

CONTRIBUTIONS to the HISTORY of the POLYZOA. By the  
 Rev. THOMAS HINCKS, B.A., F.R.S.  
 (Plate II.)

I.—THE "GERM-CAPSULE."

In a previous paper<sup>1</sup> I have given a brief account of my observations on the "germ-capsule" of the Polyzoa, with special reference to Dr. Nitsche's criticisms on the researches of the Swedish naturalist Smitt.<sup>2</sup> Since the publication of that paper I have had the opportunity of further investigation, and have both confirmed the results already announced and cleared up some points which were involved in doubt. I have also had the advantage of studying the complete exposition of his views, which Nitsche has since given us,<sup>3</sup> and of which his communication to this Journal was only "a preliminary sketch." Under these circumstances I propose to discuss more fully the very interesting question as to the true nature and function of the so-called "germ-capsule."

I shall first, however, bring together the accounts of this structure which have been given by various authors, so as to exhibit the history of opinions respecting it.

The dark, circular bodies ("germ-capsules" of Smitt), which are generally present in many of the zoecia, on any given polyzoary, are much too conspicuous to escape the notice of observers, and accordingly we find a reference to them in most works on the Polyzoa. Amongst the earlier writers Ellis describes and figures them under the name of "black spots." "These," he says, "are nothing but the dead polypes, or remains of the animals once inhabiting these cells, of which I had evident proof in my last journey to the sea-coast; for after I had examined this coralline (*Bugula plumosa*), with its polypes alive in sea-water, I laid the specimen aside, and upon examining it again some time after, I found the lifeless contracted animals exhibited the appearance above mentioned" ('Nat. Hist. of Corallines,' 1755, p. 34).

Dr. Grant, in his remarkable papers "On the Structure and Nature of *Flustra*,"<sup>4</sup> has noticed the small red or brown spots in the centre of the cells of *Flustra foliacea*, which he considered to be "the last remains of the dead polypi."

<sup>1</sup> 'Quart. Journ. of Micros. Science' for July, 1871, p. 235.

<sup>2</sup> *Ibid.*, for April, 1871.

<sup>3</sup> 'Beiträge zur Kenntniss der Bryozoen,' ii Heft. 3. 'Ueber der Anatomie und Entwicklungsgeschichte von *Flustra membranacea*,' 1871.

<sup>4</sup> 'Edinburgh New Phil. Journ.' for 1827, pp. 107 and 337.

In describing *F. carbasea*, too, and comparing it with the former species, he speaks of "the same dark round spots in the centre of those cells which have lost their polypi." In his account of the development of the ova he remarks that they "first make their appearance at the narrow base of the cells as very small, pale-red, gelatinous spheres, and the polypi of such cells are generally removed, and only a small, round, dark brown spot is seen in their stead, in the centre of the cells;" and he adds the important observation—"When the ovum has escaped from the cell *the dark round spot in the centre of the cell enlarges, and a new polypus shoots out at that point* . . . The same cells may repeatedly produce ova and polypi, and the whole zoophyte retain its energy for several seasons." It would seem, therefore, that he noticed a change taking place in the dark body, and connected with it the appearance of a new polypide in the zoecium, and so far anticipated the observations of Smitt.

J. V. Thompson<sup>1</sup> noticed that the lower portion of the stomach (which he calls "the viscus") acquired a spherical shape, and opaque yellowish colour, and persisted after the death of the polypide in many of the Polyzoa; and he regarded the body thus formed as "most probably an ovum or ovarium."

Farre, in his well-known paper on the "Ciliobrachiata Polypi,"<sup>2</sup> gives an account of these bodies, and conjectures that they are probably connected with the process of reproduction, though whether they were to be regarded as ovaries or immature ova he was unable to determine. "From their dark colour," he says, "they are generally very conspicuous, especially as they remain in the cells long after the animal has perished and disappeared from them. From this circumstance it might be imagined that they resulted from decomposition, were they not also frequently seen in the living animal. Moreover, they have a definite form and size, and, when removed from the cell and carefully examined, are found to consist of a delicate transparent membrane, enclosing a brown granular matter, to which their colour is due." This observation is an important one.

In a paper on *Cellularia* (*Bugula*) *avicularia*,<sup>3</sup> Pallas, Nordmann has described the structure to which Smitt gives the name "germ-capsule," and rightly regards it as formed

<sup>1</sup> 'Zoological Researches and Illustrations,' 1830, art. v.

<sup>2</sup> 'Philosophical Transactions' for 1837, p. 400.

<sup>3</sup> 'Voyage dans la Russie Méridionale et la Crimée, exécuté en 1837, sous la direction de M. Anatole de Demidoff,' 1840, vol. iii, 702, note.

out of a portion of the body of the polypide, though he mistook its function, and considered it to be an egg.

Van Beneden<sup>1</sup> regards the "round, dark-coloured bodies" which he noticed in *Flustra foliacea* through the walls of the zoecia as eggs. He describes them as destitute of cilia, and quite motionless, and says that they are hatched in the deserted cells, for he had seen very young individuals in the old zoecia. From some of his figures we may, I think, infer that he had observed the development of a polypide from the "germ-capsule," though he misinterpreted the appearances that came under his notice.

In plate viii, fig. 4 *n*, a germ-capsule is represented in a zoecium of *Alcyonidium gelatinosum*, from which an elongate body, which is clearly a rudimentary polypide, is sprouting. The description explains that it is a "young polypide originating from a bud;" but the supposed "bud" is evidently one of the dark bodies which Van Beneden has elsewhere described as ova. It may also be remarked that the figure very fairly represents the general appearance of the polypide in course of development from the germ-capsule.

In plate vii, figs. 15 and 16 are described "as young polypes attached to the valves of the egg," but are really polypides budding from the germ-capsule, which Van Beneden, as we have seen, identified with the ovum.

