XXXIV.—THE DEVELOPMENT OF THE OYSTER (OSTREA EDULIS L.).*

By Dr. R. HORST.

I.—HISTORICAL.

More has been written on the history of the development of the oyster than on that of any other invertebrate. The cause of this doubtless is the circumstance that from time immemorial the oyster has been considered a great delicacy, and that therefore attention was early directed to its development.

Brach [1] (1690) seems to have been the first to use the microscope in observing the embryo of the oyster. According to this author, the oysters found in the Venetian waters produce spawn towards the end of spring, during the entire summer, and in the beginning of autumn, which spawn they discharge into the water. During this time the central round and fleshy part of the oyster diminishes in volume and loses its succulence, while the branchia and the edge of the mantle assume a harder and more solid appearance. The liquid seen in the shell round the body in the beginning looks whitish, clear, and fluid, but later changes to a blackish mass having the consistency of pap.

When this mass is examined under the microscope, one finds in it eggs in two different stages of development: (1) Some entirely white, not altogether spherical, and resembling pellets; these eggs are quiescent and consequently less developed; (2) Others which are also white and round, but a little more compressed; they have the form of a grown oyster and show a black line in the place where the little valves will open. These last-mentioned eggs, moreover, move about and maintain a spiral motion in the mother shell. This continues until the eggs are more developed (*usque ad perfectiorem animationis gradum*). Later the oyster closes its shell, so that the water from the outside cannot penetrate into it, and the mother oyster becomes very lean, because she has to feed her offspring. During this time the young oysters gradually

* "*De Ontwikkelingsgeschiedenis van de Oester.*" From *Tijdschrift der Nederlandsche Dierkundige Vereeniging*. Supplement No. 1, Leyden, 1883–84. Translated from the Dutch by HERMAN JACOBSON.

[1] D. Jac. Brachii: *Observ. CCIII, De ovis Ostreorum. Ephemer. Acad. Leop. Nat. Cur.*, Ann. VIII, 1690, p. 506.

assume the form of the grown oyster, and become of a black color. Either owing to the lack of water, or because they need no movement for their further development, they remain quiescent in the shell until they are ejected by the mother oyster, and then they adhere to various objects, such as wood, mud, stones, &c.

Leeuwenhoek[2] (1695) seems to have known and observed the eggs of the oyster independently of Brach. From a letter dated the 18th day of the calends of September, we learn that an oyster opened on August 4th was found filled with an enormous number of young oysters, which moved about rapidly in the water by means of the small organs which projected from their shells and which they drew in when they died (*velum auct.*). They resembled the grown oyster as much as one egg resembles the other, but they were so small that, according to Leeuwenhoek's calculation, it would take 1,728,000 to make a ball one inch in diameter. Leeuwenhoek seems also to have observed younger stages of development; at least in a later letter (dated the 15th day of the calends of September) he states that he found in some oysters a number of small unborn young, which were much less developed than those which he had previously observed, and which he could not be sure were alive.

Two years later he wrote to the Royal Society of London[3] that one day, when eating oysters at the house of a relative at Rotterdam, he found one which was partly filled with a gray mucus. As he was in doubt whether this mucus contained oyster eggs, he took some home and examined it under a microscope, when he found that his supposition was correct, as this apparent mucus was entirely composed of young oysters.

Baster[4] (1759) added but little to the above observations. He does not agree with Leeuwenhoek and others who say that the sexes are separated among the oysters. He thinks that the oyster is a genuine hermaphrodite, because it cannot move about at will and consequently cannot approach the female for the purpose of impregnation.

Home[5] (1826) says but little of the spawn of the oyster, and what he says is not very accurate, much less so, in fact, than the statements of persons who had preceded him, and whom he does not even quote in his work. He says that about the end of June the eggs issue from the ovaries, and that towards the end of July none are found either in the ovaries or in the oviducts; that the moment the egg leaves the oviduct a kind of purplish mucus is secreted, which probably serves as nourishment to the oyster during its stay in the cavity of the mantle. Once in that cavity, the eggs often fall a prey to little aquatic worms which slip into the shell. His paper is accompanied by several figures of the brood of the oyster.

---

[2] A. van Leeuwenhoek: *Arcana Naturæ*. Opera, T. II, Epist. 92 and 94.

[3] Philosophical Transactions, vol. xix, 1698, p. 798.

[4] Job Baster: *Natuurk. Uitspanningen*, 1759, p. 73.

[5] On the mode of breeding in the oyster. Phios. Transact., 1827, p. 39, Plates II and IV.

Lovén[6] (1848) cannot be passed by in silence, for his exhaustive researches on the development of the *Modiolaria*, *Cardium*, *Montacuta*, and *Mytilus* serve as the basis of our knowledge of the embryology of the Lamellibranchiata. Although he has not observed the development of the oyster, nor that of any other form of the group *Monomyaria*, he has studied the representatives of widely different families of the *Dimyaria*, and the results of his researches have, therefore, a wide scope. He describes in succession the expulsion of the polar globule, the cleavage, the inclusion of the vegetative by the animal pole, the formation of the velum, the origin of the shell, the origin and differentiation of the intestinal canal, &c.

Davaine[7] (1852) is the first who gave a detailed description of the development of the oyster. According to him, the period during which the oyster contains spawn extends from the beginning of June till the end of September. He also observed spawn in the beginning of May; but this must be attributed to the higher temperature of the shallow basins where he observed it. After having directed attention to the difficulties encountered in studying the development of the oyster, caused by the circumstance that the eggs are retained in the cavity of the mantle, whence they cannot be removed without bringing their development to a standstill and causing their death, he describes the changes observed in the egg before it begins to segment. Sometimes the germinative vesicle is missing altogether, while in others another smaller vesicle is found attached to the germinative vesicle. Sometimes there is a germinative vesicle half the usual size, while at other times there are two of the same size, but only half the size of the ordinary vesicle. (This description leads us to believe that Davaine had at that period observed in the egg of the oyster some of the phenomena of fecundation made known to us at the present day through the researches of Hertwig, Selenka, Fol, and others.)

The first stage of segmentation which was observed consisted in the formation of four *blastomeres*. These are of different sizes, and generally three small segments are found adherent to a larger one. These segments, or cells, divide several times, diminish in volume, but increase in number, so that finally the egg contains nothing but small cells. Finally, the egg which had been round becomes heart-shaped. The incision which gives this last-mentioned form to the egg soon disappears, and at two points of the outline vibratile cilia begin to appear. Opposite these groups of vibratile cilia there appeared on the edge of the egg a transparent streak. This is the beginning of the hinge of the valves. During the following period the vibratile cilia become longer and more distinct, and a crown of them is formed, which indicates the

[6] S. Lovén: *Bidrag till Kännedomen om utvecklingen af Mollusca Acephala Lamellibranchiata. K. Vetensk. Akad. Handlgr.*, 1848.

