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CONTENTS.

No. 1. — *The Histology and Development of the Eye in the Lobster.*

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Table of Contents.

Introduction.

Through the kindness of Mr. Alexander Agassiz it was my privilege to spend the greater part of the summer of 1887 at the Newport Marine Laboratory. During the preceding winter I had been interested in the structure of the eyes in Arthropods, especially in the inversion of the retina in Arachnoids and my instructor, Dr. E. L. Mark, had called my attention to the importance of ascertaining whether the retina in the compound eyes of Crustaceans was inverted or not. At about this time Kingsley ('86[a]) published his preliminary account of the development of the compound eye of Crangon, and claimed that in this crustacean, as in spiders, the retina was inverted. For reasons which I shall mention in the course of this paper, Kingsley's account did not seem fully satisfactory to me, and consequently I decided to study for myself the development of the eye in a crustacean. My visit to the Newport Laboratory offered an excellent opportunity to collect embryological material for such a study. During August and September spawning lobsters were easily obtained, and I therefore determined to study the eye in the lobster, *Homarus americanus*, Edwards. A series of lobsters' eggs were collected, and before leaving Newport my observa-

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XVII.

tions had been carried far enough to satisfy me that the retina in the lobster was a simple ectodermic thickening. On returning to Cambridge from Newport, the study of the lobster's eye was continued in the Embryological Laboratory at Harvard College, under the direction of Dr. Mark. Here I completed the observations on the development of the eye, and studied its histology. In the fall of 1888 a brief preliminary account of the results which are now presented in full was published in "The Proceedings of the American Academy of Arts and Sciences," Vol. XXIV. pp. 24, 25.

In procuring at Newport the necessary stages in the development of the lobster I proceeded as follows.

Female lobsters with eggs were obtained from the fishermen, and kept in floating latticed boxes which were anchored in the small cove beside the Laboratory. A few eggs were taken daily from each lobster. The reagents which I employed in killing the eggs were Kleinenberg's picro-sulphuric acid, Perenyi's fluid, a saturated aqueous solution of corrosive sublimate, and hot water. The eggs which were prepared with corrosive sublimate were rendered almost useless by the subsequent formation of a fine precipitate. Those which were killed in Kleinenberg's picro-sulphuric acid and in Perenyi's fluid gave fair results; the latter reagent left the yolk in good condition for cutting. The best results, however, were obtained by the use of hot water. Eggs which had been prepared in this way could be easily shelled, and the embryos could be readily dissected from the yolk. The separation of the embryo from the yolk proved to be a great advantage, and obviated the necessity of cutting the yolk, a tedious process in an egg as large as the lobster's.

In the following account of the development of the lobster's eye, the stages which it is necessary to describe are taken from different sets of eggs. These sets were from different lobsters, consequently I cannot state with exactness their relative ages. I shall therefore characterize them by their most evident structural peculiarities. Beginning with the earliest stage and proceeding to the later ones, I have lettered them A, B, C, D, E, and F. Set A is in the stage of the "egg-nauplius"; in this set the characteristic three pairs of appendages are easily distinguishable. In set B the thoracic appendages have begun to form. This stage corresponds very closely to what Reichenbach ('86, Plate III. Fig. 11) has designated in the crayfish as stage H. In stage C the first trace of pigment in the retina is visible. Stage D is from the same series of eggs as stage C, but is seven days older than C. In both

stages C and D, the abdomen of the embryo is recurved, and reaches forward covering the space between the optic lobes. Stage E corresponds to the time of hatching. Stage F is represented by a young lobster one inch in length.

The younger stages which follow the hatching of the lobster are obtained with considerable difficulty, and I am under obligations to several of my friends for material which covers this period. For some lobsters in the "Schizopod" stage I am indebted to Mr. Sho Watase. Mr. H. H. Field and Mr. Carl H. Eigenmann kindly collected for me some young lobsters one inch in length. From Mr. F. L. Washburn I received the eyes of several half-grown lobsters, six to eight inches in length. The material which I used in studying the histology of the eye in the adult was very kindly supplied to me by A. T. Nickerson and Company, of Charlestown, Mass.

Methods.

The methods of staining, embedding, etc., which I have employed, are those known to all students of modern histology. In one case, the staining of nerve-fibres, I have used a method which I accidentally discovered while experimenting with Weigert's hæmatoxylin.

In employing this method it is necessary to stain the sections on the slide. The way in which I have stained sections on the slide has already been described ('87, p. 175). Further experience has shown, however, that the successful employment of this method necessitates a careful observance of certain precautions. These I have not sufficiently emphasized in my former account, and I therefore redescribe the method, calling especial attention to the precautions. The method consists in a cautious use of Schällibaum's fixative. The fixative which I have employed is composed of clove oil three parts and Squibb's flexible collodion one part. The mixture before being used should be allowed to stand for about a week. After several months it may become ineffective. When working, I usually employ the fixative frequently enough to follow its changes, and at the first signs of failure I make a new mixture. If for any reason I have not used the fixative for some time, I test it with a few waste sections before employing it with valuable material. In using it a moderate amount is applied to the slide, and the sections in paraffine are placed on it. The slide and its sections are now subjected to a temperature of 58° C. for fifteen minutes. It is important to observe carefully both the length of time during which the slide is heated and the temperature to which it is raised. At the end of fifteen

minutes, the slide, while warm, is thoroughly washed with flowing turpentine. This can be applied conveniently from a small wash-bottle. All of the paraffine should be removed from the slide before it becomes cool, otherwise on cooling some paraffine may solidify. This is liable to loosen the film of collodion. The wash of turpentine should be continued not only till the paraffine is thoroughly removed, but till the slide is cool. Then, and not till then, can the turpentine be safely replaced by alcohol, first 95%, then 70%, 50%, and 35%, and finally it can be immersed in water. After once having got the slide with its sections into water, the subsequent treatment with alcohol and water seems to have no effect in loosening the sections, although the film of collodion will dissolve easily in ether. I have very generally employed this method of staining for two years, and as it obviates the difficulties which arise from maceration or partial penetration of dyes, I use it in preference to staining *in toto*. I have lost very few sections by it, and such accidents as I have had were due, I believe, to a neglect of some of the precautions which have been mentioned.

The method of staining nerve-fibres which I have employed consists of a modified use of Weigert's hæmatoxylin. The tissue which was stained by this method was for the most part killed in hot water, although I have also successfully stained nerve-fibres which were killed in chromic acid and Kleinenberg's picro-sulphuric acid. Sections of the optic nerve which had been mounted on the slide and carried into water were treated for about half a minute with an aqueous solution of potassic hydrate $\frac{1}{10}$%. They were then *thoroughly* rinsed in distilled water and transferred to Weigert's hæmatoxylin. Here they remained for about three hours at a temperature of 50° C. They were then rinsed again in distilled water, carried through the grades of alcohol, and after being dehydrated with alcohol of about 99%, they were cleared in turpentine and mounted in benzole balsam. Each nerve-fibre when so treated had a distinct blue-gray outline. The sections do not overstain even when they are kept in the dye for a prolonged period, and there is of course no subsequent decoloring. This method yields fair results when applied to nerves from any part of the lobster's body, but it is especially successful in treating that portion of the optic nerve which intervenes between the retina and the optic ganglion.

The Histology.

The two movable eye-stalks of the lobster are situated one on either side of the rostrum, at the angle which that structure makes with the

anterior edge of the carapace. The form of the eye-stalk approaches that of a short cylinder terminated by a hemisphere. The cylindrical part of the stalk resembles the general surface of the body in that it is covered with a firm, calcified cuticula. Excepting a portion of the surface next the rostrum, the whole of the hemispherical part during life is black, and covered with a flexible cuticula. The black area defines the position of the retina. That portion of the hemispherical surface which is not black, and which faces the rostrum, is covered with a peninsula-shaped piece of inflexible cuticula. A broad isthmus of the same kind of cuticula connects this with the shell of the cylindrical part. The absence of the retina from the peninsula-shaped portion of the hemisphere is due in all probability to the fact that the field of vision for this part of the hemisphere is cut off by the rostrum. The remainder of the hemisphere, that part on which the retina is developed, faces away from the lobster's body, and its field of vision is not permanently obstructed by any part of the animal.

A section perpendicular to the surface, and cutting the eye-stalk in a region where the cylindrical and hemispherical parts unite, is shown in Figure 26. The thick, calcified cuticula of the cylindrical part is indicated at *cta.* On the inner surface of this cuticula is a thin hypodermis (*h d.*). The hypodermis is bounded on its inner face by a basement membrane (*mb.*). The cuticula of the hemispherical part (*crn.*) is thin and flexible. It can be designated by the name corneal cuticula. (Compare Patten, '86, p. 544.) Resting on the deep face of the corneal cuticula is the thick cellular layer, named by Lankester and Bourne the ommateum (*omm'.*). The proximal face of the ommateum is limited by a basement membrane, which is continuous with that bounding the corresponding face of the undifferentiated hypodermis. The ommateum is continuous with the hypodermis, and in fact can be regarded as a thickening of that layer. Carrière ('85, p. 169) has already pointed out in the eye of Astacus a similar relation between the hypodermis and ommateum, and he believes that this relation holds good for all Decapods.

On inspecting the external face of the corneal cuticula, one finds it divided into an immense number of square facets, one of which is shown in Figure 2. Although as a rule the outline of the facet is square, it is not invariably so; for on the margin of the retinal area close to where the ommateum passes over into the undifferentiated hypodermis, the outline often becomes somewhat irregular, and more frequently presents the form of a hexagon than of a square (Fig. 59). The number of facets in each eye of an adult lobster is about 13,500.

In the ommateum the cells are arranged in specialized groups or ommatidia. There is a single ommatidium under each corneal facet, consequently in any given eye the number of ommatidia equals the number of facets. The cellular composition of each ommatidium is best understood from a comparison of longitudinal and transverse sections. Figure 1 represents a longitudinal section through an ommatidium. The thick lamellated layer (*crn.*) at the distal end is the corneal cuticula. Directly below this is a thin layer of cells, the corneal hypodermis (*crn. h d.*). Following on the corneal hypodermis are the cone-cells (*cl. con.*). They are very long, and extend from the corneal hypodermis inward till their proximal ends disappear in the deep part of the retina. In reality they terminate upon the basement membrane. Their distal ends in the region of the crystalline cones are surrounded by pigment-cells, to which I give the name distal retinulæ (*rtn'. dst.*). These, like the cone-cells, extend to the deeper part of the retina. Here the proximal retinulæ and accessory pigment-cells occur. The proximal retinulæ are elongated cells (*rtn'. px.*), and contain black pigment. They surround the rhabdomes (*rhb.*). The accessory pigment-cells are irregular cells, which fill the space between the deep ends of the proximal retinulæ. They contain a pigment which is whitish by reflected and yellowish by transmitted light. Their nuclei are shown at *nl. pig.*, Figure 1. The last two kinds of pigment-cells described rest upon the basement membrane (*mb.*); below this membrane the fibres of the optic nerve can be seen (*n. fbr.*).

From this description it will be seen that the ommateum lies between the corneal cuticula and the basement membrane, and is composed of the following kinds of elements: cells of the corneal hypodermis, cone-cells, distal retinulæ, proximal retinulæ, and accessory pigment-cells. The numbers and positions of these cells are best made out from transverse sections. The several kinds of cells will be discussed in the order named.

The Corneal Hypodermis.

That the corneal cuticula in Decapods is separated from the cone-cells by an intervening layer of cells is a view which has been held only by recent investigators. Grenacher ('79, p. 123), in his account of the eyes in Decapods makes no mention of such a layer, and leaves one to conclude that the cone-cells abut against the cuticula. Claus ('86, p. 57) suspected the presence of a corneal hypodermis in Decapods, Schizopods, and Stomatopods, but his search for it was in vain.

The view that the cuticula and cone-cells are in contact, is strongly contrasted with that maintained by Patten ('86, pp. 626, 642). According to this writer, the corneal cuticula is due to the activity of a layer of cells, the corneal hypodermis, which intervenes between the cuticula and the cone-cells. Patten has identified the corneal hypodermis in the following genera of Decapods: Penæus, Palæmon, Pagurus, and Galathea. It has also been described by Kingsley ('86, p. 863) in the eyes of Crangon, and by Herrick ('86, p. 43) in the eyes of Alpheus. Carrière ('89, p. 225) has recorded it in the eye of Astacus, and there is now good reason for believing that a corneal hypodermis exists in the eyes of all Decapods.

Patten's statement ('86, pp. 665, 666) that the corneal hypodermis "has been invariably overlooked by Grenacher," and Kingsley's assertion ('86, p. 863) that the existence of the corneal hypodermis "was utterly ignored by Grenacher," are perhaps a trifle too strong. It seems much more probable that Grenacher confused the nuclei of the cone-cells and corneal hypodermis. He evidently never saw both kinds of nuclei in the eye of the same Decapod. In some cases he may have described the nuclei of the cone-cells, in other cases those of the corneal hypodermis. In both instances what he described he took to be the nuclei of the cone-cells. In the eye of Mysis, I believe that he ('79, p. 118) described the nuclei of both the cone-cells and corneal hypodermis, although in this case he was of the opinion that both sets of nuclei belonged to the cone-cells. Where only one set is figured, it is difficult to decide whether he has given the nuclei of the cone-cells or of the corneal hypodermis. So far as I am aware, there are always in each ommatidium of a Decapod *two* hypodermal nuclei, and *four* nuclei in the cone-cells. This numerical relation is sufficient to distinguish the groups of nuclei, but it can only be employed satisfactorily where transverse sections at the proper niveau are given. Unfortunately, in the Decapods, Grenacher did not figure any such sections, and it is therefore difficult to decide in particular cases which kind of nuclei he has described.

In the lobster a well differentiated corneal hypodermis has already been pointed out (Fig. 1, *crn. hd.*). In transverse sections this presents the appearance of squares of granular protoplasm (Fig. 3). Each square contains two nuclei, and is bounded by a membrane. A narrow space filled with granular substance separates the membranes of adjacent squares. From the longitudinal section (Fig. 1) it will be seen that these squares are relatively thin, so that their proportions are somewhat like those of square tiles. The outer face of the tile is flat; its inner

face is hollowed, however, so that its centre is the thinnest part. In a few cases the corneal hypodermis has appeared as cubical blocks, rather than as tiles. This thickened condition probably indicates an increased functional activity, and the more frequently occurring tile-like condition may correspond to a quiescent stage.

The two nuclei contained in each square are placed some distance apart, and on one of the diagonals of the square (Fig. 3). Their long axes are approximately parallel to the other diagonal. In a given eye all the squares agree in having the nuclei on parallel diagonals. The presence of two nuclei in a square indicates that the square consists of two cells. Any membrane separating the two cells must necessarily pass between the two nuclei, but all attempts to discover such a membrane have failed. However, for a reason which will be given shortly, I believe that the protoplasm of the hypodermal square is divided by the diagonal which lies between the nuclei. In the centre of each square several oval or round outlines are usually visible (Fig. 3). These are vesicular bodies which occur in the distal ends of the cone-cells, and which can be seen through the very thin corneal hypodermis.

The corneal cuticula is the result of the activity of the corneal hypodermis. Viewed from the surface, the cuticula is divided by narrow bands into square facets (Fig. 2). Each facet is external to a hypodermal square. The proximal and distal faces of each facet, as can be seen in the transverse section (Fig. 1), are very nearly flat, the proximal face only being a trifle convex. This convexity, however, is so slight that one cannot attribute to the facet the character of a lens.

When a piece of corneal cuticula is cleaned by treating it with potassic hydrate, and is then examined in water, the markings which are visible with difficulty in preparations mounted in balsam are easily seen. Each facet in addition to its narrow limiting bands has a faintly marked diagonal band which divides the square into two equal triangles (Fig. 2). In the different facets of a given eye the diagonal bands are parallel. Newton ('73, p. 327, Plate XVI. Fig. 3), in describing the structure of the eye in the lobster, states that each facet is crossed by *two* diagonals at right angles to each other. This statement I cannot confirm, for, although I have searched with care, I have never succeeded in finding more than a single diagonal in each facet. In the middle of the diagonal there is an irregular hazy patch. This at times has a distinctly marked cross in it. When the cross is present, one of its axes lies in the diagonal band, the other extends at right angles to the band (Fig. 2).

Whether all of these markings extend through the substance of the

cuticula, or whether they are confined to its surface, is difficult to say. The production of the cuticula is such a uniform process that one would naturally expect to find that the marking extended through it, for the successive layers would be similarly marked, and thus bands would be established extending from its deep to its superficial face. Concerning the vertical extension of the bands between the facets there is no question, for in transverse sections of the cuticula (Fig. 1, *x*) they reappear in their proper positions, and extend from one surface to the other. Owing to the roughness of the cut face, they are much less readily detected in sections than when viewed from the outer surface of the cuticula (compare Figs. 1 and 2). The diagonal band and its central spot have not been observed in transverse sections, even when the plane of section is in the most advantageous position for demonstrating these structures. Notwithstanding their apparent absence, both may be present, although indiscernible. For even in the superficial view, when the outline of the facet was so readily visible, the diagonal band was only faintly seen. In transverse sections, where the distinct boundary of the facet is visible with difficulty, one should not expect to see the much fainter diagonal. On comparing the diagonal band and the boundary of the facet by focusing through the corneal cuticula, I was unable to distinguish a greater vertical extension in the one than in the other. Since it has been shown that the boundary of the facet extends through the cuticula, this observation supports the conclusion that the diagonal band also extends through it.

Patten ('86, pp. 626, 627) has described in the facet of Penæus a band which has many resemblances to the diagonal band in the lobster. It is not diagonal, however, but transverse, and divides the square facet into two equal rectangles, in which the sides are in the proportion of one to two. I have already given my reason for believing that the diagonal band in the cornea of the lobster extends through the substance of the cuticula. Patten states that the transverse band in Penæus is only a superficial structure, and says ('86, p. 627) that in cleaning the cuticula "when the treatment with caustic potash has been carried to excess, all markings disappear except the contours of the facets." I have subjected the corneal cuticula of a lobster to a boiling solution of potassic hydrate (75%) for a quarter of an hour, and, although the potash completely cleaned the cuticula, the outlines of the facets, the diagonal band, and its spot were as readily visible after this treatment as before. A second and third trial with the same piece of cuticula did not noticeably effect the markings. In this respect, then,

the diagonal band in the lobster is materially different from the transverse band in Penæus, and I conclude that in the cornea of the lobster the limiting and diagonal bands are essentially similar in that they both extend through the cuticula.

In all probability the bands between the facets were produced during the secretion of the cuticula by the interference of the partitions which separate the hypodermal squares. If this be true, it is probable that the diagonal bands represent a like interference. It is important to notice that the diagonal band in the cuticula corresponds to the imaginary diagonal which lies *between* the nuclei of each hypodermal square, never to the diagonal which crosses the nuclei (compare Figs. 2 and 3). This diagonal then corresponds to the position in which one would look for a membrane between the pair of hypodermal cells; and although such a structure has not been observed, the diagonal band in the cornea is a strong indication of its presence.

Admitting this to be the significance of the diagonal band, it is but natural to expect that, if deeper cells touch the cuticula, they would pass outward *between* the hypodermal cells. The fact that the hazy patch which lies in the middle of the facet is always on the diagonal band, and directly external to the distal tips of the cone-cells, leads to the belief that this patch marks the place where the cone-cells pass between the cells of the hypodermis and touch the cuticula. I am not of opinion that the patch is produced by the secretion of the cone-cells, although I have no evidence that the cone-cells cannot produce cuticula at their distal tips. It seems to me more probable that they have given rise to the patch by a series of interrupted interferences with the activity of the corneal hypodermis. If such be the case, a distinct cross might be produced when the area of interference was definitely circumscribed. When the area was not so sharply bounded, a hazy patch with indistinct outlines might be the result.

From the facts which have been presented, I conclude that each hypodermal square consists of two flattened cells, triangular in outline, and very intimately applied on their longest sides.

The Cone-cells.

One of the most important questions in the anatomy of the cells of the crystalline cones (retinophoræ) concerns the relation which these cells bear to the rhabdome. Max Schultze was the first to maintain ('67, p. 407) that the cone-cells and rhabdomes were separate structures. Grenacher's researches lead to the same conclusion. As an oppo-

nent of this view, Patten ('86, p. 670) has claimed that the cone-cells and rhabdome were continuous, and in fact that the rhabdome of the compound eye was only an enlargement of the proximal end of the cone-cell. Kingsley ('86, p. 863) in his description of the eye in Crangon supported Patten's view.

Of those authors who maintain the separateness of the cone-cells and rhabdome, no one, I believe, has given a fully satisfactory account of the way in which the proximal ends of the cone-cells terminate. Grenacher, in describing the eye in Palæmon said ('79, p. 123): "Die fein ausgezogene Spitze dieser Pyramide [the cone-cells] durchsetzt, bevor sie in contact mit der Retinula tritt, zuerst eine in Form eines Hohlcylinders sie umhüllende Pigmentmasse um sich dann in das Vorderende der Retinula eine Strecke weit einzusenken." A more detailed account was given by Schultze, who, after stating ('68, p. 10) that in some crustaceans the cone-cells appeared to terminate a little in front of the distal end of the rhabdome, said that in the crayfish "geht der Krystallkegel nach unten in vier Spitzen aus, welche sich aus den vier Kanten der Oberfläche entwickeln und das obere Ende des nervösen ebenfalls vierkantigen Sehstabes umschliessen. Die vier Spitzen legen sich dabei an die Kanten des letzteren an und laufen als lange feine Fäden auf der Oberfläche des Sehstabes herab, diesen umklammernd und mit ihm oberflächlich verbunden aber durch Maceration isolirbar. Gegen das Ende spitzen sie sich fein zu und verlieren sich auf der Oberfläche des Körpers, den sie umfassen." This account is the most complete of any that I have seen, and yet that Schultze was not fully satisfied that he had seen the proximal termination of the cone-cells is probable from the fact that he says the fibres *are lost* on the surface of the rhabdome.

The relation of the rhabdome to the cone-cells, and the way in which these cells terminate in the lobster, is as follows. As in other Decapods, each ommatidium in the eye of the lobster contains four crystalline cone-cells. Together these cells form an elongated pyramid, with its base next the corneal hypodermis and its apex on the basement membrane (Fig. I, *cl. con.*). At the distal end of the ommatidium, in the region which corresponds to the base of the pyramid, the four cells are closely applied to each other. This condition is maintained till the deeper part of the ommatidium is reached. Here the four cells, reduced to fibres, separate and end independently on the basement membrane.

A transverse section of the distal ends of the cone-cells is shown in Figure 4. On the external faces of each group of four cells there is a

distinct bounding membrane (*mb. pi ph.*). This can be called the peripheral membrane. The four cells in each group are separated one from another by delicate membranes (*mb. i cl.*), which often show undoubted continuity with the peripheral membrane. These membranes, since they lie between the cone-cells, can be called the intercellular membranes. The distal end of each cell contains coarsely granular protoplasm and a nucleus (Fig. 4, *nl. con.*). The nuclei usually lie in the external angles of the cells, and do not readily take up coloring matter. The terminal granular protoplasm of the four cells forms a distal cap (Fig. 1, *cap.*). This cap fills the concavity on the proximal face of the corneal hypodermis, and its central distal tip probably passes between the pair of hypodermal cells and touches the cuticula. The spot or cross which is thus probably produced in the centre of each facet has already been described.

Below the cap of granular protoplasm is the crystalline cone. The firm peripheral membrane of the cap is continued over the cone and proximal part of the cone-cell. The distal end of the cone in cross-section is a square with rounded angles. At this end there is no indication of a division of the cone into four segments corresponding to the four cells. A transverse section midway the length of the cone (Fig. 5) shows no features essentially different from those of the section across the distal end. The proximal end of the cone in cross-section is nearly circular (Fig. 6). On the sides of this end of the cone one often notices small re-entrant angles (Fig. 6, *x*). The peripheral membrane dips into these. The angles are usually four in number, never more, and occupy positions which indicate the planes of separation between the four cone-cells. In some cases delicate membranes originating from the angles divide the substance of the cone into its four constituents (Fig. 6, *mb. i cl.*). These membranes correspond in position to the intercellular membranes at the distal end of the cone-cells. The substance of the cone is very finely granular. The four constituents of each cone terminate very nearly at one level. In passing in a proximal direction through a series of sections, the substance of the cone is last seen as a thickening which flanks the cell membranes, especially the intercellular membranes. (Compare Figs. 1 and 6.)

Below the cones the outlines of the four cone-cells are well marked by both peripheral and intercellular membranes (Fig. 7). The intercellular membranes are continuous with those seen in the proximal ends of some cones. In this region the cells contain coarsely granular protoplasm. In passing from the deep ends of the cones to the proximal

retinulæ, the most striking difference noticed in the cone-cells is a diminution in their diameter. (Compare Figs. 1, 6, and 8.) On a level with the distal ends of the proximal retinulæ, the groups of cone-cells still retain their four-parted character (Fig. 9, *cl. con.*). Each group is easily traced between the retinulæ till it approaches the distal end of the rhabdome. The change which here takes place is represented in Figure 12. Of the four ommatidia which are shown in this section, the one indicated at *a* is cut slightly above the rhabdome. In the case of ommatidia *b*, *c*, and *d*, the plane of section passes through the end of the rhabdome. In each of these three, it will be noticed that the rhabdome is surrounded by four bodies, which correspond in position to the four cone-cells. The four ommatidia which are drawn in Figure 12 are in no way exceptional, but represent a very usual condition. Many such cases have been examined, and whenever the tip of the rhabdome was in the section, it was invariably surrounded by the four bodies previously mentioned. When, on the other hand, the plane of section did not pass through the rhabdome, only the four cone-cells were present. The round bodies at the sides of the rhabdome can be traced from section to section, and I therefore believe them to be fibres. Moreover, there is no break observable in their continuity with the cone-cells, and I therefore further believe that they are the fibrous prolongations of the cone-cells. They have one peculiarity which is worthy of comment. As the cone-cell passes over into the fibre, a considerable diminution in its diameter takes place. This is accomplished at the distal end of the rhabdome, and within a space equal to the thickness of one or at most two sections (7.5–15 μ). Occasionally there is to be seen a group, in which one or two cells have been reduced to fibres, and the remaining ones are as large in transverse section as an individual in ommatidium *a* (Fig. 12). The conclusions which are arrived at from the study of sections are confirmed by isolation-preparations. Figure 28 represents a portion of an isolated group of four cone-cells from a single ommatidium. In the distal part of the specimen the four cells are intimately bound together, but at the proximal end they appear as four separate fibres. As in the transverse section (Fig. 12), the continuity of the fibrous and thicker portion of the cone-cell, and the rapid reduction of the cone-cell to form the fibre, are plainly seen. The cone-cells are usually somewhat separated before they reach the rhabdome. It can scarcely be said that they touch the rhabdome, although this is the region in which they are nearest to it. As the fibres pass into the deeper part of the retina they are found to lie nearer the periphery of the ommatid-

ium. They lie between the proximal retinulæ, but at some distance from the rhabdome (Fig. 14, *cl. con.*). They still retain, however, the same relative positions in the ommatidium. Their peripheral location is maintained (Fig. 17) till they are very close to the basement membrane.

The changes which the fibres undergo as they approach the basement membrane is shown in Figure 19. In this section the plane of cutting was slightly oblique to the basement membrane. Of the three ommatidia which are here represented, those indicated at *c* and *d* are cut at about the same level, and very close to the basement membrane. Ommatidium *b* is cut farther from the membrane than either *c* or *d*. The fibres of the cone-cells are closer to each other in *c* and *d* than in *b*. As this condition is generally true in other sections, it follows that, as we approach the basement membrane, the fibres of the cone-cells converge. The convergence is also shown in Figure 21. Of the ommatidia here figured, *b* is cut farthest from the basement membrane. In it the four cone-cells (*cl. con.*) can be seen, and between them a dot which represents the proximal end of the rhabdome (*rhb.*). Nearer the basement membrane is ommatidium *a*, in which the four cone-cells can be recognized, and to one side a fibrous area. The rhabdome does not extend as deep as this. The fibrous area represents a region in which the plane of section passes through an elevation on the distal face of the basement membrane. Ommatidium *d* is still nearer the membrane. The cone-cells are here brought more closely together, and are surrounded by the fibrous substance of the elevation. The form of the elevation is now seen to be that of a cross. At *x* is shown a basal section of the cross-shaped elevation surrounded by four large openings through the basement membrane. The cone-cells are no longer visible at this level, and I therefore believe that without penetrating the basement membrane they terminate in these elevations. This belief is further supported by the fact that in transverse sections of the basement membrane the cone-cells distinctly end in the substance of these elevations (Fig. 29, *cl. con.*).

The facts obtained from a study of the lobster's eye support the claim made by Schultze and Grenacher, that the cone-cells and rhabdomes are separate structures. In the case of the crayfish, Schultze, moreover, saw the prolongations of the cone-cells, and traced them into the deeper part of the retina. It is probable that in the crayfish, as in the lobster, the fibrous ends of the cone-cells terminate in the basement membrane, but this Schultze did not see. Such an omission is by no means sur-

prising; for when we reflect upon the methods at his command, it is remarkable what success he had in tracing the course of the fibres, and in demonstrating the relation of the cone-cells and rhabdome.

Patten has advanced the view that the cone-cells are provided with an axial nerve-fibre, and that the cone itself is the true perceptive element. I shall defer the consideration of this topic till I describe the innervation of the retina.

The Distal Retinulæ.

Surrounding each crystalline cone are two pigment-cells, the distal retinulæ. These cells not only surround the cone, but extend as fibres into the proximal part of the retina (Fig. 1, *rtn'. dst.*).

The relation which the distal retinulæ sustain to the cone can be studied most readily in transverse sections. In a section passing through the distal end of the cone (Fig. 4, ommatidium *a*), it will be observed that of the four lateral faces which the cone presents, two, the lower and left-hand ones, are covered by a single retinula (*rtn'. dst.*). The retinula is thickest at the lower left-hand angle of the cone, and becomes thinner the farther it extends on the two adjacent faces. At the more distant edges of these two faces the retinula terminates. Thus the retinula is composed of a central portion and two blade-like extensions. Each blade covers one face of the cone. The second retinula is essentially like the one just described, but lies at the upper right-hand angle of the cone and covers its upper and right-hand faces. In this way the four faces of the cone are sheathed by a pair of retinulæ.

On inspecting the arrangement of the retinulæ in adjoining ommatidia (Fig. 4), it is evident that they are so placed that the thick end of each blade-like portion is opposite the thin end of the blade of a neighboring retinula, and that, in passing along the space between the cones, as one retinula becomes thicker the other becomes thinner. The delicate membranes which separate the blades consequently extend obliquely across the spaces between the cones (Fig. 4). In the space which is left between the angles of four adjoining cones the membranes of the retinulæ are very much thickened. That this is a thickening in the membrane of the retinula, and not due to substance produced by the cone-cells, seems probable for two reasons. First, the membrane is often somewhat thickened in regions between two retinulæ, and where the cone-cells could not well touch it. Such thickenings are directly continuous with the larger ones already mentioned (Fig. 4).

Secondly, in isolation-preparations the thickenings always remain attached to the retinulæ; the cones, on the other hand, are covered with membranes of uniform thickness. The thickening in the membrane is not characteristic of the whole length of the retinula, but is peculiar to the region corresponding in level to the distal end of the cone (Fig. 1).

The foregoing description applies to the structure of the distal retinulæ as seen in the plane of Figure 4. This plane passes through the outer ends of the cones. In other regions the retinulæ present somewhat different conditions. The relation of the retinulæ to the hypodermal squares is shown in a section (Fig. 3) which is slightly more superficial than that just described. The two retinulæ which were located at the two angles of the cones here occupy the corresponding angles of the hypodermal squares. They do not, however, entirely cover the four lateral faces of the square, as they did those of the cone, but from the angles at which they are located they extend over half of each of the adjoining faces. It follows from this that together they flank only one half of the lateral exposure of the square. The blades are now no longer wedge-shaped in transverse section, nor do they overlap neighboring blades, but each one stretches completely across the space in which it lies. Of the lateral surface of the square, that half which is not sheathed by its own pair of retinulæ is covered by the arms of four adjacent retinulæ. Consequently, six retinulæ in all touch each hypodermal square. Two of these belong to the ommatidium which is represented by the square; four belong to adjoining ommatidia. The relation of these will be readily seen by referring to Figure 3.

In passing from the plane in which each cone is surrounded by its own pair of retinulæ to the one in which the corresponding hypodermal square is surrounded by six retinulæ, the blades of the two retinulæ proper to the cone undergo a gradual narrowing; so that, instead of each blade covering the whole of one face of the cone, it covers less and less, and eventually sheathes only one half of the corresponding face of the hypodermal square. As the blades of the retinulæ become narrower, they expose the surface of the cone, but this is still kept covered by the retinulæ of adjoining ommatidia. In any ommatidium there are four blades which become narrow, consequently there are four regions in which adjacent retinulæ touch the cones; and as there is a separate retinula for each region, it follows that four additional retinulæ here come in contact with the cone.

The distal retinulæ touch the cuticula along the band which marks the boundaries of the facets. That the retinulæ contribute to the formation of the cuticula is very improbable, although I believe that it is largely through their interference that the outlines of the facets are produced.

The lateral surfaces of each cone are completely enclosed by retinulæ; the pair of retinulæ belonging to the cone play the principal part. That portion of each retinula which encloses the proximal two thirds of the cone is densely pigmented (Fig. 1). In transverse sections through the pigmented region one can see that each cone is *completely* surrounded by a pigment band. On a level with the middle of the cone each retinula contains a nucleus (Figs. 1 and 5, *nl. dst.*). This is imbedded in pigment. The membranes of the retinulæ are less distinct in the pigmented region than near the distal end of the cone. The only membrane which was observed (Fig. 5) was one which corresponds to the thickened membrane shown in Figure 4. At the proximal end of the cone, the retinulæ rapidly contract till they are reduced to fibres (Figs. 6 and 7, *rtn'. dst.*). The pigment is present for only a slight distance below this level. The fibres of the retinulæ are grouped in pairs, and in this relation extend to the proximal part of the retina. It is noticeable that the two fibres which constitute a pair are derived, not from a single ommatidium, but from two adjacent ommatidia. These fibres when seen in longitudinal sections were probably mistaken by Newton ('73, pp. 328, 329) for an investing membrane. At least, in all attempts to demonstrate the existence of such a membrane I have failed, and there is so strong a resemblance between the fibres of the distal retinulæ and the structure which Newton figured ('73, Plate XVII. Fig. 15) as the cut edge of an investing membrane, that I am inclined to think them identical. Transverse sections from the proper region would have settled the question whether these bodies were fibres or membranes, but unfortunately Newton has not figured any such sections.

The pair of fibres in passing from the basal ends of the cones to the proximal retinulæ retain the same relative position, and are only slightly reduced in diameter. (Compare Figs. 7 and 8, *rtn'. dst.*) Deeper than this, they are still identifiable, and can be distinguished from the fibres of the cone-cells by their slightly greater diameter, and by the fact that they are always in pairs. They lie in the space between four ommatidia. (Compare Figs. 12, 15, and 18.) Till within a very short distance of the basement membrane they maintain the condition shown

in Figure 18, *rtn'. dst.* Beyond this I have not been able to trace them with certainty. The groups are no longer observable, and it is probable that the fibres have separated. I know that in this region the other cells suffer a very considerable rearrangement; and such being the case, it would be a very difficult matter to identify single fibres, especially fibres as small as these are. I have not found any satisfactory method of staining the fibres so as to distinguish them, as in the case of the fibrous ends of the cone-cells. I can therefore claim to have traced the fibres only to within about 20 μ from the basement membrane.

As I have already mentioned, the distal face of the basement membrane has cross-shaped thickenings on it. In the angles which the arms of the cross make with each other, the basement membrane is perforated. There are consequently around each cross four openings through the membrane. Each opening, however, lies between two crosses, so that in reality only one half of each opening belongs to a given cross, or, if one counts whole openings only, half of the four openings, i. e. two openings, belong to each cross. The crosses correspond in number and position to ommatidia, hence there are also two openings for each ommatidium. In each opening, beside three or four large fibres which will be described later, one finds a single small fibre (Fig. 21, *rtn'. dst.*). That this fibre represents the continuation of the fibrous end of a distal retinula seems probable, for two reasons. First, the diameters of this fibre and of the fibrous part of the distal retinulæ are so nearly the same as to be undistinguishable. Secondly, the number of fibres which pass through the basement membrane, two for each ommatidium, agrees with the number of distal retinulæ in each ommatidium. I therefore believe that the small fibres which are seen in the openings through the basement membrane are the proximal continuations of the fibres of the distal retinulæ. If this explanation be true, then it is only natural to expect that, as a pair of fibres approaches the basement, the individual fibres should separate, one passing through each opening. As I have already explained, the fibres, while separated, could be identified only with great difficulty.

If the fibres pass through the basement membrane, as I believe they do, they terminate only a short distance below it. For at about 15 μ below the membrane all of the fibres are of nearly the same size, i. e. somewhat larger than the large fibres which pass through the membrane (Fig. 22). In this region, then, the smaller fibres have either increased to the size of the larger ones, or diminished till no trace of them is left. The fibres here are in groups, however, and these are directly continu-

ous with the groups which pass through the membrane. Each group of large fibres as it passes through the membrane consists of either three or four individual fibres. If the smaller fibres disappear, the groups below the membrane should consist of three or four fibres also; if, on the other hand, the smaller fibres increase in size, the deeper groups should consist of four or five fibres. By either method of change there would be groups of four fibres, so that it is the groups of three or five fibres which will be decisive. As a matter of fact, the fibres are very commonly in groups of three, and not in groups of five; consequently I conclude that the smaller fibres dwindle out a short distance below the basement membrane.

The distal retinulæ have not been identified in many Decapods. Carrière ('85, p. 169) has described them in the eye of Astacus. In Penæus, Patten ('86, p. 634) has observed four cells which belong to the pigmented collar of the retinophora. Two of these, the inner ones, evidently correspond to the distal retinulæ of the lobster. They surround the cones. The other two, the outer ones, appear to have no homologue in the lobster's eye.

The Intercellular Spaces of the Retina.

In the region of the retina which lies between the proximal ends of the cones and the distal border of the deeper band of pigment, the groups of cone-cells and the pairs of distal retinulæ are separated by considerable intervening space (Fig. 1, *spa. i cl.*). This space is filled with a fluid which contains a very small amount of albuminoid substance. Patten ('86, Plate 31, Fig. 73, *x*) has figured a similar fluid-filled space in Penæus. On the application of heat this albuminoid substance in the lobster coagulates and forms larger or smaller vesicular bodies, which vary much in size. They are usually loosely attached to the cone-cells and the fibres of the distal retinulæ. They readily take up coloring matter. They have never been observed in fresh retinas when teased in normal salt solution, nor in maceration-preparations. It was probably these bodies which Newton ('73, p. 329, Fig. 15, *c'*) described as the nuclei on the investing membrane.

In addition to the albuminoid substance which I have described, one occasionally meets with a thin layer of homogeneous material which lies slightly in front of the rounded ends of the proximal retinulæ. This forms a dividing membrane which separates the retina into a proximal and distal portion. The membrane is of course pierced in many places. There is an opening in it for each pair of distal retinulæ, and

each group of cone-cells. In many cases the membrane has not been observed. It was noticed by Newton ('73, p. 328), and as it is non-cellular it is probably a feeble representative of what Herrick ('86, p. 44) has described as a "chitinous" framework in the deeper part of the retina in Alpheus.

The Proximal Retinulæ.

The proximal retinulæ are pigment-cells which closely invest the rhabdome. With the brownish accessory pigment-cells they constitute the proximal band of brownish black pigment on the distal side of the basement-membrane (Fig. 26, *pig. px.*). In some cases they appear to terminate distally in rounded knobs, each of which contains a nucleus (Fig. 1, *rtn'. px.*). In other instances, and these are of frequent occurrence, their distal ends, in addition to having a swollen nucleated part, are prolonged into delicate fibres (Fig. 30). These fibres when present extend toward the outer surface of the retina, and are applied, not to the cone-cells, but to the fibrous portion of the distal retinulæ. The fibres have been traced only a short distance beyond the rounded ends of the cells from which they originate. As the region into which they extend is one readily studied in both sections and maceration preparations, and as these methods of study have given no evidence of fibres other than that of the very short ones already mentioned, it seems fair to conclude that the distal retinulæ terminate as fine fibres a short distance in front of their nucleated portions.

In transverse sections the distal retinulæ first clearly appear in the plane represented in Figure 9. Here each group of four cone-cells is surrounded by a circle of seven retinulæ. The section from which this figure was drawn is in a slightly oblique plane. In moving from right to left, one passes into deeper and deeper regions. In the more superficial part of the section, the right-hand half, each retinula contains a nucleus, which is surrounded by a small amount of pigmented cell-substance. In the deeper part of the section, the left-hand half, the plane is below the region of most of the nuclei, and one sees the seven retinulæ densely filled with pigment. In the next section (Fig. 10), the retinulæ are broader in transverse section. In their expansion they have so far encroached on the space which they surround that it is only large enough to allow the passage of the four cone-cells. The contraction of the space within the circle of retinulæ takes place almost in one plane, as can be seen in the longitudinal section (Fig. 1). In the plane of Figure 10, the retinulæ show a tendency to group themselves.

One can recognize an odd, usually larger retinula, which occupies the lower right-hand corner of each group. The remaining six retinulæ are disposed in pairs. In Figure 11, which represents a plane of section deeper than that shown in Figure 10, the retinulæ, although somewhat reduced in thickness, present nevertheless the same method of grouping as was pointed out in Figure 10. In this plane one also notices next the odd retinula, a nucleus. This is remarkably constant in its occurrence, both as to position and as to the fact that there is always a *single* nucleus. When compared with the nuclei of the surrounding retinulæ, it is found to resemble them very closely. The nuclei of the seven retinulæ are characterized by their sharply marked oval outlines, and by the possession of one or two very distinct nucleoli (Fig. 30, *nl. px.*). In both of these respects the single nucleus agrees so closely with the nuclei of the retinulæ, that, were it not for its somewhat smaller size and deeper position, it could not be distinguished from them. The regularity with which it occurs, and its structural peculiarities, incline me to believe that it represents a reduced retinula in which pigment has never been developed. This belief is further supported by the fact, that the additional nucleus is always found next the larger retinula, which from its great size seems to have replaced a second cell. It is therefore probable that each ommatidium of the lobster's eye possesses eight proximal retinulæ rather than seven, and that one of these is rudimentary.

Below this additional nucleus, the proximal retinulæ pass around the rhabdome. In this region they are deeply pigmented, and so completely envelop the rhabdome that I am of opinion that no appreciable amount of light gains access to it except through the cone-cells. The cone-cells, it will be remembered, extend through the central region of each group of proximal retinulæ, until they almost impinge on the distal end of the rhabdome. Thus, by excluding the retinulæ, they form a transparent shaft, which leads to the distal tip of the rhabdome, and by which that structure can receive light. The rhabdome in transverse section has a four-sided outline. Three sides of the rhabdome are occupied each by a pair of retinulæ. These pairs are composed of the same couples which were previously noticed. (Compare Figs. 10 and 14.) The fourth side of the rhabdome is occupied by the seventh or odd retinula. Thus, again, it is noticeable that this retinula occupies a position where, if perfect symmetry were shown, we should expect two retinulæ. The rhabdome in transverse section is broadest midway of its length. In this position the retinulæ are small, as if closely pressed

against its sides (Fig. 14). Below its middle transverse plane the rhabdome becomes gradually smaller and smaller, till finally it terminates about 15 μ from the basement membrane. As the rhabdome contracts in size, the retinulæ enlarge. (Compare Figs. 14 and 17.)

As I have already mentioned, the retinulæ are definitely arranged around the rhabdome, and this arrangement persists nearly to its proximal termination; but between the end of the rhabdome and the basement membrane the retinulæ rearrange themselves. This rearrangement of the retinulæ is a step preparatory to their passing through the apertures in the basement membrane, the general structure of which has already been described. It will be remembered that under each ommatidium the distal face of the membrane presents a cross-shaped thickening, and that in each of the four angles which the arms of the cross make with each other there is an opening (Fig. 21). The openings are oval in outline, especially on the distal face of the membrane. One end of a given oval lies in the angle of the cross, and the crosses are so close to each other that the other end of the same oval lies in the angle of a neighboring cross. Each opening then lies in the angles of two adjoining crosses, and through it pass two groups of retinulæ, one from each of the two ommatidia to which the crosses correspond.

The four groups into which the retinulæ of a single ommatidium are divided pass one through each of the four surrounding apertures. Three of the groups consist of pairs of retinulæ; the fourth group is represented by only a single retinula. Although these groups agree numerically with the groups of retinulæ, which, as I have already shown, surround the rhabdome, they are not composed of the same individual retinulæ.

For convenience of comparison, numbers can be assigned to the different retinulæ. This has been done in ommatidium *c* (Fig. 15), where the large odd retinula is numbered 1, and the remaining retinulæ, proceeding in a circle to the left, are numbered 2 to 7. On this plan of numbering, the four groups of retinulæ which have been already indicated as surrounding the rhabdome are composed as follows. What may be called the first group is formed of retinulæ 2 and 3, the second group contains retinulæ 4 and 5, the third retinulæ 6 and 7, and the fourth retinula 1. It will be observed (Fig. 15) that the seven retinulæ are also divided into four other groups by the fibres of the cone-cells. Three of these groups are composed of pairs of retinulæ, the individuals of which lie nearest the angles of the rhabdome. In Figure 15, omma-

tidium *c*, these three groups are represented by retinulæ 1 and 2, 3 and 4, and 5 and 6. The fourth group is composed of the single retinula number 7.

The four groups thus defined are identical with the ones which pass through the four openings in the basement membrane. In Figure 21 the four openings which surround the cross (*x*) can be designated from their positions as the upper, lower, right-hand, and left-hand openings. The upper and lower openings each present the transverse section of four large fibres. The right- and left-hand openings are each occupied by three large fibres. The source of these fibres can be ascertained by comparing Figures 20 and 21. In ommatidium *c* (Fig. 20) retinulæ 5 and 6 unite with retinulæ 1 and 2 of ommatidium *d*, and thus constitute the four fibres which pass through the upper aperture (Fig. 21). In a similar way, retinulæ 1 and 2 of ommatidium *c* unite with 5 and 6 of an ommatidium which lies below *c*, and pass as four fibres through the lower opening (Fig. 21). Retinulæ 3 and 4 of ommatidium *c* (Fig. 20) unite with retinula 7 of an ommatidium to the left of *c*, and emerge as three fibres through the left-hand opening (Fig. 21). Retinulæ 7 of *c*, and 3 and 4 of *b* (Fig. 20), unite and form the three large fibres of the right-hand opening (Fig. 21). This plan of distribution is repeated in each ommatidium, and thus brings about the groups of three or four fibres which occur in each opening through the basement membrane. The groups of fibres are distinguishable for only a very short distance below the basement membrane. The individual fibres of each group soon separate, and in the deeper part of the optic nerve they never again present this grouping. The description of the termination of the fibres will be deferred to a later part of this paper.

The relation of the rhabdome to the cone-cells in Homarus has already been described. That they are separate structures, as Schultze and Grenacher have asserted, I believe there can be no doubt. I have seen nothing which favors the view held by Patten, namely, that the rhabdome is an enlargement in the proximal part of the cone-cells. In Homarus the rhabdome has the general form of a spindle. In transverse section, however, it is not circular, but square. Its four sides are thrown into ridges, the crests of which extend across the sides at right angles to its longest axis. The inner face of each proximal retinula is thrown into corresponding undulations. The rhabdome and retinula are so adjusted to each other that a crest on one fits into a furrow on the other. (For a similar condition in Penæus, compare Patten, '86, Fig. 72.) The retinulæ and rhabdome are thus intimately bound

together. On comparing opposite faces of the rhabdome, it will be seen that the crests of one side are in the same horizontal plane as those of the other; but on comparing adjoining faces, it will be observed that the crests of one correspond to the furrows of the other.

In the rhabdome of the lobster I have not found a complicated system of plates, such as Patten describes in Penæus. The substance of the rhabdome in the fresh condition is apparently homogeneous, but in hardened preparations it is finely granular and stratified. The strata are at right angles to the long axis of the rhabdome, and the rhabdomes often break transversely. The stratified condition of the rhabdome, and the close relation which the proximal retinulæ bear to it, support the conclusion that the rhabdome is the product of the proximal retinulæ.

In the structure of the rhabdome there is one peculiarity which, although I cannot explain it, requires some comment. In transverse sections the square area of the rhabdome is often divided into four smaller squares by two intersecting lines (Figs. 13 and 43). I made this observation before I had studied the relation of the distal tip of the rhabdome to the cone-cells, and I concluded then, that, if Patten was correct in believing that the cone-cells and rhabdome were continuous, these four divisions of the rhabdome must correspond to the four cone-cells. I recognized the fact, however, that, if such was the case, the group of cone-cells in the region of the rhabdome was turned through an angle of 45° as compared with its position at the surface of the retina (contrast Figs. 4 and 13). After having satisfied myself that the cone-cells and rhabdome were separate structures, I was forced to the conclusion, that the four segments of the rhabdome were independent of the four cone-cells. That there can be no question of the independence of these two structures is shown by the condition of the cone-cells and rhabdome in Mysis. In all Decapods, so far as I am aware, the cone is formed of four cone-cells, and the rhabdome has four segments; in Mysis, however, the cone is formed of only *two* cells, although the rhabdome has *four* segments.[1]

I can offer no explanation of the cross lines which occur in the rhabdome. As Grenacher ('79, p. 124) has observed, one might at first take them for the outlines of such parts of the rhabdome as were produced by individual retinulæ. There are, however, seven retinulæ, and only four segments. Not only do the numbers disagree, but the position of the lines in the rhabdome is difficult to explain. If the lines are related to the retinulæ, it would be natural to expect that they would coincide

[1] My attention was called to this fact by my friend, Mr. H. H. Field.

with the junction of two retinulæ. As a matter of fact, three lines do come between retinulæ, but the fourth one abuts against the middle of the large odd retinula (Fig. 34). This relation of the cross-lines and retinulæ persists from the earliest stage in the production of the rhabdome, and although the lines are doubtless formed during this process they show a strange independence of the retinulæ.

An exactly similar relation between the cross-lines and retinulæ has been described by Grenacher ('79, p. 124) in Palæmon. I cannot agree with Grenacher in believing that the four lines are due to the fact that only four retinulæ are concerned in the production of the rhabdome. The relations of the retinulæ and rhabdome are the same in the young lobster (Fig. 58) in which the rhabdome is being produced as in the adult. This fact was not known to Grenacher. It shows, I believe, that the rhabdome is the product of the surrounding seven retinulæ, and that the problematic lines have some other significance than that of indicating regions of production.

The Accessory Pigment-cells.

These cells occupy the open space at the base of the ommatidia. They are characterized by possessing a pigment which, as I have before stated, is brownish by transmitted and whitish by reflected light. The cells are bounded proximally by the basement membrane, and their distal ends rarely reach beyond the middle of the rhabdomes (Fig. 1). They are extremely irregular in form, and seem to fit themselves to a cavity of almost any shape. Their function seems to be that of filling what would be otherwise an unoccupied space, as though to lend solidity to the tissue in the base of the retina. (Compare Figs. 13 and 16.) Their nuclei are irregular in form and size (Fig. 18, *nl. pig.*). Judging from the number of nuclei, two or three cells are associated with each ommatidium. The number, however, is variable. The physical properties of the pigment which these cells contain are very characteristic. Streaks of this pigment, and even whole cells, are to be met with in the open space on the proximal side of the basement membrane.

Cells similar to those which I have called accessory pigment-cells have been described by Carrière ('85, p. 169) in Astacus, and by Patten ('86, p. 636) in Penæus. It is highly probable that the yellow pigment which Grenacher ('79, Fig. 114) figured in the base of the retina of Mysis represents accessory pigment-cells as well as the dark pigment which he described ('79, p. 124, Fig. 117) in Palæmon.

The Innervation of the Retina.

The study of the termination of the nerves in the retina is of particular importance, since it affords a means of identifying the perceptive elements. Wherever these elements may be, the ultimate branches of the nerve-fibres must unquestionably lead to them; hence the importance of discovering the termination of the nerve-fibres.

Students who have investigated the compound eyes of Arthropods have held two opinions as to the position in which the nerve-fibres terminate. One school has maintained that the fibres terminate in the crystalline cones, and that therefore these bodies are the perceptive elements. The other school has endeavored to show that the fibres end in the region of the rhabdome, and that for this reason the rhabdome is the perceptive element. I shall not attempt to give an historical account of this subject, but only call attention to the fact, that of late years the majority of writers have expressed the opinion that the rhabdome is the perceptive element, and that the cone is merely dioptric in function. This conclusion has been recently criticised by Patten, who believes the cone to be the perceptive body.

Many of Patten's statements are based upon observations which were possible only by his methods of investigation. On this account, as well as for the reason that his paper is the most important recent contribution to the study of nerve-termination in compound eyes, I shall not refer to the older publications, but limit myself to what he has presented in his article on "Eyes of Molluscs and Arthropods," and to such papers as have appeared since the publication of that work.

When comparing Patten's statements on nerve-termination with those of other recent investigators, I was inclined to believe, since Patten used new and probably better methods of study, that his results were more trustworthy. The contrast between his views and those which are more generally accepted is so striking, however, that in beginning a study of the nerve-terminations the first step to be taken was necessarily one of confirmation. I was unable to obtain the same species of Crustaceans as Patten had used, but I believe that I was safe in assuming that the difference which may exist between the innervation of the retina in Penæus and Homarus could not be a fundamental one, and that the more important feature which had been demonstrated in one genus could be shown in the other. I consequently prepared sections of the retina of Homarus according to the methods which Patten had recommended, and although I was careful in both preparation and

examination of these sections, I was entirely unsuccessful in discovering any trace of nerve-fibres such as Patten had described. I therefore resolved to try his methods of maceration. This I did, following closely his directions as to the strength of solutions, length of time during which reagents should be employed, etc., but my results were again negative. Still adhering to the reagents which he had recommended, especially chromic and sulphuric acids, I varied the time during which the eyes were treated, hoping thereby to obtain a combination more favorable for Homarus. The separation of the elements of the retina was often very successful, but I never saw in any of my preparations systems of nerve-fibres which resembled those figured by Patten. In almost all cases the isolated parts of the retina presented many delicate fibrous projections. These projections might be interpreted as shreds of broken nerve-fibres, although in no case did they show a systematic arrangement. Moreover, they were found on all kinds of tissue. For these two reasons, I believe that they were not broken nerve-fibres, but simply shreds of tissue. The substance of the cones was finely granular, and was never penetrated, so far as I could discover, by any fibres. My results from both sections and isolation preparations were invariably negative; and as my observations had been made upon somewhat over sixty lobsters' eyes, I concluded that in Homarus there was no evidence in favor of the method of nerve-termination which Patten had described. As I have previously mentioned, it is highly improbable that the methods of innervation in the retinas of Penæus and Homarus are fundamentally different, and since I have found in the retina of Homarus no confirmation of Patten's views, I am of opinion that he must be mistaken as to the method of nerve-termination in Penæus. Many of Patten's figures of the individual nerve-fibres in Penæus ('86, Plate 31, Figs. 69, 70, 71) resemble so closely the fibres which I have seen in all of my isolation preparations, and which, for reasons already given, I am persuaded are not nervous, that I am forced to believe that Patten has mistaken for nerve-fibres shreds of non-nervous tissue.

My criticism of Patten's results refers only to those which he obtained from a study of the Crustacea. No one, so far as I am aware, has fully confirmed his views concerning the nerve-terminations in this group. Kingsley ('86, p. 864) claims to have seen the axial nerve-fibre in Crangon, but he was unable to trace its finer ramifications in the cone. He states ('87, p. 57), however, that the method of preparation which he employed was not intended especially for the fibres, and that therefore it is not surprising that they were not identifiable. Herrick

('89, p. 168) could not distinguish fibres in the cones of Alpheus, although, like Kingsley, he admits that his failure may be due to the method which he used. Relative to nerve-terminations, the evidence which the work of these two investigators presents can scarcely be called critical, and I therefore hold to my former conclusion, namely, that the fibres which according to Patten represent the nerve-terminations are in reality not nerve-fibres at all.

After having reached this conclusion, I was naturally led to look elsewhere for the true nerve-fibres. It occurred to me that, in order to be certain that I was dealing with nerve-fibres, it was safer to begin studying them in regions where their identity was beyond question. I therefore examined maceration-preparations of parts of the larger nerves from the lobster's body. These nerves were readily resolved into a number of fibres, which in transverse section were enormous when compared with such fibres as the axial nerve-fibre figured by Patten ('86, Plate 31, Figs. 72, 74, 108). I then studied in a similar way the optic nerve. The fibres in this nerve were smaller than those from the other nerves which I had macerated, but they were much larger than those figured by Patten. Each fibre (Fig. 36) possessed a distinct sheath, and its contents were marked by lines which extended parallel to its long axis. These lines I interpreted as indications of fibrillæ which composed the fibre. In addition to the large fibres, the optic nerve, as well as the other nerves, showed, when macerated, the fibrous shreds which I have previously mentioned. They were very insignificant in amount, forming, I should judge, not more than a fraction of one per cent of the whole optic nerve, and I was never able to trace them as continuous fibres for any considerable distance. I believe that here, as in the retina, they arose from an artificial tearing of the tissue.

At about this time I happened to find the modification of Weigert's method of staining nerve-fibres, which I have described in the Introduction. As soon as I was aware of the results which could be obtained by this method, I applied it to a series of transverse sections of the optic nerve. The series extended from the retina to the optic ganglion, and demonstrated conclusively, I think, that the proximal ends of the seven proximal retinulæ, after passing through the basement membrane, as I have described, continued inward as fibres, and finally passed into the substance of the optic ganglion. Figures 21, 22, 23, 24, and 25 illustrate steps in the passage from the retina to the ganglion. In Figure 21 the groups of three or four proximal retinulæ are seen as they pass through the basement membrane. Figure 22 is taken at a level imme-

diately below the basement membrane. Here two groups of four fibres, and one of three, can be distinguished. Below this level the groups of three and four fibres are no longer to be recognized. The fibres diminish rapidly in diameter as they leave the retina. Figure 23 represents a transverse section of the fibres at one fourth the distance from the basement membrane to the distal face of the ganglion. Figure 24 represents a similar section midway between retina and ganglion. Figure 25 represents the fibres as they enter the ganglion. The same kind of fibres have been identified in the substance of the ganglion. These fibres, I believe, are the true fibres of the optic nerve, and, as I have shown, they connect the seven proximal retinulæ of each ommatidium with the optic ganglion.

The termination of the nerve-fibres in the proximal retinulæ is so directly opposed to the method of termination which Patten has described, that, before making a final statement based on a study of the lobster only, it seemed prudent to seek confirmation in other species. This I have done, and I can now state that the termination of the nerve-fibres in the retinulæ has been demonstrated in Eupagurus, Cambarus, and Gammarus. From this I conclude that it is highly probably that in the compound eyes of all Crustacea the nerve-fibres terminate in the retinulæ.

This method of nerve-termination, namely, the direct continuity of the nerve-fibre and the perceptive cell, has also been demonstrated by Watase ('89, pp. 34–36) in the eyes of Limulus.

There are some interesting phases in the transition from the nerve-fibre to the retinula. On examining the transverse sections of nerve-fibres at a level slightly below the basement membrane, one observes that it is in the form of a transparent cylinder the periphery of which has scattered over it a few pigment granules. As the fibre passes through the basement membrane the pigment increases in quantity, and when the retinula is reached the nerve-fibre is represented by a transparent axis in its centre (Fig. 19, *ax. n.*). The nervous axis is transparent, because it contains no pigment granules, while the peripheral portion of the retinula is densely pigmented. In this way the nerve-fibre proper is continuous as a transparent axial shaft from below the basement membrane to a level in the retina, which corresponds to the middle of the rhabdome. From this level to its distal end the retinula is completely filled with pigment, no trace of a transparent central axis being visible. (Compare Figs. 19 and 14 with Figs. 11, 10, and 9.) The transparent nervous axis of each retinula terminates, as I have said before,

on a level with the middle of the rhabdome. When it is cut very close to its distal end, the nervous axis is seen to lie almost next the rhabdome. I have never seen a case, however, in which the axis and rhabdome were not separated by a line of pigment granules. In transverse sections which have been thoroughly depigmented, the distal half of each rhabdome is surrounded by a great number of bodies which resemble coarse granules (Fig. 32, *fbr'*.). These bodies are limited almost entirely to the distal half of the rhabdome. At first I supposed that they were the colorless skeletons of pigment granules, but they were easily distinguished from the latter by their larger size and sharper outline. It then occurred to me that, since these bodies were found only about that portion of the rhabdome which was distal to the nervous axis, they might therefore be the cut ends of the finer fibrillæ into which that axis had been resolved. If such was the case, these bodies were in reality fibres, not granules. In order to determine whether they were fibres or granules, I examined oblique sections of the rhabdome. Figure 33 is taken from one of these sections. The granular body in the figure is the rhabdome, and the transverse bands are the strata in its substance. The projection of the long axis of the rhabdome in this figure would be a vertical line. The lower end of the figure is proximal, the upper end distal. Owing to the fact that the rhabdome is cut obliquely, what is seen at its proximal end belongs on one side of it, and what is seen at its distal end belongs on the opposite side. The first proximal dark band in the substance of the rhabdome is very nearly midway between its ends. At the proximal end of the rhabdome three distinct fibre-like bodies are seen. These are in reality longitudinal sections of the greatly compressed retinulæ, which have been noticed in transverse sections. (Compare Figs. 15 and 18.) At the distal end of the rhabdome, in place of the three retinulæ, there are a great number of fine fibres. The fibres occur only around the distal half of the rhabdome, and I believe that in transverse sections these fibres are represented by the small round bodies previously described. From the distribution of these small fibres and their relation to the distal end of the nervous axis, I am of opinion that they represent the fibrillæ of the nerve-fibre.

The entrance of the fibres of the optic nerve into the proximal retinulæ is of itself strong evidence that the rhabdome, not the cone, is the perceptive body. This conclusion is further supported by the ultimate distribution of the optic fibrillæ. If it be admitted that the rhabdome is immediately concerned in the perception of light, it is only

natural to expect that this structure would be accessible to the light. As I have already shown, the cone-cells form a transparent axis, which leads directly to the rhabdome, and through which light could readily reach that structure. Once having penetrated to the rhabdome, it is probable that, either in the substance of the rhabdome itself, or in the superficial layer of pigment which immediately surrounds the rhabdome and in which the fibrillæ are, the light is transformed into that kind of energy which is transmitted by nerve-fibres.

The Development.

In discussing the development of the eyes in Arthropods, the more recent investigators have given much attention to the general plan of these organs. One of the objects of their researches has been the reduction of the eyes of these animals to a single structural type. If such a type were found to exist, it would very probably reproduce the essential structural feature which the eye of the ancestral Arthropod possessed. The desirability of ascertaing if there is a common type for the eyes of all Arthropods is evident, for upon the nature of the answer to this question must depend to some extent the conclusions concerning the phylogenetic relationship of the group, and its different classes. Possibly in the phylogeny of two classes of Arthropods the eyes may have originated independently. Of course organs independently developed could not be homologous, and they might be so differently constructed that it would be impossible to reduce them to a common type. Notwithstanding the difficulty in homologizing the eyes of one class of Arthropods with those of another, the homologies among the members of a single class are much more readily determined, and many important comparisons can be safely made. It would, therefore, seem more prudent to limit investigations to the eyes of a single class until they were well understood, rather than institute comparisons between the eyes of different classes, where, from the limitations of our knowledge, such comparisons must be more or less hazardous.

The Plan of the Eye.

The work of different investigators has already suggested several structural types for the compound eyes of Arthropods, but the differences which some of these types present are of such a fundamental character, that to accept one is to reject another. It was with the hope of gaining confirmation for some one type that I was led to study the

development of the eye in a Crustacean, and, as I have previously explained, the species most available for such a study was the lobster.

The results which have been presented in the more recent papers on the embryology of the compound eyes require a brief notice before the development of the eye in the lobster is described. What is said in this connection is purely introductory; no criticism of the views of different authors will be made until after the development of the lobster's eye has been described.

The writers who have thus far published accounts of the development of compound eyes can be grouped under four heads, depending upon the type of eye which their researches indicate. The first type is that represented by the eye of Peripatus. Patten ('86, p. 688, '87, p. 211) is of the opinion that the compound eyes of Hexapods, as well as Crustaceans, are constructed upon this plan. Each eye should then consist of a closed vesicle which was produced by an involution of the hypodermis. The eye would be composed of three layers, which in the order of their positions are as follows: first, the superficial hypodermis; second, the outer wall of the vesicle; and third, the inner wall of the vesicle. Patten is of opinion that in the eye of an adult individual these three layers are modified in the following way: the superficial hypodermis becomes the corneal hypodermis; the outer wall of the vesicle is so far reduced as to be inconspicuous, and the inner wall gives rise to the retina. The retina includes the crystalline cones and the pedicels (rhabdomes). Patten supports these conclusions mainly from theoretical grounds, but he believes that he has found evidence of the existence of this type in the development of the compound eyes of Vespa, Blatta, and the Phryganids.

The second structural type which I shall mention has been advocated by Kingsley ('87, p. 51) in his description of the development of the compound eye of Crangon.[1] In this type the eye results from a vesicular infolding, as in that which was proposed by Patten, but it differs from the latter in the fate which is ascribed to the two walls of the vesicle. According to Kingsley, the outer wall of the vesicle is not reduced, but gives rise to the retina. In it are developed the crystalline cones and the pedicels (rhabdomes). The inner wall of the vesicle, instead of forming the retina, as Patten believed, is converted into a part of the optic ganglion.

The third structural type is that which is presented by Reichenbach ('86, pp. 85–96) in his account of the development of the crayfish.

[1] See the note on page 41.

Here a hypodermal involution takes place, and a vesicle is produced, but the cavity of the vesicle is soon obliterated. The mass of cells which results from the fusion of the walls of the vesicle now divides into an outer and an inner layer. These two layers do not necessarily correspond to the outer and inner walls of the original vesicle. The superficial hypodermis and outer layer of the infolded mass fuse, and give rise to the retina. The crystalline cones are developed in that part of the retina which is derived from the superficial hypodermis; the rhabdomes probably originate in that part which is derived from the outer layer of infolded cells; the inner layer of cells becomes ganglionic.

Bobretsky's ('73) account of the development of the compound eyes in Astacus and Palæmon agrees in its essential features with the description which Reichenbach has given for the eyes in the crayfish. Bobretsky, however, does not describe an involution in the optic disks. As Reichenbach suggests, the fact that Bobretsky did not have the opportunity of studying very early stages may explain his failure to observe the involution. In other respects, the accounts are essentially alike, and there is little doubt that the plan of eye which Bobretsky's researches indicate is the same as that suggested by Reichenbach's studies.

Each of the three structural types which have thus far been described are dependent upon the formation of a hypodermal vesicle. The fourth type is simpler than any of the three preceding ones, in that a vesicle is not necessarily produced, the retina being supposed to originate as a simple thickening in the superficial hypodermis. This type has been advocated by Herrick ('86, p. 43) in his account of the development of Alpheus. The researches of Nusbaum ('87, pp. 171–186) on the development of Mysis indicate the same type. Neither in Grobben's ('79) account of the development of the eyes in Moina, nor in Claus's ('86, pp. 307–324) description of those in Branchipus and Artemia is any mention made of an involution. These authors might, therefore, be cited as favoring the fourth type of eye, although it is to be observed that the special question of the vesicular origin of the eye is not discussed by them.

The advocates of the fourth type find support, not only in the embryology of the Crustacea, but also in that of the Hexapods. According to Carriere ('85, pp. 181–186), the compound eyes of some Hymenoptera and Lepidoptera develop as simple thickenings of the hypodermis.

Of the four types which have been mentioned, the one with which the development of the lobster's eye accords will be seen from the following description.

The first traces of the eyes in the development of the lobster are the optic disks. These disks lie one on either side of the median plane, and are for a considerable time the most conspicuous structures in the anterior region of the embryo. In the early stages of development the disks face ventrally, but as the head of the animal becomes differentiated they come to face almost in the opposite direction, i. e. dorsally. At stage A (Fig. 37) the optic disk, so called, is oval in outline rather than disk-shaped; its longer axis is transverse to the principal axis of the embryo. From that portion of each disk which is near the median plane a band of tissue extends posteriorly, and connects the disk with the ventral plate of the embryo. The disk and the band with which it is connected to the ventral plate are distinguished from the surrounding tissue by their greater number of nuclei. The disks comprise the tissue from which both retina and optic ganglia develop.

A section passing through an optic disk in a plane perpendicular to the longitudinal axis of the embryo is shown in Figure 38. In this case the section is from the right optic disk. The left side of the section is farthest from the median plane; the right side is near that plane. Since *at this stage* the disk faces ventrally, and since the ventral edge of the section is uppermost in the figure, it is the posterior face of the section which is presented. To the right and left of the disk one can see the undifferentiated ectoderm with its occasional nuclei. This ectoderm is directly continuous with the tissue of the disk; in fact, the disk is only a local thickening in the ventral ectodermic layer of the embryo. It is due to its greater thickness that the disk contains more nuclei than the surrounding ectoderm. The deep face of the ectoderm, both of that which is undifferentiated and that which forms the disk, is limited by a delicate but distinct basement membrane (Fig. 38, *mb.*).

Some idea of the method of growth in the optic disk can be gained from a study of its nuclei. It will be noticed that the nuclei in the deeper part of the disk are rather small and irregularly grouped when compared with those which are found next its outer surface. These superficial nuclei form an almost regular series, which extends from one margin of the disk to the other. They are usually also characterized by having their long axes perpendicular to the surface of the disk. When they increase by division, their planes of separation are in most cases either parallel or perpendicular to the outer surface of the disk. When the plane of separation is perpendicular to the surface of the disk, the tendency for such divisions is to increase the diameter of the disk. When, on the other hand, the plane of separation is parallel to the

surface of the disk, the tendency is to thicken it. In order to determine the distribution of these two methods of division, the planes of separation in the superficial nuclei of four disks were carefully observed. Each disk can be divided into halves by a plane parallel to the sagittal plane of the embryo. That half of the disk which lies near the median plane can be called the proximal half; that which is farther from the median plane, the distal half. Among the superficial nuclei of the distal halves of the four disks which were examined there were seen thirteen cases of division. In all of these cases the tendency was to broaden the disk. There was no case where the division of the nucleus would have thickened it. In the proximal halves of the disk there were six cases of division observed; five of these tended to thicken the disk, and one would have broadened it. It is therefore apparent that in the superficial layer of each disk the proximal half is becoming thicker, while the distal half is becoming broader.

The deep nuclei of each disk, those lying below the row of superficial nuclei, divide in different planes. Among these nuclei in the four disks which were examined, seven instances of division were noticed. Five of these were in planes which would have thickened the disk; the remaining two would have broadened it. This part of the disk consequently shows a tendency both to become broader and thicker. Of these two tendencies, that which would thicken the disk is the stronger.

The method of growth which has been described for different parts of the optic disk can be easily distinguished only in its earlier stages. The subsequent changes which affect the structure of the disk render it rather difficult to follow in detail the growth of the disk as a whole; but in general the broadening of the distal superficial region, the thickening of the proximal superficial part, and the broadening and thickening of the deeper parts are continued.

The most important changes in the differentiation of the optic disks are the following: first, the separation of the retina and optic ganglion by the formation of the basement membrane; second, the production of the optic nerve; and third, the differentiation of the ommatidia. These three changes will be considered in the order named.

The first step in the differentiation of the retina and optic ganglion occurs at stage B. Figure 39 represents a section from the optic disk of an embryo of this stage. The plane of section in this case corresponds to that of Figure 38. The chief difference observable between the disk at stages A and B is its greater thickness in the older embryo. Not only has the disk thickened, but it has spread laterally, so that the small

angle which is seen on the outer margin of the disk in stage A (Fig. 38, *x*), and which indicates a tendency on the part of the disk to grow over the adjacent ectoderm, is represented in stage B by a very acute angle (Fig. 39, *x*), while the disk itself forms an actual fold, which covers a portion of the undifferentiated ectoderm.