Reid<sup>2</sup> describes a prolongation of the stomach below, which he regards as an "appendix" of the digestive sac, or a "separate organ." "Its inner surface," he says, "is so thickly covered with reddish-brown granules, or, more properly speaking, minute cells, as to be quite opaque." He remarks that this "appendix" is, in some cases, much larger in proportion to the stomach than in others. He also observed many bodies, "each composed of reddish-brown nucleated cells, enclosed in a membrane" amongst the broken-down zoecia, which he considers to be ova.

Dalyell<sup>3</sup> notices the "dark globular substance" which is found in many of the cells of *Bugula ciliata*, and figures the same body in *B. avicularis*. He speaks doubtfully of the opinion that it is the residuum of the body of the polypide, but has no special observations of his own to record.

In a paper on *Flustrella hispida*,<sup>4</sup> Dr. Redfern has suggested,<sup>1</sup> 'Recherches sur l'Anatomie, la Physiologie et l'Embryogenie des Bryozaires,' 1845, p. 58.

<sup>2</sup> "Anatom. and Physiol. Observations on some Zoophytes," *Annals Nat. Hist.*, xvi, 1845, p. 385.

<sup>3</sup> 'Rare and Remarkable Animals of Scotland,' vol. i, p. 240, 1847.

<sup>4</sup> 'Flustrella hispida and its Development,' *Quart. Journ. Mic. Sci.*, vol. vi, p. 96, 1858.

gested a new interpretation of the "dark bodies," by naming them "unciliated ova or statoblasts."

In 1861 I published a "Note on the Ovicells of the Cheilostomatous Polyzoa,"<sup>1</sup> in which the "germ-capsule" was regarded as an egg, but an egg of different character from those which I supposed to be produced in the ovicell. It was described as a non-ciliated ovum developed in the zoecium,<sup>2</sup> and only liberated after the death of the polypide. The view which I then entertained was that it might prove to be the equivalent of the statoblast of the *Phylactolamata*.

We come now to Smitt's observations on the "dark bodies," which were published in 1863 and 1865.<sup>3</sup> In his first paper, after an historical review of the literature of the subject, he gives the result of his investigation into the various modes of development by gemmation which prevail amongst the Polyzoa. Amongst these he places reproduction by the formation of a germ-capsule (grodtkapsel). In the following passage he explains his use of this term:—"As will appear from what follows, the 'dark bodies' in their composition and significance approach most nearly the egg-formation ('äggbildning'), which Allman, in the case of the freshwater Bryozoa, has named *statoblast*. As, however, the former not only serve as receptacles for eggs, which escape as embryos, but also, as will appear hereafter, contain within them buds for the formation of a new polypide in old cells from which the original polypides have disappeared, I shall employ in what follows the name 'grodtkapslar' (germ-capsules)." He then describes the germ-capsule as it occurs in various species, and points out that it originates from the digestive sac of the polypide, to which, indeed, it bears a striking resemblance in structure and appearance. He had seen one, definitely formed, which was still firmly attached to a portion of the stomach-walls. He had observed further (in *Acyonidium parasiticum*), that in old zoecia, the polypides of which had vanished, the germ-capsule was often to be seen attached to newly formed buds. The relation, however, between the two was not so intimate but that the buds, especially when advanced in development, often broke loose from the germ-capsule and lay free in the zoecium. In this case he did not succeed in establishing the connection of the bud from

<sup>1</sup> 'Quart. Journ. Mic. Sc.' for October, 1861.

<sup>2</sup> Nitsche and Claparède were quite right in supposing that at this time I mistook the germ-capsule for an ovum. I shall refer to this hereafter.

<sup>3</sup> "Bidrag till Kännedomen om Hafs Bryozoernas utveckling," 'Ups. Univ. Årsskrift,' 1863; "Om Hafs Bryozoernas utveckling och fettkroppar," 'Öfversigt af Kongl. Vet. Akad. Förh.,' 1865.

its origin with the germ-capsule and its derivation from the latter. In *Lepralia Pallasiana* he noticed one portion of the germ-capsule of a lighter colour than the rest, and at the extremity of this part a process of a light-grey colour and homogeneous granular substance was budding. In another case a bud was attached to the side of the light portion, furnished with a crown of rudimentary tentacles.

In his second paper (1865) Smitt has embodied the results of further observation, in addition to those already obtained, and has supplied illustrative figures, which are most of them, however, much too small to exhibit satisfactorily the structural details. I shall bring together here some of his observations on the different species that came under his notice, as I shall have to refer to them hereafter when I give the results of my own investigations.

In *Scrupocellaria scruposa* a dark mass was noticed in the older cells, at whose side a bud was placed, which had already the rudiments of tentacles.<sup>1</sup>

In *Bugula fastigiata* the germ-capsule exhibited the same character as in the last species, but the buds in this case were much more distant from it, and their relation to it was difficult to determine.

In a zoecium of *Flustra membranacea*, a germ-capsule was seen from which tentacles and the cavity of the alimentary canal had been developed by budding.

In *Eucratea chelata* a kidney-shaped germ-capsule was met with, light-coloured at one end, and at the other thickly covered with dark spots. The new parts arising from it (digestive canal, with the crown of tentacles and muscles) were already fully developed.

In a specimen of *Alcyonidium gelatinosum* a germ-capsule was found attached to the stomach-wall, and another of lighter colour lying near it; and from this Smitt infers that several germ-capsules may be developed successively from the walls of the stomach.

In *Membranipora unicornis*, a germ-capsule of an oval form was observed near a bud which exhibited twenty-four rudimentary tentacles.

In connection with the development of the germ-capsule Smitt describes a mass of oil-globules ("fettkroppsmassa") formed in a particular way, which constitutes a foundation for the production of the new parts.<sup>2</sup>

<sup>1</sup> "Vid hvars sida ligger en Knop, som nyst fått de första anlagen till tentakler," p. 23, plate v, fig. 1 g.

