

**On the Development of Tubulipora, and on some  
British and Northern Species of this Genus.**

By

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With Plates 8—10.

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**Introduction.**

THE principal object of the observations described in the present paper was to test the conclusion, at which I formerly arrived, that a process of embryonic fission is of normal occurrence in Cyclostomatous Polyzoa. The process had already been demonstrated in *Crisia* (15) and in *Lichenopora* (16), and I am now able to show that the development of *Tubulipora*<sup>1</sup> takes place on essentially the same lines. In the course of these observations it became apparent that the discrimination of the British species of *Tubulipora* had not been characterised with sufficient precision.

The satisfactory determination of the species of Cyclostomatous Polyzoa is not an easy task. There are perhaps few cases, even in this group, in which the synonymy is in a more involved state than in the genus *Tubulipora*. Many of the specific diagnoses which have hitherto been given are based on immature specimens, or are for other reasons insufficient for purposes of identification, and the compilation of unduly long lists of synonyms is for this reason undesirable.

<sup>1</sup> A preliminary note (17) on this subject was published, in which the genus appears as *Idmonea*.

The question is further complicated by difficulties in deciding which names have the greatest claim to be assigned to particular species.

Before proceeding to the accounts of the species the scope of the paper may be stated. I have given diagnoses of two Northern species, one of which I believe to be new, and of all the forms ordinarily recognised as British species of *Tubulipora*, with the exception of *T. lobulata*, Hassall.

I have not had a sufficient supply of this supposed species to enable me to come to any clear conclusion about it. Many of the colonies which I have found on shells in the deeper Plymouth dredgings (20—30 fathoms) agree well enough with Hincks's description of this form. I have also seen similar specimens from the Liverpool district, kindly lent to me by Professor Herdman; but I have not been able to examine uninjured mature colonies. In the absence of perfect ovicells, it is possible that some of the specimens supposed to be *T. lobulata* may be worn examples of other species of *Tubulipora*. I prefer, therefore, to express no opinion with regard to this form.

The paper is divided in the following way :

I. Structure of the colony and of the ovicell. (The terms "œciostome" and "œciopore" are here proposed.)

II. History of the species and genus.

III. Synonymy, diagnoses, and accounts of the species. (New species, *T. aperta*.)

IV. The nature of certain vesicles found in the tentacles and other parts, with a few statements relating to the budding and the structure of the adult zoëcium.

V. Description of the development. (The terms "axial lobe" and "lateral lobes" are here proposed.)

VI. The morphology of the internal parts of the ovicell.

#### I. Structure of the Colony and of the Ovicell.

A colony of *Tubulipora*, as of other Cyclostomes, takes its origin in the well-known circular primitive disc (Pl. 8,

fig. 2) formed by the calcification of the body-wall of the metamorphosed larva. The early zoarial development is well described by Barrois (1, p. 70, pl. iv, fig.), whose account perhaps refers partly to *T. phalangea* and partly to *T. plumosa*; and it results in all species in the formation of a colony which is at first pyriform or fan-shaped. The terms "proximal" and "distal" will be used with relation to the primitive disc. The distal curved margin of the colony is bounded by the "terminal membrane" (16, p. 93), which consists partly of an uncalcified cuticle (ectocyst) and partly of underlying protoplasmic structures. The terminal membrane does not remain as a continuous sheet, since portions of it are continually cut off by the upgrowth of the calcareous septa which form the lateral walls of the zoëcia or ovicells. Each of these structures is thus closed by a derivative of the original terminal membrane, and this name may consequently be applied also to the uncalcified distal wall of each unit of the colony (fig. 24). Both the zoëcia and the ovicells are added to, after their first formation at the growing edge, only by the prolongation of parts of the calcareous tubes which have already been developed, though this is not altogether true of the Lichenoporidae, in which the character of the colony is altered by the subsequent development of "cancelli." It thus follows that a young *Tubulipora* colony is identical, so far as its calcareous structures are concerned, with the proximal part of the same colony at a later stage of its existence; and that in order to understand what a particular colony or ovicell was like at an early period of its development, it is only necessary to imagine the distal parts of the colony suppressed.

The form of a particular colony is due to the behaviour of its terminal membrane, which is identical in its extent with the growing margin. Should this remain undivided, and continue to grow symmetrically, a pyriform or flabelliform colony will result, according to the relative activity of growth in the longitudinal and transverse directions. Under certain circumstances, probably due to unfavourable conditions, the colony becomes mature by developing an ovicell without losing its

pyriform shape. I have found mature colonies of this type commonly in at least three of the species described in the present paper, namely in *T. phalangea*, *T. flabellaris* (fig. 4), and *T. aperta* (fig. 2).

In other cases the transverse growth of the terminal membrane is more active, and the flabelliform character becomes more marked (figs. 1 and 5), its lateral edges commonly growing proximally so as more or less to encircle the primitive disc. This flabelliform shape typically occurs in well-grown colonies of *T. flabellaris* and *T. aperta*. In other species the terminal membrane commonly divides at an early stage, so that there is a cessation of growth between the two parts of the divided membrane. The colony then grows into two lobes, which usually diverge from one another. This form of growth is well indicated by Pallas (33, p. 248) in his original account of *T. liliacea* (= *T. serpens*, auct.). Colonies of this species, as well as those of *T. phalangea* and *T. plumosa*, often become mature in this condition; but in all three species further divisions of the terminal membrane<sup>1</sup> usually take place, the colony thus becoming variously lobed. In *T. liliacea* alone of the forms described in this paper, there is in many cases a marked tendency for the lobes to become free and erect; and an *Idmonea*-like form thus results.

The common basal part of a colony consists of a mass of pyramidal tubes with pointed proximal ends, the arrangement being comparable with that of a honeycomb, all the "cells" of which look in one direction, represented in *Tubulipora* by the growing margin of the lobe. The base of the colony, or basal lamina, is the sum of the lower walls of the more proximal parts of the zoëcia. It is completely adherent to the substratum in many species of *Tubulipora*, but it may grow out freely from it, and the colony thus becomes erect. Each zoëcium is developed at the growing edge by the formation of a new radial septum in connection with the basal

<sup>1</sup> A commencing division of the terminal membrane is indicated on the right side of fig. 1.

lamina, and grows at first in a more or less horizontal, centrifugal direction. As its length is added to at the growing edge, its upper wall gradually rises above the general level of the colony, and some of the zoëcia thus form projecting ridges (fig. 1). As the zoëcium rises up in this way, its basal wall splits off from the basal lamina, between which and itself a cavity thus originates. This cavity is the beginning of a new zoëcium, which continues to grow in the same manner.

It follows from this description that each zoëcium proximally reaches the basal lamina, as in *Lichenopora* (16, woodcut, p. 84); a younger zoëcium always originating from the basal side of an older one, and making its appearance distally to it after a certain time.

As the zoëcium continues to grow longer, its distal part becomes free from the common basal mass of the colony. It may become completely free on all sides, and it then, by the activity of its own terminal membrane, develops into a curved tube, which is generally cylindrical, though in some cases with an oval transverse section and orifice. Very commonly in *Tubulipora* the zoëcium does not become free on its basal side, where it remains connected with one or more of its younger neighbours. In this way it forms the beginning of a row, usually uniserial, of connate zoëcia, as show in figs. 1, 5, and 9. The adjacent zoëcia of a series are separated by a flat septum, corresponding with the intersecting plane of two cylinders. Any one of the middle zoëcia of a simple series will thus have four flat walls (fig. 1).

The shape of the orifice corresponds with that of the zoëcium, being at first angular in the case of serial zoëcia. If, however, growth of these goes on actively, the series may be resolved above into its constituent units, each of which then becomes cylindrical with a round orifice.

The ovicell of *Tubulipora* is an enlarged zoëcium. This is shown by several facts, the most striking of which is that when young it has a polypide, and then differs in no way from an ordinary zoëcium. The proximal end of the ovicell thus takes part in the formation of the basal lamina. On looking

down into the mouth of the open calcareous funnel (fig. 4.7), which is the condition of the young ovicell at the time when it commences to expand distally, a tubular cavity can be seen, which passes down to the basal lamina and represents the ovicell in its zoëcium stage.

The upper wall of the expanded distal part of the ovicell is thickly perforated by pores (fig. 1). These pass through the calcareous layer; they are wider internally and constricted externally, where they are closed by a cuticle, the pore being entirely filled with a few cells. The pores are always much more numerous in the upper wall of the ovicell than in the walls of the zoëcia, as Waters has pointed out (45, p. 277, and in other papers). It is perhaps probable that the function of these pores is mainly respiratory, to provide for the gas-exchange which must be necessary for the development of the great mass of larvæ which are formed inside the ovicell. The definitive assumption of the ovicell-character by a zoëcium is thus marked by a great increase of the porosity of its upper wall.

In some species, and notably in *T. flabellaris* (fig. 4, ovicell 2) and *T. aperta*, the more porous part can in some cases be seen to be separated from the less porous part by a sharp line. The proximal part has the appearance of a zoëcium; and we thus have an external indication of the time at which the fertile zoëcium became definitely an ovicell.

An ordinary zoëcium was seen to become, sooner or later, free from the common basal part of the colony, unless it remained connected with it by forming one of a connate series or of a fasciculus of zoëcia. The corresponding process in the ovicell is the formation of its tubular portion ending in the orifice. This part, in all respects comparable with the up-standing free part of an ordinary zoëcium, is, however, developed late, and can only be seen in ovicells which are nearly mature. The ovicell, in fact, remains a part of the common basal mass of the colony for a long period, during which its distal end is expanding and increasing the space available for the growth of the embryos. Before the distal

expansion begins the ovicell has become separated by younger zoëcia from the basal lamina, and its floor is thus formed by their proximal parts. The upper part or roof of the ovicell spreads out horizontally as the conspicuous, porous, calcareous film usually described as the ovicell. If no fresh zoëcia were formed at the growing edge, the roof of the ovicell would be a simple fan-shaped film. But new zoëcia continue to grow in the same way as if no ovicell were present (Pl. 10, fig. 32). The floor of the ovicell, formed by the upper walls of the younger zoëcia, or really by the septa dividing its own body-cavity from that of these zoëcia, thus rises into radial ridges which encroach on its cavity. As these become more vertical they meet the growing horizontal roof of the ovicell, and with further prolongation stand up from it at a right or obtuse angle.

In most of the species investigated the zoëcia which are younger than the ovicell are arranged in connate series. But whereas the proximal parts of the fertile lobes have their zoëcia in obliquely transverse, alternate rows (fig. 5), these series usually become radial in the region of the ovicell. In other words, a young zoëcium which has reached the roof of the ovicell in the manner just indicated does not become free, but remains connected with the expanding growing edge by a still younger zoëcium. A radial series of connate zoëcia thus results, and the roof of the ovicell is divided into two lobes, one on each side of the zoëcial series. After a time the series may become completely free from the growing edge, and the two adjacent lobes of the roof of the ovicell may then unite distally to the series.

In my preliminary note (17, p. 212) I have stated that the zoëcia may thus be left as columns passing freely through the cavity of the ovicell. I believe that this statement is not correct for *Tubulipora*. The cavity of the ovicell may indeed surround the zoëcium, or series of zoëcia, on the proximal, lateral, and to some extent on the distal sides; but I have found no evidence that two lobes which have become contiguous on the distal side of a zoëcium ever really unite, as

they certainly do in *Lichenopora*. In transparent preparations it can be seen that the cavities of the two lobes remain separated by a vertical radial septum, the upper edge of which is generally indicated as a line on the roof of the ovicell even in dried colonies (fig. 5.s.).

As the radial series of zoëcia are formed all round the periphery, the ovicell itself consists of a cavity which branches dichotomously at the proximal end of each series. In large, actively growing colonies (fig. 5) the ovicell usually branches in a palmate manner, and the primary lobes may undergo further dichotomy once or more. The extent to which the ovicell branches is not a specific character, but is probably dependent partly on nutrition and partly on temperature. Figs. 2 and 4 represent mature fertile colonies of *T. aperta* and *T. flabellaris* respectively, and fig. 1 a fertile lobe of *T. plumosa*. The ovicell shown in the last figure is much more complicated than that shown in the former two; but it must be distinctly understood that the ovicell of *T. flabellaris* and *T. aperta* may be large and much branched in vigorous colonies.

After the ovicell has reached a certain size it develops its tubular portion, ending in the orifice through which the larvæ make their escape. Here, however, there is some modification in the course of the development as compared with an ordinary zoëcium. While the orifice of the latter is merely the part which, for the time being, forms the distal end of the zoëcium, the lobes of the ovicell undergo a considerable amount of growth, in most cases, after the orifice is fully formed. Sooner or later, however, the peripheral ends of the lobes, closed merely by a soft terminal membrane during growth, become completely calcified, except in the abnormal specimens of *T. aperta* (fig. 2), described under the heading of that species, in which accessory openings may be formed by the outgrowth of the lobes into tubular passages which more or less resemble the real orifice of the ovicell. The complete calcification of the peripheral ends of the lobes of the ovicell takes place, as in other Cyclostomes, by the encroachment of the calcareous

roof on the terminal membrane, which is, so to speak, gradually constricted until it completely disappears.

My study of *Tubulipora* has fully confirmed the conclusion stated in my paper on *Crisia* (13, p. 128), that the form of the orifice of the ovicell is of great importance for the discrimination of the species. As I am convinced that this structure will become increasingly important in the systematic study of the Cyclostomata, I venture to think that a special terminology may be convenient for descriptive purposes; and I therefore propose to term the passage by which the larvæ escape from the ovicell the "œciostome," and its actual external orifice the "œciopore." The œciostome is usually a tubular or funnel-shaped structure, as in the species of *Tubulipora* here described, and in many other Cyclostomes. The part connecting the cavity of the ovicell with the œciopore may be termed the "tube" of the œciostome, whatever its shape. The tube is not a necessary part of the œciostome, since it is absent in *Crisia aculeata*, Hassall, in which the œciopore represents the entire œciostome.

The structure of the wall of the tube is commonly different at its two ends. The proximal portion is often pierced by pores identical with those in the roof of the ovicell, of which it is a direct continuation (fig. 1), while the distal portion is imperforate. Valuable specific characters are afforded by the shape, size, and relations of the œciostome, and by the size and position of its tube and œciopore.

The constancy of the characters of the œciostome has been verified by the examination of numerous specimens of several species from various localities. While the shape and size of the entire colony, and therefore of the ovicells, has been shown to be highly variable, the œciostome retains its character, whatever the condition of the colony. I do not, of course, mean to assert that there is no variation in the œciostome. Variation does occur, sometimes within fairly wide limits; but it is usually possible to decide the species at once by an inspection of its œciostome. In order to do this it may be necessary to have a fully developed œciostome, since the

specific characters are not completely shown in the immature condition of this structure. There are occasional cases in which the œciostome of a given colony may appear intermediate between two species. In most of these cases comparison with other specimens will, however, usually leave no doubt of the existence of a definite character for the œciostome of each species, in spite of the occasional occurrence of difficult cases.

The value of the characters of the œciostome in diagnosing a species is strikingly illustrated by the specimens of *T. flabellaris*, Fabr., which have come into my hands. Fig. 4 is an Arctic specimen of this species, dredged by Colonel H. W. Feilden on July 1st, 1895, in Barents Sea, and presented by him to the Cambridge Museum of Zoology. Although the colony is very much smaller than the form of this species figured by Smitt (40, pl. ix, fig. 6), it possesses no less than six complete ovicells, each with a fully formed œciostome (1—6), five of which are visible in the position in which the colony lies, besides one immature ovicell (7). The ovicells are crowded and are very small, exhibiting hardly any of the lobing which may occur in this species as in others. The principal characteristic of the species, the flattened shape of the œciostome, is nevertheless as well marked in each ovicell as it is in the lobed ovicells of a larger colony, sent to me by Dr. Nordgaard from Hammerfest.

The above case can hardly be regarded as a mere individual abnormality. I have examined four specimens (including the above) from Colonel Feilden's collection, and all of them showed the same peculiarities. Two other colonies (about the same size as the above) had each four small, contiguous ovicells with fully formed œciostomes, and an immature fifth ovicell. The last consisted (unlike the others) of two diverging lobes, which may, however, have been formed from two larvæ. One lobe had two ovicells with œciostomes, and at least one immature ovicell, and the other lobe had one ovicell with a fully developed œciostome. In every ovicell the long flattened œciostome, which I regard as the distinguishing

feature of this species, was developed on precisely the same type.

A case of the abnormal development of four contiguous ovicells has been described by me (13, p. 166, pl. xii, fig. 13) in *Crisia ramosa*. These cases are interesting as showing the essential similarity of the ovicell and the zoëcium. The production of an ovicell is probably induced by the development of an embryo from one of the eggs which so commonly occur in young zoëcia, most of which do not ordinarily become fertile.

The simple ovicells of the specimens of *T. flabellaris* from Barents Sea are similar to those which were figured by Savigny (37, pl. vi, figs. 4.2 and 5.2), and described by Audouin under the names of *Proboscina Boryi*, and *P. Lamourouxii*. Ovicells of a similar type are known in *Diastopora suborbicularis*, Hincks, and in many fossil forms. They are figured, for example, by Gregory (12, pl. i, fig. 6; pl. iii, fig. 3), and this type of ovicell is given by Walford (41, p. 73) as a characteristic of his genus *Pergensia*, although I cannot agree with him in thinking that the character shows any approach to the Cheilostome genera *Lekythopora* and *Pæcilopora*. It appears to me probable that the stunted specimens of *T. flabellaris* above described have reverted to a more primitive condition (a conclusion borne out by the evidence of fossils) in developing a less complicated form of ovicell than is usually produced in other recent species, and even in *T. flabellaris* itself. This reversion may be regarded as due to the small size of the colony, in conjunction with the successful development of primary embryos in several contiguous zoëcia. It is probable that this points to a time when the ovicells were ordinary zoëcia, and that the restriction in the number of fertile zoëcia now so characteristic of Cyclostomes is not a primitive feature of the group.

