On the Fœtal Membranes of Chelonia.

(Contributions to the Embryology of Reptilia II*)

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With Plates I—X.

Our knowledge of the fœtal membranes of Reptilia is confessedly still very imperfect. It is generally assumed that they resemble more or less closely those of Birds. Kölliker is altogether silent, Balfour gives very meagre information, on the subject in their respective treatises on Embryology, while Hertwig in his Lehrbuch treats Reptilia throughout as presenting the same appearances as Birds on this point. Recently Strahl (No. 5), Hoffman (Nos. 6 & 7), Ravn (No. 9) and Perenyi (No. 16) have touched on the subject but their observations are confined mostly to the earlier stages.

Whilst collecting embryos of Chelonia, I became aware of the fact that there are some very notable features presented by the fœtal membranes of these animals which, so far as I am aware, have hitherto been entirely overlooked. These features appeared to me so remarkable and interesting that I thought it worth while to inves-

* I shall consider the article on "the Formation of the Germinal Layers in Chelonia" by Mr. Ishikawa and myself, and published in this Journal Vol. 1 and also in Quart. Jour. of Micro. Sci. Vol. 27 as the first of this series of contributions to the Embryology of Reptilia.

tigate the whole history of these membranes in this group. The following embodies the results of my study on this subject.

The species which I have investigated are Clemmys (or Emys) Japonica, Gray, and Trionyx Japonicus, Schlegel. In earlier stages, the fœtal membranes of these two species are very much alike but in later stages they present differences which, in my opinion, are highly significant. For convenience of treatment, I shall divide the present article into three parts, as follows :—

I. Earlier Stages of the Amnion.
II. Origin of the Allantois.
III. Later Stages of the Fœtal Membranes.

And in each part, I shall treat the two species separately, generally giving the description of Clemmys first, as that species seems to have more primitive relations in its fœtal membranes. At the conclusion, I have put together some suggestions on the theoretical bearings of the facts brought forth under the head of General Considerations.

I. Earlier Stages of the Amnion.

a. Clemmys Japonica.

The first stage of which I shall give a description is represented in surface view in Figs. 1. and 1 *a*. Pl. I. There is at this period a deep horse-shoe shaped groove bounding the anterior end of the embryonic region—the "Vordere Grenzfurche" of German authors. The posterior wall of this groove is the head of the embryo, while its anterior wall is the first rudiment of the anterior fold of the amnion. The structure and relations of these parts will become clear from the sections to be described directly. The medullary groove is still open thoughout its length, its posterior part being wider apart than its anterior portion. The dorsal opening of the blastopore is very distinct. At the posterior end of the embryonic region, there is, in the specimen figured, a low semilunar fold bounding the embryo from behind. It gives one the impression of its being the posterior fold of the amnion. Such folds are not, however, found by any means in all the embryos, and even when present, are not always of the same figure and distinctness as in the figure. As the subsequent history shows, these inconstant folds at the posterior end of the embryo take no share whatever in the formation of the permanent amniotic sac.

Round the head-end of the embryo, there is an irregularly semicircular transparent area of the blastoderm. In this area, there is usually an opaque line also semicircular and concentric with the cephalic groove (Fig. 1). Round the posterior end of the embryo, and along its sides, there is a broad horse-shoe shaped opaque streak which is caused by the abundant accumulation of yolk-granules—the germinal wall. The mesoblast, at this stage, extends into the head of the embryo proper, but anteriorly, laterally, and posteriorly the opaque horse-shoe shaped streak marks the limit of its extent. Hence the transparent area in front of the embryo is as yet free from the mesoblast.

In Fig. 58, Pl. VII. (See also Diag. I. Pl. X.), a median longitudinal section of the head end of the embryo is represented. It is evident from this section that the deep horse-shoe shaped groove at the anterior end (*a. l. f.*) is bounded posteriorly by the head (H. F.) of the embryo, while its anterior wall forms the first rudiment of the anterior fold of the amnion (Amn). The amnion is thus laid in the region into which the mesoblast has not yet found its way, and therefore, of necessity, consists at first only of the epiblast and hypoblast. In Fig. 59 (Pl. VII.), a transverse section of the same region is represented. From this and Fig. 58 (Pl. VII.), the characters of the two layers in the amnion will be easily understood. Where the layers reach the level of the general surface of the blastoderm, the epiblast presents a thickened ridge along the whole upper edge of the groove. As it is by the growth backward of this edge that the amnion comes to cover the embryo, this ridge of the epiblast must be the seat of an active growth. There is also in the median line a thickened ridge (Fig. 59, c.) of the epiblast which starting from the bottom of the groove reaches as far as the level of the blastoderm, fitting in its upward course the still open medullary groove of the head of the embryo.