<sup>2</sup> The following is the passage referred to:—"Ett bland Bryozoernas egenomligaste reproduktions sätt är deras Groddkapselbildning, vid hvilken lika-

In 1870 the accomplished biologist, Edouard Claparède, whose early loss every student of science must deplore, published in Siebold and Kölliker's 'Zeitschrift' a paper on "The Anatomy and Development of the Marine Bryozoa,"<sup>1</sup> in which he reviewed Smitt's theory of the germ-capsule, and offered a very different interpretation of the facts on which he supposed it to be grounded. The "brown body" he regards as a secretion from the endocyst, and in nowise endowed with any reproductive function. The supposed buds which have been noticed in adult zooecia, and which he had himself examined, he considers to be the result of a "retrogressive metamorphosis" of the original polypides, which, under certain circumstances, shrink back into this rudimentary condition, passing through the same stages in their decline as in their progress towards maturity, but in an inverse order.

With reference to the first point it is sufficient to remark that the development of the germ-capsule from the body of the polypide has been conclusively established by direct observation, and is placed beyond a doubt; while the extraordinary theory invented to account for the presence of buds within the adult zooecia is not only unsupported by any analogy or positive evidence, but gratuitously creates a difficulty where none is presented by the actual facts. The bud from the endocyst in the adult zoecium (to which Claparède refers, and *not to the germ-capsule bud*) exactly resembles that in the forming zoecium on the margin of the polyzary, and has no doubt a similar history.

In 1871 Smitt's views were again subjected to criticism by Dr. Hinrich Nitsche.<sup>2</sup> He agrees with the Swedish zoologist in regarding the "brown bodies" as originating from the polypide, but denies that they have any reproductive function. He has found in them Diatomaceæ, sponge-spicules, thread-cells, &c., a fact which clearly proves that they once formed a part of the stomach of the polypide, and which is also fatal, as he thinks, to Smitt's view of their office. He contends that they never give origin to buds, as this observer affirms, and

ledes en fettkroppsmassa, om också på ett annat sätt upkommen, utgör grundlaget för de nya delarnes uppträdande." 'Om Hafs-bryozoenas utveckling,' p. 23.

<sup>1</sup> "Beiträge zur Anatomie und Entwicklungsgeschichte der Seebryozoen," 'Zeitschrift' for December, 1870, p. 147.

<sup>2</sup> "Some interesting points concerning the mode of reproduction of the Bryozoa," 'Quart. Journ. Mic. Soc.' for April, 1871.

"Beiträge zur Kenntniss der Bryozoen," ii Heft. 3. "Über die Anatomie u. Entwicklungsgeschichte von *Flustra membranacea*," 'Zeitschrift für wissensch. Zool.,' xxi Bd., 4 Heft.

have nothing to do with the appearance of fresh polypides in the adult zoecia. The buds which are frequently met with in zoecia from which the original tenant has disappeared, are a product of the endocyst and not of the "brown body;" but as they are commonly developed in close proximity to the latter they have been mistaken for a part of it, and hence the error of interpretation. As I shall point out hereafter the endocyst-bud is totally distinct from the germ-capsule-bud. Both are of common occurrence; Nitsche is correct in his account of the former, but has overlooked the latter.

In a paper in this Journal, already referred to, I have briefly replied to Nitsche's statements by detailing my observations on the formation and development of the germ-capsule which are confirmatory of Smitt's views. The latter has also published a short rejoinder,<sup>1</sup> in which he expresses his confidence in the results previously announced, and refers to my paper for corroborative evidence.

I may conclude this historical survey by mentioning that, in a paper<sup>2</sup> very recently published, Nitsche has recorded the occurrence of the germ-capsule in one of the freshwater Polyzoa (*Alcyonella*). He states that in a specimen which came under his observation the ovary and embryos occupied so fully the upper space in the zoecium that the polypide was pressed down, and, as it were, forced into a "retrogressive metamorphosis," which resulted in the formation of a "dark body."

It appears from this historical sketch (1) that the dark-coloured, more or less spherical bodies that occur in the zoecia of the Polyzoa have attracted very general attention; (2) that several of the earlier observers had determined their formation out of a portion of the body of the polypide; (3) that the definite structure which they exhibit had been noticed and accurately described by Farre; (4) that in one or two cases the connection of these bodies with the appearance of fresh polypides in adult zoecia had been surmised or imperfectly observed long before the doctrine of the germ-capsule was enunciated by Smitt.

I shall now proceed to describe the origin and development of the germ-capsule more fully than in my previous paper, and shall be able to render the details more intelligible by the aid of the accompanying figures (figs. 1—7.)

Every student of the Polyzoa must have noticed that the

<sup>1</sup> "Remarks on Dr. Nitsche's Researches on Bryozoa," 'Quart. Journ. Micr. Sci.' for July, 1872.

<sup>2</sup> "Betrachtungen über die Entwicklungsgesch. u. Morphologie der Bryozoen," 'Zeitschrift' for 1872, 4 Heft, p. 467.

life of the individual polypides is comparatively ephemeral. In most cases a large proportion of the zooecia are found to have lost their original tenants, while at the same time the polyzoary retains its full vitality, and along the margin fresh additions are constantly being made to it by the growth of new buds. Not uncommonly almost all the zooecia covering the lower or older portions of a tuft of *Bugula* or *Bicellaria*, for example, are thus emptied of their polypides; but towards the upper extremities of the branches all are occupied by an active population, and along the outer edge zooecia are to be seen in every stage of development. The disappearance of the polypide, however, is a comparatively unimportant incident in the life of the colony; and ample provision exists for securing new tenants for the deserted dwellings. The zooecium which has lost its polypide is, in time, filled by another, and may very possibly be the home of a succession of occupants.

The renewal of the polypides in the adult zooecia is effected in two ways—(1) by the formation of a germ-capsule, and (2) by gemmation from the endocyst or inner wall of the zooecium.