References to the oëciostome in any form hitherto described as *Tubulipora* or *Idmonea* are curiously rare; and most authors do not seem to have considered the possibility of the occurrence of this essential part of the ovicell. Smitt (40)

has described it in *Idmonea atlantica* (p. 443), in *I. serpens* [= *T. liliacea* of the present paper] (p. 446), in *T. fimbria* [= *T. aperta*] (p. 455), in *T. flabellaris* (pp. 456, 457), and in *T. lobulata* (p. 457). The descriptions there given are not, however, sufficiently precise to be used in discriminating the species, nor are they illustrated by figures which really show their character. Waters (44, pp. 256—259, and 43, p. 339) has described the œciostome in one or two species of *Tubulipora* or *Idmonea*; and Kirkpatrick (22, p. 22, pl. iv, figs. 6 a, 6 b) has described and figured the œciostome of *I. pulcherrima*. These are almost the only references I have been able to find to the œciostome of recent species of *Tubulipora*. It appears to me that a *Tubulipora* colony reaches its fully adult condition when the ovicell, with its œciostome, is fully formed. If this view be correct, the importance of the œciostome as a specific character is intelligible. Colonies in which this structure is not yet developed are in a state of immaturity. It is perhaps as reasonable to characterise a species of *Tubulipora* without taking account of its œciostome as it would be to describe a new species of *Cervus* without describing the form of the antlers. It is unfortunately impossible to describe the œciostome of a *Cyclostome* in the majority of cases, and particularly in fossil specimens; but I think the description of this structure should be an essential part of a diagnosis wherever it can be given.

The absence of the œciostome in a given case may depend on the season of the year at which the specimen was obtained. It is, for instance, somewhat difficult to find the œciostomes of the British species in colonies collected in the spring, in which the formation of the ovicell is beginning; but it is easy to find them in uninjured healthy colonies collected in the summer.

The following table illustrates the use which can be made of the œciostome in distinguishing the species treated of in this paper. The "lower" surface of the colony is that by which it is fixed, so that "upwards" means away from the basal surface:

- 1 { Zoœcia more or less obviously arranged in connate series,  
at least in well-developed colonies . . . . . 2  
Zoœcia not in connate series, even in the fertile lobes.  
Oœciostome with a well-developed tube, usually more  
or less free, the oœciopore being larger than an orifice  
and looking upwards . . . . . T. aperta (Pl. 8, fig. 2)
- 2 { Oœciopore much larger than an orifice, opening upwards  
or obliquely horizontally  
. . . . . T. plumosa, W. Thoms. (fig. 1)  
Oœciostome or oœciopore not larger or only slightly  
larger than an orifice . . . . . 3
- 3 { Tube of the oœciostome recumbent on a zoœcium or  
series of zoœcia, the oœciopore opening horizontally  
or downwards . . . . . 4  
Tube of the oœciostome free, greatly compressed, the  
oœciopore being slit-like  
. . . . . T. flabellaris, Fabr. (fig. 4)
- 4 { Oœciopore larger than an orifice, opening horizontally  
. . . . . T. liliacea, Pall. (=T. serpens, auctt.) (figs. 7, 8)  
Oœciopore concealed, smaller than an orifice, looking  
downwards . . . . . T. phalangea, Couch (figs. 5, 6)

The average size (in thousandths of a millimetre =  $\mu$ ) of the oœciopores and of the orifices is stated in the following table, the greater diameter of the oœciostome being added in *T. phalangea*, the only species in which the oœciopore is narrower than the oœciostome:

	Oœciopores.	Orifices.
<i>T. phalangea</i> . . . . .	120 (oœciostome, 150)	160
<i>T. flabellaris</i> . . . . .	165	175
<i>T. liliacea</i> . . . . .	260	165
<i>T. aperta</i> . . . . .	280	170
<i>T. plumosa</i> . . . . .	355	185

It should be expressly noted that the diameter of the oldest zoœcia of a colony may be much smaller than that of the younger zoœcia. The above averages are taken from zoœcia which have reached their full size.

## II. History of the Species and Genus.

The tenth edition of the 'Systema Naturæ' gives the diagnosis of certain species referred to the genus *Tubulipora*, of which the first or type species is *T. musica*, the organ-pipe coral. Amongst these (p. 790) occurs *T. serpens*.

The twelfth edition contains (p. 1271) a diagnosis of *T. serpens*, as "*T. tubulis cylindricis erectis brevissimis distantibus axillaribus, basi repente dichotoma divaricata.*" This is practically identical with that given in the tenth edition, to which a reference is given, with the further reference 'Amœn. Acad.,' i, p. 105, t. 4, f. 26.

The species is thrown up on the shores of the Baltic, while a similar but smaller form occurs in the Mediterranean, the only locality mentioned in the former edition.

A reference to the first figure which is quoted by Linnæus, namely, to that contained in his 'Amœnitates Academicæ' (vol. i, 1749), leads to the conclusion that the original description did not refer to the species which is now usually known as *Idmonea serpens*. The figure is on a plate headed "p. 312," and the description is on p. 209 [not 105]. The figure, with which the description agrees, represents a stone bearing a closely adherent species, consisting of an open network of tubes with single pores at considerable intervals, usually at the angles of the meshes. It is hardly possible to recognise any similarity to any species of *Tubulipora* or *Idmonea*; but, on the contrary, the figure is strikingly suggestive of the Alcyonarian *Sarcodictyon catenatum*, Forbes, and closely resembles the figure of that species given by Herdman in the 'Proc. Liverpool Biol. Soc.,' vol. ix, 1895, pl. viii, fig. 2.

Whether the description of Linnæus referred to *Sarcodictyon* or to an *Alecto*-like form must be left an open question,<sup>1</sup> but I think that it can have had no connection with any species of *Tubulipora* or *Idmonea*.

In 1755 (9, p. 74) Ellis described, under the name of the

<sup>1</sup> Milne Edwards (20, p. 331) believed that it referred to an "Aulopore."

“small purple Eschara,” the form which is now commonly known as *Idmonea serpens*. The purple colour and the parallel arrangement of the zoëcia are expressly mentioned. The figures *e* and *ε* on pl. xxvii represent the species as growing on a substance which is doubtless the stem of the “sickle coralline” (*Hydrallmania falcata*), as appears from the description, on p. 75, of the *Cellepora* shown on the same stem. The occurrence on this species of Hydroid is eminently characteristic of the “small purple Eschara.”

In 1766 (33, pp. 248, 249) Pallas described the same species under the name of *Millepora liliacea*, referring to Ellis’s description and figures; and it is given as *Millepora tubulosa* in the well-known work of Ellis and Solander (10, p. 136).

In the enlarged thirteenth edition of the ‘*Systema Naturæ*’ (1788) Gmelin complicates the question by describing the species under no less than three different names.<sup>1</sup> The first of these (tom. i, part 6, p. 3754) is *Tubulipora serpens*. Linnæus’s diagnosis is repeated, but a reference to former editions of the ‘*Systema*’ is omitted, while the small purple Eschara of Ellis, and *Millepora liliacea* of Pallas are given as synonyms. The second (p. 3790) is *Millepora tubulosa*, Ell. and Sol., the small purple Eschara of Ellis appearing a second time as a synonym. The third (p. 3790) is *Millepora liliacea*, Pall., and *Tubulipora serpens*, Linn., is given as a synonym.

It appears to me that the Linnæan name must be rejected, and, following the ordinary laws of priority, that the choice must lie between *Tubulipora liliacea*, Pall. (1766), and *T. tubulosa*, Ell. and Sol. (1788). If the tenth edition of the ‘*Systema Naturæ*’ is adopted as the commencement of the binomial system, Pallas’s name has the right to be accepted; while the adoption of the twelfth edition as the starting-point would necessitate the employment of *T. tubulosa*, Ell. and Sol. I shall follow the example of Mr. Hincks<sup>2</sup> in regarding as valid Pallas’s

<sup>1</sup> As has already been pointed out by Lamouroux (25), p. 66.

<sup>2</sup> See his remarks on *Flustra securifrons*, Pall., on p. 122 of the ‘*British Marine Polyzoa*’ (1880).

names, published in the year before the part of the twelfth edition of the 'Systema Naturæ' which referred to Zoophytes.

I have come to the conclusion, from my study of the development, that it is not possible to separate "Idmonea" liliacea generically from the British forms recognised as "Tubulipora," although I claim no novelty in that conclusion. It thus becomes necessary to consider whether the genus which includes the two species should be called Idmonea or Tubulipora.

The genus Tubulipora was founded by Lamarck (23) in 1816, while Idmonea is due to Lamouroux (25), and dates from 1821. Lamarck's type-species is *T. transversa*, said to be found on *Fucus* in the Mediterranean. The small purple *Eschara* of Ellis, and *Millepora tubulosa* of Ellis and Solander, are given as synonyms, and from this, with the diagnosis, it might be concluded that *T. liliacea*, Pall., is the type-species of the genus Tubulipora. H. Milne Edwards has, however, figured (30, pl. ix, figs. 3 and 3a) a specimen from the Paris Museum with the statement (p. 218, note) that it is the one from which Lamarck's description was taken. He regarded the species as an *Idmonea* (29, p. 332), a course which is hardly justifiable considering that it was the type-species of the earlier genus Tubulipora. If, then, we are to accept Milne Edwards' figures as a correct representation of Lamarck's species, *Idmonea* becomes, on his showing, a synonym of Tubulipora.

If a generic distinction between Tubulipora and Idmonea, in the ordinarily understood sense, can really be maintained, this is a regrettable conclusion, since it results in the substitution of Tubulipora for Idmonea, and would necessitate the use of some other generic name for the species usually understood to belong to Tubulipora. If Lamarck's type-specimen is still in existence, and the evidence that it is the type-specimen is satisfactory, I suppose there is no option but to regard the synonyms which he himself gave for *T. transversa* as erroneous. But as the evidence is perhaps not quite certain, and as, moreover, it is not clear that any

generic difference between *Tubulipora* and *Idmonea* can be maintained, I shall regard the species described in this paper as members of the genus *Tubulipora*.

The type-species of Lamouroux' genus is *Idmonea triquetra*, a fossil form from the "terrain à polypiers" (Bathonian) of Caen. The description might lead to the inference that the species is erect, but Gregory (12, p. 134) states that it is always an encrusting form, and has justly remarked that it is therefore impossible to define *Idmonea* as consisting only of erect species. If this is so, it becomes very difficult to draw any line between *Tubulipora* and *Idmonea*. Dr. Gregory's catalogue includes no species of *Tubulipora*, but he distinguishes (p. 134) a family *Idmoniidae* from the *Tubuliporidae* mainly by the existence of regular transverse rows of zoecia in the former. I do not think that this distinction can be maintained, either as the character of a family or even of a genus. Lamarck's type-species of *Tubulipora* was defined as having its zoecia in transverse series, and this feature is strongly marked in other recent species which are ordinarily included in that genus. The only character in Dr. Gregory's diagnosis of *Idmonea* (p. 134) which is not applicable to many species of *Tubulipora* is the ridged or triangular cross-section of the branches, and it is very doubtful if this is really a valid generic difference.

From a superficial examination of the ovicells of *Idmonea atlantica*, and from a consideration of Smitt's description and figures (40, p. 443, pl. iv, figs. 5, 7), it appears to me that this form at least is closely allied to *T. liliacea*.

### III. Synonymy, Diagnoses, and Accounts of the Species.

The material on which the following account was based was collected mainly in the Salcombe Estuary, in South Devon, in March and April. I have to thank Dr. A. M. Norman for having recommended me to choose that place as a base of operations. Other specimens were collected by myself while working at the Plymouth Laboratory and on other parts of

the English coast, and in Norway. I have to express my great indebtedness to my friends who have kindly given or lent me specimens from other localities; and particularly to Professor Herdman and Miss Thornely for specimens from the Liverpool district; to Professor M'Intosh for material from Scotland; to Dr. O. Nordgaard for specimens from Norway; and to Dr. F. M. Turner for material from Guernsey. I must also express my obligation to Mr. A. H. Church for determining one or two seaweeds on which my specimens were found, and for some observations on the amount of annual growth of the colony; and to Mr. S. D. Scott for some observations on the excretory vesicles.

#### Tubulipora, Lamarck.

Zoarium with a distinct basal lamina, adnate or erect, beginning as a pyriform or flabelliform colony, which may become lobed by the division of the terminal membrane. Lobes short and adherent, or longer and dichotomously divided once or more often, sometimes becoming erect. Zoœcia with a free, cylindrical, terminal portion; or connate in obliquely transverse series, in which they are separated by flat septa corresponding with the intersection of two cylindrical zoœcia. The series are arranged alternately on opposite sides of the axial line of the lobe, but the transverse arrangement usually becomes radial in the distal part of the fertile lobes. Ovicell an enlarged zoœcium, which extends into the intervals between the parallel or radial series.

The number of the tentacles is usually eleven or twelve in the three species I have studied by means of sections. Of these, *T. phalangea* and *T. plumosa* seem to have eleven tentacles in most cases, Milne Edwards (30, p. 195, note), giving the number as twelve for the former. In *T. liliacea* I have counted twelve tentacles in most cases, a number agreeing with Dalyell's statement (6, p. 86); but one polypide had thirteen, and several had eleven.

#### *T. liliacea*, Pallas (figs. 7—9).

*Tubulipora* and *Idmonea serpens*, auctt. (not *Tubipora serpens*, Linn. [27, p. 1271], nor Fabr. [11, p. 428]).

Small purple *Eschara*, Ellis (9, p. 74, pl. xxvii, figs. c, e).

*Millepora liliacea*, Pallas (33, p. 248).

*Millepora tubulosa*, Ell. and Sol. (10, p. 136).

*Millepora tubulosa* and *M. liliacea*, Linn. Gmel. (28, p. 3790).

*Tubipora serpens*, Dalyell (8, p. 85, pl. xviii, figs. 11—15).

*Tubulipora serpens*, Johnst. (19, pl. xxxi, figs. 4—6; and 20, pl. xlvii, figs. 4—6). Couch (5, pp. 105 [part], 106). Smitt (40, pp. 399, 444, [part], pl. iii, figs. 4a—4c, 5a, 5b; pl. ix, figs. 1, 2a, 2b). Busk (2, pp. 25, 26 [part], pl. xxii, figs. 1—3).

*Idmonea serpens*, Hincks (18, p. 453, pl. lxi, figs. 2, 3). Levinsen (26, p. 76, pl. vii, figs. 6—10).

Zoarium adnate or erect, its form being greatly influenced by the substance on which it is growing; commonly dividing several times dichotomously. Zoecia curved for the most part in one plane, with the serially connate, alternate arrangement strongly marked, though sometimes obscured in small or irregular colonies. In well-branched colonies the inner zoecia are much longer than the outer ones, so that the height of the transverse series diminishes greatly in passing from the inner to the outer side. Ectocyst usually vitreous and hyaline. Oecioostome about 260  $\mu$  in diameter, slightly larger than the orifice of a zoecium, opening horizontally.

Common on Hydroids (especially *Hydrallmania falcata*), from 20 to 40 fathoms; but also found on *Cellaria* from the same depth, and on red seaweeds from shallower water.

This is the "small purple Eschara" of Ellis, and the *Tubulipora* or *Idmonea serpens* of most writers. I have explained on p. 86 the reasons for rejecting the familiar specific name.

The distinctive feature of this species is the form of the oecioostome (figs. 7 and 8). In size it is intermediate between the corresponding structure of *T. plumosa* and that of *T. phalangea*, and is somewhat larger than the orifice of an ordinary zoecium. The difference between the oecioostome of *T. liliacea* and that of *T. phalangea* (figs. 5 and 6) is not always apparent at first sight, the oeciopore being often concealed in both cases. But whereas in the latter species it is seldom possible to see the oeciopore in any position in which the uninjured colony may be placed, it is nearly always

possible in *T. liliacea* to see it by inclining the colony in a suitable direction. The oeciopore typically opens horizontally; or, in other words, its plane is vertical to the upper or exposed surface of the ovicell. The edge of the oeciopore may be slightly everted, so as to form a narrow brim, or there may be no eversion; and the upper lip may be horizontal and more prolonged than the lower lip.

In all cases the oeciopore is relatively large, varying from  $230\ \mu$  to  $270\ \mu$ , that of an ordinary zoecium being  $145\ \mu$  to  $190\ \mu$ . When the structure is placed in a suitable position it is possible to see some way down the tube of the oeciostome (fig. 7). This cannot be done in *T. phalangea*.

The tube is moderately long, and is recumbent on a zoecium or series of zoecia. It may occur on the proximal side of the series, and look towards the oldest part of the colony, or it may be placed on the distal side and look towards the growing edge.

*T. liliacea* is very common on certain Hydroids, particularly on *Hydrallmania falcata*, a fact familiar to many of the older naturalists, and on *Sertularella*. It is easily obtained from the masses of Hydroids brought up by trawlers in water of twenty fathoms or more. The form of the entire colony varies a good deal. It may remain closely attached to the narrow stem of the Hydroid, its basal lamina curving round the stem and thus giving rise to very irregular colonies; or it may remain attached merely by a small central area, and grow out into free, erect branches, as in the var. *radiata* of Hincks. In this condition it assumes a typical *Idmonea*-form, having a very strongly marked alternate arrangement of connate plates of zoecia.

In a particularly fine specimen of this form, from the Trondhjem Fjord, which I owe to the kindness of Dr. Nordgaard, a single series consists in some cases of as many as eight zoecia, the inner ones being very much taller than the outer ones. The tip of the longest branch is about 11 mm. from the centre of the colony. The oeciostome belonging to this branch is on the distal side of the seventh series (of one

side of the branch) from the bifurcation preceding the ovicell; whereas in another branch the œciostome is on the proximal side of the eighth series of one side, the ovicell itself beginning immediately after the fifth series.

The ovicells of this colony extend through a region of four or five transverse series of zoœcia on each side of the fertile lobe. The shape of the ovicell is of course affected by the strongly marked alternate arrangement of the series, and its roof is thus a comparatively narrow, curvedly zigzag band, running along the middle of the lobe, and giving off an interserial lobe on the convex side of each bend. The ovicell may thus be described as consisting of a regularly undulating axis, with an alternately pinnate arrangement of simple lobes extending between the series of zoœcia. The ends of the branches are bifurcated, but the same ovicell extends into both halves of the fork by division of its main axis. The same arrangement is figured by Smitt (40, pl. iv, figs. 5 and 7) in *Idmonea atlantica*.

A great contrast to this *Idmonea*-like colony was afforded by a fine specimen from the Liverpool district kindly lent to me by Professor Herdman. A narrow branch suddenly expanded into a nearly semicircular fertile lobe, 6 mm. in transverse diameter. The zoœcia in this lobe had a *Tubulipora*-like arrangement, consisting of radial series, which showed a distinct tendency to become frayed out into separate zoœcia at their upper borders. The œciostome had the typical form, and other colonies from the same locality were in no way different from the more ordinary type of *T. liliacea*.

