III. "Preliminary Note on Embryonic Fission in *Lichenopora*." By SIDNEY F. HARMER, M.A., Fellow of King's College, Cambridge, Superintendent of the University Museum of Zoology. Communicated by A. SEDGWICK, F.R.S. Received November 3, 1894.

I have shown on a previous occasion* that the primary embryo of *Crisia* gives rise to numerous larvæ by a constantly repeated process of embryonic fission, and I have suggested the probability that this method of development will be found to be characteristic of Cyclostomatous Polyzoa in general. Observations recently made on *Lichenopora verrucaria*, Fabr., obtained on the coast of Norway,† have enabled me to prove the occurrence of embryonic fission in a second genus of Cyclostomata, although the details of the development are remarkably different from those of *Crisia*.

The colonies of *Lichenopora verrucaria* occur in great numbers on fronds of *Laminaria saccharina*, growing just beneath low-water mark. The colony is regularly plano-convex, with a diameter, in the full-grown condition, of about 5 mm.; and it is attached by its flat surface to the sea-weed. Embryonic development commences with the beginning of the formation of the colony, and the earliest stages can only be followed by examining the initial stages of the colony itself.

The growth of the young colony closely resembles that of *Tubulipora flabellaris*, Fabr., as described by Barrois.‡ The colony originates from a circular disc, which, as Barrois has shown, results from the calcification of the outer part of the body-wall of the larva after its fixation. This disc is continued into the primary zoœcium, which buds off simultaneously, on its side turned towards the sea-weed, two new zoœcia, more or less parallel with itself. *The first brood of embryos is normally developed from the egg formed in one of these two zoœcia*, although the egg is in some colonies formed in a younger zoœcium.

The colony continues to grow in the form of a compressed funnel, which at first lies on one of its flattened sides. By further growth, the mouth of the funnel soon curves round so as to look directly away from the sea-weed, its rim meanwhile extending in a plane parallel to the surface of attachment, so as to overlap and finally cover the disc from which the colony originated. The adult colony may

* 'Quart. Journ. Mic. Sci.,' vol. 34, 1893, p. 199.

† For a part of this material I am indebted to the kindness of Dr. Brunchorst and Dr. Nordgaard, of the Bergen Museum.

‡ 'Recherches sur l'Embryologie des Bryozoaires,' 4to., Lille, 1877, pl. 4.

be compared with a funnel with a basal angle of nearly 180°, passing off into a short stalk, which is curved round so as to lie between the base of the funnel and its attachment.

The funnel is composed of a multitude of closely packed pyramidal tubes, whose wider ends open at the surface in the manner of the cells of a honey-comb. These are continuously formed at the margin of the colony, where fresh tubes are constantly cut off, simultaneously with the extension of the margin, by the upgrowth of calcareous septa. The body-cavity is here closed in on the upper side by an uncalcified body-wall. The new septa are developed at the growing edge in such a way that two kinds of tubes are formed. These give rise respectively to the zoœcia and to the ovicell. The zoœcia all reach the base of the colony, where they are in close contact with one another. In growing upwards they diverge, so that a set of pyramidal spaces, narrow below and widening above, originate between them. These spaces, from which the ovicell is developed, acquire complete calcareous walls, their roof remaining at first membranous. Each contains a part of the body-cavity, cut off from the growing edge of the colony, and the spaces may accordingly be compared with zoœcia, in which, however, no polypide-buds are formed.

The membranous roof of these interzoœcial spaces becomes calcified, thus forming a "crust" which extends horizontally between adjacent zoœcia. The side walls of the spaces then break down, and a large continuous cavity thus results. This cavity, the *ovicell*, lies superficial to the bases of the zoœcia, some of which pass through it as free columns which project beyond its roof. The ovicell later acquires one or more trumpet-shaped openings to the exterior.

The mature ovicell contains several hundred larvæ in various stages of development. These, constituting the first brood, have all been derived from the primary embryo which normally develops in one of the two zoœcia first formed from the primary zoœcium.

The beginning of the developmental processes was found in a colony consisting of three zoœcia only. Each of these contained a "brown body" and a mature polypide. The polypide of the primary zoœcium, like that of one of the two secondary zoœcia, possessed a testis, attached to the lower end of its alimentary canal. That of the remaining zoœcium had an egg in the corresponding position.

A precisely similar egg was found, in one or two young colonies, in a polypide-bud, where, from its position, it had probably been developed from the outer (mesodermic) layer of the bud. Eggs are not necessarily confined to a single polypide in the colony, but in a condition in which they can be recognised as eggs, they do not appear to be developed in most cases except in the polypide destined to give rise to a primary embryo. The testis, on the contrary, may be regarded as a normal possession of every polypide. It usually gives

rise to an enormous number of spermatozoa. Fertilisation has not been observed, although a testis may be developed by a polypide which carries an egg, and although free, ripe spermatozoa have been noticed in the immediate neighbourhood of young primary embryos.

The primary embryo in its older stages is always in the immediate neighbourhood of a "brown body," a structure which was found, with rare exceptions, in the younger stages as well. Unless it should hereafter appear that a "brown body" may be formed by the degeneration of a part of a polypide, the presence of this structure in a zoœcium containing an egg or a very young embryo clearly indicates that the egg itself belongs to the second polypide which tenants the zoœcium.

Every colony normally gives rise to an ovicell, although cases are not uncommon in which degeneration sets in at an earlier or later period, resulting in the atrophy of the embryonic tissues or in their failure to develop further.