The separation of the retina and its ganglion is accomplished by the production of a basement membrane. This is gradually developed in the substance of the disk between the regions of the retina and the optic ganglion. In order to distinguish the newly formed membrane from the original basement membrane which bounds the under surface of the disk, I shall speak of the former as the *intercepting membrane*. The intercepting membrane (Fig. 39, *mb. i cpt.*) takes its origin from the basement membrane on a line a little within the lateral edge of the disk. From this position it extends at this stage as a delicate lamella for a short distance through the tissue of the disk. The direction of its course is approximately parallel to the outer surface of the disk, and it divides the distal portion of the disk into two masses, one of which is superficial, the other deep. The superficial mass is the first portion of the retina to be differentiated, and, as I have previously stated, the growth in this region is chiefly lateral. The deep mass is the beginning of the optic ganglion. The intercepting membrane does not extend so far as to separate the superficial portion of the disk from the deeper part in the proximal half. This condition is what one might expect, since in the proximal region of the disk the superficial nuclei divide in such planes as to thicken the disk, and a membrane which would separate the deep and superficial parts would be a source of interference in the process of thickening.

The intercepting membrane is not an involution of the original basement membrane, but is produced by the activity of the ectodermic cells between which it lies. There is no reason for doubting, I believe, that at this early stage (B) it is strictly an ectodermic secretion. At this stage it is fan-shaped, the handle of the fan being formed by that part of the membrane which is in contact with the original basement membrane. The plane of the fan is parallel with the outer surface of the disk. In sections which are either anterior or posterior, but parallel to that shown in Figure 39, portions of the intercepting membrane are often visible, and may be apparently unconnected with the basement membrane. This is due to the fact that the plane of section cuts the anterior or posterior edge of the fan without including the handle.

The chief difference between the intercepting membranes at stages

B and C is the greater extension of the membrane at stage C. (Compare Figs. 39 and 41.) The retina is now much more completely separated from the ganglion than formerly. The superficial and deep portions of the proximal part of the disk are, however, still continuous.

In stage D (Fig. 45) an important step is taken in the development of the membrane. It splits at this stage into two layers, one of which adheres to the retina, and the other to the optic ganglion. The retinal and ganglionic layers of the membrane have probably been distinct from the time of their formation; but until stage D is reached, the double nature of the membrane is not apparent. Occasionally in stage C one notices at the point where the intercepting and basement membranes unite a re-entrant angle (Fig. 41, *x*). This in some cases extends a short distance between retina and ganglion, and doubtless represents the first step in the separation of the components which form the intercepting membrane.

In stage E (Fig. 46) the membrane has completely severed the superficial from the deep ectoderm, and the separation of its retinal and ganglionic constituents extends over a broader area than in the previous stage.

The subsequent changes in the intercepting membrane consist in a complete separation of its retinal and ganglionic portions. This separation is effected by the withdrawal of the optic ganglion from the superficial ectoderm. In the adult, the ganglionic membrane remains relatively thin, but the retinal membrane becomes much thickened. This membrane, which has already been described as the basement membrane of the adult retina, is not uniformly thickened, but presents local elevations, each of which is in the form of a cross. The four apertures which pierce the membrane in the angles of the cross-shaped elevations, and the relation which adjoining crosses and apertures bear to one another, have already been described. The proximal face of the basement membrane is nearly flat (Fig. 29). The cross-shaped elevations occur on its distal face. The substance of the membrane is apparently homogeneous, and contains no traces of cells or nuclei. The fact that its substance is alike throughout favors the idea that it has been derived from a single source. From stage E to the adult condition a few mesodermic cells have been noticed next its proximal face (Fig. 1, *cl. ms d.*). These cells are not intimately attached to it, and I am of opinion that they contribute little or nothing to its composition.

From the foregoing account I draw the following conclusions concerning the growth of the basement membrane of the eye. In its earliest

stages the basement membrane is strictly ectodermic in origin. In the adult condition it is much thicker than in its early stages, and the greater part of its substance has probably come from the ectoderm, although mesodermic cells rest against its proximal face, and possibly may contribute to its formation.

From the description which I have given, it is evident that the optic disks are thickened regions in the superficial ectoderm, and that these disks are cut by an intercepting membrane into two parts, one deep, the other superficial. The deep part is converted into the optic ganglion ; the superficial part becomes the retina. So far, then, as the development of the retina in the lobster is concerned, it supports the view that the compound eye in Crustaceans is developed from a simple thickening of the ectoderm.

In describing the formation of the retina and optic ganglion in the lobster, I have made no mention of an involution. Both Reichenbach and Kingsley have described an infolding in the formation of the eyes, — the former in Astacus, the latter in Crangon, — and it is therefore only natural to look for a similar condition in the eyes of Homarus. Any evidence of an involution in the production of the lobster's eyes is to be sought in the early stages of development. I regret that in the very early stages my material is deficient, and I have not grounds enough to warrant the statement that no involution occurs. All that I can state is, that in all stages which I have examined I have not been able to find any evidence of an involution. The youngest individual which I have studied was one in which the optic disk was about two thirds as thick as that represented in Figure 38. Excepting its thinness and the smaller number of its nuclei, it presented essentially the same appearance as the one which is figured. It will be noticed that near the centre of the disk in Figure 38 there is a space devoid of nuclei. It occurred to me that such a space might represent the last traces of an involution, and I therefore plotted carefully the nuclei in five pairs of disks, some of which were less mature than the disk shown in Figure 38. The result of the plotting was that the light space which is seen in Figure 38 proved to be an individual peculiarity, and I did not find in the arrangement of the nuclei in the other disks any evidence of an involution.

The plotting of the nuclei, however, brought to light the method by which the disks increased in size. This has already been described, and offers, I believe, an explanation of the fact that in some cases, as for instance in the crayfish, the formation of the eye is attended with an involution, while in other instances, as in Alpheus, no involution is present.

It will be remembered that the superficial layer of nuclei in the optic disk of the lobster was divided into two regions. The one farther from the median plane has been called the distal region; the one nearer, the proximal region. The broadening of the distal region produced the retina. By a proliferation of its cells the proximal region resulted in the formation of the optic ganglion. It is my opinion that this proliferation of cells represents what is produced in the case of some Crustaceans by an involution, and that either an involution or proliferation, or possibly a combination of both processes, occurs in the eyes of all Crustaceans. Whichever process characterizes the development of a given eye, it must be borne in mind that the involution or proliferation is connected with the formation of the ganglion only, and takes no part in the production of the retina. The latter is a simple thickening in the ectoderm; the optic ganglion is developed either as a proliferation or involution of the ectoderm which lies close beside the retina. The results at which various investigators have arrived, different as they may at first appear, can be harmonized, I believe, by this interpretation of the origin of the retina and optic ganglion.

In his account of the development of the eye in the crayfish, Reichenbach ('86, p. 85) has described an ectodermic involution, which occurs nearly in the centre of the optic disk. That portion of the disk which is farther from the median plane than the region of involution gives rise to the retina, so that the region of involution in the crayfish occupies a position which corresponds to the region of proliferation in the lobster. Not only do the two regions correspond, but the masses of tissue which are developed from each have certain peculiarities common to both animals. In the case of the crayfish the mass of tissue which results from the involution becomes divided into an outer and an inner wall. These two walls are separated from each other by a band of nuclei, which are larger and lighter in color than the surrounding nuclei. In the lobster the ganglionic tissue which arises by proliferation is divided into an outer and an inner part. The separation is effected by a band of nuclei, which in position and structure resemble the band figured by Reichenbach. (Compare Reichenbach, '86, Plate XII. Fig. 174, and Plate III. Fig. 41 of this paper.) The similarity presented by the bands of nuclei in the lobster and crayfish supports the conclusion that the involution in the crayfish and the proliferation in the lobster are homologous structures.

An objection to this comparison might be raised on the ground that, according to Reichenbach's statement ('86, p. 93), the involution in the

case of the crayfish gave rise to a mass of tissue which formed on the one hand the deeper part of the retina, and on the other a portion of the optic ganglion, while the cells which arise by proliferation from this region in the lobster produce only a part of the optic ganglion. But, as Patten ('87, pp. 208, 209) has shown, Reichenbach himself was not certain that any part of the infolded ectoderm contributed to the formation of the retina. Reichenbach found it difficult to locate exactly the position which the developing rhabdomes occupied. On page 92 in his account he describes a part of the outer wall (Ausserwand) of the infolded ectoderm, and states his belief that in it the rhabdomes develop; in fact, he describes certain red bodies which he says are without doubt the rhabdomes themselves. On page 96 he admits that the layer in which he supposed the rhabdomes originated may be a layer of nerve-fibres. Granting this interpretation, it is no longer possible to consider the previously described red bodies as rhabdomes. Reichenbach does not make this last statement, but his description implies it when he states that, although the region of the red bodies may not be the region of the rhabdomes, yet the rhabdomes doubtless originate in a somewhat more superficial part of the outer wall. Apparently he has not identified the rhabdomes in their new position; at least, he makes no such statement in his text or description of plates. Since he has also admitted that the red bodies may not be rhabdomes, I cannot see that he has positively identified any structure as a rhabdome. Such being the case, it is difficult to understand on what grounds he can maintain the assertion that the rhabdomes develop in the outer wall. If this assertion cannot be defended, then it is possible that they may develop in the superficial hypodermis. This would be analogous to the condition presented in the lobster.

If the rhabdome in the eye of the crayfish is developed, as I believe it is, in the superficial hypodermis, and not in the outer wall of the infolded hypodermis, the objection which was suggested in homologizing the involution in the eye of the crayfish with the proliferation of cells in the eye of the lobster has no weight.

In the development of the eye of Crangon, according to Kingsley's ('86[a]) account, there is also an optic invagination. If what I have attempted to show in regard to the eyes of the crayfish be true, then this invagination in Crangon should be connected with the formation of the ganglion only. This, as I have already stated, is not the view held by Kingsley, for he maintains that the outer wall of the invaginated pocket gives rise to the retina, and only the inner wall is concerned in the pro-

duction of the ganglion. This is fundamentally different from the condition found in the lobster. The difference, however, is due, I believe, to the fact, that in describing the later stages of development Kingsley has pointed out a cavity which he believed to be the cavity of the invagination, but which in reality is not. The cavity which he has marked *oc* in his Figures 3, 4, and 5, is unquestionably the cavity of involution, but the space marked *oc* in his other figures is, in my opinion, a part of the body cavity.

My reason for this belief is as follows. The cavity of an involution such as is found in the anterior median eyes of spiders or the median eyes of scorpions is, when it has lost its connection with the exterior, a closed ectodermic sac. That such a cavity should be occupied by migrating mesodermic cells seems to me extremely questionable, for in order to enter the cavity it would be necessary for the cells to penetrate one wall of the vesicle. This of course is not impossible, but it is not borne out by analogy with the Arachnoids. The cavity which Kingsley has marked *oc* in Figure 7 is occupied by several mesodermic nuclei, and what is more important, perhaps, is that it is apparently connected with other cavities in the embryo. These cavities also contain mesodermic tissue. Excepting Figures 3, 4, and 5, the cavities marked *oc* I believe to be homologous, and I further believe that they represent, not the cavity of involution, but the space which intervenes between the infolded pocket and the superficial ectoderm. This is a part of the embryonic body cavity, and is of course readily accessible to mesodermic cells. The fate of the real cavity of involution is not so easily discovered. Probably, as in the case of the crayfish, it is obliterated in the mass of tissue from which the retinal ganglia arise.[1]

If the interpretation which I have suggested in the preceding paragraph be admitted, the development of the eye in Crangon is essentially the same as in the lobster and crayfish. The proliferation in the optic disks of the lobster is represented by an involution in the disks of Crangon. The cavity of the involution disappears in Crangon, and its walls give rise to ganglionic tissue. The part of the superficial ecto-

[1] Since this paper was written, I have received a copy of the third part of Kingsley's studies on the development of Crangon. As the following quotation will show, Kingsley ('89, p. 20) has materially changed his views as to the formation of the retina: "I may say here that I am inclined to believe that I fell into error in my account of the development of the Compound Eye of Crangon, and that the invagination or inpushing which I there described as giving rise to the ommatidial layer of the eye, in reality gives rise to the ganglion of the eye which in the adult is contained within the ophthalmic stalk."

derm which is immediately external to the ganglionic involution thickens and produces the retina.

The mode of development which Patten has suggested for the compound eye of Arthropods has not received any support, so far as I am aware, from the embryology of the Crustacean eye. The only observations which go to confirm Patten's opinion are those of his own on Vespa, Blatta,. and the Phryganids. Possibly the compound eyes of Crustaceans may be developed upon a different plan from those of Hexapods. Certainly the evidence which Patten has given for the Peripatus-like type of the compound eye of Hexapods has not been found in any of the Crustacea. According to Patten's view of the origin of the compound eyes, the corneal hypodermis should arise on the sides of the optic area, and spread over the retina until the latter is entirely covered. This constitutes the closing of the shallow vesicle. When I come to describe the differentiation of the ommatidia, I believe it can be shown beyond a doubt that in the lobster the corneal hypodermis arises, not by any lateral growth from the edge of the optic area, but by a simple process of delamination. The cells of the corneal hypodermis are the differentiated superficial cells of that thickening in the hypodermis which produces the retina. Thus the plan which Patten has suggested for the compound eyes in Arthropods is not supported by the evidence derived from the development of the lobster. Patten himself ('87, p. 202) admits that in Vespa he did not see the closure of the hypodermis over the retina, and that in Blatta and the Phryganids ('87, pp. 208 and 211) the process is very obscure.

The researches of Carrière point to a type of compound eyes for the Hexapods which is similar to that exhibited by the lobster. It is possible that the vesicular origin of the compound eyes of Hexapods, owing to their obscure method of formation, may have been overlooked by Carrière, but I am inclined to believe, after a consideration of both sides of the question, that the evidence favors the simpler method of origin, and therefore that the compound eyes of Hexapods as well as Crustaceans arise as simple hypodermal thickenings.

In Mysis, according to Nusbaum ('87, pp. 171–185), the development of the eye follows essentially the same course as that which I have described in the lobster. The optic disks are formed and the ganglionic and retinal portions are differentiated in the same manner in both cases. The development of the retina is slightly complicated in Mysis by the fact that, instead of lying in one plane, or very nearly so, the retina is strongly folded on itself, so as to give the appearance of two lamellæ, an

internal and an external one. The retinal elements are differentiated earliest in the internal lamella. As the eye becomes more distinctly separated from the body, the internal and external lamellæ are unfolded so that they are no longer distinguishable as separate parts. The retina is developed from the thickened layer of hypodermis. So far as Nusbaum's observations extended, the ganglion is produced without an involution.

The development of the compound eye in Alpheus has been studied by Herrick ('86, '88, and '89). The course of development is almost identical with that of the lobster.[1] The optic disks after they thicken are cut by a basement membrane into a ganglionic and a retinal portion. There is no involution connected with the formation of the eye.

In the introduction to the development of the lobster's eye, mention was made of four structural types which the work of different investigators indicated as possible plans for the compound eyes of Crustacea. I have given reasons for excluding three of these. The type of eye which Patten has advocated is unsupported by the embryology of the Crustacea. Reichenbach and Kingsley misinterpreted structures in the eyes which they studied, and were consequently led to erroneous conclusions. If the interpretations which I put on the work of these two investigators be admitted, all studies on the development of the compound eyes of Crustacea point to one conclusion, namely, that in these eyes the retina originates as a thickened layer of hypodermis, and is not modified by any form of involution. The involution when present is connected with the formation of the optic ganglion only. In the production of the ganglion, the involution can be replaced by a proliferation of the cells.

The Optic Nerve.

The development of the optic nerve[2] is intimately connected with the formation of the intercepting membrane. Before the formation of this

[1] I have had an opportunity of examining Dr. Herrick's unpublished plates on the development of Alpheus, and Dr. Herrick has kindly looked over my figures of the lobster. The correspondence between the method of growth in the eye of Alpheus and Homarus is certainly very close. The few differences that were noticed were such as might be expected between different species. I take this opportunity of thanking Dr. Herrick for his kindness in extending to me the use of his plates.

[2] The optic tracts of a lobster consist of four principal parts. The first of these is the retina, from which nerve-fibres lead to the optic ganglion. These three

membrane the retina and ganglion is one continuous mass of cells (Fig. 38). When the intercepting membrane is formed, the retina and ganglion are apparently separated (Fig. 39). I am of opinion, however, that this separation is only apparent, and that in reality the two structures are still in connection. At least in this stage and in stage C (Fig. 41) nuclei are frequently found lying directly across the membrane. These nuclei present so normal an appearance, and their occurrence is so frequent, that I cannot believe that their position is due to accidental displacement. My only way of accounting for the place which they occupy is by supposing that the basement membrane is perforated where they are found. The membrane was probably produced in the form of a net, through the meshes of which the retina and ganglion retained their original connection. Either this is true, or it must be admitted that the retina and ganglion were first connected, then separated, and finally reconnected; a supposition which seems to me unnecessary as well as improbable. From stage C to the adult condition the retina and ganglion are unquestionably connected by nerve-fibres. If the conclusion arrived at concerning the origin of the optic nerve is correct, it follows that the optic nerve cannot be properly described as an outgrowth either from the retina or from the ganglion, but it must be considered as a remnant of the original connection which existed between retina and ganglion. Patten ('87, p. 196) has described essentially the same method of origin for the optic nerve of Vespa. The formation of the optic nerve from tissue which represents the original connection of a portion of the optic ganglion with the superficial ectoderm is doubtless a reproduction of the method by which that nerve arose phylogenetically.

The fact that the fibres of the optic nerve are from the outset attached to the proximal ends of the retinulæ is of significance in determining the plan of the eye. Of the four structural types of compound eyes which have been suggested, that which Kingsley has presented involves the inversion of the middle or retinal layer. Mark ('87, pp. 91, 92) has shown that when the retina is inverted, as in the anterior median eyes of spiders, the nerve-fibres are at first attached to the morphologically deep ends of the retinal cells, and that the attachment afterwards migrates toward the other ends of these cells. From the fact that in

parts, retina, nerve, and ganglion, are contained in the eye-stalk. The fourth part is a second bundle of nerve-fibres which connect the optic and cephalic ganglia. In using the term optic nerve I refer to that collection of fibres which unites the retina and optic ganglion.

Crustaceans the nerve-fibres are always attached to the proximal ends of the retinulæ, it can be argued that the retina in this group has never been inverted, but retains its original position, and that any structural plan which involves the inversion of the retina is therefore probably wrong.

The Differentiation of the Ommatidia.

In the development of the compound eye in the lobster, the deposition of pigment and the differentiation of the ommatidia take place at about the same time. These changes occur at stage C. (Compare Figs. 39, 41, and 42.) At this stage (Fig. 41) it will be observed that the retinal layer is thickest at the lateral margin of the disk (the extreme left in Fig. 41). The retina becomes thinner as one proceeds from the margin toward the median plane (from left to right in the figure). The thickest part of the retina, it will be recalled, was the part first to be separated from the ganglion by the intercepting membrane. As it was the first part of the retina to be separated, so it is the first part in which the ommatidia are differentiated and pigment is deposited.

The first steps in the differentiation of the ommatidia are seen in Figure 42. Here the nuclei in the thicker part of the retina have separated into two bands, one distal (*y*), and one proximal (*x*). The distal band, as I shall presently show, can be further separated into a superficial and deep layer. These two layers are close to the outer surface of the retina, and approximately parallel with it.

The arrangement of the nuclei which make up the distal band is most easily observed when the retina is viewed from the surface. The grouping of these nuclei, from the time when the ommatidia are differentiated to the adult condition, is so characteristic that the fate of the individual nuclei can be easily traced. For the sake of simplicity I shall therefore designate the different nuclei, from their first appearance in groups, by the names of the cells in which they are ultimately found, although it is to be borne in mind that in the early stages the cell walls are not as yet differentiated.

Viewed from the surface, the superficial layer of the distal band of nuclei presents the appearance which is shown in Figure 43. In this layer there are two kinds of nuclei, one elongated, the other roundish. The elongated ones are always in pairs. They ultimately become the nuclei of the corneal hypodermis. These hypodermal nuclei arise from among the superficial nuclei of the distal band, and do not originate, as Patten believed ('86, p. 645), from a fold which grows over the retinal

area. Of course the number of pairs of hypodermal nuclei equals the number of ommatidia. In the earliest stages in which the ommatidia have been seen there were always three or four pairs of hypodermal nuclei, so that it is probable that the first step in differentiation is the simultaneous production of three or four ommatidia.

The second kind of nuclei in the superficial layer are roundish and arranged in circles of six around each pair of hypodermal nuclei. The circles are so combined that each nucleus plays a part in three circles; and as there is one circle for each ommatidium, it follows that only one third of each nucleus belongs to a given ommatidium, or, if one estimates the nuclei as units, only one third of each circle of six nuclei, or two nuclei, belong to an ommatidium. These nuclei represent the cells which in the adult have been called the distal retinulæ, and of which there was a single pair to each ommatidium.

The deep layer in the distal band of nuclei lies directly below the superficial layer (Fig. 42). The nuclei which constitute this layer are all of one kind, and are arranged in groups of four (Fig. 44). They represent the cells of the crystalline cones. The centre of a given group of cone-nuclei is directly below the centre of a pair of hypodermal nuclei. At this stage the cone-cells can be observed as elongated pyramids, which lie with their bases in the region of their four nuclei, and their apices extending into the deeper part of the retina (Fig. 42).

The nuclei of the proximal band show at this stage no special arrangement. They migrate to the deeper part of the retina, and there undergo further change. Between them and the basement membrane the pigment is deposited.

The most noticeable changes which the retina as a whole now undergoes are two. First, it thickens until it is throughout nearly as thick as in the region where the ommatidia were first differentiated. (Compare Figs. 45 and 46.) Second, the number of ommatidia greatly increases. These two changes, the thickening of the retina and the production of new ommatidia, go hand in hand and spread over the general surface of the eye, from the region in which the first ommatidia appear. It is worthy of notice that the new ommatidia are constructed from the undifferentiated cells which immediately surround the area of ommatidia already formed. Cells once incorporated in a given ommatidium never in any way contribute to the formation of other ommatidia. Moreover, in the differentiation of an ommatidium no cells are left between it and the neighboring ommatidia, so that ommatidia once adjoining each other remain so. In other words, new ommatidia are not

produced between old ones, but only on the edge of the ommatidial area.

The changes in the ommatidia themselves can be studied most readily in longitudinal and transverse sections of the retina. Figure 47 is an enlarged drawing of that portion of the retina which is marked by a bracket in Figure 46. It will be noticed that in this stage, E, the nuclei are limited for the most part to the distal half of the retina. The middle of the retina is occupied by a band of pigment, which gradually fades as it approaches the basement membrane. The space between the basement membrane and the ganglion is relatively narrow, and is occupied chiefly by nerve-fibres. Returning now to the nuclei in the distal half of the retina, it is to be observed that the general arrangement which was pointed out in the last stage also persists here. The nuclei of the distal retinulæ are still in circles of six (compare Figs. 47 and 48, *nl. dst.*), and are very close to the external surface of the eye. In the centre of each circle is seen a round pink body, the tip of the cone-cells (Fig. 48 *con.*). Directly below the level of the nuclei in the distal retinulæ are the pairs of nuclei belonging to the corneal hypodermis (Figs. 47 and 49, *nl. crn.*). Each pair of corneal nuclei surrounds the distal end of the cone.

Below this level one meets the four nuclei of the cone-cells (Figs. 47 and 50, *nl. con.*). From the side view (Fig. 47) it will be seen that the groups of cone-cells are spindle-shaped in outline, and have their nuclei arranged in a transverse plane at the thickest part of the spindle. The nuclei which in stage C formed the proximal band are scattered in this stage between the deep ends of the cones (Fig. 47, *nl. px.*). They are not definitely arranged. In order to estimate the number of nuclei in the proximal band for each ommatidium, I counted these nuclei as seen in a series of tangential sections. In the outermost section in which the proximal nuclei occur there were six nuclei around each cone. These nuclei, however, were arranged in circles similar to the circles of the corneal nuclei; consequently for each ommatidium there were only two nuclei in each circle of six. The remaining nuclei were all embraced in the two succeeding deeper sections. In each of these two sections there were about nine nuclei around each cone. The arrangement of these nuclei was extremely irregular, and it was consequently difficult to estimate the number of nuclei which belonged to one ommatidium. Most of the nuclei were situated between three cones, therefore, about one third of the nuclei around a given cone can be considered as belonging to the ommatidium represented by that cone. As there were in

these two sections about eighteen nuclei around each cone, it follows that one third of this number, or six, represents approximately the number of nuclei for each ommatidium. If then the deeper sections contain six nuclei for each ommatidium and the outermost section two, the total number of proximal nuclei for each ommatidium must be eight. I do not mean to imply that this estimate can be insisted upon as absolutely invariable; but I wish to show that, as these nuclei represent the proximal retinulæ in an adult lobster's eye, and as there are eight such retinulæ and about eight of these nuclei to an ommatidium, the change which the eight embryonic cells undergo in becoming adult retinulæ is chiefly that of arrangement, and certainly does not involve any considerable increase in numbers.

At stage E, which was the one last described, the young lobster was about to escape from the egg-shell. The next stage, F, is that of a lobster about one inch in length. At this stage the optic lobes are represented by optic stalks, and the distal rounded end of each stalk is occupied by the retina. Figure 51 represents a longitudinal section of a single ommatidium from this stage. The distal end of the ommatidium is covered with a well developed corneal cuticula. The cuticula is marked out into hexagonal corneal facets (Fig. 52). The facets of course indicate the arrangement of the ommatidia. This arrangement at the first differentiation of ommatidia was such that hexagonal and not square facets would have resulted if a cuticula had been then produced.

Directly below each corneal facet is a pair of crescentic nuclei, those of the corneal hypodermis (Fig. 53, *nl. crn.*). These nuclei have in all preceding stages shown a tendency to become elongated and crescentic in outline, but it is in this stage that this peculiarity reaches its highest development. Between each pair of hypodermal nuclei the distal end of the cone-cells is usually seen (Fig. 53, *con.*). The four cone-cells with their nuclei occur immediately below the corneal hypodermis (Figs. 51 and 54, *nl. con.*). The cone itself is already formed in part, and lies below the nuclei of the cone-cells. Proximally the four cone-cells can be traced to near the middle of the retina; here they are no longer distinguishable. The proximal end of the cone itself terminates as four processes, one on the outer lateral wall of each cone-cell (Fig. 56). Surrounding the cone about midway on its length are the nuclei of the distal retinulæ (Figs. 51 and 55, *nl. dst.*). In transverse sections of stage F, these nuclei show the same grouping in circles of six as they showed in previous stages. The outlines of the retinulæ are not visible.

The substance in which the nuclei lie contains a few granules of pigment. Below the proximal end of the cone the nuclei of the proximal part of the retina can be seen. These are not so definitely arranged that they can be counted. They occur on several planes. Fortunately, their cells in this stage have very distinct outlines, and a short distance below the nuclei one can see with perfect clearness the seven retinulæ which surround each rhabdome (Fig. 57, *rtn'. px.*). Occasionally, as is seen in Figure 57, the nucleus of the retinula occupies a position in its cell as deep as the plane of this section. The proximal retinulæ contain a few pigment granules. On account of the great similarity of the groups of proximal retinulæ, I have not been able to plot and superimpose sections with certainty; and as the nuclei of the proximal retinulæ are placed at different levels I have not succeeded in identifying an eighth nucleus, which, it will be remembered, was pointed out in the histology of the adult eye as probably representing a degenerate retinula.

At this stage the first trace of the rhabdome appears (Fig. 57, *rhb.*). It is a cylindrical thickening in the centre of each group of proximal retinulæ, and extends from a short distance below the crystalline cone very nearly to the basement membrane. From its earliest appearance it is divided into four segments, which bear the same relation to the surrounding retinulæ as they do in the adult. (Compare Figs. 58 and 34.) Nothing has been observed in the development of the rhabdome which indicates the significance of the four lines by which the segments of the rhabdome are separated.

Owing to a lack of distinctness in the tissue near the basement membrane, I have been unable to identify the individual retinulæ in that region. What I have observed is, that fibres pass from the retina through the basement membrane and into the optic ganglion. Presumably these fibres are from the proximal ends of the retinulæ, and are grouped as I have described in the retina of mature lobsters.

At this stage the only observation which I have made bearing on the question of nerve termination is as follows. In each proximal retinula near the rhabdome there are one or two fibres which extend nearly the whole length of the retinula. In transverse sections they of course appear as dots (Fig. 58, *fbr'.*), and might be mistaken for the remains of pigment granules were it not for their sharper outlines and the regularity of their arrangement. I am of opinion that they are the first indications of nerve-fibrillæ, which, as I have pointed out in the section on Histology, lie in the adult eye next the rhabdome.

The cells which I have thus far described in the differentiation of the ommatidia are unquestionably ectodermal in origin. In stage F certain nuclei appear which may have another origin. It will be recalled that in stage C (Fig. 41), although the intercepting membrane is well developed, the retina and optic ganglion are still closely applied to each other. In stage D (Fig. 45) the retina and ganglion have separated enough to form an intervening space of considerable extent. In stage E (Fig. 46) this space not unfrequently contains several nuclei. These are smaller than the ectodermic nuclei in the retina, and of about the size of those in the ganglion. Their chromatine differs from that of both the retinal and ganglionic nuclei, in that it has the form of very distinct particles which give the nucleus a decidedly granular appearance. Moreover, these nuclei, which I believe to be mesodermic in origin, are variable in shape, whereas the different kinds of ectodermic nuclei possess characteristic forms (Fig. 47). In stage F the space between the retina and ganglion also contains a few mesodermic nuclei, and similar ones are noticeable in the base of the retina (Fig. 51, *nl. pig.*). The latter are different from the nuclei of the proximal retinulæ (Fig. 51, *nl. px.*), and resemble so closely the nuclei which in the adult have been described as belonging to the accessory pigment cells, that I believe them to be the nuclei of those cells.[1]

From stage F to that of the fully grown lobster the changes in the retina are, with one exception, rather insignificant. The parts of the retina increase considerably in size, especially at the distal end of the ommatidium, and additional pigment is deposited in the distal and proximal retinulæ. The only change of importance which the eye undergoes before full maturity is reached is a rearrangement of the ommatidia. It will be remembered that up to stage F the ommatidia were so arranged in relation to each other that the resulting corneal facets were hexagonal in outline. In the adult lobster the facets are square. The change from the six- to the four-sided facet is effected, I believe, by a partial slipping of rows of ommatidia on each other. Imagine, in Figure 55, a row of ommatidia extending in the direction of the arrow and on either side, and parallel to this another row. Only one ommatidium in each of these two lateral rows is given in the figure.

[1] When the preliminary notice of this paper was written, I was somewhat in doubt as to the origin of the accessory pigment-cells. I had not then had the opportunity of studying stage F, and I was of opinion that these cells were probably of ectodermic origin. I believe that the evidence which is now at hand indicates that they are cells derived from the mesoderm.

Suppose the individual ommatidia of the three rows to be arranged in reference to one another as the four in Figure 55; i. e. the ommatidium of one row covering the open spaces between two ommatidia in the adjoining row. Under these conditions hexagonal facets would be produced. But now imagine the middle row to move in the direction of the arrow through the distance of half the thickness of an ommatidium. After the completion of this movement, the ommatidia of the middle row are directly opposite the ommatidia of the adjacent rows. With this arrangement the ommatidia can be grouped in *square* blocks of four, nine, etc. This is the grouping which obtains in the adult retina, and the facets resulting from it are square in outline. In the more primitive arrangement, that with hexagonal facets, the ommatidia can also be grouped in blocks of four, nine, etc. These blocks, however, are never square in outline, but *lozenge-shaped* (Fig. 55).

The process of rearranging the ommatidia is accomplished at a period in the growth of the young lobster much later than that at which the nerve-fibres have arranged themselves in relation to the openings in the basement membrane. Such being the case, one would expect to find in the deeper part of the adult retina traces of the more primitive arrangement. This is seen, I believe, in the lozenge-shaped outline which groups of four ommatidia present in the deeper part of the retina. A good instance of this is to be seen in Figure 14, although it is apparent in almost all of the transverse sections which include the proximal retinulæ. One might say that the ommatidia were rooted to the basement membrane when the hexagonal system prevailed, and that the rearrangement fully affected only their free distal ends.

The movement suggested as a means of rearranging the ommatidia not only explains the new position of the ommatidia, but also accounts for the situation in which the nuclei of the distal retinulæ occur. In Figure 55 each ommatidium is surrounded by a circle of six nuclei. These belong to the distal retinulæ. Instead of describing them as being in circles of six, it might be said that there is one nucleus at each corner of every cone. Thus, cone *x* (Fig. 55) has nuclei 1, 2, 3, and 4 at its four corners, and cone *y* has in a corresponding way nuclei 5, 6, 7, and 8. If the cones were to move as I have already described, and were to carry their surrounding nuclei with them, the result would be that nucleus 5 would come to lie next to nucleus 2, and 7 next to 4, and so on. In other words, a pair of nuclei would occupy each space between the adjoining angles of four adjacent cones. This is the position which the nuclei of the distal retinulæ occupy in the retina of an adult lobster (Fig. 5).

Several investigators have already described the development of the ommatidia in the compound eyes of the higher Crustaceans. The different accounts disagree especially in two particulars; first, as to the source of the different structures in the retina, and, secondly, as to the number and arrangement of the cells in an ommatidium. In describing the development of the retina, I have already discussed the first difference, and need here only recall my conclusion; namely, that the retina, including the corneal hypodermis, crystalline cones, retinulæ, and rhabdome, originates as a simple hypodermal thickening, and that no part of it is derived from the deeper ectoderm, which becomes the central nervous system. As to the number of cells which constitute an ommatidium, it will be recalled that in the lobster there are at least sixteen in each ommatidium; two in the corneal hypodermis, four cone-cells, two distal retinulæ, eight proximal retinulæ one of which was rudimentary, and a small, but variable number of accessory pigment-cells. The last are probably mesodermic in origin; all of the others are derived from the ectoderm.

The several accounts of the corneal hypodermis given by various authors differ principally in the number of cells which are said to be found in each ommatidium. Reichenbach ('86, p. 91) and Nusbaum ('87, p. 179) state respectively that in Astacus and Mysis there are four hypodermal cells in each ommatidium. Nusbaum's statement is further supported by Grenacher ('79, p. 118), who describes four cells under each facet in Mysis. Herrick ('89, p. 167) has found two hypodermal cells in the ommatidium of Alpheus. Patten states that the number of corneal cells in the ommatidia of all Decapods which he has examined is two.

All the direct evidence that I have seen points to the conclusion that the ommatidia of the Decapods possess two cells in the corneal hypodermis. Reichenbach's observation directly opposes this view. I have not had the opportunity of examining the same species as Reichenbach did, but I have studied a representative of the fresh-water crayfishes, *Cambarus Bartoni*, and there is no question that in the ommatidium of this species only two corneal cells are present. The nuclei of these two cells lie in the angles of the hypodermal squares, each one directly above a nucleus of a cone-cell. When viewed from the surface, it is difficult to say whether there are two or four hypodermal nuclei, because the four nuclei of the cone lie so near to the hypodermis and resemble its nuclei so closely. It seems to me possible that in his surface view Reichenbach ('86, Fig. 226) may have drawn with

the hypodermal nuclei those of the cone-cells, thus giving four instead of two.

The four nuclei in the corneal hypodermis of each ommatidium, as described by Nusbaum in the case of Mysis, had already been seen by Grenacher, who further stated that the nuclei were arranged in pairs at two levels. Grenacher does not describe nuclei in the two segments of the crystalline cone. In the retina of *Mysis stenolepis*, the four nuclei which were described by Grenacher are easily identified, but I cannot agree with Grenacher's statement ('79, p. 118) that all four belong to the same category. The more superficial pair unquestionably belong to the corneal hypodermis; but the deeper pair, I feel confident, are the nuclei of the crystalline cone. The conclusion to be drawn from this interpretation of the work of Reichenbach, Nusbaum, and Grenacher is, that in Decapods and Schizopods each ommatidium possesses two cells in the corneal hypodermis and only two.

Concerning the number of cone-cells in the ommatidium of Decapods, different writers very generally agree. Reichenbach, Kingsley, Herrick, and Patten all state that there are four cone-cells in the Crustaceans which they have studied.

In the cone-cells the number four, according to Grenacher, is characteristic not only of Decapods, but, excepting the Schizopods, it is the distinguishing feature of the Podophthalmata. In Mysis, Grenacher states that the cone has two, instead of four segments. I have studied the eyes of *Mysis stenolepis*, Smith, and my observations confirm this statement. Notwithstanding Grenacher's assertion, Nusbaum ('87, p. 179) claims that the nuclei of the cone-cells in Mysis are grouped in fours. I am confident that there are only two nuclei in the adult cone, and having seen no evidence of a suppression of two nuclei, I must consequently side with Grenacher in his belief that the cone of Mysis is composed of only two cells.

The differentiation of the retinulæ into distal and proximal groups is more complete in the lobster than in the majority of other Decapods studied. As a result of this incomplete differentiation, it is often impossible to get exact statements from the descriptions of different authors concerning the number and position of the retinulæ.

Reichenbach ('86, p. 93) maintains that in Astacus, after the four cone-cells, and as he believes the four hypodermal cells, were differentiated, the remaining cells became pigment-cells (retinulæ). Essentially the same account is given by Nusbaum ('87, p. 180) for Mysis. Kingsley ('87, p. 53) states that, in addition to the corneal hypodermis,

each ommatidium in Crangon at first consists of four vertical series of nuclei, each series containing five nuclei. This would give a total of twenty cells for each ommatidium. After deducting four, the number of cone-cells, from twenty, the original number of cells, there remain sixteen cells to be accounted for, presumably as pigment-cells. I have examined the eye of an adult *Crangon vulgaris*, and I find in it, as in the lobster's eye, two distal retinulæ and seven proximal retinulæ. This can scarcely be reconciled with Kingsley's account, unless one admits an extensive suppression of cells. Such a suppression seems to me scarcely probable, and I am therefore inclined to believe that there has been some error in Kingsley's method of counting. Possibly the series of nuclei were so placed that they were shared by neighboring ommatidia, and did not all belong to one ommatidium. This, however, could only be settled by re-examining the early stages of Crangon.

Herrick ('86, p. 44) describes seven retinulæ in the ommatidium of Alpheus, and makes the statement that they do not possess nuclei. He then describes some undifferentiated ectodermic cells, the nuclei of which can be seen in the space between the cones. As this is the position which in the young lobster is occupied by the nuclei of the proximal retinulæ, and as Herrick has not identified any nuclei for the proximal retinulæ in Alpheus, I am inclined to regard the deeper nuclei of this group as belonging to these cells. The more superficial of the nuclei described by Herrick are apparently arranged in circles of six around each cone. (Compare Herrick, '86, Figs. 1 and 2.) As in the early stages of the lobster this arrangement was characteristic of the nuclei in the distal retinulæ, it is possible that these superficial nuclei in Alpheus may represent the distal retinulæ.

Reichenbach ('86, p. 92), Kingsley ('87, p. 52), Nusbaum ('87, p. 179), and Herrick ('89, p. 167) describe an ingrowth of mesodermic tissue between the retina and ganglion, and in Mysis, according to Nusbaum ('87, p. 180), these cells, as in the lobster, give rise to what I have called the accessory pigment-cells.

From the investigations which have been summarized in the preceding pages, it is difficult to draw any general conclusion concerning the number of retinulæ in the ommatidia of the higher Crustacea. Reichenbach and Nusbaum make no statement as to the number of these cells in Astacus and Mysis. Kingsley's enumeration of them in Crangon seems to be erroneous. Admitting the undifferentiated ectodermic nuclei in Alpheus to be the nuclei of the retinulæ, Herrick's statement

that there are seven retinulæ in the ommatidia of this Crustacean coincides fairly with the results obtained from the lobster.

From the histological evidence of the adult, on the other hand, writers are generally agreed that the ommatidia of Decapods possess seven proximal retinulæ. It is probable, however, that this statement requires some qualification. It will be recalled that, in describing the proximal retinulæ of the lobster, I referred to an additional nucleus which apparently represented an eighth rudimentary retinula. I have identified this eighth nucleus in the ommatidia of Cambarus, where, as in the lobster, it lies in a plane different from that of the other seven nuclei. If the eighth nucleus should be present in approximately the same plane as the other nuclei, it could be identified only with great difficulty. It is my belief that it often occurs in this position, and probably for this reason it has generally escaped the attention of investigators, for I am of opinion that it is present in the ommatidia of all Decapods. When, therefore, the statement is made that the ommatidia of a certain Decapod contains seven proximal retinulæ, the probabilities are that the ommatidium in reality contains eight proximal retinulæ, one of which is rudimentary.

Concerning the Schizopods, Grenacher states ('79, p. 119) that in Mysis there are more than four proximal retinulæ, but how many more he is not certain. In *Mysis stenolepis* my own observations have shown me that there are certainly seven pigmented proximal retinulæ. This number agrees with the number of functional retinulæ in Decapods, and my opinion is that in Mysis, as in Decapods, an eighth rudimentary proximal retinula may be expected.

The presence of distal retinulæ in the ommatidia of Decapods seems to have generally escaped attention. Patten and Carrière, however, describe these cells in Penæus and Astacus, and the fact that they are easily recognized in the eyes of Homarus, Cambarus, and Eupagurus inclines me to the belief that they form a constant element in the ommatidia of all Decapods. They have also been seen in the retina of Mysis. In the eyes of this genus their nuclei occupy the position inditated by *d* in Grenacher's Figure 112. It is of interest to observe that their permanent position in Mysis is an early and transitory one in the lobster. (Compare Grenacher, '79, Fig. 112 *d*, with Figs. 48 and 55 of this paper.) In both the Decapods and Mysis the number of distal retinulæ is two.

The Types of Ommatidia.

With the conclusions arrived at in the foregoing account as a basis, an ommatidium can be constructed which will serve as a type for the ommatidia of all Decapods. Omitting the accessory pigment-cells, this typical ommatidium would be composed of sixteen cells as follows: two cells in the corneal hypodermis, four cone-cells, two distal retinulæ, and eight proximal retinulæ. In a similar way a typical ommatidium can be constructed for the Schizopods. This type would differ from that proposed for the Decapods, in that its crystalline cone would be formed of two, instead of four cells.

The ommatidia of the Schizopods and Decapods, as the development of the lobster shows, are closely related. The arrangement of the ommatidia by which hexagonal facets are produced is permanent in Mysis, and temporary in the lobster. The distal retinulæ are grouped in the adult Mysis in a way which is reproduced only in the early stages of the lobster. In Mysis the outline of the nuclei in the corneal hypodermis, as seen in sections tangential to the retina, is strikingly crescentic. This form is temporarily assumed by the corresponding nuclei in the young lobster (Fig. 53). Thus it is evident that the ommatidia of the lobster pass through a stage in which they closely resemble the permanent condition of the ommatidia in Mysis. For this reason, I believe that the ommatidium of Mysis represents a type ancestral to that of the lobster.

The only important difference which exists between the ommatidium of Mysis and that of the lobster in its early stages is that in the latter the cone consists of four cells, while in Mysis it is composed of only two. If one admits that the ommatidium of Mysis is the forerunner of that of the lobster, this difference in the number of cone-cells can easily be explained on the supposition that the cells which form the cone in Decapods divided once more than those in Schizopods. If these two types of ommatidia are thus related, it is only natural to expect that this process of cell-division may connect the ommatidium of Mysis with that of some lower Crustacean.

The ommatidia in the eyes of Amphipods are constructed upon a type which seems thus connected with that of Mysis. In Gammarus, for instance, I have found that the ommatidia possess an undifferentiated corneal hypodermis, a crystalline cone of two cells, and five retinulæ. If one desires to convert this type into that of Mysis, or through Mysis into that of the Decapods, the necessary change merely involves

the division and differentiation of cells. The two cone-cells in the simpler type would remain unaffected in Mysis; in the Decapod they would divide once, thus producing a cone of four cells. By division, the five retinulæ of the Amphipod would become the ten retinulæ of the higher type. These ten retinulæ are differentiated into two sets, eight proximal retinulæ which surround the rhabdome, seven of them possessing nerve-fibres, and two distal retinulæ which envelop the cone, but have no nervous connections. If the ten retinulæ of the higher type were developed from the five retinulæ of the lower type, it follows, since all of the five retinulæ possessed nerve-fibres, that those of the ten retinulæ which do not possess nerve-fibres must be considered as degenerate. The degenerate cells of the higher type of ommatidium are consequently the eighth proximal retinula and the two distal retinulæ. The structural condition of these three cells favors this view. The eighth proximal retinula is identifiable only through its nucleus. Each distal retinula, as I have previously described, possesses a proximal fibre. This fibre passes through the basement membrane with the nerve-fibres of the proximal retinulæ, but it is very much smaller than these fibres, and terminates without reaching the optic ganglion. This condition is easily interpreted as one of degeneracy.

The process by which distal and proximal retinulæ were probably differentiated from unmodified retinulæ is easily suggested. A characteristic distinction between the ommatidia of the higher and lower Crustacea, as, for instance, between Gammarus and Homarus, is that in the former the cone and rhabdome are very close to each other, whereas in the latter the cone proper and rhabdome are separated by considerable space. Without attempting to assign physiological reasons, the statement may be made that it seems necessary that the sides of the cone should be sheathed with pigment. In the ommatidia of Gammarus this is accomplished by the distal ends of the five retinulæ; these reach beyond the rhabdome and envelop the cone. They thus form a funnel, in the large central cavity of which the cone rests, while the neck of the funnel is occupied by the rhabdome. Imagine now the division of these five retinulæ into ten, and the separation of the cone from the rhabdome. It is easy to understand how two of the ten retinulæ may retain their connection with the cone, while the remaining eight adhere to the rhabdome. The two retinulæ connected with the cone would lose their nervous function and become simple pigment-cells. The retinulæ which remain attached to the rhabdome would continue as perceptive cells. The separation of the rhabdome and cone not only offers an

explanation of the way in which the distal and proximal retinulæ have arisen, but it also accords well with the fact that the proximal retinulæ end distally in fine fibres which stretch toward the cone, and are applied to the fibres of the distal retinulæ.

If what has been said of the growth of ommatidia be true, the course which the development of these structures takes in the case of the lobster must be somewhat different from that by which they arose phylogenetically. In the lobster the division of the nuclei is entirely completed before the ommatidia are differentiated. Consequently, after differentiation has occurred, no further cell-division ensues among the elements of an ommatidium. This fact, however, is by no means a serious objection to the view which I have expressed, for of the two processes, cell-division and the differentiation of ommatidia, it is only necessary to imagine that in successive generations the differentiation was retarded until a stage was reached in which all cell-division was accomplished before the differentiation of ommatidia began. It is of interest to observe, however, that in the lobster the planes of division among the nuclei, which eventually enter into the formation of ommatidia, correspond in direction to the plane in which the nuclei of the ommatidium in Gammarus would divide, should this ommatidium be converted into that of the lobster. Thus the plane of nuclear division which was so characteristic of the distal superficial part of each optic disk in the lobster may have a phylogenetic significance.

In how far the ommatidia of all the Crustacea can be brought into relation by a process of cell-division such as I have outlined, and what constitutes the simplest form of an ommatidium, are questions which require careful and extensive comparative study, and which I am not able to discuss here. Suffice it to say, that between the ommatidia of the higher and lower Crustacea there is reason to conclude that such a relation as I have pointed out probably exists.

Cambridge, October 1, 1889.

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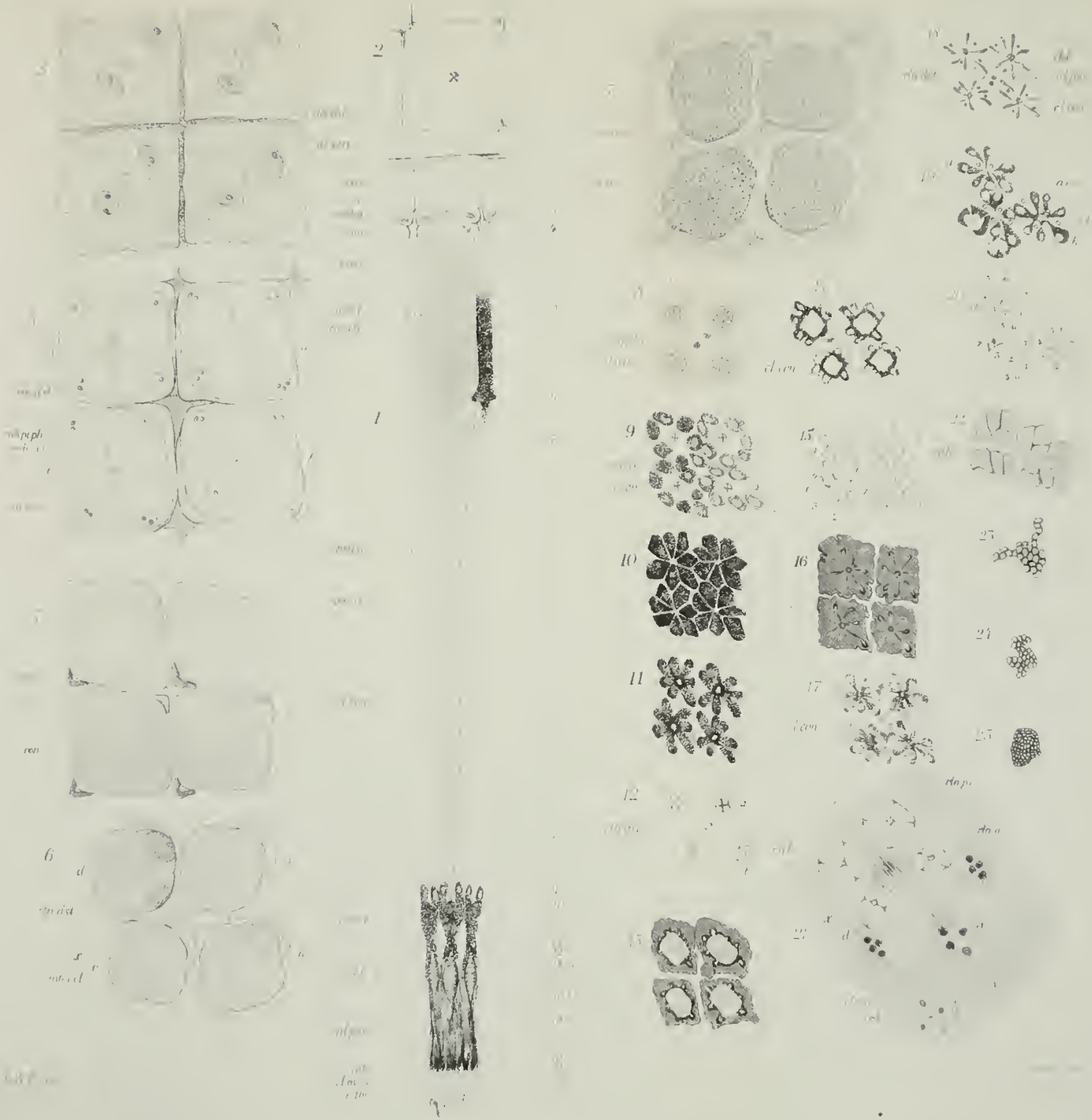


EXPLANATION OF FIGURES.

All the figures were drawn with the aid of an Abbé camera. Unless otherwise stated, the figures are from specimens stained with Grenacher's alcoholic borax-carmine and mounted in benzol-balsam. Where sections have been depigmented the reagent employed was an aqueous solution of potassic hydrate ¼% (see Parker, '87, p. 175). Figs. 1 to 36 refer to the *histology* of the adult lobster's eye. Figs. 37 to 59 inclusive deal with the *development* of the eye.

PLATE I.

All figures on this plate illustrate the *histology* of the lobster's eye.

Fig. 1. A longitudinal section of an ommatidium. This is a composite figure, its parts having been drawn to one scale from various sections, and afterwards combined. The distal retinula on the right side of the cone contains its natural pigment; that on the left side has been depigmented. The letter *x* indicates the position of the band which limits the corneal facet. The numbers to the right of the figure correspond to the numbers of the following figures of transverse sections, and mark the level at which the latter were taken. × 105.

The remaining figures on this plate (*Nos.* 2–25) *are transverse sections either of ommatidia or bundles of nerve-fibres. In each case the sections were studied and drawn from their distal faces. Figs.* 2 *to* 20 *are magnified* 375 *diameters; Figs.* 21 *to* 25, 575 *diameters.*

" 2. A corneal facet. This specimen was cleaned in a boiling solution of potassic hydrate and studied in water.

" 3. Four pairs of cells from the corneal hypodermis. Around the lower right-hand pair of cells the outlines of the six surrounding distal retinulæ are indicated in part by dotted lines.

" 4. Four groups of cone-cells. The ommatidia to which the cone-cells belong are indicated by the letters *a*, *b*, *c*, and *d*. These letters are used to indicate corresponding ommatidia in deeper sections.

" 5 to 20 represent transverse sections through ommatidia in the various regions indicated as follows: —

" 5. The middle region of four cones. Completely depigmented.

" 6. The proximal ends of four cones. The re-entrant angle on the surface is indicated at *x*. Completely depigmented.

" 7. Slightly below the proximal ends of the cones.

" 8. Beyond the distal ends of the proximal retinulæ.

" 9. The distal ends of the proximal retinulæ.

" 10. The thick distal portion of the proximal retinula.

" 11. The proximal retinulæ immediately above the distal termination of the rhabdome.

" 12. At the distal ends of the rhabdomes. Completely depigmented.

Fig. 13. The rhabdome between its distal end and middle. In this section the accessory pigment-cells of each ommatidium are apparently separated by an intervening space from those of neighboring ommatidia. This space is probably the result of shrinkage and subsequent rupture.

" 14. In the same plane as that shown in Fig. 13. Partially depigmented.

" 15. The middle of the rhabdome. The distal retinulæ of ommatidium *c* have been numbered. Completely depigmented.

" 16. The proximal end of the rhabdome. The accessory pigment-cells in this section have probably been ruptured, as in Fig. 13.

" 17. In the same plane as that shown in Fig. 16. Partially depigmented.

" 18. The proximal tip of the rhabdome. Completely depigmented.

" 19. The proximal retinulæ close to the basement membrane. Partially depigmented.

" 20. A diagram of Fig. 19. The proximal retinulæ of the different ommatidia have been numbered to correspond with those of ommatidium *c* in Fig. 15. The retinulæ of ommatidium *c* are tinted pink.

" 21. Transverse section of nerve-fibres as they pass through the basement membrane. The line *y z* shows the plane of section for Fig. 29; *x* indicates the cross-shaped thickening in the basement membrane. Completely depigmented and stained in Weigert's hæmatoxylin. (See page 4.) × 575.

" 22, 23, 24, and 25 represent transverse sections of the fibres in the optic nerve. Weigert's hæmatoxylin. × 575. The planes at which these sections were taken are as follows: —

" 22. Directly below the basement membrane. The fibres are in groups of threes and fours.

" 23. At one fourth the distance from the basement membrane to the optic ganglion.

" 24. At half the distance between the membrane and ganglion.

" 25. At the surface of the ganglion.

ABBREVIATIONS.

ax. n.	Nervous axis of retinula.	*mb. pi ph.*	Peripheral membrane.
cap.	Protoplasmic cap of cone-cell.	*n. fbr.*	Nerve-fibre.
cl. con.	Cone-cell.	*nl. con.*	Nucleus of cone-cell.
cl. ms d.	Mesodermic cell.	*nl. crn.*	" corneal hypodermis.
con.	Cone.	*nl. dst.*	" distal retinula.
crn.	Corneal cuticula.	*nl. pig.*	" accessory pigment-cell.
crn. h d.	Corneal hypodermis.	*nl. px.*	" proximal retinula.
cta.	Cuticula.	*omm'.*	Ommateum.
enc.	Brain.	*pig. dst.*	Distal band of pigment.
fbr'.	Fibrillæ.	*pig. px.*	Proximal band of pigment.
gn. opt.	Optic ganglion.	*r.*	Retina.
h d.	Hypodermis.	*rhb.*	Rhabdome.
mb.	Basement membrane.	*rtn'. dst.*	Distal retinula.
mb. i cpt.	Intercepting membrane.	*rtn'. px.*	Proximal retinula.
mb. i cl.	Intercellular membrane.	*spa. i cl.*	Intercellular space of retina.

The other abbreviations which occur on the plates are explained in the description of the figures with which they are found.

PLATE II.

Figs. 26 to 36 deal with the *histology* of the lobster's eye; Figs. 37 to 39, with its *development*.

Fig. 26. Vertical section through that portion of the eye-stalk where the transition from the undifferentiated hypodermis to the ommateum is accomplished. The open space x is due to shrinkage. × 31.

" 27. A group of the four cone-cells of an ommatidium and the attached corneal hypodermis. Isolated and studied in Muller's fluid. × 365.

" 28. Proximal end of a group of four cone-cells where they separate as fibres to pass around the rhabdome. Isolated and studied in Muller's fluid. × 365.

" 29. Transverse section of the basement membrane. The distal face is uppermost; the proximal face below. The section is taken in a plane which would be represented in Fig. 21 by the line $z\ y$. × 575.

" 30. A rhabdome and its seven surrounding proximal retinulæ. At the distal end the free tips of the seven retinulæ can be seen. At the proximal end the rhabdome and the four groups of retinulæ which pass through the basement membrane are visible. Isolated and studied in chromic acid $\frac{1}{50}\%$. × 200.

" 31. An individual proximal retinula. Isolated and studied in chromic acid $\frac{1}{50}\%$. × 200.

" 32. Transverse section of a rhabdome and its surrounding cells. The plane of section is about half-way between the middle and distal end of the rhabdome. Completely depigmented with potassic hydrate. × 460.

" 33. Oblique section of a rhabdome from the same series of sections as Fig. 32. The upper end of the figure is distal; the lower, proximal. × 460.

" 34. Transverse section of a rhabdome and its surrounding retinulæ. The nervous axis of each retinula is distinctly stained. Completely depigmented; stained with Kleinenberg's alum-hæmatoxylin. × 460.

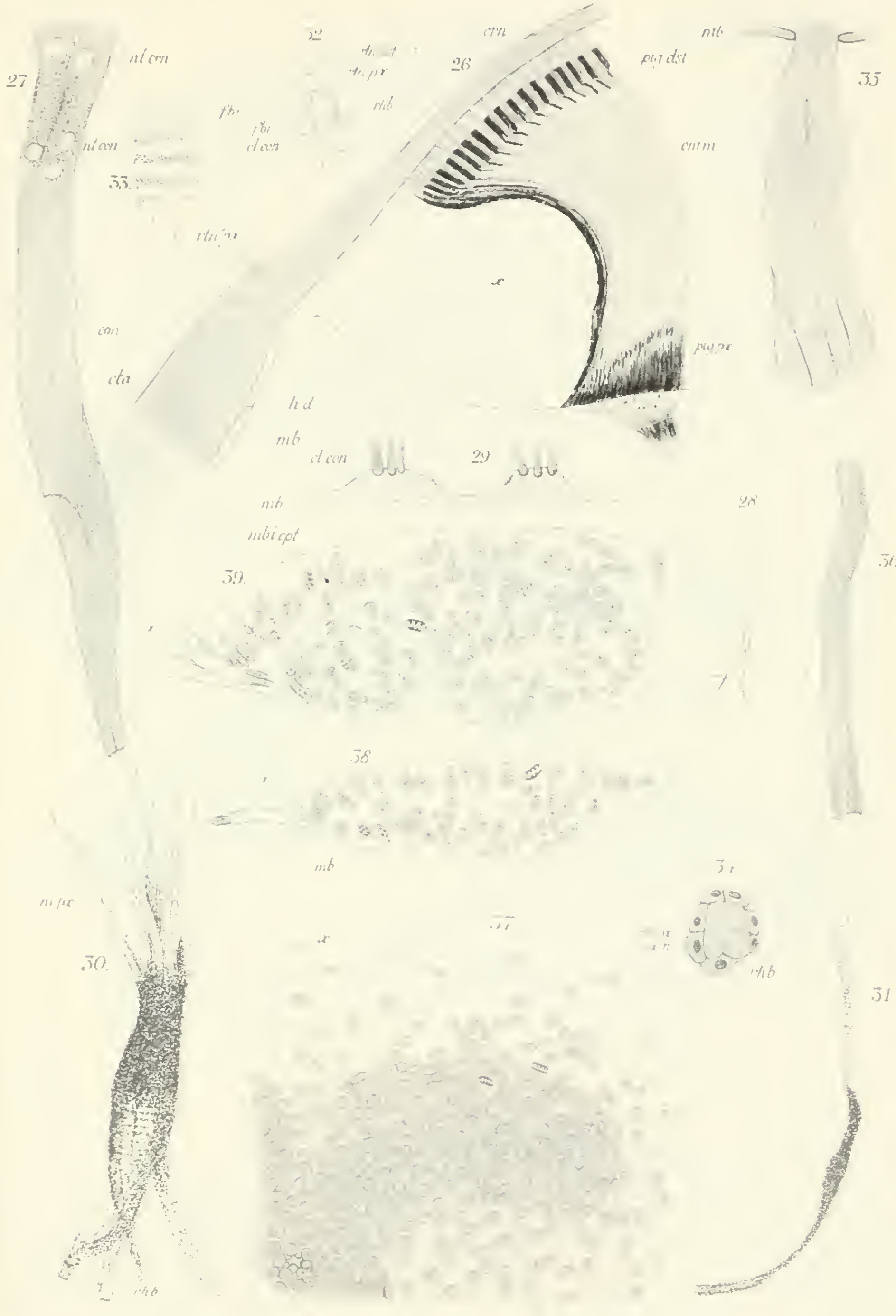
" 35. Longitudinal section of a bundle of nerve-fibres extending through the basement membrane toward the optic ganglion. Depigmented; Weigert's hæmatoxylin. × 575.

" 36. Optic nerve-fibre. Isolated and studied in Müller's fluid. × 575.

" 37. Superficial view of a left optic lobe. Enough of the right lobe is drawn to indicate the position of the median plane ($x\ y$). x is anterior; y is posterior. Stage A (see page 2). × 280.

" 38. Posterior face of a section from a right optic disk cut transversely to the longitudinal axis of the embryo (see page 34). At x is an angle formed by the growth of the retinal cells over the undifferentiated ectoderm. Stage A. × 280.

" 39. A section from the optic disk of an embryo in stage B. The plane of cutting corresponds to that in Fig. 38. In this figure x indicates, as in the preceding one, the angle between the undifferentiated ectoderm and the growing retina. × 280.


27
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cta
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cl con
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PLATE III.

All figures on this plate illustrate the *development* of the lobster's eye.

Fig. 40. A section through the left optic lobe and left half of the supra-œsophageal ganglion. The plane of section is tangential to that part of the surface of the egg on which the embryo rests. The position of the median plane is indicated at $x\,y$. The surfaces tinted with deeper pink in the figure represent areas containing nuclei in the specimen; those in lighter pink, areas in which no nuclei were present. The optic lobe is divided into two parts by a band of large, faintly colored nuclei, which, with the smaller surrounding nuclei, are shown in the figure. To the right of the nuclei the broad tinted marginal area represents the retina, r. The remainder of the optic lobe gives rise to the optic ganglion. Stage C (see page 2). × 280.

" 41. Posterior aspect of a transverse section of a right optic lobe. The plane of section corresponds to that in Fig. 38; x is the angle which indicates the separation of the retinal and ganglionic constituents of the intercepting membrane. Stage C. × 280.

" 42. This figure is taken from a region which corresponds to the left-hand portion of Fig. 41. Although from the same set of eggs the embryo from which Fig. 42 was drawn was somewhat more advanced than that from which Fig. 41 was taken. At x the proximal band of retinal nuclei can be seen; at y the distal band is shown. Stage C. × 460.

" 43. The superficial layer from the distal band of retinal nuclei; seen from the external surface of the retina. Stage C. × 460.

" 44. The deep layer of the distal band of nuclei. These are seen in optical section somewhat within the outer face of the retina. Stage C. × 460.

" 45. A transverse section of an optic lobe from a lobster at stage D. The plane of section corresponds to that of Fig. 38. As in Fig. 40, the deeply tinted areas were nucleated; the lighter areas were without nuclei. × 145.


40
gn opt.
enc.
43
nl con
nl dst
44
nl con.
41
mb opt
gn. opt.
h.d
nl dst
nl con.
n fbr.
nl con
42
gn opt
mb opt
45
gn opt
enc

PLATE IV.

All figures on this plate, except Fig. 59, illustrate the *development* of the lobster's eye.

Fig. 46. A transverse section of an optic lobe at stage E (see page 2). The plane of section and the method of coloring the figure are the same as in Fig. 45. × 145.

" 47. An enlarged drawing of that portion of the retina which is in brackets in Fig 46. Stage E. × 460.

" 48. A view of the external surface of the retina. The distal ends of four ommatidia are seen. Stage E. × 460.

" 49. A transverse section of four ommatidia in the region of the hypodermal nuclei. (Compare Fig. 47.) Stage E. × 460.

" 50. A transverse section of four ommatidia in the plane which the nuclei of the cone-cells occupy. Stage E. × 460.

" 51. Longitudinal section of a single ommatidium. Stage F. × 460.

" 52. Four corneal facets seen from the external surface. Stage F. × 460.

" 53 to 58 represent transverse sections of four ommatidia at Stage F. The numbers on the left side of Fig. 51 indicate the heights at which these sections were taken, and correspond to the numbers of the following figures. In Figs. 53 to 58 the magnification is 460.

" 53. A transverse section in the region of the corneal hypodermis.

" 54. A transverse section through the region in which the nuclei of the cone-cells occur.

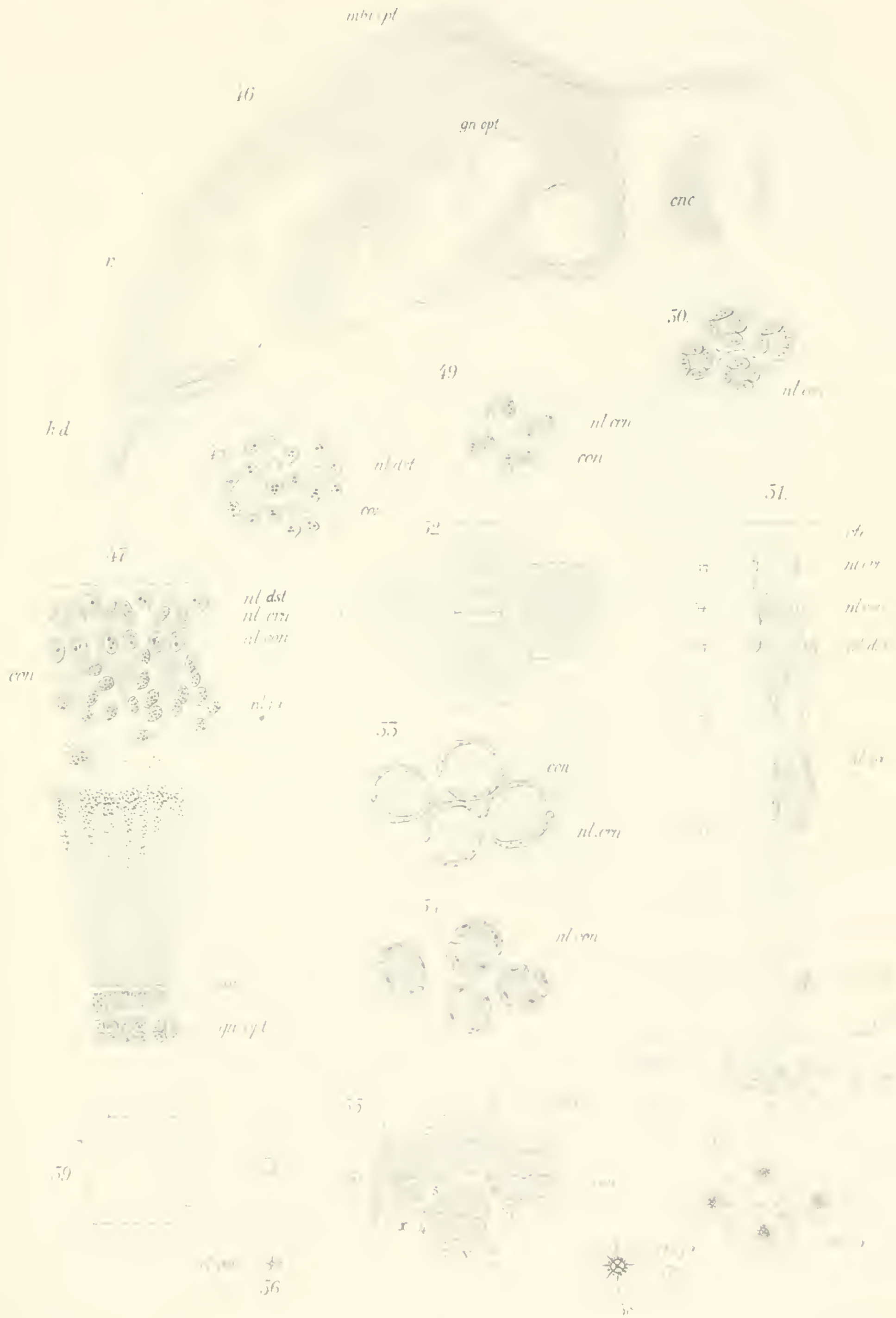
" 55. A transverse section in the same plane as the nuclei of the distal retinulæ.

" 56. A transverse section of the proximal ends of two cones.

" 57. A transverse section through the rhabdomes and proximal retinulæ.

" 58. A transverse section of a rhabdome from Fig. 57. Fig. 58 was drawn with a higher magnification than Fig. 57 in order to show the relation of the proximal retinulæ to the segments of the rhabdome. × 640.

" 59. A corneal facet from near the periphery of the retina in an adult lobster. The hexagonal outline is noteworthy. This specimen was cleaned in boiling potassic hydrate and examined in water. × 280.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No. 2. — *On the Rate of Growth of Corals.* By Alexander Agassiz.

We know as yet comparatively little regarding the rate of growth of corals under different conditions. Dana has given, in his "Corals and Coral Islands," * a *résumé* of our knowledge on the subject, so that it is only necessary for me here to refer the reader to his account of the statements of Darwin, Stuchbury, Duchassaing, Verrill, and others, relating to this subject.

The specimens figured in this communication have been kindly sent me by Lieut. J. F. Moser, commanding the U. S. Coast and Geodetic Survey steamer "Bache." They were all taken (as stated by Mr. Hellings, the cable manager) off the cable laid between Havana and Key West, in June, 1888, from a portion of the cable repaired in the summer of 1881; so that the growth is about seven years. Lieutenant Moser writes: "Taken from the shore end of the International Cable; the specimens were taken between the triangular buoys and the outer reef, the shore end being that portion between Key West and the outer reef." The Coast Survey maps indicate a depth of from six to seven fathoms, and this portion of the cable is most favorably situated as regards food supply, being directly in the track of the main flow of the tide as it sweeps in and out from the outer reef into Key West Harbor, and over the flats to the northward.

Some of the specimens belong to different species from those of which the rate of growth was already known.

Orbicella annularis (Plates I. and II.) shows a much greater increase in the thickness of coral formed than the case mentioned by Verrill, where the thickness formed in sixty-four years was not more than about eight inches. The specimens sent by Lieutenant Moser grew to a thickness of two and a half inches in about seven years.

* Coral and Coral Islands, by James D. Dana. Third edition. New York, 1890. (Pp. 123, 253, 418.)

The *Manicina areolata* (Plate III.) shows also a very rapid rate of increase. This corresponds to the rate of growth of allied genera (*Mæandrina labyrinthica*) observed by Pourtalès at Fort Jefferson, Tortugas.

The *Isophyllia dipsacea* (Plate IV.) shows a still more rapid increase.

Of course, we are unable to state that these corals began to grow the first season the cable was laid; but, judging from the favorable locality in which the corals were found, it is not probable that more than a few months passed before some of the swarms of pelagic coral embryos which must have floated past the cable found a place of attachment.

The specimens have all been figured of the natural size.

The figures all show, with the exception of those of Manicina, the size of the cable to which the corals were attached.

Cambridge, August, 1890.

EXPLANATION OF THE PLATES.

PLATE I.

Orbicella annularis Dana (natural size).

The thickness of the coral at the edge of the mass varies from $\frac{3}{8}$ to $\frac{3}{4}$ of an inch. The greatest height of the mass above the cable is $2\frac{1}{2}$ inches.

PLATE II.

Orbicella annularis Dana (natural size).

The thickness of this specimen is very much less than that of Plate I. It varies at the edge of the mass from $\frac{1}{8}$ to $\frac{1}{4}$ of an inch. The greatest height above the cable is $2\frac{1}{4}$ inches.

PLATE III.