I think there can be no doubt that the form of œciostome which I have described is quite characteristic of this species. Although I first noticed it in a number of specimens from the Plymouth district, it is not a local peculiarity, since I have found precisely the same form in the specimens which have just been alluded to from Trondhjem and Liverpool, as well as in a series of colonies from Hydroids dredged in St. Andrews Bay (20 to 27 fathoms), kindly given to me by Professor McIntosh. The variations in the size of the œciopore

are indicated by the following list of measurements of the transverse diameter :

Plymouth (on red seaweed)	.	.	.	220 $\mu$ .
St. Andrews (on Hydroid)	.	.	.	230 $\mu$ .
Plymouth (on Hydroid)	.	.	.	260 $\mu$ .
Trondhjem	.	.	.	265 $\mu$ .
Plymouth (on Hydroid)	.	.	.	280 $\mu$ .
Liverpool (probably on Hydroid)	.	.	.	300 $\mu$ .

The average of this series of measurements is 260  $\mu$ .

### *T. phalangea*, Couch (figs. 5, 6).

*Tubulipora phalangea*, Couch (5, p. 106, pl. xix, fig. 7 [figure bad]).

Johnston (20, p. 273 [part], pl. xlvi, figs. 1—4). Busk (2, p. 25, pl. xxiii, fig. 2).

*Tubulipora flabellaris*, Hincks (18, p. 446, pl. lxiv, figs. 1—3).

*Tubulipora verrucaria* and *T. verrucosa*, Milne Edwards (20, pp. 337, 328, 323, pl. xii, fig. 1).

Zoarium entirely adnate, variously lobed, sometimes consisting of a series of divaricated lobes, sometimes almost circular in outline, and then reaching a maximum diameter of at least 15 mm. In stunted specimens the terminal membrane may not divide, but gives rise to a single small fertile lobe, the whole colony being pear-shaped. Zoecia serially connate, the series alternate near the base of elongated branches, but becoming radial in fertile lobes. The series are commonly resolved above into their component elements, the zoecia having a longer or shorter free cylindrical portion; but they may remain entirely connate to their ends. Zoecia narrow and long compared with those of most other species. Oocystome (fig. 5) about as large, at its widest point, as an orifice, averaging 150  $\mu$  in diameter, the tube bent completely round, so that the oocypore (fig. 6), which averages only 120  $\mu$  in its longer diameter, looks down on to the roof of the ovicell, and can rarely be seen without dissection of the colony. The tube of the oocystome is adnate to a series of zoecia, and its upper exposed surface is convex. The primary zoecium diverges from the plane of attachment to a greater extent than in most species, and the proximal part of the colony is usually rather deep and narrow.

Common (in Devonshire) on red seaweeds, shells, and stones from about three fathoms to moderately deep water. I have seen one specimen from the Outer Hebrides.

The reasons for maintaining that this species is distinct

from *T. flabellaris*, Fabr., are given below, under the account of that species.

The œciostome of *T. phalangea* is shown in figs. 5, 6. The convex upper surface is really the outer part of the wall of the tube, which has the form of a  $\Omega$ , one limb of which rises vertically from the roof of the ovicell, the other being shortened and opening downwards. It results from this arrangement that it is quite impossible to see the adult œciopore in the great majority of cases without breaking off the series of zoœcia which bears the tube, and turning it over until the œciopore becomes visible. It is then seen to have the form shown in fig. 6, being conspicuously smaller than that of *T. liliacea*. The diameter of the œciopore varied from 110 to 135  $\mu$  in five specimens measured (average 118  $\mu$ ), the widest part of the entire tube varying from 110 to 180  $\mu$  (average 139  $\mu$ ) in the same specimens. The œciostome may be quite symmetrical, or it may be distorted so that the œciopore looks obliquely downwards. When the œciostome is typically developed (as in the great majority of cases), it differs to a striking extent from that of any other species described in this paper.

In its typically developed form this species is distinguishable by its very long and slender zoœcia, the ends of which are more commonly dissociated from their neighbours (and are therefore completely cylindrical) than in *T. plumosa*, with which it commonly occurs. The character of the oldest zoœcia is of some value in distinguishing the species. While *T. plumosa* is usually depressed in the oldest part of the colony, this species has rather the opposite tendency, and the primary zoœcium usually grows upwards at a considerable angle from the plane of support, the interval being occupied by the proximal ends of the next zoœcia.

The general characters are well described by Couch (5, pp. 106, 107), though his fig. 7, pl. xix (wrongly given as fig. 8 in the text), is excessively bad. H. Milne Edwards (29, pl. xii, figs. 1, 1b, &c.) gives excellent figures of this species, accompanied by some anatomical details (pp. 323, &c.), under the

name of *T. verrucaria*, Fabr., accidentally given as *T. verrucosa* in one place on p. 328. The name employed by Milne Edwards cannot be retained, since the *Madrepora verrucaria* of Fabricius is a *Lichenopora*. From an inspection of the original description and figures I can see no sufficient reason for believing that the fossil *Diastopora plumula*, Reuss, is identical with the present species or with *T. flabellaris*, Fabr., although Pergens (34, p. 9) considers the specific name given by Reuss to be the correct name of one of the forms to which the name *T. flabellaris* has been ascribed.

*T. phalangea* is common in the Salcombe Estuary, at a depth of 3 to 5 fathoms, on red seaweeds, where it occurs in company with *T. plumosa*, and on dead shells. It is equally common at Plymouth from 3 to 15 fathoms; and I believe that the greater number of specimens of *Tubulipora* found on shells in the shallower parts of the Plymouth district belong to this species. In the deeper water (20 to 30 fathoms) a considerable proportion of the specimens may belong to the form identified by Mr. Hincks as *T. lobulata*, Hassall; but I am at present unable to express any positive opinion with regard to Hassall's species.

I have seen a typical specimen of *T. phalangea*, kindly lent to me by Professor M'Intosh, from the Outer Hebrides; but the rest of my material has been obtained from Devonshire. *T. phalangea* is very variable in the form assumed by the colony. It may consist merely of a single small, fertile lobe, the whole colony being then pear-shaped, and closely resembling the *Obelia tubulifera* of Lamouroux (25, p. 81, pl. lxxx, figs. 7, 8), a Mediterranean form with which it may be identical. It may consist of a small number of well-separated lobes, or it may have an almost completely circular outline. Colonies of the last type may reach a diameter of nearly an inch. The complexity of the ovicell varies greatly with the size of the colony, the large colonies having very complicated ovicells with numerous palmately arranged lobes extending between the radial series of zoecia; fig. 5 being by no means

an extreme case of this kind. The smaller colonies have simpler ovicells, but this is also the case in other species.

My Salcombe specimens were dredged in March and April; and an examination of this material gives some hints with regard to the meaning of the differences in size. A very large number of colonies found on shells were small and pyriform, although in many cases possessing a mature ovicell; while other small colonies consisted of only two or three lobes. These colonies were nearly all brown, and more or less encrusted with foreign matter. Here and there an old lobe had recommenced to grow, and had given rise to a fresh and clean lobe, whose brilliant white colour (in spirit specimens) forms the most striking contrast with the older lobes. The colonies of *Tubulipora* have in fact the power, which is probably common to all Cyclostomes, of regenerating new zoœcia from various parts of the old colony (cf. 13, p. 141). In the species now under consideration a small part of the edge of the old colony here and there becomes active, so that a series of fresh lobes, with narrow bases, may be seen growing out from various parts. These lobes have in many cases acquired a considerable size by the beginning of April, and have developed mature ovicells. A few quite young, healthy colonies were found amongst these specimens. It is probable that these last were colonies which had recently commenced their existence, that the brown specimens belonged to a previous year, and that the fresh lobes proceeding from them were entirely recent growths. If this is a correct inference, it may be suggested that the small brown colonies were produced late in the year when the temperature was becoming low, so that although they became mature so far as the external characters of their ovicells were concerned, they were unable to grow large. There was of course no doubt that the finely developed specimens were actively growing when they were dredged.

I think it probable, therefore, that the difference in the development of the entire colony may, in some cases at least, be of a seasonal nature.

I may here refer to some interesting remarks which have  
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been made to me by Mr. A. H. Church, whom I had consulted on the growth of *Tubulipora*. Mr. Church informs me that *Rhodymenia ciliata*, a red seaweed on which I obtained nearly all the material (*T. phalangea* and *T. plumosa*) which I have used for sections, is an annual. It follows, therefore, that even the largest colonies (some 12—15 mm.) found on this seaweed must represent the growth of one year. Mr. Church informs me that *R. ciliata* usually dies in the winter, the middle of which period may be regarded (for Algæ) as February, but that the specimens I dredged (in a sheltered estuary) at the beginning of April must have grown in the preceding year. I have not noticed processes of regeneration in colonies growing on seaweeds, the evidence from which is not entirely concordant with that from shells. The specimens growing on *Rhodymenia* (and the same is true of specimens of *T. plumosa* collected at the same season on *Saccorhiza bulbosa*) show no apparent discontinuity of growth, nor were any stunted mature colonies observed in this situation. The colonies were probably far too large to have grown in the year in which they were collected; and although the growth may have been less active or dormant during the winter, there was no interruption sufficient to give rise to a marked discontinuity, as in the specimens growing on shells. It may, however, be noticed that there is no reason for assuming that these latter were the growth of the year immediately preceding. They may be evidence of unfavorable conditions more than one year before, in which case the absence of similar colonies on the *Rhodymenia* growing in the same locality would be due to the fact that this plant is an annual. I think it follows from the observed facts that growth may start at any time when the species is breeding, and that a colony which begins existence in the summer continues to live through the winter, and produces ovicells in the spring.

Mr. Church informs me that in some cases of regeneration which he has observed (on a glass bottle) the central part of the colony had decayed, leaving the new growths with a vacant

space in the centre. I have had no opportunity of examining cases of this kind.

Hincks (18, p. 447) has referred to a curious lobed *Tubulipora*, about an inch in diameter, which he has met with in Salcombe Bay. I have obtained some specimens which appear to correspond with Mr. Hincks's description. One or two of these colonies were from the Salcombe Estuary, and had the oeciostomes of *T. phalangea*. Two others were sent to me from Plymouth by Mr. Church, and had the oeciostomes of *T. plumosa*. The variety is a very curious one, and is characterised by its nearly circular outline and by the great crowding of the zoecia, the series being placed very close together, and the lobes of the well-branched ovicells being correspondingly narrow. On closer examination a considerable difference (no doubt specific) between the Plymouth and the Salcombe specimens becomes apparent. A perfect colony of the former measures about 15 mm. in diameter; it is composed of twelve well-marked lobes, and closely resembles the form of *T. plumosa* which is found on *Saccorhiza*. These lobes can be readily made out without any magnification, whereas the Salcombe specimens do not appear obviously lobed when examined with the naked eye.

I regard this variety as due to an excessive growth of the edge of the colony, resulting, by the mutual pressure of the lobes, in a crowding of the zoecia, and in the acquirement of a circular form. This appears to me to be a further instance of the tendency of different species of *Tubulipora* to assume the same general form as the result of some unknown factors in the environment.

*T. flabellaris*, Fabricius (fig. 4, described on p. 82).

*Tubulipora flabellaris*, Fabr. (11, p. 430).

*Tubulipora flabellaris*, Smitt (40, p. 401, pl. ix, figs. 6—8).

? *T. flabellaris*, Levisen (26, p. 76, pl. vii, figs. 1—3).

Zoarium entirely adnate, more or less fan-shaped in form in well-developed specimens. Stunted colonies may occur, as in the preceding species. Some of the zoecia are free, others are in connate series, which are more or less

developed, and become radial in fertile lobes. Oeciocostome consisting of a greatly compressed tube, whose oeciopore is slit-like. The longer diameter of the slit averages about  $165 \mu$  ( $130-180 \mu$ ), being equal to or somewhat less than the diameter of an orifice. The tube is not recumbent on a series of zoecia, but stands up freely from the roof of the ovicell, its two narrow edges being placed in a radius of the colony.

This seems to be an essentially Northern species, and I have no evidence of its occurrence in British waters. I have examined specimens from Greenland (the locality from which the type-specimens came), Barents Sea (50 fathoms, growing on *Cellularia peachii*), and Hammerfest; and I have also obtained what I believe to be a young form of this species from Godösund, Björne Fjord, Norway. The specimen figured (fig. 4) is a stunted, somewhat abnormal form of this species from Barents Sea (see the description on p. 82), but it well illustrates its characteristics by showing five perfectly typical oeciostomes.

Professor Smitt (40, pp. 400—402, 454, 458), who is followed in this respect by Mr. Hincks, regards *T. phalangea* of Johnston as identical with *T. flabellaris*, although he believes the original *T. phalangea* of Couch to be identical with *T. lobulata*, Hassall. It appears to me that the characters of the oeciostome are amply sufficient to separate *T. phalangea* from *T. flabellaris*. I first became acquainted with the oeciostome of the latter in two colonies from Hammerfest, kindly sent to me by Dr. Nordgaard. The collection of Polyzoa given to the University Museum of Zoology by Miss E. C. Jelly contained a moderate number of specimens on seaweed from Greenland. The form and size of the oeciostome were identical in these and in the Hammerfest specimens. The colonies from Greenland, although very small and stunted (one of them, with only twenty-seven zoecia, possessing a complete ovicell), did not resemble the Barents Sea specimens from deeper water in possessing a multiplicity of ovicells.

It can hardly be doubted that the Greenland specimens, sent by Miss Jelly, belong to Fabricius' species. The flabelliform shape, the connate series of zoecia, the occurrence on seaweed, and the small size (given by Fabricius as  $1\frac{1}{2}$  lin. in transverse diameter), all agree closely with the original description. The species has been more fully described by Smitt, who gives excellent figures. In two of these (40, pl. ix, figs. 6, 8), re-

presenting specimens from Spitzbergen, the peculiar form of the flattened œciostomes, with their radially arranged flat sides, is indicated, while the flattened form is expressly mentioned on p. 457. I have not seen specimens so finely developed as that shown by Smitt in his fig. 6, in which the radial serial arrangement of the zoœcia is strongly marked (as many as twenty being stated to occur in one series). The difference between Smitt's specimens and those examined by me may, however, be seasonal, as suggested under the last species.

It may be remarked that Smitt's conclusion that *T. phalangea* is a synonym, partly of *T. lobulata*, Hass., and partly of *T. flabellaris*, Fabr., does not appear to have been based on an examination of actual specimens of the first-named species.

*Tubulipora aperta*, n. sp. (figs. 2, 3).

*Tubulipora fimbria*, Smitt (40, pp. 401, 452, pl. ix, fig. 5).

? *Tubulipora fimbria*, Levinsen (26, p. 75, pl. vi, figs. 45—50).

Zoarium entirely adnate, pyriform, flabelliform, or lobed. Zoœcia not serially connate, or only exceptionally united in very short series. Ectocyst with few pores. Œciostome about 280  $\mu$  in diameter, larger than an orifice, more or less funnel-shaped; the œciopore opens upwards, and is circular or oval. Tube of the œciostome usually more or less free, and diverging from the zoœcium on which its base is recumbent, the edge of the œciopore often resting on the wall of another zoœcium. Accessory openings sometimes present at the ends of the lobes of the ovicell.

Common on the fronds of *Laminaria saccharina* in Norway. My largest colony is 5.25 mm. in transverse diameter.

This species, which I believe to have hitherto received no distinctive specific name, has been described and figured by Smitt under the name of *T. fimbria*. This name, applied by Hincks to *T. plumosa*, Thomps., was given by Lamarck to an immature specimen of *Tubulipora*, of which the locality is not recorded, and I give my reasons for not accepting it on page 107. The name *aperta* is suggested in reference to the wide œciopore, which is usually clearly visible from above,

and is not concealed either by the zoëcia or by other parts of the œciostome. The specimens on which my account of this species is based were found principally at Godösund, a small island off the north of Tysnäsö, at the entrance to the Björne Fjord in Norway. They were not uncommon on the fronds of *Laminaria saccharina*, where they occurred in company with *Lichenopora verrucaria*, Fabr. Most of the specimens collected at the end of June had fully developed ovicells. Specimens collected at Lervik, in the Hardanger Fjord, at the same period in a previous year were, however, not provided with ovicells. Smitt describes the species as occurring on *Laminariæ* and other Algæ from the Gullmar Fjord (in the south of Sweden) to Spitzbergen, so that the species may fairly be regarded as a Northern one.

I think there can be no doubt of the specific distinctness of this very beautiful form, which is more easily recognised, at all stages of its growth, than are most of the European species of *Tubulipora*. It differs strikingly from the other species here described in having its zoëcia isolated, or only associated two or three together. The connate arrangement found in other forms is usually completely absent; and even in the fertile lobes the zoëcia stand up for the most part singly from the roof of the ovicell, the lobes of which may thus unite distally to the zoëcium. Even in these cases the suture or septum between the two ovicell-lobes is easily seen near the growing edge, and I have no reason to suppose that contiguous lobes really fuse at any time.

The zoëcia are more clearly marked off from one another in the basal part of the colony than is the case in most species, the proximal part of a zoëcium being very convex as far as the suture where it joins another zoëcium. In other species parts of the zoëcia may form more or less extensive flat surfaces, as is well seen in the connate series or in the basal adherent parts of the colony. The ectocyst of *T. aperta* has a delicate appearance, and there are noticeably fewer pores on the zoëcia than in most other species. Numerous concentric lines of growth, passing transversely across the zoëcia, are clearly

marked, as Smitt points out. The zoëcia are relatively large, averaging about  $175 \mu$  in diameter.

The oëciostome more nearly resembles that of *T. plumosa* than that of the other species here described, but it differs from it in the fact that the basal region of the tube, which is perforated by pores, is commonly partially free (fig. 3), whereas in *T. plumosa*, as in *T. phalangea* and *T. liliacea*, the porous part is wholly adnate to a zoëcium, and only the non-porous termination of the tube is free. The oëciopore typically opens upwards, or away from the basal surface of the colony. The proximal part of the tube is attached to a zoëcium, and is followed by a considerable free length of tube (part of which is porous), which dilates upwards, so as to be more or less funnel-shaped. This funnel-shaped portion commonly grows away from the first zoëcium and towards the free part of a second zoëcium, on which its edge rests. In *T. plumosa* the whole of the tube is recumbent on the same zoëcium or zoëcia. In some specimens of *T. aperta*, and especially when the tube is wedged in between two zoëcia which are near one another, the arrangement above described is not so obvious. The oëciopore is circular or oval, and is of considerable size, its longer diameter usually varying from  $200 \mu$  to  $370 \mu$ , and averaging about  $280 \mu$ . One abnormally small oëciopore was only  $135 \mu$ , and one unusually large one was  $435 \mu$ , but the usual range is given by the figures first stated. The edge of the oëciopore may be slightly everted, or evenly circular or oval. In some cases it is somewhat indented on one or both sides, and may then closely resemble that of *T. plumosa*.