In the semicircular transparent area in front of the anterior horse-shoe shaped groove, the epiblast consists of two layers of pavement cells, of which the upper is especially flat and seems to be of stiff consistency. The hypoblast in the region directly in front of the groove consists of polygonal cells. The opaque semicircular line in the transparent area already spoken of seems to be due to a special accumulation of the hypoblastic (Fig. 58.) cells. A little in front of this line, the hypoblast becomes suddenly a mass of five yolk granules with nuclei scattered among them. At the periphery of the transparent area this passes rather abruptly into a bed of large yolk spherules.

The fact that the amnion in Reptilia, consists, when first laid, only of the two primary layers was made known by Strahl (No. 5), Hoffman (No. 6), Perenyi (No. 16), and Ravn (No. 9). Hoffman pointed it out as a point of great difference between the amnion of Reptilia and that of Birds, but it is now well known that, in Birds also, the amnion consists at first only of the epiblast and hypoblast. Kölliker refers to the fact in his classical work (zweite Auf. p.188. and Fig. 85), and Ravn (No. 8) has worked out the point elaborately. Van Beneden and Ch. Julin (No. 11) also observed the same fact in the

Rabbit and Bats and named the two-layered amniotic cap the "Proamnion." Fleischmann has also found the same state of things in the cat. It seems therefore an established fact that the head-fold of the amnion, when first laid, consists throughout the Amniota only of the epiblast and hypoblast and is therefore of the nature of Proamnion. In Reptilia, this point is made perhaps more conspicuous by the subsequent history of the fœtal membranes than in other groups.

It will be seen from this stage that the head of the embryo sinks from the first below the level of the blastoderm. Apart from any phylogenetic significance, there is mechanical necessity for its sinking in this manner. As soon as the development begins, the white of the egg is rapidly absorbed from the part over the blastoderm which becomes adherent to the inner surface of the shell membrane. There is therefore no space into which the head can grow except towards below. In removing embryos from the eggs, I availed myself of the fact of the blastoderm becoming adherent to the shell membrane, for, with a stout pair of scissors, I could easily cut a watch-glass shaped piece of the shell with the shell membrane and the embryo adherent to it, and inverting it, I could pour the preservative fluid into it, thus using it like a veritable watch glass, only excelling it in this that it keeps the embryo and the blastoderm stretched in their natural positions.

I am inclined to think that the semilunar ridge at the posterior end (Fig. 1) is also caused by the posterior heavy end of the embryo sinking into the space below. Its section is almost exactly like that of the lateral fold of the permanent amnion (Figs. 30 and 30*a*, Pl. V.). Such adventitious ridges seem to be produced here and there without any regularity (cf. also Fig. 2). They are of a transient nature and take no part in the formation of the amnion.

As later stages will show, the whole amniotic sac is produced solely by the growth backward of the anterior fold in conjunction with the lateral folds which rise gradually from before backward.

In the stage with two or three mesoblastic somites, as shown in Figs. 2 and 2*a*, Pl. I. (see also Diag. II. and II'. Pl. X.), the amniotic fold has extended nearly half over the body of the embryo whose anterior part has sunk meanwhile more and more below the level of the blastoderm. The posterior edge of the amniotic hood presents a horse-shoe shaped outline, being caused by the lateral fold of each side extending more posteriorly than the median part. There are again some irregular folds (*a*) in the posterior parts of the embryonic region.

Figs. 30–33 (Pl. V.) show a series of transverse sections selected from different parts of this embryo, Fig. 30 being the most posterior and Fig. 33 the most anterior.