Manicina areolata, Ehrenb

1. Seen in profile. The thickness above the cable is one inch.
2. Same, seen from above.

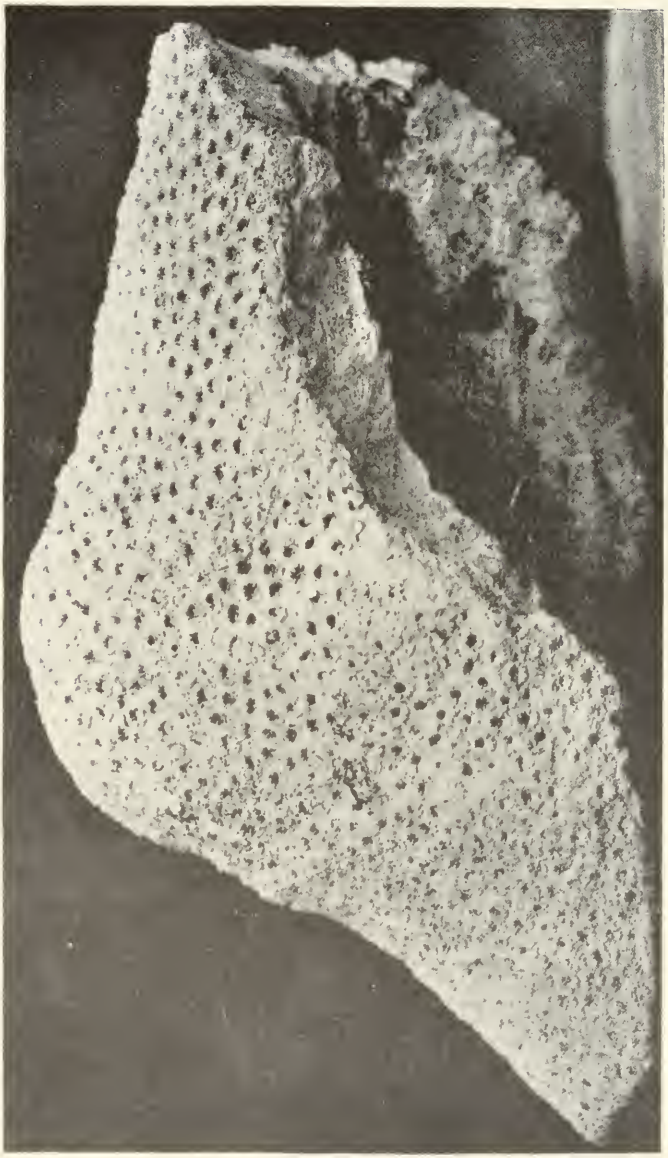
Both figures natural size.

PLATE IV.

Isophyllia dipsacea Ag. (natural size).

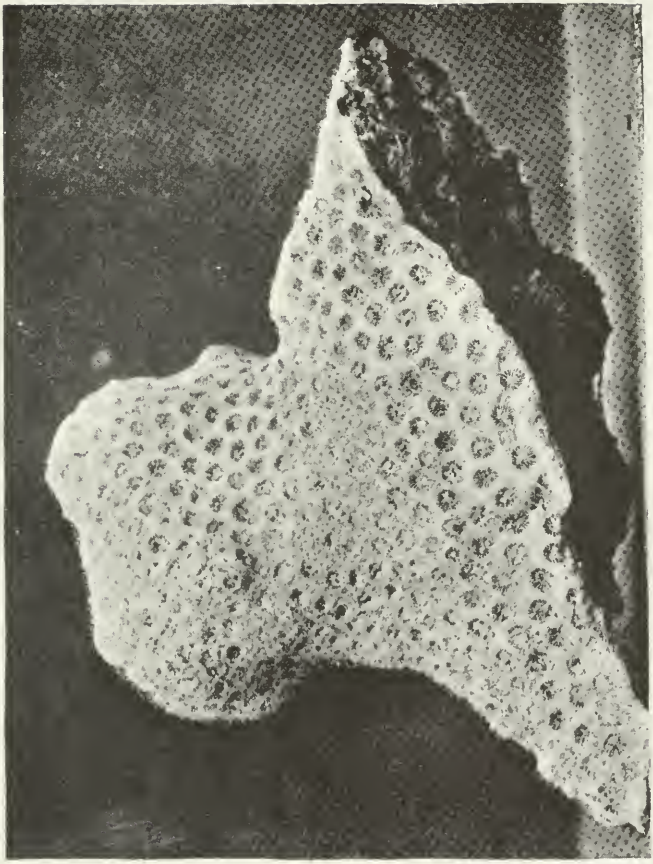
The greatest thickness is $2\frac{1}{2}$ inches

PLATE I.



ORBICELLA ANNULARIS *Dana*.

PLATE II.



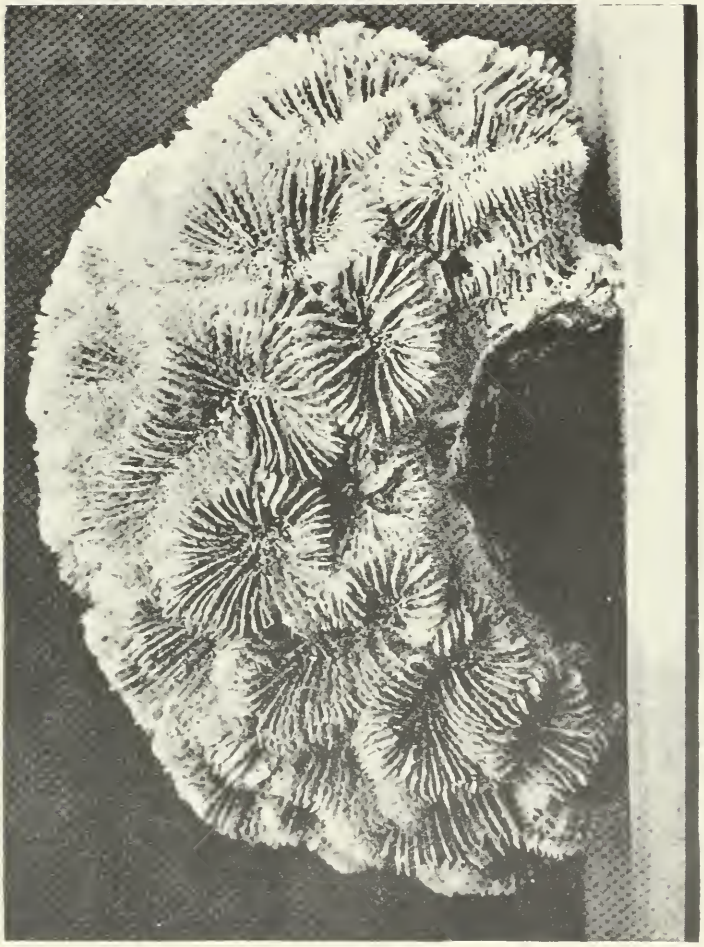
ORBICELLA ANNULARIS *Dana*.

1.

2.

MANICINA AREOLATA *Ehrenb*

PLATE IV.



ISOPHYLLIA DIPSACEA *Ag.*

No. 3. — *Preliminary Account of the Fossil Mammals from the White River and Loup Fork Formations, contained in the Museum of Comparative Zoölogy.* Part II. *The Carnivora and Artiodactyla by* W. B. Scott. *The Perissodactyla by* Henry Fairfield Osborn.

This paper, the second upon the Fossil Mammals of the Museum of Comparative Zoölogy, is a continuation of the one published by the writers[1] in August, 1887, upon the White River Mammalia, and includes a number of additions to and corrections of the results there described. It is, however, especially devoted to a consideration of the upper Miocene or Loup Fork mammals collected in Nebraska by Messrs. Garman and Clifford, and in Kansas by Mr. Sternberg. The specimens from these different localities exhibit a considerable range of specific variation.

The Loup Fork species here described have for the most part been long established, but these collections add much to our knowledge, and enable us to determine very fully the structure of forms which have been known hitherto only from fragments. Of such new observations we may mention: (1) the determination of the foot structure of *Merycochœrus;* (2) of *Blastomeryx;* (3) the restoration of *Cosoryx;* (4) discovery of the mandible of *Ælurodon hyœnoides;* (5) the discovery of an exceedingly large feline animal; (6) observations upon the molars of the equine series; (7) the manus and pes of *Aceratherium;* (8) the skeletal characters and restoration of *Aphelops fossiger;* (9) the homologies of the elements of the molar teeth in the rhinoceroses; (10) the brain characters of *Aphelops* and *Mesohippus;* (11) the discovery of a Loup Fork species of *Chalicotherium.*

We have again to express our thanks to Dr. F. C. Hill, Curator of the Geological Museum at Princeton, for his skilful excavation and mending of the specimens, and to Mr. R. Weber for the very accurate series of drawings which accompany this paper.

Geological Museum, Princeton, N. J., July 8, 1890.

[1] The authors, as initiated in their Memoir upon the Uinta Mammalia, have divided the subjects for their present and future joint papers.

CARNIVORA.

CANIDÆ.

ÆLURODON, Leidy.

(Syn. *Epicyon*, Leidy. *Canis*, Leidy, in part. *Palhyæna*, Schlosser.)

The dogs of this genus are the most abundant of the Loup Fork *Canidæ*, and, as their relations and systematic position have been very generally misunderstood, it will be well to describe them in some detail. The special peculiarity of the genus is to be found in the development of a large anterior basal lobe on the superior sectorial, as in the cats. The postero-internal cone (metaconid) of the lower sectorial is much reduced, and in some species almost disappears. The talon of this tooth is rather short, and consists of an internal and external cone or tubercle, being of the basin-like character. The premolars are remarkably heavy, and possess well developed basal conules. There are four well marked species of this genus, of which the best known is

Ælurodon sævus, Leidy (Cope).

(Syn. *Canis sævus*, Leidy. *Ælurodon ferox*, Leidy. *Ælurodon sævus*, Cope.)

This species is characterized by the very small size of the internal cusp of the upper sectorial, and by the nearly straight and slender mandible; the incisors are rather small, and the first upper molar is very large and subtriangular in shape. The skull as figured by Cope (American Naturalist, XVII.) presents a rather short, narrow muzzle, and is in general quite bear-like in appearance. Notwithstanding its peculiarities of dentition, this animal is an unmistakable dog, and the structure of the skull, vertebræ, limbs, and feet is characteristically cynoid. The metapodials are, however, somewhat less elongated proportionally than in existing dogs.

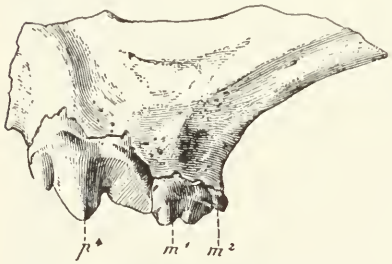


Figure 1. — *Ælurodon sævus*, fragment of right superior maxillary × ⅔.

Ælurodon Haydeni, Leidy.

(Syn. *Canis Haydeni*, Leidy. *Epicyon Haydeni*, Leidy.)

This species is very large, and is remarkable for the short, massive mandible and the strong upward curvature of the posterior portion of the alveolus, so that the inferior tubercular molars may almost be said to be inserted in the ascending ramus. In Dr. Leidy's type of the species (Ext. Mam. Fauna, Dak. and Neb., Plate I. fig. 10) the third lower molar is inserted by two fangs, and in

the Cambridge specimen by only one; but this does not appear to be a constant character. The postero-internal cusp (metaconid) of the lower sectorial is reduced to a rudiment, and the talon is much shortened antero-posteriorly. Pm. 1 and 2 are relatively quite small, while $\overline{pm}$. 3 and 4 are quite high and massive.

Ælurodon Wheelerianus, Cope.

(Syn. *Canis Wheelerianus*, Cope. *Ælurodon Wheelerianus*, Cope.)

This species is nearly as large as the preceding one, but differs from it (1) in the much less strongly curved alveolar region, and (2) in the very large size of the external upper incisor, which at the base is nearly as large as the canine. The species is represented in the collection by the facial region of a very old individual, the teeth of which are worn down to mere stumps. The face appears to be proportionately longer than in *Æ. sævus*, the orbit lying somewhat farther back; it is also very deep, and encloses an unusually large nasal chamber.

Ælurodon hyænoides, Cope.

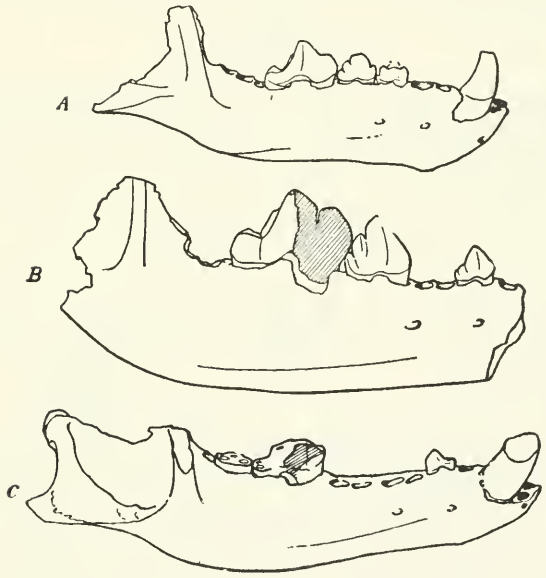


Figure 2. — Mandibles of *Ælurodon* × ½. A. *Æ. hyænoides*; B. *Æ. Haydeni*; C. *Æ. sævus*.

This, the smallest species of the genus, has been described by Cope from the superior dentition: "The second and third premolars are robust and somewhat swollen at the inner base. Each has a short heel, but no median posterior lobe. The principal lobe is robust, in the third [pre]molar as wide as long at the base.

The internal anterior lobe of the superior incisor [sectorial] is very large, and its apex is distinct from the inner side of the rest of the tooth. It is relatively larger than in *Crocuta brunnea*. . . . The first true molar is somewhat wider near the inner extremity of the crown than at the external extremity." (Bulletin U. S. Geological and Geographical Survey of the Territories, Vol. VI. p. 388.)

The Cambridge collection contains a mandible which should almost certainly be referred to this species. It is proportionately short, stout, and of nearly uniform depth, not tapering anteriorly as in *Æ. sævus;* the symphysis is very obliquely placed and the chin abruptly rounded, giving the jaw a somewhat cat-like appearance. The first and second premolars are small, and the latter is implanted by a fang which is but imperfectly divided into two; the third and fourth premolars are low but strong, and differ from the corresponding teeth of the other species in the presence of a small *anterior* basal cusp. The sectorial is large, and has a well developed metaconid; the talon is obliquely worn upon its outer side, showing a different mode of opposition of the teeth from that which obtains in *Æ. sævus.* The incisors are very closely crowded together, and the median one is pushed very far back out of the line of the other two.

MEASUREMENTS.

	m.		m.
Length, inferior molar series	.032	Blade of sectorial (ant. post.)	.013
" " premolar series	.031	Talon " "	.006
" sectorial (m. 1)	.019		

? Ælurodon ursinus, COPE.

(Syn. *Canis ursinus*, Cope.)

Some large specimens agree best with the figures and descriptions of the *Canis ursinus*, but they are so damaged as to render any final reference of them impossible. Indeed, it is by no means clear that the species here named can be regarded as distinct.

The systematic position of *Ælurodon* has been somewhat disputed. Leidy placed it provisionally among the *Felidæ* (*op. cit.*, pp. 68 and 367). Cope, though referring it to the *Canidæ*, has regarded it as the forerunner of the hyænas. "I nevertheless suspect that this genus is the ancestor of the *Hyænidæ*, through the intermediate forms *Ictitherium* and *Hyænictis.*" (American Naturalist, Vol. XVII. p. 244.) Professor Cope has, however, informed us that he does not attach much importance to this view. Schlosser has adopted the same opinion, but believes that *Æ. sævus* should be generically separated from the other species. "Der *Canis sævus*, Leidy, wird von Cope zur Gattung *Ælurodon* gestellt, indess offenbar ohne hinreichenden Grund, denn sowohl der Schädelbau, als auch die Beschaffenheit der einzelnen Zähne, namentlich des oberen Pr. 1 sprechen sehr für die Zugehörigkeit zu den echten Caniden, wäh-

rend die beiden übrigen *Ælurodon*-Arten sich höchst wahrscheinlich als Vorläufer der Hyänen erweisen werden." (Beitr. z. Paläont. Oesterr. Ungarns, Bd. VIII. p. 252.)

In these statements Schlosser has been misled by the fact that the specimen of *Ælurodon sævus* which was figured by Cope is very old, and the teeth so much worn down that the anterior lobe of the upper sectorial is hardly distinguishable. The specimens before us demonstrate clearly that Cope's reference of the species is correct, and that *Æ. Wheelerianus* and *hyænoides* cannot be generically distinguished from it. The only characters of *Ælurodon* which in any way resemble those of the hyænas are (1) the massive premolars, (2) the presence of an anterior basal cusp on the upper sectorial, and (3) the reduction (in some species) of the postero-internal cusp of the lower sectorial. These resemblances are obviously merely analogical, and are of far less importance than the characters of the skull and limbs, which are distinctively cynoid. These animals are genuine dogs, if somewhat peculiarly modified, and to regard them as ancestors of the hyænas is to ignore the close connection between the latter and the viverrines, besides being improbable on geographical grounds.

CANIS.

? Canis vafer, Leidy.

This small alopecoid is represented in the collection by a mandible with broken teeth and some other fragments. It agrees almost exactly with Leidy's type (*op. cit.*, Plate I. fig. 11), except that the diastema between the canine and $\overline{\text{pm}}$. 1 is shorter. The small size of the sectorial places the species in the microdont division of the alopecoid series. M. 2 is very elongate antero-posteriorly, and m. 3 is implanted by two fangs. The mandible is very slender, much

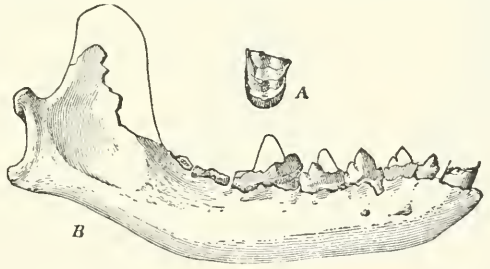


Figure 3. — ? *Canis vafer* × $\frac{3}{4}$. A. First superior molar; B. Mandible.

curved, and non-lobate. The first upper molar is nearly quadrate in shape, the metaconule being almost as large as the protocone, and placed upon nearly the same antero-posterior line. The cingulum is internally very greatly enlarged and thickened, and is disposed symmetrically around the inner side of the crown, instead of being confined to the postero-internal angle, as is usual among the recent *Canidæ*.

The head of the radius is less transversely extended and more discoidal than in recent dogs, apparently indicating the retention in some degree of the power of supination.

FELIDÆ.

FELIS.

? Felis maxima, sp. nov.

This species is founded upon a well preserved humerus from the Loup Fork of Kansas. The chief peculiarity of the specimen is its great size, which very much exceeds that of any living feline. In construction it closely resembles the humerus of the lion, with some minor differences. The external tuberosity rises high above the head, and is somewhat less rugose; the deltoid ridge is exceedingly broad and massive, and descends far down upon the shaft; the outer condyle for the capitellum of the radius is less decidedly convex; the internal epicondyle is very prominent and massive, and is surmounted by a large epicondylar foramen. The presence of this epicondylar foramen shows that the specimen before us cannot be referred to *Smilodon*, for the humerus of *S. necator* figured by Cope (American Naturalist, Vol. XIV. p. 857) has no such foramen. The supinator ridge is somewhat broken, but it appears to have been proportionately less robust than in the lion. The following table will exhibit the great size of this specimen. The measurements of the humerus of *Smilodon* are taken from Cope's figure.

FIGURE 4. — Humerus of ? *Felis maxima* × $\frac{1}{3}$; internal and anterior views.

MEASUREMENTS.

	Smilodon necator.	*Felis leo.*	*F.? maxima.*
	m.	m.	m.
Humerus length	.384	.313	.429
" width of distal end	.087	.054	.072
" antero-posterior diameter proximal end	—	.088	.118

Another cat, perhaps a smaller individual of the same species, is represented by a phalanx of the median row, which is of the characteristically asymmetrical shape, so as to allow the retraction of the claws. It agrees best in shape with the median phalanx of the fourth posterior digit of the lion, but is much larger, measuring 37 mm. in length, and the proximal end is 20 mm. wide; in the lion these dimensions are 27 and 14 mm.

A third very large feline is indicated by the proximal end of a radius from the Loup Fork of Nebraska: it agrees closely in shape and size with that of the lion.

Still another cat is represented by the third and fourth metatarsals from the same horizon and locality. The mode of interlocking, the shape and character of the proximal articular surfaces, are very cat-like, but the bones are short and massive, showing strikingly different proportions from those to be observed in the recent forms.

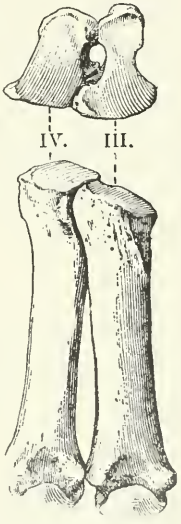


FIGURE 5. — Third and fourth metatarsals of unknown feline × ½.

MEASUREMENTS.

	Felis leo. m.	? m.
Metatarsal III., length	.119	.089
" " width proximal end .	.021	.022
" IV., length	.115	.093
" " width proximal end .	.015	.018

These specimens show that the number of cats occurring in the Loup Fork formation is much more considerable than has hitherto been supposed. Unfortunately, however, these remains are not associated with teeth, so that they cannot be referred to their proper genera and species.

? Pseudalurus intrepidus, LEIDY.

This species is doubtfully indicated by a humerus, lacking the proximal end, which is distinctly feline in character, but remarkable for the very weak development of the supinator ridge.

MUSTELIDÆ.

Carnivora of this family are not certainly known to occur in any American formation older than the Loup Fork, and they are very rare even in that formation. The mustelines are represented in the collection by only a fragment of a lower jaw supporting pm. 4. In the absence of the molars, it is impossible to determine to what genus this specimen should be referred; but it would appear to agree best with the *Mustela parviloba* of Cope.

ARTIODACTYLA.

OREODONTIDÆ.

MERYCHYUS, Leidy.

Merychyus elegans, Leidy.

The genus *Merychyus* is abundant in the Loup Fork, but has been known hitherto chiefly from the dentition. The Garman collection contains some portions of the skeleton, which are therefore of great interest. These specimens show that the genus has departed but little from the type of the family, *Oreodon*, but present, nevertheless, some important approximations to the ruminants.

The ulna and radius show no tendency to coalesce, and the former has the shaft considerably more reduced than in *Oreodon*. The radius differs in many ways from the ordinary oreodont type; the groove for the intertrochlear ridge of the humerus is narrower, the inner flange of the head smaller and less oblique, the outer larger and more concave, and the upward projection from the anterior edge much better developed, almost as in a true ruminant. The shaft is broader and more flattened, the walls much thinner, and the medullary cavity larger. The distal end is less expanded and thickened, and the tendinal sulcus barely indicated. The facets for the scaphoid and lunar are very distinctly separated; the former is shaped much as in *Oreodon*, but more deeply incised and more obliquely placed; between the two is a very deep notch, which penetrates from the posterior side through nearly half the thickness of the radius. This notch is indicated in *Oreodon*, but is not nearly so deep. The only bone of the manus which is preserved is the magnum, the shape of which, however, shows that it has moved entirely beneath the scaphoid, and has a deeply concave facet upon its ulnar side which embraces the side of the lunar almost in a semicircle. No facet for the second metacarpal is to be seen upon the radial side of the magnum, whence it follows that the third metacarpal was in contact with the trapezoid, and that an adaptive reduction of the manus had commenced, which, except in *Merycochœrus*, is unknown in other oreodonts.

Of the tibia only the distal end is preserved, and this portion differs but little from that of *Oreodon;* the astragalar facets are somewhat more deeply grooved and of more unequal size, and the fibular surface is deeper, as if the distal end of the fibula had commenced to wedge itself between the tibia and the calcaneum. The pes is higher and more slender than in *Oreodon*, but shows few important changes. The middle and external cuneiforms are united, but the limits of the two elements are plainly shown by the step cut in the distal surface. Metatarsal II. occupies the whole of the distal surface of the mesocuneiform, and abuts against the side of the ectocuneiform, while metatarsal III. is confined to the latter alone. *Merychyus* thus presents the curious condition of an adaptively reduced manus and an inadaptively reduced pes. The metatar-

sals are relatively very long and slender, more so than in any other member of the entire family, though far from reaching the elongation seen in the true ruminants; the lateral digits are especially slender, though proportionately as long as in *Oreodon*. The phalanges are likewise long and slender, but the unguals are still plainly of the true oreodont pattern.

Another specimen of this species is the skull of a very young animal with the milk dentition, which shows some interesting differences from that of *Oreodon*. In the latter genus, as in the Tragulina and the older selenodonts generally, the third upper milk molar, d. 3, is of a triangular shape, having only the posterior crescents developed, with the anterior portion elongated and trenchant, while *Merychyus* agrees with the true ruminants in the fact that this tooth is like a permanent molar, consisting of four crescents.

Of all known oreodonts *Merychyus* is perhaps the one which most closely approximates the true ruminant type. This is apparent in the elongated and more or less prismatic crowns of the true molars, in the increased size and complexity of pm. 2, in the character of the milk dentition, in the structure of the long bones of the skeleton with their large medullary cavities and thin walls, as well as in the adaptive method of reduction assumed by the manus.

MERYCOCHŒRUS.

Merycochœrus cenopus, Scott.

The type of this species is the specimen consisting of a beautifully preserved manus and pes contained in the Garman collection from the Loup Fork of Nebraska, which unfortunately are not associated with teeth. It is therefore possible that they may belong to some already described species, though they do not agree well in size with any of them.

The foot structure of this genus has been briefly noticed by Cope, who states that the feet are tetradactyle, and that "the os magnum is entirely beneath the scaphoid, and there is a distinct trapezium. The posterior foot is constituted as in *Eucrotaphus*." (Proc. Am. Ass. Adv. Sci., 1884, p. 484.) The manus in *Merycochœrus* agrees much more closely with that of *Merychyus* than with that of any other genus of the family. The carpus is higher in proportion to its breadth than in *Oreodon*, and very much higher as compared with the height of the metacarpus, thus giving the manus very different proportions in the two genera. When the individual carpal bones are compared, we find many differences of detail. The scaphoid has lost its cuboidal shape and become higher, narrower, and deeper (antero-posteriorly); the proximal surface has a convex anterior ridge which is very oblique, rising to a high point on the ulnar, and dying away on the radial side. The distal surface is anteriorly much narrower than in *Oreodon*, broadening however behind; the magnum facet is much larger, and the trapezoidal smaller and more lateral. The trapezium appears not to have been in contact with the scaphoid. The lunar is very peculiar, especially in the great downward prolongation of the beak-like process, which is wedged in between the unciform and magnum, and almost reaches the metacarpals. The proximal

surface has not the simply convex shape seen in *Oreodon*, but rises high towards the ulnar side, and is much depressed on the radial. The distal surface is occupied by the long concave and obliquely placed facet for the unciform, that for the magnum being altogether lateral. This is the culmination of a tendency already noticeable in *Protoreodon* of the Uinta formation, the earliest known member of the family, and more marked in *Oreodon*, namely, the movement of the magnum away from the lunar and under the scaphoid. In *Merycochœrus* (and *Merychyus*) the lunar does not rest upon the magnum at all, touching it only laterally. The cuneiform is much like that of *Oreodon*. The pisiform is very different from that seen in the earlier genera of the family, and shows a tendency to assume the form characteristic of the pigs, though relatively much larger than in those animals. Compared with that of *Oreodon*, it is shorter, heavier, and especially much more expanded at the free end. No trapezium is preserved in connection with this specimen, and as no facets for it are clearly distinguishable on the other carpals, it may not have been developed. The trapezoid is very different from that of *Oreodon*, in being very much higher, narrower, and deeper; the facet for the scaphoid is oblique and almost as much posterior as superior; behind, the bone is drawn out into a projecting process, not abruptly truncated by the facet for the trapezium, as it is in *Sus*. The significant characters of the trapezoid are shown by the distal surface, which is constituted as in the pigs, having a large facet for mc. II. and a small one for mc. III.; in the pig the two facets are of nearly the same size. The magnum is very peculiar; as Cope has shown, it lies entirely beneath the scaphoid and internal to the lunar; its proximal surface is occupied by a large, slightly convex facet for the scaphoid, very different in shape from the same facet in *Oreodon*, as it lacks the abruptly rounded posterior rising; the ulnar side is even more deeply concave than in *Merychyus*, encircling the convex lunar. The unciform differs but little from that of *Oreodon*, except that the proportions of the proximal facets have changed, that for the lunar being considerably the larger.

The metacarpals are relatively much shorter and broader than in *Oreodon*, the lateral digits are somewhat reduced, though not very much, while the median ones have greatly increased in thickness. In proportions the metacarpus is quite like that of *Sus*, though as in all the oreodonts the keels of the distal trochleæ are confined to the palmar surface. Mc. II. is short, stout, and compressed; it articulates by a narrow surface with the trapezoid, but is excluded from the magnum. Mc. III. is very swilline in appearance, but its proximal end is not much extended transversely; on each side of the magnum surface is a facet for the trapezoid and unciform, the latter considerably the larger, while in the pig they are of nearly equal size. Mc. IV. is of about the same breadth and thickness as mc. III.; its proximal end is transverse, as in the pig, not oblique, as in *Oreodon*. Mc. V. is not preserved in the specimen, but the facet for it on the unciform shows that its head was flatter than in *Oreodon*, and that it did not rise so much upon the external side of the unciform.

The phalanges resemble those of *Oreodon*, except for their greater stoutness,

and, as compared with the metacarpus, their greater length, for the three phalanges of the fourth digit are together as long as the metacarpal. The unguals are of the same general shape in the two genera, but broader, more depressed, and with the ends less pointed in *Merycochœrus*.

The pes in the species of *Merycochœrus* from the John Day and Deep River beds differs less from that of *Oreodon* than does the manus, but the species before us appears to show an important departure from that type. The astragalus is shorter, broader, and more massive than in *Oreodon*, and the distal trochlea has a broader surface for the cuboid. The calcaneum is not preserved. The cuboid is low and broad; the surface for the astragalus is broader than that for the calcaneum, reversing the proportions seen in *Oreodon;* the calcaneal surface is also of a different shape, as it does not project outwards, and its external margin is straight, not rounded; unlike the pigs, this facet is not notched on its outer margin. The astragalar surface is not so deeply concave as in the White River genera, and another difference lies in the presence of a broad shallow groove which separates the articular surface into anterior and posterior portions. The peroneal sulcus is shallow. The distal end is almost entirely taken up by the large facet for mt. IV., that for mt. V. being very small and more lateral than distal; in *Oreodon* it is entirely distal. The navicular does not differ sufficiently from that of the earlier genera to require description. The ento-cuneiform is relatively large, and in general resembles that of *Oreodon*, but has a larger bearing upon mt. II. The ento- and meso-cuneiforms are missing, but they were doubtless ankylosed together as in all the other members of the family.

As a whole, the tarsus has changed in an opposite sense to the changes in the carpus, having become lower and broader, while the carpus has become narrower and remarkably high.

The metatarsus is suilline in general appearance; the median digits are short and massive, while the laterals are reduced, especially in length, being not only proportionally but absolutely shorter than in *Oreodon Culbertsoni*. Mt. II. has an exceedingly small surface for the mesocuneiform, but the head is not oblique as in *Sus*. Mt. III. has a minute facet upon the tibial side of the head, which appears to encroach upon the mesocuneiform; and if this is the case, we have here the beginnings of an adaptive reduction of the pes, which is not known to occur in any other member of the family. Except for its heavier proportions, mt. IV. is like that of *Oreodon;* mt. V. has a smaller, more concave and obliquely placed facet for the cuboid than in the latter genus.

Merycochœrus and *Merychyus* thus agree with each other, and differ from other oreodonts in which the foot structure is known in the adaptive reduction of the manus, and it is interesting to note that this adaptive method has been independently assumed in several distinct lines of artiodactyles, e. g. the true ruminants, the pigs, and the camels. A study of the oreodonts shows that they are not closely connected with any existing artiodactyles, and it is difficult to see how the same result could be so often reached independently, unless it be the effect of the similar mechanical conditions to which the extremities are subjected.

MEASUREMENTS.

	Merycochœrus cenopus.	*Merychyus elegans.*
	m.	
Carpus, height	.030	
" breadth	.044	
Lunar, height	.025	
" breadth proximal end	.014	
Metacarpal II., length	.049	
" " breadth proximal end	.008	
" III., length	.064	
" " breadth proximal end	.019	
" IV., length	.057	
Phalanges of IV. digit, length	.057	
	m.	
Astragalus, height	.039	.027
" breadth	.023	.014
Metatarsal II., length	.050	.056
" III. "	.062	.067
" " breadth proximal end	.015	.009
" IV., length	.066	
" V., "	.051	

SUIDÆ.

DICOTYLES.

Several species of peccaries have been described from the Loup Fork beds. The Clifford collection contains two jaw fragments, apparently of different species. One of these differs from existing species in the fact that the last lower premolar is of much simpler construction than the molars, and more perfect specimens would probably show that this represents a distinct genus; but it would be premature to propose a name for it in the absence of more complete material.

FIGURE 6. — Fragment of mandible of Peccary × ⅔.

GELOCIDÆ.

BLASTOMERYX, COPE.

This genus of true ruminants is abundantly represented in the collection. The type species, *B. gemmifer*, Cope, is from the Loup Fork, and differs from the closely allied *Cosoryx* chiefly in the brachyodont dentition. The later described species from the John Day formation not improbably belong to *Palæomeryx*, from which *Blastomeryx* is distinguished by the absence of the characteristic fold on the lower molars, and the greater narrowness and compression of the molar crowns.

The Skull.

A little of the superior wall of the cranium is preserved in one of the specimens, which probably belonged to a young animal, as the horn is a mere rudiment. The frontals are extended back of the orbits and form a considerable part of the cranium, but they are shorter than in *Cariacus*. Distinct though not prominent ridges converge from the back of the orbits, and probably unite behind in a sagittal crest, though as this part of the cranium is broken away the existence of a sagittal crest cannot be certainly affirmed. If present at all, it must have been a mere indication. The orbits are large, and have sharp superior borders. In *Cosoryx* and *Antilocapra* the horn arises directly over the orbit, and the same is probably true of the John Day species of *Blastomeryx;* but in the Loup Fork species of the latter genus the base of the antler has shifted its position somewhat, so as to spring from the posterior portion of the orbit, and it is also directed obliquely backwards, which apparently is the beginning of a process which results in the position of the pedicels observed in *Cariacus*. So much of the frontals as is preserved shows no trace of any sinuses, only the ordinary diploetic structure of the cranial bones. The bases of the antlers are much farther apart than in the deer, and are not connected by any intervening ridge. The coronal suture is nearly straight. As usual in ruminants, the parietals have coalesced into a single large bone, which clearly makes up most of the roof of the cranium. In the anterior portion the supra-orbital ridges are carried over from the frontals and converge to a point. Only the anterior part of the parietal is preserved. The inferior surface of this, and of the frontals as well, is deeply channelled by the winding and complex cerebral convolutions. Of the *dentition* we possess only a superior molar, and several inferior molars of a smaller species. The upper molar is very cervine in structure. The crown is brachyodont, and nearly as broad as long, while in *Cosoryx* it is strikingly narrow as well as hypsodont. The valleys are deeper and the external crescents more flattened than in *Palæomeryx*, while the internal crescents are somewhat simpler. The cingulum has almost disappeared, but a small basal pillar occurs between the inner lobes, as in many deer. The lower molars have low and rather narrow crowns; the valleys are shallow, and disappear after a comparatively short time of attrition. The cingula are but faintly indicated. As compared with the molars of *Cariacus*, those of *Blastomeryx* are simpler in the uncomplicated inner crescents of the upper teeth and the shallower valleys.

The Skeleton.

The *scapula* is much like that of *Cosoryx*, though with some difference, the neck is more contracted, the coracoid more prominent, and the acromion more overhanging. The glenoid cavity is small, nearly circular in shape, and quite deep; the anterior or coracoid border is thin and curved, the glenoid border much thickened and nearly straight. The spine is not very high and divides the blade into unequal fossæ, the postscapular being much the larger, and the acromion overhangs the neck, but does not nearly reach the margin of the glenoid cavity.

The *humerus*. The proximal end of this bone is not preserved in any of the specimens; the shaft is rather short and slender, and shows a distinct sigmoid curve; an indistinctly marked deltoid ridge runs for some distance down the shaft. The distal end is moderately expanded and thoroughly cervine in appearance; the inner condyle is much the wider, and the intercondylar ridge is sharp and prominent. The anconeal fossa is deep and narrow, but does not perforate the bone. A moderate internal tuberosity forms a downward projection at the postero-internal angle. The ridges for muscular attachment are but feebly developed.

The *radius* is entirely distinct from the ulna, no co-ossification between the two occurring at any portion of their length. The proximal end is much expanded, as this bone carries nearly the entire weight of the fore limb, and covers the whole of the distal end of the humerus, the ulna being confined to the posterior aspect. The groove for the intercondylar ridge is deep, and emarginates the anterior and posterior edges. Two small facets for the proximal end of the ulna occur on the posterior side, the inner one very small, the outer larger and quite deeply concave. The shaft is long, slender, and considerably flattened, forming in section a transversely directed oval. The distal end is expanded and thickened, and is deeply grooved in front by the tendinal sulcus. On the external side there is a strong and roughened extension, which fits into a corresponding depression in the side of the ulna. The facets for the carpus are separated by a strongly defined ridge, and are placed very obliquely to the axis of the bone. That for the scaphoid is deeply concave in front and as markedly convex behind, and is continued well up on the posterior side of the bone. This portion has the greatest antero-posterior diameter. The lunar facet is smaller and less deeply incised. External to it is a small oblique surface which articulates with the cuneiform.

The ulna is much reduced, though still retaining its independence. The olecranon is rather short and much compressed, though of considerable fore and aft depth. As the radius has usurped the entire distal end of the humeral trochlea, the sigmoid notch of the ulna is shallow, and the internal radial facet has become minute, though the external one forms quite a protuberance. The shaft is exceedingly slender and compressed; for most of its length hardly more than a thread of bone. The distal end is somewhat expanded, though very small, and deeply excavated on the inner side for the protuberance of the radius. The cuneiform facet is saddle-shaped, and sends down a well marked process on the outer side.

The *pelvis*, so far as it is preserved, is much like that of *Cosoryx*, though the ilium has a longer neck, and was apppreently even less everted than in that genus. The ischium is rather short.

Little of the *femur* is preserved. The head is small and compressed, and rises little above the ridge connecting it with the great trochanter. The rotular trochlea is very broad, with rounded and somewhat more prominent internal edge; the outer edge is lower and sharper. The condyles are rather small and widely separated; above the inner one there is a small but distinct plantaris rugosity.

The *tibia* has a large trihedral head, with large external and small internal surfaces for the femoral condyles, and prominent bifid spine. The cnemial crest is very well developed, and just posterior to it on the external side is a very deep tendinal sulcus. The shaft is quite long and stout, with oval section and broad distal end. The surfaces for the astragalus are deeply incised, and the external one is somewhat the larger. The tongue is broad and thick, corresponding to the breadth of the groove in the astragalus. The internal malleolus is very long, and forms a tongue-like projection from the antero-internal corner.

The *fibula* is as completely reduced as in any ruminant. The proximal end is ankylosed with the tibia, where it forms a short sharp process. The distal end is not represented in any of the specimens, but from the structure of the tibia it is plain that it was a small nodule wedged in between the distal end of the tibia and the fibular process on the calcaneum. Between the two distal fibular facets of the tibia is a groove for the reception of the rudimentary shaft.

The *carpus* is like that of recent deer; the bones of the proximal row are high and narrow, those of the distal row low and broad. The scaphoid is deep antero-posteriorly, and broader in front than behind, where it is much narrowed by the great lateral extension of the lunar; the proximal surface is directed very obliquely backwards and inwards, and is deeply incised so as to form a very firm interlocking joint with the radius; this facet is divided into a strongly convex anterior portion, and an as strongly concave posterior portion. The lunar is curiously shaped; it is broadest in front and behind, and contracted in the middle; the anterior surface is transverse, the posterior very oblique. The radial surface is directed obliquely inwards parallel to that of the scaphoid. The distal surface is divided nearly equally between the magnum and the unciform, which meet at a very open angle, and the "beak" is barely indicated. The inner face of the lunar is nearly vertical, the outer very oblique, as the upper part of the bone is considerably wider than the lower, corresponding to the reduction in width of the proximal portion of the cuneiform. The latter bone has a broad distal surface and small saddle-shaped facet for the ulna, which is prolonged well down upon the postero-external surface. The cuneiform rises above the level of the lunar, and presents a small oblique surface, which articulates with the radius. The pisiform facet is high and very narrow. The trapezium is not preserved in any of the specimens, but its presence is demonstrated by a small facet on the postero-internal angle of the trapezoid. It was obviously very small and did not reach the scaphoid. The trapezoid and magnum have coalesced; the proximal surface of the compound bone is mostly occupied by the scaphoid, the facet for which is low and concave in front, rising behind to a low broad convexity; the distal surface is nearly flat. The unciform is narrower and higher than the

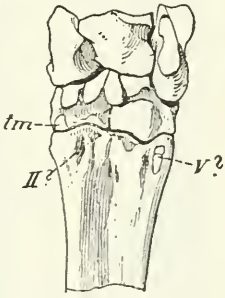


FIGURE 7. — Carpus of *Blastomeryx*, nat. size, posterior view.

trapezo-magnum; its proximal surface is divided obliquely into facets for the lunar and cuneiform. The unciform projects below the level of the trapezo-magnum, and so presents upon the radial side a small facet for the corresponding projection of mc. III.

The metacarpus consists of the III. and IV. metacarpals, which have coalesced to form a cannon-bone, and the II. and IV., which are very slender, styliform bones, perhaps interrupted in the middle of the shaft. The cannon-bone is more slender than the anterior one of *Cosoryx* figured by Cope (Am. Nat., 1881, p. 547). The proximal surface is unequally divided, considerably the larger part belonging to mc. III., which projects above the level of mc. IV., and so comes into contact with the unciform. This arrangement occurs also in *Dremotherium* (see Gaudry, Enchainements, Fig. 142), and to a much less degree in *Antilocapra*. The shaft of the cannon-bone is broader and flatter proximally, becoming narrower and more rounded distally, and the distal trochleæ are completely encircled by sharp keels, as in existing ruminants. On the posterior side of the proximal end are two small facets, probably for the heads of the lateral digits. At all events, much of the shafts of the metacarpals II. and V. were preserved in the shape of very slender and compressed splint bones.

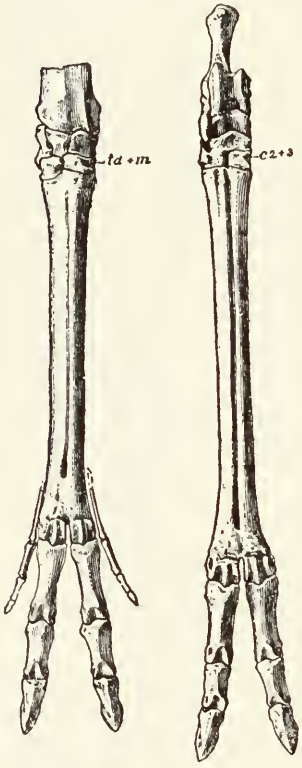


FIGURE 8. — Manus and pes of *Blastomeryx* × $\frac{2}{3}$.

The phalanges are long and slender, and so asymmetrical as to produce a decided convergence of the toes. The proximal ends of the first row are deeply grooved for the keels of the metapodials, but are not emarginated in front as are those of the recent Pecora. The ungual phalanges differ from those of the deer and antelopes only in their greater slenderness. The phalanges of the lateral digits are of about the same proportionate size as in existing *Cervidæ*.

The tarsus is also cervine in character, and differs little from that of *Palæomeryx* (*Cervus*) *Flourensianus* as figured by Fraas (Fauna von Steinheim, Taf. VIII. fig. 24). The astragalus is high, narrow, and deeply grooved, and the distal end shows hardly more than an indication of the ridge which passes between the navicular and cuboid. The calcaneum is long and much compressed, though with considerable depth, antero-posteriorly in the lower third (in *Palæomeryx* the calcaneum is thicker and more rounded); the cuboidal facet is narrow, pointed in front and quite concave from before backwards; the sus-

tentaculum is short, but broad and thick, and the fibular facet is high, but short and narrow. As compared with the calcaneum of recent deer, that of *Blastomeryx* has less antero-posterior diameter below, and a somewhat less thickened tuberosity at the free end, quite unimportant differences. The cuboid and navicular are firmly co-ossified, as in *Palæomeryx* and all existing Pecora; these bones are quite low, and the navicular rises but little in front to fit the distal groove of the astragalus, but on the postero-internal side it sends up a strong and high process, which makes the astragalar facet very deeply concave; distally the navicular shows two facets, a large one for the compound cuneiform, and a much smaller one for the entocuneiform. On the distal surface of the cuboid, besides the large facet for mt. IV., is seen a minute, oblique infero-lateral one, obviously for a rudimentary fifth digit. The only other tarsal bone preserved in the specimens is the compound cuneiform, which is rather low, narrow, and deep; in front it is nearly on a level with the cuboid, but behind descends somewhat below it, and thus affords a lateral attachment to mt. IV. The presence of a distinct entocuneiform is demonstrated by the facets for it upon the navicular and cannon-bone.

The metatarsus presents some features of much interest. Rosenberg (Zeitschr. f. wiss. Zool., Bd. XXIII.) has shown that in the sheep embryo there are at one stage four complete metatarsals; he states, however, that the lateral ones are ultimately absorbed. In *Blastomeryx*, as in *Amphitragulus*, and probably all existing Pecora and Tylopoda, there are at least three elements which enter into the formation of the posterior cannon-bone; viz. mt. III. and IV., and the proximal portion of mt. II. The latter, though ankylosed with mt. III., shows its limits distinctly; it has a small facet for the entocuneiform, and ends below in a point. Mt. V. was obviously present, as upon the postero-external side of the cannon-bone there is a shallow groove, and upon the cuboid, as already stated, there is a small facet for the head of it. An examination of the metatarsus of a modern ruminant seems to show that the portion articulating with the entocuneiform is the head of mt. II.; whether mt. V. be also present is more difficult to decide, but in existing forms there is no portion which can be identified with it, while in *Blastomeryx*, though undoubtedly present, it does not coalesce with the cannon-bone. There is nothing in any of the specimens to indicate that any portion of the distal ends of the lateral metatarsals were retained, though doubtless phalanges were preserved, as in the deer.

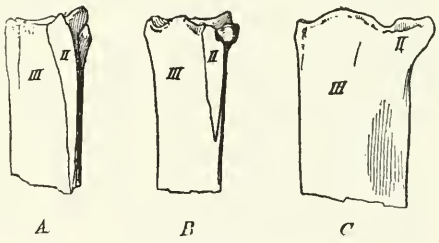


FIGURE 9. — Proximal end of posterior cannon-bones × $\frac{2}{3}$, internal view; A. *Amphitragulus*; B. *Blastomeryx*; C. *Antilocapra*.

In this brief, but fairly comprehensive review of the osteology of *Blastomeryx*, we have seen nothing which can be opposed to the view expressed by Profess-

Cope, that this genus should be placed in the ancestral line of the distinctively American deer. *Alces*, *Tarandus*, and *Cervus* are really immigrants from the Old World, and do not belong in this category; but the truly American types, of which *Cariacus* is the chief example, have a peculiar skull structure, first pointed out by Garrod, which seems to show that the American deer were separated from those of the Old World at a comparatively early date, though it is very questionable whether both series could have independently acquired the extraordinary peculiarity of the deciduous antler.

COSORYX, LEIDY.

Cosoryx furcatus, LEIDY.

This very interesting animal is represented in the collections of Garman and Sternberg by several specimens, which enable us to add materially to the descriptions hitherto published. These descriptions are so brief that the relationships of this genus have been very generally misunderstood. Schlosser says: "In Nordamerika finden sich im oberen Tertiär zwar Geweihe von Hirschen, Kiefer derselben sind indessen noch nicht mit Sicherheit ermittelt, wenigstens nähern sich die Gebisse des *Dicrocerus* Cope, *Merycodus* Leidy, *Cosoryx* Marsh, zweifellos eher den Antilopen, besonders dem lebenden nordamerikanischen Genus Antilocapra, als den Hirschen. Sie sind zugleich viel einfacher gebaut und schliessen sich namentlich die Marken sehr bald, was bei den Hirschen erst in einem ziemlich späten Stadium der Abkauung auftritt. Das Gleiche dürfte wohl auch der Fall sein bei *Blastomeryx* Cope = *Cosoryx gemmifer*, trotzdem Cope denselben als Stammvater von *Cervus* und *Cariacus* betrachtet. Die von Marsh behauptete Existenz von Seitenzehen bei *Cosoryx* dürfte wohl mit Recht bezweifelt werden; die Hand hat Cope abgebildet und zeigt dieselbe keine Spur von etwaigen Griffeln. Wenn auch die systematische Stellung dieser Formen noch nicht völlig klar gelegt erscheint, so können wir doch mit grosser Wahrscheinlichkeit annehmen, dass wir hier einen eigenen Seitenzweig der Ruminantier vor uns haben, als dessen letzter Rest die merkwürdige nordamerikanische Gabelantilope zu betrachten ist. Die Verästelung des Geweihes ist bisweilen fast so stark wie bei den echten Hirschen. Wahrscheinlich war es von Hornmasse überzogen — den verwachsenen Haaren des Bastgeweihes. Für diese Annahme spricht die auffallende Glätte der von Cope und Leidy abgebildete Geweihfragmente." (Morph. Jahrb., Bd. XII. p. 70.)

As we shall see, some of these inferences are probably quite correct, others are equally probably misleading. This group of closely allied species is not confined to the "upper Tertiary" or Loup Fork beds, but appears first in the lower middle Miocene of Oregon in the John Day beds, where the genus *Blastomeryx* is abundantly represented by some large species. Now *Blastomeryx* is, so far as we can at present determine, almost identical with the type variously named in Europe *Palæomeryx* and *Dremotherium*, about the only difference of importance being the absence of the characteristic "Palæomeryx fold" on the

lower molars. *Cosoryx* is very closely allied to *Blastomeryx*, and is distinguished from it chiefly by the much more hypodont molars. The bones of the various Loup Fork species of this genera cannot be distinguished apart in the absence of associated teeth, and it is quite probable that the John Day species of *Blastomeryx* will prove to belong to a different genus from the Loup Fork species.

The Dentition.

One undoubted specimen of *Cosoryx* contained in the Cambridge collection consists of a fragment of the superior maxillary containing one molar, the lower jaw with first and third molars, an antler, the sacrum, all the lumbar and the five posterior dorsal vertebræ in unbroken succession, the scapula, humerus, pelvis, and posterior cannon-bone. The resemblance of these bones to *Antilocapra* is very striking, and fully justifies what Schlosser has said with regard to the relationships of the two genera. The second upper molar is not much extended in the antero-posterior direction, and has a fairly high crown, though not hypsodont to the same degree as in the prong-buck; the median fold of enamel on the external wall, or, more properly speaking, the projecting anterior horn of the postero-external crescent is less strongly developed than in the recent form, and the corresponding horn of the anterior crescent hardly projects at all. The valleys are shorter and wider than in *Antilocapra*, and though the tooth is in an advanced state of wear, they are still quite deep, in contrast to what occurs in the lower molars. The lower incisors and canines are all broken away, but from the alveoli and remaining fangs it may be seen that they were of the ordinary ruminant pattern, probably not very long; they decrease in size from the median incisor outwards, and the canine is the smallest of the series. The premolars, three in number, are represented only by their alveoli, which shows them to have been very small. The most anterior is implanted by a single root, the others by two. Leidy's figure (*Merycodus necatus*) shows them to possess considerable complication, but they are less molariform and more trenchant than in *Antilocapra*. The true molars are more truly hypsodont than in the upper jaw; the first is very small, but the third resembles that of the modern genus exceedingly closely.

The same may be said as to the form of the mandible itself; the horizontal ramus is very long, compressed, and rather shallow, and with an extremely long diastema between the canine and premolar 3; the ramus is less rounded on the external side than in *Antilocapra*, and in that genus there is no such descent of the upper margin in front of the premolars as occurs in *Cosoryx*. The symphysis is short (much shorter than in *C. trilateralis*, Cope) and much contracted, and on a level with its posterior edge is a large single mental foramen. The antler is branched like the one figured by Leidy with the name of *Cervus Warreni*, but with a much longer beam, and the tines meeting at a more open angle. The beam is longer and the tines shorter than in any of the antlers figured by Cope, except, perhaps, the imperfect specimen named *Cosoryx* (*Dicrocerus*) *teres* (Wheeler, Pl. LXXXII. fig. 6). The antler is composed of dense bone, with a

smooth and here and there furrowed surface, a texture which, as Schlosser has remarked, is very different from that of a deer antler. The burr is very large and prominent, but a vertical section shows that the beam passes into the pedicel without any perceptible break or change in the tissue. In *Cosoryx* the burr is very variable, as may be seen from Cope's figures. In this collection are some specimens without any burr, others with a single burr, and some with two or three. They can hardly be regarded as an evidence that the antler was deciduous.

The Skeleton.

The *vertebræ*, so far as they are preserved, resemble very much those of *Antilocapra*. Owing to the fact that only the posterior part of the column is preserved in the specimen, it will be most convenient to describe them from behind forwards. The only caudal represented is like the second of the prong-buck, but a little more complete, and clearly shows that the tail was short, as may also be inferred from the sacrum. This caudal is short and narrow, especially in front, with short wide transverse processes near the posterior end. There are a pair of rudimentary prezygapophyses, and an exceedingly minute neural canal, which will just allow the passage of a needle, and a corresponding neural spine. In the prong-buck the second caudal has neither canal nor spine, and the transverse processes are wider.

The *sacrum* consists of four completely ankylosed vertebræ. The first has a broad depressed centrum, well developed prezygapophyses, and much enlarged pleurapophyses, which occupy most of the sacral surfaces of the ilia. The spine is coalesced with the others into a high and arched ridge. In the prong-buck the spines are more distinct. The other sacrals have expanded pleurapophyses, but only the second has any contact with the ilium. The centra decrease rapidly in size from the first posteriorly, and that of the last is exceedingly depressed and thin. The whole sacrum is quite strongly arched from before backwards. The lumbar region is quite long, and consists of six vertebræ, which are slenderly constructed; the centra are anteriorly comparatively narrow and trihedral in section, posteriorly they are broader and more depressed. The spines are low and comparatively broad, and are inclined well forward, with concave anterior borders. The transverse processes on the first lumbar are short, depressed, but comparatively broad; these processes lengthen as we pass backwards, but are very slender as compared with those of *Antilocapra*, and the neural spines are lower than in that genus. The zygapophyses are of the interlocking cylindrical type usual among artiodactyles, and there are no metapophyses. We may infer with considerable confidence that the number of dorsal vertebræ was thirteen; on this assumption, the most anterior dorsal of this specimen is the ninth. In this the centrum is short and trihedral in section, with the inferior border sharp and arched from before backwards; the spine is rather short, and directed very obliquely backwards; the transverse processes are short and slender, and have well marked facets for the tubercles of the ribs; the prezygapophyses are flat and placed on the pedicels of the neural arch, and, separated

from them by a short interval, arises a pair of small metapophyses. The tenth is the anticlinal vertebra; the spine is at first very oblique, but curves, and in its upper portion is vertical. In other respects this vertebra is like its predecessor. On the eleventh the spine is directed slightly forwards, but the end is rounded like that of the anterior dorsals; the metapophyses have approached the median line so as to touch the post-zygapophyses of the tenth, while the post-zygapophyses of the eleventh have assumed the cylindrical shape found in the lumbar region. The twelfth and thirteenth vertebræ are much like lumbars in their construction, and are distinctly longer than the three antecedent vertebræ; the spines have the nearly straight thickened free ends seen in the lumbars, and the metapophyses have disappeared. The transverse processes, however, are very short, though they still retain the rib-facets, even on the thirteenth.

The *ribs*, so far as can be judged from the fragments, are narrow and very slender. Of course this may be true only of the posterior part of the series.

The *scapula* is characteristically ruminant. The glenoid cavity is nearly round and quite shallow, the coracoid process is prominent, recurved and thickened at the end; the neck is very long and much contracted, the borders sloping away from it very gradually; the coracoid border is thin and rounded at the edge, it curves gently forwards and upwards from the neck; the glenoid border is very much thickened and somewhat overhanging, from the neck it is nearly straight, and forms a right angle with the very thin suprascapular border. The spine rises abruptly from the neck into the high acromion; the latter overhangs very slightly, in sharp contrast to the condition found in *Antilocapra*. The spine divides the blade into unequal fossæ, the prescapular being much the smaller, as is ordinarily the case among the ruminants. Except for the nearly straight inferior edge of the spine, and the consequent lack of an overhanging acromion, this scapula very closely resembles that of the prong-buck.

The *humerus* has a broad and flattened head, which projects but little beyond the shaft. The external tuberosity is large, and curves over the deep bicipital groove; the internal tuberosity very small; both are much less developed than the corresponding processes in *Antilocapra*. Proximally the shaft is broad and compressed, below it is rounded and slender. No ridges for muscular attachment are more than very faintly indicated. The distal end is broken away, but in all probability it was like that of *Blastomeryx* described above.

The *pelvis* is also entirely ruminant in character. The ilium has a short, deep, and much compressed neck, expanding into a curved and strongly everted plate, which projects a considerable distance in front of the sacral attachment. The ilium is somewhat tribedral in section, the median rounded ridge of the plate being more prominent, and the expansion itself smaller than in the prong-buck. The ischium is very long; above the acetabulum its superior border shows the convexity so usual in the recent ruminants, though in a less marked degree. The tuberosity of the ischium is very long and prominent, and directed straight outwards; behind the tuberosity the ischium is prolonged further than in the prong-buck. The cannon-bone belonging to this specimen is broken, and its

proximal end obviously diseased, so that it does not merit description; the only fact of importance which it shows is the comparative slenderness of the bone.

So far as the material will enable us to judge, the feet of *Cosoryx* differ in no important respect from those of *Blastomeryx*, and the same statement applies to the long bones of the limbs.

Restoration of Cosoryx furcatus.

(See Plate I.)

This drawing is made from the specimen already described, completed by fragments of others, while the feet are drawn from *Blastomeryx;* the cervical vertebræ are represented only by the axis, the others being conjectural, as are also the anterior dorsals. The skull is taken chiefly from that of the closely allied European genus, *Pa'æomeryx*, and from specimens of the large *Cosoryx teres*, Cope, belonging to the Smithsonian Institution. The fortunate association of the mandible in the same specimen with the vertebræ, pelvis, scapula, etc., gives a very useful standard as to the length and character of the skull, position of the molars, etc. It may be assumed with some confidence that the drawing gives a fairly accurate representation of the animal. Marsh's account of the feet of *Cosoryx* shows that they were constructed much like those of *Blastomeryx*. In general appearance *Cosoryx* seems to have had the same light, graceful build as *Antilocapra*, but with a very different skull and deer-like antlers. The proportions of the limbs also differ somewhat, the hinder cannon-bone being considerably longer than the fore, while in the prong-buck they are of nearly the same length. *Cosoryx* was a much smaller animal, the bones are all more slender than in *Antilocapra*, and the carpal and tarsal bones are much higher and narrower proportionately.

The view held by Cope that *Cosoryx* is the ancestor of *Antilocapra* is very probably the true one. So far as the dentition, the vertebræ, and the limbs are concerned, the differences between the two genera are only such as might be expected to occur between a Miocene and a recent ruminant. A distinction of some importance, however, consists in the character of the horns. In *Cosoryx* they are branched, but probably not deciduous antlers; in *Antilocapra*, a core with a horny sheath, which, however, differs strikingly from the horn of the typical Cavicornia. But the unique branched horn of *Antilocapra* not improbably indicates, as has been suggested by Cope, a remnant of a former branching of the bony core itself, and so this difference does not preclude a genetic connection between the two forms. In *Cosoryx* the antler was almost certainly covered with skin; its smooth surface, as Schlosser points out, shows that it could not have been naked, as in the true deer.

Both *Blastomeryx* and *Cosoryx* are probably to be derived from the species referred to the former genus which occur in the John Day beds, but there is no form yet known in the White River which could have given rise to these John Day ruminants. The latter are most probably descended from some *Palæomeryx* of the Old World, which migrated to this continent. The very close con-

nection between these American genera and the *Amphitragulus*, *Dremotherium*, etc. of St. Gérand le Puy is obvious from the most superficial comparison.

The collection contains specimens probably indicative of other species of *Cosoryx*, some of them much larger than *C. furcatus;* but in the absence of associated teeth, it is not possible to refer them to their proper categories.

PERISSODACTYLA.

ANCHITHERIIDÆ.

MESOHIPPUS, Marsh.

The Brain.

Mesohippus had a large and well convoluted brain. The length and breadth indicate that it weighed about one third as much as the brain of the recent horse, while if we estimate the body weights of the fossil and recent animals by the relative size of the humeri, the brain of the Miocene species was proportionally heavier. The cerebrum of the horse is, however, much more highly convoluted, and the frontal lobes are relatively broader. The *Mesohippus* brain is distinguished in a marked manner by the longitudinal direction of the parietal and occipital sulci, and by the deep transverse frontal sulci, as contrasted with the oblique sulci of all recent ungulates. In fact, in this respect it bears a marked general resemblance to the brain type of recent Carnivora, and conforms with the higher Ungulata of the Eocene.

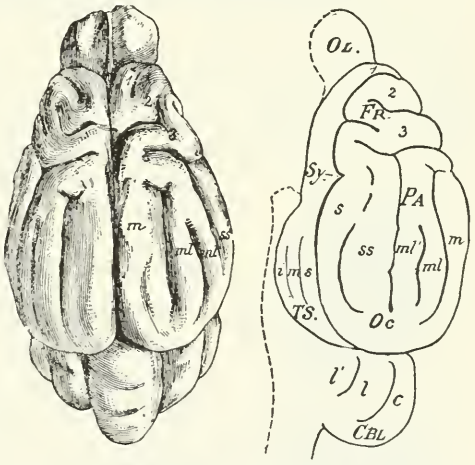


Figure 10. — Brain of *Mesohippus Bairdii* × ⅔. From above, and from side.

On either side of the longitudinal fissure is a long deep fissure forking anteriorly and marking off the median gyrus, *m*, of the parieto-occipital region. Parallel with this is a short fissure, which separates the two medilateral gyri, *ml*, *ml'*. The third fissure extends to the posterior transverse, and thus entirely separates the supersylvian gyrus, *ss*, from the medilateral. The fourth fissure is shallower. There are three transverse frontal fissures (Fr. 1, 2, 3) which divide this lobe into three gyri; the median fissure extends almost to the longitudinal fissure, and sug-

gests the crucial sulcus of the Carnivora. The sylvian fissure is very shallow. The temporo-sphenoidal lobe is very prominent, and is divided into three gyri (*s*, *m*, *i*) by two sulci. Beneath the third frontal gyrus is a vertical sulcus, parallel with the sylvian.

The cerebellum has a large central lobe with transverse simple furrows.

The Dentition.

There are a few new points to be noted in regard to the teeth of *Mesohippus*, which bear upon the dentition of the horses in general, and are clearly shown in

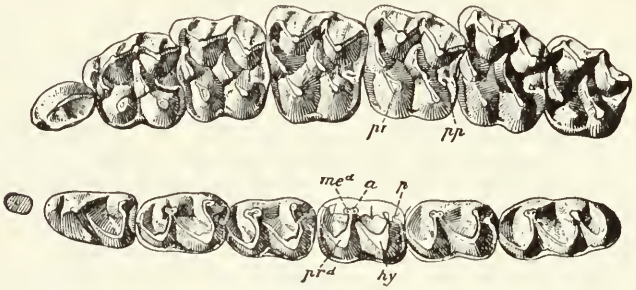


Figure 11. — Superior and inferior molars of *Mesohippus Bairdii* × ½.

a series of unworn crowns of the upper and lower jaws. Scott has already pointed out that the incisors in this genus are simple, there being no indication of the infolding of the enamel, such as is seen in *Anchitherium aurelianense*. In some of the John Day species of *Anchitherium* the enamel is not infolded, as observed in the lower jaw of a specimen referred to *A. equiceps*, Cope.

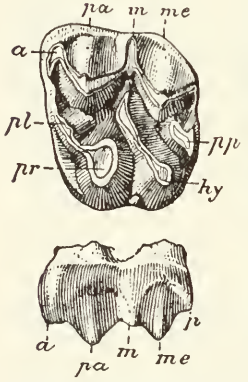


Figure 12. — Superior molar of *Anchitherium longicriste* × ½. Superior and external view. Cope collection.

The upper molars of *Mesohippus* clearly show the first step in the formation of the *posterior pillar*, *pp*, which is so conspicuous a feature in *Anchitherium*, in the posterior valley. This can also be observed in a still simpler stage in a specimen of *Anchilophus* from the French Phosphorites. Step by step with the development of this cusp appears the *posterior pillar*, *p*, in the lower molars, behind the entoconid; this accessory cusp can be traced back to the teeth of *Epihippus*. When it finally unites with the entoconid, in *Hipparion*, it forms the posterior twin cusp (*b*, *b*, Rütimeyer), which is analogous to the anterior pair formed by the union of the metaconid and *anterior pillar*, *a* (*a*, *a*, Rütimeyer).

Thus the transition from the *Mesohippus* to the *Anchitherium* molars is very gradual, as shown in the accompanying figures. By tracing back the rise of

the eleven elements which compose the upper *Equus* molar, we find that six belong to the primitive sextubercular bunodont crown. Two elements of the ectoloph, the *anterior pillar* and *median pillar*, rise from the simple primitive basal cingulum of the *Hyracotherium* molar; the same mode of development, we have just seen, is true of the *posterior pillar*. The eleventh element, the fold of the postero-external angle of the crown, *p*, is not prominent until we reach *Equus*. The term "posterior pillar" is taken from Lydekker; the other terms, "median" and "anterior," are applied to parts which have an analogous origin from the basal cingulum. The remaining coronal cusps are readily identified with their homologues in the primitive tritubercular molar.

? Anchitherium parvulus, Marsh.

(Syn. *Equus parvulus*, Marsh.)

Among the Loup Fork specimens collected by Clifford are found two lower molars, m_1 and m_3, which are almost identical in size with those of *Mesohippus Bairdii*. The crown of m_1 measures: antero-posterior, .011 m.; transverse, .009 m. Unlike the *Mesohippus* molars, there is no external cingulum. The "posterior pillar" has the same degree of development as in *Anchitherium*. The fangs are separate. There is no trace of cement. Marsh has described a diminutive horse (*Equus parvulus*), estimated at two feet in height, from the same beds, and it is highly probable that these teeth belong to this species. The generic reference is of course very uncertain. The brachydont crowns point either to *Merychippus* or *Anchitherium*, but the stage of development of the coronal pattern approximates most closely that in the latter genus, being a little more advanced than in *Mesohippus*.

RHINOCERIDÆ.

ACERATHERIUM.

The Manus and Pes.

The characteristics of the pes of *Hyracodon* from the lower White River beds have been fully enumerated by us.[1] They are principally as follows: cuboid not supporting astragalus anteriorly; lateral digits reduced and not spreading; ectocuneiform not articulating laterally with mts. II. We may subsequently find that the feet of the later species of *Hyracodon* varied in some of these respects, although this is not probable, owing to the fixity of foot-types once established. We have, however, no present means of distinguishing between the *Metamynodon* and *Aceratherium* foot-bones.

On page 169 of the first Bulletin a high, rather slender tarsus was described,

[1] See Scott, E. M. Museum Bulletin, No. 3, May, 1883, p. 19. Also, Osborn, Mammalia of the Uinta Formation, May, 1889, Part IV. "Evolution of the Ungulate Foot," p. 549.

which probably belongs to the *Aceratherium* of the lower beds. It differs widely in its proportions from other specimens found in this collection, which belong either to the *Aceratherium* of the higher beds, or to *Metamynodon*. The best preserved specimen of this second type (marked a^8) is comparatively short and broad, with spreading digits and rugose surfaces for muscular attachment (Figure 13). The proportions of the metapodials to the tarsals are similar to those in *Ceratorhinus*. The calcaneum has a powerful tuber; the ectal astragalar facet is very convex; the sustentaculum is narrow, and its oval facet is continuous with the inferior; the cuboidal facet is nearly horizontal. About one fifth of the astragalus rests upon the cuboid. The relations of the cuboid, navicular, and ectocuneiform repeat those observed in *Rhinocerus*. The mesocuneiform is very short, giving mts. II. a wide articulation with the ectocuneiform. The metatarsals are powerful, the lateral pair having approximately the same length as in *R. indicus*. This type of foot is related directly to that of *Aphelops*.

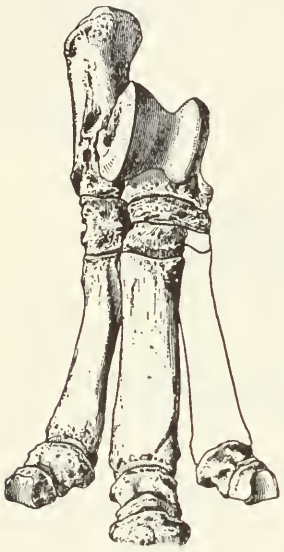


FIGURE 13 — Right pes of *Aceratherium* × $\frac{1}{4}$.

The manus and pes of a third specimen (marked a^6) show several interesting differences. In the pes, the metatarsals are of the same proportions, but the calcaneo-cuboidal facet is oblique and narrow, resembling that in *Hyracodon*, and the sustentaculum is very small. The remains of the carpus show that the species to which this specimen belonged had a greatly reduced fifth digit, constituting a functionally tridactyl manus. The evidence for this is in the greatly reduced lunar-magnum facet, which is invariably characteristic of tridactylism.[1]

It may be noted here that among the carpals of *Titanotherium* there is a well preserved lunar, which has its magnum facet much reduced anteriorly, so there is little question that we shall yet discover a tridactyle species of the genus.

The Rhinoceros Molars.

The peculiarities of the molars of *Aphelops* will be made more clear by a few observations upon the molars of the rhinoceroses in general. The three main crests of the lophodont crown may now be distinguished in part by terms which express their homologies with the elements of the sextubercular superior and quadritubercular inferior molars of the primitive ungulate, *Phenacodus*. In the upper molars, the outer crest is formed by the union of the primitive paracone

[1] See Osborn, Mammalia of the Uinta Formation, p. 567. It is possible that these feet belong to *Metamynodon*.

and metacone, to which is joined the anterior pillar (see *Mesohippus*, p. 88); it may be called the *ectoloph*. As the anterior crest is formed by the union of the protocone, protoconule, and paracone, it may be termed the *protoloph*. The posterior crest, which unites the primitive metacone, the metaconule, and the hypocone, may be termed the *metaloph*. The outer surface of the ectoloph in the primitive molar of the Rhinoceros is marked by three vertical ridges corresponding to its three primitive component elements, *me, pa, ap;* one or all of these disappear in the flattening of the surface. It will be observed that nothing corresponding to the 'median pillar' of the superior molar of the horse is developed. In the lower molars (the paraconid disappearing), the union of the metaconid and protoconid forms the anterior crest, or *metalophid*, while the hypoconid and entoconid unite to form the *hypolophid*.

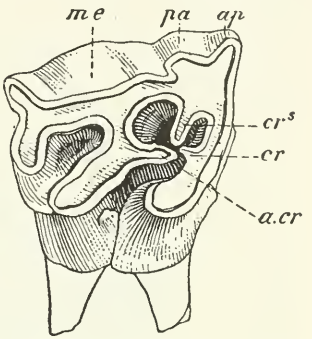


FIGURE 14. — Superior molar of Rhinoceros (sp. indet.) × ½. After De Blainville.

The secondary enamel folds, which are developed from the three crests, bear a most interesting analogy to those observed in the horse series, beginning with *Protohippus;* they are outgrowths of the same regions of the crown and subserve the same purpose. They are moreover of like value in phylogeny. The useful descriptive terms introduced by Busk, Flower, and Lydekker, should be adopted in part.[1] These secondary elements consist, first, of three folds projecting into the median valley, one from the ectoloph, the *crista;* one from the protoloph, the *crochet;* one from the metaloph, the *anticrochet*. Secondly, the ectoloph unites with the posterior cingulum and metaloph. Thus the anterior and posterior valleys may be cut off by the union of these folds into from one to three 'fossettes,' precisely analogous to the 'lakes' in the horse molar, except that they are not filled with cement.