[7] C. Davaine: *Recherches sur la génération des huîtres*, with 2 pl., in *Comptes Rendus et Mém. de la Soc. de Biologie*, vol. iv, 1852, p. 297.

front part of the body, while opposite (therefore at the posterior part) the hinge is found. The central mass becomes more clearly defined, and is separated from the ectoderm by a certain space. Later, the two valves of the shell become visible round the hind part of the body. The central mass is divided into two parts, one of which, of a darker color, perhaps corresponds to the liver, while the other, which begins to exhibit dilating and contracting movements, becomes the intestinal canal. The shell of these embryos is already composed of a calcareous substance.

While the embryo continues to grow the ciliary apparatus increases in dimensions, so that it seems to form, so to speak, a separate organ from the rest of the body, by means of which the embryo can swim in any direction. Gradually the basis of the ciliary apparatus decreases in size, so that finally it is attached to the body only by a thin stem, which breaks in due time. The ciliary apparatus which thus becomes detached has the shape of a round cushion, having in the center an opening which corresponds to the mouth aperture. The digestive canal assumes the shape of a retort, inclosing the liver in its concave part; the wide part of the retort forms the stomach, and the narrow part the intestines, which, owing to their general development, elongate and form a loop, which is plainly visible. Davaine was not able to observe with any degree of certainty either the mouth or the anus or the organs of sight and hearing. The appearance of the branchia is indicated by a very distinct vibratile movement on the side of the body. At the same time there was observed below the mouth aperture a small pear-shaped and transparent organ, the rapid pulsations of which show that it is the heart. The embryos probably remain in the mantle cavity of the mother oyster more than a month. Their number in a good-sized oyster has been estimated at 1,125,000.

De Lacaze-Duthiers[8] (1854), who, after Davaine, had occupied himself during two summers with the study of the development of the oyster, has in several respects continued and completed the observations of his predecessor.

1. The oyster is a hermaphrodite. Fecundation takes place in the efferent canals of the genital gland, and segmentation commences immediately after the eggs have been set free. The egg is generally divided into four, sometimes two, and rarely three segmentation spheres. From these first four spheres there are formed, as it were by a budding process, small transparent hyaline spherules, which increase so as soon to cover entirely the dark and granular spheres forming the vitellus, so much so that soon there can be distinguished in the egg a peripheral and a central portion; the embryo then becomes heart-shaped; at the depression which corresponds to the dorsal part there

---

[8] H. De Lacaze-Duthiers: *Mémoire sur le développement des Acéphales Lamellibranches* (Ostrea) in *Comptes Rendus de l'Ac. de Sc. Paris*, vol. xxxix, p. 103. Also *Nouvelles observations sur le développement des huîtres*, same work, p. 1197.

appear two tufts of vibratile cilia. Finally, the shell is formed from two thickenings of the epiblast, resembling a pair of watch-crystals of great transparency, attached on each side to the dorsal depression. The two halves in growing approach each other, finally join, and form the hinge. This, therefore, is not the first to appear.

The central and opaque part of the embryo is then detached from the peripheral part, first at the dorsal side and finally at the ventral side, except in two places, namely, the places occupied by the mouth and by the anus. At this latter point the central part is again joined to the peripheric layer, or epiblast, by a cylindrical stem, which elongates and finally is transformed into the intestines. The stomach is formed in the upper portion of the central mass, and the liver in the lower portion. Two groups of vibratile cilia encircle the pole opposite the shell like a wreath, which is the beginning of the trochal disk, and in the center of which the mouth forms. The intestine and the stomach form a distinct cavity, which is lined with ciliated epithelium. Soon the shell has grown so large that it incloses the entire body; in front of the anus there is found an appendage resembling a rudimentary foot. Although the trochal disk principally serves as an organ of locomotion, it has also something to do with respiration, and probably also with the taking of food. Even in the more developed larvæ neither branchia nor heart could be observed, nor any movement of the trochal disk, as stated by Davaine.

2. He succeeded once in keeping the larvæ alive, outside the mother shell, for thirty, and at another time for forty-three days. In order to follow the development of the intestines, the larvæ were fed on different colored substances. The mouth seems to be placed between the trochal disk and the foot-shaped appendage in front of the anus; it is a long funnel lined with vibratile cilia, the upper lip being formed by the disk itself, and the lower lip by the appendage in question. A tubular organ which is found in the center of the trochal disk has, in less developed larvæ, been mistaken for the mouth. The stomach is narrower in the middle, in the place where the intestines are attached. The intestines, forming a loop, turn toward the left side of the stomach. Then the lobes of the liver become hollow, and the characteristic granules commence to show themselves in the parenchyma. The streaks of fibrous appearance change to bundles of muscles, and attach themselves to the trochal disk, which they force back into the shell. He has never seen the trochal disk, or velum, detach itself spontaneously, but it sometimes happens that the shell in closing abruptly either cuts it off wholly or in part. The hinge of the shell is provided with teeth, as in young mussels. Finally, the otoliths also make their appearance in the form of vesicles which inclose granules, agitated by a very lively movement and placed under the mouth at the base of the lower labium or lip.

Coste[9] (1861), the zealous advocate of fish-culture in France, describes

---

[9] *Voyage d'exploration sur le littoral de la France et de l'Italie*, 2d ed., 1861, p. 93.

the appearance of the embryos of the oyster when seen through the microscope, and he gives some tolerably exact illustrations of them. As it is possible to keep these larvæ alive, outside of the mother shell, for several days, he thinks that this may become an important industry.

De la Blanchère[10] (1866) reports almost exactly the same as Davaine and Coste. He also gives four good drawings showing larves of the oyster, in which he shows the longitudinal muscles and the dorsal and ventral muscles which cause the velum to be drawn back into the shell. He says that, according to the observations of Mr. Gerbe, when the larve of the oyster becomes properly defined, the velum dies, as the branchiæ develop, so that it is probable that they have their origin in this organ.

Gwyn Jeffreys[11] (1869) observed the spawn of oysters when he examined an oyster fishery in the river Roach in Essex. He compares the larvæ to the grains of seed of the shepherd's-pouch. He says that the body can be seen through the transparent shell; the central portion is opaque, almost black, and probably represents the liver. The front part only is provided with vibratile cilia.

Saunders[12] (1873) exhibited, at the session of July 10 of the East Kent Natural History Society, live larvæ of oysters, and stated that they have a small shell, the two valves of which are convex, while in the grown oyster one is convex and the other flat.

Salensky[13] (1874) gives in his *Bemerkungen über Haeckels Gastræa theorie* good illustrations of the three different phases of the development of the oyster larvæ. These illustrations serve as an example of the development of the lamellibranchiates, which, according to him, have no alimentary organ. The embryo is originally composed of two layers without an internal cavity, and the intestinal cavity only makes its appearance later in the endoderm.

Möbius (1877), in his charming little work, *Die Auster und die Austernwirthschaft*, gives some illustrations of the first stages of the development of the *Ostrea edulis*. He also gives a very accurate drawing of the larva (with the adductor muscle); by mistake, however, this figure is reversed, so that the velum is placed below. He found that the young oysters leave the mother when they have reached the size of 0.15 to 0.18 millimeter.