In one or two colonies the proximal part of the exposed portion of the ovicell had the characters of an ordinary zoëcium, the pores being very few and widely scattered. At the level where the ovicell commences to enlarge, in these cases, the pores become suddenly numerous, and the zoëcium takes on the character of an ovicell. The line where the pores become more numerous probably corresponds with a time at which the embryonic structures reached a certain stage of development. The same peculiarity in the ovicell was also

noticed in some of the proximal ovicells of the specimens of *T. flabellaris* from Barents Sea described on p. 82.

I have observed one or two interesting variations in this species. In two or three colonies, zoëcia of double the normal width occur, with an orifice measuring as much as  $380 \mu$  in its major axis, but having the normal diameter in its minor axis. In one of these cases a groove down the large zoëcium indicated that its size was due to the absence of the septum which should normally have divided it into two zoëcia. A similar large zoëcium was found in a colony of *T. flabellaris* from Greenland. I have not seen more than one of these giant-zoëcia in a single colony, and they do not occur at all in most cases. It is not impossible that they may be zoëcia which made an abortive attempt to develop into ovicells.

In one instance an œciostome was recumbent on a giant zoëcium (cf. the remarks given in Waters' paper, 45, p. 277), but there was no similar relation in the other cases. Walford (42, p. 80) has characterised his genus *Cisternifera* (said to be Cheilostomatous) by the occurrence of giant-zoëcia in the colony, and has in the same place (p. 79, pl. v, figs. 14, 15) described similar giant-zoëcia or "cistern-cells" in "so-called *Diastoporæ*" from the Great Oolite. These latter, at any rate, appear to me to correspond with the large zoëcia of *T. aperta* and *T. flabellaris*.

A more interesting variation was noticed in two colonies in which an ovicell had developed accessory œciostomes (fig. 2). Since the ovicell of *Tubulipora* is an enlarged zoëcium, its œciopore is homologous with a normal orifice, and it follows that an ovicell should have only one œciostome. This is actually the case in most species, and in most colonies which I have seen of *T. aperta*. When the growth of the ovicell is completed, each of the lobes other than that ending in the œciostome normally becomes closed by a porous calcareous film. In the abnormal colonies of *T. aperta*, however, one or more of these lobes has not closed completely, but has grown at its distal end into a tube, which may completely simulate

the normal œciostome, which can be seen in the more proximal part of the ovicell.

One of these cases is a small pyriform colony (fig. 2), beginning with the usual primitive disc, which measures 185  $\mu$  in diameter. One ovicell is present, with a normal œciostome, its tube (fig. 3) being long and to a large extent free, and the œciopore measuring 265  $\mu$ . To the apparent right of the œciostome one of the lobes of the ovicell ends in an accessory œciostome (fig. 2.1), 105  $\mu$  in diameter; while on the other side three lobes have accessory œciostomes. Of these, No. 2 measures 165  $\mu$ ; No. 3 is not yet fully formed; and No. 5 is 90  $\mu$  in diameter. A smaller tube (4), at the end of a very small ovicell-lobe, had closed except for a minute terminal pore.

A second case is that of a portion of a larger colony. The fragment is rather more than 2 mm. in transverse diameter, and has five ovicell-lobes, each of which has an accessory œciostome, a normal one being present more proximally. One of these closely resembles the normal œciostome, while another has about the same diameter at its base, but then becomes much constricted, finally opening by an orifice much smaller than a normal orifice.

I have not had time to examine sections of this species, but it appears to me highly probable that the accessory œciostomes are functional in providing a means of escape for the larvæ which find their way into the lobes to which they respectively belong.

*Tubulipora plumosa*,<sup>1</sup> W. Thompson (fig. 1).

*Tubulipora plumosa*, W. Thompson, in Johnston (20, p. 274 [immature]).

*Tubulipora phalangea* (part), Johnston (20, p. 273, especially the statements given on the authority of Mr. Peach).

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<sup>1</sup> Thompson's name first appeared in 1847. In the same year Reuss ("Foss. Polyparien d. Wiener Tertiärbeckens," in Haidinger's 'Naturwiss. Abhandl.,' Band ii, Abth. 1, 1848, p. 39) described *Defrancia pluma* and (p. 51) *Diastopora plumula*. The former, at any rate, is doubtless a *Tubulipora*, and is given as a member of this genus by Manzoni ('Denkschr.

*Tubulipora flabellaris*, Johnston (20, p. 274, pl. xlvii, figs. 5, 6 [immature]). Busk (2, p. 25 [part], pl. xxiv, figs. 1—3; pl. xxv, fig. 2).

♀ *Tubulipora flabellaris*, Busk (3, p. 23, pl. v, figs. 1, 1a—1c).

The locality given in the text is Station 315 [Falkland Islands], and the specimens figured presumably came from that locality. On this account I regard the determination of the species as uncertain, in the absence of any description of the œciostome.

*Tubulipora fimbria*, Hincks (18, p. 448, pl. lx, figs. 3, 3a [immature]).

Zoarium completely adnate, variously lobed, reaching a diameter of an inch in the finest specimens. The serial, connate arrangement of the zoœcia is strongly marked, the series becoming radial in fertile lobes. Zoœcia large. Œciopore much larger than an ordinary orifice, averaging about 355  $\mu$  in its greatest diameter. The tube is funnel-shaped, and the œciopore opens directly or obliquely upwards, one of its edges being usually somewhat indented. Tentacles containing (homogeneous) excretory vesicles (see p. 113).

Common in the cavities and on the outside of the remarkable nodular rooting bulbs of *Laminaria* (*Saccorhiza*) *bulbosa*, where it reaches its greatest size, and on red seaweeds from shallow water.

I have examined large numbers of specimens of this species from Salcombe, Devonshire, and from Plymouth. I have also obtained typical specimens from Guernsey and from Roscoff.

This well-marked species appears frequently in the literature of the subject in its immature form, in which condition it has been supposed to be adult. Its real adult condition has been presumably mistaken for *T. liliacea* (*T. serpens*, auctt.) by most writers; but it is clearly alluded to by Johnston (20, p. 273), who quotes Mr. Peach as the authority for stating that it luxuriates in the bulb of *Laminaria bulbosa*, and that it reaches the diameter of nearly an inch. It is there given as a form of *T. phalangea*, while on the next page Johnston describes the species in its young state as *T. flabellaris*.

These specimens were sent to Johnston as *T. plumosa* by K. Acad. Wien, xxxviii, Abth. 2, 1878, p. 20, sep. copy; it has, moreover, a considerable resemblance to Thompson's species. The specific names *pluma*, *plumula*, and *plumosa* are similar in meaning, but they are sufficiently distinct in sound. I think there is no practical inconvenience in reviving Thompson's name, and in a group where the synonymy is so involved it is advisable to retain any name that can possibly be used when it is moderately certain what was originally meant by it.

Mr. W. Thompson, whose name I have adopted. The description and figures given by Johnston leave no doubt in my mind that Thompson's *T. plumosa* is the form of which I have given a diagnosis above. The flat central region of the colony, which alone is developed in Johnston's figs. 5 and 6 (pl. xlvi), is eminently characteristic of the present species. This form is indeed not invariably assumed by it, but is very distinctive when it does occur. In this condition the zoëcia are often strongly ridged transversely, in the manner described in Johnston's work, and the serial arrangement of the zoëcia is hardly apparent unless the colony is looked at from its distal edge. The shortness of the tubes alluded to by Johnston is of course due to the fact that they are immature.

Specimens with this depressed central region are usually easy to distinguish from *T. phalangea*, with which the species is associated on red seaweeds. The radial ridges formed by the more projecting zoëcia are the commencements of the series of zoëcia. As the colony increases in diameter, the freshly added parts of these projecting zoëcia project more and more, younger zoëcia are developed connately with them on their lower side, and the serial arrangement becomes as strongly marked as in any other species of *Tubulipora*.

*T. plumosa* is described by Hincks (18, p. 448, pl. lx, figs. 3 and 3a) from immature specimens as *T. fimbria*, Lamk. Fig. 3 of this author shows the beginning of an ovicell on the right side, although the septa between the ovicell and the contiguous zoëcia are not all indicated. Mr. Hincks expresses a doubt as to the identity of this species with *T. fimbria*, Lamk., but accepts the name with some hesitation on Smitt's authority. Smitt's *T. fimbria* is, however, in my opinion, a different species, and it is here described as *T. aperta*. The figure of *T. "fimbria,"* given by Milne Edwards (29, pl. xiv, fig. 2) from a specimen labelled by Lamarck, does not specially resemble *T. plumosa*.

The distinctive feature of *T. plumosa* is the oöciostome (fig. 1), which is a wide, funnel-shaped structure, looking up-

wards or obliquely upwards, the oëciopore being conspicuously larger than an orifice. Its tube is recumbent on a series of zoëcia, and does not often become completely free, as is normally the case in *T. aperta*. The shape of the oëciopore is usually complicated by a slight fold or indentation of one side, as shown in fig. 1, or of both sides. The size of the oëciopore varies from 270  $\mu$  to 430  $\mu$ , the average being 355  $\mu$ .

*T. plumosa* reaches its largest size in the cavities of the bulb-like bases of *Laminaria* (*Saccorhiza*) *bulbosa*. One of the finest colonies I have seen was approximately circular, with a diameter of 21 mm., and its peripheral parts were formed of sixteen separate lobes, some of them bifurcated. These colonies are attached to the seaweed by remarkable ridges on their under side,<sup>1</sup> similar to those which have been figured by Waters (44, pl. vii, figs. 2, 3) in an Australian form, termed by him *T. fimbria*, forma *pulchra*, MacG., and by Busk (3, pl. v, fig. 1.b) in *T. "flabellaris."* The ridges do not project greatly, and their general arrangement is radially dichotomous. As the colony increases in diameter, the ridges increase in length, often dividing or undergoing a cessation of growth. When the ridge is re-formed it commonly grows in such a way as to prolong the direction of its more proximal portion. In one case a ridge was observed measuring 1.36 mm. without interruption, but the ridges are usually much shorter than this. If the ridge is narrow its axis may be occupied by a single row of pores, which correspond with the ordinary zoëcial pores, but are considerably larger. If the ridge is broader the number of rows of pores is correspondingly increased, and large areas of the lower side are sometimes in the form of broad, irregular, porous areas, which radiate out into narrower ridges towards the distal part of the colony. In some cases the ridges are broken up into short pieces, only large enough to contain a few pores, sometimes only a single pore. If the base of the colony is, by reason of an irregularity in the surface of the seaweed or for any other cause, separated

<sup>1</sup> The colonies can be conveniently removed from the seaweed by prolonged boiling with caustic potash.

from its base of support, these short ridges may grow out into short foot-like columns of support.

The lobes of this form of *T. plumosa* are often narrow, with nearly parallel radial sides. In well-grown colonies the parallel sides of adjacent lobes are commonly in close proximity, and they may then unite by means of these attaching processes, which grow towards one another and fuse. This may occur distally, but not proximally, so that narrow fenestræ are left between the united lobes, and these are most easily seen from the back of the colony. A colony whose lobes have thus united may have an almost completely circular edge, and may at first sight appear to have an undivided terminal membrane. That this is not the case can usually be seen by careful examination, and the original lobes are indicated not only by continuing to develop their zoœcia in alternate, connate series, but also by a slight undulation of the growing edge, due to the fact that the distal border of each lobe has a convexity which has a shorter radius than that of the entire colony. Somewhat similar colonies of this species growing on shells have been described above (p. 99).

I have not found these attaching ridges or processes on specimens of this species growing on other seaweeds, nor have I found them in any other species. It appears, therefore, possible that the ridges are, from some cause, a special adaptation connected with the occurrence of *T. plumosa* on this particular seaweed.

*T. plumosa* appears to be a shallow water form. Its fondness for *Saccorhiza bulbosa* has been already referred to. It is dredged at Plymouth in great numbers on *Cystoseira granulata* from a few fathoms depth. On this seaweed the colonies are small and irregular in their growth, owing to the small diameter of the stems round which they grow. I obtained numerous specimens, which were much more convenient for examination, growing with *T. phalangea* on *Rhodymenia ciliata* from the Salcombe Estuary. The flat surfaces of this seaweed induce a regular growth in the *Tubulipora*, which are thus well adapted for the preparation

of sections which it is desired to obtain in given planes. My study of the development of this form has been entirely based on material obtained from this source.

I have found *T. plumosa* on the empty carapace of a large crab (*Cancer pagurus*), but I have not obtained many specimens which I could certainly refer to this species on shells or stones. Its typical habitat may be considered to be the surface of seaweeds from shallow water, but some of the specimens of *Tubulipora* from shells in deeper water may also belong to the same species. Should it, in fact, prove identical with *T. lobulata*, Hass., this name would have priority over *T. plumosa*.

#### IV. The Nature of certain Vesicles found in the Tentacles and other Parts, with Remarks on the Structure of the Adult Zoëcium and on the Budding.

The account of the occurrence of these vesicles must be preceded by some statements with regard to the development of the polypide-buds and the structures connected with the orifice of the adult zoëcium.

##### a. Budding and Structure of Orifice.

There are no really detailed accounts of the budding of *Cyclostomes*, though some information is given by Ostroumoff (32).

I have not satisfied myself with regard to the manner in which the first rudiment of the bud is derived from the terminal membrane. The young bud (fig. 23) is bounded externally by a more or less solid mass of cells of some thickness, which may be regarded as the protoplasmic part of its terminal membrane, and is probably in the main ectodermic. Within this, two or three excretory vesicles appear at a very early stage in all the three species investigated. More internally is a deeply staining two-layered mass of cells, at first forming a hollowed plate, concave externally, but soon taking the form of the well-known vesicular polypide-bud of *Ectoprocta*. In correlation with the fact that the proximal ends of the zoëcia

are narrow and pointed, the younger stages of the bud are longer than is usually the case in the Gymnolæmata; and a longitudinal section of the entire mass of protoplasmic structures appears as a sharply acute-angled triangle, filling up the narrow pointed tube which is at present the only representative of the future zoëcium.

It may be assumed, on the analogy of other cases,<sup>1</sup> that the inner layer of the vesicular bud is ectodermic, and the outer layer mesodermic. The distal part of the bud gives rise to the tentacle-sheath, into which the tentacles project; while the proximal part develops into the remainder of the polypide, in much the same manner as in other Ectoprocta.

Immediately on the distal side of the two-layered polypide-bud, which can be distinguished by the great readiness with which it takes up colouring matters, there appears at an early stage a cavity, lined by a thin layer of cells, which ultimately gives rise to that part of the introvert which lies between the calcareous "orifice" of the zoëcium and the "diaphragm" which forms the distal end of the tentacle-sheath. This cavity is figured and described by many writers on the Ectoprocta. It is shown by Nitsche (31, pl. xxxv, fig. 2) and by Prouho (36, pl. xxiii, figs. 1 and 3), and it appears to be of general occurrence throughout the Ectoprocta. Davenport (7, and elsewhere) having termed the cavity of the tentacle-sheath the "atrium," this space, with its wall, will be alluded to in future as the "vestibule," without thereby implying any exact homology with the similarly named part of Polyzoön larvæ. I have previously figured the vestibule of a young Cyclostome-bud (15, pl. xxii, fig. 1), although the space in question was then erroneously described as the tentacle-sheath.

In some cases the young vestibule appears as an invagination of the ectoderm of the terminal membrane, but it is often difficult to obtain direct evidence on this point.

The vestibule of the adult zoëcium is usually a space of considerable length, the diaphragm being a constriction between it and the tentacle-sheath, as originally described by

<sup>1</sup> Cf. especially Seeliger (38).

Nitsche in *Membranipora membranacea*. The vestibule is lined with a flexible cuticle, which can be made out in longitudinal sections through an adult orifice as a collapsed tube continuous externally with the chitinous part of the terminal membrane of the zoëcium, and internally with the diaphragm, through which the tentacles are protruded.

In a living, perfectly healthy colony, each zoëcium is seen to be closed by a delicate terminal membrane, perforated by a minute hole at its centre, the membrane and its perforation being stretched across the extreme end of the calcareous zoëcium. A similar membrane closes the young ovicells, and appears to be stretched continuously over the edges of the calcareous septa which are forming the walls of new zoëcia at the growing margin of the colony. The size of the perforation in the membrane of the adult zoëcium can be altered in a way which suggests the alterations in the diameter of the pupil of the eye, though I have not succeeded in demonstrating the mechanism of the movements. Before protrusion of the tentacles the pupil, or in reality the opening of the introvert, is widely dilated, and the tentacles are pushed through it.

The perforated terminal membrane appears to be similar to what Jullien (21, p. 38) has described as the "irisoidea" in Cheilostomes (*Microporella malusii*), although Pergens (35, p. 509) has adversely criticised Jullien's results on this point.

In colonies which are still alive, but less healthy, the terminal membrane may no longer appear flush with the surface of the zoëcia, but may be sunk down to some little distance from the orifice (fig. 29), and be deeply concave distally or upwards. There is little doubt that this is the result of an unhealthy condition; but it is important to notice that the position of the terminal membrane can vary in the tube because in sections and in colonies which have been mounted whole the distal ends of the zoëcia are often completely empty of cellular structures for a distance equal to once or twice the diameter of the zoëcium. The same phenomenon is noticed in the ovicells, in which the growing edge of the living body-wall is usually at some distance from the edge of the cal-

careous part. I regard these as post-mortem changes due to the action of reagents, and I think it probable that in the healthy zoëcium or ovicell the distal end of the body-wall is in the immediate neighbourhood of the edge of the calcareous wall which it secretes.

The pupil-like opening seen in the terminal membrane of living colonies is doubtless the external opening of the vestibule. When the membrane is in its proper place it is probable that the body-wall of this region is of no great thickness; but in the more usual retracted condition, which is probably artificial, the irisoid (adopting Jullien's name), or in other words the terminal membrane of the zoëcium, generally appears as a thick mass of nucleated protoplasm.