The accompanying diagram is taken from a fossil molar figured by De Blainville. (Osteogr. Gen. Rhin, Plate XIII.) It is remarkable in exhibiting all the primary and secondary elements, for they are very rarely combined in a single tooth. Similar accessory folds are frequently developed in the lower molars.

[1] The terms 'protoloph' and 'metaloph' are, however, substituted for 'anterior collis' and 'posterior collis' of Lydekker. The term 'anterior pillar' = 'first costa,' and 'paracone' = 'second costa.' The mode of evolution of the 'pillar' must have been similar to that in the horses, where Lydekker has proposed this term for the 'posterior pillar.' It is very appropriate, because the pillars in their earliest development can be shown to rise independently from the cingulum (see *Mesohippus*, p. 88), and not as folds of the main elements of the crown, as we should infer from their fully developed stage.

APHELOPS, Cope.

The generic characters of *Aphelops* have been given by Cope as follows. Dentition, I. $\frac{2-2}{1-1}$, C. $\frac{0}{1}$, P. $\frac{4-4}{3-3}$, M. $\frac{3}{3}$; post-glenoid and post-tympanic processes in contact but not co-ossified; digits, 3–3; nasals hornless. To these characters may be added: magnum not supporting lunar anteriorly; absence of the 'crista' and invariable presence of the more or less strongly developed 'crochet' and 'anticrochet' in the superior molars.

The specific nomenclature of *Aphelops* is in confusion. The type of *A. (Rhinoceros) crassus*, Leidy,[1] is a last upper molar, which is closely similar to that of *A. megalodus;* the characters of the milk molar associated with this type cannot be used in definition.[2] The penultimate upper molar, the type of *A. meridianus*, Leidy,[1] corresponds in the development of the two 'crochets' to the same tooth in *A. fossiger*, Cope, but the posterior 'fossette' is not enclosed by the strong cingulum as in the latter species. *A. (Aceratherium) acutum*, Marsh, is identical with *A. fossiger*. *A. malacorhinus*, Cope, resembles *A. meridianus* in the open posterior fossette and the development of the 'crochets.' It is impossible, however, to clear up this synonymy without bringing the original types together for comparison. General characteristics of all these types are the invariable development of the 'crochet,' absence of the 'crista,' usual development of the 'anticrochet.' The specific names proposed by Cope are here adopted because they are established upon a very complete knowledge of the skull as well as of the teeth.

Aphelops fossiger, Cope.

Dentition: I. $\frac{1}{1}$, C. $\frac{0}{1}$, P. $\frac{4}{3}$, M. $\frac{3}{3}$. First premolar simple, conical, sometimes absent; nasals not overhanging premaxillaries; foramen lacerum medium confluent with foramen ovale; occiput broad and low; limbs short and bulky; molars with well developed 'crochet' and 'anticrochet.'

In the figure given by Marsh (Am. Journ. Sci., Oct., 1887, p. 3) and by Cope (Am. Nat., Dec., 1879, p. 771 *e*), the third and fourth premolars have both the 'crochet' and 'anticrochet.' There is some ground for the supposition that the skull here described belongs to a different species, since the 'anticrochet' is not developed in the premolars. This reference is therefore provisional.

This is apparently the only species which is represented in this collection. All the specimens are from Kansas, and include several skulls and well preserved bones from all parts of the skeleton, enabling us to give a complete description and restoration of the animal.

[1] See Ext. Mamm. Fauna, Dak., p. 228.

[2] Cope has nevertheless employed the 'cristæ' developed in this milk molar in his definition of *A. crassus*. "On the Extinct Species of Rhinoceriidæ of North America," etc., Bull. U. S. Geol. Survey, Vol. V. No. 2, p. 237.

The Brain.

One of the most interesting features of *Aphelops* is the very large size of the brain. The walls of the cranium are solid. There are no vacuities or air-cells in the diploë of the mid-region of the brain-case, such as attain from 1 to 1½ inches in thickness in *Ceratorhinus*. Thus the brain is relatively much larger

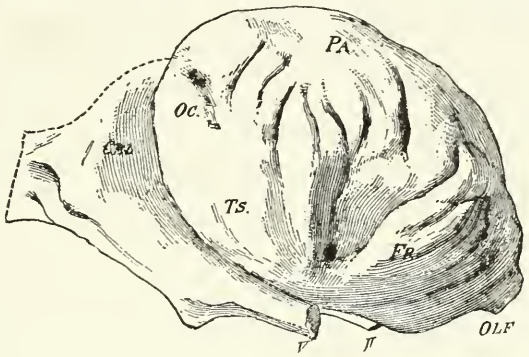


Figure 15 — Brain of *Aphelops fossiger* × ⅓. Lateral view of intracranial cast.

than that of the recent rhinoceros, and presents a marked advance upon that of *Aceratherium occidentale*. The bulk of the fore- and mid-brain, or the divisions in front of the cerebellum, is approximately as follows :—

Aceratherium, 420 c.c. *Aphelops*, 1240 c.c. *Ceratorhinus*, 720 c.c.

The bulk of the entire brain is: *Aphelops*, 1470 c c. *Ceratorhinus*, 850 c.c. The relative body weight of the two animals can be roughly estimated from a comparison of the femora as *Aphelops* 4, *Ceratorhinus* 3. It thus appears that the steady brain growth of the ungulates during the Eocene and early Miocene periods reached its highest point in some families of the later Miocene, and was followed by a degeneration.

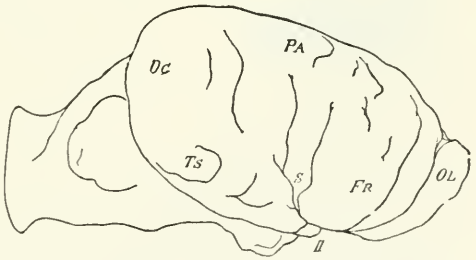


Figure 16 — Brain of *Ceratorhinus Sumatrensis* × ⅓. Lateral view of cast.

The cerebellum in *Aphelops* is small and partly overhung by the hemispheres. The lateral view of the hemispheres shows a very marked predominance of transverse sulci, which radiate from the vertical sylvian fissure, *S*, so that in the basal view of the frontal lobes the fissures are antero-posterior. The dorsal surface of the cast is somewhat imperfect, giving an incomplete reproduction of the parietal and occipital regions. The superior

sulci of the frontal lobe are directed obliquely backwards to the longitudinal fissure, thus reversing the direction observed in the recent ungulates.

The Skull and Dentition.

The *skull* (Plate III.) is broad in relation to its length, owing to the shortening of the ant-orbital region and the recession of the nasals. The maxillaries spread very widely for the powerful series of molars, while the *premaxillaries* are slender. The orbit is placed above the first molar. The *nasals* are compressed anteriorly, and extend only so far as to overhang the premaxillary suture. A marked feature of the skull is that the upper surface is in a nearly straight line from the supra-occipital ridge to the tip of the nasals, while in *A. megalodus* it is concave. The orbit is very slightly overhung by the supra-orbital process. The zygomatic arch is deep vertically, but compressed laterally. The post-glenoid process is deep and narrow; it has contact with the post-tympanic of variable length. The remarkable feature of the post-tympanic is its extension into a broad flat plate behind the auditory meatus. The occiput is broad and low, and does not overhang the condyles; it is deeply cleft in the median line. On the base of the skull, the foramina rotundum and spheno-orbitale are confluent, as observed by Cope. The foramen ovale is either confluent with or separated by a slender ridge of bone from the foramen lacerum medium.

The *molars* and *premolars* are remarkable for the extreme flattening of the outer surface of the ectoloph, all trace of the three vertical ridges having disappeared. The first premolar is a simple conical tooth implanted by a single fang; it is apparently inconstantly developed, for Marsh makes no mention of it in his description of *A. (acutum) fossiger*. The inner angles of the protoloph and metaloph unite by the 'crochet' in pm^2 and pm^3 to enclose the median valley, as in *Aceratherium*. The fourth premolar resembles the molars except in the non-development of the 'anticrochet' The true molars are characterized as follows: by the constriction of the inner portion of the protoloph into a separate column; by the strong development of the 'crochet,' which in m^1 and m^2 unites early with the metaloph to enclose the anterior 'fossette'; by the development of the 'anticrochet' at the inner angle of the metaloph and ectoloph; by the complete enclosure of a posterior 'fossette' in the first and second molars.

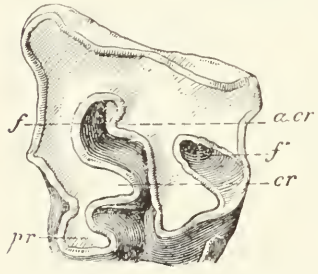


Figure 17. — First superior molar of *Aphelops fossiger* × ½.

The inferior molars are of the simple rhinoceros pattern, there being no trace of accessory folds. The first premolar is missing; the second is separated by a rather narrow diastema from the large lateral tooth. Between the pair of large semi-procumbent caniniform teeth are two small incisors.

The lower jaws are very massive, with a strongly arched lower border. The condyles are broad and elevated. The posterior border is broad, but not rugose.

The Skeleton.

(Plate III.)

Vertebræ. — The atlas resembles that of *R. unicornis*, with extremely broad transverse processes. A well preserved axis has a low tuberosity representing the spine; there is some doubt whether this is the normal adult condition, although the absence of the spine would accord with the low occiput and hornless nasals. The cervicals 3–6 have deeply opisthocœlous centra, rather high and narrow in proportion, with powerful zygapophysial processes. The inferior lamellæ of the transverse processes project downwards and forwards, and expand very slightly at the tip; the width of this lamella increases somewhat in C. 6; the superior lamellæ project opposite the vertebrarterial canal. The sixth and seventh cervicals apparently have slender elevated spines, in the remainder the spines are low or tuberous. The centrum of C. 7 is subcircular in front and broad posteriorly.

The dorsals are represented by a number of vertebræ in the mid-region. The centra are laterally compressed with distinct keels; the zygapophysial facets are very small and horizontal; the metapophyses are well developed. The length of the spines in the anterior dorsal region was apparently as in *R. javanus*. No lumbars are found in this collection.

Fore limb. — The *scapula* is very short and heavy. The general outline is triangular; the glenoid border is concave; the coracoid border is convex; the superior border rises to a point above the spine; the upper third of the spine shows a very stout recurved acromial process.

The *humerus* is remarkably short and heavy, and is distinguished by the unusually elevated position of the deltoid ridge, which is much higher upon the shaft than in the recent rhinoceroses. The tuberosities are heavy and sessile: the external condyle is unusually prominent. The *ulna* has a deep, powerful olecranon process and stout trihedral shaft, which is suddenly compressed inferiorly for the cuneiform articulation. The proximal and distal faces of the *radius* are subequal; the shaft is very slightly arched and closely united with that of the ulna, giving this segment a very massive appearance.

The structure of the *manus* is in keeping with the short and heavy upper segments; it is broader and more powerful than in any of the recent rhinoceroses. The three short, widely spreading digits are faced by rugose areas for the attachment of powerful muscles. Mtc. III. is much the largest; the lateral metacarpals, II. and IV., are short and directed outwards; the phalanges are short and wide, especially the distal series. As in all tridactyle forms the carpal displacement is extreme; the scaphoid covers the whole upper surface of the magnum anteriorly; the lunar is rather small, and rests anteriorly wholly upon the unciform; posteriorly the pivotal process of the magnum supports the lunar; the cuneiform is high and narrow. The trapezium is missing in both the carpal series before us, but is indicated by the usual facets upon mtc. II. and the trapezoid. The magnum is broad and quadrilateral. The unciform has an unusually wide mtc. III. facet, and is vertically compressed.

Hind limb. — There is a complete left innominate bone, which gives all the characters of the *pelvis*. The upper surface of the ilium, unlike that of *Ceratorhinus*, is nearly flat. The supra-iliac border is evenly arched, and, as the ischial and acetabular borders are of approximately the same length, the ilium is unusually symmetrical. The ischium and pubis are in a plane perpendicular to that of the ilium; the pubic symphysis is short; the obturator foramen is an elongate oval. The tuber-ischii is not very prominent. The border extending from the tuber to the symphysis is evenly rounded.

The *femur* is relatively longer and more slender than the humerus, having the form and proportions observed in *Ceratorhinus*. The great trochanter stands out widely; below this the shaft is of a broad flattened section; the lesser trochanter presents a long low ridge; the third trochanter is only half as prominent as in the recent rhinoceros, and is not recurved. The *tibia* is characterized by a marked asymmetry of the tuberosity; the internal malleolus is not prominent; the popliteal space is deeply excavated; the astragalar facets are shallow. The *fibula* is of the same proportions as in the recent rhinoceros.

The *tarsus* is unusually short and spreading. The astragalo-tibial facet is flattened laterally, and shows little fore and aft play; the ectal and sustentacular facets are either confluent or slightly separate; the inferior is distinct and separate; the cuboidal facet is extremely broad. The cuboid is shallow, with subequal calcaneal and astragalar facets; posteriorly it articulates with both the navicular and ectocuneiform, anteriorly with the latter only; it has a very deep posterior hook. The presence of the entocuneiform is indicated by the articular facets for it. The mesocuneiform is narrow and deep. The ectocuneiform is very broad; this bone and the navicular have the same proportions as in the rhinoceros. The middle digit is much the largest of the three, and Mts. III. has a considerable cuboidal facet.

The following measurements are made from specimens which belong to different individuals, *a*, *b*, *c*, etc.; they therefore cannot be used in estimating the exact proportions of the different parts. The proportions have, however, been very carefully determined in the accompanying restoration of the skeleton.

Measurements.

Skull.

		m.
Spec. *s.*	Total length, sagittal crest to end of nasals	.490
"	Breadth, outside zygomatic arches	.360
"	Depth, penultimate molar to top of cranium	.235
"	Occiput, diameter of, transverse, .268 m.; vertical	.198
"	From occiput to anterior end of orbit	.340
"	Antero-posterior, diameter molar-premolar series (pm. 115 m., m. 150 m.)	.265
"	Diameter first molar, antero-posterior .057 m., transverse . .	.070
"	" second " " .068 "	.070
"	" third " " .058 "	.052

		m.		m.
Spec. *s.*	Diameter fourth premolar, antero-posterior	.045;	transverse .	.065
"	" third " "	.035	" . .	.050
"	" second " "	.028	" . .	.032
"	" first " "	.017	" . .	.017
"	Lower jaw, length, angle to front of canine			.470
"	" depth, tip of coronoid to inferior border			.295

Vertebræ.

Spec. *h.*	Atlas, greatest width, .356 m.; greatest depth	.100
Spec. *pp.*	Axis, greatest width, .18 m.; length of centrum	.090
"	" " depth, spine to base of centrum, estimated . .	.140
Spec. *p.*	Fifth cervical centrum, antero-posterior .074 m., vertical .068 m., transverse .076 m.	
Spec. *o.*	Twelfth dorsal centrum, antero-posterior .075 m., vertical .055 m., transverse .058 m.	

Appendicular Skeleton.

Spec. *c.*	Scapula, vertical diameter, approx., .295 m.; glenoid cavity, ant. post.	.900
"	Humerus, length of, .308 m.; breadth, head and tuberosity . .	.155
Spec. *a.*	Radius, length, .285 m.; breadth, proximal, .093 m.; distal .	.098
"	Ulna, greatest length, .36 m.; sigmoid facet to cuneiform facet	.295
"	Carpus, greatest transverse diameter, .130 m.; ditto vertical .	.057
"	Mtc. III., breadth . . .070 m.; length	.116
"	" II. " . . .043 "	.100
"	" I. " . . .040 "	.092
Spec. *e.*	Left innominate bone, diameter, antero-posterior	.495
"	Length of pubis, .185 m.; of ischium, .20 m.; of ilium . . .	.340
Spec. *f.*	Femur, length of, .46 m.; diameter, head and great trochanter .	.165
Spec. *g.*	Tibia, length of, .37 m.; width, proximal	.140
Spec. *q* and *r.*	Tarsus, tuber calcis to distal facet of mts. III., approx. .	.220
"	" transverse diameter	.108
"	Second metatarsal, length	.088

RESTORATION. (See Plate II.)

The restoration of *Aphelops fossiger* confirms Cope's statement that the proportions of the animal were rather those of the hippopotamus than the rhinoceros. The body was long, the chest deep, the limbs and feet short and massive, and supplied with powerful muscles. The skeleton is about 9 feet long and 4 feet 6 inches high. Thus *Aphelops* presented a wide contrast to its tall, comparatively slender predecessor, *Aceratherium*, of the lower Miocene. The increase in brain capacity shows that its nervous organization kept pace with its general muscular and skeletal development. We may infer that the extinction of *Aphelops* was due to climatic changes, rather than to any defects in its internal organization, because the brain, teeth, and feet are, in themselves, as adaptive as in any of the present persisting types.

Comparison with Aceratherium and Rhinocerus.

There is nothing, however, which precludes the supposition that the American lower and upper Miocene Aceratheria are genetically related.

All portions of the skeleton of *A. occidentale* are now known to us, excepting the scapula, pelvis, and dorso-lumbar vertebræ; they indicate an animal in the same stage of skeletal evolution as the recent tapir; the proportions are practically similar; the displacement of the carpals and tarsals is in a corresponding stage. The mode of progression was also probably similar, for all the articular facets and protuberances for muscular attachment present innumerable points of resemblance. Cope[1] first pointed out the tapir resemblances in *Aceratherium*, especially in the separation of the foramina spheno-orbitale and rotundum ovale and foramen lacerum medium; the separation of the post-glenoid and post-tympanic; and the form of the femur. We have shown that this resemblance applies to the carpus[2] and tarsus; it is also true of the humerus and forearm, and of the atlas and axis. The remaining cervicals are widely different; it is probable, also, that the pelvis and scapula were different. This is of course simply an instance of functional and structural parallelism. It follows that an enumeration of the differences between the recent tapir and rhinoceros would also embrace the majority of the features which distinguish *Aceratherium* from *Aphelops*, for the latter is in most respects a fully developed rhinoceros.

Thus, if the descent from *Aceratherium* to *Aphelops* took place, it was accompanied by wide-spread modifications of the skeleton. In *Aphelops megalodus* we find a probable transition species. Its proportions are more intermediate. The narrow elevated occiput, the less degree of separation of the foramina of the skull, the lophodont character of the first upper premolar, the small development of the 'anticrochet' in the superior molars, — these characters all point towards *Aceratherium*.

A. fossiger is a highly modified form, with its broad occiput, simple first premolar, and confluent cranial foramina. In many respects the modifications it exhibits are simply steps towards the recent rhinoceros type; for example, its tridactylism, the extreme displacement of the podials, and the characters of the spinal column. But there are many points in which *Aphelops* differs from the recent rhinoceroses; namely, the sub-triangular shape of the scapula, the very elevated position and sessile character of the deltoid ridge of the humerus, the spreading manus, the oval obturator foramen, and the comparatively feeble development of the third trochanter. The marked peculiarity of the upper molars is the development of both the 'crochet' and 'anticrochet,' and absence of the 'crista.' This combination is very distinctive, since all the living rhinoceroses present combinations of the 'anticrochet' and 'crista.'[3] The molars of *Aphelops*

[1] Bull. U. S. Geol. Surv., Vol. V. No. 2, p. 235. Also, "On Extinct American Rhinoceroses and their Allies," Am. Nat., Dec., 1879, p. 771 c.

[2] Osborn, "Evolution of the Ungulate Foot," Mem. Uinta Mamm., p. 550.

[3] See Flower, "On some Cranial and Dental Characters of the Existing Species of Rhinoceroses," Proc. Zoöl. Soc., 1876.

resemble in this respect those of *R. tichorhinus*. Briefly stated, in all living forms the protoloph is simple, and the accessory folds are developed, first from the metaloph, then from the ectoloph; while in the known extinct American forms the ectoloph is simple, and the protoloph develops a fold to which a fold of the metaloph is sometimes superadded.

In view of these facts, together with the numerous divergences in the skeleton, there is strong corroboration for the opinion advanced[1] by Scott in 1883, that *Aphelops* should not be regarded as ancestral to any of the recent foreign species, but rather as the last known of an extinct American series. The question is still an open one whether its distribution was confined to this continent.

CHALICOTHERIOIDIA.[2]

CHALICOTHERIUM, Kaup.

Specimens of this genus are rare in American formations, and have not as yet been reported from the Loup Fork. Marsh[3] has mentioned the occurrence of it in the John Day Miocene of Oregon, and in view of the discoveries of Forsyth Major and Filhol, it is altogether probable that the foot-bones from that formation, which Marsh has referred to the Edentata under the names *Moropus distans* and *M. senex*,[4] belong to the same genus. A third species of the same genus is announced by Marsh[5] from the Loup Fork, *M. elatus*, which is probably represented in the Garman collection from the Loup Fork of Nebraska.

Chalicotherium elatum? Marsh.

(Syn. *Moropus elatus*, Marsh.)

The specimen is a portion of a right superior maxillary containing the third and fourth premolars and the first molar. The premolars have a flattened ectoloph connected by two convergent crests, with a large internal cone which is cleft at the summit; the base of this cone is surrounded by a strong internal cingulum. The ectoloph is worn by two symmetrical incisions alternating with the transverse crests in the third premolar, but in the fourth these incisions are asymmetrical. The first molar is partly of the Titanotherium type, with its

[1] E. M. Museum Bulletin, No. 3, 1883, p. 17.

[2] Gill, Arr. of the Fam. of Mammals, Smithsonian Misc. Coll., No. 230, p. 271. This order was properly defined by Gill, but was erroneously placed among the Artiodactyla, owing to the reduced condition of the superior incisors. Filhol's forthcoming memoir upon the Mammals of Sansan will probably enable us to determine its phylogenetic relations.

[3] American Journal of Science and Arts, 3d Series, Vol. XIV. p. 362.

[4] Ibid., pp. 249, 250.

[5] Ibid., pp. 250, 251.

protocone isolated, but the hypocone, as in all known Chalicotherioids, is united with the metacone by a low ridge (metaloph).

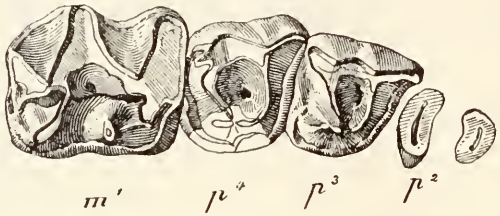


FIGURE 18. — Superior premolars and first molar of *Chalicotherium elatum* × ⅔.

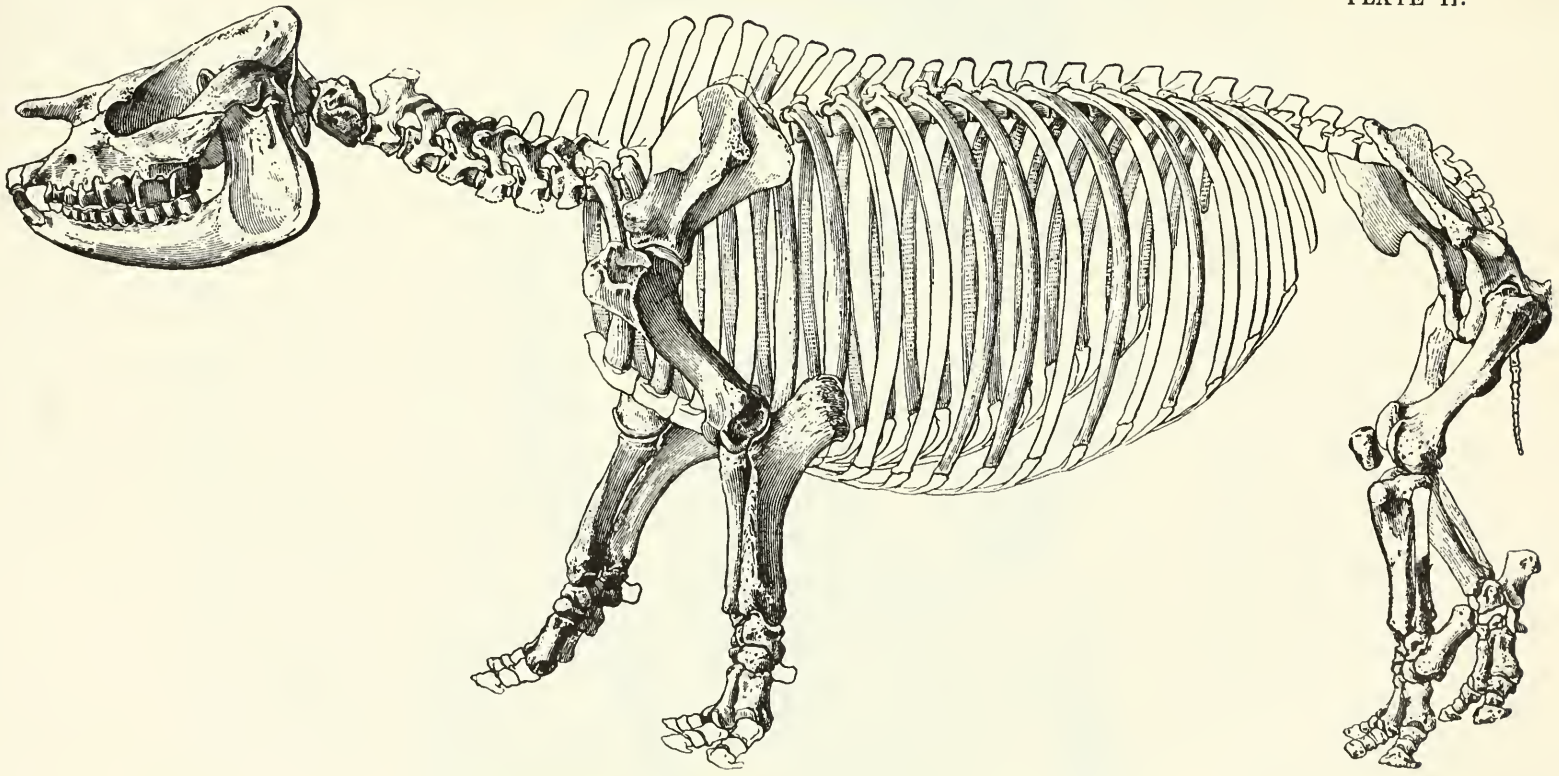
The available figures and descriptions are so imperfect that the relationships of this species to those of the Old World cannot be definitely made out. It is, however, decidedly smaller than that which occurs at Pikermi (*Ancylotherium*).

MEASUREMENTS.

	m.		m.
Third premolar, antero-posterior diameter,	.024 ;	transverse,	.025.
Fourth " " "	.025 ;	"	.028.
First molar, " "	.036 ;	"	.033.

RESTORATION OF THE SKELETON OF COSORYX FURCATUS.

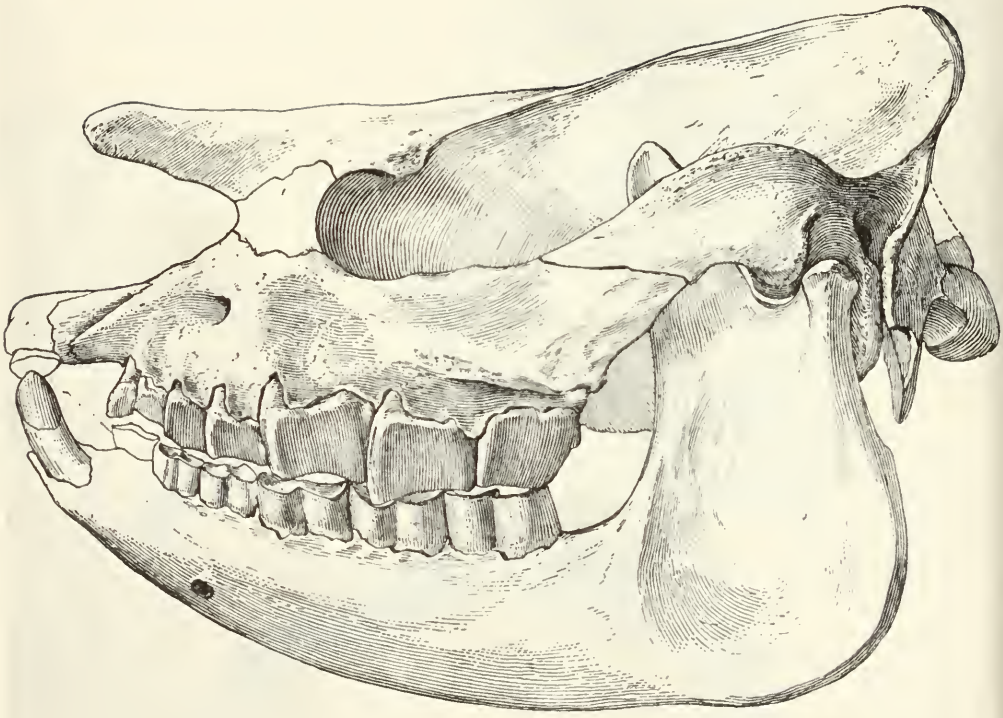
One sixth natural size.



RESTORATION OF THE SKELETON OF APHELOPS FOSSIGER.

One twelfth natural size.

PLATE III.



Skull of Aphelops fossiger.

One sixth natural size.

No. 4. — *Cristatella: the Origin and Development of the Individual in the Colony.* By C. B. DAVENPORT.[1]

CONTENTS.

I. Introduction.

AT the suggestion of Dr. E. L. Mark, I began, in the spring of 1889, the study of fresh-water Bryozoa. While at the Laboratory of the United States Fish Commission, at Woods Holl, Mass., where, through the kindness of Mr. A. Agassiz, I had the opportunity of spending the

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XIX.

following summer, I gathered most of the material for this study. I found an excellent place for collection in Fresh Pond, Falmouth, where Fredericella and Plumatella were also gathered. Upon my first visit to this pond (July 5th), I found at its outlet Cristatella exceedingly abundant on the leaves of the pond-lilies. A month later, the same locality yielded very few specimens; but about September 5th I found them plentiful again, and at the same time noticed the phenomenon described by Kraepelin and by Braem, — that some of the statoblasts of Plumatella had already hatched. Colonies of from five to twenty individuals were observed with the two halves of the statoblast still adhering to their bases. A few colonies of Cristatella were also gathered in the latter part of August from Trinity Lake, New York.

The material collected was killed with a variety of reagents. Cold corrosive sublimate gave the best results. In staining, I always found Czoker's cochineal the most satisfactory dye for the study of the embryonic cells of the bud.

As Haddon ('83, pp. 539–546) has reviewed the most important part of the bibliography of budding in Phylactolæmata which had been published at the time of his writing, I shall be relieved from giving here any extended historical account of the earlier researches. The contributions of Nitsche ('75) and Hatschek ('77) are well known. Reinhard has published a preliminary article ('80[a], '80[b]) on this subject in the Zoologischer Anzeiger; but his two more important papers ('82 and '88) I have unfortunately not seen. Braem's ('88, '89[a], and '89[b]) three preliminary papers concerning budding in fresh-water Bryozoa correct some erroneous statements of Nitsche, and support Hatschek's view of the origin of the polypide. The results at which I have arrived concerning this last problem are similar to those of Braem, but his work has apparently been done chiefly on Alcyonella, mine on Cristatella. Finally, I believe there will be found in this paper something new on the organogeny, which Braem does not seem to have especially studied, and which may be of general morphological importance. For these reasons, it has seemed to me desirable that I should publish my observations and conclusions, and I am the more inclined to do so because our views are not in all points the same.

In the matter of nomenclature, my studies have not led me to a final conclusion as to the homologies of the axes of the individual, and therefore I fall back by preference on non-committal terms. The individual is bilaterally symmetrical. Parts nearer the mouth end of a line joining mouth and anus (i. e. nearer the margin of the colony) will be desig-

nated "anterior" or "oral"; parts nearer the anal end, "posterior" or "anal." To parts nearer the roof of the colony will be applied the term "superior," or "tectal"; to those nearer the sole, "inferior." Parts situated at either side of the sagittal plane of the individual are "lateral," and either right or left, — the individual facing the margin of the colony. In naming organs, I have preferably used the terms employed by Kraepelin ('87). I adopt the term polypide simply because it is a convenient name for a number of organs closely united anatomically, and arising from a common source embryologically.

II. Architecture of the Colony.

The colony of Cristatella, as is well known, consists of a closed sac, which is greatly elongated in old specimens, and has a flattened base or "sole," and a convex roof. The wall of this sac is known as the wall of the colony or cystiderm (Kraepelin). Suspended from the dorsal wall, and hanging in the common cavity of the colony, which may be called the *cœnocœl*, are to be seen numerous polypides in different stages of development. A more careful observation shows that the polypides lying nearest the median plane of the colony are the largest and oldest, those nearest the margin, conversely, smallest and youngest (Plate I. Fig. 1). All young colonies of Cristatella have been derived from one of two sources, eggs or statoblasts. According to Nitsche ('72, p. 469, Fig. 1), there are two polypides of the same age first developed in the cystid, which is a product of a fertilized ovum, and regarding these he fully agrees with Metschnikoff's ('71, p. 508) statement, "Die beiden Zooiden entwickeln sich wie gewöhnliche Knospen."

Nitsche ('75, pp. 351, 352) observed that in Alcyonella the primary polypides are placed with their oral sides turned from each other, and that the younger buds arise in the prolongation of the sagittal plane of the older polypides, and from that part of the cystid lying between the œsophagus of the older buds and the margin of the colony.

As Braem ('89[b], pp. 676–678) has shown, there is but one primary bud in the statoblast embryo. The younger buds formed in the statoblast arise on the oral side of the primary bud.

In Cristatella, says Braem ('88, p. 508), the newly hatched statoblast embryo already exhibits to the right and left of the adult primary polypide two nearly complete daughter individuals of unlike age, which are generally followed by two other sisters in the same relative positions, and a fifth in the median plane, — oral with respect to the

mother bud. These buds may produce new ones until the whole colony has attained the size of a pea; then young buds arise analwards of the primary polypide, and as the margin of the colony is protruded on each side of this point, the colony becomes heart-shaped. The two upper lobes of the heart are regions of great reproductive activity; they separate from each other, and thus transform the heart-shaped colony into an elongated one. Through the heaping together of buds effected by this process, a misproportion between the area (Flächenraum) and the circumference of the colony results, and the buds, which lie in longitudinal rows, soon come to be crowded. After this, they each give rise to only two daughter buds, a lateral and a younger median one.

To these observations of Braem I have little to add. I have figured (Plate X. Fig. 88) a young colony of Cristatella, containing about thirty polypides. This was taken in the latter part of July, and is probably an egg colony. My reasons for thinking so are, that the statoblasts of the preceding year form colonies in the early spring; that statoblasts of any year have never been seen, like those of Alcyonella, to hatch in the fall; and that there are, occupying the centre, two polypides of very nearly equal size and development, and probably therefore of nearly equal age. Surrounding these are eight younger individuals, nearly equal to each other in size, and these are in turn followed by two generations, of thirteen and seven individuals respectively, — the last generation evidently being as yet incomplete.

As Kraepelin ('87, pp. 38, 139, 167) clearly states, the Cristatella colony is comparable with those of Pectinatella, Plumatella, etc., and may be derived from them by imagining a condensation of those branching colonies. The radial partitions seen in Figure 88, *di sep. r.*, Plate X., are thus homologous with the lateral walls of the branches of a Plumatella colony; and just as in the latter, so here young individuals arise near the tips of the branches, and the older individuals degenerate. As in Plumatella, young individuals are produced not only distad of older, but also laterad, thus founding new branches, so in Cristatella we find young buds having the same positions. These facts will be better appreciated by a reference to Figure 1, which shows a portion of the margin of a mature colony. It is here clearly seen, (1) that, as has long been known, the youngest individuals are placed nearest to the margin, and that therefore, as one passes towards the centre, one encounters successively older and older individuals; and (2) that, as Kraepelin ('87, Fig. 134) has already figured, the older individuals are arranged in a quincunx fashion.

The bit of the margin figured may be regarded as typical, not only on account of its symmetry, but also because of the fact that the youngest individuals are placed at the normal distance from the margin. Although I have seen these conditions repeated in enough instances to assure me of their normal nature, yet, owing to a crowding of polypides, both among themselves and to the margin of the colony, and also to the consequent displacement of polypides, the appearances which I am about to describe are often obscured.

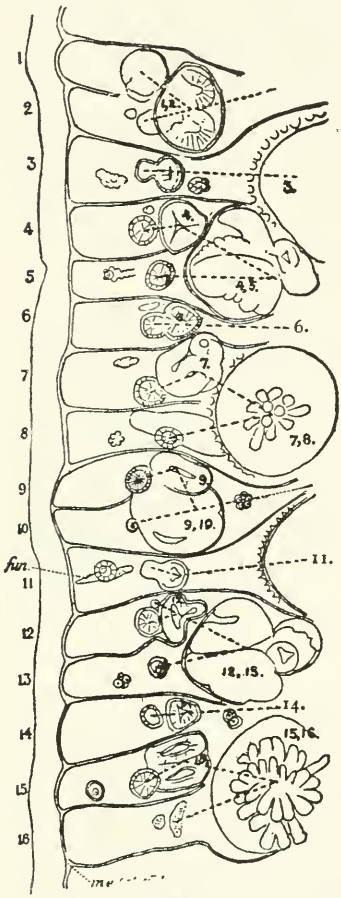


FIGURE A.

First, the interrelations of the individuals included within compartments 1–8 are exactly repeated in compartments 9–16. The same repetition holds true for the remainder of this side of the colony. On the opposite side, the number varies from six to eight. At the ends of the colony, owing to crowding of individuals, it is difficult to count with accuracy. Since all individuals are derived from preceding ones, the conclusion seems reasonable that the inhabitants of these eight branches were derived from a common ancestor. It is interesting that from each of these ancestors the same number of branches and an almost equal number of individuals are produced, and that the corresponding individuals in each of these families, e. g. Figure A, 4, 5 and 12, 13, and 7, 8 and 15, 16, are similar in position, and of the same stage of development.

Secondly, most individuals figured have given rise to two individuals; some, on the contrary, to but one. Of the two individuals produced, one (the older) passes into a second (new) compartment, and so forms a new branch. The younger, however, remains in the ancestral compartment, and thus continues the ancestral branch. See, e. g., individual

4, 5, of Figure A. The buds which give rise to new compartments may be called lateral buds, in accordance with Braem's terminology; those which prolong the ancestral branch, median buds. Where only one individual arises, it is a median bud. These conclusions regarding the relationship of buds are based solely upon the length of the radial partitions, the inner extremities of which correspond to the angle formed by two branches in branching genera like Plumatella.

Thirdly, while the lateral buds, Figure A, 4, 5, and 12, 13, give rise directly to new buds, median buds of the same or younger age, 6, 14, have moved to a considerable distance from their mother buds before giving rise to new individuals. The effect of this is, that the median bud comes to lie, not alongside of the lateral bud, but in a quincunx position relatively to it.

Fourthly, lateral buds (branches) may arise from either side of the budding individual. Although most of the branching in the part of the colony figured in the cut is to the right, yet the youngest lateral buds are being given off to the left. So in compartments 4, 6, 7, 12, the funiculus indicating the point where the median bud will arise.

To recapitulate: The descendants of common ancestors are arranged similarly in the same region of the colony; a lateral and a median bud may arise from a single individual, the first forming a new branch, the latter continuing the ancestral one; median buds migrate towards the margin before producing new buds; and new branches are formed on either side of the ancestral branches.

III. Origin of the Individual.

Two essentially different views of the origin of the polypide in the adult colony of Phylactolæmata have been maintained within recent years. The first is that advanced by Nitsche ('75, pp. 349, 352, 353), and adopted by Reinhard[1] ('80[a], p. 211, '80[b], p. 235). According to these authors, the outer of the two layers of the colony-wall gives rise, either by a typical or a potential invagination, to the inner cell layer of the bud, — the layer from which the lining of the alimentary tract and the nervous system both arise, — and pushes before it the inner layer

[1] Reinhard says in his preliminary article, "Meiner Meinung nach entwickelt sich die Knospe in Folge einer Verdickung des Ectoderms, in welche dann die Zellen des Entoderms eindringen," but Brandt's abstract of the paper read by Reinhard before the Zoölogical Section of the Russian Association, places entoderm for ectoderm, and *vice versa*, — a rendering more in accordance with Reinhard's statements in the context.

of the colony-wall, which thus becomes the outer layer of the bud Hence the buds arise independently of each other.

The second view is that advanced by Hatschek ('77, pp. 538, 539, Fig. 3). He asserted that in Cristatella "Die Schichten der jüngeren Knospe stammen von denen der nächst älteren direct ab." Finally, Braem ('88, p. 505) agrees essentially with Hatschek, and believes that a typical double bud, although it does not always appear, is the fundamental condition. His preliminary account clearly shows that precisely the same condition of affairs, except in so far as modified by the less metamorphosed condition of the ectoderm, exists in Alcyonella as in Cristatella.

A. Observations.

1. *Origin of the Bud.* — The result of my own work has been to lead me to a conclusion differing from both of these two views, but more like the second than the first. By my view, as well as by Braem's, Nitsche's two types of single and "double" buds are united into one. I would not say, with Hatschek, that the two layers of the younger bud arise directly from those of the next older, but that each of the corresponding layers of the younger and next older buds arises from the same mass of indifferent embryonic tissue. In some cases, each of the layers of the daughter polypide does arise from the corresponding layers of the very young mother bud. In other cases each of the two layers out of which the two layers of the older bud were constructed contributes cells to form the corresponding layers of the younger bud, but the cells thus contributed have never formed any essential part of the older bud. All gradations between these two types occur. For convenience' sake, we may always call the older polypide the mother; the younger polypide, the daughter. Figure 3 (Plate I.) shows a well advanced bud (Stage VIII.) which consists of two layers of cells, an inner, *i.*, composed of a high columnar epithelium arranged about a narrow lumen; and an outer, *ex.*, of more cubical cells. In a region (I) on the bud which is near the attachment of its oral face to the body-wall there is a marked evagination of the contour, caused in part by a thickening of the outer layer, and in part by a slight increase in the diameter of the inner. This thickening o the wall is the first indication of the formation of a younger bud, which is to arise at this place. Figures 22, II., 16, VI. (Plate III.), and 11, VI. (Plate II.) show later stages of buds originating in the same manner as that of Figure 3. The mother bud has grown larger, as has also its lumen. The outline in its upper oral region has become much folded as

a result of cell proliferation, and a deep pocket has been formed lined by a layer of cells which are still a part of the inner layer of the mother bud. The outer layer of the latter has also been protruded by the activity of the inner layer, and its cells go to form the outer layer of the young bud. Still another point is to be observed. The centre of the young bud has moved away from the centre of the neck of the mother bud, and thus the former lies nearer to the margin of the colony than the latter. Figure 17, VII. (Plate III.) shows a still more advanced stage in the development of the bud, in which it is sharply separated from its parent, but its inner and its outer layers are still in direct continuity with the inner and outer layers respectively of the mother.

I have selected this series from the many which might have been chosen to show the origin of the polypide, because it is an intermediate type between two extremes, and because by it the other cases receive an easy explanation. All cases of budding, however, seem to conform to this general law: the greater the difference in age between the youngest and the next older bud, the greater the distance between the points at which they begin to develop. Thus the typical case of a "double bud" is that in which two buds appear to arise at the same time. They originate, as Nitsche observed, from a common mass of cells. A case of two buds, one only slightly younger than the other, is seen in Figure 5. By comparing with Figure 3, in which the older polypide is older than VII., Figure 5, the difference between the younger buds will be apparent. On the other hand, Figure 4 illustrates a comparatively late formation of the younger bud. The older bud had attained a stage corresponding to Figure 18 (Plate III.), but the younger bud is not older than that seen in Figure 22, II. Just as in the latter case the two layers of the older bud went respectively into those of the younger, so in the present case a direct continuity can be traced between the cells of the inner and outer layers respectively of the younger and older buds. The evidence that the cells composing the inner layer of the young bud have not arisen directly from the ectoderm is derived not only from the continuity of both cell layers of the two buds, but from the presence of the apparently unmodified ectodermic cells lying above the inner layer of the young bud, and sharply marked off from it. Figure 6 shows a later stage of this same type, in which the layers of the young bud are seen well formed, but still very sharply separated from the overlying ectodermal cells. These series afford an interpretation of the extreme type of budding shown in Figure 2, which is not uncommon. The mother polypide has reached a stage corresponding to Figure 18, Plate III. To the left of the neck of

the polypide and towards the margin is the funiculus, *fun.* Between it and the neck of the polypide the cœlomic epithelium is thickened and its cell boundaries have become evident. Directly above this region, and immediately above the muscularis, is a row of cells, which stain deeply and show other evidences of being embryonic. These are directly continuous with the neck cells of the older polypide, exactly as was the case with the cells of the inner layer in Figures 4 and 6 (Plate I.). In fact, they are in every way comparable with these. Figures 8 and 9 (Plate II.) show slightly later stages. The funiculus has moved farther from the parent bud, the future outer layer (*ex.*) has become thicker, and its cells are columnar and sharply marked off from each other. The inner layer (*i.*) of the new individual is represented by a thicker, stolon-like mass of cells, which is in direct continuation with the inner layer of the mother bud, from which it was doubtless derived.

A stage which, on account of the greater distance of the funiculus from the older polypide, I believe to be slightly more advanced than Figure 8, is shown in Figure 9. In the section drawn, the inner cell mass (*i.*) exhibits few nuclei, but they are more numerous in adjacent sections. The band of protoplasm connecting this young bud with the mother is perceptibly smaller than in the preceding stage. The cells of the inner layer form a mass sharply marked off from the ectoderm; those of the outer layer are greatly thickened, as in the last stage.

A peculiar thickening of what I regard as Nitsche's "Stützlamella" takes place between the young bud and the mother polypide. This is shown in Figures 9 and 10 at *mu.* It is not stained by Czoker's cochineal, and the circular muscle fibres, here cut transversely, are very conspicuous in the midst of it. As I have noticed this appearance only in the cases of young buds which have originated like those of Figures 9 and 10, and of others of about their age, (and it is in these buds and at this age that migration from the older polypides takes place,) I believe that there is some connection between this condition of the muscularis and the disturbance which such a migration must cause.

I have already (page 106) referred to the fact that in some cases median buds are found far removed from the mother polypide, although in an early stage of development. Stage IV. is the youngest in which such buds have been found.

The cells of the mass destined to form the inner layer of the bud multiply rapidly after they have reached a proper position, and there is considerable protrusion of the cœlomic epithelium into the body cavity. The fact, that during its extensive migration the bud increased only

slightly, whereas it now begins to develop rapidly, leads to the presumption that it has ceased to migrate, and has come to a state of comparative rest, relative to the surrounding ectodermal cells.

One of the first indications of further development is seen in the arrangement of the cells of the inner layer, which is such that their nuclei come to lie near the surface of a hemisphere whose convex side is turned toward the cœnocœl. The beginning of this process is seen in Figure 10 (Plate II.), and, further progressed, in Figure 11. Figure 14 exhibits a still later stage in the development of the polypide. In the lower portion of the two-layered sac of this figure a separation of the cells (*lu. gm.*) has begun. This is the first indication of the atrium.

In all cases there exists at this stage a condition of the ectoderm like that shown in Figures 5 and 14. The absence of ectodermal cells directly over the bud may be accounted for by supposing that they have come to lie upon, and form part of, the neck of the polypide. While it would be impossible to deny that they *might* migrate through the cells composing the neck of the polypide, and thus come to form the nervous elements, a careful study of the successive stages figured will not show the slightest evidence of any such migration, nor is it *a priori* probable, from what is known of the action of epithelium the world over, that such a migration would occur.[1]

According to the description of Nitsche ('75, p. 353), there is a lumen in the bud of Alcyonella (where the ectoderm is much less metamorphosed than in Cristatella), which is always in direct communication with the outer world, the bud having been formed by a typical invagination. Braem ('88, pp. 506, 507), however, states that he has never seen in Alcyonella this communication of the bud cavity with the outer world. In the much more obscure process of polypide development in Gymnolæmata the lumen first appears after the cells of that mass from which the bud is to arise have arranged themselves in two concentric layers. In Endoprocta, according to Nitsche ('75, p. 374) and Seeliger ('89, p. 179), the lumen arises by a virtual or actual invagi-

[1] Since writing the above paragraph I have cut some sections of Plumatella in which this process is much clearer, owing to the absence of secreted bodies in the ectoderm. Instead of a few ectodermal cells dropping down upon the upper part of the neck of the polypide, as is the case in Cristatella, there is a cup-shaped invagination of the ectoderm, which is quite deep, and thus gives rise to an elongated "neck." That none of these ectodermal cells go to form any part of the polypide proper is certain in Plumatella. But it is also true, that ectodermal cells are thus incorporated into the neck of the polypide, and probably into the stolon which proceeds from it.

nation and remains always in communication with the surrounding medium. In Cristatella the lumen is formed in the bud at the time when its diameter perpendicular to the roof of the colony slightly exceeds that parallel to it. As Figure 14 (Plate II.) shows, this cavity (*lu. gm.*) first makes its appearance in the distal part of the central mass of cells. There are always cells lying above the lumen, and thus cutting off the ectoderm from contact with it. The two layers from which, according to my view, all of the cells of the adult polypide are derived, are now completely established; and the cavity has already appeared which, by enlargement, out-pocketing, and the concrescence of its walls, gives rise to the atrium, and the lumina of the alimentary tract and supra-œsophageal ganglion.

The bud elongates, and often at this time, preparatory to giving rise to a new bud from its upper marginal angle, becomes bent or curved, the concavity always being next the daughter bud (see Figs. 3, 5, 11, and 22). By this change in form the bud becomes bilaterally symmetrical.

2. *Origin of the Alimentary Tract.* — The first organ derived from the two-layered sac is the alimentary tract. Nitsche ('75, p. 356) described the process of its formation in a very clear manner; but I believe he is in error. The original lumen of the bud represents, he says, the atrium and the lumen of the alimentary tract. The part lying nearest the attached end of the bud gives rise to the former; the latter is derived from the lower part of the lumen. These two regions become separated by the invagination of the two layers of the bud along a furrow on each side of the bud; just as though the walls of a two-layered hollow rubber ball were pressed together by a finger of each hand acting at opposite sides until the points of the fingers should be separated by the four layers of the ball only. By this process, mouth, anus, and the entire gut, would of course be formed at one time. Reinhard ('80[a], p. 212) appears to agree with Nitsche as to the method of origin of the alimentary tract. Braem ('89[b], pp. 677, 678) describes and figures diagrammatically this process in the statoblast of Cristatella. In the median plane of the bud there is an out-pocketing from the anal side of the atrium which involves both layers of the bud; it assumes the form of a comma, its blind end curving forward to meet the blind end of a lesser evagination of the oral part of the atrium, — the œsophagus. The blind ends of these two pockets meet, and by the breaking through of the intervening tissue their lumina freely communicate with each other, thus completing the alimentary tract. He adds: "Auch bei den Polypiden der fertigen Colonie der Darm durch Verwachsung eines analen

und eines später auftretenden oralen Schlauches, an deren Bildung freilich das äussere Knospenblatt nur secundär sich betheiligt, zu Stande kommt."

My own observations are nearly in accord with the statements of Braem, as opposed to Nitsche's. The older bud of Figure 11 (Plate II.) shows the first indication of the lumen of the posterior part of the alimentary tract near the attached portion of the bud. The cells of the inner layer are multiplying, and the lumen of the bud is broader here than elsewhere. The position of a daughter bud, VI. (on the oral side of the one under consideration), sufficiently indicates that the point marked *rt.* is in the region of the future anal opening. Figures 12 and 13 (Plate II.) show further stages in this same process. The lumen of the intestine is formed, not by constricting off a part of the original lumen of the bud, but by the rearrangement of cells at the progressing blind end of the pocket, which gradually moves towards the distal part of the larger or bud cavity. It is important to establish the fact that the alimentary tract is formed in the inner layer of the bud, and that its cells alone line the digestive cavity. Figures 20 and 21 (Plate III.) represent two successive sections out of five which pass through the inner layer; namely, the second and the third counting from the attached to the free end of the bud. The sections were cut at right angles to the plane of Figure 11 nearly along the lines 20 and 21 respectively. It will be seen that the inner layer alone is implicated in the lining of the alimentary pocket at this early age. They also show clearly the incorrectness of the statements of Nitsche on this point. Figures 24, 25, and 26 (Plate IV.) are three sections cut through a bud of about the age of that represented in Figure 13 (Plate II.), and at right angles to the plane of the latter, and in the direction of the lines 24, 25, and 26 respectively. A section cut beyond the end of the intestine, in Figure 13, is not represented. It shows that the lumen of the alimentary tract is absent at this plane. A comparison of Figures 20 (Plate III.) and 26 (Plate IV.) shows that the lumen of the bud, *lu. gm.* (which we may call the atrium from its resemblance to a space having the same relations in Entoprocta), has increased in volume owing to a growth of the lateral walls. On account of the more rapid elongation of the anal than of the oral side, the axis of the alimentary tract comes to take a horizontal position, as shown in Figures 17 and 18, Plate III. (Compare also Figs. 27–29, Plate IV.) The blind end of the digestive sac comes very close to the blind end of another pocket formed on the oral side, the œsophagus, and soon the two communicate directly. At the same time, the inner cell-layer of the

middle portion of the alimentary tract has been quite cut off from that of the atrium by a constriction, the beginning of which is seen at *ex.*, Figure 24 (Plate IV.) and in a later stage at *ex.*, Figure 28. The cells of the outer layer are next pushed into the place of constriction and remove the alimentary tract at this point still further from the atrium, as is shown in Figures 18 (Plate III.) and 28, *ex.* (Plate IV.). The error of Nitsche is explainable on the ground that he believed the stage of Figure 18 to be the earliest in the development of the alimentary tract.

3. *Origin of the Central Nervous System.* — Metschnikoff ('71, p. 508) first clearly recognized that the supra-œsophageal ganglion of Phylactolæmata is derived from the inner cell-layer of the bud, — the same layer which gives rise to the inner lining of the alimentary tract. Nitsche ('75, pp. 359, 360) described and figured in an insufficient and not wholly accurate way the process of the formation of this organ. According to my observations, the central nervous system arises directly over the middle of the horizontally placed alimentary tract in the position marked *gn.* in Figure 18, Plate III. (compare also Figs. 17 and 28, *pam. gn.*). The process by which the ganglion with its internal cavity (Plate VIII. Fig. 73, *lu. gn.*) is formed will be more easily understood if the reading of the text be accompanied by reference to the following sections. Figures 17, 18, 19, Plate III., and Figure 73, Plate VIII., show successive stages in sagittal section. Figures 27–29, Plate IV., from a single individual, are vertical right-and-left sections, the positions of which are indicated by the lines 27, 28, 29 of Figure 17. Figures 30–32 are similar sections from an older individual (see lines 30, 31, and 32, numbered at the lower border of Fig. 18), and Figures 33–38 are from a still older polypide (compare lines 33–38, Fig. 19). By a study of these sections, it is seen that the cells forming the floor of the brain, *pam. gn.*, are derived from the inner layer of the bud, and indeed from the very region of the layer which furnished cells to line the alimentary tract (Plate II. Fig. 13, Plate IV. Figs. 25 and 24, *ga.*), and therefore that the layer of cells forming the floor of the ganglion is directly continuous posteriorly through the anal opening (Plate II. Fig. 13, *an.*) with the wall of the rectum, and anteriorly with the lining of the œsophagus. The first marked differentiation of this region is effected by the sinking of the centre of the floor of the neural tract (Fig. 18, *gn.*), thus forming a shallow pit, which opens directly into the atrium above.

The *closure of the walls of the ganglion* above must now be considered. Concerning this process, Nitsche says: "Die Ränder dieser Einstülpung [my 'shallow pit'] wachsen nun wie die Ränder der Medullarrinne

eines Wirbelthierembryos gegen einander, und wie in letzterem Falle eine hohle Röhre von der dorsalen Leibeswand des Thieres abgeschnürt wird, so wird hier eine hohle *Blase* von der Wand des Polypids abgeschnürt. In unserem Falle ist aber die Wandung an der diese *Abschnürung* vor sich geht, zweischichtig." The two layers referred to were those of the median walls of a pair of invaginations of the latero-anal sides of the wall of the atrium, — the beginnings of the lophophoric arms (*br. loph.*, Figs. 37, 38, Plate IV., and Figs. 61, 62, Plate VII.).

The process of closure is in reality somewhat different from Nitsche's conception of it. The axes of the pockets which go to form the lophophoric arms are, at first, directed inward, upward, and slightly oralward (Plate I. Fig. 7, *br. loph.*). By means of these invaginations the cell layers lining the atrium on opposite sides are brought into contact at a point between the rectum and the ganglionic pit (Plate V. Fig. 43, *loph.'*). This approximation of the walls may, perhaps, better be said to be a continuation upward of the process by which the alimentary tract was cut off from the atrium (after the lumen of the former was formed), and by which cells of the outer layer of the bud came to intrude themselves between these two regions (Plate IV. Fig. 35, *ex.*); for the lateral furrows, by the formation of which this act is performed, are, on each side, continuous with the lophophoric pockets, and above end blindly in them. By the approximation and fusion of the inner layers of the atrium several things are accomplished. The posterior wall of the brain is formed (Plate IV. Fig. 39, *loph.'*), the anus is carried farther up (compare Plate III. Fig. 19, and Plate VIII. Fig. 73, *an.*), and by a continuation of the constricting process the cavities of the lophophore on opposite sides of the polypide are brought into communication between the ganglion and the rectum at a point opposite the letters *lu. gm.* in Figure 63 (Plate VII.), whereas they formerly communicated only outside the alimentary tract.

Oralward from the lophophoric pockets there is a thickening of the inner layer above the floor (*pam. gn.*) of the ganglion on each side (Plate IV. Figs. 28 and 31). Later, each of these thickenings becomes a fold involving the inner layer of the bud only (Plate IV. Fig. 35). The upper and lower halves of this pair of folds respectively fuse in the sagittal plane, the last point at which the union occurs being near the œsophagus (Plate III. Fig. 19). Anteriorly the rim of the shallow brain-pit rises up as a third fold, and the ganglion becomes a sac whose mouth is bounded by the edges of the folds, the advance of which causes it to become more and more constricted. These folds are the pair of folds

above the cavity of the ganglion, and the one between the cavity of the ganglion and the œsophagus. The outer layers of these three folds respectively fuse immediately behind the œsophagus; the inner layers are constricted off, but without closing the neck of the sac. Consequently the neck of the ganglionic sac, instead of opening into the atrium, now abuts upon the inner cell-layer at the angle between the floor of the atrium and the œsophagus. The lower layers of the horizontal folds thus become the upper wall of the ganglion (Fig. 35, *tct. gn.*); the upper layers form the new floor of the atrium (Fig. 73, *pam. atr.*), which lies between the lophophore arms, is continuous with its median walls, and passes over into the walls of the alimentary tract both in front and behind. The outer layer of the young bud only secondarily makes its way in between the upper and lower layers of these folds. It ultimately takes the form of a double layer embracing a space, which is the epistomic canal. (Plate VIII. Fig. 73, *lu. gn.*, Plate V. Fig. 52, *lu. gn.*, *can. e stm.*)

4. *Origin of the Kamptoderm.* — While the alimentary tract, lophophore arms, and nervous system are being marked out in the lower portion of the bud, these organs become farther removed from the wall of the colony by an enlargement of the atrium to meet the demands of the augmenting volume of the lophophore. *Pari passu* with this enlargement of the atrium, its walls diminish in thickness (compare *kmp. drm.*, Fig. 73, Plate VIII., with Fig. 18, Plate III.). This is rather the result of a failure of the cells to multiply in proportion as the area of the wall increases, than of a decrease in the number of cells already formed. Both the inner and outer cell-layers of the bud take part in the formation of this wall, as is evident from the figures. The wall of the atrium was called "tentacular sheath" by Allman ('56, p. 12) and Nitsche, but Kraepelin ('87, p. 19) employs the name "kamptoderm" for this structure. I prefer this term to "tentacular sheath," and have employed it both on account of the reasons given by him and because it may be easily inflected, whereas "tentacular sheath" may not. The kamptoderm, then, is formed of the upper portion of the bud, and both of its cell-layers are concerned in its formation and persist in the adult.

5. *Origin of the Funiculus and Muscles.* — Nitsche ('75, pp. 353, 354) did not see the origin of the *funiculus*, but states that it suddenly occurs lying close along the oral side of the bud, to which one end is attached. Its proximal end is fastened, he says, to the inner layer of the colony-wall, and by the growth of the latter between the funiculus and the neck of the bud this end retreats from the young polypide. Braem

('88, p. 533) asserts that the funiculus arises as a longitudinal ridge on the outer layer of the oral wall of the young polypide at the time of the formation of the alimentary tract, and that the cells of this ridge are cut off from the bud to form the funicular cord. Soon after this, embryonic cells from the inner layer of the young polypide penetrate into the midst of the cord through its proximal end, and thus lay the foundation of the statoblast.

Concerning the origin of the *muscles*, Nitsche ('75, p. 354) states that they are simple elements of the outer cell-layer of the bud, which were originally situated in the angle of attachment of the bud to the inner layer of the colony-wall, and that by the growth of this wall they become drawn out into spindle-shaped cells.

I have decided to treat of these two organs together, since their origin and development are curiously similar. According to my belief, both arise, in part at least, from the inner cell-layer of the colony-wall. At a stage slightly earlier than that of the first appearance of the fully formed funiculus (Plate II. Fig. 11, *cl. fun.*), I have always found a disturbed condition of the cœlomic epithelium. This is particularly noticeable on that side of the young lateral bud upon which the median bud is about to arise. In some cases I have seen the cells of this layer taking on all the characters of wandering cells, as seen at *cl. fun.*, Figure 22, Plate III., where some have already begun to group themselves into a funiculus-like cord. At Figure 57, *cl. fun.*, Plate VI., the funiculus is seen lying close to the oral wall of the polypide. That it has not arisen in precisely the manner described by Braem is probable from this figure alone, for the proximal end of the funiculus is not yet connected with the wall of the colony. If my view is correct, this connection arises only secondarily (Fig. 2, *fun.*). I am, however, inclined to believe that the distal end of the funiculus arises in a different way from the proximal, and in the manner described by Braem. My evidence for this is, that I have twice seen at this point cells in the act of dividing so as to contribute daughter cells to the funiculus. Figure 53, Plate VI., shows the condition of the distal end of the funiculus, *fun.*, which passes, without any line of demarcation, into the outer layer of the bud; this layer is normally one cell thick, but in the region of funicular formation it is two cells thick. The proximal end of the funiculus is, at this stage, attached to the cœlomic epithelium of the roof of the colony, *tct.* That an attachment should occur in this manner, and become quite intimate, is not strange, considering the origin of the funiculus from amœboid cells, and the fact that, even at a late

stage of development, this character is still retained by much of its tissue. (See, for example, Fig. 77, *fun.*, Plate IX.)

The great *retractor* and *rotator muscles* have, I believe, like the funiculus, a double origin. They arise from the outer layer of the bud, on the one hand, and from the cœlomic epithelium on the other. The first indication of the differentiation of the muscle cells consists in a disturbance in the upper lateral edge of the outer layer of the bud at about the stage of Figure 17, Plate III. This is shown in dorso-ventral sections through this region (*cl. mu.*, Figs. 24, 26, Plate IV.). Later, the disturbance becomes more marked, and cells having a semi-amœboid character appear to be proliferated (*cl. mu.*, Fig. 33, Plate IV.), and to migrate from the bud towards the cœlomic epithelium. During this process the cells of the latter layer also are active, and some of them, elongating, reach towards the young polypide, as seems to be clearly shown at *cl. mus.*, Figure 54, Plate VI. It is significant that, since each of the two upper lateral edges of the bud lies near a radial partition, the muscles also are always formed in close proximity to one (*di sep. r.*, Fig. 54, Plate VI.; Fig. 30, Plate IV.). It will thus be observed that, both in the case of the funiculus and of the muscles, the end which is attached to the wall of the colony arises at a point which is remote from that of its attachment to the adult. The migration to the later positions will be treated of farther on. (See page 141.)

6. *Origin of the Body-wall.* — As already shown (page 104), the body-wall of the individual of a Cristatella colony includes not only the endocyst of authors, — the roof and the sole, — but also the radial partitions.

Braem ('88, pp. 506, 507) concludes "dass die polypoide Knospenanlage . . . nicht allein das Polypid nebst den Tochterknospen liefert, sondern dass auch die zugehörigen Cystide aus ihr und zwar aus ihrem Halstheil entwickelt werden." I believe that a portion of the "cystid," or body-wall, is thus formed in Cristatella, but not the whole.

If one compares the relations of the polypide to its daughter bud in Figures 3 (Plate I.) and 17 (Plate III.), and reflects that later the daughter bud is to be found still farther from the mother bud, he is forced to one or the other of two conclusions: either the young bud is pushed from the mother by a proliferation of cells from the neck of the polypide without causing an increase in the length of the body-wall itself, or there is an actual increase in the length of the body-wall, produced either by the proliferation of cells already existing in it, or by the addition and subsequent proliferation of cells from the neck of the mother

polypide; and this increase in length, occurring between the polypide and bud, carries the two apart. Unfortunately, I am unable to state definitely how this migration of the young bud away from the mother is effected. If the ectoderm increases in length between the two buds by the proliferation of cells already existing in it, that fact ought to be evinced by a distorted condition of the old cell-walls of the highly metamorphosed cells of the ectoderm. For, since most of the active protoplasm is at the base of the ectoderm, its area will increase faster than will the area of the surface of the ectoderm; and the latter will either rupture or stretch, or else the ectoderm will become concave on its outer side. An application of these criteria to sections of the body-wall in the budding region leads to the conclusion that the ectoderm of Cristatella increases here very slightly, if at all, by a proliferation of cells already existing in it. A search for cell division in this region has yielded the same negative results. There can be no doubt that cells are added to the ectoderm from the neck of the polypide. The process takes place, however, after the daughter bud is well established at some distance from the mother bud. The proliferation of these cells ruptures the old cell-walls of the ectoderm, and increases the area of the body-wall. I shall have occasion to speak of this process more fully in treating of the later period to which it belongs.

There remains, then, the conclusion, that the cells which go to form the inner layer of the young bud are pushed from the neck of the next older bud by a proliferation of cells in the stolon-like mass, without causing an increase in the area of the body-wall itself. Moreover, I have seen cell proliferation in the stolon-like mass. Another series of facts will lead us to this same conclusion.

Though the body-wall does not increase by cell proliferation between buds, it does so, I believe, at the margin of the colony. This, it is true, cannot be directly observed with ease, since the multiplication of cells, which tends to increase the breadth of the colony, must also occur at the margin, and one cannot be certain what dimension of the colony wall will be augmented by any given case of nuclear division. My belief rests on the following evidence. (1) In the same adult colony the distance of the youngest bud from the margin is not the same in all regions. This is not what we should expect if the distance of the youngest polypides from the margin remained unchanged during the growth of the colony. (2) There is a gradual increase in the amount of metamorphosis exhibited by the cells as one passes from the margin towards the middle of the roof. Figure 60 (Plate VI.) shows a rather

marked example of a very common, although not universal, condition of the lateral margin of the colony. The epithelium of the margin is composed of columnar cells, which are higher (54 μ) than those of the roof (48 μ), and also of a less average diameter (8.4 μ) than the latter (18.2 μ). Moreover, the cells are very little metamorphosed. In passing towards the roof (*tct.*), the cells are seen to become more and more metamorphosed, the secreted bodies (*cp. sec.*) becoming relatively larger. Figure 55 represents the margin in a more metamorphosed state than Figure 60. Although this condition of things is not incompatible with the idea of a passive margin, it strongly suggests that this region is one of proliferation, by which cells are added to the roof, and thus the distance from the youngest polypide to the margin is virtually increased. This conclusion receives a very important confirmation from the study of the origin of the radial partitions, the treatment of which must be deferred for the moment. Although new cells are being added to the roof at the margin, yet the distance from the youngest polypide to the margin is not greater in old than in young colonies. How, then, is the approximate constancy of this distance maintained? Evidently it can only be by the process (which I have already shown must take place) of migration of some of the young buds at the base of the ectoderm, particularly in the case of median buds. The tendency of the migration of young buds towards the margin is to diminish the distance between the front of the budding region and the margin of the colony. The tendency of cell proliferation at the margin is to increase that distance. The actual distance is the resultant of these two opposing factors, and may be less or greater in different parts of the same colony, according as the one or the other is the more active. If we assume, further, that the cells added to the roof and sole from the margin plus those derived from the necks of the polypides are equal in amount to those lost by the degeneration of individuals in the middle of the colony, we have a sufficient explanation of the fact, observed long ago, that the adult colony of Cristatella maintains a nearly constant width.

7. *Origin of the Radial Partitions.* — I know of nothing on this subject by any previous author. The radial partitions consist of a muscularis covered on both faces by a very thin epithelial layer (Plate X. Fig. 95, 1). The muscle fibres of the muscularis arise from the already formed longitudinal muscles of the wall of the colony at the region of transition from the sole to the roof (Plate VI. Fig. 55, *mu.*). As the muscle fibres move into the cœnocœl, they carry before them the cœlo-

mic epithelium of the region from which they arise. It is owing to this method of origin that the epithelium comes to clothe both faces of the partition. The process by which the muscle fibres move into the cœnocœl appears to be this. The end of a fibre nearest the roof becomes fixed to a certain part of the muscularis of the roof, and is left behind with it when the margin is carried outward (potentially) as the result of cell proliferation. Thus from a nearly horizontal position the fibres attain a direction at first oblique, and then perpendicular to the sole. In some instances the upper ends of the fibres move through an arc of more than ninety degrees, so that they are ultimately directed upward and inward, i. e. towards the centre of the colony. (Compare *mu*, *mu'*, *mu''*, Fig. 55, Plate VI.). This process is also indicated in two horizontal sections (Plate X. Figs. 95 and 96), the former being nearer the sole than the latter. This is a region of active budding, and in consequence new compartments or *branches* are being rapidly formed. The numbers 3, 4, 5, and 6 (Figs. 95, 96) show the positions of young partitions, which are shorter above than below, owing to the oblique position assumed by the innermost muscle fibres of the partition. The oblique position is due to the fact already demonstrated (Fig. 55, Plate VI.), that the tectal end of the muscle of the partition first appears at the margin nearer the sole than the roof. At 2 (Fig. 96) there is apparently an interesting case of the formation of a new partition by the detachment of certain fibres from the muscularis of an old one. The fibres, moving away laterally, take with them a covering of cœlomic epithelium. Near the sole this process has progressed farther than it has nearer the roof, so that in Fig. 95 the detachment appears complete, whereas in Fig. 96 the union is still visible. This method of formation is intelligible when one considers that the muscularis of the partition often contains more than a single layer of muscle fibres. Thus, in Figure 87, *mu.*, there are two or three layers of fibres in the section. Figure 86 represents a section cut vertically and at right angles to a partition near its union with the marginal wall of the colony, and shows three fibres of the longitudinal or inner layer of the muscularis lying side by side in the partition.

B. — Comparative and Theoretical Review of the Observations on the Origin of the Individual.

What bearing have the facts here adduced on those given for other groups of Bryozoa, and what is their probable significance in relation to the general problem of non-sexual reproduction?

1. *Origin of the Polypide.* — Lateral budding (as distinguished from linear budding, such as occurs in Turbellaria, Chætopods, &c.) may be roughly classified under two types, in one of which the young individual arises *directly* from the body-wall of the parent, as in Hydra. In the other, the young arise, one after the other, from a mass of embryonic material derived from a parent individual, — from a stolon, as in Salpa. In the group of Bryozoa both of these methods seem to be present. In such a form as Paludicella (Allman, '56, pp. 35, 36, Korotneff, '75, p. 369) we have an example of the direct type; in Pedicellina we have a stoloniferous genus. Also in the marine Ectoprocta examples of both types appear to occur (e. g. Flustra, Hypophorella). To which of these classes does budding in Cristatella belong? It seems to me that we have here an instructive example of a transitional condition. The young polypide of Figure 3 arises directly from the mother polypide, and may represent a case of the first class. Is the type of Figure 2 a representative of the stoloniferous class? It seems to me that it partakes of the essentials of that class, although, as I have shown, it may be united by intermediate stages with the first class. I understand a stolon, in its morphological sense, to signify a mass of embryonic cells derived from a parent individual, and capable of reproducing non-sexually one or more daughter individuals at some distance from that parent. The condition shown in Figure 15, Plate II., in which the embryonic cells of the two layers represent the stolon, may fairly be said to answer to this definition. The mass of cells (III.) represents, then, the distal end of the stolon. But the stolon does not end here, although its further progress towards the margin is delayed. Not all of its cells go to form the polypide which arises at this place. On the contrary, some of them remain in the "neck" of the new polypide, in an indifferent histological condition, and later give rise, either directly, or by the intervention of a typical stolon, or by both, to one or two new buds. Those cells of the neck which do not thus pass over into new buds for the most part degenerate (page 144). According to this view, the neck of the polypide is to be regarded as at first essentially a portion of the stolon.