#### 1. RENEWAL OF THE POLYPIDE BY THE FORMATION OF A GERM-CAPSULE.

If we examine a specimen of one of the erect, plant-like Polyzoa, we shall find, as I have stated, along the upper edge of the branches zooecia in course of formation, and exhibiting every degree of development; immediately below these will be zooecia in which the polypides are fully formed, but immature; below these, again, will extend a zone, inhabited by adult polypides, in full vigour and activity; further down still we shall probably encounter dwellings for the most part destitute of tenants. Of course these divisions are not invariable, nor are they separated by any hard lines; but such is the general character of the polyzoarium. In most of the tenantless zooecia dark, more or less spherical bodies occur, which occupy somewhat different positions, but exhibit a definite and uniform structure. They are generally placed about the middle of the zooecium, and are commonly attached to the (so-called) funiculus, by which the polypide is connected with the base of its dwelling (fig 1 a). It is a mistake to speak of these bodies, at least in their normal and perfect condition, as lying free within the cavity of the zooecium; they occupy the same position as the lower portion of the digestive sac of the polypide, and, like it, are firmly attached to the funiculus. Immediately below the "dark

body," to which I shall apply Smitt's name ("germ-capsule"), and in contact with it, is a small oval body, of a pale gold colour, and minutely granular structure, which is included within the funiculus (fig. 5 c). In zooecia containing a polypide it occupies a similar position in relation to the base of the stomach. The germ-capsule is found at times separated from the funiculus, but in the species which I have most closely studied (belonging to the genera *Bicellaria* and *Bugula*) it usually occurred as I have described it; and I am inclined to believe that when detached it has lost the power of further development, and probably decays away. This, however, is a mere conjecture; it is not a little remarkable that in their *figures* neither Smitt nor Nitsche has clearly indicated the connexion of the germ-capsule with the funiculus.

The germ-capsule exhibits a very definite structure; it consists of a mass of granular matter inclosed in a delicate membrane, the inner surface of which is covered with spots of a rich, reddish-brown colour. It bears the closest resemblance, in general aspect and in colour, to the stomach of the polypide, the reddish spots at once reminding the observer of the hepatic cells of the latter. If direct proof were wanting, it would be difficult to avoid the conclusion that it has originated in some way or other from this portion of the polypide. This point, however, has been conclusively established. J. V. Thompson and Nordmann<sup>1</sup> have both described the survival of a portion of the digestive sac, after the disappearance of the rest of the polypide, as a dark spherical body, which they supposed to be an egg or ovary. Smitt has seen a germ-capsule attached to a piece of the stomach-walls. I have met with a polypide in an early stage of decay, having a fully formed germ-capsule at the base of its body. Nitsche has also observed the development of this structure from the polypide in *Flustra membranacea*.

Further, I have traced the course of its development in *Bicellaria* and *Bugula*. This is so fully described in my former paper in this Journal that I shall only briefly refer to it now in connection with the illustrative figures. The first

<sup>1</sup> "En soumettant à un examen microscopique soigneux un certain nombre de cellules de Polypes des espèces *Cellularia*, *Bowerbankia*, *Flustra*, *Eschara*, &c., on ne tardera pas à découvrir que, dans beaucoup de ces cellules, le Polype est déjà mort, qu'il ne reste plus une trace des tentacules, mais qu'une partie du corps du Polype (principalement la cavité digestive) s'est convertie en une masse ronde ou oblongue ayant des contours parfaitement arrêtés, et qui montrent, a ne pas pouvoir s'y méprendre, la forme et la nature d'un œuf." On *Cellularia avicularia*, in Demidoff's 'Voyage dans la Russie Meridionale,' vol. iii, p. 702, note.

step towards the formation of the germ-capsule is a slight constriction of the walls of the stomach at a certain point (fig. 7 *c, c*). This constriction increases, until at length the lower portion of the stomach assumes a somewhat globular shape, and hangs at the base of the body like a distinct organ, communication with the rest of the digestive system being maintained through a narrow channel (fig. 6 *a*). When the polypide loses its vitality and decays, this globular appendage survives as a separate structure, and remains, as I have described it, attached to the funiculus (fig. 2 *a*).

In its first stage, after separation from the polypide, the germ-capsule is more or less surrounded by a mass of pale yellow globules (fig. 1 *a*), the "fettkropfsmassa" of Smitt, which this author regards, if I rightly understand him, as discharging a nutritive function and contributing to its further growth. As development proceeds they disappear.

At this point I may remark that the whole aspect and history of the germ-capsule would naturally lead us to conclude, apart from the developmental changes which I am about to describe, that it is much more than "the mere remains of a decaying polypide." Its definite form and structure, its constant occurrence, its connexion with the funiculus, its persistency, all suggest that it must have some special part to play in the life-history of the Polyzoon.

The first change that seems to take place is an increase of size. This was noticed by Grant, as before mentioned.

In one of the zoecia, on a specimen of *Bugula*, I have met with a germ-capsule which had attained unusually large dimensions; it was oblong in form, and occupied a considerable portion of the cavity. This was, no doubt, abnormal; but some increase of size appears to precede the actual commencement of development. After a time a light space makes its appearance on the upper surface of the capsule (fig. 2 *x*), and at this point a small swelling or bud is subsequently developed, which is of a light greyish colour, while the lower portion of the capsule retains its rich deep red. This bud enlarges (fig. 3), and the germ-capsule assumes an oblong form, tapering very slightly upwards. In a short time the tentacles are distinguishable in the anterior portion of the bud (figs. 1 *a'*, and 5 *b'*), and below them the commencement of a pharynx and œsophagus, the lower and deeply coloured portion of the capsule occupying the place of the stomach.<sup>1</sup> As development proceeds the tentacles

<sup>1</sup> I am unable to describe more minutely the development of the various parts, as I have not examined the germ-capsule under compression. I can merely record the general appearance which it presented in different stages of growth.

lengthen, and the different portions of the alimentary canal are more distinctly defined, and, at last, a fully formed polypide fills the place of the one which has disappeared from the zoecium (fig. 4). *From the first the polypides thus developed from the germ-capsule are distinguished by the dark reddish-brown colour of the walls of the stomach, while those which bud from the endocyst, whether in the new or adult zoecia, do not exhibit this character until they have attained maturity.*

Nitsche considers that the "brown-bodies" arise in *Flustra membranacea* from the decay of the polypide, and are formed by a kind of encysting of the greater part of the products of this decay.<sup>1</sup> The observations which I have just detailed do not allow me to accept this statement as a correct expression of the facts. In *Bicellaria* and *Bugula*, at least, the germ-capsule (or "brown-body") consists of a portion of the stomach of the polypide that survives the rest of the organism as a separate structure.