The young zoëcium with its polypide-bud has been seen to consist of the following parts (cf. 15, pl. xxii, fig. 1):—an external terminal membrane (irisoid), a vestibule, and the two-layered vesicular bud. Further examination has shown, however, that the outer layer of the bud is reflected at its distal end into a thin membrane (fig. 23, *s. m.*), which encloses the whole bud, a cavity occurring between it and the bud. In older polypides the alimentary canal, the retractor muscles, and the reproductive organ, whether ovary or testis, lie in this space, which is the body-cavity. The reflected layer seen in the young bud may probably be regarded as the somatic mesoderm. This perhaps throws some light on the morphology of the cavity lined by the inner layer of cells of the secondary embryo (cf. 15, p. 223, pl. xxiv, fig. 23). The inner layer applies itself closely to the dorsal ectoderm in the region which will give rise to the primary polypide bud. If that bud were developed by an invagination of the entire dorsal wall, and the shape of the cavity of the inner layer were simplified by the eversion of the sucker, the cavity in question would closely resemble what has just been described as the body-cavity of the bud.

#### ò. Excretory Vesicles.

The most casual inspection of sections of the three species of *Tubulipora* which I have specially studied reveals the

presence of remarkable brown vesicles in various parts of the polypides and ovicells (see figs. 20, 22), provided that the material was prepared with certain reagents. As I have, moreover, found these vesicles also in decalcified preparations of *T. aperta*, it is highly probable that they are of normal occurrence in a portion of the genus at least, and perhaps throughout the whole genus, and that they play some important part in the physiology of the colonies. What that part may be is somewhat doubtful. I have hesitated whether to consider them as reserve-stores of nutritive material or as excretory bodies; but the balance of evidence appears to me to incline towards the latter view.

I first found the vesicles in sections of material which had been prepared with corrosive sublimate. The vesicles are with this preparation excessively resistant, and therefore retain their form and their yellowish-brown colour in sections of colonies which have been decalcified with nitric acid, embedded in paraffin, and stained with hæmatoxylin or borax carmine. They are found principally in one of three places: (a) beneath or in the terminal membranes of the zoecia and buds; (b) beneath or in the terminal membrane of the ovicell; (c) in the tentacles. They occur in the first two situations in *T. plumosa*, *T. liliacea*, and *T. phalangea*; and in the first, at least, in *T. aperta*, of which I have not examined sections. So far as I know at present the occurrence of the vesicles in the tentacles is almost restricted to *T. plumosa*; and so constant have I found this character (during the spring months) that I have used it as a means of distinguishing sections of this species from those of *T. phalangea*. In one case, however, excretory vesicles occurred in the tentacles of a specimen of *T. phalangea*, determined as such by the characters of its œciostome. The colony contained an old ovicell (early stage G), but most if not all of its polypides were degenerating, and the whole colony was unusually heavily charged with excretory vesicles. It thus appears that the vesicles may occur in the tentacles of *T. phalangea* under certain circumstances; but I think it is none the less true that in the early spring, on the coast of

Devonshire, the tentacles of *T. plumosa* normally contain these vesicles, and those of *T. liliacea* and *T. phalangea* do not normally contain them.

I spent some time at the Plymouth Laboratory during the spring, for the purpose of endeavouring to decide the nature of these vesicles. Material was unfortunately not plentiful, but some results were obtained. The most convenient way of studying the vesicles was to dissect out the fresh polypides of *T. plumosa*, and after separating the tentacles from one another to examine them in sea water. Although there is some difficulty in dissecting out the polypides, decalcification cannot well be employed, because the vesicles are at first readily altered by reagents.

The vesicles of *T. plumosa* do not occur in the lumen of the tentacles, as might at first be supposed; but they are situated in the external epithelium on the abaxial side of the lumen (fig. 26). In specimens obtained in the early spring no trace is seen, in fresh material, of the typical vesicles found in sections, but the epithelium contains a row of greenish refractive vesicles, which are commonest near the tips of the tentacles, but may also occur more proximally. These vesicles are not bounded by any distinct membrane, but appear rather as drops of a fluid substance contained in the epithelium. Other smaller granules of yellowish pigment (*p.*) occur here and there in the epithelial cells, but these have a more solid appearance, and are not affected by reagents in the way characteristic of the larger vesicles.

In sections, on the contrary, the vesicles appear to be bounded by a sharply defined membrane; and it was therefore necessary to consider whether they might be symbiotic *Algæ*. With the view of testing for starch and cellulose, I added a solution of iodine in potassium iodide to the fresh tentacles, with somewhat surprising results. The vesicles, which were at first more or less irregular in outline, immediately rounded themselves off and became darker in colour, an active Brownian movement at once becoming apparent in their interior (showing that they are really fluid). This lasted for a brief period,

at the end of which (fig. 27) each of the homogeneous greenish vesicles took on the appearance of the sharply contoured spherical bodies seen in sections, a certain number of brownish granules being precipitated in their interior, and usually coming to rest on the inside of the wall of the vesicle, the fluid contents of which are now colourless.<sup>1</sup> The subsequent addition of strong sulphuric acid gave no blue colour, and did not greatly alter the vesicles. These changes took place in the same way in vesicles which had been freed from the polypides during the dissection.

The greenish vesicles were found in the fresh material in the tentacles (in *T. plumosa* alone) and beneath the terminal membranes, i. e. in precisely the same places as those in which they had been previously noticed in sections.

The above-described reaction was due to the iodine and not to the potassic iodide. This was shown by the fact that a solution of potassic iodide (*a*) in distilled water, (*b*) in sea water, was added to other specimens without producing any effect. On adding a fragment of iodine to either solution the characteristic precipitation at once took place. The same result was produced by adding sea water in which a fragment of iodine had been rubbed up.

It soon became apparent, however, that iodine was not alone in precipitating the contents of the homogeneous vesicles. The same result was produced by the following reagents:—distilled water, solution of corrosive sublimate (in fresh water or sea water), strong ammonia, osmic acid.

The darker (brown) colour assumed by the vesicles in the first experiment is not merely the effect of staining by the iodine, since it occurs with other reagents, even with distilled water. In all cases the colour of the homogeneous vesicle at once becomes darker, and an appreciable interval occurs during which nothing else can be made out. The Brownian movement then commences, the granules being at first invisible individually. The vesicle soon contains numerous minute

<sup>1</sup> The vesicles are very similar to those which have been figured by Durham ('Quart. Journ. Mic. Sci.,' xxxiii, pl. 1, fig. 3) in *Spatangids*.

granules in active movement. These become larger, and on coming to rest form the granules seen even in sections in the interior of the vesicles. One fresh vesicle always gives rise to one precipitated vesicle.

The amount of the precipitate produced by various reagents is not identical. Ammonia gives rise to a specially copious precipitation, the vesicles now looking very dark, and sometimes dissolving after a prolonged action of the ammonia. The addition of strong potash now broke up the precipitated granules, with some indication of solution, during which a purplish colour appeared. Osmic acid similarly gives rise to a very dark-coloured precipitate; but when added to vesicles which have recently been precipitated by corrosive sublimate, it merely slightly darkens their granules.

In most of the above-described experiments no trace was seen in the fresh material of precipitated vesicles, but these were observed in one or two specimens. It is, I think, probable that precipitation of the granules takes place during life in old vesicles; but it seems clear that the young stages of these bodies consist merely of a homogeneous fluid.

While the above reagents produced precipitation of the vesicles, others dissolved them completely. 90 per cent. alcohol at once dissolves them without precipitation, and the same effect is produced by 30 per cent. alcohol, which does not affect the yellow granules above described in other parts of the tentacles. The vesicle is indicated as an empty space in the tentacle after the addition of alcohol. Nitric acid dissolves the fresh vesicles, giving rise to a red-brown mass. Dilute acetic acid has no effect.

When the vesicles have been precipitated, their behaviour towards reagents is entirely different from that of fresh vesicles. Alcohol, even weak alcohol, readily dissolves the latter, but it has no effect on vesicles which have been precipitated with corrosive sublimate, as is obvious enough from the fact that they are seen in sections.

The vesicles of some sublimate-material which had been kept in 70 per cent. spirit for seven or eight months were ex-

traordinarily resistant. After decalcification of the colonies with dilute nitric acid the vesicles were practically unaffected by the following reagents:—sulphuric acid (dilute and pure), nitric acid (even when the strong acid is heated), strong ammonia, 4 per cent. potash, ether, chloroform, benzole. Gmelin's test for bile-pigments was tried without any results, and the murexide test for uric acid was also negative.

The freshly precipitated vesicles, on the contrary, were less resistant. Thus, after precipitation with distilled water, 90 per cent. alcohol had some effect on them, while a 4 per cent. solution of potash at once dissolved them. After the action of corrosive sublimate (15 minutes), followed by distilled water (25 minutes), even strong potash had practically no effect.

In some cases, though not in all, ammonia added to the vesicles, freshly precipitated by distilled water, first turned them purplish, and then dissolved them. Certain pigmented granules or cells observed in the terminal membranes of the zoecia of *T. plumosa* also turned purplish on adding distilled water.

*T. phalangea* and *T. liliacea*.—Although the tentacles of these species do not usually contain homogeneous vesicles, they possess in their places structures which consist of a large number of minute vesicles (fig. 28). Each compound vesicle probably corresponds with a single cell, and its reactions are different from those of the homogeneous vesicles, which occur in the terminal membranes of the same species, as in *T. plumosa*. The homogeneous vesicles are precipitated by various reagents, and then take on the form seen in sections, whether they occur in the tentacles (*T. plumosa*) or in the terminal membranes. The compound vesicles of *T. phalangea* and *T. liliacea* under no circumstances give rise to what I may call the "formed" excretory vesicles.

The tentacles of *T. phalangea*, as of other Cyclostomes I have examined, contain pigmented granules in various parts of their external epithelium. Two of these (*p.*) are seen in the distal part of the tentacle shown in fig. 28. They do not give the reactions characteristic of the other structures.

The fresh compound vesicles of the tentacles of *T. pha-*

lancea are dissolved by strong ammonia, by 4 per cent. potash, by 90 per cent. alcohol, and by nitric acid. Osmic acid also destroys them.

They are not affected by corrosive sublimate, nor are they broken up by acetic acid. After being fixed with corrosive sublimate, they are no longer affected by osmic acid, nor by distilled water.

On adding distilled water the fresh compound vesicles lost the boundaries of their constituent vesicles, and turned a diffuse red-purple, that colour becoming soon restricted to numerous granules, which disappeared on adding ammonia. The homogeneous vesicles of the terminal membrane were precipitated by distilled water; some of these (probably the more delicate ones) were dissolved by ammonia, while others remained and turned purple inside.

Several facts in the above experiments suggest that there is some connection between the well-known purple colour of certain species of *Tubulipora* and the homogeneous or compound vesicles. The change from a greenish to a purplish colour was specially marked on adding distilled water to the compound vesicles, and it also occurred in the homogeneous vesicles, under certain circumstances, as the result of treatment with ammonia or potash. The purple colour is, however, not entirely due to the action of reagents. The branches of *T. liliacea*, for instance, are commonly purple during life, the colour occurring as a purple pigment in the cells of the terminal membrane, as correctly stated by Smitt (39, p. 22), and in other parts. This purple pigment was not affected by the successive action of distilled water, ammonia, and potash, nor by acetic acid.

It seems to me probable, however, that the purple colour often seen in dry preparations of species of *Tubulipora* may in many cases be due to post-mortem changes of the excretory vesicles. This view was confirmed by an observation on a colony of *T. liliacea* which, when alive, had no trace of purple, but assumed that colour after being washed with fresh water and dried. The colour is not seen in colonies preserved

in spirit (which dissolves the vesicles), nor in those treated with corrosive sublimate (which precipitates the homogeneous vesicles); but colonies which have been allowed to dry, after washing with fresh water, are commonly of a characteristic purple colour. This colour is usually not noticeable during life in *T. plumosa*, healthy colonies of which are yellowish; but it is conspicuous in specimens which have been dried without being put in spirit.

I have found very pale greenish, homogeneous vesicles in *Diastopora patina* in the brown bodies, and apparently in the body-cavities. These were precipitated by sublimate, ammonia, or iodine in potassic iodide; but the details of the reactions were not altogether similar to those in *Tubulipora*. I have also seen structures somewhat resembling the compound vesicles of *T. phalangea* in the tentacles of a *Stomatopora*, perhaps *S. major*.

Experiments made with indigo-carmin, carminate of ammonia, and Bismarck-brown on living specimens of *Tubulipora* gave only negative results. The vesicles did not appear to take up any of these pigments, although control-experiments, made with species of *Bugula*, gave results similar to those I had previously arrived at (14). The cells which take up indigo-carmin in *B. flabellata* are the same as the "gelbe Tropfen" described by Claparède (4, pl. viii, fig. 1b, t.). Since these are normally of a yellow or yellowish-green colour, they are not unlike the homogeneous vesicles of *Tubulipora*. They are not precipitated, however, by distilled water, iodine, sublimate, or ammonia; and taking this fact in conjunction with the difference in their behaviour to indigo-carmin, it may be concluded that they do not closely resemble the vesicles of *Tubulipora*.

The result of the previous reactions seems to be that there is some substance in solution in the homogeneous vesicles which is precipitated by any reagent (not being a solvent of that substance) which alters the density or constitution of the solvent. The action of distilled water may be due to osmosis from the vesicle, while it is possible that substances like cor-

rosive sublimate have some specific action on the substance itself. The precipitate, once formed, behaves to reagents quite differently from its antecedent state in solution in the vesicle. Alcohol, for instance, dissolves the contents of the fresh vesicles without precipitation; but the precipitated contents become entirely resistant to alcohol, except immediately after their formation by distilled water.

Different colonies vary a good deal in the extent to which the vesicles are developed; but those obtained in the summer appear to have a much greater development of the vesicles than those of the same species found in the spring. I have examined summer specimens in preserved material only; but in many of them the excretory vesicles are very much more conspicuous than in the spring colonies. Their walls become very dark, and may be so thickened as to greatly diminish the lumen, while the contents may appear as a single solid concretion. The number of the vesicles may often be very greatly increased in the summer. This was observed especially in *T. plumosa*, in which summer specimens had almost the entire length of the tentacle occupied by a single row of closely packed vesicles.

These facts seem to indicate that the vesicles are not normally discharged to the exterior, although it would not appear difficult for their fluid contents to escape through the epidermis of the tentacles. In many of my preparations excretory vesicles appear to have been forced to the outside of the epithelia which normally cover them. I am inclined to regard this as an artefact, the fluid vesicles being squeezed out as the result of the contraction induced at death by the action of reagents, and being precipitated outside the body by those reagents. This is indicated by the fact that I have never seen them on the morphologically outer side of the ectocyst of the vestibules of the zoëcia or of the terminal membrane of the ovicell.

The increase of the number of the vesicles in the later part of the year is a reason for regarding them as excretory, and this view is confirmed by their dark colour and by the con-

cretion-like contents which may appear within them. Their occurrence in the terminal membranes of buds (even of young ones) as well as of the polypides and ovicells might suggest the view that they were nutritive.

Davenport (7, pp. 34—, pl. vi, figs. 54, 56, 57, 59) has described certain mesoderm cells (which have also been observed by Braem) in the budding regions of *Paludicella*. These contain refractive bodies which are not altogether unlike the vesicles which I have described above, and they are regarded by both Braem and Davenport as nutritive. It appears to me that these bodies are not comparable with the vesicles of *Tubulipora*; but there is enough appearance of similarity to make it worth while to call attention to the resemblance.

I can hardly doubt, however, that the *Tubulipora* vesicles have a close similarity to the "Exkretbläschen" which have been described by Eisig (8, pp. 725—) in *Capitellidæ*. The reactions of these bodies, and particularly the resistant way in which some of them behaved to mineral acids and potash, led Eisig to the belief that they contained chitin as one of their constituents, and that this substance was to be regarded as one of the normal nitrogenous excreta. The reactions which I have described agree so well with Eisig's results that the view that the vesicles are of an excretory nature appears to me to be greatly strengthened thereby. If the insoluble substance which is precipitated by various reagents is really chitin, or some similar body, the normal homogeneous vesicles may perhaps be considered to contain a substance which could be called chitinogen, which, though itself soluble, readily passes into an insoluble state. The vesicles might conceivably be employed in giving rise to the chitinous parts of the terminal membranes or vestibules of the zoœcia, although their number would appear disproportionately large on this hypothesis. It is perhaps more likely that their occurrence in the tentacles and terminal membranes is due to a tendency to deposit the excretory substances in the peripheral parts of the colony, and to the advantage of removing waste products of metabolism from the polypide-buds and embryo-

phores, where specially important processes of growth are taking place.

It would be interesting to know the fate of the vesicles when a brown body is formed. I have not as yet obtained any satisfactory evidence on this point, the colonies found in the spring having been almost completely devoid of brown bodies. It is not improbable that the vesicles found in the tentacles, at least, are in some way got rid of when a brown body is formed.

#### V. Description of the Development.

The ovicell of *Tubulipora* is in its development, in certain respects, intermediate between that of *Crisia* and that of *Lichenopora*, a conclusion which might be expected from a consideration of the adult characters of the three genera. The account given in my preliminary note (17) of "*Idmonea serpens*" really refers mainly to what is here termed *Tubulipora plumosa*, though I now find that the sections on which that account was based were partly prepared from *T. phalangea*.

The following account refers indifferently to *T. plumosa* and *T. phalangea* if no species is mentioned. Where statements are made with regard to *T. phalangea*, it must be understood that the evidence for the specific determination was, unless the contrary is stated, the absence of excretory vesicles in the tentacles. This negative evidence is not so satisfactory as the positive evidence, afforded by their presence, that a given specimen belongs to *T. plumosa*; since it is possible to overlook in the sections vesicles which are not very numerous. It may be noted that the material used for the study of the development of these two species was derived almost entirely from a single haul of the dredge which brought up *Rhodymenia ciliata*, on which *T. plumosa* and *T. phalangea* alone were discovered.

The specimens of *T. liliacea* were from Hydroids in deeper water at Plymouth, and the species was determined before they were decalcified.

The account of the development will, as far as possible, be described as a series of stages corresponding with those which I have formerly described in *Lichenopora* (16, p. 99). Those stages were characterised partly by the degree of development of the embryo and embryophore,<sup>1</sup> and partly by the condition of the fertile polypide. This latter degenerates at an earlier stage in *Tubulipora* than in *Lichenopora*, and the correspondence between the developments is therefore not exact.

The stages selected for descriptive purposes are thus as follows:

Stage A. Formation of the definitive egg (fig. 10).

Stage B. Division of the egg, and degeneration of the fertile polypide (figs. 11—13).

Stage C. [Not represented in *Tubulipora*.]

Stage D. Formation of the embryophore. The fertile zoecium is still cylindrical, or slightly expanded distally, and its brown body becomes closely surrounded by a distinct cellular investment (figs. 14—18, 21).