We must finally mention some reports regarding two other species, namely, the American oyster (*Ostrea virginiana*) and the Portuguese oyster (*Ostrea angulata*).

According to Brooks[14] the American oyster (*Ostrea virginiana* List),

[10] H. de la Blanchère: *Industrie des Eaux*, 1866, p. 69.

[11] British Conchology, vol. v, 1869, Supplement, p. 165.

[12] Quart. Jour. Microsc. Science, vol. xiii, 1873, p. 493.

[13] *Archiv für Naturgeschichte*, 1874, p. 150, Plate V, Figs. 1, 2, and 3.

[14] Studies from the Biological Laboratory of Johns Hopkins University, No. 4, Baltimore, 1880, plates I–X.

is unisexual; its eggs are fecundated and develop outside the mother oyster. The progress of segmentation depends a good deal on the temperature and other circumstances. In some cases the embryo, provided with vibratile cilia, is formed two hours after fecundation; but the ordinary duration of the process is not less than twenty-four hours, and may even extend over more than two days. At the beginning of segmentation the egg assumes an oval shape, the thick end becomes the animal pole (formative, Brooks), and the small end the vegetative pole (nutritive, Brooks). This latter corresponds to the dorsal side of the embryo. During violent movements of the vitellus the first polar globule issues from it. There does not seem to be any segmentation cavity such as is observed in the eggs of other mollusks. After repeated segmentations of the animal spheres, whose number is still further increased by other spheres, originating in the vegetative part, a layer of ectoderm cells is formed which covers the vegetative sphere, and as it grows larger completely envelops it. The vegetative sphere is first divided into two entodermic cells, whose number afterwards increases to six and more. The embryo is flattened out, and the ectoderm and entoderm become detached from each other. Finally, the entoderm is invaginated, so that in form it resembles a shallow cup with a shallow gastric cavity. The embryo now undergoes an important change; a crown of vibratile cilia is formed, and in the dorsal part, transversely to the great axis of the body, a depression begins to appear which represents the blastopore. This finally closes, and the entoderm, a mass of cells, is inclosed in the peritoneal cavity. But prior to this there appears, at each extremity of the depression of the blastopore, a small irregular transparent body; these are the two valves. A couple of hours later, the embryo has considerably increased in size, and there may be seen forming in the entoderm a cavity which is lined with a vibratile epithelium. This cavity communicates with the outside by an aperture which is almost opposite the shell, so that small molecules can enter. The edges of the aperture may turn toward the outside and thus act as a suction apparatus. Meanwhile the shell has assumed a regular shape, and has grown so much that it covers nearly half the surface of the body. Soon a second aperture appears, through which the intestines communicate with the outside; this is the anus; while the stomach now becomes pear-shaped. Its larger part is turned forward, and on the fourth or fifth day a diverticle appears on each side of the stomach; these are the two halves of the liver, in the sides of which small globules of oil may be seen which strongly refract the light.

The study of the development of the American oyster, therefore, teaches us these four things:

1. That there is a gastrular stage caused by invagination.

2. That the blastopore closes, and that the anus and the latter do not coincide.

3. That the shell appears at a point originally occupied by the blastopore.

4. That a first and then a second opening is formed connecting the mesenteron with the exterior almost opposite the place where the blastopore is found; and that one of these openings becomes the mouth and the other the anus.

Winslow[15] (1881), while on board the American vessel Saratoga, during the summer of 1880, observed the development of an oyster from the Bay of Cadiz, which he took to be the common oyster (*Ostrea edulis*). but which, as Dr. Hoek has already remarked, was probably the Portuguese oyster (*Ostrea angulata*). As Mr. Winslow did not discover any embryos in the shell, he attempted artificial fecundation and was entirely successful. After five hours the eggs had produced well developed larvæ, provided with a velum, a shell, and a mesenteron, all of which could be plainly distinguished. The manner in which the development took place resembled very much that of the *Ostrea virginiana*.

Bouchon-Brandely[16] (1882) has studied the mode of propagation of the Portuguese oyster (*Ostrea angulata*) which at present is acclimatized at the mouth of the Gironde. This oyster is unisexual; its eggs develop outside of the mother, and may, therefore, be cultivated in sea-water. He believes if experiments made in this respect with the *Ostrea edulis* did not succeed, this is caused by the considerable quantity of albumen which the liquid of the mantle cavity contains, in which the larvæ of this oyster develop. According to Bouchon-Brandely, this essential difference in the organization of these two species makes all attempts at cross-breeding absolutely impossible, and thereby also excludes the possibility of a bastard form which some oyster cultivators say exists. Experiments made in this respect have proved entire failures. The fecundation of the *Ostrea angulata*, on the other hand, has proved successful. The eggs and the spermatozoa, when in water, preserve their vitality for several hours. Excellent results were obtained by using the sexual products taken two or three hours previous from the genital organs. The embryos began to move, according to the temperature, in from 7 to 12 hours after fecundation. The shell formed about the sixth or seventh day.

Finally, Ryder[17] (1883) speaks of the mode of fixation of the larvæ of the American oyster. Assisted by Col. Marshall McDonald, he succeeded in obtaining larvæ of the eggs of the *Ostrea virginiana* artificially fecundated. These larvæ, after twenty-four hours, adhered to the sides

---

[15] An account of an experiment in artificially fertilizing the ova of the European oyster (*Ostrea edulis*). Report of Ferguson, commissioner of fisheries of Maryland, 1881.

[16] *De la sexualité chez l'huître ordinaire* (*O. edulis*) *et chez l'huître portugaise* (*O. angulata*). *Comptes Rendus*, &c., vol. xcv, p. 256.

[17] On the mode of fixation of the fry of the oyster. Bulletin of the U. S. Fish Commission, vol. ii, 1882, p. 383.

of the glass vessels in which they were. They became so firmly fixed that a strong current of water could not detach them. He could not discover with any degree of certainty in what manner they were attached; but, although he admits the possibility of the existence of a filamentous byssus, he supposes that the fixation takes place by means of the edge of the mantle which protrudes from the shell; because he has often seen the larva resting on its side, and the edge of the mantle protruding from the valves. Before the larval period comes to an end the straight line of the hinge disappears more or less as the shell grows. When the larva has become fixed, new layers of shelly matter are deposited round the edges, presenting a prismatic structure. During this growth the hinge end is slightly lifted up, so that it is clear that shell matter is deposited along the edge. The lower valve is so firmly attached to the collector by the organic matrix of the shell (the conchyoline) that it cannot be torn from it without breaking it.

II.—Personal Researches.