In his criticism on Smitt's views the same able observer maintains, as we have seen, that certain buds, originating from the endocyst, which often occur in adult zoecia, had been mistaken for buds from the germ-capsule. When I first commented on this statement I had not seen these endocyst-buds, but my observations left no doubt on my mind that Smitt was substantially correct in his account. I have since, however, carefully examined them, and can now state that they differ essentially in general appearance as well as in position from the budding germ-capsules. It must be admitted, at the same time, that Smitt has given a handle to his critics; for I have satisfied myself that in several instances he has actually confounded the two bodies, and has thus been led to give a form to his statements which has naturally suggested doubts as to the accuracy of his observations. For example, in describing the "groddkapsel" of *Bugula fastigiata* and its development, he speaks of the bud as situated at some distance from it, and says that it was difficult to determine the relation between the two. On referring to his figure (pl. v, fig. 2) it is evident enough that the supposed bud from the germ-capsule is in reality one of the endocyst-buds described by Nitsche. So, again, in his account of *Scrupocellaria scruposa* he tells us that in one of the zoecia a bud with rudimentary tentacles was observed by the side of one of the "dark bodies." This would be a very incorrect description of the germ-capsule and its bud; and accordingly on reference to the

<sup>1</sup> Ueber die Anatom. u. Entwicklungsgesch. von *Flustra membranacea*, p. 86.

figure (pl. v, fig. 1) it appears that in this case also we have to do with an endocyst-bud, the characteristic appearance of which is very accurately given! Elsewhere (as in his account of *Alcyonidium parasiticum*) Smitt remarks that the buds are sometimes so slightly connected with the germ-capsule that they break loose from it, especially as they advance in development, and lie free in the zooecia. Hence Claparède represents him as teaching that the young polypide creeps out of the capsule and attaches itself near it! Nothing of the kind could possibly take place in the case of the germ-capsule, which is not a structure distinct from its bud, but organically one with it. It is clear that in this case Smitt has seen the development of the endocyst-bud into the polypide alongside the "groddkapsel."

These mistakes on the part of this distinguished observer have certainly given some show of reason to the strictures of Claparède and Nitsche, but, on the other hand, these writers have not assigned their due weight to the passages in which he has correctly and clearly described, or to the figures (*e. g.* pl. v, figs. 5, 17, 18, 19), in which he has represented the development of the germ-capsule into the polypide.

It is hardly necessary that I should refer at any length to the objections and arguments of Dr. Nitsche. If the observations now recorded are worth anything they conclusively establish the doctrine of the germ-capsule as I have stated it.

One point is much relied upon by Nitsche; he states that he has found in the interior of the brown bodies diatomaceæ, sponge-spicules, thread-cells, &c., evidently the remains of the polypide's last meal before its dissolution, and this fact he considers fatal to Smitt's theory. I have never observed anything of the kind; but inasmuch as the germ-capsule is a portion of the digestive sac, it is not at all improbable that it may occasionally retain portions of the food at the time of its separation from the polypide. But I fail to see how this should interfere with its further development. If, however, in such cases development be arrested, it is nevertheless true according to my observations, that in others it takes place.

Many points in the history of the germ-capsule remain to be determined. Not unfrequently the zooecia over a large portion of the polyzoary, are found to contain "dark bodies," a number of which show no signs whatever of growth, while others are already budding. It would be interesting to know under what conditions development takes place; and whether the germ-capsule discharges any other function than that which has just been described. Smitt asserts that it sometimes acts as an ovary, and that he has observed the

ova in the interior of one taken from *Alcyonidium mytili*, Dalyell. One is tempted to imagine that there may have been an error of observation in this case, but the point should be thoroughly investigated.

Both Grant and Farre noticed that occasionally two of the "dark bodies" were present in a single zoecium, and Smitt has confirmed the observation; but it remains to be determined how the second originates.

It may be remarked, in conclusion, that the germ-capsule cannot properly be brought into comparison with the statoblast, from which it differs essentially in its origin, structure, and function.

I pass on to notice very briefly the second mode in which the polypide is renewed in the adult zoecium.

## 2. RENEWAL OF THE POLYPIDE BY GEMMATION FROM THE ENDOCYST.

In adult zoecia, in which the polypides are already decaying, a bud is sometimes observed sprouting from the endocyst, in which the rudimentary crown of tentacles is soon traceable (figs. 8, 9), and which exactly resembles the polypide-bud of the newly formed zoecium on the margin of the polyzoary. It originates about the middle of one of the sides of the zoecium, and, no doubt, passes through the same course of development as the last named. I have met with such a bud in a zoecium containing a fully formed capsule,<sup>1</sup> and it is certainly not a little puzzling to find this double provision for the supply of a fresh tenant. What the precise relation may be between these two modes of reproduction, I cannot at present pretend to say; nor can I answer Claparède's query, "Wozu dann aber die Keimkapsel, wenn dieselbe so leicht entbehrlich ist?" But I have not the least doubt that the two modes exist, and that between them they keep up the succession of polypides so long as the life of the colony continues in vigour.<sup>2</sup>

## 3. REPRODUCTION BY OVA—THE OOECIUM.

The reproductive organs of the Polyzoa have been carefully studied, and the position of the ovary and testicle, the development of the ova, their fertilisation by the spermatozoa in the perigastric cavity, and their final conversion into cili-

<sup>1</sup> So far as my observation goes, the endocyst-buds are of rare occurrence as compared with the germ-capsules.