Stage E. The investment of the brown body becomes vacuolated, so as to give rise to a cavity. The ovicell expands distally (figs. 19, 20, 22, 25, 32).

Stage F. Commencement of embryonic fission.

Stage G. Fully formed ovicell (figs. 1—8, 33).

#### Stage A.—Formation of the Definitive Egg.

The eggs are developed at a very early stage by the polypide-buds, as in *Lichenopora* and *Crisia*. This precocious occurrence of the eggs appears to be in some way correlated with a colonial habit, and cases of this kind are familiar to every student of colonial Ascidians and of Hydroids. The

<sup>1</sup> The term "embryophore" will be used below to denote the structures, in relation with the primary embryo and its derivative secondary embryos, which are on the proximal side of the vestibule. The principal contents of the ovicell are thus the embryophore, containing the embryo and the fertile brown body, the vestibule, and the terminal membrane.

phenomenon has been described in Cheilostomes (*Bugula*) by Claparède (4, p. 166).

The eggs appear as part of the outer or mesodermic layer of the polypide-bud. In some colonies they are very numerous. Thus in one case (*T. plumosa*) a young bilobed colony contained twenty-three individuals in which an egg or eggs had become unmistakable. Some of these were fully formed polypides, others very young buds, the youngest belonging to a stage when the bud consisted of a two-layered cell-plate which had not yet become vesicular. All stages intermediate between these extremes were represented.

In most of the zoëcia there is only a single egg; in six cases there are two, and in one case three eggs; the position being at or near the proximal end of the polypide-bud or the cæcum of the polypide, as the case may be. Each egg (whatever the number in a zoëcium) is surrounded by a very distinct follicle (fig. 10) of cells, in which a follicle-cavity is usually visible.

There can be no doubt of the normal occurrence of eggs in the manner above described, since they are repeatedly noticed in the sections. I think, moreover, that there is clear evidence that the eggs occur especially in young lobes. When a lobe possesses an ovicell belonging to one of the later stages, although eggs may not be altogether wanting, they cease to be the conspicuous feature that they form in young lobes during the breeding period. It is thus probable that the successful development of an egg, with the resulting modification of the fertile zoëcium into an ovicell, diverts the energies of the lobe from the production of fresh eggs to the nutrition of the embryos, although new lobes may be formed from the same colony and give rise to new ovicells.

The mature egg reaches a diameter of  $24\ \mu$  or even  $28\ \mu$  (*T. plumosa*), and this measurement is larger than those previously recorded for *Crisia* ( $17.6\ \mu$ ) and *Lichenopora* ( $16\ \mu$ ). It possesses a distinct germinal vesicle and germinal spot, and it commonly has a paranuclear body lying in its protoplasm. This body might possibly be a male pronucleus, against which is to be set the fact that the nucleus of the egg

shows no sign of alteration; or it might be a centrosome, a view which hardly appears likely, from the fact that it stains readily with hæmatoxylin. I have not discovered the nature of this body.

In stage B (fig. 13) I have seen what I believe to be spermatozoa in the follicle cavity; but I have not observed the fertilisation of the egg.

I have never found a testis in an ovigerous zoëcium, contrary to what may happen in *Lichenopora*. The testes appear in the majority of zoëcia, and usually in all those which produce no eggs, in the same position as the ovaries of the female polypides; the colony being thus monœcious. The young testis is distinguishable from the young ovary owing to the fact that it consists of a small group of nuclei at the proximal apex of the cæcum of the polypide. The testes grow concurrently with the polypide to which they belong, and they occur at all stages of the development of the ovicell. Owing to the great size they reach, they form a very conspicuous feature of sections, and can readily be seen in colonies mounted whole. They fill up the proximal end of the zoëcia with a great mass of developing or mature spermatozoa, and they may reach the length of  $670 \mu$  (*T. plumosa*). When the testis is mature, the ripe spermatozoa may be seen extending up the side of the polypide, and may even be massed between its tentacle-sheath and body-wall. I have not ascertained the mode of escape of the spermatozoa.

The testes are thus produced in the great majority of the zoëcia, while ovaries are developed in but few, and an embryo in an extremely restricted number. This seems to make it probable that cross-fertilisation takes place, the great number of spermatozoa that are produced being probably in some way discharged into the surrounding water before fertilisation is effected.

The occurrence of large testes had no relation to the age of the corresponding ovicell; whilst in *Lichenopora* (16, p. 127) there was evidence of the disappearance of the testes with increasing age of the ovicell. The apparent difference

between the two genera may be due to the fact that in *Lichenopora* the ovicell dominates the entire colony, whereas in *Tubulipora* new fertile lobes can be developed in colonies which possess an old ovicell (fig. 1). It must further be noted that the specimens of *Tubulipora* were collected early in the year, and therefore early in the breeding season.

**Stage B.—Division of the Egg, and Degeneration of the Fertile Polypide.**

The number of polypides which become actually fertile is a strictly limited one, as in *Lichenopora*. The bilobed condition so often characteristic of the young colony is usually correlated with the development of two ovicells. These are at first ordinary zoëcia, as in *Lichenopora*; and in *T. flabellaris* and *T. aperta* the proximal end of the ovicell not uncommonly has the external characters of a zoëcium, the increased number of pores which denote the ovicell beginning in some cases suddenly when the zoëcium has reached a certain length. But in all species it is easy to see, by looking down into the young ovicell at a time when it is commencing to expand, that the dilated part of the ovicell is continuous with a prismatic or pyramidal cavity which runs proximally into the general series of zoëcia. A convenient way to demonstrate the fact that the proximal end of the ovicell is morphologically a zoëcium is to stain a colony which possesses a young ovicell without decalcifying, and to embed it in paraffin. By scraping away the lower or basal wall of the colony, and then dissolving out the paraffin and mounting whole, a view of the lower surface can be obtained without having the details obscured by the relatively thick, calcareous, basal lamina. In preparations of ovicells of a suitable age made in this way (fig. 30) the young embryophore may be demonstrated in a part of the ovicell whose floor is the basal lamina, and in fact in a cavity which in no way differs from an ordinary zoëcium.

The fertile zoëcia of *Lichenopora* are usually differentiated at an extremely early stage in the life of the colony. In

*Tubulipora* the entire colony cannot be looked upon as an individual of the third order to the same extent as can that of *Lichenopora*; but a certain amount of individuality may be recognised in each of the ovicell-bearing lobes. The fertile zoecium is, in fact, differentiated at a very early stage in the development of a lobe. This may be understood by reference to fig. 1, in which a young ovicell is beginning to develop at the right of the figure. The development of the first ovicells of the colony begins in *T. plumosa* in the immature stage which was considered by Thompson and Johnston as the adult condition of this species.

The phenomena of the selection of the fertile zoecia are probably more primitive in *Tubulipora* than in *Lichenopora*, in which the differentiation of the ovicell may have been thrown back to an early stage in the development of the colony, in correlation with the high degree of individuality which is possessed by the entire colony in that genus.

Internal evidence that the ovicell is at first a zoecium is afforded by the invariable presence in it of a brown body, indicating the previous existence of a polypide. This may be called the "fertile brown body," as in the case of *Lichenopora*.

In the latter the fertile polypide is not the first inhabitant of its zoecium, as is indicated by the simultaneous presence in it of a brown body, a functional polypide, and an embryophore. In *Tubulipora*, on the contrary, the first polypide of the fertile zoecium becomes fertile, and no new polypide is developed in the normal ovicell after the first brown body is formed. In cases of abnormal development, however, the entire embryophore may degenerate, and a new polypide-bud may make its appearance. In a single case only I have found a brown body (in addition to the normal brown body) on the proximal side of an embryophore in stage E. This may be interpreted as evidence of the degeneration of a polypide before the formation of the definitive fertile polypide.

It is not easy to obtain evidence showing the exact stage at which degeneration of the fertile polypide takes place in

Tubulipora, and this is probably because the stage is of short duration. Two possibilities have to be considered,—(a) that degeneration takes place while the polypide is still a bud; (b) that it occurs after the polypide has become functional. The latter view is probably the correct one, and if this is so, Tubulipora occupies an intermediate position in this respect between *Crisia*, in which the polypide degenerates while it is still a two-layered bud, and *Lichenopora*, in which two functional polypides successively occupy the young ovicell.

The question clearly turns on the observation of the stage at which the egg begins to develop. No trace of development is found in the eggs of polypide-buds, and on the assumption that the brown body is formed by the degeneration of a bud, it would be necessary to assume that the large eggs which are so commonly noticed in the ovaries of polypides have missed their chance of developing, and would later have degenerated. Positive evidence that the fertile brown body is formed from a polypide, and not from a mere bud, is afforded by the fact that the youngest embryophores found with a brown body and partially developed embryo occur in fully formed, long zoecia, and not merely in immature zoecia still in process of development at the growing edge.

Even more direct evidence is, however, afforded by the stage shown in fig. 11 (*T. plumosa*), which represents what is certainly a case of the division of the egg. The darkly stained bodies marked *f* probably represent degenerating eggs or their follicles. This would indicate that in the event of more than one egg occurring in a single ovary, only one of the eggs actually develops. The figure shows the cæcum of the fertile polypide, which from its size, and from the avidity with which its tissues have taken up hæmatoxylin, was clearly only just mature. Its rectum contains Diatoms, a fact which proves that the polypide had commenced to feed. A second, precisely similar polypide, containing Diatoms, and provided with an egg in the same condition as that of the first specimen, also occurred in the same colony. Most of the buds and young polypides in this colony, if not all of them, possessed either

one or two eggs, and one unmistakable ovicell was also present; no other development had taken place.

This is the only colony in which I have obtained certain evidence of the period at which the egg begins to develop; but taken in connection with the next described series of cases, the conclusion may be drawn that the degeneration of the fertile polypide normally takes place shortly after the polypide has become functional. This is in accordance with the fact that ovaries or eggs are not found in the older polypides of a colony, indicating that they are in some way absorbed or degenerate if development does not begin in them shortly after their parent polypide has become mature.

The occurrence of more than one polypide in the fertile zoecium of *Lichenopora* is associated with the fact that each of the ordinary zoecia of the young colonies also possesses a brown body and a polypide. This is not the case in *Tubulipora*, in which there are normally no brown bodies (in the species investigated) in the young colonies. It is not impossible that this may have something to do with the season at which my material was collected. My specimens were obtained during March and April, a time when growth is taking place with great energy, probably after a period of winter rest. I have found brown bodies commonly in colonies of *Tubulipora* obtained in Devonshire during the summer months. It is not impossible that the excretory vesicles which have been described above provide a means of eliminating excretory matters which would otherwise accumulate in the stomachs, and induce the formation of brown bodies. Whether this be the case or not, the entire absence of brown bodies in a large proportion of the specimens of *Tubulipora*, even in quite large colonies, is a fact in striking contrast with the normal occurrence of brown bodies in the young zoecia of *Lichenopora*.

Evidence of the degeneration of a fertile polypide was obtained in ten cases, four of which appear to belong to *T. plumosa* and six to *T. phalangea*. The results of the examination of these cases were quite concordant, all of them

pointing to the degeneration of a polypide at a stage when the embryo consists of about 2—4 blastomeres, at first enclosed in the original follicle of the egg, the follicle ceasing to be distinct in the later stages. In two of these cases additional evidence that the degeneration was a normal stage in the development of the ovicell was afforded by the fact that it was in the position relatively to an obvious ovicell which it might have been expected to occupy, from the fact that two ovicells are so commonly found in young colonies. Fig. 12 shows the beginning of the degeneration of the fertile polypide. The section cuts the edge of the mass of tentacles, which in the next few sections are obscurely defined, showing that degeneration is taking place. Parts of the alimentary canal are visible in the section figured. The nuclei of the follicle are not so regularly arranged as in the case of unfertilised eggs. The embryo has two cells, which lie in a distinct follicle-cavity.

Fig. 13 (*T. phalangea*) shows a later stage, drawn with a higher power. The brown body, which is only indicated in the figure, still shows some traces of the parts of the alimentary canal of the fertile polypide, whereas a fully formed fertile brown body shows no such traces, and consists of a granular pigmented mass, containing a few nuclei. The embryo certainly possesses three blastomeres, while the elongated nuclei of two of the cells of the egg-follicle are clearly seen. The follicle contains a minute deeply stained body, which is almost certainly the remains of a spermatozoon.

The terminal membrane of the fertile zoëcium plays an important part in the development of the future ovicell. The evidence afforded by this and the next stage appears to be that the orifice of the vestibule closes at the degeneration of the polypide, and that the terminal membrane retires some little distance within the calcareous orifice. It is, however, difficult to be certain how far this regression is normal, and how far it is an artefact.

[Stage C (functional polypide + embryophore) of *Lichenopora* is not represented in the development of *Tubulipora*.]

**Stage D.—Definitive Formation of the Embryophore.**

The appearance of the ovicell in this stage is very characteristic, and from the frequency with which it occurs in my sections I conclude that the stage is of relatively long duration. I have examined about seventeen ovicells in this stage of *T. plumosa*, twenty-seven of *T. phalangea*, and one of *T. liliacea*. It appears to me that the embryophore of the first species is normally distinctly larger than that of the second, while that of the third species differs from the other two in its great length.

Fig. 15 shows an embryophore of *T. plumosa* at the beginning of this stage. The brown body is fully formed, but appears young, and it is not yet surrounded by any very definite investment of cells. The embryo has two obvious blastomeres, and the follicle-cavity in which they lie is in the immediate neighbourhood of the brown body. The cord of cells running proximally from the follicle is the shrunken remains of the somatic mesoderm of the fertile polypide. The terminal membrane is thickened, and its staining properties indicate that it is in a state of active growth. It is continuous internally with a mass of cells which extend from it to the brown body. This mass contains four excretory vesicles, though a larger number were visible in some of the other sections of the same ovicell.

The length of the embryophore, from the proximal end of the follicle to the distal tip of the terminal membrane, is 200  $\mu$ .

Fig. 14 (*T. phalangea*) illustrates the condition in which the terminal membrane is usually found in this stage. The distal end of the embryophore projects into the cavity of the young ovicell as a knob, which appears to be quite free from the wall of the ovicell. The brown body is fully formed, and has a more compact appearance than that of the former specimen.

Fig. 18 is a slightly older embryophore of *T. plumosa*, from a colony in which excretory vesicles were specially

numerous. In the section drawn they form a large axial mass, lying in the solid tissue on the distal side of the brown body. The details of this tissue are not shown, but it does not differ in any essential respect from the similar region of fig. 16.

Two embryonic cells are seen, the two large nuclei shown to the right of the follicle-cavity probably belonging to the original egg-follicle. While in the younger ovicells shown in figs. 14 and 15 the follicle is in the immediate neighbourhood of the brown body, it is here separated from it by some intervening tissue, the existence of which, and the occurrence of a definite cellular investment to the brown body, are indications that the embryophore is more advanced in its development than was that of the former figures.

The investment of the brown body has in fact become a perfectly definite structure, sharply marked off from the surrounding tissues. The part of it which lies distally to the brown body has become thickened, and the nuclei are here arranged in several layers, while they occur in a single layer at the sides of the brown body. Distally to the thickened part is a slit-like cavity, which will be termed the vestibule. The morphology of these parts will be considered in the final part of the paper.

Fig. 16 is a still later stage (*T. phalangea*), as is shown by the more advanced development of the embryophore and of the embryo. The latter now consists of a considerable number of cells, still lying in a follicle-cavity. The embryophore is rather longer than before, and the investment of the brown body is now thickened laterally and proximally, as well as distally. A special growth of the investing tissue is taking place proximally to form the "nutritive tissue," destined hereafter to form the reticulum in which the secondary embryos lie. As it appears probable that this reticulum is directly or indirectly concerned in the nutrition of the rapidly growing mass of embryos, the term here suggested may conveniently be used for descriptive purposes. The investment of the brown body in fig. 16 shows some signs distally of

being continuous with the vestibule. The terminal membrane is deeply invaginated medianly; and this is in fact a general feature of ovicells in this stage. In sections which are not median the invagination may not be seen; and in some cases, as in fig. 18, it is obscured by the great development of the excretory vesicles. The existence of the invagination may, however, be looked on as the general rule; and it is probable that the vestibule is really continuous with, and has been developed by invagination from, the terminal invagination, though it is not easy to demonstrate this continuity. The wall of the vestibule, during the beginning of stage D, is closely surrounded by the other tissues of the solid distal half of the embryophore, so that the whole of its limits cannot, in most cases, be made out with certainty. Excretory vesicles were but slightly developed in this ovicell (fig. 16).

Fig. 17 is a somewhat oblique longitudinal section of the distal half of an ovicell in about the same stage as fig. 16. Part of the median invagination of the terminal membrane is seen as a slit-like cavity. The section shows the investment of the brown body, and the way in which it is connected with the vestibule, the junction being constricted like the neck of a flask. This is a normal arrangement, as is also (in *T. phalangea* at least) the oblique position of the neck of the flask-like connection.

Fig. 24 (Pl. 10) represents an ovicell of *T. plumosa* in an unusual condition. While the embryo and the proximal half of the embryophore are in stage D, the remainder of the ovicell has the form characteristic of stage E.

It can hardly be doubted, from the sections of stage D, that the ovicell at this time does not differ, or hardly differs, externally from a zoëcium. The young ovicell lies completely in series with the ordinary zoëcia, and there is no indication of a distal dilatation of its cavity.

In Fig. 24, however, the distal end of the ovicell is clearly dilated, and this expansion has been accompanied by the vacuolation of the previously solid or semi-solid distal half of the ovicell, which now contains a spacious cavity, with excre-

tory vesicles and a few cellular contents. The vestibule has well-defined walls lying in the body-cavity of the ovicell. The terminal membrane has become distinct; it closes the body-cavity at its distal end, and is somewhat thickened, except at the middle.

Fig. 21 represents an ovicell of *T. liliacea* in stage D. Although I have only one series of sections of this species in the stage in question, its characters correspond so closely with those of the succeeding stage (fig. 20) that I regard it as a normal ovicell. If this be admitted, it follows that there is a marked difference between *T. liliacea* and the other two species (*T. plumosa* and *T. phalangea*), its embryophore being much longer than anything which occurs in them, and being in fact as well developed as that of *Lichenopora*. Fig. 21 is drawn to the same scale as figs. 16 and 18, so that comparison is easy.

The other features of the section resemble those found in the other species. The distal part of the ovicell is still solid, and contains but few excretory vesicles (not seen in this section); the vestibule can be made out, and the brown body has a thick investment continuous proximally with the embryophore, and having distally a split leading to the vestibule. The existence of the nutritive tissue shows that the ovicell is at the end of stage D, a conclusion which is also indicated by the length of the embryophore.