2. *Interrelation of the Individuals in the Colony.* — The interrelation of individuals in the colony in Cheilostomata has been most carefully investigated from a morphological standpoint by Nitsche ('71, pages 35, 36), who showed that, in opposition to Smitt's theory, each new individual arose from a single preceding one, and that the latter, in order to increase the breadth of the colony, might give rise to two individuals

instead of one. Reichert ('69, p. 311, Fig. 28, Plate VI.) has shown that in Zoöbotryon (one of the Ctenostomata) "an der Mantelfläche, und zwar einseitig, inseriren die Bryozoenköpfe mit Alternation in parallelen, wie es scheint, langgezogenen spiralig verlaufenden Reihen angeordnet." Nitsche ('75, p. 370) states that the buds in Loxosoma arise from the mother alternately on opposite sides, and that the younger the bud, the nearer it is to the foot of the parent individual.

Both Hatscheck ('77, pp. 517, 518, Fig. 33, Plate XXIX.) and Seeliger ('89, p. 176) show that in Pedicellina young individuals are developed in the plane of the older ones, and are successively formed at the growing tip of the stolon, towards which the œsophageal side of all individuals is turned. This relation is the same as that which we have found in Cristatella. In Cheilostomata, however, it is apparently the anus which is turned towards the budding margin.

Thus, throughout the group of Bryozoa, we find that the position which young buds assume in relation to older individuals is very definite.

I am inclined to believe that the radial partitions of Cristatella separate the morphological equivalents of the isolated branches of such a form as Plumatella punctata (see Kraepelin, '87, Taf. V. Figs. 124, 125). The type of budding which gives rise to the series of median buds may, then, be represented, as seen from the side, by Figure B. The margin (*) will then represent that portion of the body-wall of the youngest individual, which will give rise to a part of the body-wall of the next younger individual. The process by which the body-wall of the individual of Cristatella is formed is therefore, in my opinion, different from that which Braem describes in the case of Alcyonella, for he maintains that in Alcyonella the proper body-wall of an individual arises later than its polypide. In fact, the tip of the branch of Alcyonella is somewhat different from that of Cristatella. In the former, it is occupied by the polypide of a budding individual; in the latter, a part of the body-wall of the budding individual is pushed out beyond the polypide. In the former, the foundations of the daughter polypide are pushed out upon the body-wall of the mother, and begin to form their own proper body-wall; in the latter, the young bud migrates away into the modified part of the body-wall of the mother, which forms the extremity of the branch, and which now becomes a part of the body-wall of the daughter polypide. This distal part of the body-wall grows independently of the polypide by interstitial growth, and thus differs from any part of the body-wall

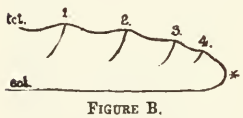


FIGURE B.

of the individual of Alcyonella, for all of it, according to Braem, is derived from the neck of its own polypide. This last method of origin of the body-wall I believe to be also present in Cristatella, as well as in Alcyonella, as I shall have occasion to show later (page 144).

In Paludicella, according to both Allman ('56, pp. 35, 36) and Korotneff ('75, p. 369), the formation of the body-wall of the new individual is begun before the appearance of the polypide. In Cheilostomata, as both Nitsche ('71, p. 22) and Vigelius ('84, p. 75) have shown, and in Ctenostomata, as demonstrated by Ehlers ('76, pp. 91, 92), the "zoœcium" arises before the polypide takes on its definite form.

3. *Origin of the Layers.* — Although later researches have only confirmed the conclusion arrived at long ago, that in Tunicates cells from all three germinal layers of the parent pass over into the bud, the facts in Bryozoa have seemed not to favor the view of the fundamental nature of this process. To be sure, Hatschek ('77, pp. 517–524) believed that he had found evidence of a condition in the budding of Pedicellina exactly comparable with that in the budding of Tunicates; but the more recent studies of Harmer ('86, p. 255) and Seeliger ('89) have failed to confirm his results, if they have not satisfactorily explained the source of his error.

What is the relation of the condition I have described in Cristatella to the question of the transmission of a part of each germinal layer to the bud, and in how far do the conditions here agree with our present knowledge of the budding process in other groups of Bryozoa? Although my results accord with Hatschek's in this, that the youngest and next older buds are intimately related, that the corresponding layers in each are derived from the same cell layers, and that the inner layer of the bud is not derived directly from the overlying ectoderm, they do not strengthen the idea of the fundamental importance of his doctrine, "Die Schichten der jüngeren Knospe stammen von denen der nächst älteren direct ab." Moreover, they afford no evidence of the accuracy of his conclusion, that the inner layer of the bud is composed of entoderm; indeed, since this inner layer does not give rise to the alimentary tract alone, as he supposed, but to the nervous system also, the facts in Cristatella tend to weaken his hypothesis. In order to determine finally just what the origin of the stolon from which the inner layer arises is, it will be necessary to study the origin of the first-formed polypides. This I have not yet been able to do. Our present knowledge on the subject is still in an unsatisfactory state.

Allman ('56, pp. 33, 34) has described and figured some stages in the

development of the egg, but without referring to gastrulation, or the layers involved in the first polypide.

Metschnikoff ('71, p. 508) and Nitsche ('75, p. 349) maintain that the outer layer of the embryonic "cystid" goes to form the inner layer of the primitive polypides, and that its inner layer forms the outer layer of the polypides.

Reinhard ('80[a], pp. 208–212) is more explicit concerning the early stages than preceding authors. Apparently the egg segments regularly, and undergoes embolic invagination. The blastopore closes. There is a circular groove in the anterior part of the embryo (Barrois's mantle cavity), and from the cap or "hood" which the mantle cavity surrounds, the wall of the "cystid" or colony-wall is subsequently formed. The embryo is already composed of three layers, "an outer, the tunica muscularis, and the entoderm." All three layers of the "hood" share in the formation of the polypides, but the fate of each layer is not clearly described.

Haddon ('83, p. 543) suggests that the gastrula is to be regarded as one in which the alimentary tract is retarded in development, and that the enlarged cœlomic diverticula, such as occur in Sagitta, etc., line nearly the whole of the so-called archenteron. From the small mass of true entoderm at the pole opposite the blastopore the alimentary tract arises. This suggestion, unfortunately, has no positive facts for its support, and could be of service only upon the assumption that the alimentary tract of the first polypide is formed from the *inner* layer of the "cystid"; but this assumption is contrary to the observation of all who have written on this subject.

Kraepelin ('86, p. 601) has also observed the "gastrulation," but he believes that it is to be interpreted as the precocious formation of an enterocœl, in which case the invagination to form the first polypide is to be regarded as the true gastrulation, the inner layer of the cystid as mesoderm, and the inner layer of the bud as entoderm.

By far the most satisfactory and complete account of the embryology of fresh-water Bryozoa is that of Korotneff, '89. The genera studied were Alcyonella and Cristatella. Since the development takes place inside of an œcium, the use of the section method is necessary for the elucidation of the details of the embryological processes. Apparently the egg segments regularly and forms a blastula. Loose cells are given off from the inner surface at one pole of this blastula. These arrange themselves in an epithelium, lying immediately inside of the ectoderm, over a part only of its inner surface; so that while the upper two-thirds

of the embryo has two layers, the lower third is one-layered. The cavity of the lower third contains some scattered cells, which, the author hints, may be representatives of the mesoderm, while the cavity in which they lie may represent an enterocœl. The author regards the inner layer of the upper two-thirds as true entoderm. The method of its formation recalls that of the entoderm of some Cœlenterata, as demonstrated by Metschnikoff. There is no epithelial invagination, such as Kraepelin maintained, and therefore the cavity which the inner layer lines cannot be regarded, says Korotneff, as an enterocœl. Later, the entire embryo becomes two-layered by an extension of the inner layer. The two polypides arise from two distinct invaginations of the double-layered wall.

Unfortunately, Korotneff does not demonstrate by figures the method of origin of the alimentary tracts of the first polypides; but there is little reason to doubt that it is essentially like that in other buds. If it is admitted that the inner layer is entoderm, as Korotneff maintains, then the entoderm takes no part in forming the digestive epithelium; but the latter is derived solely from ectoderm.

In his discussion of the theoretical bearing of his results (p. 404), the author seems to maintain that the polypide is to be regarded neither as an individual (Nitsche's view), nor, on the other hand, as an assemblage of organs homologous with organs of the same name in other groups; but rather as a new structure, developed upon the cystid, to aid in its nutrition.

In criticism of Korotneff's view, that the loose cells given off from one pole of the blastula are entoderm, I may point out that this process bears quite as much resemblance to the process of "mesenchyme" formation (as described by Korschelt for the Echinoids), as it does to the origin of the entoderm in some Cœlenterates. Compare Figs. 13 E and 182, in Korschelt und Heider's Lehrbuch der Vergleichenden Entwicklungsgeschichte.

Braem ('89[b], pp. 676, 677) has shown that the primary polypide of the statoblast arises from the cell layers of the statoblast, exactly as the primary polypide of the egg embryo does from those of the "cystid," and the alimentary tract is formed as in buds of Cristatella.

To sum up: The outer layer of the colony-wall is ectodermal in origin; the inner layer arises by an embolic (?) invagination of the blastula, and would therefore appear to be entoderm, although the possibility of its being homologous with the mesoderm in other forms is perhaps not excluded. The first polypides so arise that their inner layers are

formed by an invagination of the outer layer of the colony-wall, and their outer layer from the inner layer of that wall.

In *Endoprocta*, Seeliger ('90, pp. 176–187) has shown decisively that the inner layer of the bud is derived solely from the ectoderm, and that this inner layer gives rise to the digestive epithelium of the alimentary tract, to the nervous tissue of the brain, and to the outer layer of the tentacles. Here mesenchymatous cells, representing undoubtedly mesodermal tissue, come secondarily to surround the polypide as a loose outer tissue. In Loxosoma the same is probably true.

The conditions of budding in *Gymnolæmata* are more difficult to understand. In Paludicella the bud seems to arise as in Phylactolæmata (Allman and Korotneff). The same is probably true for Alcyonidium (Haddon, '83, p. 523, Plate XXXVIII. Fig. 23). In the Cheilostomata, however, the fact of the great development of a loose mesenchyme-like tissue obscures the process, and makes it difficult of interpretation. This tissue, which is known under three probably homologous terms, — "Funiculargewebe," Nitsche, "Parenchymgewebe" in part, Vigelius, and "Endosarc," Joliet, — is to be considered as representing the funicular and cœlomic tissues of Phylactolæmata. The most careful observations on the origin of this tissue are those of Joliet ('77, pp. 249, 250, and '86, pp. 39, 40) and Vigelius ('84, p. 76). Both authors assert that this tissue is derived from cells given off from an epithelium at the distal end of the budding individual. Vigelius ('84, pp. 19, 79) believes that this epithelium is ectodermal, and that it is the sole rudiment of this layer; but Ostroumoff ('85, p. 291) and Pergens ('89, p. 505) have shown that the ectoderm persists and secretes in its cells the calcareous ectocyst. It seems more probable, however, that the "funicular tissue" arises from the inner layer of the body-wall (Nitsche, '71, p. 37, Plate III. Fig. 5, *c*.), and is the equivalent of the cœlomic epithelium of Cristatella. The fact that many of these mesenchymatous cells conglomerate in the formation of the polypide sufficiently accounts for the origin of its outer layer of cells. The origin of the inner layer is problematical, if, as is asserted to be the case by several authors, the bud is not formed in the region of the body-wall.

It will be premature to speculate upon the significance of the facts of budding in the Ectoprocta until we shall have gained a more complete knowledge of the ontogeny of the group, and of the relationship of the Cheilostomatous to the Phylactolæmatous type through comparative agamogenetic studies. It may appear in the end, that, under certain circumstances, undifferentiated embryonic tissue, derived from a

certain germ layer, can assume the task of building organs in budded individuals similar to those derived from a different layer in the sexually produced individual.

Whatever may be the truth of the conclusions reached by Haddon ('83, pp. 548, 549, 552) and by Joliet ('86, pp. 54–56), that the nervous system and the alimentary tract arise from two distinct layers, or kinds of cells, in the species studied by them (and their evidence is certainly not conclusive even for these), their attempts (Haddon, '83, p. 540, Joliet, '86, p. 57) to apply their results to the Phylactolæmata are not justified by the observations which are here presented, nor by those which have been made upon most Gymnolæmata and Endoprocta.

4. *Origin of the Alimentary Tract.* — There is a curious difference between the Endoprocta and the Ectoprocta in the development of the organs of digestion. Seeliger ('89, pp. 182–184) has shown for Pedicellina, that the œsophagus *and stomach* arise as an evagination of the oral wall of the young bud, which secondarily becomes connected with the proctodæum. Haddon ('83, pp. 517, 518) has shown for Flustra, Barrois ('86, pp. 73–86) for Lepralia, Braem ('89[b], pp. 677, 678) for the statoblast polypides of Cristatella, and the present paper for the polypides in the adult Cristatella, that the œsophagus only is formed on the oral side, the stomach arising with the rectum on the anal side of the atrium. In all cases the œsophagus is formed first (Plate II. Fig. 13). A comparison of my Figure 18 with Figure 41, Plate XXX., of Hatschek ('77), shows a striking resemblance between the two. The form of the alimentary tract and the depression to form the ganglion are practically identical; and were the tentacles to arise directly from the immature lophophore arm (*br. loph.*, Fig. 18), and from the circumoral fold which has already appeared, it would be difficult to decide whether the anus opened outside or inside the circlet of tentacles, — whether, at this stage, the Cristatella polypide were ectoproct or endoproct.

5. *Origin of the Central Nervous System.* — The only observations on the origin of the brain in Bryozoa relate to Phylactolæmata and Endoprocta. In buds of Pedicellina, the ganglion is formed, according to Hatschek ('77, p. 520), as an invagination of the floor of the atrium, which later becomes cut off as a hollow sac. Harmer ('85, pp. 274, 275) has studied the origin of the ganglion in the bud in Loxosoma. He states that it is derived from the floor of the vestibular [atrial] cavity, and (apparently on purely theoretical grounds) that this latter is ectodermic. "In a longitudinal section through a fairly advanced bud

(Fig. 15) it is seen that a narrow slit-like diverticulum of the vestibule passes behind the epistome. This diverticulum, which remains in very much the same condition throughout life, does not give rise *in toto* to the ganglion, which is merely formed by a differentiation of some of its ectodermic cells." Harmer further doubts Hatschek's account of the formation of the ganglion in Pedicellina, and believes that the lumen of Hatschek's hollow sac is in reality the commencement of the fibrous tissue which occupies the centre of the ganglion in the adult, and which in optical sections might easily be mistaken for an empty space. "Similarly," he continues, "Nitsche has described the ganglion of *Alcyonella* as originating as a diverticulum from the tentacle sheath. I regard it as probable that the explanation which I have suggested for *Pedicellina* will hold also for *Alcyonella*." The conditions which every student of the embryology of Phylactolæmata has stated since Metschnikoff's paper in 1871, and which my own results reaffirm, do not warrant Harmer's conclusions. The nerve fibres are very evident in the adult ganglion of Cristatella, and in addition to them there is a cavity, ontogenetically derived from the atrium, which, as Saefftigen ('88, p. 96) has also shown for Phylactolæmata, contains no histological elements (Plate V. Fig. 52).

6. *Origin of the Funiculus and Muscles.* — The origin of the so-called funicular tissue in Gymnolæmata has been described already (page 126). This same tissue also gives rise, according to Vigelius ('84, pp. 34, 35) and others, to the retractor muscles of the polypide. As I have already shown (pages 115–117, Figs. 22, 54), in writing of the origin of these tissues in Cristatella, the cœlomic epithelium gives off cells, some of which take on an amœboid appearance, and, uniting together, form that end of the funiculus which is attached to the colony-wall. Other cells from the cœlomic epithelium pass directly to the adjacent outer layer of the bud, to form the nascent retractor and rotator muscles. Both of these organs are, however, formed in part from cells composing the outer layer of the bud, — itself closely related ontogenetically to the cœlomic epithelium.

These facts would seem to confirm the conclusion which the similar relation of the two layers would suggest, namely, that the cœlomic epithelium of Phylactolæmata is the homologue of the "endosarc" of Gymnolæmata.

IV. Organogeny.

1. *Development of the Ring Canal.* — Nitsche ('75, p. 358) describes the ring canal as a furrow arising from the opening of each of the lophophoric pockets, and running towards the oral side of the bud. In a later stage, both layers become deeply implicated in this furrow, and the ring canal is completed by a growing together of the edges of the furrow.

Braem ('89[b], p. 679) merely states that he cannot fully agree with Nitsche's description of the formation of the ring canal.

As a result of my own studies on this subject, I have reached the conclusion that the circumoral branch of the ring canal makes its first appearance in the median plane in the oral region at about the time that the depressions of the lophophoric pockets are first indicated. The formation of both organs is preceded by a preliminary thickening of the inner layer of the bud (Plate IV. Fig. 26, *br. loph.*, and Plate III. Fig. 17, *can. circ.*). It is only later, after the lophophoric pockets have attained considerable depth, that the groove of the incipient "ring canal" appears continuously on the side of the polypide, extending from the pre-oral region to the lophophoric pockets (Plate IV. Figs. 33, 35, 37, *can. circ.*).

As indicated in the successive stages of Figures 18 and 19, Plate III., the thickening of the inner layer anterior to the mouth is followed by a fold at this point involving both layers. The fold is deepest in the pre-oral part of the median plane, and becomes shallower as it proceeds posteriorly. Finally, the outer-layer cells of the lips of the fold approach each other and fuse, thus forming a true canal (Plate IV. Fig. 33, *can. circ.*). Kraepelin ('87, p. 57, Figs. 72, 73, *qb.*) asserts that this canal does not communicate at its neural ends with the cœnocœl, but that it is always closed by a strong "Querbrücke" connecting the "Kamptoderm" with the alimentary tract. By making sections of the colony parallel to the sole, dozens of individuals are cut through the entire length of the circumoral ring canal. Although I have examined many individuals cut in this way, I have never succeeded in finding in Cristatella this closing "Querbrücke"; but in both young and old specimens, sections nearly corresponding to Kraepelin's Figure 72 show a perfectly uninterrupted semicircular space surrounding the œsophagus, and opening freely into the cœnocœl on each side of the brain (Plate IX. Fig. 78, *can. circ.*). I must therefore conclude that in Cristatella the fluids of the cavities of the circumoral branch of the ring canal, and therefore

of the tentacles also, are in free communication with the fluids of the common body cavity. As Figure 51, Plate V., shows, the posterior ends of the ring canals open into a pair of cavities which are the bases of the lophophoric pockets, and by a comparison of Figures 61–63, *can. circ.*, *can. circ.'*, Plate VII., it will become apparent that they each become confluent with a furrow which passes up the lophophore arm, and from which the outer lophophoric row of tentacles is developed. Further, by a comparison of *can. circ.''*, *can. circ.'''*, in Figures 61–63, Plate VII. (dextro-sinistral vertical sections), and Figure 50, Plate V. (horizontal section, compare also Fig. 52, a sagittal section), it will be seen that from the tip of the lophophoric arm a groove (*can. circ.''*) passes down upon the side opposite to the ascending groove (*can. circ.'*), and, reaching the base, turns abruptly anteriorly (*can. circ.'''*, Fig. 50), and finally, in a later stage, becomes confluent with its fellow of the opposite side in the median plane just behind the epistome and above the brain. It would be quite unnecessary for me to give figures showing the course of this supraganglionic canal (cf. Fig. 52, Plate V.). It has long been recognized, and is shown in Kraepelin's ('87) Figure 66, Taf. II. This is probably what Verworn ('87, pp. 114, 115, Figs. 20 a, 20 b, Taf. XII.) has described as a "segmental organ." Braem ('89^{b}, p. 679) has given to it the name "Gabelkanal." The "Ringkanal" of Nitsche is, then, to my mind, merely the circumoral portion of a groove which is elsewhere unclosed to form a proper canal and which lies at the base of all tentacles. My reason for avoiding another term for the unenclosed portion of the "canal" is, that I regard the whole as morphologically equivalent to the ring canal of Gymnolæmata, which is said to be closed throughout.

2. *Development of the Lophophore.* — The early stages in the formation of this organ are well known, both from the descriptions of Nitsche ('75, pp. 357, 358) and the earlier ones of Allman and others.

I have already (page 114) shown how the cavities of the lophophoric pockets become confluent between the rectum and ganglion, and how their opposed walls, formerly passing over into each other through the floor of the brain, are now anteriorly continuous by means of the new floor of the atrium, and posteriorly are fused together.

The union of the inner layers of the two opposed walls of the lophophore arms (Plate V. Fig. 44, *loph.'*) continues, however, for some distance above the floor of the atrium, up to within a short distance of the tips of the young arms (Plate VII. Figs. 61, 62, *loph.'*). As the arms grow longer, the relative extent of their free and fused portions remains

approximately the same. The free ends of the arms are shown in Figure 99, Plate XI., just above *loph'*. The polypide figured here is only slightly older than that of Figure 77, Plate IX. The connection between the two arms is not one of contact merely, for in the region of fusion one can count roughly three layers of nuclei, whereas each of the two free portions of the same cell layer contains but one layer of nuclei (Fig. 99).

Before the atrial opening is formed, a separation of the two arms begins to take place. This process commences at the base of the arms, and proceeds upward as the tentacles of the inner row successively reach a certain stage of development. As the work of separation progresses, the cells of the connecting band lose their capacity for becoming stained and appear vacuolated. The vacuoles increase in size until the connection between the arms is reduced to a series of fine threads (Plate VIII. Fig. 75, *loph.'*), which are probably sundered when the tentacles of the inner row (*can. crc.''*, Fig. 76) bend at right angles to their former position to become parallel to those of the outer row. In attempting to find an explanation of this process, it must first be ascertained how the arms of the lophophore grow in length. One is perhaps inclined to think of a terminal growth, but this does not take place. So far as I can judge from an examination of many longitudinal sections of the arms, cell proliferation goes on throughout the whole length of the arm, and with nearly equal rapidity in all parts. The distance between the centres of the terminal tentacles is about the same as in the case of the more fully developed proximal ones, but they are closer together in the young arm than in the adult one. This being the case, there ought to be as many (incipient) tentacles in the young as in the adult, and I find that to be, so far as I can determine, very nearly or exactly the case.

The horseshoe-shaped lophophore being characteristic of the Phylactolæmata, a study of its development is important, since it may be expected to throw light on the phylogeny of the group. We have in Cristatella, Plumatella, and Fredericella, a series in which the arms of the lophophore are shorter and shorter, in correspondence with other changes, by which is effected a gradual transition to the Gymnolæmata, which have a circular lophophore. In Gymnolæmata, the ring canal lies at the base of all tentacles in the adult. The anus lies outside the circle of this canal. The brain lies within the lumen of the canal.

Nitsche ('71, pp. 43–45) has given the best description extant of the

development of the lophophore in Gymnolæmata. At a very early stage, the rudiments of the tentacles, he says, are seen lying in a U-shaped line, surrounding the mouth in front, but unclosed behind. The same is true for Paludicella (Korotneff, '75, p. 371). The post-oral tentacles make their appearance at the posterior free ends of the row of tentacles. They are bent slightly downward, so as to be concealed by the tentacles above. At a later stage, the tentacles lying next to the anus gradually come to lie nearer to the anal side of the mouth opening, the nearly parallel lateral rows lose their compressed appearance, and a circular basin is formed whose walls are constituted by the corona of tentacles.

In Pedicellina (Hatschek, '77, pp. 520, 521) the tentacles arise as five pairs of papilla-like processes in the upper part of the atrium. Two additional pairs are formed later nearer the anal opening. In the adult (Nitsche, '69, p. 21) the tentacles are arranged with bilateral symmetry, and so that the plane of symmetry passes through two inter-tentacular spaces, which are thus the only unpaired spaces; they are also much broader than the others.

One might be inclined to ask by what modification of the condition of the tentacles in Endoprocta we may suppose the condition in Ectoprocta to have arisen, but the question is not a fair one. I have already (page 127) shown that the young bud of Cristatella has many points of similarity to a well advanced Endoproct. This similarity leads me to the conclusion that the common ancestor of the Endoprocta and Phylactolæmata more nearly resembled the former than the latter group. But the Endoprocta are not that common ancestor; rather they are themselves more or less modified descendants of it. The proper inquiry is, To what ancestral relation between tentacles and anal opening does a comparison of the ontogeny of Endoprocta and Ectoprocta point, and by what modifications of that ancestral type may the two divergent types of the present be derived? Eliminating for a moment the evidently cœnogenetic character of the lophophore arm, an early stage of either Endoprocta or Ectoprocta reveals a U-shaped band from which tentacles are to arise. This band completely encircles the mouth, and passes posteriorly as far as the anus. This is the condition of the Endoproct bud, with only five of its seven pairs of tentacles formed; it is also the condition of the Cristatella bud of Stage XIII. (compare Figs. 19, 44). Starting from this common condition, that of the adult Endoproct, on the one hand, was attained by the addition of two pairs of tentacles posteriorly, thus nearly completing the circlet

behind the anus. The condition of the adult Ectoproct, on the other hand, was reached by the curving oralwards, and the meeting of the free ends of the rows of tentacles between the mouth and anus, thus shutting the anus outside of their circle. In evidence of this latter assertion, I submit the following comparative statement.

As Nitsche has shown for Gymnolæmata, the tentacles on the ring canal are first arranged in two rows, placed bilaterally, and meeting in front, but not behind. Later the hindermost of the tentacles move forward and toward the median plane, thus completing the circlet of tentacles at a point behind the mouth, but in front of the anus. I believe the circumoral ring canal plus the early invaginations of the lophophoric arms in Phylactolæmata to be homologous with the ring canal of Gymnolæmata in its early stage; like the latter, it is closed in front, but has two free ends behind. The difference lies in the greater development of the posterior ends of the canal, which latter have become thrown into a vertical fold to afford space for more tentacles. At this stage of development it would be difficult to say whether the anus opened within or without the corona of tentacles. As in Gymnolæmata the circle is completed by a movement inward of the posterior tentacles, so in Phylactolæmata the corona of tentacles is completed in front of the anus by the two anterior processes, *can. crc.'''*, Figure 50 (cf. Fig. 44), of the lophophore arm, which come to unite just behind the epistome, Figures 52, 81, *can. crc.'''* The lumen of this process of the lophophore arm thus forms that portion of the ring canal which, as I shall show directly, is the morphological equivalent of the most posterior portion of the ring canal in Gymnolæmata. The tentacles which arise from this portion of the ring canal are ontogenetically, and therefore phylogenetically, the youngest. As in Gymnolæmata, so here the moving forward of the most posterior tentacles obliterates the basin-like floor of the atrium, such as we see in Endoprocta, and leaves the anal opening far outside the circlet of tentacles.

The answer to the question, How may the horseshoe-shaped tentacular corona of Phylactolæmata be homologized with circular ones? is involved in the answer to the preceding query. Nitsche ('75, p. 357) believed the lophophoric arms to be "primary tentacles," and the tentacles borne on them to be secondary tentacles. "Gar nicht ohne Weiteres mit den Tentakeln der Infundibulata von Gervais zu vergleichen." The only evidence which he offers in support of his theory is the fact that the tentacles on the lophophore arm arise later than the arm itself.

The tentacles of Phylactolæmata may be distributed into two groups. The first includes those which arise from the circumoral branch of the ring canal. The ring canal, from which they spring, begins to be formed at nearly the same time as the lophophoric arms. These tentacles are undoubtedly homologous with those of the same region in Endoprocta and Gymnolæmata. The second group of tentacles includes those which are borne upon the lophophore arms and upon the supraganglionic ring canal. Are these comparable with the posterior tentacles of Gymnolæmata? I believe they are, and for the following reasons. Nitsche's reason for supposing that they are not is unsatisfactory, since, if we regard the lophophore arms as mere upward folds of the wall of the ring canal, we should expect to have the tentacles arise later than the arms. The fact that the tentacles of the lophophore arm arise much later than those of the circumoral region is what we should expect, since the posterior tentacles arise later than the circumoral ones in both Endoprocta and Gymnolæmata, — a criticism which Hatschek ('77, p. 541) has already applied. In direct support of my belief are the facts, (1) that the ring canal is continuous along two sides of the lophophore arms, which would be the case if they were mere upward folds of the wall of the ring canal; (2) the structure of the tentacles is the same as that of the oral ones, and the relation of their intertentacular septæ to the ring canal of the arms is the same as that of the septæ of the oral tentacles to their ring canal, as Kraepelin ('87, pp. 55, 56) has shown. If both circumoral and lophophoric tentacles find their homologues in Gymnolæmata, we have only to conceive of an elongation of the posterolateral angles of the lophophore of Gymnolæmata, after the forward movement of the posterior tentacles, to effect the condition which is found in Phylactolæmata.

The significance of the fusion of the lophophore arms is difficult to determine. I had thought it might be possible to find a phylogenetic explanation for it, by regarding the unfused tips of the arms in Cristatella as homologous with the short arms of Fredericella. In studying Plumatella, however, where the length of the lophophore arms is intermediate between that of Cristatella and Fredericella, I have been able to find no trace of this fusion. It does exist, however, in Pectinatella. I have had no material of Lophopus, upon which it is important to study this point. The evidence so far seems to indicate that this fusion of the arms during the period of their development is a secondarily acquired adaptation to some condition concerning the nature of which I am ignorant.

3. *Development of the Tentacles.* — Nitsche ('75, p. 359) observed that both layers of the bud went to form the tentacle in Phylactolæmata, and that the inner layer was derived from the outer layer of the polypide; the outer, on the contrary, form the inner cell layer. He states, moreover, as already mentioned, that the oral tentacles arise first, then those of the outer row of the lophophore arms, of which the basal are fully formed before the terminal ones. The tentacles of the inner row, he says, are formed last, and in Alcyonella are yet lacking when the polypide is first evaginated.

My own observations confirm in general those of Nitsche. The longest tentacles in a polypide of about the age of that shown in Figure 77, Plate IX., are those arising from the region of transition from the circumoral ring canal (*can. crc.*) to the outer lophophoric ring canal (*can. crc.'*). The tentacles lying near the median plane, and in front of the mouth, are somewhat shorter than these (75 μ : 52 μ). The tentacles situated near the proximal extremity of the inner lophophoric ring canal (*can. crc.''*) are still shorter (50 μ). Those situated at the tips of the lophophore arms are at this stage about 30 μ in length. The tentacles behind the mouth, arising from the supraganglionic part of the ring canal (*can. crc.'''*), are shortest of all at this stage (15 μ).

The two layers which, as we have seen, go to form the upper wall of the ring canal in all its parts, are the ones which give rise to the tentacles. In Figure 74, *ta.'*, Plate VIII. (compare Fig. 51, *ta.'*), young oral tentacles are cut transversely at different heights. The circumoral part of the ring canal is seen at a point (*can. crc.*) near which it opens into the cavity of the lophophore arm. The plane of the section passes obliquely upward and anteriorly from this point. The most posterior tentacle in the lower part of the figure is cut at the base. The calibre of the canal (including its walls) is evidently much enlarged at this point. The enlargements of the canal at the base of the tentacles are seen also in Figure 78, *can. crc.*, Plate IX. The more anterior tentacles in Figure 74 show the two layers well marked, but as yet enclosing no lumen. Since the tentacles arise from the ring canal at intervals only, the ring canal is a tube (or groove) whose lumen is alternately constricted and expanded laterally as well as vertically. The lumen is, indeed, often so small between the tentacles that the ring canal appears divided into separate chambers by a series of transverse septæ, which, however, are always penetrated by an opening (Fig. 78, *can. crc.*). Figures 73 and 77, *ta.'*, show, in longitudinal section, successive stages in the development of the oral tentacles. The formation of tentacles begins by a rapid cell

proliferation at intervals in the upper wall of the ring canal; thus a projection is formed at each of these points, which constantly elongates to form the tentacle. Figures 70 and 69 (Plate VII.) are longitudinal sections of two later stages in the development of tentacles. The inner layer, *ex.* (Fig. 70), becomes gradually thinner as the tentacle grows older, and its cells finally become thread-like (Fig. 69, *ex.*).

Figure 81 (Plate IX.) shows the arrangement of the tentacles about the mouth and over the ganglion in a young polypide. The supraganglionic part of the ring canal is cut tangentially just behind the epistome (*can. circ.*^{III}). I have often noticed that, in polypides of about the age of that of Figure 77, or older, certain of the nuclei seen in a cross section of a tentacle stain more deeply than the others. These nuclei are usually two or three in number on each of the lateral surfaces of the tentacles. They are evident in Figure 81. I do not know what this difference in staining properties signifies. Vigelius ('84, p. 38, Fig. 23) describes and figures a condition of the nuclei in Flustra, as seen on cross-section, which is similar to that just described. The deeply staining nuclei in Flustra lie on the inner face of the tentacle, are larger than the others, and belong to cells which possess no cilia.

Nitsche ('71, p. 43) described the development of the tentacles in Flustra as though they were derived exclusively from the inner layers of the bud; but Repiachoff ('75^{a}, pp. 138, 139, '75^{b}, p. 152) showed that in Cheilostomes both cell layers of the bud took part in their formation, and he figures an early stage which is quite similar to my Figure 70.

4. *Development of the Lophophoric Nerves.* — It has long been known that a large nerve passes along the middle of the upper wall of each lophophore arm, connecting proximally with the corresponding side of the ganglion. No observations have been made, so far as I know, upon the origin of this organ. Evidently there are, *a priori*, two possibilities. Either (1) the lophophoric nerve is formed by a direct outgrowth of the ganglion, or (2) it arises in place from the inner layer of the bud, which, since it here forms the outer layer of the lophophoric pocket, is the same as that from which the ganglion itself is constructed. By a careful study of this nerve in many stages of development, and from sections in different directions, I have come to the conclusion that it arises as an outgrowth of the walls of the ganglion, and that it penetrates between the outer and inner layers of the arm.

The facts which have led me to this conclusion are these. First, during the formation of the brain, soon after its lumen is cut off from its connection with the atrium, its cells begin to divide rapidly (Plate V.

Fig. 51, Plate VII. Figs. 63, 68); but that the new cells so formed do not all remain in the brain is indicated by the fact that the brain does not increase very rapidly in size. (Compare Plate III. Fig. 19, and Plate IX. Fig. 77.) This rapid cell division would be inexplicable upon the assumption of an origin *in situ*. Secondly, at an early stage the lophophoric nerve is already seen extending from the brain to the adjacent inner layer, with which it remains in contact. A longitudinal section through the middle of this nerve shows a prolongation of the lumen of the brain extending into it, so that its upper wall passes directly into the upper wall of the brain, and its lower wall into the corresponding part of the central organ (Plate VII. Fig. 68, *lu. gn.*, *n. loph.*). The proximal part of the lophophoric nerve is thus to be regarded as a pocket of the brain. The existing condition is not what we should expect if a cord of cells derived from the outer layer of the lophophoric arm had secondarily fused with the brain. Thirdly, I have never found any good evidence that cells were being given off from the outer layer of the arm at its tip to form the nerve, where we should look for such a process, if anywhere; on the contrary, the nerve is quite sharply marked off from the outer layer at this point, as will be seen by reference to Figures 64–67 (Plate VII.). These figures represent successive transverse sections from a young lophophore arm of about the stage of development of that shown in Figure 71. Figures 65–67 were drawn from one arm in about the position indicated by the lines 65–67 in Figure 71. Figure 64 was drawn from the opposite arm of the same individual, and in about the region of Figure 65. In Figures 64 and 65 there is a small space between the nerve (*n. loph.*) and the overlying cells of the inner layer (*i.*). This may be due to shrinkage, but in any event it indicates a complete independence between the two cell masses which it separates. Over the nerve the cells of the layer *i* are shorter than elsewhere. This might be considered as an indication that the cells had recently divided in order to give up cells to the nerve, which, on this assumption, would be formed *in situ*. Three appearances, however, indicate that the cells of the layer *i.* have been rather subjected to crowding at this point, as though by a mass of cells forcing their way between them and the layer *ex.*, and gradually increasing in volume. (*a.*) The surface of the layer *i.* is raised above the general level directly above the nerve. (*b.*) The cells of the layer *i.* are somewhat broader over the nerve than elsewhere, and the nuclei are shorter, but thicker. These are the conditions which we should expect in an epithelium subjected to pressure by the intrusion of a mass of cells at its base, for in volume the crowded cells compare

fairly with their neighbors, whereas, if they had by division given rise to nerve cells, they should all be smaller. (*c.*) In Figure 67, which is a section immediately in front of the advancing tip of the nerve, the position corresponding to that opposite the nerve in the preceding sections is indicated by an asterisk (*). The nuclei are here crowded together, indicating pressure. Fourthly, there is a considerable difference in size between the nuclei of the cells of the layer *i.* of the lophophore and the nerve cells. This is not what one would expect upon the assumption of the formation of the nerve directly from the overlying cells. Fifthly, a longitudinal section through the young lophophoric nerve (Plate VII. Fig. 71) shows a more active cell division in it than in the walls of the arm (compare Fig. 64, *n. loph.*), and a crowding together of nuclei of the outer layer of the arm, *i*, at its distal end, rather than a passage of nuclei into the nerve.

The conclusion to which I have arrived from considering these facts is that the *peripheral nervous system in Phylactolæmata arises from the brain as an outgrowth of its walls.*

5. *Development of the Epistome.* — The epistome was regarded by Lankester at one time ('74, p. 80) as homologous with the foot of Mollusca, and on another occasion ('85, p. 434) as representing the preoral lobe of Annelids, — a view for which Caldwell ('83) first produced evidence from comparative embryology. In view of such divergent opinions, and of the occurrence of an organ which is possibly its homologue, in quite aberrant genera, such as Phoronis, Rhabdopleura, etc., a careful consideration of its origin and development is desirable.

After the ganglion is fully formed, its oral face remains in contact in front with the posterior wall of the œsophagus (Plate V. Fig. 52, Plate IX. Fig. 77), and on each side with the outer wall of the lophophoric pockets by means of the lophophoric nerves (Plate VII. Fig. 63, *n. loph.*). The outer layer of the bud penetrates between the ganglion and rectum, but not between the ganglion and the œsophagus (Fig. 51,*). This layer also comes to lie between the floor of the atrium above, the ganglion below, and the lophophoric nerves on either side, having made its way in from behind as a double cell-layer enclosing a flat cavity (Plate V. Fig. 52, Plate VI. Fig. 56, Plate VIII. Fig. 74, *can. e stm.*). My description of the process by which the inner layer comes to envelop the ganglion above and behind differs considerably from Nitsche's, already quoted (page 114). As the ganglion becomes farther removed from the floor of the atrium, the cavity above it (*can. e stm.*) enlarges, and the two lateral walls of this canal, each composed of

two layers of cells, both belonging to the outer layer of the bud, form the "Verbindungsstrang des Ganglions mit dem Lophoderm" of Kraepelin ('87, p. 63, Taf. II. Fig. 59, *vs.*). (See Plate V. Fig. 51, Plate VI. Fig. 56, and Plate IX. Fig. 80,*.) This canal is the only one by which communication between the body cavity and the cavity of the epistome can occur. It may be called the *epistomic canal* (Plate V. Fig. 52, Plate VIII. Fig. 72, *can. e stm.*).

The epistome proper arises at the point where the epistomic canal ends blindly, above and in front of the brain (Plate VIII. Fig. 73, Plate IX. Fig. 77, *e stm.*); it is a pocket, the outer wall of which is continuous on its under surface with the œsophageal epithelium, and on its upper surface with the floor of the atrium. The growth of this organ is disproportionately great after the first evagination of the polypide. That part of its wall which is turned towards the alimentary tract is then much thicker than the remaining part; it forms the posterior wall of the pharynx (Plate VIII. Fig. 72, *e stm.*; compare Plate IX. Fig. 81). Is the epistome innervated by fibres from the brain, as maintained by Hyatt ('68, pp. 41–43)? I have not succeeded in finding such fibres, and the conditions of the formation of the epistome, cut off as it is from the brain at every point, make such a connection improbable.

Allman ('56, Fig. 8, Plate XI.) and Korotneff ('75, p. 371) have shown for Paludicella, and Nitsche ('71, p. 44) has shown for Flustra, that an epistome-like fold occurs at an early stage of development, but is absent in the adult. Such an organ has been described by Allman ('56, p. 56) and other observers in Pedicellina, and it is still more prominent in Loxosoma, in which the relation of the epistome to the body cavity is similar to that in the Phylactolæmata.

The constant occurrence of this organ in the development of Bryozoa, and its presence in so many aberrant genera which seem to be somewhat allied to this group, can only be interpreted, it seems to me, as signifying that it is an ancient and morphologically important organ. The manner of its development in Cristatella seems to throw very little light, however, upon its significance; it arises rather late, and does not become of any considerable size until the atrial opening is made.

6. *Development of the Alimentary Tract.* — The later development and histological differentiation of the alimentary tract have not been heretofore carefully studied.

At the stage at which we left the alimentary tract (Plate III. Fig. 19) only two parts were clearly differentiated, the œsophagus and the intes-

tine. In the next stage shown (Plate VIII. Fig. 73), further changes are seen to have taken place. The most prominent is the down-folding of the lower wall of the intestine at its middle region to form the cœcum. Even at this early stage histological differentiation of the cells of this region has occurred to such an extent that the lumen of the cœcum is nearly obliterated by the great elongation of some of the cells lining it. This condition of affairs will be understood by studying the cross section of the cœcum at a later stage, as shown in Figure 94, Plate X. The cavity of the rectum has also enlarged, and its cells have taken on the regular columnar appearance which exists in the adult.

At a still later stage (Plate IX. Fig. 77), the position of the cardiac and pyloric valves, separating respectively the œsophagus (*œ.*) from the stomach (*ga.*), and the cœcum (*cœ.*) from the rectum (*rt.*), is clearly indicated. The blind sac is still further elongated and well differentiated from both stomach and rectum. In order to attain the adult condition (Plate VIII. Fig. 72), the oral portion of the alimentary tract has merely to become divided, by a difference in the character of its cells, into pharynx (*phx.*) and œsophagus (*œ.*), the stomach (*ga.*) to increase in diameter, and the blind sac (*cœ.*) to elongate. The anus (*an.*) finally comes to lie at the apex of a small cone, or sphincter valve.

The histological changes which the cells of the different parts of the alimentary tract undergo are considerable, and will be treated of in order, beginning with the

Œsophagus. — At a stage a little later than Figure 77, the œsophagus, as is shown in Figure 84, Plate X., has a small diameter relative to that of the rest of the alimentary tract (cf. Plate VIII. Fig. 72, *œ.*), and its inner lining is composed of high columnar epithelium, like that of the oral groove. The shape of the cells is not greatly different in the adult; but they become vacuolated, and since these vacuoles lie near the base of the cells, and either nearer to or farther from the lumen than the nuclei, the latter acquire that irregular arrangement referred to by Verworn ('87, pp. 111 and 112).

Stomach. — Figure 93 (Plate X.) represents a section across the stomach immediately below the cardiac valve, from the same individual as that from which Figure 84 was taken. The proximal ends of all cells stain more deeply than the distal ends, but the cells are all alike as far as regards receptivity to stains. Already, in certain regions, the cells are higher or lower than the average, and have even begun to group themselves as typical ridge- and furrow-cells. Figure 82 is a section through the same region as Figure 93, but from an adult individual. The ridge-

cells are distinguishable from those of the furrows by their greater height, their weaker attraction for dyes, and their vacuolated and granular appearance. Moreover, the cell boundaries of this epithelium are gradually lost. Kraepelin ('87, p. 51) has argued that the elongated cells are the true digestive cells, and that the deeply dyed cells of the furrows are, functionally, liver cells.

Cœcum. — Figure 94 is from a cross section of the cœcum at the stage of Figures 84 and 93. The cells are more differentiated here than at any other part of the alimentary tract. They stain uniformly, however, except for a narrow light zone next to the lumen, and all reach to the muscularis. The digestive cells are swollen at their free ends; the liver cells, on the contrary, are thickest at the base. Figure 83 is from a section of the proximal part of the cœcum of an adult. The changes which the cells have undergone are of a similar character to those experienced by the gastric epithelium, only there has been an exaggeration in this region of the features shown by the stomach. Figure 85 represents a section near the blind end of the cœcum of an adult. The diameter of the tube is smaller here than in the section last described, but the inner epithelium is thrown into still higher ridges and more profound furrows. Nearly all of the cells, however, seem to extend to the muscularis. The "liver" cells do not extend so far towards the blind end of the cœcum as this region. The cytoplasm is not at all stained. Evidently, here the process of digestion reaches a maximum. The circular muscles of the muscularis are *striped*, and are developed here to an extraordinary degree, and the cœlomic epithelium is greatly thickened, another evidence, it seems to me, of the intimate relation of this layer to the muscularis. The number of ridges is not constant in different parts of the alimentary tract of the same individual, and varies somewhat for the same region in different individuals. In sections corresponding in position to Figure 83, I have, however, usually found six ridges.

7. *Development of the Funiculus and Muscles.* — It has already (page 117) been pointed out that the fixed ends of both the funiculus and muscles originate at a great distance from their position in the adult. Thus the funiculus originates upon the *oral* face of a young bud. As this bud grows older, the fixed end of its funiculus becomes gradually farther and farther removed from its neck towards the margin, until finally the funiculus is inserted upon the colony-wall at the margin, or even upon the sole. So the retractor and rotator muscles arise together on each side of the polypide and in the angle formed by the colony-wall and the radial partitions. Later (Plate V. Figs. 44, 45, *mu. ret.* + *rot.*)

they are found on the partitions immediately below the colony-wall. Still later (Plate VI. Fig. 59, *mu. rot.*, *mu. ret.*) we see them on the lower portion of the partition, and finally (Fig. 56, *mu. rot.*, *mu. ret.*) they are found attached to the sole, at some distance, it may be, from the radial partition.

The question arises at once, How do these changes of position take place? Examination shows that the union between the cœlomic epithelium and the cells of that portion of the funiculus which is attached to the roof is very slight after the funiculus has passed to some distance from the mother polypide. Although occasionally I have seen the cells of the fixed end closely applied to the cœlomic epithelium, the only connection between the two is usually effected by means of amœboid cells (Plate V. Figs. 46–48, *cl. mi.*). On cross sections of the fixed end of the funiculus these cells (Fig. 49, *cl. mi.*) are seen to surround it as a loose layer, and in longitudinal sections some of the amœboid cells are seen to be connected with the cœlomic epithelium. It is difficult to determine the origin of these cells, but they have the position and character of the cells of which the funiculus was exclusively composed before the entrance into it of the ectodermal plug described by Braem. The only explanation of the migration of the funiculus which occurs to me has been suggested by the facts given above; namely, that the "migratory cells," by which the funiculus is attached to the cœlomic epithelium, change their position, carrying with them the funiculus. Remembering that the cœnocœl is filled with a fluid in which the funiculus floats, and that by the growth of the funiculus it is elongated in proportion as the distance from its origin to the cœcum increases, this hypothesis does not seem improbable, although its truth can hardly be tested by the study of preserved material. When the funiculus has reached its permanent position its attachment to the cœlomic epithelium is more intimate. Meanwhile the end attached to the polypide has become more and more attenuated (Plate IX. Fig. 77, *fun.*), until, in the adult, I have usually been unable to discover any attachment. In any case, it must certainly be broken when the polypide begins to degenerate.

The migration downward of the ends of the muscles which are attached to the partition is even more difficult of explanation. During this migration their point of origin seems to be in the muscularis of the partition itself. The fixed point of the muscle in the adult is probably in the muscularis of the sole, since I have traced muscle fibres through the cœlomic epithelium, and to the muscularis (Plate VI. Fig. 58, *mu.*

ret.). The insertion is in the muscularis of the polypide (Fig. 56), but I have not been able to determine the precise relation between the muscle fibres of the great cœlomic muscles and those of the muscularis. A comparison of Figures 44, 59, and 56 shows quite plainly that both the retractor and the rotator muscles originate from a common mass of muscle cells, and become distinct from one another by a separation of their points of attachment to the polypide. The retractor muscles (*mu. ret.*) are attached to the œsophagus immediately below the ganglion (Plate IX. Fig. 78); the rotator muscles (*mu. rot.*), on the contrary, to the lateral walls of the opening leading from the cœnocœl (*cœn.*) to the cavity of the lophophore arms. These two regions are near to each other in the young polypide, but become constantly more widely separated with the growth of the lophophore. Compare Figure 78 with Figures 74 (Plate VIII.) and 51 (Plate V.), which are younger stages, cut somewhat above the level of Figure 78, and more than twice as highly magnified.

I have been able to obtain in thick sections various stages in the development of the muscle fibres, some of which are shown in Figures 89 to 92 (Plate X.). In the earlier stages, all parts of the muscle cell stain uniformly in cochineal. Later, the cell body becomes differentiated into two portions, easily distinguishable by their different receptivity to the dye. The more retractile portion becomes greatly elongated, highly refractive, and incapable of being stained. A mass of indifferent protoplasm, including the nucleus, still remains stainable (Fig. 90). The undifferentiated portion continues to diminish relatively to the whole mass of the cell, which has greatly increased in size, until little remains but the nucleus, placed on one side of the muscle fibre (Figs. 91, 92). Figure 92 is one of the retractor muscle fibres, in a partly contracted state. The end placed uppermost in the figure was that which abutted upon the muscularis of the œsophagus. Its more intimate relation to the muscularis could not be traced.

8. *Origin and Development of the Parieto-vaginal Muscles.* — These consist of two sets, the lower, or *posterior*, and the upper, or *anterior*. The posterior arise earlier. At about the time when the neck of the polypide begins to disintegrate in order that the polypide may become extrusible, a disturbance is seen in the cells of the outer layer of the kamptoderm immediately below the neck of the polypide, and in the cœlomic epithelium opposite to them (Plate XI. Fig. 97, *mu. inf.*). As a result, several cells of each layer become organically connected with those of the opposite layer, and give rise to muscle cells. A later stage of

such a process is seen at Figure 98. · By the time the atrial opening is established these cells have become plainly muscular (Plate IX. Fig. 79). Farther up in the angle of attachment of the kamptoderm to the roof of the colony, the cœlomic epithelium and the outer layer of the bud are both seen to be somewhat disturbed (Fig. 97, *mu. su.*). At different points, a single one of these cells reaches across, and later becomes differentiated into a genuine muscle cell (Fig. 99, *mu. su.*). Of these there may be three rows.

9. *Disintegration of the Neck of the Polypide.* — The neck of the polypide, having fulfilled its function as the most important part of the stolon, must now give way to allow of the extrusion of the nearly developed polypide. The first indication of this process is the formation within the cells of the neck of a secreted substance (*cp. sec.'*), apparently like the secreted bodies of the ectoderm. This metamorphosis first involves the outer and middle cells of the neck only (Plate XI. Fig. 97, *cev. pyd.*). Later (Plate IX. Fig. 77, *of. atr.*) a depression occurs in the ectoderm. This is due, I believe, to a cessation of cell proliferation at the centre, although it remains active at the edges of the neck. The depression gradually deepens until the atrium is closed by a thin layer of cells only (Fig. 98). The cells of the side of the neck do not disintegrate, but go to form the "Randwulst" of Kraepelin ('87, p. 40). The cells of this region remain unmetamorphosed. Only a thin layer of cells now stands between the polypide and the outside world. This ruptures, as is shown in Figure 99, and by the relaxation of the muscularis, which is thickened about the atrial opening into a sphincter (Fig. 98, *spht.*), the polypide is ready to expand itself.

10. *Development of the Body-wall.* — As already stated (page 117), Braem believes that the whole body-wall in Alcyonella is derived from the neck of the young polypide, after it has begun to give rise to daughter polypides; and I have given my reasons for believing that in Cristatella a portion of it at least is derived from the margin.

In addition to this, cells are undoubtedly added to the body-wall, as Braem states, after the time of origin of the buds. Particularly after the formation of the median bud, the neck appears to continue to furnish cells to the ectoderm. Figure 73,* Plate VIII., shows such a mass of cells. Later stages show that these cells secrete a gelatinous substance within their protoplasm (*cp. sec.'*, Plate XI. Figs. 97, 98); they gradually increase in width and height from the neck outward (Figs. 97–99), and at the same time become more and more completely metamorphosed. The result of the addition of these cells from the neck of the polypide is to

carry the body-wall at the region of the atrial opening to a considerable height above the level of that portion of the roof lying between polypides. (Compare Fig. 73, Plate VIII.; Figs. 98 and 99, Plate XI.) This method of origin of the body-wall is of much less importance in Cristatella than in Alcyonella, since the extent of the proper body-wall about the atrial opening is much less in the former than in the latter case.

The development of the gelatinous bodies deserves further attention. Kraepelin ('87, p. 24) concluded, from a study of the condition in a statoblast embryo, that they are formed by a metamorphosis of the cell protoplasm, beginning at the outer end of the cylindrical cell, and finally involving, in some cases, the entire cell, together with its nucleus. Some appearances which I have noticed in the ectoderm of Cristatella lead me to conclude that the origin is not always so simple as Kraepelin describes. Figure 79, Plate IX., shows at *cp. sec.* a number of small gelatinous masses occurring at various regions in the protoplasm. Such an appearance is quite common, and must be interpreted, it seems to me, as the formation of the gelatinous balls by an intra-cellular metamorphosis of the cytoplasm. The balls, flowing together, produce the larger masses. The metamorphosed matter from several cells may also fuse into one mass (Plate VI. Fig. 55, *cp. sec.*). The final result of this process of cell metamorphosis in the ectoderm is a frame-work of old cell walls, having a thin layer of protoplasm and nuclei at its base, and inclosing the great gelatinous balls. Such a condition exists near the centre of the colony between adult polypides, and is shown in Figure 100, Plate XI.

Summary.

1. Most individuals give rise to two buds, of which one forms a new branch, the other continues the ancestral branch.

2. The median buds migrate away from the parent polypide to a considerable distance before giving rise to new buds.

3. The descendants of equal age from common ancestors are arranged similarly in the same region of the colony.

4. New branches are formed upon either side of ancestral branches.

5. The greater the difference in age between the youngest and the next older bud, the greater the distance between the points at which they begin to develop.

6. In typical "double buds," both polypides arise from a common mass of cells at the same time. From the neck of old polypides a stolon-

like process of cells is given off to form median buds. Between these two extreme types, intermediate conditions occur.

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7. The alimentary tract is formed by two out-pocketings of the lumen of the bud in the median plane, one forming the œsophagus, the other the rectum and stomach. The blind ends of these two pockets fuse, and thus form a continuous lumen.

8. The central nervous system arises as a shallow pit in the floor of the atrium; the pit becomes closed over by a fold of the inner layer only of the polypide, which thus forms a sac, the walls of which become the ganglion.

9. The kamptoderm arises by the transformation of the columnar epithelium of the two layers of the wall of the atrium into pavement epithelium.

10. The funiculus arises from amœboid cells derived from the cœlomic epithelium.

11. The retractor and rotator muscles arise together from the cœlomic epithelium of both body-wall and bud, and in the angles formed by the radial partitions and the body-wall.

12. The wall of the colony grows by cell proliferation at its margin.

13. The radial partitions arise as follows: certain muscles of the muscularis at the margin of the colony leave the latter, and are carried into the cœnocœl, taking with them a covering of cœlomic epithelium.

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14. Budding in Cristatella presents conditions transitional between direct and stoloniferous budding.

15. Throughout the group of Bryozoa, the youngest and next older buds are intimately related, and the place of the origin of the younger buds relatively to the older is determined by a definite law.

16. Cristatella differs from Alcyonella in possessing a region of the colony-wall, — the tip of the branch, — which grows independently of the polypides.

17. Each of the layers of the younger bud arises from a part of the same cell mass as that which gave rise to the corresponding layer of the next older bud.

18. The digestive epithelium and the nervous tissue are both derived from one and the same layer of cells, the inner layer of the bud.

19. The alimentary tract of Cristatella at an early stage is similar to that of a young Endoproct.

20. Harmer's conclusion, that the ganglion of Phylactolæmata arises exactly as in Endoprocta, is not confirmed.

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21. The "ring canal" lies at the base of all tentacles.

22. The circumoral region of the ring canal in Cristatella is in free communication with the cœnocœl in all stages of development; and not closed, as maintained by Kraepelin.

23. The two arms of the lophophore arise independently of each other. Their adjacent surfaces undergo a secondary fusion, which persists until the inner row of tentacles is about to be formed on the lophophore. The two arms then become entirely separate.

24. The ancestor of Bryozoa probably possessed a U-shaped row of tentacles, encircling the mouth in front, and ending freely behind near the anus.

25. The tentacles near the mouth are phylogenetically the oldest.

26. Both layers of the bud are involved in the formation of the tentacles.

27. The lophophoric nerves arise as outgrowths of the central ganglion, which make their way into the lophophore arms.

28. The epistome arises as a fold continuous with the wall of the œsophagus below and the floor of the atrium above, and it communicates with the cœnocœl by means of the epistomic canal.

29. The cœcum of the alimentary tract, which occurs only in Ectoprocta, is produced relatively late in the ontogeny by an out-pocketing of the lower wall of the alimentary tract at the free end of the polypide.

30. The funiculus migrates (probably with the aid of amœboid cells) from the roof of the colony to the margin, or even to the sole.

31. The "origins" of the retractor and rotator muscles migrate along the radial partitions from roof to sole. The separation of the two muscles takes place secondarily as their points of insertion separate.

32. The parieto-vaginal muscles arise from the cœlomic epithelium of the body-wall and polypide.

33. The disintegration of the neck of the polypide is begun by a metamorphosis of the protoplasm of its cells. The metamorphosed cells break away, leaving the atrial opening.

34. The part of the body-wall lying around the atrial opening arises by proliferation of cells derived from the neck of the polypide.

35. The ectodermal cells become metamorphosed by an intercellular secretion of small "Gallertballen," which fuse to form the larger ones. Often the contents of more than one cell fuse into a single large mass.

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EXPLANATION OF FIGURES.

All figures were drawn with the aid of a camera lucida from preparations of *Cristatella mucedo*.

ABBREVIATIONS.

An.	Anal side of polypidè.
an.	Anus.
atr.	Atrium.
br. loph.	Lophophore arm.
can. crc.	Ring canal, circumoral part.
can. crc.'	Ring canal, outer lophophoric part.
can. crc.''	Ring canal, inner lophophoric part.
can. crc.'''	Ring canal, supra-ganglionic part.
can. e stm.	Epistomic canal.
cav. loph.	Cavity of lophophore arm.
cev. pyd.	Neck of polypide.
cl. fun.	Young cells of funiculus.
cl. mi.	Migratory cells.
cl. mus.	Young muscle cells.
cæ.	Cœcum.
cæn.	Cœnocœl.
cp. sec.	Secreted bodies of ectoderm.
cta.	Cuticula.
di sep.	Intertentacular septum.
di sep. r.	Radial septum of colony.
ec.	Ectoderm.
e stm.	Epistome.
e t. cæl.	Cœlomic epithelium.
ex.	Outer layer of bud.
fun.	Funiculus.
ga.	Stomach.
gn.	Ganglion.
i.	Inner layer of bud.
kmp. drm.	Kamptoderm.
loph.'	Place of union of arms of lophophore.
lu. gm.	Lumen of the bud.
lu. gn.	Lumen of the ganglion.
mu.	Muscularis.
mu. inf.	Inferior parieto-vaginal muscles.
mu. lg.	Longitudinal muscle fibre of muscularis.
mu. ret.	Retractor muscle of polypide.
mu. rot.	Rotator muscle of polypide.
mu. su.	Superior parieto-vaginal muscles.
mu. tr.	Transverse (circular) muscle fibre of muscularis.
n. loph.	Lophophoric nerve.
nu. ml.	Nucleus of muscle fibre.
œ.	Œsophagus.
of. atr.	Atrial opening.
om.	Ovum.
Or.	Oral side of polypide.
or.	Mouth.
pam. atr.	Floor of atrium.
pam. gn.	Floor of ganglion.
phx.	Pharynx.
pyd. [i., ii., &c.]	Polypide.
pyd. fili.	Daughter polypide.
pyd. ma.	Mother polypide.
rt.	Rectum.
sol.	Sole.
spht.	Sphincter.
sul. or.	Oral groove.
ta.	Tentacle.
ta.'	Oral tentacle.
tct.	Roof of colony.
tct. gn.	Roof of ganglion.
vac.	Vacuole.
vlv. cr.	Cardiac valve.
vlv. py.	Pyloric valve.

PLATE I.

Fig. 1. A portion of the lateral rim of a colony. An optical section taken just below the roof of the colony, showing the arrangement of polypides. × 72.

" 2. Origin of the stolon (I.) from the neck of a mother polypide of about Stage XII. (Fig. 18). Sagittal section of mother polypide. The margin of the colony is to the left. × 390.

" 3. Earliest stage in the origin of a bud from a young mother polypide. Sagittal section. Margin to left. × 390.

" 4. Origin of a bud from a mother polypide of about the age of that of Fig. 3. Sagittal section. The margin of the colony is to the right of figure. × 390.

" 5. Sagittal section of a double bud. Margin of colony to the left. × 390.

" 6. Later stage in bud formation of same type as Fig. 4. Sagittal section. × 390.

" 7. A part of the right side of a polypide of a stage of development intermediate between those of Figs. 19 and 73. Seen from the sagittal plane. The cut surface lies to the right of the sagittal plane, and passes through the orifice of the right lophophore arm. The alimentary tract thus lies immediately above the plane of the paper. × 150.

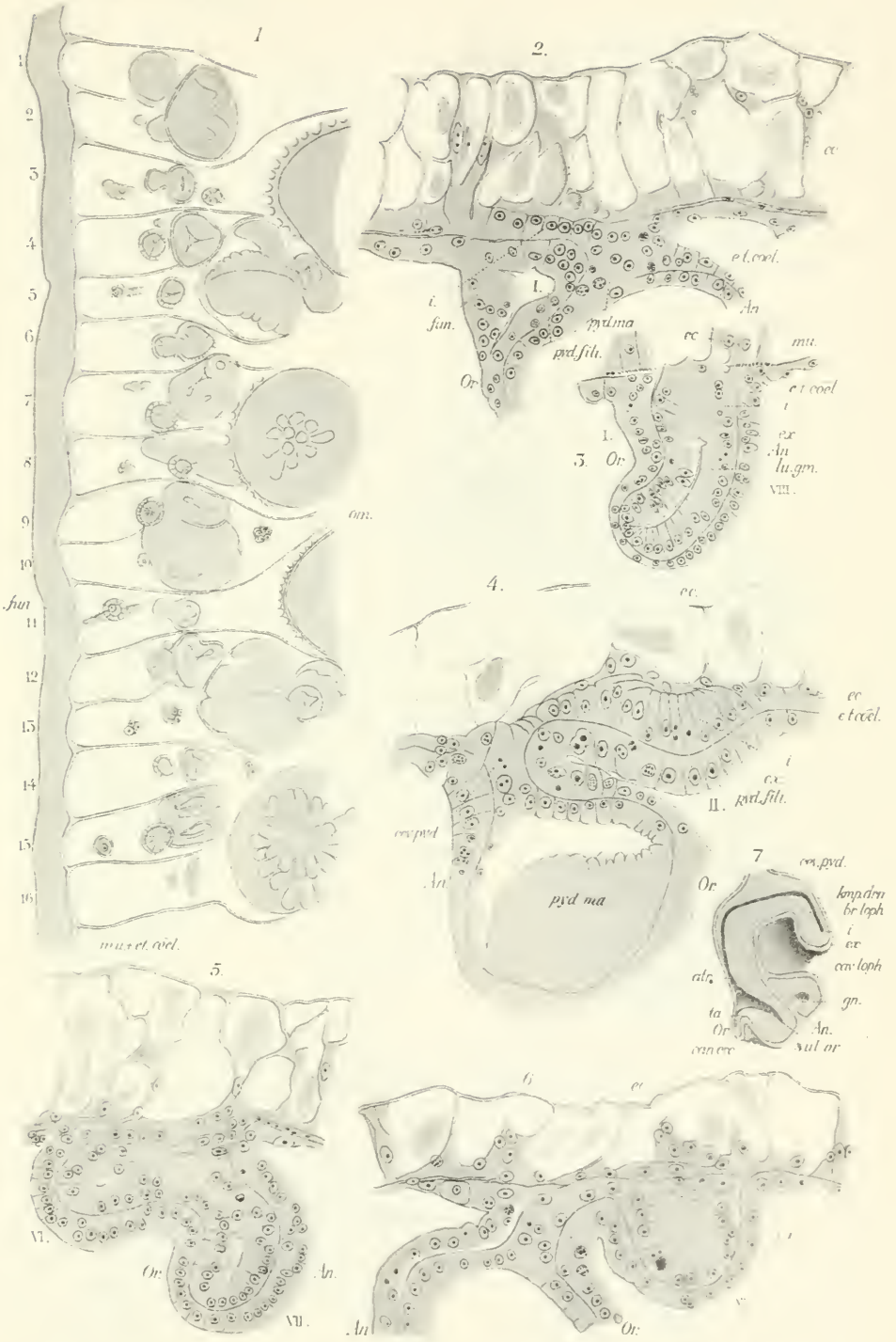

1
2
3
4
5
6
7
om.
fun
mu. et. cœl.
ec
et.coel.
i.
fun.
pyd.ma
pyd.fil.
Or
An
mu.
ex
lu.gm.
VIII.
cav.pyd.
pyd ma
II.
kmp.dru
br.loph
cav.loph
gn.
ta
mul or
VII.

PLATE II.

All figures are magnified 390 diameters, and are from sagittal sections.

Fig. 8. Stage II. in the same series as Fig. 2. The funiculus, *fun.*, has moved farther from the mother polypide. Margin to left.

" 9. Stage IV. The inner layer, *i.*, of the bud is definitely formed, and the external layer is greatly thickened. Margin to left of figure.

" 10. Stage V. The cells, *i.*, have arranged themselves in a layer, and begin to form an invagination. Margin to right.

" 11. Stage VIII. The first indications of the alimentary tract appear as a depression in the inner layer, *rt.* The funiculus, *cl. fun.*, has begun to form, as is indicated by a disturbance of the cœlomic epithelium. Daughter bud forms Stage VI. in a series beginning with I., Fig. 3. Margin to left.

" 12, 13. Successive stages in the formation of the alimentary tract.

" 14. Stage VI. The two cell-layers are now definitely formed, and a lumen has begun to appear in the inner. Margin to right.

" 15. Stage III. in the stoloniferous type of budding. Stolon has elongated greatly, and active cell division is taking place at its distal (i. e. marginal) end.


8
An
ovd ma
ovd fila
9
mu
ovd pvi
pvi fila
Or
11
mu
el fun
VI.
rt
Or
An
VII
pvi ma
Cp
pvd fun
V.
cp.sec
15
IX.
12.
An
Or
lu gm
X
24
14
el.coel
mu
lu gm
VI.
17
ovd ma
Or
fun.

PLATE IV.

All figures, except Fig. 39, are vertical right-and-left sections, and all are magnified 390 diameters.

Figs. 24–26. Three sections from a series passing from the oral to the aboral face of a polypide of about Stage X., and cutting it in the planes indicated by the lines 24–26, Fig. 13.

" 27–29. Three sections of a series cut from a polypide of Stage XI. The planes of section are indicated in the lines 27–29, Fig 17.

" 30–32. Three sections, whose positions are indicated by the lines 30–32, Fig. 18, cut from a polypide of Stage XII.

" 33–38. Six sections cut from a polypide of Stage XIII. in the directions indicated in Fig. 19 by the lines 33–38.

" 39. A horizontal section of a polypide somewhat older than that represented in Fig. 18, and passing nearly in the direction of the line 43.


24
cl mu
er
ga
25
ga
26
cl mu
br loph
27
mu
28
atr
pa n gn
er
29
an
30
cl mu
disep r
mu
cl mu
disep r
31
par gn
ga
32
an
br loph
can cr
37
cav loph
34
can cr
35
tel gn
par gn
er
36
gn
cl mus
can cr
33
or
br loph
39
lu gn
loph'
or
oe
an
lu
38

PLATE VI.

Fig. 53. Young funiculus, showing its connection with polypide. × 390.

" 54. Origin of muscles. The section passes diagonally across a partition at the left, *di sep. r.*, and cuts the polypide tangentially at the right. × 390.

" 55. Section including a radial portion, showing the position of the muscles in the partition near the margin of the colony. × 390.

" 56. Section through the retractor and rotator muscles of a polypide of about the age of that shown in Fig. 77. × 390.

" 57. Young funiculus, whose upper end is free from the cœlomic epithelium of the roof of the colony. × 390.

" 58. Section through the sole, showing the relation between the muscle cells and the muscularis of the sole. × 600.

" 59. Section across a radial partition, and both rotator and retractor muscles which are migrating from the roof to the sole. × 390.

" 60. Section at right angles to the wall of the colony, showing the elongated and unmetamorphosed cells of the margin. × 390.

PLATE VIII.

Fig. 72. Sagittal section of an adult polypide. The lophophore has been omitted. Outlines with camera lucida. Nuclei put in free hand. × 175.

" 73. Sagittal section of bud. Stage XIV. The margin of colony to left. * Ectodermal cells derived from neck of polypide. × 390.

" 74. Nearly horizontal section of a bud a little older than that shown in Fig. 73. The plane of section passes obliquely upward and forward. The tentacles are cut at different heights. × 390.

" 75. Transverse section of lophophore arms before separation. The connecting band, *loph.'*, is reduced to threads. The polypide has already evaginated. The section figured is the seventh from the distal end of the arms, — about 40 μ distant. × 390.

" 76. Transverse section of lophophore arms immediately after separation. The tentacles arising from *can. cec.''* were previously fused. × 390.

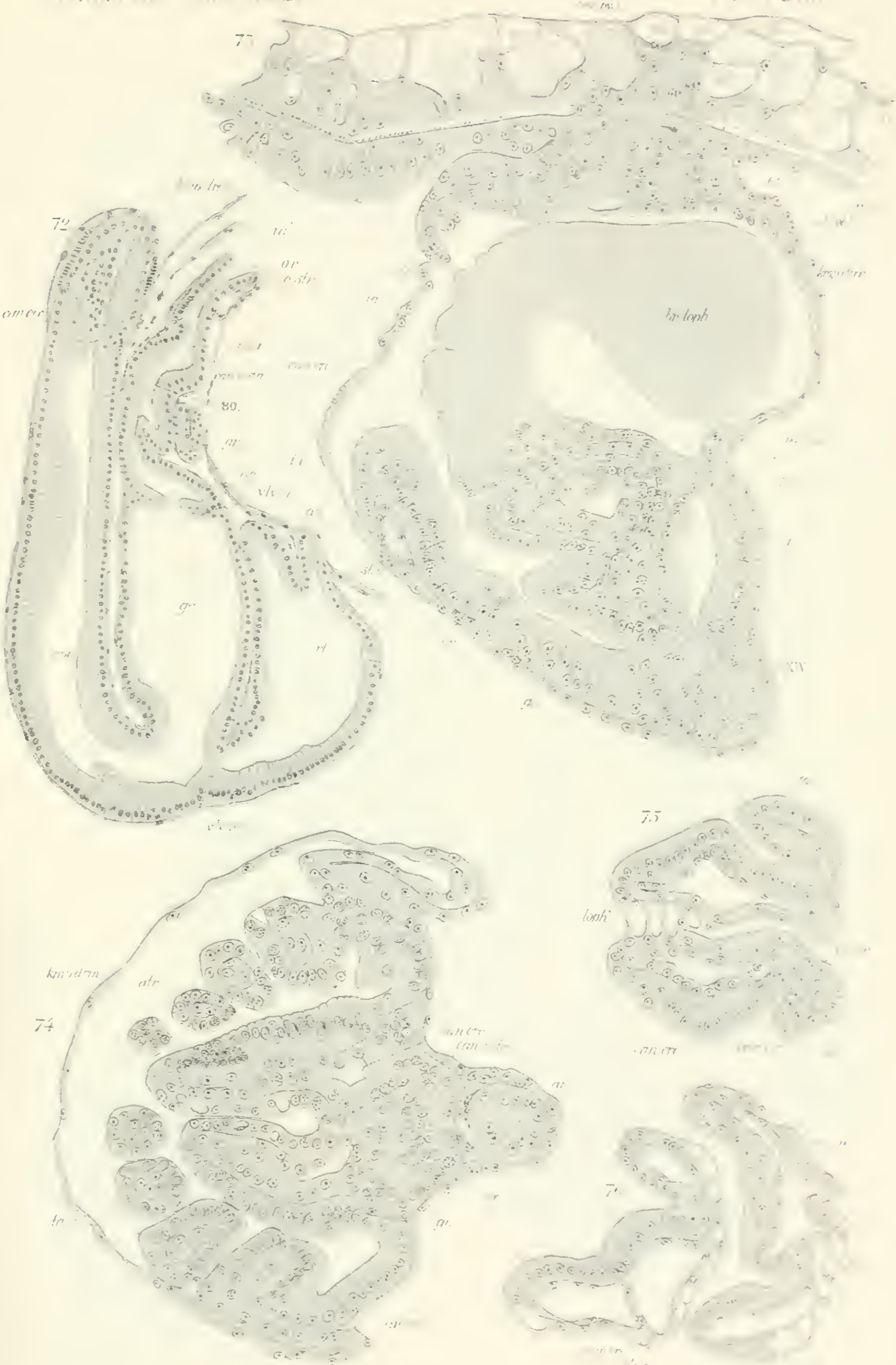

72
73
74
75
br. loph
loph
80.