<sup>2</sup> Amongst the Hydroids we know that there may be a frequent fall and renewal of the polypides during the life of the zoophyte.

ated embryos, have been described by various writers. A question, however, has arisen respecting the precise function of the oecium (ovicell) with which the *Cheilostomata* generally are furnished. Huxley was the first to suggest that it is a kind of marsupium, with which the ova pass from the zoecium, and are there matured into ciliated embryos.<sup>1</sup> This theory was challenged by myself in a paper,<sup>2</sup> in which I supported the view previously taken by Reid, and endeavoured to show that the ova found in the oecia are produced there. The eggs which are developed within the zoecium I considered to be of a different kind; I supposed that they continue unciliated, and are only liberated at the death of the polypide. This paper has been recently criticised by Nitsche,<sup>3</sup> who adopts Huxley's opinion, and supports it by fresh observations. It is also referred to by Smitt, as affording confirmation of views at which he himself has arrived. Under these circumstances it seems desirable that I should state how far the opinions expressed in this paper have been modified by further observation. When it was written (1861) the true structure of the oecium had not been determined, and we were ignorant of the real significance of the germ-capsule. The latter I undoubtedly mistook for an ovum, distinct in kind from that contained in the oecium, and which I fancied might prove to be a sort of winter-egg. With respect to the marsupial theory, I now believe that the ova produced and fertilised in the zoecium are probably conveyed into the ovicell, and there complete their development, though I am still unable to understand how the transference is accomplished. At the same time I am by no means prepared to abandon the opinion that ova are in some cases developed within the oecium itself. The observations which I have recorded in my paper of 1861, and which are supported by those of Reid, previously published, have lost none of their force to my own mind. The later researches of Smitt have led him to adopt a similar view.<sup>4</sup> He has observed the

<sup>1</sup> "Note on the Reproductive Organs of the *Cheilostome Polyzoa*," 'Quart. Journ. Mic. Sci.,' vol. iv, p. 191.

<sup>2</sup> "Note on the Ovicells of the Cheilostomatous Polyzoa," 'Quart. Journ. Mic. Sci.,' vol. iv, p. 278, 1861.

<sup>3</sup> "Beobachtungen über die Entwicklungsgeschichte einiger Chilostomen Bryozoen," 'Zeitsch. f. Wissensch. Zool.,' xx Band, 1 Heft.

<sup>4</sup> Nitsche, in his criticism on my paper, has hardly given a fair account of Smitt's testimony. He says that Smitt has arrived at the same results as Huxley in the case of *Scrupocellaria scruposa*, and that he merely quotes the observations leading to a different conclusion made by myself on other species. On this passage Claparède has remarked, "This is a misrepresentation of the actual state of the case, inasmuch as Smitt fully confirms both Huxley's statements and those of Hincks."

asexual development of ova both within the zoecium and the oecium. In the ovicell of *Crisia eburnea* he has traced their formation by a kind of budding, and, in the absence of spermatozoa, their development into the embryo. In *Leprakia Peachii* and *L. Pallasiana* he describes the same mode of egg-formation as taking place within the zoecium. On this point Claparède has remarked that it is scarcely to be supposed that Smitt, to whom we owe such accurate observations on the male organs of many species, should have overlooked the spermatozoa, if present; and he adds, "It seems to me much more probable either that in the species observed the sexes are distinct, and that Hincks and Smitt were unacquainted with the male, or that Parthenogenesis has a place in the history of the Bryozoa."<sup>1</sup> More can hardly be said at present, but the subject is one of peculiar interest, and worthy of the special attention of students.

In connection with the development of the ova and their passage into the oecium the following observations may be worth recording. In a specimen of a species of *Bugula* ova were met with in considerable abundance, appearing as small spherical bodies of a rather bright yellow colour. Only one was observed in a zoecium, which usually lay at the very bottom of it, below the base of the polypide. Many of the zoecia were furnished with fully-formed ovicells containing yellow bodies, bearing a general resemblance to the ova, but usually of larger size; these did not contain eggs. On other zoecia the ovicell was only partially developed, or, if completed, was empty, and in these an ovum was very generally present. It was difficult to imagine in what way it could be conveyed, in the absence of cilia or other means of locomotion, from its position at the base of the zoecium to the marsupium at its summit. In a single instance I observed an egg in a different situation; it lay beside the polypide, at a very short distance below the top of the zoecium, and was affected by all its movements. When the polypide was expanded it was drawn upwards and retained between the œsophagus and the wall of the zoecium; when it was retracted, it was drawn slightly downwards. It seemed as if a vigorous movement might at any moment discharge it into the zoecium. I could only conjecture that perhaps after all the action of the polypide might be mainly instrumental in effecting the transference to the marsupium, though I am bound to say that, considering all the circumstances of the case, the agency seems hardly adequate to the work.

<sup>1</sup> "Beiträge zur Anatom. u. Entwicklungsgesch. der Seebryozoen," *Zeitschr. für Wissensch. Zool.*, xxi Band, 1 Heft, p. 165.

Amongst the *Ctenostomata*, which are destitute of ovicells, the egg is developed into the ciliated embryo within the zoecium, and is liberated after the disappearance of its tenant. In all probability the embryo is itself the cause of the death of the latter, for as it increases in size it occupies a large portion of the cavity, and the polypide is displaced and crushed down towards the bottom.

In *Vesicularia spinosa* I have observed an ovum in the upper part of a zoecium which was of a dark brown colour, and surrounded by a delicate envelope. Myriads of spermatozoa were swarming in the perigastric cavity, while the polypide was withdrawn to the very base of its dwelling. In other cases the ovum had attained a much larger size, occupying nearly two thirds of the cavity, and had acquired a fine rose colour. The polypide had either altogether or in great part disappeared. In other cases, again, the rose-coloured embryo was found in the empty zoecium, equipped with its cilia, and ready for escape.

The oecium, which is so prominent a feature of the Cheilostomata, exhibits, in certain genera at least, a somewhat complex structure, which has been admirably demonstrated by Nitsche<sup>1</sup> in the case of *Bicellaria ciliata*. In this species the opening of the helmet-shaped marsupium is closed by a sub-globular membranous capsule (fig. 10 *x*) which is attached by its base to the polyzoary immediately in front of it. Through this capsule passes obliquely a muscular band (fig. 10 *m*) which is attached to its inner surface above, and below to a point near its base, and by means of this muscle the capsule can be withdrawn from before the opening of the oecium, so as to permit the escape of the embryo (fig. 11 *x*). I have witnessed the action of the muscle, and the vigorous retraction of the capsular operculum, even when the ovum was as yet in a very rudimentary condition. The retractor is attached at the centre of the upper part of the capsule, and as it contracts the membranous wall is inverted, and the cavity above is proportionally enlarged. By this beautiful apparatus a sufficient space is provided for the embryo in all stages of its development, and its escape at last is secured without any injury to the structure of the oecium, which may probably serve as the nursery of several generations.<sup>2</sup>

<sup>1</sup> 'Zeitsch. für Wissensch. Zool.,' xx Band, 1 Heft, pp. 3, 4.