Development of the colony and of the egg go on *pari passu*. The details of the segmentation of the egg are even more difficult to observe than in *Crisia;* but stages were found in which the number of embryonic nuclei progressively increases. By the time that the embryo comes to consist of four or five cells, it is surrounded by other cells which form the commencement of a follicle. This structure is at first composed of loosely-arranged cells, hardly distinguishable from the "funicular tissue" which occurs in the body-cavity generally. The follicle becomes more compact, and finally assumes a form which has a striking similarity to a stage described by Kraepelin* in the early development of *Plumatella*. In this condition the embryo consists of a small spherical mass of protoplasm, including a few nuclei. It is supported by a structure resembling the suspensor which supports the embryo in flowering plants. This suspensor contains a very fine lumen, and a section which passes longitudinally through its axis accordingly shows two rows of nuclei, one row belonging to each of the walls on opposite sides of the lumen. The suspensor and the embryo are surrounded by a common investment of cells; and the whole arrangement is attached either to the testis of the polypide or to the lower end of the alimentary canal when no testis is present. The embryo, with its investment, hangs down freely into the body-cavity, and it is always in close connexion with the "brown body" to which allusion has already been made.

Kraepelin and Braem† are agreed in deriving the corresponding structure in Phylactolæmata from a rudimentary polypide-bud, the

* 'Abhandl. Naturwiss. Ver. Hamburg,' vol. 12, 1893 (Bryozoen), pl. 2, figs. 67, 68.

† Leuckart and Chun's 'Bibliotheca Zoologica,' vol. 2, part 6, 1890; see explanation of fig. 171 (pl. 15).

part which I have termed the suspensor corresponding with the inner layer of the bud, and the outer investment with its outer layer. Although this interpretation would make the agreement between *Lichenopora* and the Phylactolæmata closer than would otherwise be the case, I have not succeeded in showing that the arrangement has really the morphological value of a polypide-bud.

The polypide now begins to pass into the condition of a new "brown body," with which the old "brown body" fuses. The embryo, with its investments, hangs down into the zoœcium from the wall of the "brown body," which has meanwhile moved up the zoœcium to the neighbourhood of the orifice. In this position it remains during the later stages, becoming much complicated by the processes which succeed.

The suspensor ceases to be sharply defined as such, its cells merging with those which surround the "brown body" and the embryo. The latter comes to lie close to the "brown body;" and after a large increase in the number of its nuclei, begins to undergo fission. But whilst in *Crisia* the primary embryo remains throughout in the condition of a coherent mass of cells, which buds off successive embryos into the ovicell, that of *Lichenopora* early divides up into a considerable number of irregular pieces, which ultimately give rise to the secondary embryo. In the earlier stages of the process it is easy to show that the pieces are continuous with one another, or that, from their position and structure, they have recently been separated from one another. In older ovicells it may be difficult to demonstrate the existence of the process of fission, since the number of embryos is increased, to a considerable extent at least, by the binary division of small masses of cells which have all the appearance of young embryos. The details of the fission are, in fact, more similar to those which occur in the fission of the "Urknospen" of certain Tunicata (*Doliolum*,* &c.) than to those which occur in *Crisia*.

After the first brood of larvæ are hatched the colony may develop new primary embryos at several points in the ovicell. These form the starting points for the development of a fresh brood of larvæ. Thus, early stages in the embryonic development may be found, not only in the youngest colonies, but also in the largest, fully-formed colonies. These latter differ from the young colonies in containing the set of cavities constituting the original ovicell. The primary embryos of the second generation may readily be recognised in sections by means of the characteristic "brown body," to which the follicle containing the embryo is attached. Their earliest stages have not so far been traced; but the later stages, in which fission is commencing, are, in all important points, identical with those of the first generation.

* Uljanin (B.), 'Fauna und Flora G. von Neapel,' X Monogr., 1884, pp. 108 *et seq.*

After the commencement of fission the follicle may contain numerous egg-like cells, which are probably identical with the giant cells which I have previously described in the ovicell of *Crisia*. Although it is not impossible that these cells may play some part in the formation of the secondary embryos, this is rendered improbable, not only by the analogy of *Crisia*, but still more by the fact that the early stages in the development of the primary embryo take place before such cells can be recognised in the ovicell.

The following results may be deduced from the preceding statements:—

1. The ovicell is not altogether external to the zoœcia, as might be inferred from some of the older descriptions of this structure. Its cavity is morphologically identical with the body-cavity of the zoœcia, and the ovicell results from the breaking down of numerous septa which at first separate from one another a set of tubes formed at the growing edge of the colony in the same manner as the ordinary zoœcia.

2. The development of the ovicell and that of the embryo normally commence at almost the beginning of the life of the colony. So long as the growth of the first brood of larvæ continues there is no development of new primary embryos; and the numerous young larvæ found in the ovicell are descendants of the single primary embryo which is normally produced in one of the two zoœcia first budded off from the primary zoœcium.

3. The process cannot well be interpreted as a form of alternation of generations. A large number, perhaps the great majority, of the secondary embryos are formed by the direct fission of pre-existing embryos, and are not budded off from a compact mass of cells as in *Crisia*.

4. Certain remarkable analogies may be detected between the development of the Cyclostomata and that of the Phylactolæmata. Further research will be necessary in order to show whether these resemblances are more than mere analogies.

IV. "The Influence of the Force of Gravity on the Circulation." By LEONARD HILL, M.B., Assistant Professor of Physiology, University College, London, and Grocers' Research Scholar. Communicated by Professor SCHÄFER, F.R.S. Received November 19, 1894.

(From the Physiological Laboratory of University College, London.)

(Abstract.)

The effect of position of the body upon the circulation of the blood is a matter of daily observation with the physician and surgeon, but