These observations were made during the summers of 1881 and 1883, at our branch station of Wemeldinge,[18] where I received all the assistance that could possibly be rendered from Messrs. Zocher and De Leeuw. The parks found in the neighborhood, in which the larvæ of the oyster were allowed to affix themselves, proved very useful for my researches. The study of the development of the oyster is beset with difficulties, which has led Professor De Lacaze-Duthiers to say with good reason that "the oyster is certainly one of the species of the group of the acephalous lamellibranchiata, the study of whose organization and development is exceedingly difficult."[19] With most of the lower grades of animals the sexes are separated, and the sexual products, when mature, are ejected; consequently fecundation takes place outside of the body. It is entirely different with the oyster. Not only do its embryos pass the first stages of their development in the mantle cavity of the mother oyster, and fecundation takes place inside and not outside, but the eggs and the spermatozoa probably meet in the excretory canals of the sexual gland. If one wishes to observe the first changes of the fecundated egg, this cannot be done, as with most of the lower grades of animals, by artificial fecundation; but one is obliged to open a certain number of oysters containing eggs. If one opens a mother oyster in the ordinary manner—that is, by cutting the adductor muscle of the shell—it soon dies, and the normal development of its offspring is consequently disturbed. Embryos separated from the mother oyster may be preserved alive in an aquarium, but they either soon become sick or their development stops entirely. Thus Professor De Lacaze-

[18] See the Sixth Annual of the Zoological Station.

[19] *Mémoire sur le développement des Acephales lamellibranches.* In *Compt. Rend.*, Paris, vol. xxxix, p. 1197.

Duthiers says that his oyster larvæ lived for more than a month in aquariums, but he could not observe any important changes in their organization, which certainly does not indicate a normal condition. I once succeeded in observing the development of oyster larvæ for a couple of hours, by making a small opening in the edge of the shell, which hurt the animal scarcely at all. I was thus enabled to introduce a small pipette into the mantle cavity and remove the larvæ, but this lasted only a short time, because with each operation so many embryos were removed that all were soon taken. It is, therefore, not possible to procure a continuous series of the different phases of the development. In addition there is another difficulty, namely, that one cannot always recognize the mother oysters from the outside. The relaxation of the adductor, and consequently the less firm closing of the valves, is a pretty sure indication that the oyster contains embryos; but this phenomenon is more marked in those oysters which contain more highly developed embryos, which are on the point of being ejected from the shell. For this reason I have often perceived more mother oysters containing advanced embryos than those which contained young embryos. And for this reason likewise the first stages of the segmentation of the egg have to a great extent remained unknown to me.

C. Davaine[20] and Professor Möbius[21] have, however, given illustrations and descriptions of some of the early phases of the segmentation of the egg of the oyster. It is there seen that after the polar globules have been ejected (Fig. 2), the egg divides, like those of other lamellibranchiata,[22] into two spheres; the smaller, the animal, and the larger, the vegetative sphere (Fig. 3). This stage is followed by another, during which the egg is composed of four spherules, three smaller than the animal pole, resting on a large vegetative spherule (Fig. 4). By repeated segmentation of the animal spheres, and the formation of smaller spheres, originating by budding from the vegetative sphere, there is formed on the animal pole a layer of small cells which gradually envelop more and more the vegetative sphere, without, however, inclosing it entirely (Fig. 5). Then the vegetative sphere also begins to divide, first into two large segments (Fig. 6), later into several cylindrical cells. Thus two layers are formed, one of which will develop into the ectoderm and the other into the entoderm (and into the mesoderm ?). At the same time the embryo loses its spherical form and, owing to a depression on the lower side, becomes slightly reniform (Fig. 7, where, however, the lower part is turned upside down). If one observes an optic section of a more advanced stage (Fig. 8), one sees that the layer of entodermic cells has a slight depression and that a genuine gastrula has been formed. There can, however, be no question of a genuine invagination, because there

---

[20] See his work already referred to, p. 34, Plate II.

[21] See his work already referred to, p. 16.

[22] The *Pisidium* seems to form an exception. Ray Lankester: Contributions to the develop. history of the Mollusca, in Phil. Transact., vol. 165, 1876.

is no cavity of segmentation; we have here, so to say, an intermediate form between an embolic gastrula and an epibolic gastrula. This latter form seems, moreover, to occur with other marine lamellibranchiata. Rabl[23] and others have also shown that these two types of the gastrula, so different in appearance, are connected together by a series of intermediate forms, and may be accounted for by the same process. The embryo of the oyster during this phase presents a remarkable phenomenon, namely, that there is not only an invagination at the vegetative pole, but also a very distinct depression at the other pole, a little below the dorsal side. When seen from the side, this depression of the embryo is noticed at once (Fig. 9, *sk*), and an imaginary line (drawn as shown in Fig. 8) shows at once that it is due to a slight invagination of the ectodermic cells. During the further development (Figs. 10 and 12) there is formed a small depression, composed of high cylindrical cells, with a narrow opening; the bottom of this depression is turned toward the dorsal pole of the embryo, while the opening is found across the large axis of the embryo. This little pouch is certainly nothing else but the preconchylian gland, as is shown by observations of more advanced stages. The opinion of Fol,[24] that in the oyster the preconchylian gland is not an invagination properly so-called, but only an ectodermal enlargement, is therefore not correct, and rests probably on observations of more advanced larvæ, in which, as in other mollusks with an outer shell, the invagination gradually disappears. This organ was first discovered by Mr. Ray Lankester in the *Pisidium* and several gasteropods;[25] later Mr. Hatschek discovered it in *Teredo*.[26] If one compares these two species with *Ostrea edulis*, it will be found that the preconchylian gland appears very early in the embryonic life of the latter. The first naturalists who have studied the history of the development of the oyster, Messrs. Davaine and De Lacaze-Duthiers, speak of an "*échancrure*" and of a "depression," which gives to the embryo a shape resembling a heart. They seem, therefore, to have known of this invagination, although they did not discover its true significance. According to the researches of Brooks, the embryo of the *Ostrea virginiana* shows also in its dorsal part a depression, which, however, according to his statement, contains the opening of the primitive intestinal canal—the blastopore. If one, however, compares Fig. 32 of his work with my Figs. 9, 10, and 12, I believe that it must be admitted as highly probable, that what Brooks has taken for the blastopore is nothing but the opening of the preconchylian gland. This view seems also to be confirmed by what he says of the origin of the shell, which actually begins to develop at the very point where the supposed blastopore is found. An

---

[23] *Entwicklung der Tellerschnecke.* Morpholog. Jahrbuch, vol. v, p. 601.

[24] *Études sur le développement des Mollusques. Archiv. de Zoologie Expérim.*, vol. iv, p. 186.

[25] See his work quoted above, p. 6.

[26] *Ueber die Entwicklungsgeschichte von Teredo.* Arb. Zool. Inst., Vienna, vol. iii.

analogous development of the shell in the lamellibranchiates has, so far, only been discovered by Mr. Rabl[27] in the *Unio*, and is so utterly different from the observations relative to the development of other mollusks that competent authorities have already demanded a full verification of the facts.

