

- h. Œsophagus.
- d. Respiratory or anterior aperture.
- i. Stomach.

- k. Intestine.
- l. Anus.
- m. Axis of the caudal appendage.
- n. A long membrane of appendage.
- o. Bundles of striated muscular fibrils.
- p. Testis.
- p'. Efferent duct of testis.
- q. Supposed ovary.
- r. Heart.

- s. Liver.
- t. Muscular bands.
- u. Ciliated sac.
- B. The body of Appendicularia.
- A. The caudal appendage.
- x. Hypopharyngeal band.
- y. Branchial bars.
- z. The system of tubules embracing the intestine.

#### PLATE XIX.

The diagrams represent imaginary sections of the principal types of the Ascidian family. Without pretending to be strictly accurate, they are sufficiently so to give a just idea of the gradations in structure among the different genera, and of the essential unity of structure which runs through the group.