PLATE IX.

Fig. 77. Sagittal section through a polypide, of which the atrial opening (*of. atr.*) has already begun to form. × 390.

" 78. Horizontal section through the circumoral part of the ring canal, *can. crc.*, showing its free communication with the cœnocœl (*cœn.*). Adult. × 175.

" 79. Vertical section through the roof of the colony (to the left) and the kamptoderm (to the right), showing their connection by the inferior parieto-vaginal muscles (*mu. inf.*) at an early stage of their development. × 600.

" 80. Horizontal section in position marked 80, Fig. 72, Plate VIII., showing epistomic canal, *can. e stm.*, and supra-ganglionic part of ring canal, *can. crc.'''* × 390.

" 81. Section cutting lophophore at base of tentacles. The arm of the right side only is shown entire. Stage of Fig. 77. × 175.

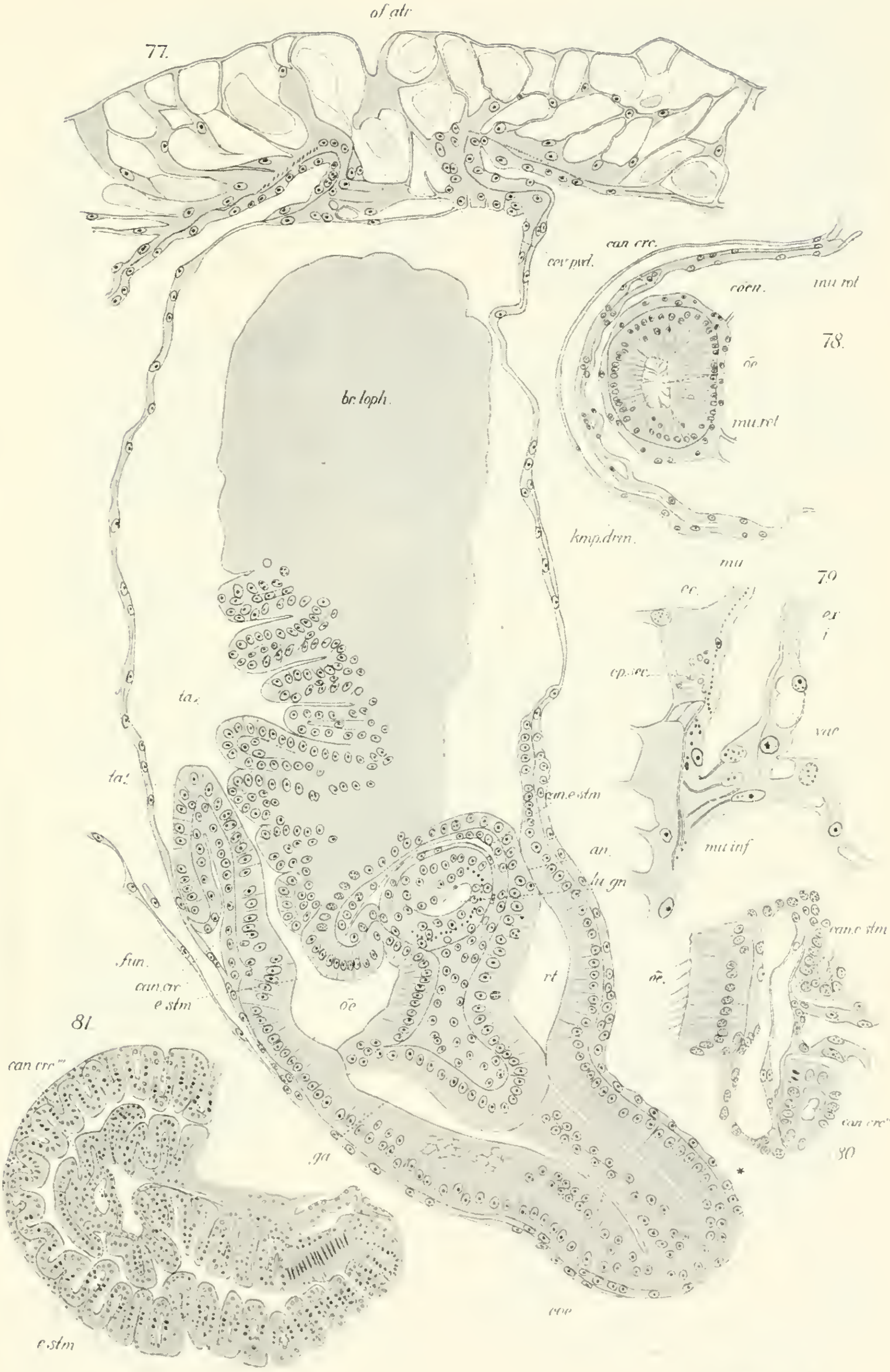

77.
of atr
can crc.
cov.pvd.
br.loph.
ta.
ta.
fun.
can.crc
e.stm
oe
rt
an.
ga
coe
78.
coen.
mu.rot
oe
mu.rot
79.
mu
cc.
mu.inf
vac
80.
can.e.stm
oe.
81.
e.stm

PLATE X.

Fig. 82. Transverse section of stomach of adult polypide. × 390. Compare with Fig. 93.

" 83. Transverse section of proximal part of cœcum of same individual as that of Fig. 82. × 390. Cf. Fig. 94.

" 84. Transverse section of œsophagus of a polypide whose atrial opening is just formed. × 390.

" 85. Transverse section of the cœcum of an adult polypide near its distal extremity. × 390.

" 86. Vertical section across a radial partition at its junction with colony-wall. × 600.

" 87. Horizontal section of radial partition at its junction with colony-wall. × 600.

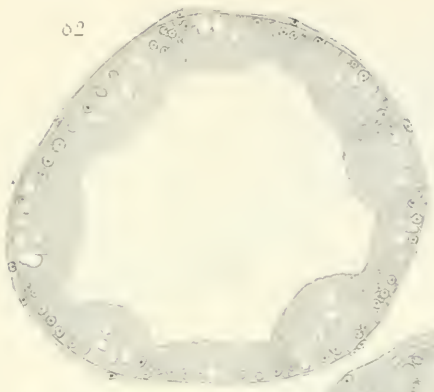
" 88. Small colony of Cristatella, drawn from transparent object, showing polypides in optical section at different focal planes. × *circa* 40.

" 89–92. Muscle fibres in successive stages of development. From thick sections. × 390.

" 93. Transverse section of stomach of the same polypide as that from which Fig. 84 was taken; representing, therefore, a considerably younger stage than Fig. 82. × 390.

" 94. Transverse section of cœcum of the same polypide as that from which Figs. 84 and 93 were taken, cut in a region nearly corresponding to the position of that shown in Fig. 83. × 390.

" 95, 96 Two horizontal sections of a part of the margin of a small colony in which radial partitions are being rapidly formed in correspondence with rapid budding. Fig. 95 lies near the sole; Fig. 96, near the roof. The same figures refer to the same partition × 300.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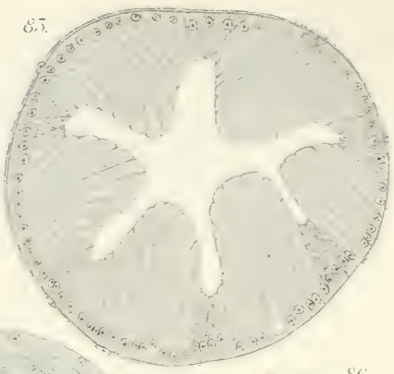
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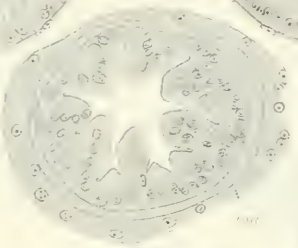
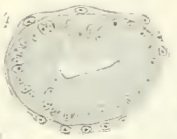

85


84


86
mx.b
mdg
tct
mdb
mdg
sol.

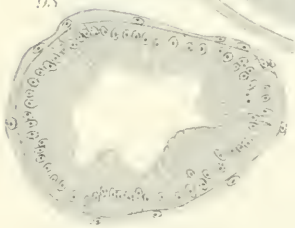

87
mx
mdb
mdb


tct
Ant.
88


89
32
mxml

90
mxml


91
mxml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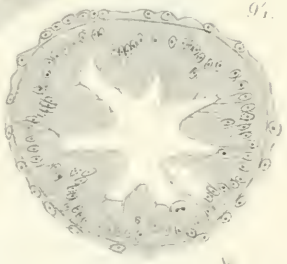
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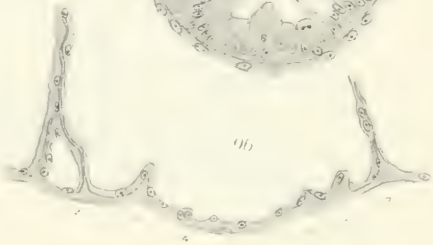
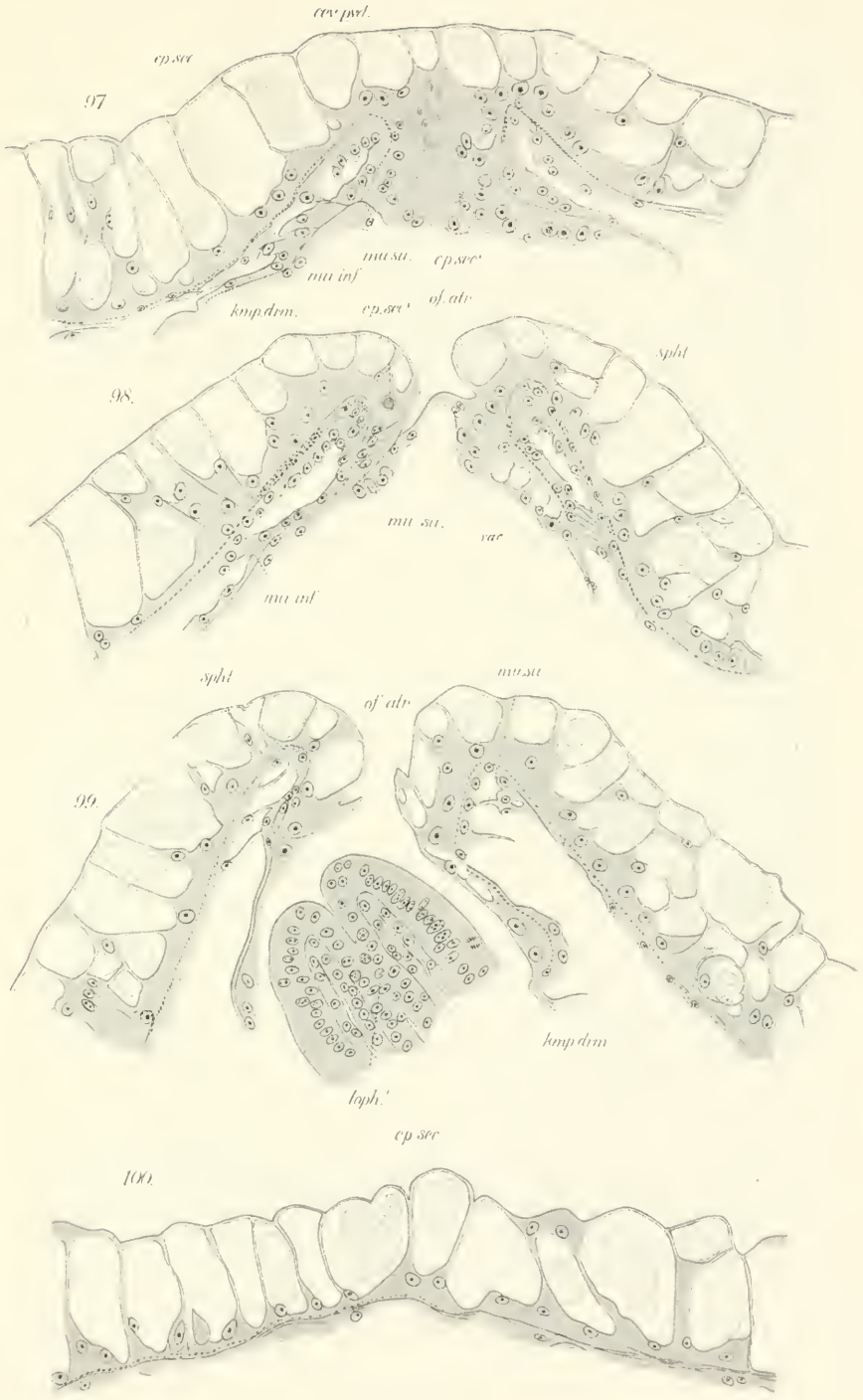

96

PLATE XI.

Figs. 97–99. Vertical sections, showing three successive stages in the degeneration of the roof to form the atrial opening, *of. atr.*, and development of the parieto-vaginal muscles. × 390.

" 100. Late stage in the development of the ectoderm, showing its extreme modification between adult polypides. × 390.


97
cvc.pvl.
ep.sec
mu.su.
ep.sec'
mu.inf
kmp.drm.
ep.sec'
of.atr
98.
spht
mu.su.
vac
mu.inf
99.
spht
of.atr
mu.su
kmp.drm
laph.'
ep.sec
100.

No. 5. — *The Eyes in Blind Crayfishes.* By G. H. Parker.[1]

In the fall of 1888 Mr. Samuel Garman placed at my disposal several crayfishes[2] which had been collected by Miss Ruth Hoppin in the caves of Jasper County, Missouri. The specimens were given to me with the suggestion that I should ascertain the extent to which their eyes had degenerated, for, judging from external appearances, these organs had become as rudimentary as the eyes of the blind crayfish, Cambarus pellucidus, Tellk., from Mammoth Cave. In order to establish comparisons it was desirable to study the eyes in C. pellucidus, and for this purpose specimens of this species were kindly furnished me from the collections in the Museum of Comparative Zoölogy. These specimens, as well as those collected by Miss Hoppin, were preserved in strong alcohol. My study of this material was carried on in the Zoölogical Laboratory of the Museum, under the direction of Dr. E. L. Mark.

Notwithstanding the general interest which zoölogists have shown in the blind crayfishes there have been very few publications on the minute structure of the eyes of these animals. The earliest contribution to this subject was from Newport, who, in discussing the ocelli of Anthophorabia, incidentally described the structure of the eye in Cambarus pellucidus. According to Newport's account ('55, p. 164), the eyes in this species would seem to be only *partially* degenerated, for although the retinal region is not pigmented, the corneal cuticula is nevertheless divided into irregular facets, or "corneales," as they are termed, "and the structure [hypodermis] behind these into chambers to which a small but distinct optic nerve is given."

The second investigator who studied the eyes of blind crayfishes was Leydig ('83, pp. 36 and 37). The material which was accessible to him was unfortunately so poorly preserved that it was of little value for histological purposes. He nevertheless satisfied himself that the cuticula in the corneal region was not facetted. He also quoted from an abstract

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XX.

[2] These crayfishes had previously been submitted to Dr. Walter Faxon for determination. They have since been described by him as a new species, under the name of Cambarus setosus, an account of which will be found in Mr. Garman's recent paper ('89, p. 237) on "Cave Animals from Southwestern Missouri."

of Newport's paper, to the effect that the eye is "ohne Hornhaut, Pigment und Nervenstäbe." The phrase "ohne Hornhaut" means, I believe, that a *facetted* cornea is not present; at least this seems to be the interpretation placed on it by Leydig, for the quotation is shortly followed by this sentence: "Dort wo man eine gefelderte Cornea zu suchen hätte — am Gipfel des Kegels — zeigt sich die Haut von der gewöhnlichen Beschaffenheit." There was greater reason for Leydig's regret that he could not consult Newport's original paper than Leydig himself appreciated; for, although he probably had no reason to consider the abstract incorrect, if his quotation from it is exact, it differs at least in one respect from Newport's account. Newport described the cornea as facetted; Leydig's quotation from the abstract states that it was not facetted. I have been unable to discover where this abstract was published, but, since Leydig quotes directly from it, the probabilities are that the discrepancy between his quotation and Newport's actual statement is to be attributed to an error in the abstract. Aside from this difficulty, it must be borne in mind that Leydig and Newport in their observations on the cornea by no means agree; for while Newport really describes the cornea as facetted, Leydig states from his own observations that it is without facets. According to Leydig, then, the eye of C. pellucidus is more completely degenerated than the observations of Newport would lead one to suppose.

The latest account of the eyes in blind crayfishes forms a part of Packard's paper on "The Cave Fauna of North America" ('88, pp. 110 to 113). Newport and Leydig studied C. pellucidus; Packard had the opportunity of studying not only this species, but also C. hamulatus, Cope and Packard, from Tennessee. In both species according to Packard the cornea was without facets, and the hypodermis was not thickened in the retinal region, but an optic nerve and ganglion were present. The results obtained by Packard thus confirm those given by Leydig.

From this brief historical review it will be observed that one of the principal questions concerning the eyes of blind crayfishes deals with the extent of their degeneration. This change has not only affected the finer structure of the retina, but it has also altered the shape of the optic stalk. I shall therefore begin with a description of the external form of the stalks.

The optic stalks of blind crayfishes are not only proportionally smaller than those of crayfishes which possess functional eyes, but they have in the two cases characteristically different shapes. In crayfishes with

fully developed eyes the stalk is terminated distally by a hemispherical enlargement; in the blind crayfishes it ends as a blunt cone. This cone-shaped outline is especially characteristic of C. pellucidus (Fig. 2). It will be observed that in this species the optic nerve (*n. opt.*) terminates in the hypodermis immediately below the blunt apex of the cone. In C. setosus (Fig. 1) the termination of the optic nerve is also at the apex of a blunt cone. In this case, however, the axis of the cone does not coincide with the axis of the stalk, as it does in C. pellucidus, but the two axes meet each other at an angle of about forty-five degrees, and in such directions that the conical protuberance at the distal end of the stalk is directed forward and outward from the median plane of the animal. The protuberance is rather more blunt in C. setosus than in C. pellucidus (compare the regions marked *r.* in Figs. 1 and 2).

Through the kindness of Dr. Walter Faxon I was enabled to examine two specimens of C. hamulatus. In this species the stalks also terminate in blunt cones. They are not so pointed as in C. pellucidus, but approach the more rounded form of C. setosus.

The three species, C. pellucidus, C. hamulatus, and C. setosus, are the only blind crayfishes thus far known in North America, and, as they agree in having a conical termination to the optic stalks, a peculiarity not observable in crayfishes with functional eyes, it may be concluded that the conical form is characteristic of the stalks in blind crayfishes. Unquestionably, this conical shape is coupled with the degenerate condition of the retina.

In describing the finer anatomy of the eye it will be more convenient to begin with the condition found in C. setosus. Figure 1 is drawn from a longitudinal horizontal section of the optic stalk in this species. The plane of section passes through the region where the optic nerve and hypodermis are in contact. This region (Fig. 1, *r.*) corresponds to the retina of other crayfishes. The optic stalk is covered with a cuticula (Fig. 1, *ct.*), which is of *uniform* thickness and which resembles the cuticula of the rest of the body. In this respect the stalk differs from that of decapods with well developed eyes, for in these, although much of the stalk is covered with ordinary cuticula, the retinal region is provided with a thin flexible cuticula. This has been named by Patten the corneal cuticula; it cannot be said to be differentiated in C. setosus. In optic stalks with functional retinas the corneal cuticula is usually facetted, but in C. setosus no indication of facets is discoverable.

The undifferentiated condition of the cuticula leads one to anticipate a simple condition in its matrix, the hypodermis. The latter is a

continuous layer of cells (Fig. 1, *hd.*) with its distal face applied to the cuticula and its proximal face bounded by a fine but distinct basement membrane (*mb.*). The layer is throughout very nearly uniform in thickness; at least it is not thicker in the region of the retina than at many other places, and the slight variations in its thickness are not in significant regions. The only feature of the retinal hypodermis which would suggest that it was unlike the rest is the somewhat closer crowding of its cells. This manifests itself in the arrangement of the nuclei in two or three irregular rows, instead of a single one. In other respects the nuclei of the retinal region and the surrounding hypodermis are essentially similar.

The optic nerve (Fig. 1, *n. opt.*) consists of a poorly defined bundle of nerve-fibres which extend from the optic ganglion to the hypodermis. The nerve-fibres are doubtless intimately connected with the cells in the hypodermis, for the basement membrane is interrupted where the nerve and hypodermis are in contact. It is probable that the basement membrane is reflected from the hypodermis to the optic nerve, although I have not been able to observe this with clearness.

Recent investigations support the conclusion that the retina in the crustacea is derived from the hypodermis. In C. setosus that portion of the hypodermis from which the retina would be derived is scarcely distinguishable from other parts of the same layer. The retina in this species, therefore, has so completely degenerated that it has at last returned to the condition of almost undifferentiated hypodermis.

That the optic nerve still retains its connection with the retinal area is, on the whole, not so significant a condition as one might at first suppose. It is probable that the optic nerve arises in this species as it does in the lobster. I have elsewhere (Parker, '90, p. 43) attempted to show that in the lobster it is not an outgrowth from either the optic ganglion or the retina, but that, as the ganglion was differentiated from the hypodermis, the optic nerve remained as a primitive connection between these two structures. So long, then, as an optic ganglion should be differentiated one might expect an accompanying optic nerve; but the nerve would be present as a passive connection between hypodermis and ganglion, rather than as a structure which had retained that position by virtue of its continued functional importance.

The foregoing account of the eye in C. setosus is based upon observations on three individuals of this species. Two of these measured, from the tip of the rostrum to the end of the telson, 6 cm.; the third, 4.2 cm. In the three individuals the eyes presented essentially the

same condition. Figure 1 is taken from one of the larger individuals. In this specimen the cuticula was somewhat thinner and the hypodermis rather thicker than in the other two. This I believe was due to the fact that the animal had recently moulted.

So far, then, as the eye of C. setosus is concerned, although the optic ganglion and optic nerve are present, the retina has undergone a complete degeneration, and is now represented by a layer of undifferentiated hypodermal cells.

The eyes of Cambarus pellucidus present a somewhat different condition from that described in C. setosus. A longitudinal horizontal section of the optic stalk of C. pellucidus is shown in Figure 2. The outer surface of the stalk is covered with a cuticula (*ct.*) of uniform thickness, and there is no indication of facets. Excepting at the apex of the stalk, the hypodermis (*hd.*) is composed of a remarkably uniform layer of cells. As in C. setosus, it is bounded on its deep face by a delicate basement membrane (*mb.*). Both an optic ganglion (*gn. opt.*) and nerve (*n. opt.*) are present, the latter being connected with the hypodermis. In all these respects C. pellucidus resembles C. setosus, but when the retinal part of the hypodermis in the two species is compared a striking difference can be seen. The retinal hypodermis in C. setosus (Fig. 1, *r.*) is, as we have seen, substantially like the remaining hypodermis of the optic stalk. The retinal hypodermis in C. pellucidus (Fig. 2, *r.*) is much thicker than the hypodermis of the stalk. With this thickened region of the hypodermis the optic nerve is connected, and there is no question, therefore, that this thickening represents the rudimentary retina. Omitting minor details, the form of the thickening is that of a plano-convex lens, the curved surface of which is applied to the concave inner face of the cuticula at the distal end of the stalk. The optic nerve is attached to the central part of the flat face of the thickening.

When the retinal thickening is carefully studied by means of radial sections, one can see that it differs from the neighboring hypodermis not only in thickness, but also in the fact that it contains two kinds of substance: a protoplasmic material uniform with that of the rest of the hypodermis, and a number of relatively large granular masses (Fig. 3, *con.*). These granular masses contain two, three, four, or sometimes five nuclei, and nuclei are also to be found scattered through the undifferentiated protoplasmic substance. The nuclei in the granular masses are slightly smaller than those in the surrounding portion of the hypo-

dermis; they are, moreover, round in outline, while the other nuclei are usually somewhat elongated. The same features can be observed in tangential sections (Fig. 6). Here, however, the outlines of the larger nuclei no longer appear oval, since these nuclei are now cut in a plane at right angles with their elongated axes. The nuclei in the hypodermis which adjoins the retinal thickening resemble the larger oval nuclei of the thickening. Nowhere in the adjoining hypodermis have the granular masses with their smaller nuclei been observed. It is therefore clear, that in C. pellucidus the retinal hypodermis is distinguished from the neighboring hypodermis, not only by its greater thickness, but also by the fact that it is composed of two kinds of substance, each with its special form of nucleus. Since the protoplasmic material of the retinal region contains nuclei which resemble those of the surrounding hypodermis, it is probable that this material represents hypodermis which has remained unmodified after the differentiation of the granular bodies. As shown in Figure 3, the granular bodies are for the most part limited to the deeper portion of the retinal thickening, and the oval nuclei occupy the more superficial part. If these oval nuclei represent undifferentiated hypodermal cells, it is only natural that they should occupy a superficial position, for it is there that the function of such cells, namely, the secretion of cuticula, could be most advantageously carried on. In tangential sections of the retinal thickening, both the nuclei of the undifferentiated hypodermis and the outlines of the cells to which they belong are distinguishable (Fig. 5). These cells when compared with those from the hypodermis of the sides of the stalk (Fig. 4) are seen to be much smaller than the latter. Like those from the sides of the stalk, however, they present no definite grouping. This accords with the fact that the cuticula presented no special markings, such as facets, etc., for such markings could of course result only from some special grouping of the secreting cells.

It is difficult to say what the granular bodies with their contained nuclei are. Doubtless they represent some element in the retina of the functional eye reduced by degeneration to this form. The ommatidium or structural unit in the retina of a crayfish consists of five kinds of cells. These are as follows: first, two cells in the corneal hypodermis, lying next the cuticula; second, four cone-cells directly below the corneal hypodermis; third, two pigment-cells, the distal retinulæ, flanking the cone-cells; fourth, seven pigment-cells, the proximal retinulæ, surrounding the rhabdome; fifth, a few yellowish accessory pigment-cells limited to the base of the retina. Excepting the accessory

pigment-cells, all the cells in an ommatidium are ectodermic in origin; the accessory pigment-cells are probably derived from the mesoderm. Of these five kinds of cells, the granular bodies probably do not represent the accessory pigment-cells, for in fully developed eyes the latter lie on both the distal and proximal sides of the basement membrane, whereas the granular bodies are found only on the distal side of that structure. The granular bodies, then, more likely represent one of the four remaining elements, all of which naturally occur only on the distal side of the membrane. It is not probable that the granular bodies represent the cells of the corneal hypodermis, for these produce the cuticula of the retinal region, and if they have any representatives, those representatives must be the distal layer of unmodified hypodermal cells already indicated in the retinal thickening. The position of the granular bodies, therefore, precludes their representing corneal hypodermis. If then the granular bodies are not accessory pigment-cells nor corneal hypodermis, they must be either distal or proximal retinulæ or cone-cells. In a previous paper I have given reasons for considering the proximal and distal retinulæ as both originating from a common group of cells, the retinulæ. These are essentially sensory in function, as contrasted with the cone-cells, which are merely dioptric. The question then narrows itself to this: Are the granular masses clusters of dioptric cone-cells or sensory retinulæ?

In determining to which of these two groups of cells the granular masses belong, the relation which the latter sustain to the fibres of the optic nerve would doubtless be of great importance, for the nerve fibres in fully developed eyes are known to terminate in the retinulæ, not in the cone-cells. Unfortunately, the histological condition of my material was such as to preclude the possibility of determining this question.

The fact that each granular mass contains several nuclei clearly indicates that it consists of several cells. The number of cells in each mass, judging from the number of nuclei, varies from one to about five, the more usual number being three or four. When one compares the condition of intimate fusion which the cells of each mass present with the normal condition of the retinulæ and cone-cells, the masses must certainly be admitted to resemble more closely the cone-cells. Moreover, the number of cells in each mass, although variable, is nearer to that of the closely united cone-cells than to that of the retinulæ. Not only do the number of cells involved and the intimacy of their fusion favor the idea that each mass represents a degenerate cone, but the

granular substance of the mass also closely resembles the granular material of a cone. For these reasons it seems probable that the granular nucleated masses in the retinal region of C. pellucidus are the degenerate representatives of the cones in normal eyes.

The fact that, of all the ectodermic elements of the retina, only the granular nucleated masses continue to be differentiated, throws them into strong contrast with the surrounding structures. The retention of these masses may mean that on account of their extreme differentiation they have had time to respond only incompletely to the influence of degeneration; or it may imply that phylogenetically they were among the earliest retinal structures differentiated. Admitting them to be degenerated cone-cells and merely dioptric in function, one can scarcely conceive how they could have been differentiated before the sensory cells which they serve. But even if they cannot be regarded as more primitive structures than retinulæ, their retention still may be significant, as an indication that the ommatidia of primitive crustaceans contained cone-cells as well as retinulæ.

Former studies have led me to believe that the difference in the ommatidia of various crustaceans could be explained on the assumption that the number of elements has been gradually increased from lower to higher forms by cell-division. The simplest conceivable representative of an ommatidium in the crustacea might then be a single cell. This would be of course a sensory cell; by its division, the more complicated ommatidia might subsequently be derived from it. In such an event, the cone-cells must be modified sensory cells; but the fact that these cells persist in so rudimentary a retina as that of C. pellucidus points rather to the conclusion, that they are probably almost as old, phylogenetically, as the retinulæ themselves, and that primitive ommatidia consisted of at least two kinds of cells, sensory cells or retinulæ, and cone-cells, derived not from degenerated sensory cells, but from the undifferentiated hypodermis.

As I have already shown, the results which Newport, Leydig, and Packard arrived at are not always in agreement. This might be explained by the fact that the organ under consideration is a degenerated one, and consequently subject to considerable individual variation. This supposition, however, is not supported by anything I have observed. The preceding account of the eye in C. pellucidus is based upon the examination of three individuals. These were respectively 6.5 cm., 5.6 cm., and 4.4 cm. long. Figure 2 was drawn from the optic stalk of the shortest individual. In all essential features the eyes of the two

other crayfishes presented the same condition as that shown in Figure 2. In the specimen 5.6 cm. in length, the granular bodies were less distinct than in the other two, but they were nevertheless recognizable, and the retinal thickening was as pronounced in this as in either of the other specimens. The fact that these three individuals show so little variation leads me to believe that the condition of the eye in the blind crayfish is not so variable as I at first supposed it would be. The same constancy is also true of C. setosus. Hence it seems to me improbable that the differences between Newport's observation and those of the later investigators are due to individual variations in the specimens studied. The fact that Newport's work was done before the development of present methods of research offers, I believe, a more natural explanation of some of his results, than the supposition of individual variations. That the methods of his time were imperfect is evident from the fact that Newport himself seems to have overlooked the ganglion of the optic stalk, a structure readily discoverable by means of serial sections. (Compare Newport's Figure 13 ['55, p. 102] with Figure 2 in this paper.) Leydig's observations, so far as they extend, are fully confirmed by my own. Packard's account differs from mine in only one particular, but that is of considerable importance; he states that there is *no retinal thickening* in the two species studied by him. This difference may possibly be due to individual variations in the crayfishes. Unfortunately, Packard does not state the number of specimens which he examined, and consequently one is uncertain how much weight to give to his general statements.

The conclusions to be drawn from the foregoing account may be summarized as follows. In both species of crayfishes studied, the optic ganglion and nerve are present, and the latter terminates in some way not discoverable in the hypodermis of the retinal region. In C. setosus this region is represented only by undifferentiated hypodermis, composed of somewhat crowded cells, while in C. pellucidus it has the form of a lenticular thickening of the hypodermis, in which there exist multinuclear granulated bodies. These I have endeavored to show are degenerated clusters of cone-cells. If Packard's observations are correct, the retina in C. pellucidus may be reduced in some individuals as much as it is in C. setosus, which I have studied, but my own examinations do not render this view probable.

Cambridge, February 24, 1890.

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EXPLANATION OF FIGURES.

ABBREVIATIONS.

con.	cone.	*mb.*	basement membrane.
ct.	cuticula.	*nl. con.*	nucleus of cone-cell.
gn. opt.	optic ganglion.	*nl. hd.*	nucleus of hypodermis.
hd.	hypodermis.	*n. opt.*	optic nerve.
		r.	retina.

The specimens from which the following figures were taken were killed and preserved in strong alcohol, and stained in Czocher's alum-cochineal. The crayfish from the optic stalk of which Figure 1 was drawn was 6 cm. long. That from which the remaining figures were made was 4.4 cm. long.

Fig. 1. A longitudinal horizontal section through the right optic stalk of Cambarus setosus, Faxon. The histological detail is given in the hypodermis only. The optic ganglion and the optic nerve are tinted. Between these structures and the hypodermis the space is filled with a loose connective tissue. × 65.

" 2. A longitudinal horizontal section through the right optic stalk of Cambarus pellucidus, Tellk. This drawing was made in the same manner as Figure 1. × 65.

" 3. An enlarged drawing from the distal end of the section which immediately follows that from which Figure 2 is taken. This figure shows the details in the retinal enlargement of the hypodermis. The space between this enlargement and the cuticula was artificially produced. × 275.

" 4. Tangential section of the hypodermis from the side of an optic stalk of Cambarus pellucidus. × 275.

" 5. Tangential section of the superficial portion of the retinal thickening in the eye of Cambarus pellucidus. × 275.

" 6. Tangential section of the deep portion in the retinal thickening of the eye of Cambarus pellucidus. This section is taken from the same series as the one from which Figure 5 was drawn. × 275.


1
n.opt.
gn.opt.
hd
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gn.opt.
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5
ct hd
mb.
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No. 6. — *Notice of Calamocrinus Diomedæ, a new Stalked Crinoid from the Galapagos, dredged by the U. S. Fish Commission Steamer "Albatross,"* Lieut.-Commander Z. L. Tanner, U. S. N., *commanding.* By Alexander Agassiz.

[Published by Permission of Marshall McDonald, U. S. Fish Commissioner.]

In 1887, Professor G. Brown Goode, Acting U. S. Fish Commissioner, was kind enough to invite me to join the "Albatross" at Panama, and to take part in the dredging operations to be carried on between that port and the Galapagos Islands.

I always hoped to have the opportunity of comparing, at some time, the deep-water fauna of the Pacific side of the Isthmus of Panama with that of the Caribbean, and to see how far the parallelism which has been traced between the littoral fauna of the two sides was carried out with the deep-water fauna. Unfortunately, I was unable to avail myself of this exceptional opportunity, although Colonel McDonald, the U. S. Fish Commissioner, detained the "Albatross" at Panama to allow me to join her at the last moment.

To have thoroughly dredged the line from Panama to the Galapagos would have been to collect material for the solution of many an interesting problem in the geographical distribution of marine animals, to say nothing of the rich harvest likely to have been gathered, when dredging in a district so prolific as that of the Bay of Panama, in shallower waters; and if the haul made at Station No. 2818, off Indefatigable Island, is at all a measure of what we may obtain in the way of novelties, the naturalist who is the first to run that line may be prepared for remarkable discoveries.

In addition to the Stalked Crinoids collected by the "Albatross," which the Fish Commissioner has kindly placed at my disposal for study, he has also intrusted to me the Echini collected by the "Albatross" on her voyage from the east coast of the United States to San Francisco. The route she followed was about the same as that taken by the "Hassler," and the material collected differed but little from the collection made by the latter vessel. The Echini were more nu-

merous; but with the exception of the young stages of a few species, and additional data regarding the geographical distribution of many species, there were no novelties brought to light. I shall take another occasion to publish a final report on the Echini.

The "Albatross" dredged on her voyage from New York to San Francisco, off Indefatigable Island, one of the Galapagos, at a depth of 392 fathoms, three imperfect specimens of a most interesting Stalked Crinoid. At the first glance, it might readily pass for a living representative of the fossil Apiocrinus; but on closer examination we found that it revealed some features which ally it with Millericrinus, and others with Hyocrinus and Rhizocrinus. It soon became apparent that we were dealing with a new type, combining structural features of all the genera above named. It has, like Hyocrinus and Rhizocrinus, only five arms; they are, however, not simple, but send off from the main stem of the arm three branches to one side and two to the other.

As in Hyocrinus, the first radials are high, the second radials much narrower than the first. The system of interradial plates is highly developed, as in Apiocrinus and Millericrinus, six rows of solid polygonal imperforate plates being closely joined together, and uniting the arms into a stiff calyx as far as the sixth or seventh radial, and to the third or fourth joints of the first and second pinnules. These two pinnules are on the fourth and fifth radials; the third pinnule is on the sixth radial; and they are all below the first axillary, which is the eighth radial, and which gives rise to the first branch from the main stem. The second and fifth, sixth, or seventh radials have syzygies.

The imperforated interradials are followed by smaller, somewhat thinner and perforated perisomatic plates, which extend to the prominent lateral plates of the food groove. The interradial calycinal plates extend along the arms for a considerable distance beyond the first branch.

The ventral surface extends nearly horizontally from the mouth to the level of the seventh radial, and this plane may be considered the greatest width of the cup, the interradial spaces arching very slightly toward the mouth, at the junction of the imperforate interradial plates with the perforated perisomatic plates.

The solid imperforate interradial plates extend over the prominent anal proboscis. The oral plates at the interradial angles of the food groove are small, but easily distinguished from the adjacent lateral and covering plates. They are separated from the so called calyx interradials by three or four rows of perforated perisomatic plates, except

on the anal interradii. The stem was somewhat curved at the upper extremity, the terminal joints expanding slightly to form a continuation of the outline of the cup of the base of the calyx. The stem tapered very gradually, and in its general appearance recalled that of Apiocrinus, expanding again towards the base, the root of which, however, was not obtained by the "Albatross." The stem is cylindrical, without cirri. In the upper third the joints are alternately ribbed transversely, or even ornamented near the base of the calyx with more or less prominent tubercles, as in Millericrinus. The uppermost joint is convex, and in the space left vacant between it and the central part of the basal ring a small lobed delicately reticulated pentagonal disk was found resting upon the upper face of the "article basal" of De Loriol. This is probably a modified anchylosed infrabasal ring, which may or may not be resorbed in older stages of the genus.

There are five distinct basals in one of the specimens; in the second their sutures can fairly be distinguished, while in the third they were completely anchylosed, much as they so frequently are in Rhizocrinus. As in Hyocrinus, the basals are about half the height of the first radials; the second radials cut deeply into the first radials.

The stem of this crinoid must have attained a length of from 26 to 27 inches; the height of the calyx to the interradials is $\frac{7}{16}$ of an inch; its diameter at the inner base of the second radials is $\frac{1}{16}$ of an inch, at the height of the third joint of the second pinnule 1 inch, at the level of the proximal face of the radials $\frac{3}{8}$ of an inch, and at the level of the suture of the basals with the uppermost joint $\frac{1}{4}$ of an inch; and the length of the arms is probably about 8 inches.

I propose to name this crinoid Calamocrinus Diomedæ, after the vessel which discovered it. I have to thank Colonel Marshall McDonald, the U. S. Fish Commissioner, for the opportunity of studying this crinoid. With his consent, a detailed account of Calamocrinus will be published in the Museum Memoirs as soon as the plates can be prepared.

Cambridge, November 28, 1890.

No. 7. — *The Origin and Development of the Central Nervous System in Limax maximus.* By Annie P. Henchman.[1]

For several years the origin of the central nervous system in Mollusks, both as to method and time of appearance, has been a matter of controversy. It has been of especial importance to determine from which of the embryonic layers its parts arise, and to ascertain if its development throws any light on the relations of Mollusks to other important groups of the animal kingdom, particularly Worms.

Since the observations of the earlier writers, down to about 1874, were carried on without the aid of sections, their conclusions do not merit that degree of confidence which is to be accorded those who have availed themselves of this means of study.

Most of the later authors agree that the central nervous system arises from the ectoderm, either by an invagination, or by a simple local thickening which later becomes detached. However, Bobretzky ('76, pp. 162–169), — the first to use sections, — while conceding that in Fusus there are invaginations of the ectoderm to form the sense organs, concludes that the supra-œsophageal and pedal ganglia arise from the mesoderm, and Bütschli ('77, pp. 227, 228) is inclined to believe that the same is true in Paludina vivipara.

Von Jhering ('74, p. 321) claims for Helix, and both Lankester ('74, pp. 382, 383) and Wolfson ('80, pp. 95, 96) for Lymnæus stagnalis, that the central nervous system arises simply from a thickening of the ectoderm.

Fol ('80, p. 664) has since pointed out, however, that Lankester's conclusions are based on an erroneous interpretation of cells ("nuchal cells"), which he believes are not at all nervous in their nature. They are the same cells which Wolfson has called the embryonic brain; but Wolfson's opinion, previously stated, has reference to the definite nervous system, not to this so-called embryonic brain.

Haddon ('82, pp. 368–370) believes that he has seen the rudiments of the cerebral and pedal ganglia of Nudibranchs in the form of thicken-

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXI.

ings of the ectoderm, and he has made sections of Purpura lapillus and Murex erinaceus which show, as he maintains, that similar rudiments are also formed in them by proliferation from thickenings of the ectoderm.

Kowalesky ('83, pp. 23–26) shows for Chiton Polii that the lateral and pedal nerve trunks are formed simply as thickenings of the ectoderm.

Rabl ('75, pp. 206–208) maintained that the supra-œsophageal ganglia and the sense organs in Lymnæus, Physa, Ancylus, and Planorbis were formed by an invagination of the ectoderm, and that the pedal ganglia were produced by delamination from the same germinal layer. He has more recently ('83, pp. 57, 58) expressed doubt as to the manner in which the pedal ganglia arise in Bythinia tentaculata, because he has seen them so connected to the ectoderm of the dorsal wall of the foot by means of cells as to indicate that they arise by proliferation from that region.

Sarasin ('82, pp. 45–48), who has also recently studied Bythinia tentaculata, and who is the only author that has hitherto followed the development of the entire nervous system in a Gastropod, contends that the whole of it arises from ectodermic thickenings, without any invagination even for the supra-œsophageal ganglia. He also believes that the pedal ganglia arise from the dorsal wall of the foot.

Fol ('80, pp. 165–169) admits no invagination for the central nervous system in aquatic pulmonates, and he even inclines to the opinion that it may be derived from the mesoderm, which, however, has itself originated from the ectoderm. He considers it an unimportant question, and therefore one which it is useless to discuss, whether the nervous system arises from ectoderm or mesoderm. If the mesoderm were derived from the entoderm, then it would be an important question. He believes that the supra-œsophageal ganglia of land pulmonates (pp. 192–195) originate by invaginations of the ectoderm, while the pedal ganglia arise from the mesoderm of the foot.

The latest investigations are those of Salensky ('86, pp. 655–759) on the development of Vermetus, one of the Prosobranchs. He concludes that the cerebral ganglia are formed by two invaginations of the ectoderm, while the pedal ganglia arise by proliferation from the ventral and lateral walls of the foot on each side of the median depression which runs along its ventral face. These ganglia arise separately, and later become connected with each other by a commissure, and with the cerebral ganglia by connectives, both of which are outgrowths from the ganglia (pp. 694, 695).

Thus we find that, of the authors cited, Bobretzky, Bütschli, and — as far at least as regards the aquatic pulmonates — Fol consider the central nervous system as originating from the mesoderm. Rabl is a little doubtful as to its mesodermic origin in Bythinia. Rabl, Fol, and Salensky are the only investigators who consider any portion of the central nervous system as arising by invagination, and then only in certain Gastropods.[1]

The following observations were made upon embryos of Limax maximus obtained from adults kept in captivity. Under favorable circumstances, they lay abundantly during the latter part of September, and through October and November. After numerous trials, the best method found was to keep about twenty-five or thirty in a large tin pail, the cover being perforated with small holes. Instead of using moss to secure the necessary moisture, the slugs were fed upon lettuce or cabbage; the latter is the better of the two. This food affords at the same time sufficient protection against desiccation, a suitable retreat for the slugs, and a place where they may lay the eggs. It should be changed every other day, — every day if the weather is warm, — and the pail should be washed thoroughly each time. One of the advantages of using a tin vessel is the ease with which it may be kept clean. Cabbage will keep longer than lettuce, and the slugs lay more abundantly when fed upon it. The eggs were generally found in the morning, sometimes at night, in bunches of from thirty to forty. They are more abundant at first than after the slugs have been kept some time in confinement; it is therefore better to obtain at intervals fresh supplies of small numbers of slugs than to procure a larger number at one time. As soon as found, the eggs were removed to a watch-glass containing water; this was placed in a tumbler already about half filled with moss or moistened paper, having a perforated tin cover. The eggs must not be allowed to become dry. For a few days they should be carefully examined under a microscope, every twenty-four hours or oftener, and all those which fail to develop should be removed at once. In the course of a few days these can be readily detected with the naked eye by reason of the greater opacity of the eggs, and the presence of a whitish spot in them due to the disintegration of the embryo.

[1] The brothers Sarasin, in later researches in Ceylon ('87, pp. 59–69) on a species of very large Helix, find that there are *two* invaginations of the ectoderm on each side of the head to form the cerebral ganglia, and Kowalesky ('83[a]) had found several years before that there were in Dentalium two deep invaginations, *one* on each side.

A very large per cent of eggs kept in this way remain in good condition until hatching, which, in a moderately warm room, occurs between the twenty-second and twenty-seventh day.

The best reagents for killing embryos were found to be either chromic acid, 0.33%, or Perenyi's fluid. The chromic material when well stained with alcoholic borax-carmine shows the differentiation of nerve cells and nuclei excellently, but it is more difficult to stain sufficiently chromic material than such as has been preserved in Perenyi's fluid. The latter may be stained with alcoholic borax-carmine or picrocarminate of lithium. Good results for the study of cell division have also been obtained by staining with Czoker's cochineal. The picrocarminate of lithium is particularly valuable in the older stages, because it brings out the nerve fibres, the latter being stained yellow, while the ganglionic cells are colored red.

To obtain the embryos in an uninjured condition, it is advisable, in using the chromic-acid method, to remove only the outer envelope *before* killing. The egg may be held between the thumb and forefinger of the left hand, while with a finely pointed stick, somewhat like a wooden toothpick, the outer membrane is gently punctured; the probe should be run under the membrane a little way, to make a larger opening, and the egg carefully pressed with the thumb and forefinger, whereupon the albumen, containing the embryo and surrounded by the inner membrane, will come out in a perfect condition. This may be dropped at once into water, if several are to be treated together, for it is more convenient to put them all into the chromic acid at the same time. When all have been shelled, they should be put into 0.33% chromic acid for two or three minutes only, simply to kill the embryo without hardening the albumen. Then they should be transferred to a watch-glass of water, to which a few drops of the acid have been added. While in this fluid, the inner membrane may be removed with needles. To accomplish this, it is advisable, in the very young stages, to make as large an opening in the membrane as possible; and then with a needle gently to press the embryo out, even if the albumen adheres to it, for the albumen becomes slightly coagulated in the weak acid, and then can easily be washed off. In the stages from the tenth to the sixteenth day, the large size of the pulsating sacs of both head and foot regions makes it extremely difficult to extract the embryos uninjured; great care must therefore be taken, and *no pressure* used. While employing one of the needles to hold the membrane, the other should be forced through the membrane, which may then be ruptured and turned back

over the embryo, being drawn off like the finger of a glove. In the older stages, not much care is necessary, because the embryos bear without injury considerable handling, and there is so little albumen left that their position is not readily changed while the membranes are being removed. When freed from the membranes and as much of the albumen as possible, the embryos are to be returned with a large-mouthed pipette to the chromic acid (0.33%), where they may be left for an hour or two; after washing in running water for two or three hours, they may be carried up to 70% alcohol by adding to the water, drop by drop, 35% alcohol; then 50% alcohol, etc. This dehydration must be made very carefully, to avoid shrinkage. The embryos are extremely delicate, and must be handled with great care through every step of the process.

In using Perenyi's mixture, it is best to free the embryos *while living* from the surrounding membranes and the albumen, removing the inner membrane under clear water. When set free, they should be transferred at once with a pipette into a dish of Perenyi's mixture, where they may remain from *two to three minutes*. They are then to be washed thoroughly in distilled water at least five minutes, put into a 5% aq. sol. of alum for thirty minutes, washed again in water, and finally carried through the grades of alcohol as in the chromic method. It is necessary to remove the embryo while living, because otherwise the albumen becomes in this reagent like a jelly, and cannot be removed without injury to the embryo. Material designed to be sectioned must not be left in alcohol longer than a month, since the albumen in the nutritive sac gradually becomes too hard to be cut, especially if prepared in Perenyi's mixture. The stages from the tenth to the sixteenth day can still be used, even if they have been thus overhardened, by removing the nutritive sac; but in the younger stages this is apt to destroy the embryo, and in the older ones — much of the albumen having been swallowed — its removal is still more certain to have the same effect. Attempts subsequently to soften the albumen by prolonged treatment with weak acetic acid proved to be only partially successful. If the embryos are to be kept at all, they should be left unstained; but the safest way is to carry them through to embedding as soon as possible.

They can be stained whole; but to do this successfully, they must be carried gradually through successively weaker grades of alcohol until a grade corresponding to the stain is reached. It is advisable to make the necessary steps from the stain to the parafine as quickly as possible.

Staining with picrocarminate of lithium has the advantage of saving time, since it acts rapidly,—the older specimens requiring only one or two hours, the younger from half an hour to an hour. A few grains of picric acid may be added to the dehydrating alcohols which follow the stain, in order to prevent the total extraction of the picric acid, and the consequent disappearance of the yellow color from the nerve fibres. If the object is too deeply stained, the differentiation of nerve tissue does not show well; the nerve fibres ought to be yellow, the surrounding nuclei pinkish red with a yellow tinge, and all the other tissue pinkish red. As this and Czoker's cochineal are both aqueous dyes, the chromic material is apt to macerate in them; neither does it stain so well in them as in alcoholic borax-carmine.

The chloroform method of embedding in parafine was used exclusively. When the embryo has been transferred by the well known method to a vial containing chloroform, the vial should be placed uncorked on the water-bath at 55° to 60° C. Pendent spoons in the large cups are not very serviceable, as the least jar sends the objects off, and it is almost impossible to recover them from the bottom of the cup without injury. It is better to have ready on the bath an empty warm glass dish, — a common salt-cellar is very good; also one filled with parafine which melts at about 52° C. The embryos are to be left in the chloroform only as long a time as is necessary for them to sink, and are then to be transferred with the chloroform to the empty glass dish. The transfer is best made by means of a warm pipette, if the embryos are small. Cold soft parafine is then added, a small piece at a time, until the chloroform has so thoroughly evaporated as to leave no trace of its odor. After remaining for fifteen minutes in the soft parafine, the embryo is to be transferred to the "harder" parafine (52° C.), where it should remain from fifteen to thirty minutes. It is important to handle the object with great care, and to carry it through the period of heating as quickly as may be; the latter is necessary, because the embryos are very apt to become brittle if subjected to the heat too long. They should be embedded within an hour or an hour and a half from the time they are first put upon the bath in the chloroform. It is especially dangerous to allow the parafine to harden about the embryo before the latter is finally embedded, because upon the remelting of the parafine the object is almost certain to fall into fragments, owing to its great delicacy.

The embedding, especially for the younger stages, must be done under a lens. It is most convenient to use a dissecting microscope, the

stage of which should be kept warm. I have found that parafine which melts between 50° and 52° C. is better for embedding than that which is harder, for the latter is liable in hardening to cause the embryo to crack.

Sections from 10 to 15 μ thick, and in the oldest stages even thicker, are better than very thin ones.

The central nervous system of Limax consists of four pairs of ganglia, — namely, cerebral, pedal, pleural, and visceral, — together with one abdominal ganglion. To these more central ganglia are joined in addition a pair of buccal ganglia, and one mantle or olfactory ganglion.

To summarize briefly in advance my conclusions: The ganglia arise separately. The components of three of the five pairs are joined together later by commissures. Secondarily-produced connectives[1] also serve to join the cerebral ganglia to the pedal, the pleural, and the buccal; the pleural to the pedal and the visceral; and the visceral to the abdominal. The growth of the ganglia is rapid; they are well formed, and in their ultimate positions by the sixteenth day. The principal changes from that time until hatching, eight or nine days later, are increase in size, and modifications of the histological conditions. According to my observations, all the ganglia, with the possible exception of the pleural, are derived directly from the ectoderm, — the cerebral in part from invaginations, the others exclusively by cell proliferation without invagination. The cerebral ganglia are formed by extensive invaginations, one on each side of the head region, just below and behind the base of the ocular tentacles. During the invagination a rapid cell proliferation takes place at the deep end of the invaginated portion of the ectoderm, and also at a region of the ectoderm corresponding to the depression between the labial tentacles and the upper lips. The lateral halves of the cerebral mass arise as two separate structures, — each from a double origin, — which are only secondarily joined. This union is the result of outgrowths from each of the ganglia which, uniting, form the cerebral commissure. The invaginations begin a little later than the proliferation of cells which gives rise to the pedal ganglia, and they remain open as narrow tubes until towards the period of hatching, or even later. In one instance they have been found in this condition as late as eight days after hatching. The cerebral com-

[1] In accordance with the usage introduced by Lacaze-Duthiers, the term *commissure* is employed for the nerve fibres joining the components of a pair of ganglia, and *connective* for those between ganglia on the same side of the body.

missure is formed a little earlier than the commissural fibres joining the pedal ganglia. The latter are connected by *two* distinct commissures, the anterior of which is formed earlier than the posterior. The visceral ganglia precede a little in their development the pleural, abdominal, buccal, and mantle ganglia. The buccal ganglia make their appearance at about the same time as the pleural, and undergo almost no change in position.

The nervous system in Limax maximus makes its appearance on the *sixth or seventh day* after the egg is laid. At this time the foot is a conical projection, less than half as long as the diameter of the more or less spherical remaining portion of the embryo, and its pulsating sac is very small. It is a stage which is only slightly older than that represented by Fol in his Planche 17–18, Fig. 7. The ocular tentacles are now distinguishable as small elevations of the head region, near the beginning of the primitive nephridial organs, but the labial tentacles are barely to be made out. The radula sac is a nearly spherical outfolding of the floor of the oral sinus; its fundus is composed of only a single layer of cells, but the part of the sac which is continuous with the wall of the œsophagus is more than a single cell deep; the lumen of the œsophagus is traceable close up to the yolk, where it ends blindly. Both the œsophagus and the radula sac are covered with a continuous layer of somewhat flattened mesodermic cells. The shell gland has the form of a large thin-walled sac containing concretions.

When this condition has been reached, the head region (Plate I. Fig. 2) exhibits no sign of cerebral invaginations, nor have I been able to find regions of cell proliferation or thickenings in the ectoderm which were referable with certainty to the cerebral ganglia.

So far as I have been able to make out, the first contribution to the formation of the pedal ganglia occurs in the form of small clusters of cells, which are still imbedded in the ectoderm of the ventral wall of the foot (Plate I. Fig. 5), from which they are subsequently detached. Each of these clusters has a spheroidal or more ridge-like form, and contains from four to eight cells. The boundaries of the cells are not sharply marked, but the whole cluster is limited by a definite outline separating it from the rest of the ectoderm. Each cell contains a nucleus, which is large, but less deeply stained than those of the ectoderm, and each nucleus has a large nucleolus, which is very deeply stained (Plate I. Fig. 1).

The region in which this proliferation takes place is definitely located,

for it lies in the same transverse plane in which the otocysts (Plate I. Figs. 3, 4) are situated, and it is found at a region in that plane intermediate between the lateral border of the foot and its middle line, but considerably nearer the former. The proliferating cells project into the cavity of the foot, and ultimately are separated from the ectoderm.

Although cells which closely resemble these are found in groups in other parts of the body wall, their nuclei do not become as large as those of the cells destined to form the ganglia. Moreover, the proliferations are constant and most abundant in the regions where the different ganglia of the nervous system take their origin. Besides, in these cases there is generally a sinking in of the surface of the ectoderm in the same region.

Somewhat later than at the stage described, usually on the *seventh day*, the external conditions still remain nearly the same, the ocular tentacles being perhaps a little more prominent, and the concretions in the shell gland more numerous.

The cells of the primitive entoderm, which surround the yolk, form a striking feature of the condition at this stage. These entoderm cells are very large, vacuolated, and only slightly stainable. They contain large ovoid nuclei, which are crowded to one margin of the cells by the nutritive contents accumulated in the cells. Each nucleus contains one large deeply stained nucleolus, and a network of chromatic substance (Plate I. Fig. 2). The ectoderm, except over the nutritive sac, consists of elongated cells, whose nuclei are so arranged as to give the appearance of two or more layers. The ganglionic cells at this time closely resemble the mesodermic cells, and this makes it difficult to distinguish between the two (Plate I. Fig. 7).

The internal ends of the primitive nephridial organs are situated one on each side of the head, immediately above and back of the ocular tentacles. These organs pass at first forwards and upwards, then in an arch backwards over the nutritive sac, and finally downward and forward. Their external openings are far back in the lateral walls of the body, behind the head region. The organs are readily distinguished in sections by their large slightly stained cells, which are arranged in a single layer around an oval lumen. The large nuclei contain each a single deeply stained nucleolus (Plate I. Figs. 2 and 6). The primitive entoderm and the nephridial organs retain this histological condition throughout the embryonic stages.

The cerebral invaginations at first appear as shallow depressions in

the ectoderm at the base of the ocular tentacles, at a point immediately below the nephridial organs. At the same time that the infolding takes place, cells, whose nuclei are larger than those of the mesodermic cells, are being proliferated from the deep surface of the invaginating portion of the ectoderm (Plate I. Fig. 6).

In the region of the ventral wall of the foot referred to in the stage previously described, there are in the ectoderm of each side of the body two groups of ganglionic cells (*prf. pd.*, Plate I. Fig. 7), one behind the other. These cells project into the cavity of the foot, and reach nearly to another small group of cells situated not far from the ventral wall. The cells of the latter group (there is one group on each side of the body) have nuclei similar to those of the cells still connected with the ectoderm. Each group lies in the position subsequently occupied by the pedal ganglion of its side of the body, and is undoubtedly the beginning of that ganglion, for the cells in the ventral wall of the foot continue to be proliferated during several days, and are found in some individuals to be in direct continuity with the ganglia after the latter have attained considerable size. In the individuals shown in Figures 7 and 9 (Plate I.), the right otocyst (Fig. 7) is seen as a closed vesicle, which is not yet wholly detached from the ectoderm. The otocysts undoubtedly vary in regard to the time of their detachment, as will be seen by a glance at the left otocyst of the same individual, which has entirely lost its connection with the ectoderm (Fig. 9).

All the other ganglia, with the exception of the one near the olfactory organ and the buccal ganglia, arise by cell proliferation from ectoderm which lies between the foot and the head region, either at or a little above the posterior angle formed by the body wall with the dorsal surface of the foot, or along a depression which runs forward from this point. This angle marks the posterior limit of a furrow which passes obliquely forward and downward, partially separating the head and visceral mass from the foot. This depression will be designated as the *pleural groove*. Of the remaining ganglia, only the visceral have begun to be formed at this time. The cells destined to form these ganglia are situated immediately above the angle produced by the pleural groove (Plate I. Figs. 8 and 9). Some of those of the left ganglion are wholly detached from the ectoderm, but those of the right (Fig. 7) are still continuous with the ectoderm, though projecting into the body cavity. The cells have large, round, faintly stainable nuclei, each containing one large nucleolus, which takes a deep stain.

Twenty-four hours later, about the *eighth day*, the pulsating sac of the foot has become still larger, and the oral sinus has extended backward and downward as a very narrow tubular passage, — the œsophagus, — which follows the surface of the nutritive sac for some distance, and subsequently opens into it. The peculiar ciliated cells of great size and spongy appearance, which occupy a linear tract along the middle of the roof of the mouth and œsophagus, are at this time very prominent (Plate I. Fig. 2, *loph. cil.*). These cells form what Fol ('80, pp. 190, 191) has called the "ciliated ridge." They persist until after the completion of the nervous system. The ingrowth of the ectoderm to form the rectum is now composed of a compact group of small cells, which shows a small lumen in its central portion, but is still closed at both ends.

The cerebral ganglia remain in nearly the same condition as that last described. About twelve hours later, between the eighth and ninth days,

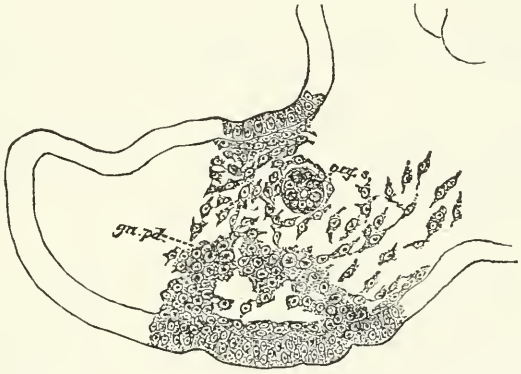

FIGURE A. — The right face of a section parallel to the sagittal plane from an embryo of the *ninth day* × 220.

gn. pd. Pedal ganglion *o cy. s.* Left otocyst.

the two cerebral invaginations have become deeper, and the two groups of cells which form the main portions of the corresponding ganglia contain a greater number of cells. (Plate II. Fig. 15.)

The pedal ganglia are also now composed of many more cells than in the previous stage. Each ganglion is usually pear-shaped, and tapers towards the posterior end of the foot. They both continue to receive accessions from the ectoderm (Figure A), and at the same time are rapidly increasing in size by division of the cells already in position. The nuclei are larger and more easily distinguished than in the previous stage from those of the mesodermic cells, the latter being more spindle-shaped than

before. The cells of the mesoderm form a continuous layer along the inner surface of the ectoderm, except where cell proliferation is taking place (Figure A).

As yet nothing is to be seen of the pleural ganglia.

The visceral ganglia have increased in size (Plate I. Figs. 10, 11, 12); they are still connected with the ectoderm (Figs. 10, 12), although a few cells with large nuclei have become detached from it (Fig. 11). The ganglion and the otocyst of the same side of the body lie in nearly the same sagittal plane. Each ganglion is situated just above the angle caused by the pleural groove. The right visceral ganglion (Fig. 10) is somewhat farther forward and more dorsal than the left (Figs. 11, 12).

About in the median plane of the body, and above the angle made by the pleural groove, are the cells which form the abdominal ganglion (Plate I. Fig. 13). The greater part of them are still embedded in the ectoderm. Although in some regions they project into the body cavity, they are nowhere wholly separated from the ectoderm. The abdominal ganglion seems to be at first more intimately connected with the left visceral ganglion than with the right, but a connective is formed with both of them a little later, and the abdominal ganglion thus appears to occupy the place of a direct commissure between the two visceral ganglia. As development proceeds, the abdominal ganglion becomes closely fused with both the visceral ganglia.

Quite an advance in external conditions is made by the *ninth day.* But individuals of the same age vary so much in the degree of development attained by both their external and internal organs, that the age assigned can be taken only as an approximation to the average condition at the time indicated.

The tentacles appear as protuberances, the labial tentacles being much smaller than the ocular; the shell gland contains more concretions, the mantle is larger and bends backward over the dorsal surface of the foot. The radula sac makes its appearance and extends backward into the foot, where it ends blindly immediately back of the pedal ganglia. In transverse sections it appears flattened dorso-ventrally; its lumen is oval, and the ectoderm lining it is more than one cell deep.

The cerebral invaginations (Plate II. Figs. 15, 19, Plate III. Figs. 25, 26) are much deeper, the infolding ectoderm is greatly thickened, and the incipient ganglia receive accessions from ectodermic depressions between the rudiments of the upper lips and the labial tentacles (Plate II. Fig. 21). The cerebral commissure (Fig. 21) is also being formed, the

cells of the median portion of each ganglion growing out to meet the corresponding cells from the opposite ganglion. The commissure at this stage is composed of a small number of cells, which are very much elongated. The fibres resulting from their elongation already make a continuous bridge from one ganglion to the other.

The pedal ganglia (Plate II. Fig. 20, Plate III. Fig. 27, Plate V. Fig. 60) consist of two small groups of cells, situated about midway between the sole of the foot and the posterior end of the radula sac. They are a little below and behind the pleural groove and the otocysts, and they are farther from each other than from the lateral wall of the foot. There is a slight indication of a commissure (Plate III. Fig. 27) joining their anterior portions to each other. The commissure is formed in the same manner as the cerebral commissure, the individual cells composing it being spindle-shaped, with their nuclei somewhat elongated in the direction of the fibres.

The otocysts (Plate II. Fig. 20, Plate III. Fig. 27, Plate V. Fig. 60) are on a level with the lower margin of the radula sac, and are nearer the pedal ganglia than in the preceding stage.

On each side of the body above the pleural groove is a group of a few cells, which are in all probability the first indications of the pleural ganglia (Plate II. Figs. 14 and 20). The centre of each cluster is seen on cross sections (Fig. 20) to be nearly on a level with the lumen of the radula sac. The cells at this stage are very small, and so loosely associated that it is difficult to distinguish them from mesodermic cells. I have not satisfactory evidence of their origin directly from the ectoderm, for, although I have found them at times very near to the ectoderm (Fig. 20), I have never found them at any stage continuous with it. On the other hand, I have not seen conditions which would warrant the conclusion that the ganglia were the result of outgrowths from either of the pre-existing ganglia.

A little before the ninth day the cells detached from the ectoderm to form the visceral ganglia (Plate II. Figs. 17, 18) increase rapidly in size, and the diameter of their nuclei often becomes four or five times as great as that of the ectodermic nuclei. The ganglia consist of elongated groups of such cells, still attached to the ectoderm above the pleural groove (Figs. 16, 18). The want of symmetry in the positions of the right and left ganglia is more conspicuous than in the preceding stage, the ganglion of the right side being considerably more dorsal and farther back than that of the left side (Plate II. Fig. 23, Plate V. Fig. 60). Owing to the infolding of the ectoderm on the right side of the body to

form the respiratory chamber (Plate II. Figs. 16, 24), the region from which the ganglionic cells arise is now located on the ventral and median walls of the infolding. The ganglia have also grown forward, and lie between the nephridial organs and the nutritive sac (Plate II. Fig. 23). In an individual cut crosswise, the posterior portion of the ganglia is found to be two or three sections back of the otocysts. Both the ganglia may be traced through five or six sections.

A little behind the visceral ganglia, and to the left of the median plane of the body, are the prominent cells of the abdominal ganglion (Plate II. Figs. 24, *ab.*).

All of these ganglia still consist of groups of loosely associated cells. Later they become more compact, and are surrounded by connective-tissue cells.

The buccal ganglia (Plate II. Fig. 22), first seen with certainty at this stage, arise, one on each side of the radula sac, at the angle between it and the œsophagus. It is to be seen from cross sections that the cell proliferations from which they spring take place from the dorsal wall of the neck of the sac, where its lumen begins to be separated from that of the œsophagus. This is also their permanent position; they are later joined together by a commissure, which results from outgrowths of the cells composing the two ganglia.

On the *tenth day* the external appearance of the embryo remains nearly the same as before, with the exception that there is an increase in the size of the embryo, and especially of its pulsating sacs. The sac of the radula has become more elongated, and the anal opening (Plate III. Fig. 31, *an.*) is formed.

The cerebral invaginations still appear, in sections parallel to the sagittal plane (Plate III. Figs. 28 and 29), as shallow depressions. The number of cells in each ganglionic group (Plate IV. Fig. 58, Plate V. Fig. 63) has increased perceptibly. At the same time the groups have extended backward, and show indications of the cerebro-pleural connectives. In specimens cut in the sagittal plane, the cerebral commissure cut crosswise may be seen above the oral opening (Plate III. Fig. 30).

The pedal ganglia (Plate IV. Figs. 54, 58, Plate V. Fig. 63) have increased in size. Their anterior borders now reach as far forward as the plane of the pleural groove, and they extend backward into the foot much farther than before. In cross sections (Plate IV. Fig. 54) they appear as rounded groups of cells, which are far apart and not yet very compact; they still continue to receive accessions by the proliferation of

ectodermic cells from the walls of the foot (Plate IV. Fig. 57, 58, *prf.*). The first decided evidence of a pedal commissure makes its appearance during this stage. It consists (Fig. 54) of a few very much elongated nerve cells, which stretch across from one ganglion to the other a little posterior to the region of the otocysts. The commissure may be traced on about half a dozen successive sections, or for a distance of some 50 or 60 μ. From its position it evidently is the beginning of the *anterior* commissure. The thickness (10 μ) of a single section contains only three or four cells, the nuclei of which have the chromatic substance so concentrated into a single nucleolus as to make the nuclei appear clearer than those of the surrounding connective-tissue cells. There is at present no trace of a posterior commissure. The otocysts are now nearer the ganglia (Plate IV. Fig. 58, Plate V. Fig. 63) than at any previous stage.

The pleural ganglia (Plate V. Fig. 63) are still inconspicuous, being composed of only a few scattered cells, which lie nearly dorsal to the otocysts, about midway between the visceral and the cerebral ganglia of the same side of the body. Many of the cells are elongated in the direction of the ganglia between which they are located, and appear to form the beginning of a connective between them.

The visceral ganglia (Plate IV. Figs. 58 and 59, *vsc.*) are still connected with the ectoderm, but project more prominently from the wall of the body, and extend forward more than before. The right (Plate IV. Fig. 59) is larger, and still lies more dorsal, than the left (Plate V. Fig. 63). The cells which compose the ganglia are numerous and large, and the nuclei of those which form the centre of the ganglion are conspicuously larger than those at the periphery. In cross sections of a stage possibly a little less developed than the one last described, the ganglia (Plate IV. Figs. 53, 56, 57, 55) lie, one on each side of the body, immediately above the pleural groove, a little below and inside the external orifices of the primitive nephridial organs. On the right side of the body the ectoderm which constitutes the anterior wall of the infolding to form the mantle chamber is seen in sagittal sections (Plate IV. Fig. 58) to be much thicker in the region adjoining the pleural groove than in that which forms the deeper portion of the infolding. The transition from the thick to the thin ectoderm is very abrupt, and is marked by a pocket-like depression. The right visceral ganglion is situated at the side and in front of this depression. Some of the cells in the anterior portion of this ganglion (Plate IV. Fig. 56) are traceable toward the median plane of the body. The left visceral ganglion

(Figs. 56, 57) is not yet as large as the right, and it consists of fewer cells.

The position of the connective between the visceral and pleural ganglia (Plate V. Fig. 63) is indicated by the presence of spindle-shaped cells with fibrous projections. The connective is at this time long, and the cells and fibres composing it are only joined to one another loosely.

As the abdominal ganglion increases in size, it extends more toward the right side of the body (Plate V. Fig. 61), and the connective be-

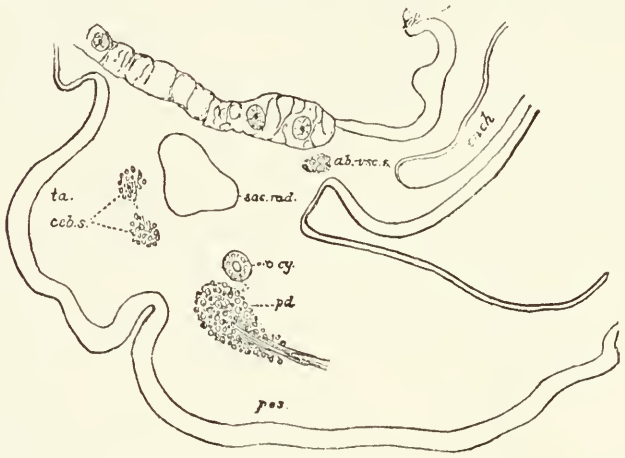

FIGURE B. — The left face of a section parallel to the sagittal plane from an embryo of the *eleventh day*. × 73.

ab.-vsc. s.	Left abdominal-visceral connective.	*pd.*	Pedal ganglion.
ceb. s.	Left cerebral ganglion.	*pes.*	Foot.
ench.	Shell gland.	*sac. rad.*	Radula sac.
o cy.	Otocyst.	*ta.*	Ocular tentacle.

tween it and the right visceral ganglion, which is hardly perceptible at this stage, is much shorter than that to the left visceral ganglion.