To return to the embryo represented in Fig. 10, we find that the entodermal area, which in a previous stage showed only a slight depression, has become a deep invagination with a tubular cavity, a genuine *protogastrea*. Behind the mouth there are found a couple of large cells, which may probably be considered as the first cells of the mesoderm, although the manner in which they originate, and the subsequent development of the mesoderm, have escaped my observation. However this may be, one finds in the embryo on the following day (Fig. 12) mesodermic cells on the upper portion of the intestinal mass. The portion on the ventral side, located below the mouth, now begins to protrude very strongly, so as to form a sort of foot which causes the embryo to resemble a young gasteropod. The blastopore continues to be very distinct, and presents a somewhat triangular form. As far as I could ascertain, it did not disappear, but remains and is transformed into the mouth or rather into the cardia. For in the same way as in embryos where the blastopore closes, the esophagus and the mouth are formed by an invagination of the ectoderm; thus in embryos where the blastopore remains, there are ectodermic cells which take a part in the formation of the upper portion of the intestinal canal.

Great changes, both internal and external, take place during the further growth of the embryo; the preconchylian gland gradually loses its primitive character of a glandular invagination, and it reassumes its primitive character and forms a thickening of the ectoderm, composed of long conical cells (Fig. 13, *sk*). A thin cuticular membrane (*s*), produced by secretion from these cells, is the first indication of the shell. As at this point the hinge is found in the grown oyster, the description of Davaine, "a transparent streak * * * this is the first indication of the hinge," is perfectly correct. The bivalve shell of the oyster, therefore, originates in a single piece, and contrary to the observations of De Lacaze-Duthiers, according to which the two valves are produced "by two thickenings of the epiblast," which are supposed afterwards to unite and form the hinge. Brooks also states that the shell of the American oyster is from the very beginning composed of two valves, which develop from a small, irregular, and transparent organ located on each side of the dorsal furrow (his blastopore).

If we call to mind the fact, already referred to, that the true nature of this furrow and the real blastopore have escaped the observation of the American naturalist, we are certainly justified in doubting the correctness of his observation.

---

[27] *Ueber die Entwicklungsgeschichte der Malermuschel*, in Jen. Zeitschr., ix, 1875.

On the contrary, the description given by Mr. Hatschek of the origin of the shell of the *Teredo* agrees perfectly with what I have observed in the *Ostrea;* and I think we are justified in considering as certain *that the shells of all mollusks originate in the same manner.* This is, doubtless, as the last-mentioned naturalist justly remarks, a very important argument in favor of the theory of the monophyletic descent of the mollusks, a theory which has been violently attacked by Von Jhering.

Meanwhile the ectoderm has become detached from the entoderm along the entire circumference of the embryo, so that for the first time a peritoneal cavity may be observed; a crown of vibratile cilia has developed above the mouth, and the surface of the velum is covered by deep cylindrical cells (Fig. 13). The entoderm has also grown considerably, and is now composed of a spacious stomach cavity, below which there is a diverticulum, still temporarily closed, but which later will communicate with the ectoderm and form the posterior part of the alimentary canal.

On the following day (Fig. 14) the shell, which has grown very much, covers a large portion of the body; it already contains carbonate of lime, as is shown when treated by acids. After steeping it for some time in acetic acid nothing remains but a thin membrane of conchyoline. The ectodermic cells, which are found on the surface of the shell, have become very thin and transparent, so that the outlines cannot be distinguished, but only the refringent nuclei. The larva (Fig. 15) takes food continually, moves about in a lively manner in all directions, and grows considerably. The velum now forms a very distinct part of the body, which is almost entirely covered by the shell. The surface of the velum, surrounded by a wreath of vibratile cilia, already shows in its center a thickening which is the beginning of the cephalic disk. An esophagus, in the shape of a funnel, leads to a large pear-shaped stomach, communicating with the outside through the intermediation of an intestinal canal.

Owing to the development of pigment at several points on the body (as on the cephalic surface, esophagus, gastric pouch, &c.), the larvæ gradually acquire a gray or bluish color. The shell now (Fig. 16) measures 0.16 millimeter in height. Its form is almost round, except the hinge, which is straight. During this period it is already furnished with small teeth, as De Lacaze-Duthiers has observed. From time to time the body of the larva may be observed to be withdrawn entirely into the shell. This is done by means of a dorsal muscle (*ds*) and a ventral muscle (*vs*) originating on the edge of the hinge in a ramified extremity, while their other extremities are inserted into the lower part of the velum. These muscles originate from mesodermic cells which, with their ramifications, cross the internal cavity of the body at several points; some of these cells which cross the dorsal part, from the left to the right valve, are gathered in a group, and form the adductor (*sp*). When the larva moves freely, the part of the body which is in front of the mouth is thrust entirely out of the shell, and is partly folded. The vibratile zone in front of the mouth is composed of a double row of long cilia. If the surface of the velum (Fig. 17) is observed from above, it will be seen that these cilia grow on two rows of cells, placed close by the side of each other and of almost rectangular shape. From each of these cells there arise two vibratile cilia, whose course may be followed into the cellular protoplasm in the colored parts. I have not been able to discover a vibratile zone in the posterior part, although the portion of the head situated below the vibratile zone of that part of the body which lies in front of the mouth is provided with short vibratile cilia. The greater part of the surface of the velum is at this period covered with a single layer of cells, exceedingly small, so that they can be distinguished only by the place occupied by their stained nuclei. Only in the middle an enlargement may be noticed, having a considerable depression toward the interior and composed of several layers of ectodermic cells (Figs. 16 and 17, *kp*). This is the cephalic plate of which we have already made mention, whence originates the superior esophagean ganglion. Its surface seems to be divided into two parts by a transverse furrow. I have not been able to observe the peripheric nerves, issuing from the cephalic plate, which Hatschek has observed in the larva of the *Teredo*. This enlargement of the ectoderm seems to have been observed in the larva of the oyster by Davaine and De Lacaze-Duthiers; but both of them at first took it for the mouth opening—an error which was afterwards recognized as such by the last-mentioned of these two observers.

The intestinal canal is also strongly developed, simultaneously with the other parts of the body. The esophagus, covered with a brownish pigment, has become elongated, and in its upper part has become widened into a funnel. The gastric cavity, greatly enlarged, is by an annular enlargement divided into an upper and lower part; in the upper part there has been formed, to the right and to the left, a large round pouch (*l*), the beginning of the liver, while the intestine begins near the narrow part of the annular enlargement, and is folded in a loop on the left side of the body, before opening into the mantle cavity. The entire inner surface of the intestinal canal is lined with a vibratile epithelium, except perhaps the pouches of the liver, the inner portion of which is difficult to observe, owing to the great quantity of black pigment.[28]

The larva represented in Fig. 16 is the most advanced phase of free larvæ which we have observed; this had been taken from the mantle cavity of the mother oyster, or had been ejected by it when placed in

[28] These are the hepatic pouches, of dark color, which form the black spot by which at an early stage in its development the oyster may be distinguished with the naked eye. This spot is generally considered by fishermen as indicating the beginning of the hinge.

an aquarium. I am not able to say anything positive in regard to the duration of the period which elapses from the time when the larvæ become free to the time when they become fixed; nor do I know what changes they undergo during this period. We have not succeeded either in producing a further development of the oyster larvæ, nor in securing their fixation, even in aquariums where there was a constant current of sea-water, or in those through which a continuous current of air was passing.[29] I have also been disappointed in my attempts to procure oysters in these phases of development by means of catching larvæ floating about in the sea. Although I have several times fished in the neighborhood of places containing collectors, by means of a trawl net, and obtained many different larvæ of annelides, crustaceans, ascidians, &c., I only once succeeded in capturing some oyster larvæ, although they doubtless move about freely in the sea for several days. We must consider the account of Engineer B. de la Grye[30] as fabulous, as he states that an oyster cultivator of the river Auray, after having squeezed the spawn from an oyster, smeared it on a stone which he immediately threw into the water, which stone soon became covered with oysters.