The general features of stage D are thus as follows:—The egg-follicle becomes replaced by what may be termed the embryonic follicle, or simply the follicle. This becomes separated from the brown body by intervening cells, which are specially well developed in *T. liliacea*. The brown body, at first without any distinct cellular investment, becomes surrounded by a mass of cells which mark it out sharply from the other parts of the ovicell; and the proximal part of this investment gives rise to a special "nutritive tissue." The vestibule makes its appearance, at first surrounded by a nearly solid mass of cells containing excretory vesicles, into which a median terminal invagination of the ectoderm projects. The

ovicell is still in the main cylindrical (or really pyramidal), and does not yet differ materially from an ordinary zoëcium.

**Stage E.—Development of the Cavity of the Embryophore and Enlargement of the Ovicell.**

The general external features of the ovicell in this stage are seen from figs. 31 and 32, both taken from one colony. The embryophore of fig. 31 is shown in back view in fig. 30, and is a rather late representative of stage D, as can be seen by comparison with fig. 16, the nutritive tissue being clearly indicated on the proximal side of the brown body. The combination of an embryophore in stage D with an ovicell in stage E has already been seen in fig. 24. The embryophore of fig. 32 is in stage E.

The cavity of the ovicell is beginning to expand distally in figs. 31 and 32, in preparation for the great increase in the size of the embryophore which is to take place during the succeeding stage. The distal end of the embryophore in both ovicells lies at the level marked *Emb.*, and it is thus interesting to note that the embryophore is still in the part of the ovicell which represents its zoëcium-stage.

The growing margin of the ovicell has already acquired the characters of stage E, consisting of a deeply staining mass of tissue which extends round the growing edge of the ovicell.

Fig. 32 shows that the growing edge is uniformly curved in the upper wall of the ovicell, while below it has an undulating course, due to the fact that the floor of the ovicell is ridged by the upgrowth of the young zoëcia in the way that has already been described (p. 79).

I believe that the position of the growing edge shown in figs. 31 and 32 is not completely normal, but that the action of reagents has caused it to shrink away from the edge of the calcareous parts. This seems to be indicated by fig. 31, in which the protoplasmic growing edge practically coincides with the distal margin of the roof of the ovicell on the left of the figure, though it has shrunk away from it to the right. Sections show that the stained line seen in the figures is

really the thickened edge of the terminal membrane, which is deeply invaginated in the middle, as was the case in the earlier stage. A longitudinal section of the ovicell thus has the form seen in fig. 22, in which the middle of the terminal membrane is greatly depressed, so as to be widely removed from the chitinous part of the membrane (ectocyst), which is tightly stretched across the open part of the calcareous funnel. I am doubtful how far this is normal. Some amount of retraction of the living tissues from the orifices of the zoëcia almost certainly takes place when the animals are killed, and it is possible that the protoplasmic terminal membrane is normally in close contact with its chitinous ectocyst. It is not easy otherwise to see how the ectocyst is formed, unless the terminal membrane is capable of attaching itself from time to time to the ectocyst, which, it must be remembered, increases in extent so long as the ovicell continues to expand.

Decalcification is a further source of alteration. Bubbles of gas accumulate during this process in various parts, and are responsible for a good deal of distortion of the protoplasmic structures. The bubbles often find much difficulty in making their way through or past the ectocyst, and an accumulation of gas between the latter and the living part of the terminal membrane may be responsible for a considerable amount of depression of the former. As, however, the tissues were well hardened before being decalcified, I think it probable that the gas would rather tear the tissues than alter the entire position of an epithelium which had lost its flexibility as the result of long immersion in spirit.

I have examined sections of nearly seventy ovicells in this stage. About half that number belonged to *T. plumosa*, eight to *T. liliacea*, and the remainder to *T. phalangea*.

Fig. 19 is a longitudinal section of an ovicell of *T. plumosa* at the beginning of stage E. The terminal membrane is deeply invaginated in a neighbouring section. The distal part of the ovicell is still nearly solid, and contains numerous excretory vesicles. The vestibule is somewhat more distinct

than before; the brown body has diminished in size, but the embryo is not greatly changed. The most noticeable difference between this and the earlier stage is in the embryophore, the proximal part of which is much more developed than before. The nutritive tissue is, in fact, now much increased in amount, and the embryo is thereby further removed from the brown body.

The nutritive tissue is becoming vacuolated in fig. 19, and further spaces are originating between it and the outermost wall of the embryophore. This leads to the condition of fig. 22, a considerably older stage (of the same species) drawn to the same scale.

Fig. 22 is from a distinctly bilobed colony, each lobe of which contains an ovicell in stage E. The two ovicells converge proximally, as can be seen from the sections, which are parallel to the basal lamina of the colony. Their proximal ends extend far down into the part of the colony which is common to the two lobes, so that it is clear that the colony was in an unlobed state when the development of the ovicells commenced.

The most important difference between fig. 22 and fig. 19 is that the part of the embryophore containing the nutritive tissue consists in the former of a long, cylindrical, thin-walled portion, containing a loose inner mass of cells which do not nearly fill its cavity. There is still no great increase in the development of the embryo.

Fig. 20 is a section of an ovicell of *T. liliacea* in the same stage, and it confirms the conclusion drawn from fig. 21 that *T. liliacea* is characterised by the great length of its embryophore. The ovicell here figured is about as much developed as fig. 19 (*T. plumosa*). The distance of the brown body from the embryo is very different in the two cases.

The condition of the ovicell towards the end of this stage is illustrated by fig. 25, representing an ovicell, probably of *T. phalangea*, cut horizontally, as is shown by its considerable breadth. The embryo has now enlarged to a marked extent, and measures 80  $\mu$  in its greatest length, which is about three

times the length of the embryo in fig. 19. Several giant-cells are seen in the immediate neighbourhood of the embryo, as in *Crisia* and *Lichenopora*. The function of these is not certain, but there is no evidence that they take any direct part in the future development.

The cavity of the embryophore has greatly enlarged, and now fills up most of the ovicell. Parts of the nutritive tissue are seen in its proximal region, and a few scattered cells belonging to this tissue occur in the middle of the cavity. The brown body is at the distal end of the cavity; and this is its usual, though not its invariable position. In some cases, during this or earlier stages, it may lie partly in the cavity of the embryophore and partly in the vestibule, demonstrating the existence of a communication between these two cavities. The vestibule is much shorter than before, so that the distal end of the cavity of the embryophore is now very near the terminal membrane. The point where the vestibule joins the terminal membrane will become the future oöciopore, the morphological "orifice" of the ovicell.

The terminal membrane is still a good deal thickened and folded at its edge, particularly on the left side of the section, and it contains the usual excretory vesicles.

The general features of stage E are thus as follows:—The fertile zoöcium becomes definitively an ovicell, and becomes obvious externally by the dilatation of its distal end. The part of the embryophore immediately distal to the follicle becomes more or less hollowed out, so that a passage is prepared by which the embryo can pass into the nutritive tissue, which is developed from the proximal part of the investment of the brown body. The part of the embryophore containing the nutritive tissue becomes vacuolated, and finally forms a wide space.

The brown body is generally left at the distal end of this space, surrounded by a mass of cells in close connection with the vestibule; but as by the vacuolation of the surrounding tissue it becomes free from other tissues, its position towards the end of this stage is variable. It may pass into the proximal

part of the cavity of the embryophore, and in one or two cases it was found in the vestibule.

The series of developmental stages grouped under the heading of stage E is really a very long one; and there are great differences between ovicells at the two ends of the series. This difference is marked in the measurements of all the parts of the ovicell.

In the early part of stage E the embryo remains for some time in the position in which it was found in the preceding stage, and its size does not at first materially increase. It is now more or less spherical, and has a diameter of about 20—25  $\mu$ . Later in stage E the follicle becomes continuous with the cavity of the embryophore. The embryo now begins to elongate in the direction of the main axis of the ovicell, and soon reaches a length of 40—50  $\mu$ , its transverse diameter being at first small. With the increase of this diameter it becomes ovoid, and then rapidly increases in size. Measurements of the embryo fairly late in stage E amounted to 80  $\mu$  for the major axis, and 50  $\mu$  for the minor axis of the same embryo. The oldest ovicell which I have found in this stage had a pear-shaped embryo 135  $\mu$  long, with its narrow end situated proximally. The ovicell had reached a considerable size, its greatest transverse diameter, as measured in a series of horizontal sections, being 1.25 mm. (= 1250  $\mu$ ). The cavity of the embryophore was spacious, and was cylindrical for about its proximal half, the distal end dilating into the form of a trefoil consisting of three lobes, the middle lobe being connected with the vestibule.

In most of the later ovicells studied in this stage the cavity of the embryophore was either cylindrical (as in fig. 22), or was somewhat dilated distally without being distinctly lobed. Beginning this stage with a length<sup>1</sup> of about 150  $\mu$ , the embryophore may reach a length of 500  $\mu$  by the end of this stage; and after the establishment of its cavity, its transverse diameter may become as much as 450  $\mu$  at its distal end.

<sup>1</sup> This measurement is taken between the points C and B in the figures on Plate 9.

In a case of rapid and continuous growth like that of the ovicell of *Tubulipora* there is of course no special significance in the measurements quoted, but they will give some idea of the dimensions of the parts during the stage in question. The measurements here given refer to *T. plumosa*.

Throughout stage E the embryo is found at the proximal end of the embryophore. At first in its follicle, the embryo begins to extend into the adjacent part of the embryophore as it begins to lengthen. Later in the stage it lies somewhat more distally in the embryophore, its long axis coinciding with that of the ovicell. The distinctness of the follicle becomes lost towards the end of this stage, and the fertile brown body diminishes in size.

#### Stage F.—Commencement of Embryonic Fission.

I have not given any figure of this stage, which does not differ materially from that of *Lichenopora*. The primary embryo increases largely in size, and divides in much the same way as in that genus (see 16, pl. x, figs. 32—35).

The details of the lobing of the ovicell are not always the same, as is shown by the varying position of the œciostome in the adult ovicell; but in several cases which I have observed in stage F the distal end of the embryophore was merely a later stage of the oldest embryophore, with a trefoil-like lumen, described in stage E. This trifold division of the embryophore is certainly a common arrangement, the median lobe being connected with the vestibule, and therefore later with the œciostome; while the other lobes form the more lateral parts of the ovicell. The lobe connected with the vestibule may be termed the "axial lobe," because, although not necessarily in the axis of symmetry of the ovicell, it is part of its morphological long axis. Other lobes will be termed "lateral lobes."

Ovicells in stage F may exhibit no subdivision of the primary lobes, but in other cases the end of each of the lateral lobes becomes bilobed. This subdivision of the embryophore is in

all cases due to the upgrowth of a zoëcium which interrupts the growth of the ovicell.

The ovicell contains (as in stage E) two principal cavities,— firstly, the cavity of the embryophore; and secondly, the cavity in which the embryophore lies. The latter may be regarded as the body-cavity of the original fertile zoëcium, and it is constantly extending itself between the series of zoëcia by the growth of the edge of the ovicell. The growth of this cavity is more energetic during this stage than that of the embryophore; so that each lobe of the latter merely enters the base of the corresponding lobe of the entire ovicell.

In one ovicell in stage F where this arrangement was obvious, the axial lobe of the entire ovicell had elongated greatly, while the corresponding lobe of the embryophore only just entered its base. The vestibule had accordingly been greatly elongated (to  $400\ \mu$ ), so as to retain its connection both with the terminal membrane and with the embryophore. The vestibule is lined with a chitinous ectocyst, and opens to the exterior by joining the terminal membrane. The fertile brown body lies freely in the middle of the large cavity of the distal end of the embryophore. The embryo, about  $225\ \mu$  long, lies in the proximal cylindrical part of the embryophore, and is clearly dividing into a number of secondary embryos. Giant-cells, similar to those of *Crisia* and of *Lichenopora*, occur in the position of the original embryonic follicle.

The total length of a trifid embryophore during this stage was  $800\ \mu$ , and the distance from tip to tip of its lateral lobes was  $720\ \mu$ . The brown body remains distinguishable during this stage, usually lying freely in the cavity of the embryophore. The partially divided primary embryo in one case formed a large, more or less spherical mass, with a diameter of  $305\ \mu$ .

#### Stage G.—Fully formed Ovicell.

This stage, which corresponds with the figures given of the mature colonies of the several species, is illustrated by fig. 33, from a decalcified preparation of *T. plumosa*. The embryo-

phore is seen to be considerably lobed in a more or less palmate way. The proximal part is cylindrical, and occupies the cavity which represents the fertile zoëcium before it became an ovicell. This part, together with the greater part of the digitate lobes, is practically solid; and consists, as in *Crisia* and *Lichenopora*, of a reticulum of nutritive tissue, containing a very large number of secondary embryos in all stages of development. The distal ends of some of the lobes can be seen to be hollow, although the thickness of the colony makes it impossible to make out all the details. The oëciostome is at the end of the lobe marked *o.*, and this is hence the axial lobe. The greatest length of the solid part of the embryophore, from the proximal end to the distal tip of the most projecting lobe, is 2.5 mm.

Sections through ovicells in this stage are readily intelligible by comparison with stage F. A comparatively young ovicell, which had a transverse diameter of about 1.5 mm. (measured in the sections), had a five-lobed embryophore. The middle lobe was in connection with the vestibule, and the two lobes of each side had resulted from the bifurcation of the primary lateral lobes. The distal end of each of the five lobes of the embryophore was hollow, while the proximal part was filled up with a mass of young secondary embryos. Excretory vesicles were numerous in the growing edge.

The fertile brown body can still be discovered, lying freely in the cavity of the embryophore, in some of the earlier ovicells belonging to this stage.

The mass of embryonic tissue increases very greatly, and in the younger ovicells it is easy to see that embryonic fission is or has recently been taking place. In the most satisfactory series I possess illustrating this point, the ovicell contained (in addition to numerous young secondary embryos) an embryonic mass, elongated in the direction of the axis of the ovicell, and measuring about 160  $\mu$  in length. This mass was very similar to the corresponding structure which I have described at the beginning of embryonic fission in *Crisia* (15, pl. xxiii, fig. 11). Karyokinetic figures were clearly seen in a large

number of the nuclei, and the mass was constricting off secondary embryos on all sides, and was further surrounded by a good many young secondary embryos of about the same size as those which were still in connection with itself.

Demonstrative evidence of the occurrence of embryonic fission during the early part of this stage was obtained in both *T. plumosa* and in *T. phalangea*. In the case of the best series of sections obtained of the latter, the species was not merely inferred from the absence of excretory vesicles in the tentacles, but had been determined, before decalcification, by the characters of the oöciostome. It appears to me that the nutritive tissue is much more abundant during this stage in *T. phalangea* than in *T. plumosa*.

The younger ovicells in this stage contain a large number of young secondary embryos, all in about the same stage as those which are being constricted off from the larger embryonic mass already described. Comparing the entire embryophore to a hand, the secondary embryos at first occupy the part which corresponds to the palm, where they form a dense mass, composed mainly of secondary embryos, which are separated from one another by a certain amount of nutritive tissue. Measurements made of this mass, in sections cut in a suitable plane, gave 250—560  $\mu$  as its greatest transverse diameter in particular cases.

As in *Lichenopora*, I am not able to say how far a secondary embryo, once formed from a larger embryonic mass, is capable of further fission. In some cases this process seemed to be clearly indicated. But even in the oldest ovicells, containing mature larvæ, ready to escape, and even actually in the tube of the oöciostome, I have in one or two cases found larger masses of embryonic tissue clearly giving rise to more than two or three secondary embryos. One of these masses noticed in an old ovicell was 90  $\mu$  long, which is about the same as the average length of a larva ready to escape from the ovicell. The dividing embryonic masses are similar to those of *Crisia*, consisting of a more or less clearly defined outer layer of cells, surrounding a central solid mass containing specially large

nuclei ( $8 \mu$ ). These nuclei appear to be characteristic of the growing tissue of the primary embryo, since they occur at a part where no separation of secondary embryos is taking place. When traced to a part where a secondary embryo is being constricted off, these large nuclei are seen to become smaller by division, and to form the smaller nuclei ( $3.5 \mu$ ) of the inner layer of the secondary embryos. Evidence of fission was not obtained in all the old ovicells.

The young secondary embryos are always embedded in nutritive tissue, whatever the age of the ovicell. In many cases the occurrence of a group of young secondary embryos in close proximity to one another probably implies recent embryonic fission. As development continues, the secondary embryos become ciliated externally, and may then become quite free in the cavity of the embryophore, the wall of which may be reduced to a thin nucleated film of protoplasm in old ovicells.

The cavity of the ovicell is ultimately almost completely filled by the embryophore, the lobes of which may be several times divided. Even the axial lobe may give off secondary lobes (fig. 33), and it is clear that this must take place in many cases from the external conformation of the ovicell. The growing edge of the ovicell is usually conspicuous at the end of any lobe which is still incomplete, but it disappears with the complete closure of the lobe by a calcareous wall. Some of the older ovicells suggest as a possibility that the number of excretory vesicles may be reduced in some way during stage G, but others were provided with numerous vesicles.

#### VI. The Morphology of the Internal Parts of the Ovicell.

There can be little doubt that the embryophore of Tubulipora corresponds in general with that of Crisia and Lichenopora; but it is not easy to decide how far the homology is an exact one.

In Crisia (15) the ovicell is at no period of its life an ordinary zoëcium. This would almost follow from the fact that its proximal end has not the character of a simple, cylin-

drical zoëcium, but begins to widen from its commencement (cf. 13, pl. xii, fig. 6). The ovicell develops a polypide-bud, which does not become a polypide, but gives rise to the tissues immediately surrounding the primary embryo. There is thus no fertile brown body. In *Tubulipora* the ovicell is at first a zoëcium with a functional polypide. Degeneration of the latter takes place at the beginning of the development of the embryo, and at a time when the polypide is still moderately young; and a brown body results. In *Lichenopora* (16) also the young ovicell is a zoëcium, but it has two successive polypides, the second of which is present until the primary embryo has developed for some time, and the embryophore has been formed.

The investigation of *Crisia* appeared to show that the rudimentary polypide-bud of the ovicell gave rise to a tentacle-sheath, which communicated with the exterior by means of a vestibule (described as "aperture" in 15). The cavity of the embryophore in *Tubulipora* is so similar to the "tentacle-sheath" of the ovicell of *Crisia* that at first I had no doubt that the two spaces were homologous. The cavity in *Tubulipora* is, however, a completely new formation, formed after degeneration of the fertile polypide. If then it is a tentacle-sheath at all, it must be that of a newly formed bud.