The buccal ganglia remain in the same condition as in the preceding stage (Plate II. Fig. 22).

By the *eleventh day* the embryo has increased greatly in size (Figure B); the tentacles are prominent, and the pulsating sac of the foot is very large. A narrow slit-like infolding of the ectoderm (compare Plate VIII. Fig. 101, *gl. pd.*) has arisen in the median plane of the body at the anterior end of the foot, into which it extends backward a short distance. It is the beginning of the foot gland. The salivary glands also make

their appearance during this stage as a pair of evaginations of the lateral walls of the œsophagus, immediately above its communication with the radula sac, and a little in front of the buccal ganglia (Plate VI. Figs. 77–80).

The cerebral invaginations still open broadly at the sides of the head (Plate III. Figs. 32–34, and Figure C). They are, however, quite deep, and in a series of sagittal sections the depression becomes deeper and deeper as one approaches the median plane, and at the same time the orifice which leads to the depression becomes narrower and narrower,

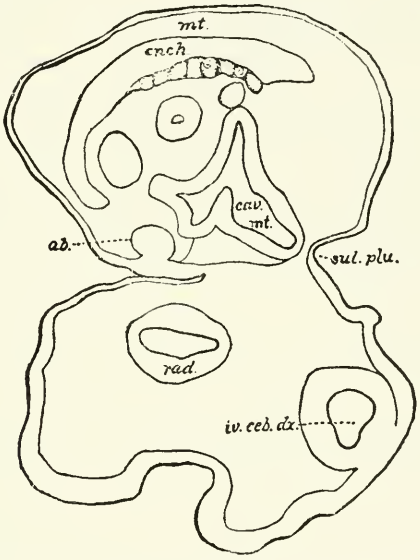

FIGURE C. — The posterior face of a transverse section from an embryo of the *eleventh day*. × 73.

ab.	Abdominal ganglion.	*mt.*	Mantle.
cav. mt.	Mantle cavity	*rad.*	Radula sac.
cnch.	Shell gland.	*sul. plu.*	Pleural groove.
iv. ceb. dx.	Right cerebral invagination.		

until it is almost slit-like (Figs. 32–40). The deep ends of the invagination are turned a little towards the median plane. These invaginated portions of the brain are composed of small, closely packed cells, whose nuclei stain deeply. The proliferated portions of the cerebral ganglia, which are deeper than the sacs (Plate V. Fig. 64, Plate VI. Figs. 70, 71), extend toward each other in the median plane, and backward and downward toward the pedal ganglia (Fig. 71). They have now become differentiated into a fibrous central part (Fig. 71), in which

are lodged the larger scattered cells with their very large nuclei, and a peripheral part, where the cells are crowded together and the nuclei are smaller (Fig. 70). They are loosely enveloped by spindle-shaped, very much elongated, connective-tissue cells (Fig. 71). Immediately above the oral cavity is the cerebral commissure (Plate VI. Fig. 80[a]). It can be traced from one side of the brain to the other, and its cross section appears as a very small round patch of fibrous substance, surrounded on the dorsal side by a layer of flat cells.

The cerebro-pedal connectives are indicated (Fig. 71) by a few cells extending from the ventral-posterior ends of the cerebral ganglia to the anterior ends of the pedal, a little in front of the cerebro-pleural connectives (Fig. 70). The latter extend from the posterior ends of the cerebral to the anterior ends of the pleural ganglia, thus diverging somewhat from the cerebro-pedal connectives. There are found in the ganglia many cells which are in different stages of division. It is owing to this cell division that the ganglia increase rapidly in size, especially after they are wholly cut off from the ectoderm; cells in the commissures and connectives are also found in process of dividing in planes perpendicular to the direction of their fibres.

The principal change in the pedal ganglia (Plate VI. Fig. 71) is due to an increase in size, particularly in the antero-posterior direction. The central portion of these ganglia has the same fibrous appearance as that described for the cerebral ganglia, and the pedal nerves can be traced for a considerable distance toward the tip of the foot (compare Figure E, page 191). The anterior commissure (Plate III. Fig. 44, Plate VI. Fig. 74) is now somewhat shorter than in the previous stage, and consists of a greater number of cells. Cell proliferation is still taking place from the ectoderm of the ventral wall of the foot (Plate VI. Fig. 71), and the ganglia continue to receive accessions from these sources. More highly magnified views of the regions of proliferation are given in Plate VI. Figs. 72 and 73.

The pleural ganglia (Plate VI. Fig. 70) are now easily recognized. Each ganglion is formed of a triangular group of cells, occupying a position immediately above and anterior to that part of the pleural groove which is nearest to the otocyst. The cells composing the ganglion are fewer than those of any of the other pairs of ganglia, but resemble them in their histological conditions; they are only loosely connected, and their fibres are elongated in the directions of the three connectives. At this stage the ganglia are not closely enveloped in connective tissue.

The pleuro-visceral connectives are well developed, especially the left

one (Fig. 70); the right one is much longer and more attenuated, since the right visceral ganglion is farther from the pleural than the left visceral. The ganglia are most distinctly seen in specimens cut in a sagittal direction.

The visceral ganglia (Plate V. Figs. 67–69, Plate VI. Fig. 70) are much larger and more elongated in the direction of the pleural ganglia — i. e. downward, forward, and outward — than they were during the previous stage. They are still connected with the ectoderm at their posterior dorsal ends, while the opposite ends are much drawn out toward the pleural ganglia (Figs. 69, 70). The right visceral ganglion (Figs. 67–69) is larger than the left, and its longest axis has a dorso-ventral direction (Fig. 68). The fibrous prolongations continue into the pleuro-visceral connectives (Fig. 71).

The abdominal ganglion (Plate III. Figs. 43, 44, 46, 47, Plate VI. Figs. 75, 76), although still connected with the ectoderm, is also larger, and projects more into the body cavity than on the tenth day. A large portion of it still lies to the left of the median plane of the body (Plate VI. Figs. 75, 76), and the connective to the left visceral is well developed (Plate III. Figs. 41, 42, Plate V. Fig. 68); that to the right is less complete (Plate III. Figs. 45, 51).

The buccal ganglia (Plate V. Fig. 62, Plate VI. Fig. 77) are now very distinct; the dorsal wall of the radula sac still contributes to their increase in size.

Cell proliferation takes place from the ectoderm bordering the entrance to the respiratory cavity. A few cells, which probably form the olfactory ganglion, are seen at this stage to be separating from the ectoderm in this region.

For the next twenty-four to thirty-six hours (*twelfth and thirteenth days*) the external appearance of the embryo remains nearly the same as on the eleventh day. In the living embryo the larval heart may be seen pulsating, and the foot gland extends somewhat farther towards the posterior extremity of the foot.

The cerebral invaginations appear simply as long narrow sacs filled with a coagulated substance; the inner ends of these sacs have grown upward as well as backward (Plate VII. Fig. 94). The proliferated portions of the cerebral ganglia (Fig. 94) are much larger, and have now assumed more nearly their ultimate positions (Plate III. Figs. 48, 49; Plate VII. Figs. 81, 82, 94) The central portion of each has become more fibrous (Fig. 81).

The connectives, both to the pedal (Plate VII. Fig. 81) and to the pleural ganglia (Plate III. Fig. 48), are well developed, and are both thicker and shorter than in the stage last described.

The pedal ganglia do not differ materially from the condition described for the eleventh day. The anterior end has increased in diameter, and has grown a little farther forward (Plate III. Fig. 50, Plate VII. Figs. 81, 91).

Both commissures are now present; the anterior (Fig. 92) is a little behind the otocysts (compare Fig. 92 with Fig. 91), and the posterior (Fig. 90) is directly above the blind end of the foot gland, and about 0.2 mm. back of the anterior commissure.

The pleural ganglia (Plate III. Fig. 48, Plate VII. Figs. 82, 83, 88) are very near the cerebral ganglia, as may readily be seen in sagittal sections (Figs. 48, 82), and the fibrous connectives to the other ganglia are plainly to be distinguished. The ganglia have become more compact and rounded, and occupy a position nearer the middle plane of the body (Figs. 86, 88).

The visceral ganglia (Plate III. Fig. 49; Plate VII. Figs. 83, 84, 86–89), although they have increased greatly in size, are still connected with the ectoderm which forms the anterior wall of the mantle chamber (Figs. 88, 89).

They have also moved inward and forward. The right ganglion (Figs. 49, 83, 87–89) is especially well developed, and much farther forward than in the previous stage. Its axis is prolonged into a nerve, which runs upward and backward, probably to the olfactory ganglion (Figs. 84, 87).

The connective from the right visceral to the abdominal ganglion passes backward and inward (Plate VII. Figs. 83, 84). Where the connective leaves the visceral ganglion (Fig. 83), the nuclei of the ganglionic cells are very large, and the fibres are very much elongated in the direction of the connective.

In specimens cut crosswise the nerve which forms the dorsal prolongation of the axis of the visceral ganglion is found far forward, in front of the anterior face of the abdominal ganglion; it passes upward and inward (Plate VII. Figs. 87, 88), and is connected with the ectoderm that forms the wall of the small infolding from the respiratory cavity (Fig. 88) referred to in the account of the tenth day. This region is at the same level as that with which the abdominal ganglion is connected farther back (Plate VII. Fig. 93). The ectodermic cells to which this nerve is distributed form the lining to an irregular infolding from the

median face of the respiratory cavity, and the lumen of the infolding connects by a narrow orifice with the respiratory chamber (Fig. 88, *cav. mt.*). I believe this is the organ first described by Lacaze-Duthiers.

A little farther forward the right visceral ganglion sends to the right side of the body a nerve (Plate VII. Fig. 89 *n.*), which passes between the wall of the mantle chamber and the primitive sexual duct, probably to be distributed to the right half of the mantle.

At this time the greater portion of the abdominal ganglion (Plate VII. Figs. 81, 82, 85, 86, 93) lies on the right side of the median plane, although it is joined to the left visceral by a large and prominent connective (Plate III. Figs. 50, 52, Plate V. Figs. 65, 66, Plate VII. Fig. 93). Since the visceral ganglia have grown inward and forward, the abdominal ganglion now occupies a position considerably posterior to them (Plate VII. Figs. 83, 86); it lies above the right side of the radula sac. Its posterior dorsal margin is still continuous with the ectoderm of the wall of the respiratory cavity (Fig. 93), but farther forward it is entirely separated from the ectoderm (Fig. 85), and is surrounded by a layer of connective-tissue cells. All the other ganglia are similarly enveloped in connective tissue except where they are continuous with the ectoderm.

The connective to the left visceral ganglion (Plate VII. Fig. 93) passes downward, forward, and outward to the left side above the radula sac.

The buccal ganglia (Plate VII. Fig. 81) are larger than on the tenth day, but are closely applied, as before, to the walls of the radula sac. Their commissure (Plate V. Fig. 65) is embraced in the angle between the œsophagus and the neck of the radula sac, and in sagittal sections presents a circular outline.

On the *fourteenth day* the upper lips as well as both pairs of tentacles are very prominent, and the foot gland has grown backward still farther into the foot (Plate VIII. Fig. 102). The salivary glands have now become elongated into tubular organs with a circular lumen and thick walls consisting of a single layer of epithelial cells (Plate VIII. Fig. 106). They reach a little farther back than the buccal commissure; in passing forward they lie on either side of the œsophagus, about on a level with its lower border. They pass along the dorsal side of the buccal ganglia, and then suddenly bend downward to open into the œsophagus.

The cerebral invaginations (Plate VIII. Fig. 96) present the same general appearance as in the stage last described, but the lumen of the sacs

is smaller (Plate X. Figs. 121, 126); in cross sections (Fig. D) it appears oval. The walls are thick, being composed of spindle-shaped cells arranged perpendicularly to the axis of the sac and so crowded that the nuclei are three or four deep.

The proliferated portion of the cerebral ganglia (Plate IX. Fig. 114) retains its pear-shaped condition, but is shorter and thicker. A ventral and

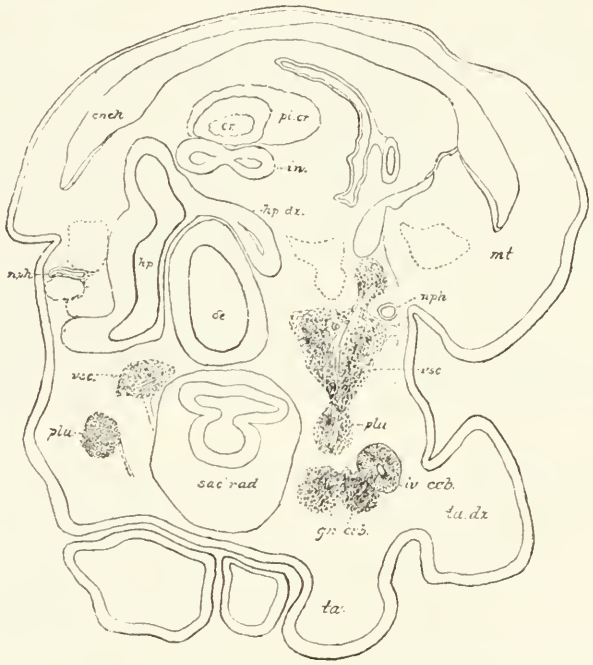

FIGURE D. — Posterior face of a transverse section from an embryo of the *fourteenth day*. × 190.

cnch.	Shell gland.	*nph.*	Nephridial organ.
cr.	Heart.	*œ.*	Œsophagus.
gn. ccb.	Cerebral ganglion.	*pi. cr*	Pericardium.
hp.	Liver.	*plu.*	Pleural ganglion.
hp. dx.	Right lobe of liver	*sac. rad*	Radula sac.
in.	Intestine.	*ta. dx.*	Right ocular tentacle.
iv. ccb	Cerebral invagination.	*ta'.*	Labial tentacle.
mt.	Mantle.	*vsc.*	Visceral ganglion.

median portion of each ganglion forms a small rounded lobe (Figure E). These lobes are near the bases of the upper lips, and in sagittal sections appear almost completely separated from the larger part of the ganglia by ingrowths of connective tissue. It is from these lobes that the pedal connectives arise. The connectives to the pleural ganglia emerge from

the larger portion of the ganglion; they are thicker and shorter than the cerebro-pedal connectives, from which they are separated by only a narrow space.

The cerebral commissure is much shorter than before (Plate X. Fig. 126), but it has not increased much in thickness (Plate VIII. Fig. 101). In sagittal sections it is seen to be composed of a central portion made up of nerve fibres cut crosswise and a peripheral layer of nuclei; but the nuclei are wanting on the face of the commissure which is in contact with the dorsal wall of the œsophagus.

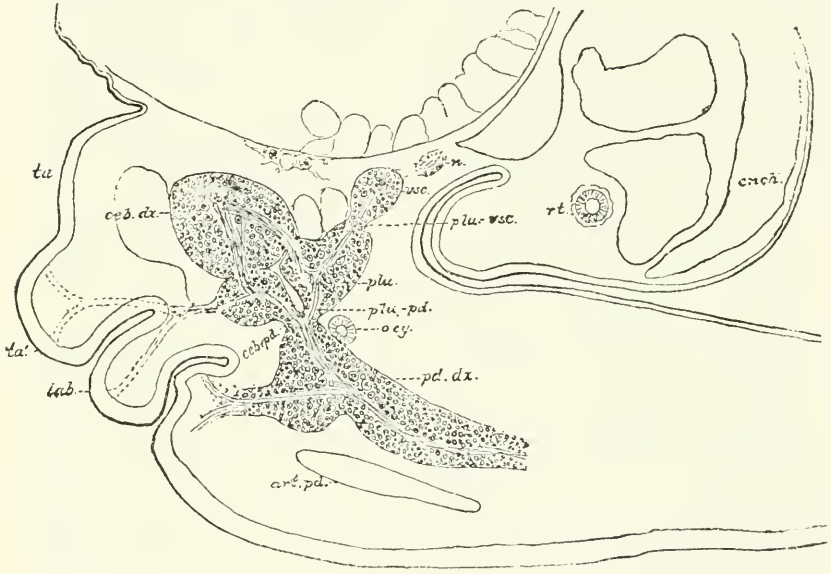

FIGURE E. — The left surface of a section parallel to the sagittal plane from an embryo of the *fourteenth day*. × 73

art. pd	Pedal artery.	*plu.-pd.*	Pleuro-pedal connective.
ceb. dx.	Right cerebral ganglion.	*plu.-vsc*	Pleuro-visceral connective.
ceb.-pd	Cerebro-pedal connective.	*pd. dx.*	Right pedal ganglion.
cnch.	Shell gland.	*rt.*	Rectum.
lab.	Lip.	*ta.*	Ocular tentacle.
n.	Nerve	*ta'.*	Labial tentacle
o cy.	Otocyst.	*vsc.*	Visceral ganglion.
plu.	Pleural ganglion.		

The pedal ganglia (Plate VIII. Figs. 97–100, Plate IX. Figs. 114, 118, 119) lie between the radula sac, which is above, and the foot gland which is below them. They are nearer together than on the twelfth day, and their anterior ends are more rounded (Fig. 114). Their pos-

terior ends are elongated and continued as two large nerves far back into the foot. In specimens cut crosswise these nerves appear as rounded patches of fibres, situated one on each side of the body, above the plane of the foot gland and about midway between it and the lateral walls of the foot. Each is surrounded by a layer of connective-tissue cells. As one approaches the pedal ganglia in passing from behind forward, the nerves increase in size and lie nearer to each other. In the region of the posterior commissure (Plate IX. Fig. 119) the ganglia are nearly as broad as in the region of the anterior commissure (Fig. 118), but they are not much more than half as thick in the dorso-ventral direction. In front of the posterior commissure they are separated by a narrow space, which is wider behind than in front, where it is terminated by the anterior commissure. The commissures are both well developed (Plate VIII. Figs. 101, 102, Plate IX. Figs. 118, 119), and owing to the approximation of the ganglia have become shorter than in the last stage. The nuclei in the region of the posterior commissure (Fig. 119) are of nearly uniform size; but in front of it each ganglion (Figs. 114, 118) contains a fibrous central portion immediately surrounded by the greatly enlarged nuclei of cells which form the most of the fibrous substance.

The pleural ganglia (Plate VIII. Fig. 106, Plate IX. Figs. 114, 116, Plate X. Figs. 123, 125, and Fig. E) have increased considerably in size, and are more compact. They have moved downward and inward; and each now lies in contact with the posterior face of the corresponding cerebral mass (Plate IX. Fig. 114), and below and in front of the ventral portion of the corresponding visceral ganglion (Figs. 106, 123, 125). They are much smaller than either the cerebral or visceral ganglia. The nuclei of their central cells are, as in the pedal ganglia, much enlarged.

The visceral ganglia (Plate VII. Fig. 95, Plate IX. Fig. 114, Plate X. Figs. 123, 125) are now entirely detached from the ectoderm, and have moved downward, forward, and inward.

The left ganglion (Plate VIII. Fig. 106, Plate X. Fig. 125) is smaller than the right, and more closely connected with the left pleural (Fig. 125) than in the previous stage. Its dorsal surface is slightly above the level of the dorsal wall of the radula sac, and its connective with the abdominal ganglion (Plate VIII. Fig. 104) is much broader than before. The right visceral ganglion (Plate VII. Fig. 95, Plate VIII. Figs. 102 and 106, Plate IX. Fig. 114, Plate X. Fig. 123) is much larger than in the last stage; it is also closely connected with the right pleural ganglion (Fig. 123). It extends dorsally much farther than the

left visceral, and also nearer to the median plane (Plate VII. Fig. 95, Plate VIII. Fig. 102, Plate IX. Fig. 120). It is in contact with the lower surface of the right end of the abdominal ganglion (Plate VII. Fig. 95).

The abdominal ganglion (Plate VII. Fig. 95, Plate VIII. Figs. 101, 102, 104, Plate IX. Figs. 115–117, Plate X. Fig. 123) is entirely unconnected with the ectoderm, and has moved forward, so that there is a considerable space between it and the pleural groove, but its posterior face extends farther back than that of the right visceral ganglion (Plate VIII. Fig. 102). The greater portion of the ganglion is now situated on the right side of the body, immediately above and to the right of the radula sac (Plate VIII. Fig. 104, Plate IX. Figs. 115–117). It is elongated, and its chief axis is directed obliquely across the body, the right end being considerably higher and a little farther back than the left end. In passing downward and forward to the left side of the body, it lies between the œsophagus and the posterior part of the radula sac. Its left end is prolonged into a connective, which passes forward and outward to join the left visceral ganglion (Plate VIII. Fig. 104, Plate X. Fig. 123). A large nerve, which passes upward and backward to be distributed to the viscera, emerges from the most dorsal portion of the abdominal ganglion on the right side of the body (Plate VIII. Fig. 104, Plate IX. Fig. 117). The histological condition of the abdominal ganglion is similar to that of the previously described ganglia of this stage. The fibrous portion, as well as the enlarged cells and nuclei, are especially prominent in the portion of the ganglion which lies to the right of the median plane of the body (Plate IX. Fig 117).

The buccal ganglia (Plate VII. Fig. 95, Plate VIII. Figs. 102, 106, Plate IX. Fig. 120, Plate X. Fig. 121) have become larger, and with their commissure (Plate VIII. Fig. 101, Plate IX. Fig. 120) stretch across the dorsal wall of the neck of the radula sac, to which they are still closely united. The nuclei immediately surrounding the central fibrous portion of the ganglion are already slightly enlarged, though the cells are not so far advanced in their histological differentiation as are those of the other ganglia. A single pair of connectives passes obliquely forward, downward, and outward, to join the buccal to the cerebral ganglia (Plate X. Fig. 121).

By the *sixteenth* and *seventeenth days*, besides a general increase in size of the external organs, the foot gland extends backward much farther

than the pedal ganglia (Plate VIII. Fig. 107), and the viscera lie rather more to the left side of the body (Figure G).

The central nervous system (Figure F) now consists of five well developed pairs of ganglia and an azygos ganglion (Figure G). The cerebral ganglia with their commissure form the dorsal portion of three nerve rings, the remainder of which are completed respectively, (1) by the cerebro-pedal connectives, the pedal ganglia, and their commissures; (2) by the cerebro-pleural connectives, the pleural ganglia, the pleuro-

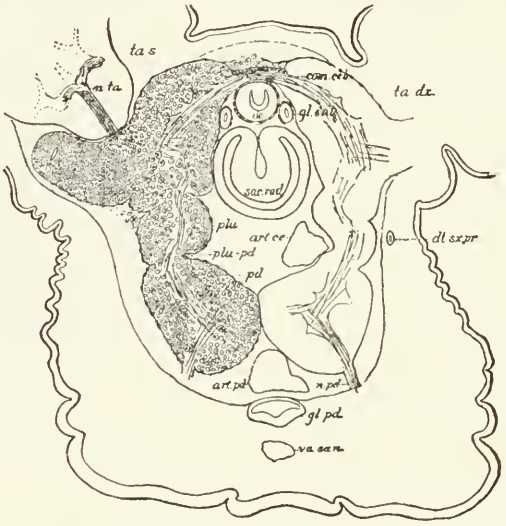

FIGURE F. — Posterior face of a transverse section from an embryo of the *sixteenth day*. × 70.

art. ce.	Cephalic artery.	*œ.*	Œsophagus.
art. pd.	Pedal artery.	*plu.*	Pleural ganglion.
com. cb.	Cerebral commissure.	*plu.-pd.*	Pleuro-pedal connective.
dt. sx. pr.	Primary sexual duct.	*pd*	Pedal ganglion.
gl. sal.	Salivary gland	*sac. rad.*	Radula sac.
gl. pd.	Pedal gland.	*ta. dx.*	Right ocular tentacle.
n. pd.	Pedal nerve.	*ta. s.*	Left ocular tentacle.
n. ta.	Tentacular nerve.		

visceral connectives, the visceral ganglia, the viscero-abdominal connectives, and the abdominal ganglion; (3) by the cerebro-buccal connectives, the buccal ganglia, and their commissure. The first and second rings are further joined to each other by means of the pleuro-pedal connectives. Each of these three rings encircles the œsophagus. The posterior end of the radula sac in the earlier stages, up to the present one, is usually found to occupy a position *above* the pedal ganglia and their

commissures; but with a greater concentration of the nervous ganglia toward one another, the sac is forced to occupy a position *below* the pedal ganglia and their commissures. The relations of the different ganglia to each other is even more definite than before, and can be more readily understood from transverse sections than from sagittal ones. The peripheral nerves from the cerebral, pedal, visceral, and abdominal ganglia are well developed; the principal changes from this time until hatching are histological.

The cerebral invaginations have become narrow and shorter, but are still open to the exterior (Plate X. Fig. 124, *iv.*). The deeper portion of the invagination, that in contact with the proliferated portion of the cerebral ganglion, has become a solid and rounded mass (Plate X. Fig. 122, *lob. lat.*), which is intimately connected with the ganglion by means of fibrous outgrowths from its ganglionic cells. It is composed of small deeply stained cells, which have undergone no such histological change as those which compose the proliferated portion of the brain. It forms a lobe on the antero-lateral face of each cerebral ganglion (Plate X. Figs. 122, 124, 127). From this time forward the principal change in the cerebral sacs consists in the gradual obliteration of the lumen of the invagination. This is usually completed somewhat later in the embryonic life; but, as previously stated, the sacs have in one instance at least been found open several days after hatching. Besides this, there is no other connection now remaining between the ectoderm and any of the ganglia, except such as is effected by means of the peripheral nerves.

The median proliferated portions of the cerebral ganglia now extend dorsally farther than in the last stage, and their commissure is much shorter (Plate VIII. Fig. 105, and Fig. F).

The pedal ganglia (Plate VIII. Figs. 103^a, 109–113) have moved forward, and are broadly in contact with the pleural ganglia. They have become more compact, and rather more triangular in shape, than before. From the ventral portion of each ganglion emerge four or five large nerves, which terminate in the ventral wall of the foot; from the dorso-lateral region two nerves are given off to the lateral walls, and the antero-ventral part of each ganglion tapers off into a stout nerve running forward to the anterior wall. The connectives with the cerebral ganglia are well developed (Plate VIII. Figs. 103, 107).

The pleural ganglia (Plate VIII. Figs. 103^a, 111–113) are nearer to the median plane than previously. The ventral posterior face of each is closely joined to the corresponding pedal ganglion (Figs. 103^a, 112),

the dorsal median face to the visceral ganglion (Figs. 103ª, 112, 113), and the anterior face to the cerebral ganglia (Fig. 107). No nerves arise from the pleural ganglia.

The visceral ganglia (Plate VIII. Figs. 103ª, 110–113) have also moved nearer to the median plane. The left ganglion is directly below

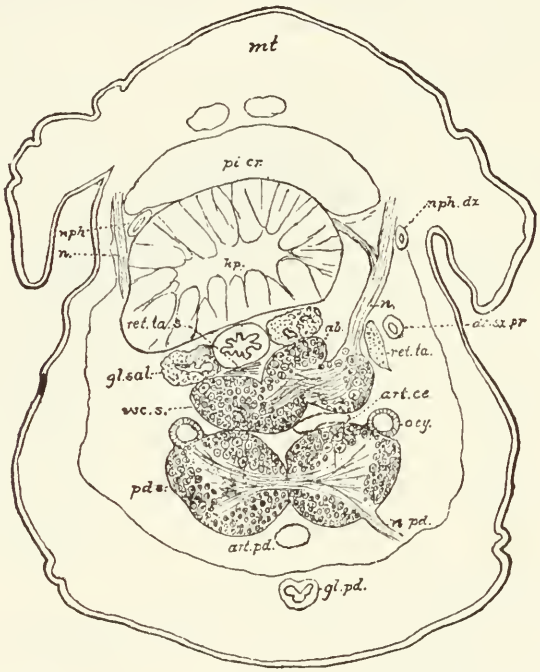

FIGURE G. — Posterior face of a transverse section from an embryo of the *seventeenth day*. × 60.

ab.	Abdominal ganglion.	*n. pd.*	Pedal nerve.
art. ce.	Cephalic artery.	*nph.*	Nephridial organ.
art. pd.	Pedal artery.	*nph. dx*	Right nephridial organ.
dt. sx. pr.	Primary sexual duct.	*o cy.*	Otocyst.
gl. sal.	Salivary gland.	*pd. s.*	Left pedal ganglion.
gl pd.	Pedal gland.	*pi. cr.*	Pericardium.
hp.	Liver.	*ret. ta.*	Retractor muscle of right ocular tentacle.
mt.	Mantle.	*ret. ta. s.*	Retractor muscle of left ocular tentacle.
n.	Nerve.	*vsc. s.*	Left visceral ganglion.

the œsophagus (Fig. 111 and Figure G), since the latter occupies a position more to the left side of the body than before. The right visceral ganglion still remains larger, and extends farther dorsally than the left (Figs. 103ª, 111, 112). It is nearer the median plane than in the

stage last described (Figure D., page 190); it lies in front and only a little to the right of the abdominal ganglion (Fig. 111).

The abdominal ganglion (Plate VIII. Figs. 109–111) is less elongated than in the last stage (Fig. 104). It is wedge-shaped, and appears as though crowded in between the two visceral ganglia from behind and above. It is so intimately connected with these ganglia that it almost appears to form a part of them (Fig. 111). But the presence, between the ganglionic masses, of connective-tissue cells, which reach nearly to the connectives, enables one to make out with some certainty the extent of each of the three ganglia. Since the planes which separate them are oblique to the transverse planes of the body, these boundaries are not always readily seen in cross sections. The right and left visceral ganglia have no *direct* commissural nerve fibres uniting them; they are joined only by such fibres as pass through the abdominal ganglion.

The buccal ganglia (Plate VIII. Fig. 108, Plate X. Fig. 124) are now entirely separated from the dorsal wall of the radula sac, from which they arose, and are surrounded by a layer of connective-tissue cells. The differentiation of their ganglionic cells is well advanced.

Summary.

1. In Limax maximus the whole of the central nervous system arises directly from the ectoderm.

2. The cerebral ganglia originate in part as a pair of true invaginations, one on each side of the body in front of the pleural groove and behind and below the bases of the ocular tentacles. In the course of their development, the neck of each invagination becomes a long, narrow tube-like structure, which remains open throughout the period of embryonic life. The main part of the cerebral ganglia is formed from cells which are detached at an early period from the deep ends of these cerebral invaginations, or from neighboring ectoderm; the portions which persist as the walls of the infoldings finally form distinct lateral lobes of the brain.

3. All the other ganglia originate by cell proliferation from the ectoderm without invagination.

4. The ganglia arise separately, and, with the exception of the abdominal and mantle ganglia, in pairs, one on each side of the body. Their connection with each other is the result of a secondary process in the development, — the outgrowth of nerve fibres.

In advanced stages, the central nervous system consists of five pairs

of ganglia and an azygos ganglion. Together these form three complete rings surrounding the œsophagus.

The relative positions of the ganglia are best appreciated from cross sections. In passing from behind forward, they are encountered in the following order: (1) the pair of pedal ganglia, which lie under the radula sac, and are joined to each other by an anterior and a posterior commissure; (2) one abdominal ganglion a little to the right of the median plane; (3) a pair of visceral ganglia occupying the posterior angle formed by the outgrowth of the radula sac from the œsophagus. They are separated by the abdominal ganglion, from which connectives pass to them; (4) a pair of pleural ganglia, not joined by a commissure, and not giving off nerves. They are united by means of connectives to the pedal, visceral, and cerebral ganglia of the same side; (5) a pair of cerebral ganglia, with their supra-œsophageal commissure and connectives to the pleural, pedal, and buccal ganglia; (6) a pair of buccal ganglia, with a commissure under the œsophagus posterior to its connection with the sac of the radula.

The mantle ganglion lies far back, and is joined to the abdominal ganglion by a large nerve.

It seems as if there could be no doubt that the infolding of the ectoderm of the anterior wall of the respiratory cavity on the right side of the body gives rise to the special-sense organ discovered by Lacaze-Duthiers ('72, pp. 483–494). It corresponds in its position and its connection with the right visceral ganglion to his description of the adult, and also to Fol's description ('80, pp. 166–168) of the origin and position of that organ in the aquatic pulmonates.

As is well known, Limax belongs to that group of Gastropods in which all the nerve centres, except the cerebral and buccal, lie on the ventral side of the intestinal tube; not to the group in which the connection between the right pleural and right visceral ganglia passes above the œsophagus, and in which that of the left lies below it. Limax, therefore, is not directly referable to Von Jhering's group of Chiastoneura, although the want of symmetry in the position of its ganglia does not allow one to say that it is orthoneuric.

The Gastropod in which the details of the origin and fate of the nervous centres have been most carefully studied is Bithynia, a chiastoneuric form, in which Sarasin has found that the abdominal ganglion is joined to the right visceral ganglion *only*, and is located at the fundus of the gill cavity. The relation is different from that found in Limax

maximus, where the abdominal ganglion is intimately fused with the right visceral, and is *also* in close connection with the left visceral ganglion.

As was to have been anticipated, the abdominal ganglion of Limax corresponds more nearly in position to that in Lymneus and other fresh-water pulmonates, as described for the adult by Lacaze-Duthiers ('72, pp. 437–500).

Of the authors who have studied the origin and development of the *cerebral ganglia* in Mollusks, Fol ('80, pp. 168, 169, 193–195) is the only one who has pursued his investigations on Limax maximus. He says ('80, p. 193): "Vers l'époque de la fermeture de la vésicule oculaire, se montrent deux autres enfoncements de l'ectoderme. L'un des deux, assez vaste et situé à la base du tentacule, à son bord intérieur, est l'origine du ganglion cérébroide; je le décriai plus loin. L'autre enfoncement, plus petit, est situé au-dessous de ce dernier, à la base du pied, et mène à la constitution de la vésicle auditive."

As to the method by which the cerebral ganglia originate, this agrees in part with that which I have found; but as to the time of origin, my investigations lead me to a different conclusion. The otocysts are present as small groups of cells (Plate I. Fig. 4), and the cellular elements which go to form the beginning of the pedal ganglia are also being proliferated (Fig. 3), before there is a trace of the invaginations which go to form the cerebral ganglia (Fig. 2).

A little later the otocysts assume the form of closed vesicles, unconnected with the ectoderm (Plate I. Fig. 9), while the cerebral invaginations are now seen as shallow pits (Fig. 6). Therefore, in Limax maximus the formation of both pedal ganglia and otocysts precedes that of the cerebral invaginations.

Sarasin ('82, pp. 1–68) maintains that in Bythinia tentaculata there are no invaginations to form the cerebral ganglia. They arise as thickenings of the ectoderm, one on each side of the body, which he calls *die Sinnesplatte*.

In the recent researches of the Sarasin brothers ('87, pp. 600–602, '88, pp. 59–69) on Helix Waltoni, of Ceylon, it is asserted that each of the cerebral ganglia is at first represented by a group of cells derived from the part of the ectoderm called "Sinnesplatte" before there is any invagination. There are two groups of these cells, one on each side of the body. Somewhat later two infoldings arise from each Sinnesplatte, one above the other. These infoldings become long, narrow

"cerebral tubes," the deep ends of which are enlarged ('88, Fig. 24). From their inner ends a rapid cell proliferation takes place, the products of which join the cerebral cells already in position. The invaginated portions later form the "accessory lobes" of the brain. At a late stage only one pair of tubes remains open to the exterior, and the openings to these are closed before the end of embryonic life. The Sarasins ('88, p. 61) do not know the precise time at which they are closed, but are certain that the openings do not persist. They express their belief that the cerebral tubes are homologous with the organs of smell in Annelids, which, according to Kleinenberg's studies on Lopadorhynchus, also originate as invaginations of the Sinnesplatte, and by cell proliferation furnish a part of the material for the brain.

Prior to any knowledge of the investigations on Helix by the Sarasins, I found very similar conditions in Limax maximus. In this case, however, there is but one invagination of the ectoderm on each side of the body. It corresponds in position to those described in Helix, being perhaps the equivalent of the upper or larger invagination in that species.

The invaginations in Limax have the form of shallow pits before any other ganglionic cells are to be seen. The cell proliferation, which results in the production of the main portion of the ganglia, takes place during their ingrowth. Possibly the proliferation from the depression between labial tentacle and upper lip represents what was originally a true invagination, and corresponds to the lower of the two invaginations described by the brothers Sarasin. In Limax maximus the external openings persist until a late stage, and occasionally even after hatching. Here, also, the invaginations form a lobe of the brain, exactly as in the case of Helix (Sarasin, '87, p. 601).

Two well developed "Seitenorgane" were found by the Sarasins ('88, p. 54) in Helix Waltoni, situated near each other in the "sense-plate"; and they think (p. 60) that these may correspond in position to the cerebral tubes of later stages.

The groups of cells embedded in the ectoderm, from which, in my opinion, the greater part of the nervous system in Limax maximus takes its origin, resemble both in the arrangement of the cells and their histological condition the "Seitenorgane" described by the brothers Sarasin ('88, pp. 53–57). But I have never observed bristles, or other terminal structures, projecting toward the outer world. Moreover, in Limax unmodified ectodermic cells usually lie between these groups of large cells and the outer surface of the body.

The Sarasins ('88, p. 57) consider these clusters of cells homologous with the "taste-buds" and "lateral organs" of vertebrates, and say that they are to be found in and at the margin of the Sinnesplatten, and along the sole of the foot, — more rarely on the sides of the foot. I think these organs are probably the same as those which I have seen in Limax, and to which I attribute simply the function of contributing to the formation of the ganglia.

Salensky ('86, pp. 685–690) describes the cerebral ganglia of Vermetus as arising from a pair of ectodermic thickenings, which early show pocket-like invaginations, and become deeper and narrower. From the inner ends of these invaginations are formed the main portion of the ganglia. The latter are united to each other by a very small commissure, composed of fibrous prolongations of the ganglionic cells surrounded by other nerve cells.

The principal difference between the method of development in Vermetus and that in Limax maximus consists in the fact that the detachment of the deep portion of the invaginations to form the ganglia in Vermetus is not effected until the invaginations have reached their ultimate size, whereas in Limax the detachment of cells from the invaginated area begins as early as does the invagination, and accompanies it during the whole of its formation.

Kowalesky ('83[a], pp. 1–54) found in Dentalium two deep invaginations, which he calls the "sincipital tubes," one on each side of the head region, a little ventral to the middle of the velar area. From the posterior deep ends of these sacs the cerebral ganglia are subsequently formed; but he is uncertain whether all the cells concerned in the involution share in the formation of the ganglia. If his Figure 65 is compared with Figures 27 and 33 A in Salensky's paper, the close resemblance in the method of origin of the cerebral ganglia in the two types becomes apparent.

Fol ('80, pp. 169, 170) asserts that the *pedal ganglia* of the aquatic pulmonates appear as condensations in an already formed mesoderm, and that they are nearer the pharynx than the ectoderm when they begin to be discernible. "One may therefore say," he adds, "that these ganglia arise from the mesoderm without prejudging the unsettled question, viz. from which of the primordial layers arises the mesoderm which forms them." Of the pedal ganglia of the terrestrial pulmonates, he says that they are diffentiated *en lieu et place* in the midst of the mesodermic tissues of the foot.

With this I cannot agree, although I admit that at the time when the groups of cells which form the ganglia begin to be proliferated from the ectoderm, it is extremely difficult to distinguish them from the mesodermic elements (Plate I. Fig. 5). It is to be observed, however, that Fol considers it an unimportant distinction, whether the ganglia are formed from groups of mesodermic cells which have themselves recently originated from the ectoderm, or by a proliferation of cells directly from the ectoderm.

I am unable to reconcile the account of the development of the pedal ganglia in Bithynia given by P. Sarasin ('82, pp. 47–49), with the conditions seen in Limax; nor can I think it probable that any considerable difference exists between nearly related mollusks in regard to the *place* whence the ganglionic cells arise. Sarasin maintains that in Bithynia the pedal ganglia arise from a *single median thickening of the ectoderm of the dorsal wall of the foot*, in the region where that wall bends over to become continuous with the posterior wall of the visceral sac. Anteriorly, in the region of the oral invagination, this median band of cells forks, and each branch becomes joined to the corresponding cerebro-pleural cell mass by a slender cord of cells. Subsequently, the posterior unique portion of the proliferated cell mass is completely divided into lateral branches by a separation which progresses from in front backward. It seems to me that, according to this account, both the pedal ganglia must be regarded as arising from a common mass of cells, and that they are not from the beginning wholly separate, as I maintain for Limax.

The relative positions of pedal ganglia and otocysts present, to my mind, a serious objection to Sarasin's view, which may not have seemed so important to him on account of his uncertainty about the origin of the otocysts. I believe it is sufficiently evident that the otocysts do not arise, as Sarasin thinks probable, from the cerebro-pleural proliferations, but independently, and from the dorso-lateral wall of the foot in the region of the "pleural groove." They ultimately lie immediately dorsal to the corresponding pedal ganglia. If Sarasin's view as to the origin of the pedal ganglia as a *median* dorsal proliferation were correct, the ganglia would have to migrate to a lower plane than that occupied by the otocysts. But there is no evidence either in Limax or the figures given of Bithynia which would confirm such a supposition. As further corroboration of my opinion that the pedal ganglia arise from the *ventral* and lateral walls of the foot, I would cite the conclusion reached by Salensky ('86, pp. 691, 692) for Vermetus. He has shown that the

pedal ganglia originate from the ventral wall of the foot, in a region and by a method corresponding to that seen in Limax maximus, as will be seen by comparing his Figures 21 C to 23 with my Plate I. Figs. 5 and 7, and Plate IV. Fig. 57. The only important difference between Vermetus and Limax lies in the fact that, in the case of the former, the cells forming the ganglion remain from the beginning a more compact mass than they do in the latter.

No one except Lacaze-Duthiers ('72, pp. 456, 457) has mentioned the existence of more than a single pedal commissure. He maintains that there are in Lymnæus as many as *three*. After speaking of the cerebral ganglia as being connected by one commissure, he goes on to say (p. 456), "Au contraire les ganglions pédieux ont trois commissures réelles." He seems, however, uncertain as to whether the most *posterior* ought to be considered a true commissure: "La troisième commissure mérite-t-elle bien ce nom? elle est constante dans les Pulmonés et se présente sous la forme d'un petit nerf grêle transversal naissant à peu près à la hauteur du troisième nerf pédieux inférieur; elle donne vers son milieu naissance à un filet nerveux trés-délié, impair médian que l'on suit dans les tissus de la fosse pédieuse sans trop pouvoir définir et limiter exactment son rôle." (p. 457.) His investigations were made exclusively upon the adult.

In Limax maximus two commissures are certainly distinguishable during a greater part of the embryonic life; no trace of a third has been seen. The adult has not been studied.

None of these authors, with the exception of Sarasin, say anything conclusive concerning the origin of the *remaining ganglia*, although Salensky (86, p. 697) speaks as if the pleural ganglia of Vermetus originated in the cerebro-visceral connectives, which are shown in his Figures 31 B to 31 F.

Sarasin asserts ('82, pp. 46, 47) that in Bithynia the pleural ganglia originate as part of the "Sinnesplatte," from which the cerebral ganglia arise, and that these ganglia, cerebral and pleural, are so closely fused with each other in the later stages of development as to form on either side of the body a single mass.

I believe that they arise in Limax maximus by cell proliferations from the lateral walls of the body, behind the cerebral ganglia, and just above the pleural groove; they are closely connected (not fused) with the cerebral ganglia only in late stages.

Sarasin ('82, pp. 50–52) says that the visceral ganglia in Bithynia

arise by cell proliferation from the dorsal margin of the ventral wall of the head or trunk region, above that which I have called the pleural groove. Further, that the right visceral (or supra-intestinal) ganglion is connected by a nerve fibre to the olfactory ganglion under the gill cavity. Farther back than the visceral ganglia he finds a median proliferation of cells lying at the ventral margin of the gill cavity, from which the abdominal ganglia arise. He asserts that there are two abdominal ganglia, — one connected with the supra-intestinal ganglion, the other with the sub-intestinal ganglion.

In Limax maximus the visceral ganglia and the abdominal ganglion arise by the same method as that described by Sarasin; but the former are produced from the lateral walls of the head region, above the pleural groove, one on each side of the body. The right ganglion in later stages is more dorsal than the left. It appears to be formed in part from the inner wall of the respiratory cavity, to which it remains connected by a nerve. It is in this region that is developed an organ which I believe to be the olfactory organ of Lacaze-Duthiers.

There is only one abdominal ganglion; this takes its origin a little to the left of the median line of the body, from the anterior margin of the body wall immediately above the pleural groove.

Sarasin ('82) is the only author who gives attention to the origin of the buccal ganglia. He describes them as arising in exactly the same manner, and in the same situation in relation to the walls of the radula sac and the œsophagus, that they do in the case of Limax maximus.

Cambridge, November, 1889.

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EXPLANATION OF FIGURES.

All the figures were drawn with the aid of the camera lucida, and were made from preparations of Limax maximus.

INDEX TO STAGES.

The Roman numerals indicate Plates. The Arabic numerals, Figures; those which are enclosed in a parenthesis belong to the same specimen. Skeleton numbers on the plates refer to the number of the section in its series.

6th day. $\left(\frac{\text{I.}}{1,\ 5}\right)$, $\left(\frac{\text{I.}}{2\text{–}4}\right)$.

7th " $\left(\frac{\text{I.}}{6\text{–}9}\right)$, $\left(\frac{\text{I.}}{10\text{–}13}\right)$, $\left(\frac{\text{II}}{15,\ 17,\ 18}\right)$, $\left(\frac{\text{IV.}}{53,\ 55\text{–}57}\right)$, $\left(\frac{\text{IV.}}{54}\right)$.

8th " $\left(\frac{\text{II.}}{14,\ 16,\ 19}\right)$.

9th " $\left(\frac{\text{II.}}{20\text{–}24}, \frac{\text{III.}}{25\text{–}27}\right)$, $\left(\frac{\text{V.}}{60}\right)$.

10th " $\left(\frac{\text{III.}}{28\text{–}31}, \frac{\text{IV.}}{58,\ 59}, \frac{\text{V.}}{61,\ 63}\right)$.

11th " $\left(\frac{\text{III.}}{32\text{–}47,\ 51}, \frac{\text{V.}}{62,\ 64,\ 67}, \frac{\text{VI.}}{70\text{–}75}\right)$, $\left(\frac{\text{V.}}{68,\ 69}, \frac{\text{VI.}}{77\text{–}80}\right)$.

12th " $\left(\frac{\text{III.}}{48,\ 49}, \frac{\text{V.}}{65,\ 66}, \frac{\text{VII.}}{81,\ 82}\right)$, $\left(\frac{\text{III.}}{50,\ 52}, \frac{\text{VII.}}{85\text{–}94}\right)$, $\left(\frac{\text{VI.}}{74\text{–}76,\ 80^{a}}\right)$, $\left(\frac{\text{VII.}}{83\text{–}84}\right)$.

14th " $\left(\frac{\text{VII.}}{95}, \frac{\text{VIII}}{96,\ 101,\ 102}, \frac{\text{IX.}}{114}\right)$, $\left(\frac{\text{VIII.}}{97\text{–}100,\ 104,\ 106}, \frac{\text{IX.}}{115\text{–}120}, \frac{\text{X.}}{121,\ 123,\ 125,\ 126}\right)$.

16th " $\left(\frac{\text{VIII.}}{107}\right)$, $\left(\frac{\text{X}}{124}\right)$.

17th " $\left(\frac{\text{VIII.}}{103,\ 103^{a},\ 105,\ 108\text{–}113}, \frac{\text{X.}}{122,\ 127}\right)$.

ABBREVIATIONS.

The right side of the animal is indicated by the letters dx., the left side by s. These letters are usually affixed to one or more of the abbreviations used to designate organs. The skeleton figures immediately under the number of a figure on the plate indicate the number of the section in the series to which the figure belongs. Consult also "Index to Stages" (p. 207).

ab.	Abdominal ganglion.	*lab.*	Upper lip.
ab.-vsc.	Abdomino-visceral connective.	*lns.*	Lens.
an.	Anus.	*lob. lat.*	Lateral lobe of brain.
buc.	Buccal ganglion.	*loph. cil.*	Ciliated ridge.
cav. mt.	Mantle cavity.	*mt.*	Mantle.
ceb.-buc.	Cerebro-buccal connective.	*n.*	Nerve.
ceb. dx.	Right cerebral ganglion.	*nph-*	Nephridial organ (primitive kid-
ceb. s.	Left cerebral ganglion.	*oc.*	Eye. [ney.)
ceb.-pd.	Cerebro-pedal connective.	*o cy.*	Otocyst.
ceb.-plu.	Cerebro-pleural connective.	*œ.*	Œsophagus.
cnch.	Shell gland.	*pd.*	Pedal ganglion.
com. a.	Anterior pedal commissure.	*pes.*	Foot.
com. buc.	Buccal commissure.	*plu.*	Pleural ganglion.
com. ceb.	Cerebral commissure.	*plu.-pd.*	Pleuro-pedal connective.
com. pd.	Pedal commissure.	*plu.-vsc.*	Pleuro-visceral connective.
com. pd. a.	Anterior pedal commissure.	*pr f.*	Cell proliferation.
com. pd. p.	Posterior pedal commissure.	*rad.*	Radula sac.
dt. sx. pr.	Primary sexual duct.	*ret. ta.*	Retractor muscle of tentacle.
dx.	Right.	*s.*	Left.
en.	Entoderm.	*sul. plu.*	Pleural groove.
gl. pd.	Pedal gland.	*ta.*	Ocular tentacle.
gl. sal.	Salivary gland.	*ta.'*	Labial tentacle.
gn.	Ganglion.	*vsc.*	Visceral ganglion.
iv. ceb.	Cerebral invagination.	*vsc.-plu.*	Viscero-pleural connective.

PLATE I.

All the figures of this plate were made from material killed in Perenyi's fluid, and all except Fig. 1 are magnified 250 diameters.

Fig. 1. A small portion of Fig. 5 more highly magnified to show the cell proliferation for the right pedal ganglion.

" 2. Posterior face of a transverse section from an individual about *six days* old. The section passes anterior to the "pleural groove," and through the region where the cerebral invaginations subsequently arise; the left side is cut a little anterior to the right. Stained in alcoholic borax-carmine.

" 3. A section from the same individual posterior to the pleural groove in the region of the cell proliferation for the pedal ganglia.

" 4. A section from the same, still farther back.

" 5. Transverse section from an embryo a few hours older than the preceding, in the region of the proliferation to form the pedal ganglion. Stained in alcoholic borax-carmine.

" 6–9. The left surface of sections parallel to the sagittal plane from an embryo of the *seventh day*. Figs. 6, 8, and 9 represent respectively the 11th, 16th, and 18th sections of the series, and are from the left half of the embryo. Fig. 7 is from the right half, and passes through the right otocyst. Stained in Czoker's cochineal.

" 10–13 exhibit the right surface of sections from another individual (between the *seventh and eighth days*) cut parallel to the sagittal plane, the anterior portion a little in advance of the posterior. Fig. 10 is a section passing through the proliferation forming the right visceral ganglion. Figs 11 and 12 are two successive sections passing through the left visceral ganglion; the latter also passes through the left otocyst. Fig. 13 shows the region of the forming abdominal ganglion. Stained in picro-carminate of lithium. In both these individuals the left ganglia and otocysts are more developed than the right.

PLATE II.

All the figures of this plate are magnified 250 diameters.

Fig. 14. A section parallel to the sagittal plane from an individual of the *eighth day*. It passes through the cerebral and pleural ganglia of the left side of the body, and also shows four cells of the left otocyst posterior to the pleural groove. The material was killed in 0.33% chromic acid, and stained in alcoholic borax-carmine.

" 15. The left surface of a section cut parallel to the sagittal plane from an embryo of the *seventh day* (but more advanced than in Figs. 6–9), passing through the cerebral invagination and a group of cells belonging to the proliferated portion of the cerebral ganglion of the right side. The material was treated as in that of Fig. 14.

" 16. A section from the same individual as Fig. 14, passing through the cell proliferation to form the visceral ganglion of the right side.

" 17 and 18 are from the same individual as Fig. 15.

" 17. A section passing through the visceral ganglion and the external opening of the nephridial organ of the right side.

" 18. The second section nearer the median plane than Fig. 17, showing the cell proliferation to form the right visceral ganglion.

" 19. From the same individual as Fig. 14, showing the cerebral invagination and proliferation of the right side, and also a cross section of the primitive kidney.

" 20–24. The anterior surfaces of transverse sections from an embryo of the *ninth day*. Material killed in Perenyi's fluid, and stained in alcoholic borax-carmine.

" 20. Portion of a section which passes through the proliferation of cells forming the pleural ganglion (dorsal to the pleural groove), and through the pedal ganglion and the otocyst of the left side.

" 21. The 37th section, which passes through the cerebral commissure and shows the proliferation of cerebral cells on the left side.

" 22. The 51st section, which passes through the buccal ganglion of the right side.

" 23. The 69th section, showing the unsymmetrical position of the visceral ganglia and a cross section of the right nephridial organ.

" 24. The 75th section of the series, passing through the abdominal ganglion and the invagination to form the mantle cavity. It is in the region where the anterior portion of the embryo is bent backward over the foot by the nutritive sac; the foot is not represented in the figure.

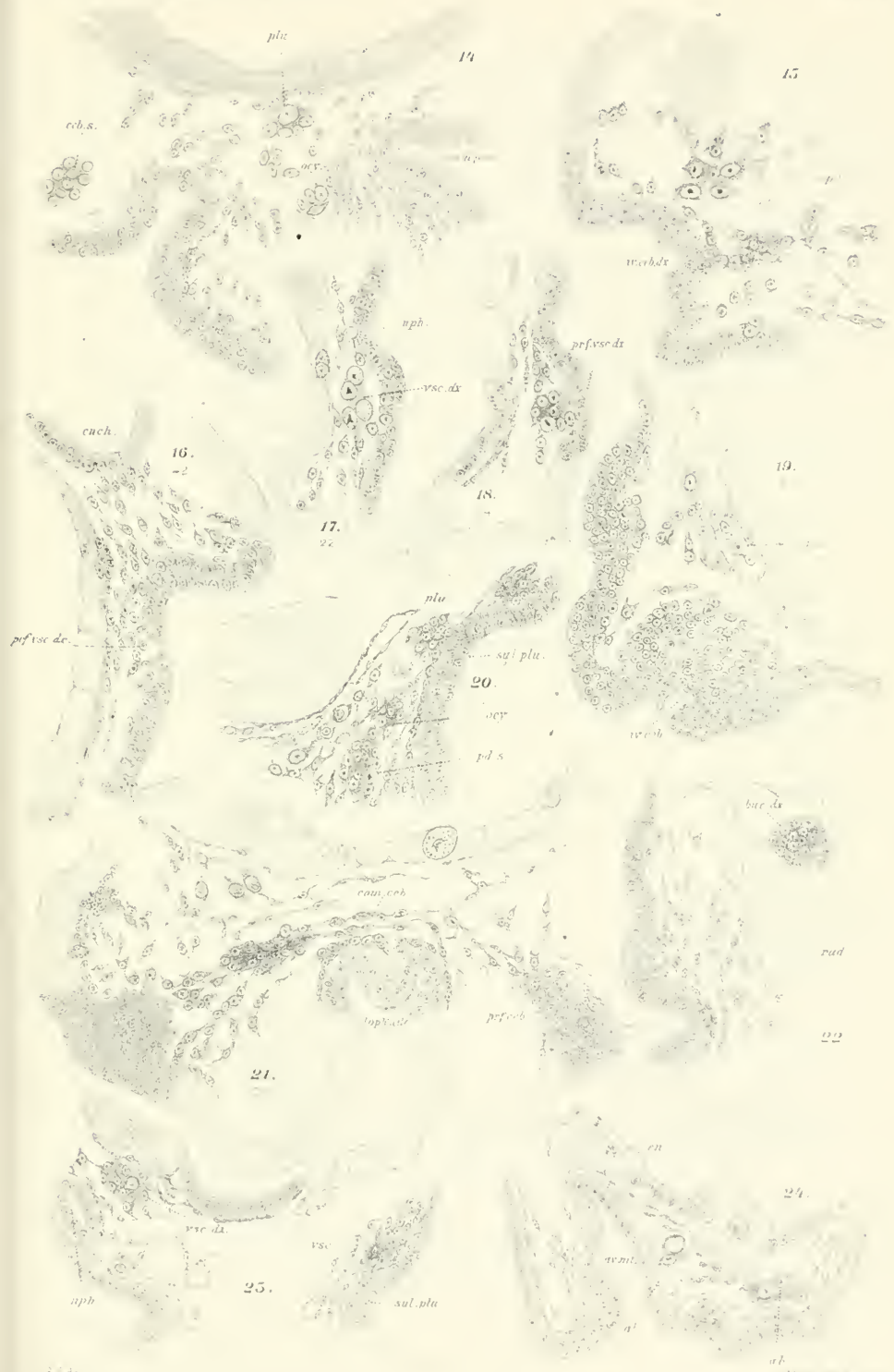
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PLATE III.

Figs. 25–27 are from the same individual (*ninth day*) as Figs. 20–24 on Plate II. They are magnified 83 diameters.

" 25. This section passes through the left cerebral ganglion, and the cerebral invagination of the right side.

" 26 shows, in addition to the cerebral invagination, that of the right eye (at the left of the figure).

" 27. Section passing through the pedal ganglia and their anterior commissure. It shows a cross section of the œsophagus, the radula sac, and the right otocyst.

" 28–31. The left surface of sections parallel to the sagittal plane from an embryo of the *tenth day*. (Figs. 58, 59, Plate IV., and Figs. 61, 63, Plate V., also belong to this series.) This individual was killed in Perenyi's fluid, and stained in picro-carminate of lithium. × 100.

" 28 and 29 are successive sections passing through the invaginations of the cerebral ganglion and the eye of the left side.

" 30 shows a cross section of the cerebral commissure.

" 31. The second section nearer the median plane than Fig. 30, showing the cerebral commissure, the position of the right visceral ganglion, and the anus already open to the exterior.

" 32–47, 51. The left surface of sections cut parallel to the sagittal plane, from an embryo of the *eleventh day*, magnified 100 diameters. Killed in Perenyi's fluid, stained in Czoker's cochineal. (Sections shown in Plate V. Figs. 62, 64, 67, and Plate VI. Figs. 70–73, also belong to this series.)

" 32–38. Seven successive sections passing through the invagination for the cerebral ganglia of the left side.

" 39. The second section nearer the median plane than Fig. 38, showing the inner sac-like end of the invagination.

" 40. The next section, showing the blind end of the invagination and the proliferated portion of the ganglion.

" 41 and 42. Successive sections (32d and 33d of the series) passing through the left pedal ganglion and the connective between the abdominal and left visceral ganglia.

" 43. Section cutting the abdominal ganglion crosswise.

" 44. The 35th section shows, in addition to the abdominal ganglion, a cross section of the anterior pedal commissure. (The 36th, 37th, 39th, and 40th sections of the series are shown in Figs. 47, 46, 45, and 51, respectively.)

" 45. Section passing through the connective between the abdominal ganglion and the right visceral ganglion.

" 46 shows the abdominal ganglion still connected with the ectoderm.

" 47. The next section to that shown in Fig. 44, passing through the abdominal ganglion.

" 48, 49. The left surface of sections cut parallel to the sagittal plane from an individual of about the *twelfth day*, magnified 100 diameters. Killed in

(See obverse.)

0.33% chromic acid, and stained in alcoholic borax-carmine. (Sections shown in Plate V. Figs. 65, 66, and Plate VII. Figs. 81, 82, also belong to this series.)

Fig. 48. A section passing through the cerebral and pleural ganglia of the right side, and also through the abdominal ganglion.

" 49 shows the proliferated portion of the cerebral ganglion and the visceral ganglion of the right side.

" 51. (See explanation of Figs. 32–47.) The section following that shown in Fig. 45. It passes through the connective between the abdominal ganglion and the visceral ganglion of the right side.

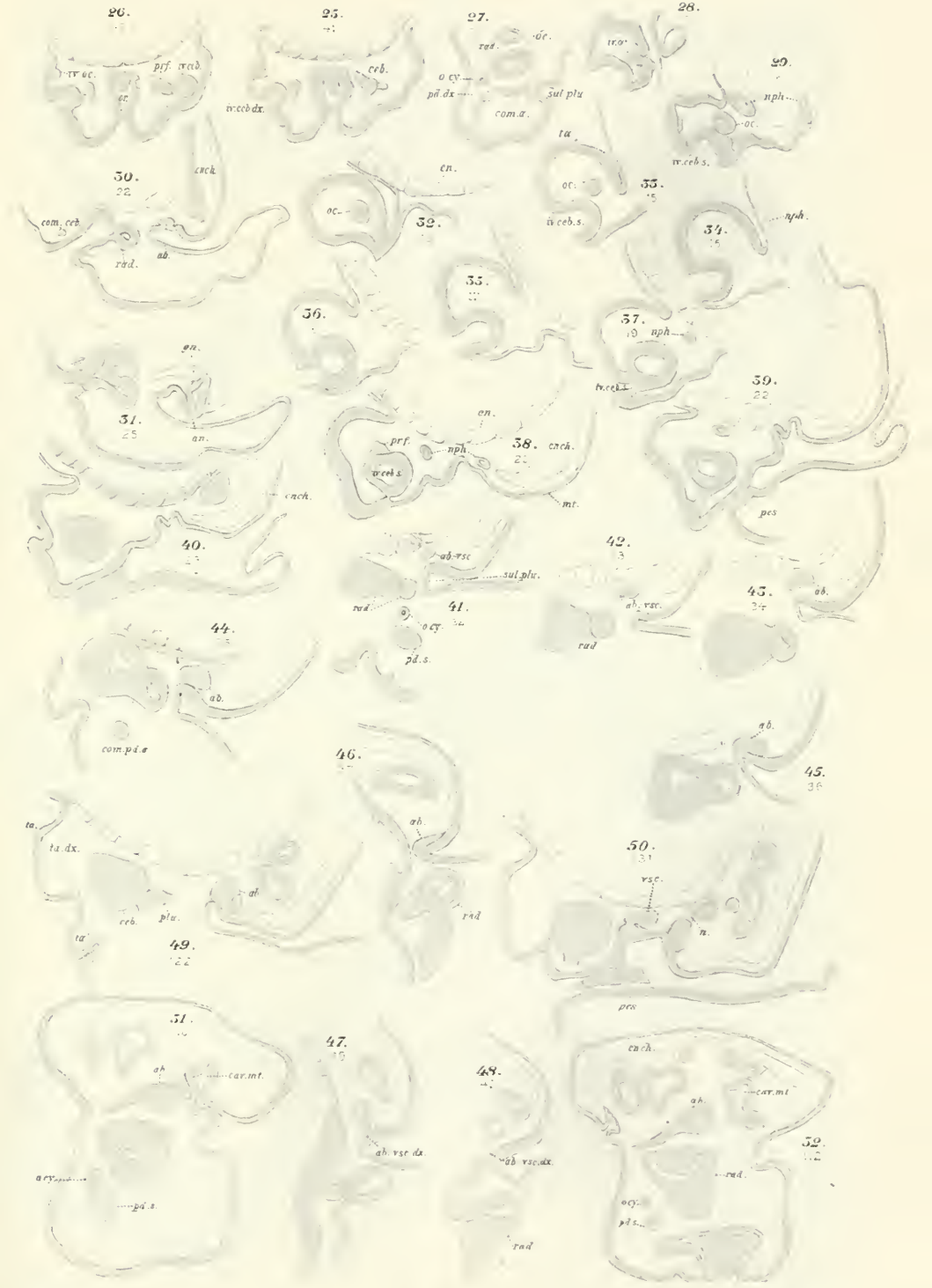
" 50, 52. The posterior surface of transverse sections of an embryo at the same stage of development (*twelfth day*) as that represented in Figs. 48 and 49. The ventral portion and the right side cut a little in advance of the dorsal portion and the left side, magnified 100 diameters. Killed in 0.33% chromic acid, stained in alcoholic borax-carmine.

Figs. 85–94, Plate VII., continue this series. The following shows the sequence of the sections: —

Section	77,	101,	103,	109,	110,	112,	113,	117,	125,	126,	128,	146.
Figure	90,	92,	91,	93,	50,	52,	85,	86,	88,	87,	89,	94.

" 50. This section passes through the left pedal ganglion and the abdominal ganglion where the latter is still attached to the ectoderm. The mantle cavity open to the exterior.

" 52. The second section in front of Fig. 50, showing that in this region the abdominal ganglion is free from the ectoderm.



A.P.H. del.

B.Meisel lith. Boston

PLATE IV.

All figures of this plate magnified 250 diameters.

Figs. 53, 56, 57, and 55 are four successive sections from the same embryo. *This was seven days old, but much more advanced than the embryos represented in* Figs. 6–13, 15, 17, and 18. Killed in 0.33% chromic acid, stained in alcoholic borax-carmine.

" 53. Posterior face of a transverse section passing through the visceral ganglia, the external opening of the nephridial organ of the right side, and the opening into the mantle chamber or respiratory cavity. (Compare Figs. 56 and 55.)

" 54. The posterior surface of a transverse section passing through the anterior pedal commissure. Embryo of about the same stage of development as the preceding, and prepared in the same way as that.

" 55. Portion of the third section following that shown in Fig. 53; it passes through the pedal and visceral ganglia of the right side.

" 56 shows both the visceral ganglia.

" 57. Portion of section showing the left pedal ganglion and cell proliferation from the ventral wall of the foot; the visceral ganglion and the external opening of the nephridial organ of the left side are also seen.

" 58, 59. Consult explanation of Figs. 28–31, Plate III.

" 58. Sagittal section passing through the proliferated portion of the right cerebral, pedal, and visceral ganglia and right otocyst. Shows cell proliferation from the ventral wall of the foot, and that the visceral ganglion is attached to the ectoderm at the margin of the mantle cavity.

" 59. A small portion of the section following Fig. 58 to show the right visceral ganglion and its attachment to the ectoderm.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cav. mt
vsc.
vsc.s.
sul. plu.
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PLATE V.

All figures magnified 250 diameters.

Fig. 60. The left surface of a section cut parallel to the sagittal plane from an embryo of the *ninth day*. The section passes through a few cells of the cerebral, the pedal, and the visceral ganglia of the right side of the body, and also shows a section of the right otocyst. Killed in Perenyi's fluid, and stained in alcoholic borax-carmine.

" 61. (Consult explanation of Figs. 28–31, Plate III.) Sagittal section (the 22d) to show the abdominal ganglion, which lies embedded in the ectoderm anterior to the pleural groove.

" 62. (Consult explanation of Figs. 32–47, Plate III.) The 32d section of the series, showing a transverse section of the cerebral commissure and a portion of the left buccal ganglion.

" 63. (Consult explanation of Figs. 28–31, Plate III.) The 15th section of the series; it passes through the left cerebral, the pedal, the pleural, and the visceral ganglia, and the wall of the left otocyst.

" 64. (Consult explanation of Fig. 62.) The 24th section; it shows the internal end of the cerebral invagination and the cell proliferation to form the larger part of the brain of the left side.

" 65, 66. Compare explanation of Figs. 48, 49, Plate III.

" 65. The 91st section of the series, showing transverse sections of the buccal commissure and the connective between the abdominal and the left visceral ganglia.

" 66. The 102d section of the series; it passes through the abdominal ganglion.

" 67. (Consult explanation of Fig. 62.) A section through the right visceral ganglion.

" 68. The posterior surface of a transverse section from an embryo of the *eleventh day*. It shows the right visceral and the abdominal ganglia. Killed in Perenyi's fluid, stained in Czoker's cochineal.

" 69. The second section anterior to Fig. 68, passing through the visceral ganglion of the right side.

(Additional sections from this specimen are shown in Figs. 77–80, Plate VI.)

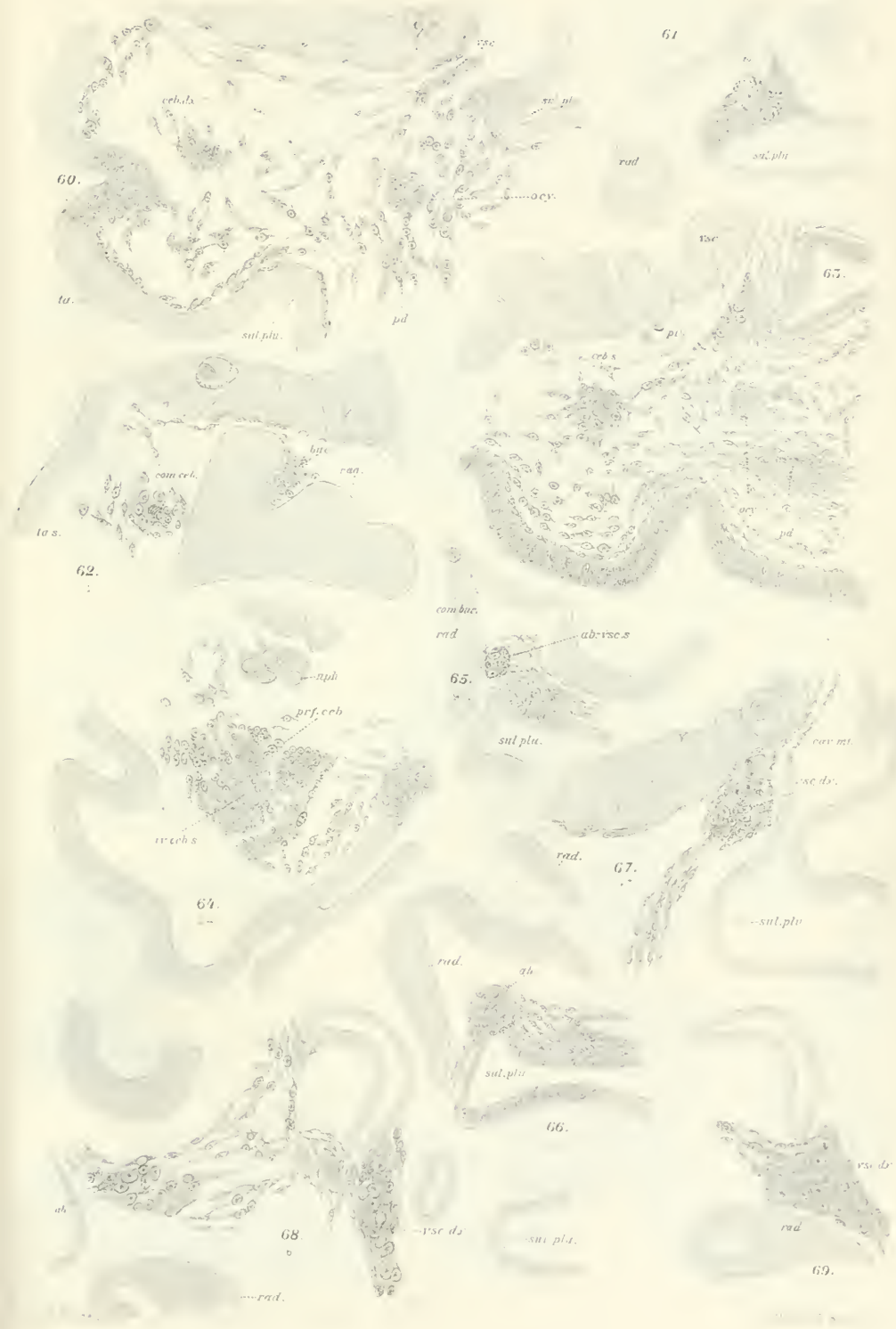
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PLATE VI.

All the figures of this plate were made from material killed in Perenyi's fluid, and all except Figs. 72, 73, and 77 are magnified 250 diameters.

Figs. 70–73. Consult explanation of Figs. 32–47, Plate III.

" 70 shows the left cerebral, pleural, and visceral ganglia in the region of the cerebro-pleural and pleuro-visceral connectives.

" 71. Section passing through the otocyst and the cerebral, pedal, and visceral ganglia of the left side. The visceral ganglion is connected with the ectoderm, and the pleuro-visceral connective is much more elongated than on the *ninth day*.