If one compares the most highly developed larvæ, described above, and the youngest among those which have become fixed, great differences in their organization may be observed. At first the shell grows very rapidly, for while it only measures 0.16 millimeter in height in a larva which is on the point of leaving the mother oyster, it measures more than 0.24 millimeter in the smallest of the fixed shells. The adductor occupies another place in the larva than in the fixed animal,[31] while in the fixed animal this muscle is found on the mouth side of the intestine, and therefore in the place of the posterior adductor of the *Dimyaria*, in the larva it is found in the ab-oral region (the hemal side, of Huxley) of the esophagus, or in the position of the anterior adductor of the *Dimyaria*. It is, therefore, probable that the adductor of the larva is homologous with the anterior adductor of the *Dimyaria*. The velum also disappears during this period, while on the other hand the branchiæ may be observed to grow. As shown by the drawing of a larva in a later phase of development (Fig. 19), the branchiæ are at first formed by filaments which are separate along their entire length, except at their bases and at their tips, where they are joined to each other. The branchiæ of *Ostrea edulis*, therefore, develop as De Lacaze-Duthiers also supposed,[32] in the same manner as those of the *Mytilus*

[29] These experiments were made in conjunction with Dr Leo de Leeuw. In order to pass air through the water, I used the apparatus recommended by Mr. Fol for journeys. This apparatus is composed of two petroleum cans (tin), provided at the top and bottom with a spigot, and joined by a rubber tube. One of the cans, filled with water, is placed at a certain height; from it the water runs into the lower can, drives the air out of it, and causes it to pass through the aquarium.

[30] H. de la Blanchère: *Industrie des Eaux*, p. 150.

[31] Professor Huxley called my attention to this fact in a letter to me.

[32] *Mémoire sur le développement de branchies.* In *Ann. des. Sc. Nat.* 4^{me} *sér. Zoologie*, vol. v, p. 43.

edulis. We therefore find in this fact another proof that, phylogenetically, the filamentous branchiæ represent a former stage, and the lamellar branchiæ a later one.

A no less important question is to ascertain how the oyster becomes fixed. It is known that some bivalve mollusks are fixed during their entire life by means of the byssus; others, on the contrary, like *Hinnites*, the *Spondylus*, &c., use this means only temporarily; and later their shell is firmly soldered to the object on which they are found. As the oyster becomes fixed at an early age, it becomes necessary to place the animal with the object to which it adheres (in short, the "collector") under the microscope, care being taken that it remains intact.

Mr. Ryder,[33] in "An account of Experiments in Oyster-culture, &c.," recommends to obtain for this purpose larvæ attached to cotton threads or to pieces of mica or glass. There is no doubt that among the substances mentioned by him glass will be the only one by which the object in view can be reached; for if the collector is opaque, microscopic observations by means of transmitted light become impossible and may prove the cause of great difficulties. I conceived the idea of using as collectors the glass slides used for mounting microscopic objects, and I was confirmed in this idea after having read an article by Prof. Karl Möbius in the *Zoologischer Anzeiger* of January 22, 1883. In order to procure living animalculæ for his microscopic observations he placed the glass slides in a wooden frame, which he put in the water about two feet above the bottom of the sea. A number of animalcules, such as *Polyps*, *Hydroids*, *Bryozoans*, *Infusoria*, &c., adhered to the slides so supported.

The apparatus used by me, which has worked very successfully, is composed of a series of wooden frames or bars, on the upper and lower edges of which a double row of small notches is cut, and in each of which a piece of a glass slide may be inserted. The central bar is provided with lateral notches, which makes it easy to take out the slides, while on the outer side a little peg holds it in place. On the lower side of the frame there is an iron band, which makes the apparatus heavier and prevents it from floating, while on the lower side of the upper edge there is a projection, which makes it possible to rest the collector on some support, so that a current of water may pass underneath. It was my intention to place this collector among the tiles used in the Netherlands for gathering the spawn of the oyster, so as to make my observations as much as possible under the same natural conditions.

The length of the collector is 210 millimeters [about 8¼ inches]—that is, almost the length of a tile—while its breadth is 180 millimeters [about 7 inches], so that on each side of the frame there may be placed six glass object-holders (English size). As it was to be feared that the larvæ would not adhere to common glass on account of its being smooth, some of the pieces of glass were ground rough; others were covered

[33] Report of Ferguson, Commissioner of Fisheries of Maryland, 1881, p. 57.

with a thin layer of hydraulic cement, which is generally used in covering the tiles. The result was that the apparatus answered its purpose admirably. The slides were left in the water 72 hours, and several larvæ became attached to them. Most of them were on the pieces of glass covered with lime, some on the rough glass, and only two on the common glass.

Microscopic examination shows that, during this period, the larva of the oyster is fixed on the collectors almost vertically, so that the hinge is at the top, and turned toward the observer (Fig. 18). The shells, which measures 0.24 millimeter in height, has still a homogeneous structure in the larva; and there may still be seen distinctly the little teeth at the hinge, traced in a straight line. Later these characteristics disappear more and more (Fig. 19) because the valves of the shell grow over or overhang the edge of the hinge, so as to form a swelling (*umbo*). The opinion of Mr. Ryder[34] that the hinge has no teeth, contrary to the observations of De Lacaze-Duthiers, may be true as far as the American oyster is concerned, but it does not apply to the *Ostrea edulis*, as I have stated above. There is deposited, all along the edge of the shell of the larva which is about to become fixed, a straight band of new shell substance, 0.012 millimeter broad, which shows the structure of the grown or secondary shell. This little band of secondary shell substance, which is naturally secreted in a liquid state along the edge of the mantle, may possibly have aided the little oyster in adhering to the piece of glass. I regret that I am unable to solve this problem satisfactorily. I believe that I have repeatedly and very distinctly noticed a small byssus; but the difficulties encountered in these investigations are so numerous that, like Mr. Ryder,[35] I have not been able to arrive at a definite result.

In the first place the almost vertical position of the little shell is very unfavorable to these investigations; moreover, the larva but rarely adheres to smooth glass, and is certain to do this only on glass covered with lime. In order therefore to observe the small object with transmitted light it becomes necessary to remove the lime, in which I succeeded pretty well; for after the slide has been held for 5 or 10 minutes in a solution of 1 per cent chromic acid, all the carbonate of lime has disappeared. By this treatment the carbonate of lime of the shell has of course also been dissolved, which causes the young oyster to undergo such modifications in its appearance, that this method has not been of any assistance to me. If one takes into consideration also the circumstance that all sorts of animalcules adhere to the young oyster and all around it (such as *Vorticella*, *Acinetians*, &c.); and that all kinds of impurities adhere to it, which cannot be removed by mechanical means without injuring the young oyster, it will be acknowledged that it is exceedingly difficult to ascertain whether or not there is a thin filamentous byssus.