Fig. 30 is from the region covered only by the lateral limbs of the horse-shoe shaped posterior margin of the amniotic hood. From this and Fig. 30*a* (Pl. V.) (the latter representing the left half of Fig. 30 under a much higher power of magnification) it will be seen that the lateral fold of the amnion, when first laid, presents two peculiarities: (1) it is purely epiblastic, and the mesoblast has no share whatever in it; (2) the fold is solid and not composed of the inner and outer limbs as represented in ordinary diagrams.

Fig. 31 is just in front of the point where the two lateral amniotic folds have united. One half of it is shown under a higher power in Fig. 31*a* (Pl. V.) The whole amnion here is composed of a solid sheet of the epiblast, the mesoblast insinuating itself between the epiblast cells only later on. The cells of this part of the amnion are in several layers, and of these, the cells of the outermost layer have undergone some process of hardening and their nuclei are stained deepest.

Fig. 32 is from the point where the head-end of the embryo is just beginning to sink below the level of the blastoderm. The mesoblast of the body has separated from the extra-embryonic part. The amnion is mostly epiblastic, although lined by the hypoblast for a short distance on each side.

Fig. 33 is from the head region which is completely sunk below the level of the blastoderm. As emphasized by Hoffmann, the head appears in the cross section below, instead of above, the blastoderm. The amnion is composed of the epiblast and hypoblast, each being only one-cell layered.

These sections show that the amnion at this stage consists, in the region of the sunken head, of the epiblast and hypoblast, and in the dorsal region, of the epiblast only. The mesoblast as yet has no share in it.

In the stage with 6 or 7 mesoblastic somites (Figs. 3 and 3 *a* Pl. I. See also Diag. III. and III'. Pl. X.), the amniotic hood has extended to the posterior end of the embryo, leaving only the region round the neurenteric canal exposed. The mesoblast has also very much increased in its distribution and has become, thoughout, split into the somatic and splanchnic layers. The cœlom has thus appeared not only within the body of the embryo proper but has extended itself into the extra-embryonic portion of the blastoderm. Although the mesoblast has originally spread from behind forward, the cœlomic cavity appears first in the neck region of the embryo and spreads gradually backward—as was pointed out by Strahl (No. 5). In the stage represented in Fig. 3, when seen through from above, the extra-embryonic cœlomic cavities of two sides, extending into the amniotic folds come close together (but are not fused) in the median dorsal line along a considerable distance in the anterior part of the dorsal region, but separate from each other before the posterior edge of the amnion is reached, and, gradually lessening in their height, are lost together with the gradually lowering lateral folds of the amnion. Thus the mesoblast now has a considerable share in the formation of the amnion.

Figs. 34–38 (Pl. V.) are a series of transverse sections selected from different regions of this embryo.

Fig. 34 is from the region where the lateral folds of the amnion are still low. When we compare this with Fig. 30, we see that in this stage the somatic layer of the mesoblast is folded and pushing itself into the hitherto solid epiblastic amniotic folds.

Fig. 35 is from the region where the mesoblastic folds or, what amounts to the same thing, the extra-embryonic cœlomic cavities are still some distance from the median line. Fig. 35 *a* represents the median dorsal portion of the amnion in the same section under a higher power. It is evident that here also, a somatic fold of the mesoblast insinuating itself, so to speak, on each side into the originally solid epiblastic amnion is separating the latter into two limbs of which the inner is the true amnion and the outer the false amnion* or serous envelope.

In Figs. 36 and 36 *a*, the mesoblastic folds have reached further dorsalward, but the amnion and the serous envelope are united in the median line. In Fig. 36 *b*, a few sections forward of Fig. 36, the mesoblastic folds have reached still further dorsalward—the most dorsalward at this stage—but still there is a distinct connection between the amnion and the serous envelope.

The mesoblastic folds maintain themselves at the level given in Fig. 36 *b* for many sections forward, and the connection between the

* In future, I shall avoid using the term "false amnion" to denote the structure here indicated and shall call it the serous envelope, as the term "false amnion" is applied to two very different structures by German and English authors.

amnion and the serous envelope is also invariably present. (Compare Fig. 3, Pl. I.).