<sup>2</sup> Reid noticed that the membrane enclosing the ova in *Bugula avicularis*, when they were fully formed, contracted and relaxed at intervals, and conjectures that in this way the escape of the embryo was facilitated; but he did not observe the muscular band.

4. THE EMBRYO OF *PEDICELLINA ECHINATA*, Sars.

The embryo of *Pedicellina* has been studied more or less by Reid (in the paper already referred to), by Van Beneden,<sup>1</sup> and by Uljanin.<sup>2</sup> The reproductive organs have also been investigated by Nitsche, but he has not described the embryo. The observations of the last-named author, of Reid, and of Uljanin, were made on *Pedicellina echinata*, Sars, while the closely allied *P. belgica* was the form examined by Van Beneden.

I have lately had an opportunity of studying the embryo of the former of these two species, and as the results obtained, after careful observation, differ materially from those already recorded, I shall give them a place in this paper.

While examining some Devonshire dredgings my attention was attracted by a *Pedicellina* which bore two ciliated bodies within the tentacular ring, apparently attached to the lophophore. On examination they were found to be embryos in an advanced stage of development which had passed from the brood-chamber and taken up temporary quarters in the tentacular crater. The movements of the mantle and ciliary lobes, to be described hereafter, were distinctly visible. After a time they detached themselves and swam about freely in the surrounding water.

The body of the embryo (fig. 15) is turbinate, and is traversed by several transverse indentations or furrows. It widens upwards from the somewhat pointed lower extremity to the top, where it is encircled by a collar-like expansion clothed with vibratile cilia (fig. 15 *b*). This is formed by a sort of contractile mantle, which can be extended and folded over the anterior surface of the body and the organs which it carries, or thrown back so as to constitute a ciliated girdle, by means of which, in great part at least, the embryo is propelled through the water.

On the anterior surface of the body, in the space enclosed by the ciliated collar, is placed an organ, furnished with two opposite lobes; one of these is somewhat produced and pointed (fig. 15 *c*), and finely ciliated round the margin, and bears an orifice from which I have seen fæcal matter ejected, and which I take to be the mouth; the other is smaller, less elevated, rounded, and set with a number of long setiform

<sup>1</sup> "Recherches sur les Bryozoaires qui habitent la côte d'Ostend," *Mémoires de l'Acad. Roy. de Belgique*, t. xix, pp. 80-2, plate x.

<sup>2</sup> "Zur Anatomie und Entwicklungsgeschichte der *Pedicellina*," *Bulletin de la Soc. Impériale des Naturalistes de Moscou*, t. xlii (1869), pp. 435-8, plate vi.

processes, which, when in motion, wave rapidly to and fro, and lash the water with much vehemence (fig. 15 *d*).<sup>1</sup> These lobes are very movable and contractile; they are sometimes extended, sometimes altogether withdrawn, the mantle in this case folding over them and enveloping the whole of the oral surface of the body. At the lower extremity of the body there is a small projection (fig. 15 *e*) by which the embryo attaches itself at pleasure, and I think (though I cannot speak with certainty) I have seen cilia at this point. I was unable to determine the internal structure, owing to the opacity of the cuticular covering. The embryo was active in its movements, but often brought itself to anchor; it would also reverse the body and creep along on the ciliated lobes as on a foot (fig. 16). I met with individuals that had permanently attached themselves, but was not able to follow the later stages of development.

It seems to me probable, however, that the oral lobes disappear, and that the tentacles are developed within the margin of the mantle-like envelope, in which we may, perhaps, recognise the membranous cup that surrounds the base of the arms in the adult polypide. But this is purely conjectural.

In comparing the foregoing account with the descriptions already published of the *Pedicellina* embryo, many important discrepancies will be noticed. There is a general agreement between the observations of Reid and Van Beneden. Both describe the embryos which they examined as presenting a somewhat funnel-shaped body, with a circle of long cilia round the upper margin. The latter noticed one or two indentations (*échancrures*), which divided the body into an anterior and posterior half. As development proceeded he observed the formation of rudimentary tentacles within the margin of the funnel, the disappearance of the cilia, and the growth of a short pedicle.

I cannot harmonise this account with my own observations, and can only suppose that the embryo of *P. belgica* differs essentially from that of its congener.<sup>2</sup> Nitsche, who was only able to make a very imperfect examination of the embryo of *P. echinata*, in specimens preserved in spirit, was, nevertheless, of opinion that it was more highly organised than the form described by Van Beneden.<sup>3</sup>

<sup>1</sup> A similar structure is of common occurrence amongst the Polyzoa embryos.

<sup>2</sup> The species investigated by Reid, however, was *P. echinata*; and unless the embryo is liberated in very different stages of development, I cannot but suspect some error of observation in this case.

<sup>3</sup> "Ueber die Anatomie von *Pedicellina echinata*, Sars.," *Zeitsch. f. Wissensch. Zool.*, xx Band, 1 Heft, p. 28.

Coming now to Uljanin's observations (which, he tells us, were made under the direction of Prof. Rud. Leuckart), we find many points of agreement, but still very weighty differences. I should be inclined to distrust my own work if the circumstances under which my observations were made did not seem to preclude the chances of serious error. The escape of the embryos from the parent was witnessed, and their structure and habits were carefully noted. I was also able to sketch them in many attitudes and from various points of view.

Uljanin describes the embryo as consisting of a symmetrical, cuticular cup in which the true sac-like body remains quite free, except at its upper margin, by which it is attached to the rim of the cup.