---

[34] Bulletin of the United States Fish Commission, 1882, p. 384.

[35] See the preceding note.

The existence of such a filament, however, seems very probable to me. This byssus would therefore serve, as in the *Hinnites*, as a temporary means of adhesion, and would soon give place to new shelly matter, which is deposited along the edge of the shell, and which, while forming, solders the larva to the collector. If no trace of a byssus is found in the grown oyster this is not a serious argument against its existence in the larva, for it is not found in grown specimens of *Unio* and *Anodonta*, which have a byssus in the larval state.[36]

If one examines the structure of the secondary shell of a small oyster which has been fixed for some days, it will be seen that it is not composed of homogeneous layers as in the larva; but that it presents a reticular structure, and is composed of small prismatic columns of lime, separated from each other by an organic substance (conchyoline) (Figs. 19 and 20). The diameter of one of these columns is about 0.012 millimeter. They are of a granulous character, as if they had been formed of small globules, one resting upon the other. These prisms, however, are not formed at the extreme edge, *i. e.*, in the most recent portion of the shell, where nothing is seen but a network of conchyoline, whose meshes are not yet filled (Fig. 20).

As is well known, the outer portion of the shell of the grown oyster, of the *Margaritana* and others, also presents a prismatic structure. If in the *Margaritana* the lime is removed from these prisms, nothing remains but the walls around the columns, which seem to be composed only of organic matter, and a small and insignificant organic remnant of the prisms.[37] According to Hessling, these layers are formed by a deposit of carbonate of lime in the prismatic cavities of the numerous thin layers of conchyoline.[38] The empty meshes which I have described above, and which are formed at the extreme edge of the little oyster shell, as well as the observations made by Tullberg on the shells of the *Margaritana*, speak strongly in favor of this opinion. The dark lines seen in Fig. 19 inside the shell seem to me to be nothing else but filaments of conchyoline; at least in breaking the shell of a small living oyster, I saw numerous gelatinous filaments between the mantle and the extreme edge of the shell.[39]

---

[36] As, according to the observations of Bouchon-Brandely, the Portuguese oyster, which is unisexual and whose eggs can therefore be fecundated artificially, adheres to some object a couple of days after fecundation has taken place, I had hoped to be able to have a better chance of studying its mode of fixation. Through the kindness of Mr. Tripota, of Vernon, I received about 50 specimens of this oyster, but the unfavorable weather which we had during the month of July was probably the cause that the larvæ, although they began to develop, did not adhere to any object.

[37] Tycho Tulberg: *Studien über Bau und Wachsthum des Hummerpanzers und der Molluskenschalen*, in *Kongl. Svensk. Vetsk. Acad. Abh.*, vol. 19, 1882.

[38] Th. von Hessling: *Die Perlmuscheln*, 1859, p. 260, vol. v, Fig. 3.

[39] This report was already in the press when I came across an article by Mr. Osborn: "On the structure and growth of the oyster shell" (Studies from the Biological Laboratory, Johns Hopkins University, vol. ii, No. 4). By the advice of Dr. Brooks, Mr. Osborn studied the formation of the oyster shell, by boring in the edge of the

It is remarkable that the lower valve does not show the reticular design of the upper valve, but undulating striæ and points joined closely to each other (Fig. 21); this different appearance of the two valves seems to be due solely to the circumstance, that the calcareous particles of the lower valve do not have the regular prismatic structure which they assume in the upper valve, and that they are smaller and of irregular shape. This difference of structure can be traced more or less distinctly throughout the entire life of the oyster; for while the upper valve has a linear structure and is composed of layers which do not adhere very firmly to each other and where the prismatic tendency can immediately be recognized, the lower valve, on the contrary, presents a denser appearance and seems to be composed of layers closely joined to each other.

As regards the difficulty of recognizing the young oyster soon after its fixation, I think that I have overcome it by using a tile covered simply with hydraulic cement, instead of a mixture of lime and sand. The numerous small uneven places caused by the grains of sand make it difficult to see the young oyster shell on the collector, even to the experienced eye of the oyster cultivator. In order to get as even a surface as possible, I used a glass tile instead of a common tile; but I do not consider this absolutely necessary. After this tile remained in the current for eight days, some small oysters became attached to it, the largest of which measured 0.85 millimeter and the smallest only 0.57 millmeter in height; and still even these latter could be distinguished by the naked eye.

I must, in conclusion, say a few words in regard to a probable enemy of the oyster. I had in my aquarium a mother oyster which from time to time ejected large numbers of larvæ. There were in the same aquarium two *Actiniæ*, such as are found in large quantities on the shell of of the oyster. I found that the larvæ diminished rapidly; and in endeavoring to ascertain the cause I found floating in the water a certain number of small bluish balls, about 2 millimeters in diameter; and at the same time I saw a similar ball issue from the mouth aperture of an *Actinia*. In examining these small balls under the microscope I discovered that they were composed of empty oyster shells pressed closely against each other, and that in fact they were the remnants of the repast of the *Actinia*. Although I do not think that, under ordinary conditions, the *Actiniæ* can easily seize the larvæ, they might nevertheless destroy a large number, if they multiplied to any great extent among the oyster parcs.

---

shell holes which were temporarily closed by means of thin pieces of glass, on which the conchyoline could be deposited. Mr. Osborn arrived at the conclusion that the shell is formed by the crystallization of carbonate of lime in the chitinous membrane. The opinion of Hessling (with whose researches Mr. Osborn does not seem to be acquainted) that the carbonate of lime is deposited in the prismatic cavities, does not, according to Mr. Osborn, seem to be borne out by the facts.

EXPLANATION OF THE PLATES.

FIG. 1. Egg of the oyster, with the germinal vesicle and spot visible within the vitellus.

FIG. 2. Beginning of development; the germinal vesicle has become invisible, and the polar globules make their appearance.

FIG. 3. First stage of segmentation; the egg is divided into two spheres of unequal size (animal sphere and vegetative sphere).

FIG. 4. More advanced stage, the egg being divided into four spherules.

FIG. 5. Stage of development where the egg shows one large vegetative sphere and several animal spheres.

FIG. 6. More advanced stage, seen from above, where the vegetative sphere is divided into two spherules.

FIG. 7. Embryo, side view, at the beginning of invagination (*gastrula*).

FIG. 8. Embryo more developed, optic section, with invagination of the entoderm and beginning of the preconchylian gland; *ec*, ectoderm; *en*, entoderm; *o*, blastopore; *sk*, preconchylian gland.

FIG. 9. Embryo a little older, side view; *v*, pediform appendix; the other letters as in preceding figure.

FIG. 10. Same stage, optic section; *me*, mesoderm; *d*, primary intestine.

FIG. 11. Embryo a day older, front view, with the primary mouth opening.