In Figs. 37 and 37 *a*, which are from the region of the heart, where the head-end is beginning to sink below the surface of the blastoderm, the mesoblastic folds have again receded from each other and the connection between the amnion and the serous envelope is again broad.

Fig. 38 is from the region of the head sunk below the level of the blastoderm, which therefore appears above the head in this section. The amnion or proamnion consists only of the epiblast and hypoblast.

The relations of different parts will become clearer, when studied in a longitudinal section.

Fig. 41 (Pl. V.) is such a section slightly out of the median dorsal line so that the extra-embryonic cœlomic cavity (cœl') of one side appears in the amnion. This section shows that the epiblastic amniotic fold reaches nearly to the neurenteric canal, while the hypoblastic fold extends only to the neck region. The triangular space between these two folds as seen in this section is occupied, for the most part, by the mesoblast enclosing a portion of the extra-embryonic cœlomic cavity. A little earlier there would have been no mesoblast in the amnion which then consisted, in the dorsal region, of the epiblast only, and in the sunken head part, of the epiblast and hypoblast. The mesoblast is now pushing itself into the solid epiblastic sheet of the amnion, dividing it into an outer and an inner limb. In Fig. 41, the posterior part of the epiblastic fold is, however, still solid. Anteriorly the mesoblast is insinuating itself between the epiblast and hypoblast. The cœlomic cavity in the mesoblast is widest in the anterior part.

One of my most important results is in regard to the connection between the amnion and the serous envelope, seen in Figs. 35–37. Contrary to what is hitherto known, the extra-embryonic cœlomic cavities of two sides are never united across with each other over the dorsal region of the embryo. A connection—quite elongated and definite in later stages—between the amnion and the serous envelope separates them to the very end of the development. That this structure causes great peculiarities in the fœtal membranes is to be expected and will become clear as later stages are described. This connection, I shall call hereafter the sero-amniotic connection. It does not extend to the sunken head part where the amnion consists of the epiblast and hypoblast, and is confined to the region behind the neck representing the original solid epiblastic sheet of the amnion or its prolongation behind.

While Fig. 3 (Pl. I.) no doubt represents the commonest and normal form in which the amnion spreads backward, it seems by no means to be the exclusive one. Fig. 14 (Pl. II.) shows one in which the posterior fold is present but a part of the left lateral fold is absent, so that the horse-shoe shaped posterior margin of the amnion is open toward the left. I have also another embryo in which a part of the right lateral fold is absent.

Now comes the most remarkable point in the development of the amnion in Clemmys. According to what is hitherto known about the amnion, one would expect that when it has reached the stage shown in Fig. 3 (Pl. I.) the posterior fold will be produced or the lateral folds will converge toward each other and thus the amniotic sac will be completely closed. Such is not the case in Clemmys. The anterior and lateral folds which starting from the head have gradually extended backward over the whole embryo do not stop at the posterior end of the embryo but continue to grow backward, although diminished in their width, until finally there is produced a tube extending backward from the posterior end of the embryo, almost as long as the body of the embryo itself, connecting the amniotic sac with the exterior. A reference to Figs. 4–7 (Pl. I.), will make the growth of this posterior tube clear. In Fig. 4, the folds have extended slightly beyond the posterior end of the embryo. Beyond this point, they suddenly come near each other, and being diminished very much in width, their continued growth backward produces a tube (Figs. 5 and 6). It will be seen that the extreme posterior point always presents a horse-shoe shaped outline, as it did when growing over the body of the embryo itself. Fig. 7 shows the stage of the greatest development of this tube in my possession. In three embryos of this stage whose lengths are 8, 8, and 8 $\frac{1}{2}$ millimeters, the length of the posterior tube of the amnion is respectively 6, 8, and 7 $\frac{1}{2}$ millimeters. The posterior opening is some distance beyond the edge of the vascular area.

The sections of this tube show that the relations of the different layers are in all essential respects exactly as in that part of the amnion proper enclosing the embryo as shown in Figs. 39 and 40 (Pl. V., from the embryo given in Fig. 5) of which Fig. 39 is from the anterior part of the tube near the embryo and Fig. 40 from about the middle of the tube. In the surface view, there is often seen a streak along the median line of the tube, which is shown by the sections to be a thickening on the floor of the tube. The structure of the similar tube in Trionyx is given in a more enlarged scale in Figs. 53–55 (Pl. VI.).