This sac can be partially everted, as it always is when the embryo is in motion. In this state its inner wall, which is covered with cilia, is turned outwards and forms a collar-like "velum" by means of which the embryo propels itself. So far the two accounts show a certain amount of general agreement.

But Uljanin makes no mention of the ciliated lobes and oral aperture; while he does describe two "ganglion-like organs" placed near two orifices in the wall of the cup, one on its margin and the other at its base, which certainly escaped my notice. It must be left to future observers to clear up these differences; meanwhile, I may remark that, judging from analogy, the structures on the oral aspect of the body which I have described and figured, are very much what we should expect to meet with in the Polyzoan embryo.<sup>1</sup>

##### 5. THE COLONIAL NERVOUS SYSTEM.

The existence of a common nervous system amongst the Polyzoa, by which the zooids composing a colony are linked together and brought into relation, was first demonstrated by Fritz Müller; his view has been adopted and confirmed by Smitt and Claparède, and opposed by Reichert<sup>2</sup> and Nitsche. Müller only succeeded in detecting the supposed nervous structure in the Ctenostomata, but Smitt in the first place, and subsequently Claparède and myself, have proved its existence in the Cheilostomata. It is most readily observed in the

<sup>1</sup> Since the foregoing has been in type I have found some notes on the embryo of *P. echinata*, accompanied by drawings, which I made several years since, and which confirm in all points the later observations recorded in this paper.

<sup>2</sup> "Vergleichende anatom. Untersuchungen üb. *Zoobotryon pellucidus*, Ehrenberg," "Aus den Abhandl. d. Königl. Akad. d. Wissensch. zu Berlin," 1869.

former; in the stem of *Vesicularia*, *Valkeria*, *Serialaria*, &c., the nerve-trunk is very conspicuous, running along one side of it and terminating at the joints in distinct ganglia (fig. 14). In the neighbourhood of the zooecia it is sometimes overlaid by a complicated plexus of nerve-threads, from which filaments pass off to the ganglia that are situated at the base of each zooecium. This structure is beautifully displayed in a specimen of *Valkeria pustulosa* preserved in fluid, which I have in my possession, and my principal object at present is to direct attention to the figures which I have given of it (figs. 12, 13).

Near the base of the internode is a mass of nucleated cells (fig. 12 c), from which threads pass off in various directions. Towards their origin they consist sometimes of a single series of cells for a short distance, and afterwards assume the usual appearance of the nervous filament.<sup>1</sup> I suppose that this cellular structure forms a portion of the plexus, which overlies the main trunk and connects the various ganglia.

That Fritz Müller has assigned its true significance to this complicated system of cords and threads pervading the stem of the polyzoon, and penetrating into the several zooecia, I have little doubt. Its general appearance and arrangement naturally suggest this interpretation, which is not contradicted by histological research as far as it has been undertaken, and is supported by various independent considerations. The movements of the avicularia and vibracula, which are quite independent of the individual polypides, and continue after they have disappeared, seem to point to some common or central nervous agency as their source.

It has been observed by Smitt, Claparède, Lovén, and myself, that a branch from the (supposed) common nervous system passes to the base of each avicularium.

The same remark may be made of the simultaneous movements of the polypides of *Mimosella*, which I have noticed in the original account of this exquisite form, and to which Fritz Müller refers in his paper.<sup>2</sup> This author also cites the energetic movements of the peduncle of *Pedicellina*, which continue after the removal of the polypide itself, and commence when as yet it is a mere rudimentary bud, as further evidence to the same effect.

Perhaps the strongest point which has been urged against this view is, the alleged non-existence of the common nervous

<sup>1</sup> In *Serialaria* I find the supposed nerve-trunk to consist of a very delicate, transparent membranous wall enclosing a fine granular matter, each granule being made up of several minute bodies agglomerated together.

<sup>2</sup> 'Wiegmann's Archiv,' 1860, p. 311.

system amongst the *Phylactolamata*, as showing that it is not physiologically necessary to the colonial life (Nitsche).<sup>1</sup>

The whole subject demands a more exhaustive treatment than it has yet received, which I trust it may soon obtain at the hands of competent observers.

RESEARCHES on the CONNECTIVE TISSUE and VESSELS of the NERVES. By LOUIS RANVIER. (With Plate III.)

(Translated from 'Archives de Physiologie,' July, 1872, p. 427.)

THE nervous tubes, which are the essential elements of nerves, are united into distinct bundles. Some authors, comparing these bundles to the primitive bundles of muscles, have described them as primitive nerve-bundles. This is, however, an error, for if there is any elementary part in the nerve which can be compared to the primitive muscular bundle, it is certainly the nervous tube, a conclusion which follows from what has been said in a former memoir.

A nervous bundle is rather comparable to an entire muscle; in fact, the nervous bundles, like muscles, differ generally in their diameter, and also, like muscles, are invested with an aponeurotic membrane. There is, then, no propriety in giving the name of primitive bundles to the bundles of nerves, and we shall call them simply nervous bundles.

A considerable nerve may be formed, in part of its course, of a single nervous bundle, or else made up of several. Each bundle is surrounded by a special connective sheath, which gives it its individuality. When several bundles combine to form a nerve they are united together by loose connective tissue, containing blood-vessels and lymphatics. In the interior of each bundle the nervous tubes are also united by loose connective tissue, traversed by blood-vessels. In order to become acquainted with these preliminary notions it is

<sup>1</sup> "Dumortier mentions a peculiarity of *Lophopus*, which indicates the existence of a colonial nervous system, such as has been discovered by Fritz Müller in *Serialaria*. He remarked, in fact, the same phenomenon in *Lophopus crystallinus* which led Müller to begin his investigations, namely, that when the cœnoecium was touched all the polypides were alarmed, whereas when a single polypide was disturbed it alone retracted. I have examined with care all parts of the cœnoecium vaginable endocyst in other genera in order to find this colonial system, but without success." Hyatt, "Observat. on Polyzoa, Sub-order Phylactolamata." From 'Proc. Essex Institute,' vols. iv and v, 1866-8, pp. 46-7.