FIG. 12. The same embryo, optic section.

FIG. 13. Embryo a day older, with a wreath of vibratile cilia, a stomachic cavity, and a beginning of a shell, *s*.

FIG. 14. More advanced stage, side view, with shell more developed.

FIG. 15. Larva still more developed, with velum, and the beginning of the cephalic plate (*scheitelplatte*); *a*, anus; *e*, intestine; *m*, stomach; *sl*, esophagus; *kp*, cephalic plate.

FIG. 16. Larva a little older, with a double pre-oral wreath of vibratile cilia, a cephalic plate, hepatic pouch, and muscles; *ds*, longitudinal dorsal muscle; *vs*, longitudinal ventral muscle; *sp*, adductor muscle; *l*, hepatic pouch; *mh*, mantle cavity; the other letters as above.

FIG. 17. The velum or rotary disk, with the double row of ciliated cells, seen obliquely from above.

FIG. 18. Larva as it attaches itself, in an almost vertical position.

FIG. 19. Little oyster, about 7 days old; the height of the primary homogeneous shell is 0.24 millimeter, that of the secondary part, composed of prisms, is 0.15 millimeter; the beginning of the branchiæ and the adductor muscle are visible.

FIG. 20. Fragment of the edge of the preceding shell, to show how the calcareous prisms are formed.

FIG. 21. Fragment of the lower valve.

Fig. 1.

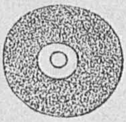


Fig. 2

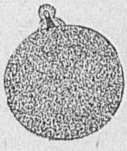


Fig. 3.

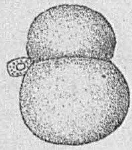


Fig. 4.

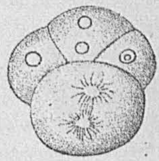


Fig. 8.

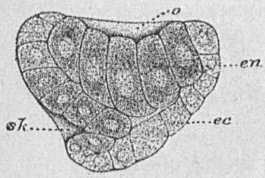


Fig. 9.

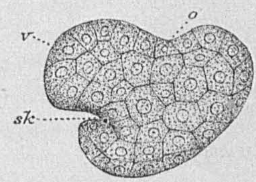
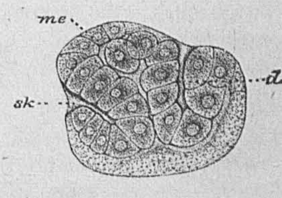


Fig. 10



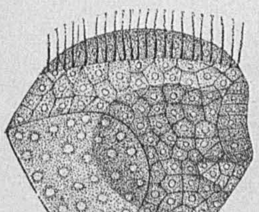


Fig. 14

Fig. 16.

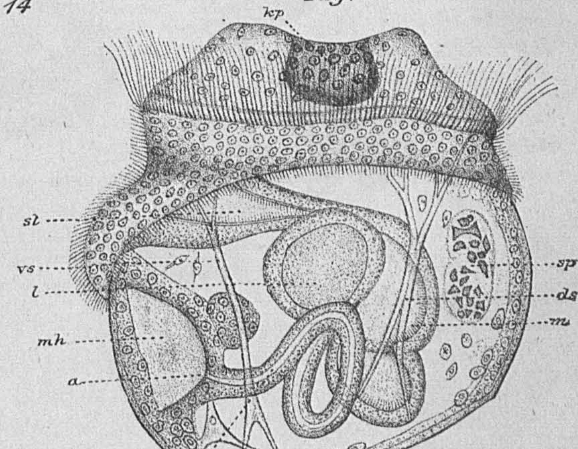


Fig. 15.

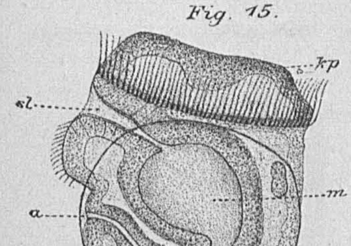


Fig 5.

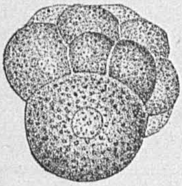


Fig. 6.

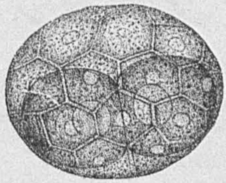


Fig. 7.

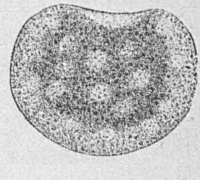


Fig. 11.

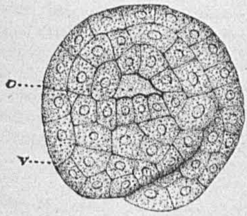


Fig. 12.

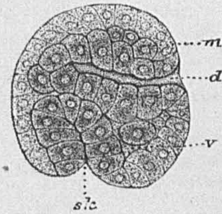


Fig. 13.

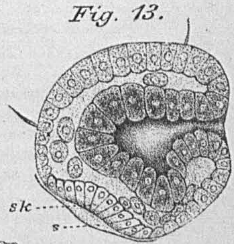


Fig. 17

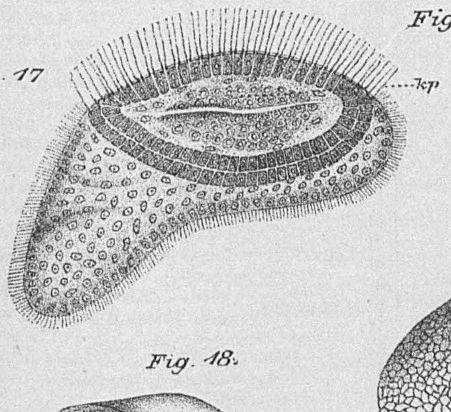


Fig. 20.

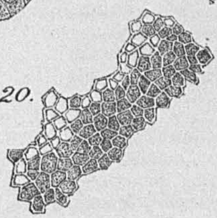


Fig 21.

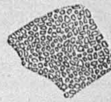


Fig. 19.

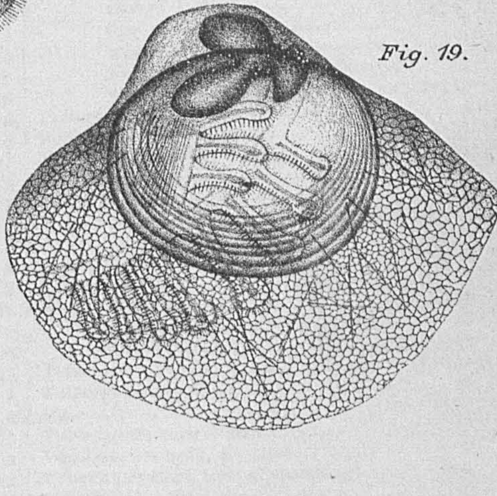
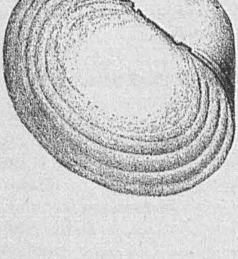


Fig. 18.



INDEX.

[NOTE.—The references are to page-figures in brackets.]