What the function of this remarkable tube connecting the amniotic sac with the exterior is,—whether it has any active function at all or is only of the nature of a remnant organ, I am unable to tell. I think it probable that it serves for conducting into the amniotic sac the nutritive matter from the white, with whose gradual disappearance from over the embryo the backward growth of the posterior amniotic tube seems to keep pace.

The condition of the amniotic sac proper at this stage when the posterior tube has already been developed is shown in the series given in Figs. 42-47 (Pl. VI.) from an embryo with twenty mesoblastic somites. An inspection of these figures shows that, over the posterior part of the embryo (Figs. 42 and 43), the amnion and the serous envelope are still adherent to each other for a considerable space: hence the extra-embryonic cœlomic cavities (cœl') of the two sides are separated from each other by a wide interval over the dorsal region. As we proceed forward, the mesoblastic folds gradually push toward the median line separating the amnion from the serous envelope, until, over the middle region of the embryo, they are separated only by a thin partition (Figs. 44 and 44*a*). This partition—the sero-amniotic connection—has now become vertically somewhat elongated and unlike Figs. 36*a* and *b* (Pl. V.) presents a string of cells in a cross-section (Fig. 44*a*). This represents the greatest vertical elongation of the sero-amniotic connection at this stage. Further forward, the mesoblastic folds become again separated by a considerable interval (Fig. 45). Anteriorly to the point where the head-end begins to sink beneath the surface of the blastederm, the cœlomic cavities of two sides which arose separately have become united across, there being no sero-amniotic connection from the beginning in this part (Fig. 46). In the head which is freely projecting into the cavity below the blastoderm, the amnion still consists only of the epiblast and hypoblast (Fig. 47).

From what has been given above, it follows that the extra-embryonic cœlomic cavities of two sides are separated from each other over the dorsal median line by the sero-amniotic connection from the neck region to the very tip of the posterior tube. In front of the neck region, i. e., in the sunken head region, the cavities become early united across. It is important to remember this fact in order to understand the relations of some parts in later stages.

In a slightly older embryo, the sero-amniotic connection has increased more in its vertical extension. Figs. 48 and 48*a* (Pl. VI.) are from the tail region, Figs. 49 and 49*a* (Pl. VI.) from the middle of the body. In the latter, the sero-amniotic connection is of a considerable length, becoming quite definite.

As to the fate of the posterior amniotic tube. At the stage (Fig. 7, Pl. I.) when it is in its highest development, the axis of the tube is the same as that of the embryo, i.e., the embryo and the tube are in the same straight line. Beyond this stage, the tube begins to become curved, at first slightly, then more and more. In Fig. 13*a* (Pl. II.) the curvature is very slight; in Figs. 13*b* and 8 (Pl. II.) it has increased greatly; in Fig. 9 the distal portion of the tube is bent at a right angle to the proximal basal part; in Figs. 10 and 15 (Pl. II.), the tube has become very irregularly curved. It will be seen that the tail end of the embryo which is at first far in front of the horse-shoe shaped distal end of the posterior amniotic tube (Fig. 7) gradually approaches the level of the latter (Fig. 9) until in Figs. 10 and 15 it has pushed itself far behind. It is now the distal end of the tube that is in front. This change of the relative positions is no doubt due to the fact that the embryo and the amniotic sac proper grows more rapidly than the posterior amniotic tube which they push aside, so to speak, in order to grow beyond it. As the curvature becomes greater, parts of the tube become fainter and fainter in appearance. For instance, in Fig. 10, a large part of the tube excepting the distal horse-shaped end and the proximal basal part, was very difficult to recognize (being represented too distinctly in the Figure). In Fig. 15 I could detect only faint traces of the tube, here and there excepting the proximal basal part which is always distinct. The oldest stage in which I detected any portion of the distal half of the posterior amniotic tube is that given in Fig. 67 (Pl. VIII.). I found there the horse-shoe shaped distal end of the tube and the portion contiguous to it, but after a most careful search, I could not connect it with the proximal part. From these facts, it appears that the largest part of the posterior amniotic tube disappears entirely, and that only the proximal part—the part nearest the amnion proper (prox pt. Figs. 9, 10, and 15, Pl. II.)—remains permanently. It will be remembered that the sero-amniotic connection extends from over the neck region of the embryo to the tip of the posterior tube. As the proximal part of the tube remains permanently this marks in all later stages the posterior end of the sero-amniotic connection. As further growth in size of the amnion proper (accommodating itself to the growth of the embryo within it) takes place mostly behind the remnant of the posterior tube, the latter and the sero-amniotic connection come to lie in the anterior part of the amnion in older embryos. The growth in size of the amnion after being closed once is therefore due mostly to the enlargement of that part which is placed behind the posterior tube enclosing the tail end in a stage like Fig. 11 (Pl. II.).