In my paper on *Lichenopora* (16, p. 114) I have alluded to this possibility for that genus. The evidence afforded by *Tubulipora* seems to be in favour of the hypothesis that the parts of the embryophore correspond with parts of a polypide-bud. This view is supported, for instance, by the great resemblance of the vestibule of the ovicell to that of the zoëcia, in its structure and in its relation to the terminal membrane. The polypide-bud would be represented by the cellular investment which appears round the brown body. This mode of origin is probably similar to those cases which have been recorded by Smitt and Hincks (18, p. lvii) among Cheilostomes, in which the young polypide-bud appears to grow out of the brown body.

The relations of the cavity of the embryophore to the vesti-

bule at first sight seem to indicate that the walls of the space represent the tentacle-sheath. There is, however, one fact which suggests a different explanation. The distal end of the wall of the embryophore in stages D and E is invariably reflected inwards, as shown in figs. 22 and 25, the reflected part usually terminating in cells which are loosely connected and lie in the cavity of the embryophore. This relation is very similar to that of what I have called above the somatic mesoderm of the young polypide-buds (fig. 23, *s. m.*). If the wall of the embryophore-cavity can really be compared with this layer, the general history of the ovicell would appear to be somewhat as follows. The ovicell is at first an ordinary zoëcium, whose first polypide develops a functional alimentary canal and an ovary. An egg begins to develop, probably while the polypide is still functional, but still comparatively young. The polypide then degenerates and forms a brown body. Certain cells arrange themselves as a definite investment round the brown body; and these cells, whose origin is obscure, probably represent a polypide-bud. A vestibule makes its appearance distally to the brown body. The body-cavity of the ovicell-bud appears as a space just inside an outer epithelial layer, which represents its somatic mesoderm. This layer lies freely in the old body-cavity, and its outer surface may be more or less covered with cells belonging to that cavity. The greater part of the rudimentary polypide-bud of the ovicell becomes a mass of nutritive tissue, in the meshes of which the secondary embryos are afterwards contained. The brown body comes to lie freely in the new body-cavity by the breaking up of the nutritive tissue. By the enlargement of the body-cavity, its somatic mesoderm is brought close to the outer calcareous wall of the ovicell, and the new body-cavity thus replaces the old one. The cavity becomes lobed in correspondence with the lobing of the entire ovicell. The lumen is visible distally, even in advanced stages, while it becomes filled up proximally by the great development of the nutritive tissue and of the secondary embryos. One of the lobes of the ovicell, the "axial lobe," is connected with the exterior by means of the

œciostome, where the vestibule opens to the exterior; and the secondary embryos ultimately escape by this passage.

The junction of the embryophore with the vestibule is somewhat complicated, and from stage D onwards there is a cellular plug between the brown body and the vestibule. This is shown in fig. 20 (*y.*), where it is still solid. In a later stage (fig. 22, *y.*) it becomes hollow, its cavity sometimes appearing completely closed, sometimes opening towards the brown body, and sometimes communicating with the vestibule. These different conditions appear to be found in ovicells of one and the same stage, and the first of them is shown in fig. 25. This figure illustrates the way in which the wall of the embryophore is reflected inwards, and the similarity with a polypide-bud (fig. 23) is marked.

It is possible that this plug of cells is the morphological representative of a tentacle-sheath. On this view, the brown body of fig. 25 does not lie freely in the tentacle-sheath (which would be a somewhat anomalous position for it to occupy), but in the body-cavity.

Sooner or later the vestibule becomes continuous with the "tentacle-sheath" (*y.*), and this with the body-cavity; the communication between the two latter being uninterrupted after the migration of the brown body to some other part of the body-cavity. A communication between the body-cavity and the exterior is not a very unusual occurrence in the Polyzoa, since the reproductive bodies escape more or less directly from the former to the outside in several cases. This is shown, in Phylactolæmata, by the escape of the statoblasts after the decay of the polypide has left an open passage to the exterior, and in certain Gymnolæmata by the occurrence of a special passage, the intertentacular organ.

The cavity of the embryophore in *Lichenopora* is probably comparable with the cavity in *Tubulipora*. The stage shown in pl. ix, fig. 27, of my former paper (16) is very similar to a *Tubulipora* at the end of stage D. The vestibule is represented by the invagination there marked "orifice;" the brown body with its investment requires no special explanation, while

the "suspensor," constituted by the inner cells between the brown body and the embryo, is probably represented in *Tubulipora* by the nutritive tissue.

The comparison with *Crisia* is less easy, but the main difference—the absence in the ovicell of that genus of a functional polypide degenerating to a brown body—has been already commented on.

Fig. 15 of pl. xxiv (15) shows a young ovicell with a bud consisting of vestibule (distally), "tentacle-sheath," and thick proximal portion, corresponding with the alimentary canal and tentacles of an ordinary polypide. Fig. 1 of the same paper is probably younger, the part there marked "tentacle-sheath" being more probably the vestibule, which is developed in Cyclostomes before the tentacle-sheath. Fig. 2 is considerably later, and its "tentacle-sheath" corresponds with the similarly marked space in the later stages; this is quite evident from the fact that a vestibule like that of fig. 3 is present in the ovicell which fig. 2 represents. Although fig. 2 is a good deal later than fig. 1, it will be noticed that its egg is in much the same state. The later ovicells formed a perfectly uninterrupted series. It thus appears to me to be sufficiently established that the vesicular bud of the ovicell of *Crisia* (15, fig. 1) gives rise to the "follicle" (figs. 3, 5, 6) of later stages. If this is the case, the cavity into which the follicle projects may be really the tentacle-sheath, which would, on this hypothesis, be much more developed than in *Tubulipora*. It seems to me more probable, however, that the cavity of the embryophore of *Tubulipora* is identical with the cavity of the "tentacle-sheath" of *Crisia*, as is indicated by a comparison of fig. 25 of the present paper with fig. 8 of my former paper (15). The apparent difference in the early stages is probably due to the fact that the development of the so-called "tentacle-sheath" of *Crisia* was not observed.

The junction of the vestibule and embryophore in the ovicell of *Crisia* (15, fig. 8) is marked by a thickening, which is by no means unlike the junction between the vestibule and the embryophore in *Tubulipora*. I can hardly doubt, therefore,

that the part which was described as "tentacle-sheath" in the ovicell of *Crisia* corresponds with the thin-walled embryophore of Stage E of *Tubulipora* (fig. 25), whatever may be the morphological character of this space.

The separation of the genera of Cyclostomes is notoriously difficult. In *Crisia*, *Tubulipora*, and *Lichenopora* we have three extreme cases, which there can be no difficulty in recognising as distinct. The fact that their ovicells belong to three entirely different types renders the ultimate definition of the genera of recent Cyclostomes a more hopeful task than it is sometimes supposed to be.<sup>1</sup> *Crisia* may be characterised as a genus in which the ovicells are modified zoëcia dilated into a pear-like form, the region of the œciostome, as in other Cyclostomes, not sharing in this dilatation. The ovicell is from the first an ovicell; and although its morphology is indicated by the appearance of a polypide-bud, the bud never becomes a functional polypide.

In *Tubulipora* the dilatation of the ovicell is usually much more marked, and the ovicell is commonly lobed. Its lobes are developed owing to the formation of zoëcia distally to the ovicell, and the latter is accordingly obliged to divide into two portions which grow round the sides of the zoëcium or series of zoëcia. The degree of lobing corresponds with the extent to which young zoëcia are developed distally to the ovicell. Two lobes may become contiguous on the distal side of a zoëcium, but probably do not fuse; and the embryophore also is composed of a series of divaricated lobes which do not unite (in the species examined). The young ovicell differs from that of *Crisia* in beginning life as an ordinary zoëcium; and the duration of this period is accurately indicated by the extent of the proximal cylindrical (or pyramidal) portion of the ovicell.

In *Lichenopora*, as in *Tubulipora*, the ovicell is at first a zoëcium, but has more than one functional polypide (in *L. verrucaria*). The principal characteristic of the ovicell is, however, the mode of growth by the addition of peripheral

<sup>1</sup> Cf. Gregory, No. 12, p. 21.

"alveoli," which are at first distinct from the cavity of the ovicell. The lobes of the ovicell, and even of the embryophore, unite with one another on the distal side of the zoëcia, which thus pass through the cavity of the ovicell as completely free columns.

Further investigations will be necessary in order to ascertain how far the distinction of genera and species of Cyclostomes can be based on the characters of the ovicells.

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 EXPLANATION OF PLATES 8—10,

Illustrating Mr. Sidney F. Harmer's paper “On the Development of Tubulipora, and on some British and Northern Species of this Genus.”

## PLATE 8.

The figures on this plate were all drawn to the same scale (camera lucida, Zeiss A obj., with front lens removed; afterwards  $\times \frac{1}{2}$ ). The pores of the zoecia are in most cases not indicated.

FIG. 1.—*Tubulipora plumosa*, W. Thomps. (p. 105). Fertile lobe, with one ovicell and the beginning of a second ovicell; from a bilobed colony (proximal ends of oldest zoecia, at the bottom of the figure, obscured by foreign substances). Salcombe estuary, 4—5 fathoms, March—April, on *Rhodymenia ciliata*.

FIG. 2.—*T. aperta*, n. sp. (p. 101). A small colony with a single ovicell, which is abnormal in possessing four accessory oeciostomes, numbered 1, 2, 3, 5. 4 is a similar structure, but its terminal membrane is completely

calcified with the exception of a minute central pore. The colony is seen to originate in the "primitive disc," the calcified body-wall of the larva. Godösund, Björne Fjord, Norway, June, on *Laminaria saccharina*.

FIG. 3.—*T. aperta*. Distal view of the same colony, to show the tube of the oeciostome. Two of the accessory oeciostomes (numbered as in fig. 2) are also seen.

FIG. 4.—*T. flabellaris*, Fabr. (p. 99). A stunted colony, in which the proximal ends of the oldest zoecia were obscured by foreign substances. The lateral parts of the colony are bent backwards round the *Cellularia peachii* on which the specimen is growing. 1—6, oeciostomes of the six mature ovicells, oeciostome 4 being concealed from view by the zoecia. The ovicells to which the oeciostomes 5 and 6 belong are seen not to have completed their growth. 7 is a young ovicell. Barents Sea, 50 fathoms, July 1; dredged by Colonel H. W. Feilden. Greatest diameter of colony, 2.36 mm.

FIG. 5.—*T. phalangea*, Couch (p. 94). Fertile lobe with a single ovicell. s. septum between two contiguous lobes of the ovicell. Salcombe estuary, 4—5 fathoms, March—April, on *Rhodymenia ciliata*.

FIG. 6.—*T. phalangea*. Zoecium, with the oeciostome, broken off from a colony, and placed in such a position as to show the oeciopore. Salcombe estuary, 4—5 fathoms, March—April, on shell.

FIG. 7.—*T. liliacea*, Pall. (p. 90). Part of ovicell, with two series of zoecia and an oeciostome. Plymouth, 30—40 fathoms, March—April, on a Hydroid.

FIG. 8.—*T. liliacea*. Fertile lobe seen from its distal end, to show the oeciostome, the upper lip of which projects so as to conceal the oeciopore, which opens horizontally. The proximal end of the lobe is the lower side of the figure. Plymouth, obtained with the last specimen on a Hydroid.

FIG. 9.—*T. liliacea*. Lobe in which no ovicell is yet apparent, to show the biserial, *Idmonea*-like arrangement of the zoecia. Plymouth, obtained with the last specimen on a Hydroid.

#### PLATE 9.

The sections figured are all longitudinal. Fig. 10 was drawn with Zeiss F, figs. 11 and 13 with  $\frac{1}{\text{X}}$  oil-immersion, figs. 12—22 with DD. All the figures were afterwards reduced  $\frac{2}{3}$ .

[The microscopical sections which are referred to as *T. plumosa* are those in which excretory vesicles were discovered in the tentacles; those referred to as *T. phalangea* are the specimens in which no excretory vesicles were seen in that position. Unless otherwise stated, the discrimination of these two species in sections depended entirely on this character.]

FIG. 10.—*T. plumosa*. Ovarian egg, in follicle (stage A).

FIG. 11.—*T. plumosa*. Stage B, the embryo consisting of two blastomeres. The cæcum of the fertile polypide (which has not yet degenerated) is seen; *f*, and the corresponding structure to the left are probably the degenerating follicles of eggs which are not developing.

FIG. 12.—*T. phalangea*. Degeneration of the fertile polypide (stage B). The tentacles, which are better seen in neighbouring sections, have lost their distinct outlines, and are obviously degenerating.  $AB = 300 \mu$ .

FIG. 13.—*T. phalangea*, stage B. Three blastomeres are seen in the follicle-cavity, which also contains a spermatozoon. The brown body still shows traces of the alimentary canal of the fertile polypide.

FIG. 14.—*T. phalangea*. Early stage D.  $AB = 165 \mu$ ;  $CB = 75 \mu$ .

FIG. 15.—*T. plumosa*. Early stage D.  $AB = 200 \mu$ .

FIG. 16.—*T. phalangea*. Late stage D, as shown by the considerable development of the cellular investment of the brown body, and particularly by the development of the nutritive tissue on the proximal side. The terminal membrane is deeply invaginated, and the vestibule is visible.  $AB = 250 \mu$ ;  $CB = 110 \mu$ .

FIG. 17.—*T. phalangea*. Late stage D; obliquely longitudinal section of the distal end of the ovicell, to show the oblique, constricted junction of the vestibule with the embryophore. The invagination of the terminal membrane is not cut so as to show its opening to the exterior.

FIG. 18.—*T. plumosa*. Rather early stage D, with very numerous excretory vesicles. The vestibule is small. The cellular investment of the brown body is thickened distally (X). There is at present no nutritive tissue.  $AB = 225 \mu$ ,  $CB = 85 \mu$ .

FIG. 19.—*T. plumosa*. Early stage E. The nutritive tissue is largely developed, and the embryophore is becoming vacuolated. The embryo has increased in size. The section passes on one side of the median invagination of the terminal membrane.  $AB = 460 \mu$ ,  $CB = 165 \mu$ .

FIG. 20.—*T. liliacea*. Early stage E. The embryophore is longer than in the other species. *y*, Plug of cells between vestibule and embryophore (see p. 148).  $AB = 630 \mu$ ,  $CB = 255 \mu$ .

FIG. 21.—*T. liliacea*. Younger ovicell (late stage D). The embryophore is much elongated, as in Fig. 20.

FIG. 22.—*T. plumosa*. Ovicell at middle of stage E. *y*, corresponding with the similarly lettered part in figs. 20 and 25, has now acquired a lumen.  $AB = 960 \mu$ ,  $CB = 355 \mu$ .

## PLATE 10.

Fig. 23 was drawn with Zeiss DD, and was not afterwards reduced. The other figures were reduced two thirds after being drawn. Figs. 24 and 25 were drawn with DD; Figs. 26—28 with F; Figs. 30—32 with A; Fig. 33 with A, the front lens of which was removed. Fig. 29 was not drawn with a camera lucida.

FIG. 23.—*T. plumosa*. Polypide-bud, partly diagrammatic; for comparison with the ovicells shown in Figs. 22, 25, &c. *s. m.* Somatic mesoderm, reflected on to the very thin tentacle-sheath, which becomes continuous with the tentacles near their proximal end. The epithelium of the stomach (below the tentacles) is derived from the inner layer of the bud, and is covered by the outer layer. The distinction between the two layers is not easily made out in the mass marked "tentacle."

FIG. 24.—*T. plumosa*. The embryophore is in stage D, and the distal part of the ovicell is in stage E. Numerous excretory vesicles occur distally. A B = 460  $\mu$ , C B = 110  $\mu$ , D E = 275  $\mu$ .

FIG. 25.—*T. phalangea*. Advanced stage E. The growing edge is much lobed and thickened on the left side of the figure. The vestibule is much shortened; it is separated by the space *y* (cf. Figs. 20 and 22, and p. 148) from the brown body, which is now almost free in the cavity of the embryophore. The outer wall of the embryophore is reflected over the wall of the space *y* (cf. the polypide-bud, Fig. 23). The embryo has greatly enlarged, and three giant-cells are shown. C B = 360  $\mu$ , F G = 385  $\mu$ ; greatest length of embryo = 80  $\mu$ .

FIG. 26.—*T. plumosa*. Tentacle, fresh, with homogeneous excretory vesicles and pigment granules (*p.*).

FIG. 27.—*T. plumosa*. Another tentacle belonging to the same polypide, after the addition of iodine in potassic iodide. The contents of the homogeneous vesicles have been precipitated.

FIG. 28.—*T. phalangea*. Tentacle, fresh, with compound vesicles and pigment granules (*p.*).

FIG. 29.—*T. plumosa*. Orifices of living zoecia. The terminal membrane has been somewhat retracted.

FIG. 30.—*T. plumosa*. Not decalcified (see p. 136). View of a colony from below, after the basal lamina has been scraped away. X and Y are zoecia, which are similarly marked in Fig. 31. G is the thickened edge of the growing margin of the ovicell (in stage E), and corresponds with G in Fig. 31. The embryophore (in stage D) lies in the proximal undilated part of the ovicell. The fertile brown body, the embryo, the beginning of the nutritive tissue, and the distal thickening of the investment of the brown body, can be made out. A B = 900  $\mu$ .

FIG. 31.—*T. plumosa*. Upper view of the same lobe. *Emb.* Level of the distal end of the embryophore. X, Y, and G are the parts similarly marked in Fig. 30.

FIG. 32.—*T. plumosa*. A similar preparation of an older ovicell in stage E. The zoëcia D project upwards into the floor of the ovicell, and the thickened edge of the terminal membrane is looped over these projecting parts. *Emb.* Level of the distal end of the embryophore.

FIG. 33.—*T. plumosa*. Decalcified preparation of an old ovicell (stage G), with nearly solid embryophore containing numerous secondary embryos. The axial lobe of the embryophore ends in the oeciostome at *o.*, and gives off another lobe to the right. The main lateral lobe of the right side is only obscurely bifurcated; that of the left side is divided into five lobes. *Z.* Proximal part of ovicell, corresponding with a zoëcium. Greatest length of solid part of embryophore to tip of most projecting lobe, 2.5 mm.

POSTSCRIPT.—Braem's interesting work, "Die geschlechtliche Entwicklung von *Plumatella fungosa*" ('*Zoologica*, Heft 23, 1897), did not appear until after my MS. was in the hands of the printers; and I am unable to refer further to his observations and conclusions on the present occasion.