" 72. A portion of the ventral wall of the foot from the 32d section, to show the cell proliferation for the pedal ganglion. × 665.

" 73. Same as Fig. 72, but from the right side of the body.

" 74–76, 80ᵇ. The posterior surface of transverse sections from an individual of the *twelfth day*. The right side cut slightly in advance of the left. Stained in picro-carminate of lithium.

" 74. The 81st section, which passes through the otocysts and both pedal ganglia in the region of their anterior commissure.

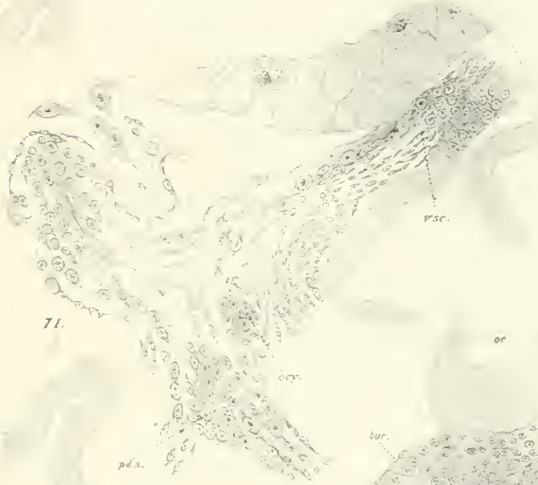
" 75 and 76. The 59th and 60th sections of the same series, showing a part of the left side of the embryo in the region of the abdominal ganglion.

" 77–80. (See explanation of Fig. 68, Plate V.) Posterior faces of four successive transverse sections through the mouth of the left salivary duct where it connects with the œsophagus. Fig. 77 shows also the buccal ganglia.

" 80ᵇ. (See explanation of Figs. 74–76.) The 107th section of the series. It shows the cerebral commissure, a few cells of the right cerebral ganglion, and the right eye.

70.

74.



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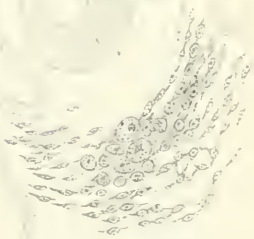

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73.

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80a.

PLATE VII.

All the figures of this plate, except Fig. 95, were made from material killed in 0.33% chromic acid, and stained in alcoholic borax-carmine. All figures are magnified 250 diameters.

Figs. 81–82. (See explanation of Figs. 48, 49, Plate III.)

" 81. The 114th section of the series; it shows the right cerebral and pedal ganglia, together with the cerebro-pedal connective, the right buccal ganglion, and the abdominal ganglion.

" 82. The 126th section of the series. It passes through a portion of the right cerebral ganglion, the right pleural and the abdominal ganglia, from the last of which a nerve runs dorsalward.

" 83, 84. The left surface of two sections (the 96th and 99th) parallel to the sagittal plane from an embryo of the *twelfth day*.

" 83. The section shows a very small portion of the cerebral ganglion, the pleural and visceral ganglia of the right side in the region of the pleuro-visceral connective, and the abdominal ganglion together with its connective with the right visceral ganglion.

" 84 shows the right visceral and the abdominal ganglia; also, a portion of the connective between the abdominal and the visceral ganglia, and a large nerve extending dorsalward from the latter.

" 85–94. (See explanation of Figs. 50, 52, Plate III.) Transverse sections, *twelfth day*.

" 85. This section (113th) shows a portion of the abdominal ganglion separated from the ectoderm.

" 86 (117th section) shows a small portion of the abdominal ganglion, as well as the pleural and visceral ganglia of the right side, together with their connective.

" 87. (126th section; compare also 125th section, Fig. 88.) A portion of the right visceral ganglion and the large nerve running dorsalward from its left dorsal margin are shown.

" 88 (125th section) shows both visceral ganglia — the left one still connected with the ectoderm — and the left pleural ganglion, together with the pleuro-visceral connective.

" 89. The 128th section, which touches the right visceral ganglion, and a large nerve running dorsalward between mantle cavity and sexual duct from the right dorsal margin of the ganglion.

" 90. The 77th section; it passes through both pedal ganglia and their posterior commissure, which is directly above the blind end of the pedal gland, the tip of which is cut.

" 91. The 103d section, which shows the right pedal ganglion and otocyst.

" 92. The 101st section, which passes through the pedal ganglia and their anterior commissure, above which is the radula sac, and below which a blood-vessel and the pedal gland are to be seen.

(See obverse)

Fig. 93. The 109th section; this passes through the abdominal ganglion at the place of its connection with the ectoderm lining the median wall of the mantle cavity. It also shows a portion of the connective from the abdominal ganglion to the left visceral ganglion.

" 94. The 146th section of the series; it shows a cross section of the neck of the cerebral invagination, and a small portion of the cerebral ganglion of the left side.

" 95. The left surface of the 54th section, from an individual of the *fourteenth day*. The section passes through the right visceral and the abdominal ganglia, showing their close connection with each other at this time, and it also cuts the right buccal ganglion. The material was killed in Perenyi's fluid, and stained in picro-carminate of lithium.

The following figures are drawn from sections of the same series as Fig. 95: Plate VIII. Figs. 96, 101, 102; Plate IX. Fig. 114. The sequence of sections is this: —

Section	52,	54,	56,	66,	82.
Figure	101,	95,	102,	114,	96.

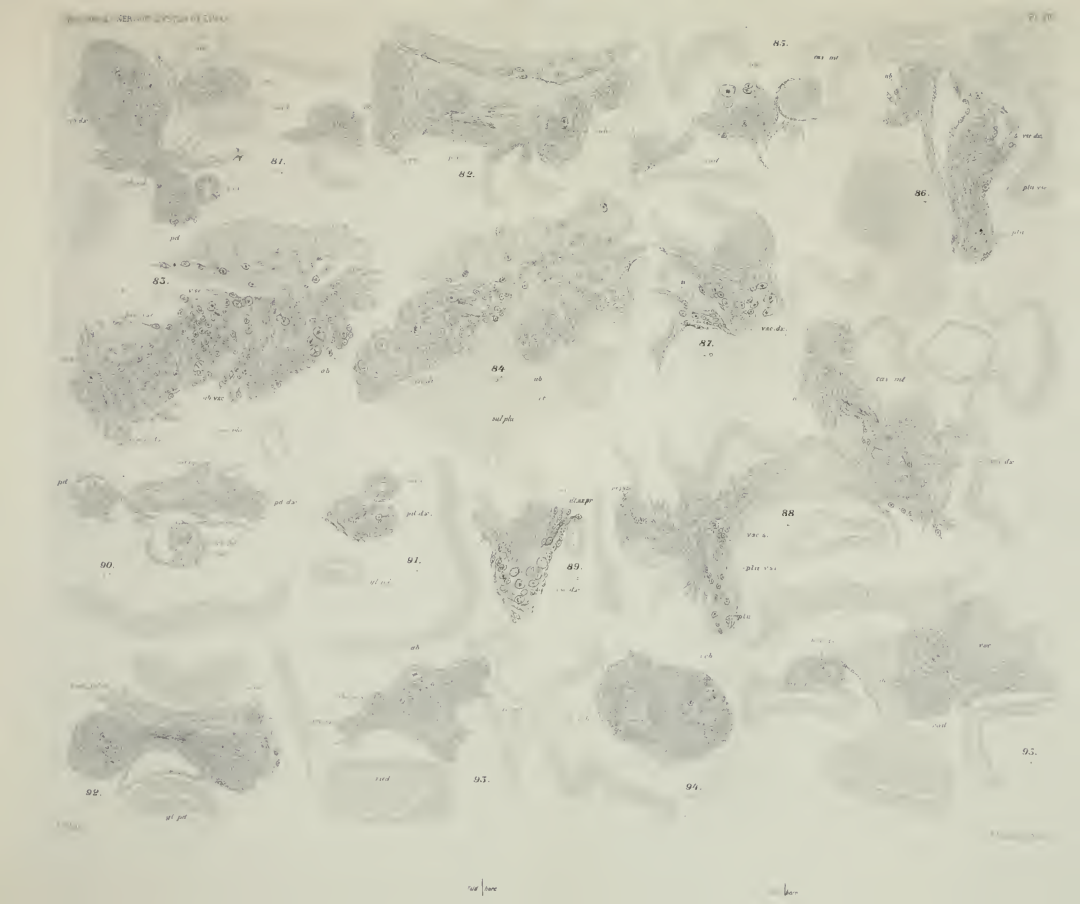
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PLATE VIII.

Fig. 96. (See explanation of Fig. 95, Plate VII.) The 82d section; it passes through the ocular tentacle, showing in section the cerebral invagination and ganglion of the right side. × 100.

" 97–100. Posterior faces of transverse sections, the right side a little in advance of the left, from an embryo of the *fourteenth day*. Killed in Perenyi's fluid, stained in picro-carminate of lithium. — Figs. 104, 106; also Plate IX. Figs. 115–120, and Plate X. Figs. 121, 123, 125, 126, belong to the same series as Figs. 97–100. The sequence of sections is: —

Section	81,	87,	92,	98,	102,	104,	109,	111,	113,	113,	115,	121,
Figure	97,	119,	98,	99,	118,	100,	115,	116,	104,	117,	123,	120,
	122,	122,	127,	139.								
	106,	125,	121,	126.								

" 97. The 81st section; it passes through the pedal ganglia, a few sections behind the posterior commissure. × 100.

" 98 and 99. The 92d and 98th sections; they pass through the pedal ganglia between the two commissures. × 100.

" 100. The 104th section, two sections in front of the anterior commissure. It shows the right otocyst in addition to the radula sac and pedal gland. × 100.

" 101, 102. (See explanation of Fig. 95, Plate VII.)

" 101. The 52d section of the series, showing the abdominal ganglion, and a cross section of the cerebral, buccal, and both pedal commissures. × 100.

" 102. The 56th section; it passes through the visceral and buccal ganglia of the right side, and a portion of the abdominal ganglion. It shows the cerebral and pedal commissures, as well as a sagittal section of the foot gland. × 100.

" 103, 103ª. The posterior surfaces of transverse sections from an embryo ot the *seventeenth day*. 0.33% chromic acid; alcoholic borax-carmine. — Additional sections from this series are shown in Figs. 105, 108–113, and Plate X. Figs. 122, 127. The sequence of sections is indicated by the following: —

Section	111,	176,	180,	186,	187,	194,	211,	212,	217,	225,	225.
Figure	103ª,	109,	110,	111,	112,	113,	103,	105,	122,	108,	127.

" 103. The section passes through the cerebral ganglia in the region of the cerebro-pedal connective. The wall of the body is not represented, but merely the ganglia, together with the œsophagus, the ducts of the salivary glands, the radula sac, and the right ocular tentacle. × 140.

" 103ª. This section (111th) passes through the pedal, pleural, and visceral ganglia in the region of the pleuro-pedal connective. A large nerve passes from the dorsal margin of each pedal ganglion to the lateral wall of the body. × 83.

(See obverse.)

Fig. 104. (See explanation of Figs. 97–100.) The 113th section; it passes through the pleural ganglia and the abdominal ganglion. A large nerve connects the abdominal ganglion with a pocket-like infolding from the wall of the mantle cavity. × 100. Figure 117 (Plate IX.) shows a portion of this section more highly magnified.

" 105. (See explanation of Figs. 103, 103ª.) The 212th section; it passes through the cerebral commissure. × 100.

" 106. (See explanation of Figs. 97–100.) This section, the 122d, passes through the right cerebral invagination, the right cerebral and buccal ganglia with their connective, and the right visceral ganglion. It also shows the left pleural and visceral ganglia with their connective. × 100.

" 107. Is a combination of two successive sections cut parallel to the sagittal plane from an embryo of the *sixteenth day*. It shows the cerebral, pedal, and pleural ganglia, with their connectives, and the otocyst of the left side. The position of the pedal gland is shown by dotted lines. Perenyi's fluid; picro-carminate of lithium. × 100.

" 108-113. See explanation of Figs. 103, 103ª.

" 108. The 225th section of the series shows the cerebral invaginations. The right one (an enlarged view of which is seen in Fig. 127) is cut lengthwise, it being still open to the exterior; the left one transversely. The cerebral ganglia and their lateral lobes, and the buccal ganglia with their commissure crossing between the radula sac below and the œsophagus above, are also shown. × 83.

" 109. The 176th section, which passes through the pedal ganglia and the abdominal ganglion. × 83.

" 110. The 180th section; it shows, in addition to the organs seen in Fig. 109, a small portion of the left visceral ganglion and the otocysts.

" 111. The 186th section; it passes through the pedal ganglia, a portion of the pleural ganglion of the right side, both visceral ganglia, and the abdominal ganglion. It also shows the connective from the abdominal to the right visceral ganglion, and a stout nerve arising from the latter. × 83.

" 112. The 187th section shows the pedal, pleural, and visceral ganglia. × 83.

" 113. The 194th section. This shows, in addition to the ganglia, the nerve which arises from the left visceral ganglion. × 83.


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PLATE IX.

All the figures of this plate are magnified 250 diameters, and were made from material killed in Perenyi's fluid, and stained in piero-carminate of lithium.

Fig. 114. (See explanation of Fig. 95, Plate VII.) The 66th section; it passes through the cerebral, the pedal, the pleural, and the visceral ganglia of the right side in the plane of the cerebro-pedal and cerebro-pleural connectives. It also shows the right otocyst.

" 115–120. See explanation of Figs. 97–100, Plate VIII.

" 115. The 109th section; it shows a portion of the abdominal ganglion at the right of the radula sac.

" 116. The 111th section; it passes through the abdominal and right pleural ganglia.

" 117. The 113th section; it shows the abdominal ganglion where it passes above the radula sac, and a portion of the right pleural ganglion. (Compare Fig. 104, Plate VIII.)

" 118. The 102d section; it passes through the pedal ganglia in the plane of their anterior commissure. It also shows the right otocyst.

" 119. The 87th section. The pedal ganglia in the plane of their posterior commissure.

" 120. The 121st section, which passes through the visceral and buccal ganglia of the right side, and shows a portion of the buccal commissure.

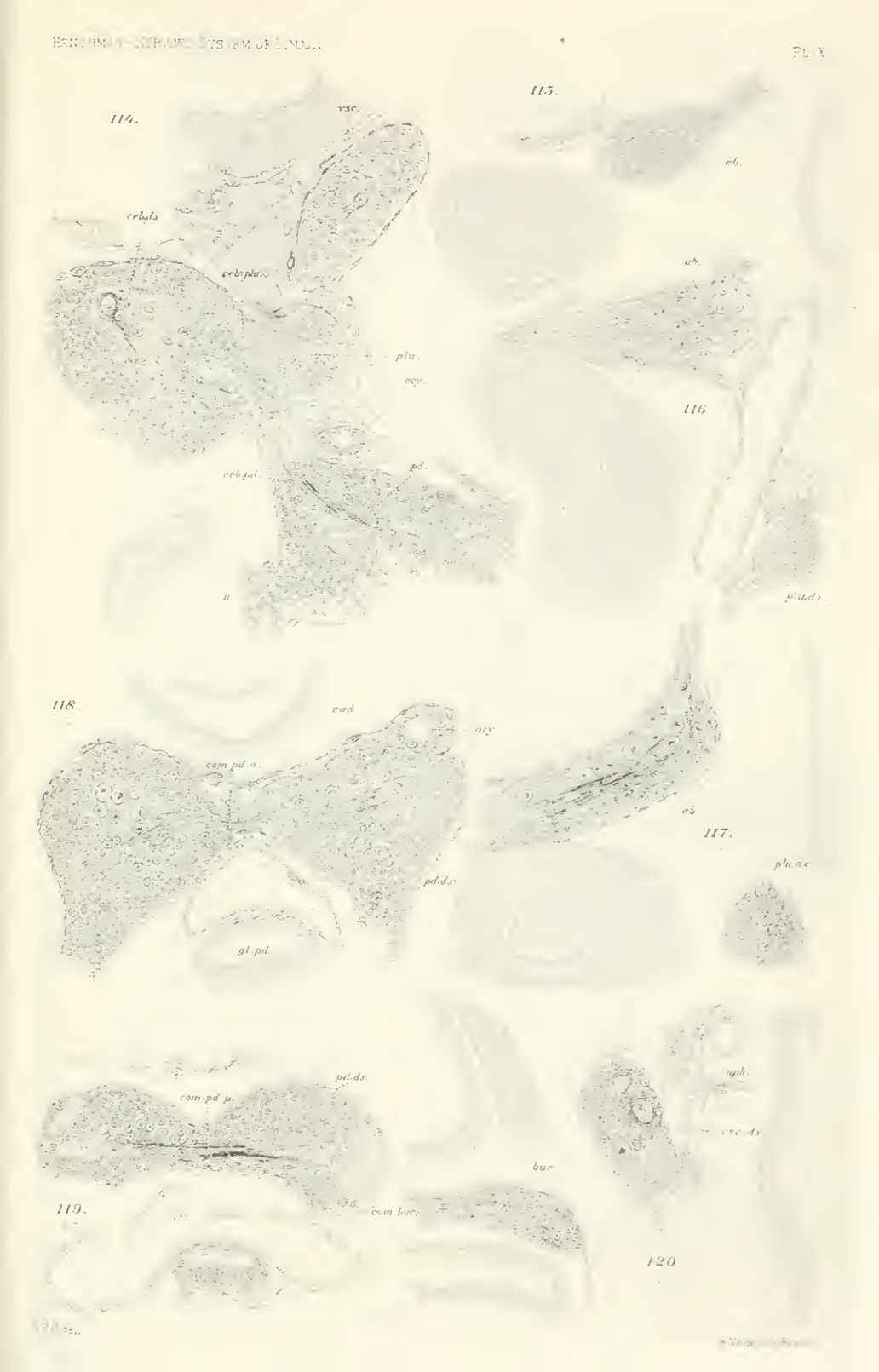
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PLATE X.

Fig. 121. (See explanation of Figs. 97–100, Plate VIII.) The 127th section; it passes through the left cerebral invagination, also through the left cerebral and buccal ganglia, and their connective. × 237.

" 122. (See explanation of Figs. 103, 103ª, Plate VIII.) The 217th section of the series. It passes through the right cerebral ganglion and its lateral lobe; it also shows the ocular tentacle and the wall of the right eye, transverse sections of the œsophagus, salivary glands, radula sac, and primary sexual duct. × 237.

" 123. (See explanation of Figs. 97–109, Plate VIII.) This section passes through the right pleural and visceral ganglia, a small portion of the left pleural and visceral ganglia, and the abdominal ganglion, which lies between the œsophagus and radula sac. × 250.

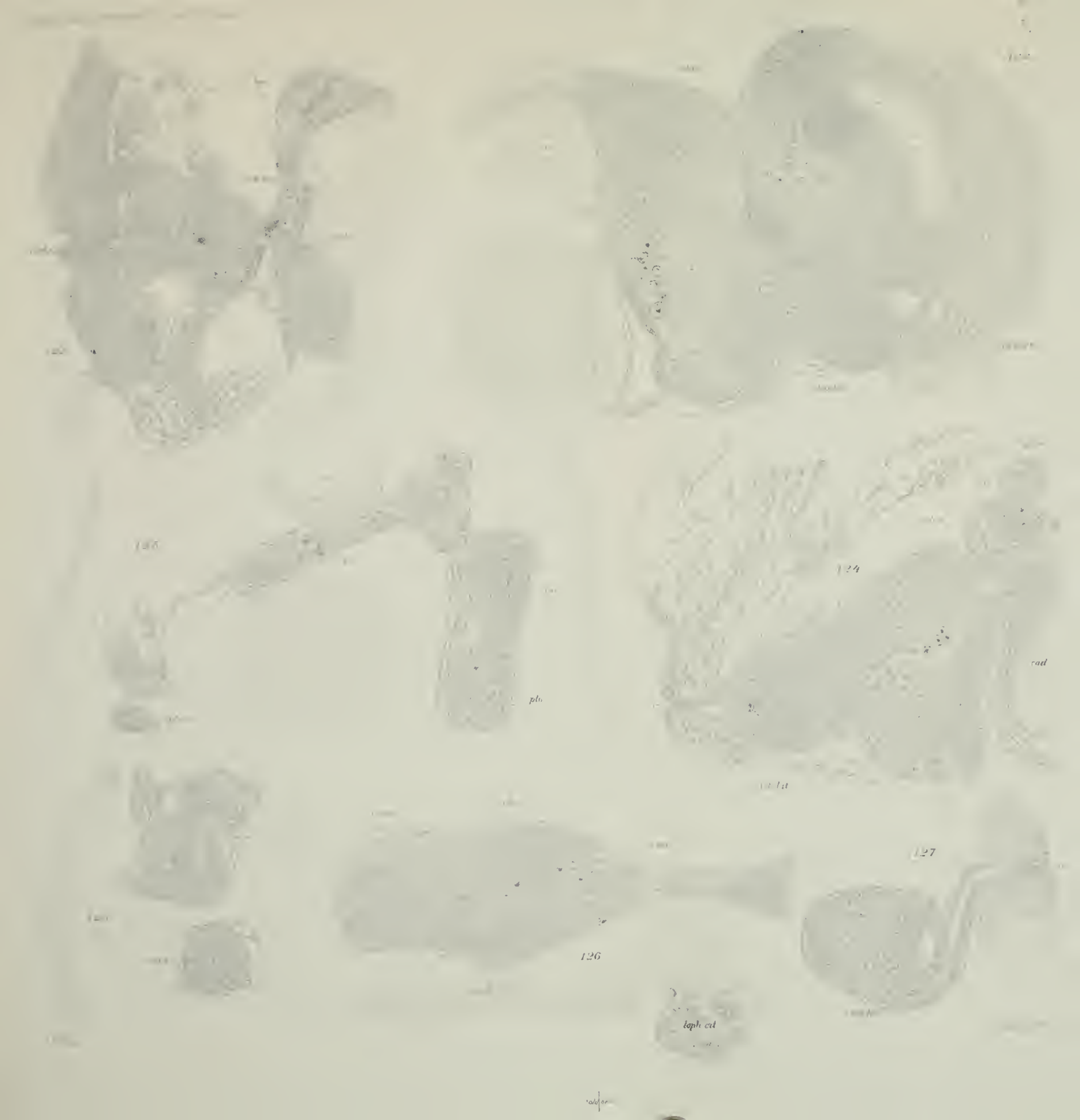
" 124. The posterior face of a transverse section from an embryo of the *sixteenth day*. The left side is cut a little in advance of the right. The section passes through the cerebral invagination, — still open to the exterior, — the cerebral ganglion of the left side and its lateral lobe, and the left buccal ganglion. It also shows in cross section the duct of the salivary gland, and a small portion of the wall of the radula sac. × 237. Perenyi's fluid; picro-carminate of lithium.

" 125, 126. See explanation of Figs. 97–100, Plate VIII.

" 125. The 122d section; it shows the left pleural and visceral ganglia, with the pleuro-visceral connective, and a small portion of the left cerebral ganglion. × 250.

" 126. The 139th section; it shows in section the left cerebral invagination, the cerebral ganglion, and the cerebral commissure. × 250.

" 127. (See explanation of Figs. 103, 103ª, Plate VIII.) The 225th section; it shows the cerebral invagination, and the right lateral lobe of the brain. (Compare Plate VIII. Fig. 108.) × 237.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No. 8. — *The Parietal Eye in some Lizards from the Western United States.* By W. E. Ritter.[1]

With a single though notable exception, the numerous authors who have written on the parietal organ in vertebrates since the papers of de Graaf ('86[a] and '86[b]) and Spencer ('86 and '87) appeared, have agreed that the structure is, or at least was in ancestral vertebrates, an eye. This belief is based entirely on the structure of the organ, no physiological experiments or observations on the habits of the animals possessing it having yet been produced in proof of its function.

Leydig ('89) alone, in a recent preliminary paper on the subject, has denied its optical nature, and has assigned to it an entirely different function; though in a second preliminary, still more recent ('90), he expresses his denial with considerably less confidence. He rejects the eye hypothesis, however, on the same grounds that have led others to adopt it; namely, on the grounds of its structure, and especially of its relation to the brain.

He believes that what is generally held to be an optic nerve is in fact merely a string of connective tissue.

Among those who believe the organ is or has been an eye, there are important differences of opinion as to its present value. By Ahlborn ('84), de Graaf, Spencer, and several other more recent writers, it is believed to be degenerate and entirely functionless in all living vertebrates. Rabl-Rückard ('86) has expressed the opinion that the organ may still be of use in furnishing its possessors with a more delicate means of detecting differences of temperature than exists elsewhere on the body. Béraneck ('87) believes that, while the structure is probably of an optical nature in some vertebrates, it has become so secondarily; that the primitive function of the epiphysis, common to the brains of all vertebrates, was something entirely unknown to us now, though not concerned with vision; but that in the Cyclostomes, the Amphibians, and the Reptiles it has taken on, secondarily, the function and form of an eye.

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXII.

But even were it established beyond question that the organ is a degenerate eye, there would still remain several quite distinct and very interesting problems to be solved. The most fundamental of these is probably that of its homology. Much has been written on this question by the various recent authors, but even less unanimity of opinion has been reached here than on the question of its structure and function. The question why the organ has remained so well developed in a few systematically widely separated groups of vertebrates, while in all others the process of degeneration has gone so far as to leave but a mere trace of the proximal portion of the epiphysis, has not been much discussed. It is not my purpose in the present paper to enter upon a discussion of the theoretical questions involved, and they are here adverted to merely to point out the need — as indicated by their importance and the discordance of the opinions now held with regard to them — of a larger body of facts on the subject than we yet possess. For the present, I confine myself to a presentation of the facts observed, and my interpretation of them as bearing upon some of the minor conclusions reached by other writers, hoping to be able to pursue the subject further in the near future, when situated in a region where an abundance and a variety of material, adult and embryonic, can be obtained, and where observations on the habits of the animals can be made.

The present work was undertaken at the suggestion of Prof. E. L. Mark. I wish here to acknowledge my indebtedness to Mr. G. H. Parker, of the Museum of Comparative Zoölogy; to Mr. J. J. Rivers, Curator of the Museum at the University of California; and to Mr. T. C. Palmer, of the United States Department of Agriculture, Washington, for material used; and also to Mr. S. Garman, of this Museum, for assistance in determining the species studied.

A word as to technique. For studying the structure of the retina it is very desirable to remove the great quantity of pigment that invariably obscures the histological elements in this region. Neither nitric nor hydrochloric acid, nor the alkalies, have any visible effect on this pigment, but the desired result was reached by the use of chlorine gas. The mounted, unstained sections were covered by a film of ninety per cent alcohol, and placed in a tight glass chamber, in which was also confined a small vessel containing a mixture of potassium chlorate and hydrochloric acid for generating the gas. By being careful that the slide on which the sections were mounted occupied a perfectly horizontal position, and was so placed that the film of alcohol could not be

drawn off by capillary attraction, the film soon became saturated with the gas, and did not need renewing. From forty-five minutes to an hour, depending on the quantity of pigment, was sufficient time in which to accomplish the work. Considerable difficulty was found in removing the chlorine from the sections. As it had thoroughly penetrated the tissue, simple washing, even though prolonged, did not wholly remove it; but by washing carefully, and then leaving the whole slide immersed in ninety per cent alcohol for twelve or fourteen hours, the gas was entirely removed. A good quality of Schällibaum's fixative held the sections perfectly through all this and the subsequent staining.

For decalcifying and hardening the tissues I have found Perenyi's fluid more satisfactory than anything else tried, the two processes being accomplished at the same time by this reagent.

Of the several species of lizards which I have studied I shall describe the structure in only three, namely, Phrynosoma Douglassii, P. coronata, and Uta Stansburiana, these being the only ones that have presented anything new or of special interest.

Phrynosoma Douglassii.

1. *External Appearance.* — Concerning the external appearance of the organ little need be said, since it differs in no essential particular from what has been amply described and illustrated in numerous other lizards. The scale marking the position of the eye is quite conspicuous, especially in very young individuals, where it is of a rather lighter color and larger size, relatively, than in the adult. In old individuals the great development of the surrounding scales and tubercles renders it somewhat less noticeable than it otherwise would be, but it is always readily distinguished, not only by its median position, but also by the absence of pigment and by its translucent appearance.

2. *The Parietal Vesicle.* — Figure 1, drawn from a sagittal section through the dorsal wall of the head, shows the form of the vesicle and its position within the parietal foramen and with reference to the external and internal surfaces of the wall. It lies within the parietal foramen, though extending somewhat above the dorsal surface of the parietal bone, firmly embedded in connective tissue, so that when the wall of the head is separated from the brain the vesicle always goes with the former. The tissues composing the dorsal wall of the head are, excepting the corneous layer of the skin, quite different immediately over the vesicle from those of the surrounding regions. The epidermal layer of the skin

elsewhere sends down irregular cone-shaped masses, which penetrate and become lost in the underlying connective tissue, thus firmly uniting the two layers. Over the vesicle, however, these processes are wholly wanting, the under surface of the epithelial layer being even, and sharply limited from the connective tissue. These processes are especially well developed immediately beyond the margin of the disk of the vesicle, where they carry the cells of the epidermal layer (*e'drm.'*) considerably deeper than their general level. The connective tissue between the vesicle and the epidermal layer is composed of fibres considerably finer and looser than those found in other places, and, furthermore, the fibres are here disposed at various angles to the surface of the skin, whereas elsewhere they are approximately parallel to this surface (*con't. tis.'*). Pigment, which is found in great abundance in the skin in all other regions of the body, is always entirely absent here. It will thus be noticed that each of the tissues over the vesicle is considerably more penetrable to light than are the corresponding ones elsewhere. The connective-tissue fibres immediately around the vesicle are arranged concentrically to its surface, and are, especially in the proximal two-thirds of their extent, considerably finer and closer than elsewhere. A kind of capsule for the vesicle is thus formed, and it is this alone which separates it from the cranial cavity. The fibres of a string of tissue extending from the distal end of the epiphysis can be traced, though with some uncertainty, to this capsule, but I find no indication of their passing through it, or even entering it, though I have given special attention to this point.

The internal surface of the cranial wall in the region of the vesicle presents a depression, which is much less marked, however, than a corresponding one in P. coronata, to be referred to hereafter. Running through the connective tissue at the bottom of this depression, and hence near the deep surface of the vesicle, are found a number of blood-vessels of considerable size and well filled with blood corpuscles (*va. sng.*). The vesicle itself is elliptical in sagittal section, the major axis, 258 μ long in the specimen figured, having the direction of the long axis of the head. In transverse section it is slightly elongated dorso-ventrally, and measures in this axis 171 μ.

The cavity in sagittal section shows a triangular outline, the base of the triangle being on the dorsal or lens side. From this outline in the sagittal section the form gradually changes to that of an ellipse in the last sections on each side that cut the cavity; so that the form of the cavity is approximately that of a broad, flat cone, the base directed

outward and the apex inward. The base of the cone is slightly concave, corresponding to the convexity of the inner surface of the lens.

The wall of the vesicle is very distinctly differentiated into lens (*lns.*) and retinal (*rtn.*) portions, the latter forming about two thirds of the whole. The lens is slightly biconvex, the two convexities being very nearly equal. The line of demarcation between the lens and the retina is a sharp one, though the two portions are plainly continuous. The cells composing the lens are large and distinct in outline, each one extending entirely through its thickness (Plate II. Fig. 5, *cl. lns.*). Their nuclei are large, easily stainable, and somewhat granular; they are uniformly situated near the internal ends of the cells. The lens is entirely without pigment.

Figure 5 represents a highly magnified portion of a longitudinal vertical section of the vesicle taken from near the median plane. In the retinal portion six regions or zones may be distinguished. Passing from the external surface toward the cavity, we find (1) a basement membrane (*mb. ba. ex.*). This is very thin, but uniform in thickness, and is of a structureless nature. From many points on this membrane fine processes radiate into the connective tissue enveloping the vesicle (Plate I. Fig. 3, *prc. r.*). These processes do not appear to be of a muscular nature, but rather the same in structure as the basement membrane from which they arise. (2) A zone containing a few scattered nuclei (*nl.'*), and fine-grained sparsely but evenly distributed pigment (*pig.*). No cell boundaries can be made out in this zone. . The nuclei, few in number, form a single layer, and are situated near the basement membrane. They are very nearly round, exhibiting no tendency to elongate in the radii of the vesicle. Areas in their centres, which are somewhat more deeply stained than the rest of the nuclei, and which are probably nucleoli, are to be seen. (3) A zone (*z.''*) in which are distinguishable neither cells, nuclei, nor pigment; only a uniform, fine-granular, slightly stainable substance, of much the same nature, apparently, as the cell substance in those regions of the retinal portion in which cell boundaries can be distinguished. Whether or not this zone represents the centrally directed ends of a layer of cells, the nuclei of which are the ones found in zone 2, I am unable to say, but it probably does. (4, 5) The next two zones are distinguished from each other only by the difference in the elements composing them, no distinguishable line of separation existing between the two. The most obvious difference between the constituent elements of these two regions is in the shape of the nuclei, those in zone 4 being approximately spherical

(*nl.*^{II}), while those in zone 5 are much elongated in the radii of the vesicle (*nl.*^{III}). The suggestion at once comes that this difference is due solely to the crowding together of the cells nearest the internal surface of the retina, and hence that the two zones should in reality be regarded as but one. If, however, the difference in shape of the nuclei were the result solely of such crowding, we should find a complete gradation from the spherical to the elongated form in passing from without inward; but such a gradation is not found in fact. Furthermore, on close examination with high powers, it is found that the nuclei differ in structure as well as in form. An irregular stellated area can be detected in the centres of some of the spherical ones which does not exist in the elongated ones; also, the entire substance of the former is slightly more granular than that of the latter. In the fifth zone cell boundaries (though not well shown in the figure) can be quite distinctly traced to the internal basement membrane; but how the cells of the fourth and fifth zones are related I have been unable to determine, since cell boundaries in the fourth zone cannot be traced. (6) The last layer may be designated as an internal basement membrane (*mb. ba. i.*), though it differs somewhat in structure from the external basement membrane, being of a granular nature. It extends over the surface of the lens, as well as over the retina, and is rather more compact in the former than in the latter region. Projecting into the cavity of the vesicle from the retinal portion are found certain structures concerning the nature of which I am not quite sure, but believe them to be secretions from the cells of the fifth zone. They are in general elongated, and pointed at their free ends, though their outlines are ragged and indefinite. They always stain most deeply at their internal free ends. In many cases, as at *, they are seen to be continuous with the cells of the fifth zone through the internal basement membrane. These structures may correspond to what de Graaf has described and figured as existing on the internal surface of the retina of Anguis, and has called "Staafjeslaag," but which Spencer and others believe to be merely a coagulum from the fluid that probably filled the cavity in the recent state. It is, however, scarcely possible to account for the structures here under consideration in this way, as is to be seen from my description and figures of them; furthermore, a coagulum (*cog.*) does exist in addition to these.

Within the substance of the retina (Fig. 5, *va. rtn.*) are found a number of cavities varying in diameter, as measured in the plane of the sections, from 5.5 μ to 22 μ. The sections of these cavities are never

quite circular, but are never much elongated. In many, though not in all, an exceedingly thin endothelial lining can be seen, and in a few instances blood corpuscles are found in the cavities (Plate I. Fig. 4, *en'th. va.* and *cp. sng.*). Although none of these cavities were found to extend through more than four or five sections, each 7.5 μ in thickness, and although in no instance was it possible satisfactorily to trace a connection between them and the blood-vessels lying outside the vesicle, it still seems quite certain that they form a network of fine blood-vessels ramifying through the substance of the retina. Owing to the fact that in some instances no lining membrane to these cavities can be found, and that their outlines are not sharply marked, the possibility of their having been artificially produced by the removal of pigment masses suggests itself; but the definiteness of the outline of many others and their endothelial lining membranes, in which much-flattened nuclei are found, strips this conjecture of its plausibility. If these are really blood-vessels, it might appear that some of them would be seen cut longitudinally; and while it is true that in many cases focusing shows the cut walls to be very oblique to the plane of the section, still no sure instance of a vessel cut lengthwise has been seen. When, however, one considers the exceeding delicacy of the endothelial lining, and the fact that no differential staining takes place, it does not seem impossible that such sections may exist, and yet escape detection. These cavities have no regularity of arrangement, but are for the most part confined to zones 2, 3, and 4. In no instance has one been seen confluent with the cavity of the vesicle.

These may possibly correspond to what Owsjannikow mentions as having been seen by him in Chamæleon vulgaris. He says: "Am hintern Rande der Retina findet sich an einigen Schnitten das Lumen eines Rohrs, von dem nicht mit Bestimmtheit gesagt werden kann, ob es einem Blutgefässe oder einem anderen Gewebe angehört." (Owsjannikow, '88, p. 16.)

3. *The Epiphysis.* — Figure 9 (Plate III.) represents a sagittal section of the epiphysis, and so much of the brain as is necessary to show the relation of the former to the latter. The entire structure, or, more properly, the combination of structures that must be considered at this time, presents the form of a curved cylinder, one end of which is produced into a cone, while the other end has a hopper-shaped excavation. In keeping with the usual method of designation, I shall call the whole structure the epiphysis, though, as the sequel will show, it is doubtful if this is justifiable. The excavated end is proximal, the

excavation being the continuation of the cavity of the third ventricle into the epiphysis. The conical end, then, is distal, and rises somewhat above the level of the cerebral hemispheres. The curved axis forms very nearly a segment of the circumference of a circle, and is directed upward and forward from its point of origin from the brain. Continuing anteriorly from the apex of the cone is a string of connective tissue (*con't. tis.*), which passes to the region of the parietal vesicle, and in the distal portion of its course comes close in contact with the dura mater of the brain. The axis of the cylinder, if we consider it as continued to the anterior termination of this connective-tissue string, describes very nearly a semicircumference. The most anterior point in the connection of the epiphysis with the brain is at the junction of the cerebrum with the optic thalamus, somewhat anterior and dorsal to the superior commissure (*com. su.*). For a short distance above its connection with the brain in this anterior part, the epithelial nature of the epiphysial wall is less distinct than at a higher level, where the wall becomes thicker, and is composed of a single layer of more or less cuboid nucleated cells, which stain readily in borax carmine or hæmatoxylin (Plate III. Figs. 8, 9, *e'th.*). Also at this level the wall becomes thrown into a highly complicated system of folds; and it is this folded epithelium, containing within its folds great quantities of blood corpuscles, that forms a large bulk of the whole epiphysis (Figs. 8 and 9, *e'th.* and *cp. sng.*).

In the section represented in Figure 9 no connection exists between the epithelium of the posterior portion of the epiphysis and the brain, and it is doubtful if such connection exists here in any of the sections of this specimen; at any rate, if it does exist, it is exceedingly thin and limited in extent. There is, however, an undoubted connection in this region in P. coronata, which will be described later; but even in this latter species the posterior wall of the epiphysis is much less developed than the anterior wall. The exceedingly thin epithelium that forms the posterior wall in P. Douglassii would, as is evident from its position and from comparison with P. coronata (Plate IV. Figs. 11 and 12), form a connection with the brain roof had not a separation taken place, either artificially or as a result of degeneration. This wall is closely applied to the anterior, concave side of the blood sinus to be presently described, and at a considerable distance above the brain is continuous with the anterior wall of the epiphysis. The space included by these walls is the hopper-shaped excavation in the proximal end of the cylinder already mentioned, — an extension of the cavity of the third

ventricle (*vnt.*[3]) into the epiphysis. Intimately connected with the distal end of the portion of the epiphysis thus far described is found a vesicle (*eph. vs.*), the thick walls of which are composed of columnar epithelium, and thus differ markedly from the folded epithelium of the anterior wall previously described. This vesicle is much flattened antero-posteriorly, its longest axis lying very nearly in the axis of the cylinder to which the epiphysis as a whole has been compared. That the structure here described is a separate vesicle, and that its cavity is not continuous with the cavity already described as a continuation of the third ventricle, admit of easy and satisfactory demonstration, not only in this particular instance, but also in all other individuals both of this species and of P. coronata of which sections have been made. In passing through the entire series of sections, it is easily seen not only that the two cavities nowhere approach more nearly to confluence than in the one represented in the figure, but also that the walls of the vesicle and those of the more proximal part of the epiphysis with which they are in relation are clearly distinct. The separateness of these two structures will appear more clearly when we come to consider the same parts in P. coronata. Passing upward and forward from the distal end of this vesicle is to be seen a bundle of connective-tissue fibres which becomes blended with the string of connective tissue already described as running from the apex of the cone to the region of the parietal vesicle. There is no indication that the epithelial wall of the epiphysial vesicle, as it may be called, passes into this string.

Covering the whole postero-dorsal convex side of the portion of the epiphysis thus far described, and even extending considerably beyond its distal extremity, is an immense blood sinus fully distended with blood corpuscles (Fig. 9, *sn. sng.*, and Fig. 8, *cp. sng.*).

Phrynosoma coronata.

1. *General Description.* — Figure 2 (Plate I.) represents a transverse section of the dorsal wall of the head, passing through the middle of the parietal eye of P. coronata. The description of the external appearance and of the vesicle and its surrounding structures given for P. Douglassii requires modification in only a few points to become applicable to this species. The depression mentioned as existing on the internal surface of the wall of the brain-case immediately under the vesicle in P. Douglassii becomes in this species a deep pit. To correspond with this pit the external surface of the wall immediately over the vesicle forms

a low, broad cone, a condition which gives quite a different general appearance to the sections in the two species. In P. coronata the vesicle is situated somewhat nearer the external surface of the cranial wall than in P. Douglassii; and the intervening connective tissue differs less, both as regards the fineness and direction of its fibres, from the adjacent tissues, than in the case of P. Douglassii. The vesicle, with its connective-tissue capsule, protrudes into the bottom of the pit considerably. The pit is bridged over by the dura mater of the brain, and thus a chamber is formed in which a great quantity of blood corpuscles is found (*cp. sng.*). It will be remembered that no such blood sinus in this region exists in P. Douglassii, but that numerous blood-vessels do occur here. In P. coronata, however, the sinus replaces the vessels.

2. *The Parietal Vesicle.* — With regard to the vesicle itself, the only points in which it differs very essentially from that found in P. Douglassii are the absence of the cavities in the retina regarded as blood-vessels, and the far less perfect development of the structures projecting from the internal surface of the retina into the cavity of the vesicle. The latter difference I am inclined to think due to the probably somewhat greater degree of degeneration of the retinal cells which secrete these structures. That this portion of the retina is more degenerated in P. coronata may be supposed from the fact that we find here considerably more pigment than in the corresponding region in P. Douglassii. However, too much stress must not be laid on the greater or less quantity of pigment, since the quantity is quite variable even within the same species. In one individual of this species pigment was found, though in small quantity, in the lens.

3. *The Epiphysis.* — Although this structure does not differ in any essential particular from what we have already seen in the preceding species, the fact that several of the points which go to make the study of the epiphysis of much interest are here well brought out, has made it seem best to describe and illustrate the organ in detail. Figures 10, 11, and 12 (Plate IV.) present vertical longitudinal sections from the same animal at different planes to the left of the median plane, Figure 12 being very nearly median, and Figure 10 farthest removed from it. It should here be said, however, that the sections are not quite vertical; so that, while the epiphysial vesicle is situated more to the left than to the right side of the sagittal plane, yet it is less so than would be inferred from the way in which it appears in the figures. The form of the epiphysis, as a whole, is nearly the same as that found in P. Douglassii, and it is composed of the same parts; — namely, a proximal

part with an anterior much-folded epithelial wall, and a posterior not folded and thinner epithelial wall; an epiphysial vesicle; a blood sinus; and a string of connective tissue extending from the distal end of the vesicle and blood sinus to the region of the parietal vesicle. In the anterior wall of the proximal portion the folding extends down somewhat nearer to the brain than is the case in P. Douglassii, and just at its junction with the brain a large blood-vessel is found filled with blood corpuscles (Fig. 12, *cp. sng.*). As already said in describing the posterior wall in P. Douglassii, the connection (opposite the letters *vnt.*[3]) with the brain is here complete and very evident, though the roof of the third ventricle (*tct. thl. opt.*) appears in the section to constitute a part of this wall.

The cells composing the walls of the proximal part are about two or three deep, but not arranged in layers. They are small, distinctly nucleated, and the nuclei are apparently perfectly round. They stain readily. On the outer surface of this wall is found, throughout most of its extent, a very thin layer of tissue, the cells of which are much flattened. This layer becomes continued from the apex of the epiphysis as the connective-tissue string (*con't. tis.*) already mentioned as passing to the region of the eye; another portion of it also becomes continuous with the pia mater of the brain.

Figure 10 represents a section through the longest portion of the epiphysial vesicle. In this plane the proximal portion of the epiphysis has not yet appeared, and is not found till we pass to a section in which the long axis of the vesicle has become considerably shortened. In the wall of the vesicle three zones or layers are found. The external one is similar to — in fact, on the posterior surface is continuous with — the thin external layer mentioned in the proximal portion. The second zone, comprising more than half of the entire thickness of the wall, is composed of cells apparently of the same nature as those described as forming the chief portion of the wall of the proximal part; but the layer is considerably thicker here than there, and on the whole rather more compact (*e'th.*, Figs. 10 and 11). The third and most internal zone is a deeply pigmented one (*pig.*). This pigment is so dense that when destroyed no distinguishable structure remains. In the presence of this pigment the species now under consideration differs entirely from P. Douglassii, where no pigment in this region is found. Again, however, attention is called to the fact that great importance cannot be attached to the presence or absence of pigment. Figure 11 shows the relation between this vesicle and the proximal portion of the

epiphysis. In this section it will be seen that a distinct line of demarcation exists between the true epithelial portions of the two walls where they come in contact. This distinctness is maintained throughout the entire series of sections. When the median section is reached, the vesicle has entirely disappeared. From the distal end of the vesicle the connective-tissue string extends forward to the region of the eye, as in the case of the proximal portion (*con't. tis.*). The blood sinus (Fig. 12) does not, in this species, come in contact with the epiphysial vesicle, but occupies the same position on the proximal part as in the case of P. Douglassii. It is much smaller in P. coronata, but in other respects is of the same nature. Whether or not this epiphysial vesicle may be homologized with the secondary vesicle in Petromyzon (Ahlborn, '83, Beard, '89, Owsjannikow, '88, Wiedersheim, '80) can be profitably discussed only after its development has been studied. So far as the condition in the adult is concerned, there is little to indicate such a homology.

I mention here an observation which may be of significance in connection with this complicated structure of the epiphysis. In both species and in all the individuals of Phrynosoma of which I have made sections favorable for exhibiting the entire dorsal surface of the brain, I have noticed that the pia mater appears to form a junction with the connective-tissue string described as passing from the distal extremity of the epiphysis to the region of the parietal eye, and also that it is thrown into several folds on the dorsal surface of the cerebellum. The membrane where folded is considerably thicker than elsewhere, contains within its folds numerous blood-vessels, and is composed of a single layer of cells very regular and distinct in outline and of a decidedly epitheloid appearance. The condition reminds one strongly of the folded portion of the wall of the epiphysis.

Uta Stansburiana.

As I have had but two specimens of this species, both preserved in alcohol, and hence not in the best histological condition, my study of it has been less satisfactory than that of the species of Phrynosoma. A few points, however, have been observed which are of some interest; but these can be presented without entering into a detailed description of the structure. Figure 6 (Plate II.) represents a portion of a sagittal section through the dorsal wall of the head and the parietal vesicle. The parietal foramen, too broad to be embraced in the figure,

is much larger here than in Phrynosoma, and the vesicle can scarcely be said to be embedded in the connective tissue of the brain roof, as in the case of Phrynosoma, but rather is suspended from the under side of the wall in a connective-tissue capsule.

The most striking features about this vesicle, as seen in the section, are its dorso-ventral flattening, and the entire separation of the lens from the retina. The lens, a well defined structure, composed of much elongated, almost fibrous, non-stainable cells, has its margins widely separated from the retina, and the intervening space is occupied by a uniformly fine granular substance (*cog.* ?), which also occupies the narrow space corresponding to what would be the cavity of the vesicle, were the lens and retina continuous at the margins of the former. The retina shows no structure beyond two deeply pigmented layers, corresponding to its external and internal surfaces, connected at short but irregular intervals by pillars of pigment, between which are seen a few scattered nuclei. This distinct separation of the margins of the lens from the retina is the only undoubted case of the kind, so far as I know, that has been seen, and if normal may be of significance in connection with the theory of the origin of the eye recently advanced by Beard ('89). I am, however, inclined to believe, notwithstanding the fact that the condition here found is apparently confirmed by the sections of my second specimen of this species, that the separation is in reality due to the extreme differentiation of the two structures, by means of which the connection between them was weakened, and then to artificial rupture by the flattening of the vesicle. The point certainly needs confirmation in more carefully preserved specimens.

I was unable to study the epiphysis in the material which I had, but no trace of anything like a nerve or even like a connective-tissue string extending from the parietal vesicle could be detected, nor were there any indications of blood-vessels or sinuses corresponding with those existing in Phrynosoma found here.

Conclusions.

The general bearing of the facts here presented I discuss at present only in connection with the question of the function, past and present, of the parietal organ. I concur in the opinion held by most of the persons who have written on the subject, that the organ is a degenerate eye, although my observations furnish, perhaps, no evidence in addition to what has been presented by former writers, in support

of the belief. From the morphologist's point of view, the evidence that would remove all doubt as to the correctness of this opinion would be that the vesicle regarded as the eyeball should be composed of elements essentially similar to elements found *somewhere* in organs known to perform the mechanical part in the act of vision; and, second, that this vesicle should be connected with the brain by a nerve comparable with the optic nerve of *some known* functional eye. I think no one familiar with the structure of the vesicle as it exists in many Lacertilia and in Petromyzon, will refuse to accept as satisfactory the evidence on the first point. The evidence on the second point is less conclusive. In many cases where the vesicle is well developed, as in Phrynosoma, it is certain that nothing which can be justly compared to an optic nerve exists. Spencer ('86 and '87) and several succeeding writers have held it as beyond doubt that in several species, notably of the genera Lacerta, Hatteria, and Varanus, there is a nervous connection between the brain and vesicle. Leydig ('89), however, in his preliminary, based on his study of Lacerta ocellata, Varanus elegans, and other forms, says "der von Spencer beschriebene Nerv ist kein Nerv sondern das strangartig ausgehende Ende der Zirbel." Lacerta ocellata is one of the forms in which Spencer ascribes, with least question, a nervous nature to the structure under consideration; but apparently Leydig has not examined either of the species of Varanus, viz. gigantea and Bengalensis, which Spencer studied; while, on the other hand, V. elegans, Leydig's species, is not mentioned by Spencer as having been studied by him. This denial *in toto* of the existence of the nerve as described by Spencer, Leydig practically repeats in his most recent contribution to the subject (Leydig, '90), and adds, as further confirmation of his opinion, that he has studied Hatteria (he does not tell us what species) and finds that here also the so-called nerve is of the nature of connective tissue. He also comes to the conclusion in this communication, that, while from the structure of the vesicle alone the organ must at least be put among the sense organs, it is yet "as good as impossible to do so while it is recognized that in the parietal structure of all the animals investigated by me not one contains a nerve, for we must hold fast to the proposition that for the equipment of a sense organ the peripheral end of a nerve is necessary." It appears to me, however, that we are not compelled to relinquish the belief that the organ was originally an eye, even though we accept Leydig's statement, as against Spencer's and others, regarding the nature of the supposed nerve in the cases which both have examined; or even should it appear that in no case does the nervous connection *now* exist.

It seems to me that Leydig has not given sufficient prominence to the possibility, not to say great probability, that the nervous connection has been lost by the modification and degeneration which the whole structure has certainly undergone; and especially must we hesitate in rejecting this explanation, when we remember that by so doing we are compelled to seek another. To be obliged to ascribe a function other than that of vision to a structure entirely like an organ of vision in most of its essential parts, and differing widely from one in no essential point, is requiring us to accept a conclusion that would throw suspicion on all our morphological reasoning. Should it be shown conclusively that the vesicle never has, in any vertebrate, *either in the adult* or *during its ontogeny*, nervous connection with the brain, then we should be obliged to abandon the optical explanation of its origin, and turn to the exceedingly difficult task of finding another. But until such knowledge is at hand, it seems to me we must suppose that the organ was produced as an eye, that in some way entirely unknown to us it lost its optical function, and that, in the consequent modification and degeneration, the optic nerve degenerated more rapidly in some cases than did the optic vesicle; and that in this way the separation which we now find took place.[1]

In previous discussions of the nature and function of the parietal organ, I believe sufficient attention has not been given to the structure and development of the epiphysis and its relation to the parietal vesicle, and especially its relation to the so-called choroid plexus. I have designated the entire structure found in connection with the roof of the thalamencephalon as the epiphysis; but, as already said, I have considerable doubt as to the wisdom of so doing. For the sake of precision it would seem best that the term epiphysis should be limited to the structure which arises as an evagination from this portion of the brain. Certain it is that the large blood sinus which I have described as a part of the epiphysis in Phrynosoma cannot be regarded as forming an essential portion of the structure, and I think it quite possible that what I have called the epiphysial vesicle is not a portion of the epiphysis, should

[1] Concerning the nervous connection between the eye and the epiphysis in Anguis fragilis, Strahl and Martin say ('88, p. 154), "Der Nerv der nach hinten am Vorderrand der Epiphyse scheinbar verschwindet, tritt von unten her in das Auge ein." Francotte ('88, p. 782) also describes essentially the same condition in this species. But such a condition would be so anomalous that C. K. Hoffmann ('88, p. 1991), notwithstanding the agreement of these independent statements, has, it seems to me with reason, expressed doubt as to the trustworthiness of the observations.

the term be limited as I have suggested that it ought to be. The distinctness of the epiphysial vesicle from the proximal portion of the epiphysis in the adult Phrynosoma is without exception, so far as my observations have gone; and if it is regarded as having been derived from the epiphysis, then we have two vesicles instead of one that have arisen in this way, and the difficulty of explaining the nature and function of the whole structure is correspondingly increased.

In his recent paper, Leydig ('90) has expressed the belief that there are two forms of parietal organs. He says: "From the posterior portion of the embryonic thalamencephalon (Zwischenhirn), especially in Lacerta agilis, two thick-walled vesicles (Blasen) bud out just in the middle line, lying one behind the other and springing from a common root (einem Wurzelpunkte). The anterior vesicle gives rise to the parietal organ, and the posterior one constitutes the epiphysis (Zirbel)." It is only, he says, from the anterior of these two vesicles (Blasen) that a vesicle (Blase) becomes cut off, and attains an eye-like character; the posterior one ends in the expanded blind terminal portion of the epiphysial thread (Zirbelfaden). But Selenka ('90) informs us, in a still more recent communication, that, after studying the development of the brain in a large number of reptiles and other vertebrates, he is unable to confirm Leydig's statement as to the origin of the parietal eye. He does find, however, in all cases, an evagination from the dorsal wall of the *fore* brain very similar to the one that forms the epiphysis from the roof of the thalamencephalon; also that the two structures elongate *pari passu*, the epiphysis becoming directed upward and forward, while the anterior evagination, which he calls the "paraphysis," becomes directed upward and backward. After the parietal vesicle is cut off from the epiphysis, the distal end of the paraphysis grows in between the vesicle and the end of the epiphysis from which it was detached, and the vesicle comes to lie on the paraphysis as on a pillow.

The relation of the two structures in the adult he does not know. C. K. Hoffmann ('85) has also described an evagination from the roof of the brain at the place of transition from the fore brain to the thalamus, which he calls the ependyma, — the beginning of the choroid plexus, — and he says that in the grown animal "it comes to take a not inconsiderable part in the formation of the epiphysis." Although there is nothing in the brief papers of either Leydig or Selenka to indicate whether or not the additional more anterior evagination seen by them is the same as that described by Hoffmann, yet, since all have studied the same forms, viz. of the genus Lacerta, it seems quite prob-

able that they have all observed the same structure. Whether or not any portion of the epiphysis as I have found it in Phrynosoma corresponds to the paraphysis of Selenka, or the ependyma of Hoffmann, can of course be determined only by studying the development of this portion of the brain.

Bearing in mind the highly vascular condition of all parts of the parietal organ, the numerous large blood-vessels surrounding the vesicle in P. Douglassii, and the great sinus in the same region in P. coronata, the sinuses of the epiphysis in both species, as well as the great quantity of blood contained in the much folded anterior wall of the epiphysis, it seems to me impossible to escape the belief that, in this genus at least, the organ must have some physiological significance. Leydig ('89) has expressed the opinion that it belongs primarily to the lymph system. From what has already been said, it is evident that I cannot accept this conclusion; but it does appear to me highly probable that the structure has become secondarily of such a character. From the numerous instances of change of function in the animal organism to which attention has been directed by Dohrn ('75), Kleinenberg ('86), Lankester ('80), Weismann ('86), and others, there are certainly no *a priori* objections to such a view, and it seems to afford more nearly a satisfactory explanation of the present condition of the organ than does any other.

Cambridge, August 15, 1890.

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EXPLANATION OF FIGURES.

All the figures are camera drawings excepting where otherwise indicated in the explanations.

ABBREVIATIONS.

cav. e'phy.	Cavity of the epiphysis.
cbl.	Cerebellum.
ceb.	Cerebrum.
chs. opt.	Optic chiasm.
cl. i.	Cells of zone 5 of the retina.
cl. lns.	Cells of the lens.
cog.	Coagulum.
com. a.	Anterior commissure.
com. p.	Posterior commissure.
com. su.	Superior commissure.
con't. tis.	Connective tissue.
cp. sng.	Blood corpuscles.
e'drm.	Ectoderm.
en'th. va.	Endothelium of retinal blood-vessels.
eph. vs.	Epithelium of the epiphysial vesicle.
e'th.	Epithelium.
la. trm.	Lamina terminalis.
lns.	Lens.
lob. opt.	Optic lobes.
m. scu.	Scale of the parietal eye.
mac. opt.	Spot marking the position of the parietal organ.
mb. ba. ex.	External basement membrane.
mb. ba. i.	Internal basement membrane.
nl.	Nucleus.
nl'.	Nuclei of zone 2 of retina.
nl''.	Nuclei of zone 4 of retina.
nl'''.	Nuclei of zone 5 of retina.
os par.	Parietal bone.
pig.	Pigment.
prc. r.	Processes radiating from the external basement membrane.
rtn.	Retina.
sn. snq.	Blood sinus.
tct. thl. opt.	Roof of the optic thalamus.
thl. opt.	Optic thalamus.
va. rtn.	Retinal blood-vessels.
vnt.[3]	Third ventricle of brain.
vs.	Epiphysial vesicle.
z''.	Second zone of retina.

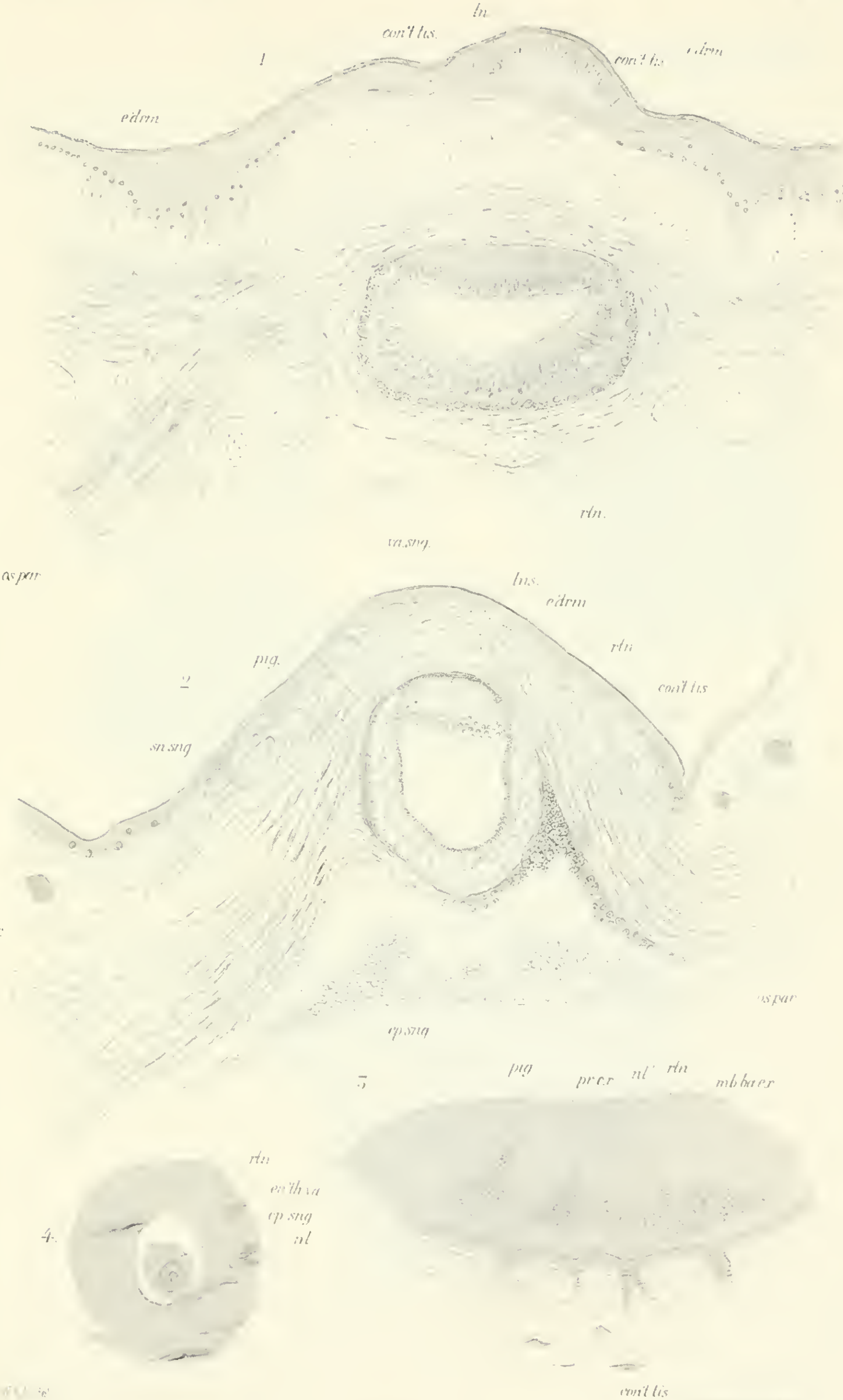
PLATE I.

Fig. 1. Left face of a section through the dorsal wall of the head of *Phrynosoma Douglassii* in the sagittal plane, and consequently passing through the middle of the parietal organ. Diagrammatic in unimportant details. × 140.

" 2. Transverse section through the dorsal wall of the head and middle of the parietal organ of *P. coronata*. Diagrammatic in unimportant details. × 140.

" 3. Section of a small portion of the deep wall of the parietal organ and the enveloping connective-tissue capsule, to show the processes radiating from the external basement membrane. × 1060.

" 4. A transverse section of one of the retinal vessels, in which a blood corpuscle is seen. × 1060.



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con'l tis
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va.sng.
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sn.sng
os.par.
os.par
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5
pig
pr.e.r
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mb.ba.e.r
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rtn
ep'th.va
ep.sng
nl
con'l tis

ABBREVIATIONS.

cav e'phy.	Cavity of the epiphysis.	*mac. opt.*	Spot marking the position of the parietal organ.
cbl.	Cerebellum.	*mb. ba. ex.*	External basement membrane.
ceb.	Cerebrum.	*mb. ba. i.*	Internal basement membrane.
chs. opt.	Optic chiasm.	*nl.*	Nucleus.
cl. i.	Cells of zone 5 of the retina.	*nl'.*	Nuclei of zone 2 of retina.
cl. lns.	Cells of the lens.	*nl''.*	Nuclei of zone 4 of retina.
cog.	Coagulum.	*nl'''.*	Nuclei of zone 5 of retina.
com. a.	Anterior commissure.	*os par.*	Parietal bone.
com. p.	Posterior commissure.	*pig.*	Pigment.
com. su.	Superior commissure.	*prc. r.*	Processes radiating from the external basement membrane.
con't. tis.	Connective tissue.	*rtn.*	Retina.
cp. sng.	Blood corpuscles.	*sn. sng.*	Blood sinus.
e'drm.	Ectoderm.	*tct. thl. opt.*	Roof of the optic thalamus.
en'th. va.	Endothelium of retinal blood-vessels.	*thl. opt.*	Optic thalamus.
eph- vs.	Epithelium of the epiphysial vesicle.	*va. rtn.*	Retinal blood-vessels.
e'th.	Epithelium.	*vnt.*[3]	Third ventricle of brain.
la. trm.	Lamina terminalis.	*vs.*	Epiphysial vesicle.
lns.	Lens.	*z''.*	Second zone of retina.
lob. opt.	Optic lobes.		
m. scu.	Scale of the parietal eye.		

* Processes secreted from the inner surface of the retina.

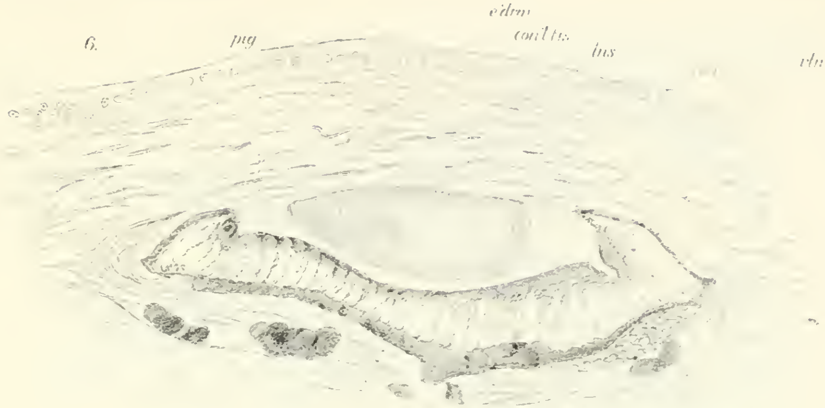
PLATE II.

Fig. 5. A portion of a section near the median plane, through the same eye as that represented in Figure 1, more highly magnified. × 570.

" 6. Sagittal section of the dorsal wall of the head, with the parietal organ of *Uta Stansburiana*. Diagrammatic in unimportant details. × 312.

" 7. External view of the parietal eye and surrounding structures in *Uta Stansburiana*. × 8.

6.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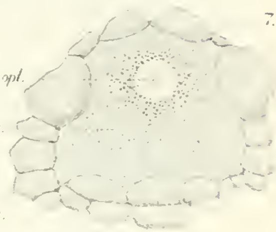
7.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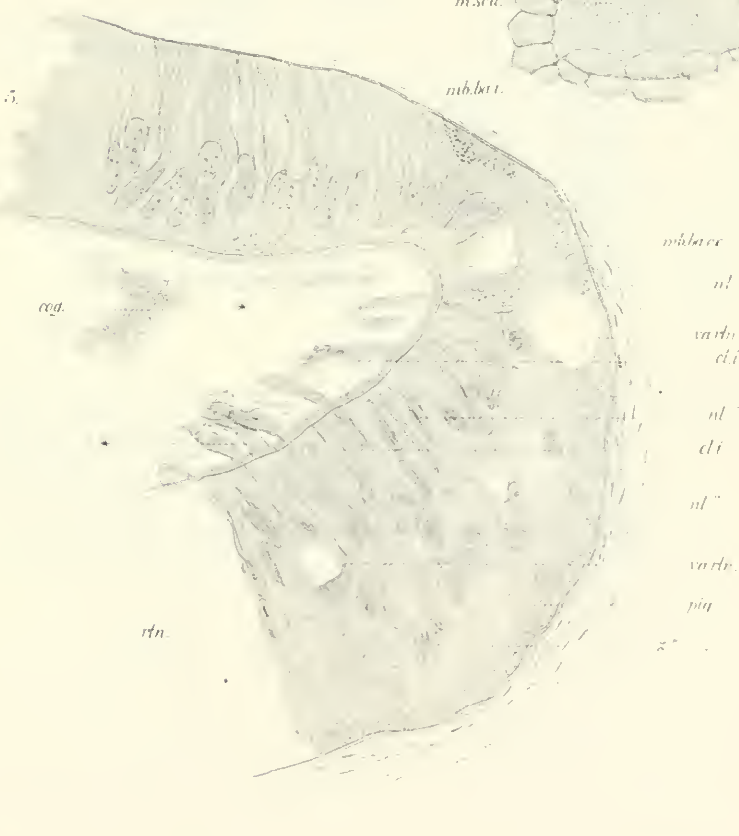
pig
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pig
rtn.

ABBREVIATIONS.

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ceb.	Cerebrum.	*mb. ba. ex.*	External basement membrane.
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cl. i.	Cells of zone 5 of the retina.	*nl.*	Nucleus.
cl. lns.	Cells of the lens.	*nl'.*	Nuclei of zone 2 of retina.
cog.	Coagulum.	*nl''.*	Nuclei of zone 4 of retina.
com. a.	Anterior commissure.	*nl'''.*	Nuclei of zone 5 of retina.
com. p.	Posterior commissure.	*os par.*	Parietal bone.
com. su.	Superior commissure.	*pig.*	Pigment.
con't. tis.	Connective tissue.	*prc. r.*	Processes radiating from the external basement membrane.
cp. sng.	Blood corpuscles.		
e'drm.	Ectoderm.		
en'th. va.	Endothelium of retinal blood-vessels.	*rtn.*	Retina.
eph. vs.	Epithelium of the epiphysial vesicle.	*sn. sng.*	Blood sinus.
		tct. thl. opt.	Roof of the optic thalamus.
e'th.	Epithelium.	*thl. opt.*	Optic thalamus.
la. trm.	Lamina terminalis.	*va. rtn.*	Retinal blood-vessels.
lns.	Lens.	*vnt.*[3]	Third ventricle of brain.
lob. opt.	Optic lobes.	*vs.*	Epiphysial vesicle.
m. scu.	Scale of the parietal eye.	*z''.*	Second zone of retina.

PLATE III.

Fig. 8. Left face of a sagittal section through a portion of the epiphysis, a short distance above its connection with the brain in *P. Douglassii*. It is in part diagrammatic, though the outlines of the figure as a whole, and of most of the foldings of the epithelium, were drawn with the camera. From the same individual as Figure 1. × 312.

" 9. Similar view of a sagittal section from the same individual, to show the relation of the epiphysis to the brain and the blood sinus. × 30.


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com
9
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lob opt
clb
tet thl opt
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ABBREVIATIONS.

cav. e'phy.	Cavity of the epiphysis.	*mac. opt.*	Spot marking the position of the parietal organ.
cbl.	Cerebellum.	*mb. ba. ex.*	External basement membrane.
ceb.	Cerebrum.	*mb. ba. i.*	Internal basement membrane.
chs. opt.	Optic chiasm.	*nl.*	Nucleus.
cl. i.	Cells of zone 5 of the retina.	*nl′.*	Nuclei of zone 2 of retina.
cl. lns.	Cells of the lens.	*nl″.*	Nuclei of zone 4 of retina.
cog.	Coagulum.	*nl‴.*	Nuclei of zone 5 of retina.
com. a.	Anterior commissure.	*os par.*	Parietal bone.
com. p.	Posterior commissure.	*pig.*	Pigment.
com. su.	Superior commissure.	*prc. r.*	Processes radiating from the external basement membrane.
con't. tis.	Connective tissue.	*rtn.*	Retina.
cp. sng.	Blood corpuscles.	*sn. sng.*	Blood sinus.
e'drm.	Ectoderm.	*tct. thl. opt.*	Roof of the optic thalamus.
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eph. vs.	Epithelium of the epiphysial vesicle.	*va. rtn.*	Retinal blood-vessels.
e'th.	Epithelium.	*vnt.*[3]	Third ventricle of brain.
la. trm.	Lamina terminalis.	*vs.*	Epiphysial vesicle.
lns	Lens	*z″.*	Second zone of retina.
lob. opt.	Optic lobes.		
m. scu.	Scale of the parietal eye.		

PLATE IV.

Figs. 10, 11, 12. The left faces of three sections of *P. coronata*, parallel with the sagittal plane, — Figure 12 nearly median, Figures 10 and 11 to the left of it. Figure 10, farther to the left of the median plane than Figure 11, passes through the longest part of the epiphysial vesicle. Figure 12 is more highly magnified, to show the histological structure. Figs. 10 and 11 × 40. Fig. 12 × 90.


12
ceb.
cp.sng
cav.ephy
e'th
cp.sng
vnt 3
thl opt
tct thl opt.
lob opt.
10
cont.tis
vs
pig
ceb
e'th
11
cont.tis
ceb
e'th
vs
pig
e'th.
cont
cav.ephy
thl opt
lob opt
thl opt
lob opt.