In all the stages hitherto described, the head of the embryo projected below the level of the blastoderm covered by the proamnion which consists only of the epiblast and hypoblast (Fig. 41, Pl. V.). On this account, in sections of this region, the head is found below the general level of the blastoderm (Figs. 33, 38, Pl. V., Fig. 47, Pl. VI.). The manner in which this anomalous state of things is brought to a close, and in which the head covered by the amnion consisting of the epiblast and the somatic mesoblast comes to lie above the hypoblast as in other parts of the body, has been described by Strahl (No. 5) and Hoffman (No. 6) and quite recently by Ravn (No. 9), The last named author (No. 8) has also studied the process in the chick and found it to be alike. My own observations agree in all essential points with the account given by these authors. The process briefly stated is as follows: As stated before, the extra-embryonic cœlomic cavities of the two sides become early united across in the head region, there being no sero-amniotic connection here. This united cavity or its mesoblast wall, in spreading itself, insinuates itself between the epiblast and hyopoblast of the blastoderm and thus pushes the hypoblast forward and downward. A comparison of Figs. 41 and 41*a* (Pl. V.) and Diags. III., IV., V. (Pl. X.) will make this point clear. In Fig. 41, the head is still entirely covered by the proamnion; in Fig. 41*a*, the extra-embryonic cœlomic cavity (cœl′) in enlarging itself, has pushed the hypoblast forward and peeled it off, so to speak, from the greater part of the proamnion covering the head, so that now the proamnion is found only on the ventral part of the head. Meanwhile, the embryo turning on its longitudinal axis comes to lie on its left side. These movements bring about the state of things as shown in Figs. 11 and 11*a* (Pl. II.) In Fig. 11 the embryo lies entirely on its left side, and a small anterior part of the head is covered by the now much reduced proamnion. In the ventral view of the same (Fig. 11*a*) the proamnion is very conspicuous, because it is transparent and without blood-vessels. A section from the head of this embryo is shown in Fig. 85 (Pl. X.). It shows how the proamnion extends now only for a short extent.

The final disappearance of the proamnion is brought about by the continued extension of the mesoblast. Although the encroachment of the proamnion takes place to some extent from behind and before, it takes place most actively from the two sides. Fig. 86 (Pl. X.) is a section similar to Fig. 85 from a somewhat older embryo.

How the proamnion has been encroached upon from both sides and has all but disappeared is very clear, if we compare these two figures. These two figures show also that the left vitelline vein (V*va*) becomes much larger than the right.

b. Trionyx Japonicus.

Earlier stages in the development of the Amnion in Trionyx are very much as in Clemmys. There is in fact no point of any importance which is different in the two species. As, however, the Trionyx embryos in my possession show very well in surface views how the extra-embryonic cœlomic cavities arise first in the neck region and gradually spread backward, I shall introduce here some figures which illustrate that point among others.

Fig. 16 (Pl. III.) is the stage closely resembling Fig. 1 of Clemmys (Pl. I.). The anterior horse-shoe shaped groove ("die vordere Grenzfruche"), the still open medullary canal, and the transparent area in front of the embryo are all very similar to the Clemmys embryo of the corresponding stage.

In Fig. 17 (Pl. III.) the amnion has extended over the anterior half of the embryo. When seen from the ventral side the whole anterior end of the embryo covered by the proamnion is projecting below the level of the blastoderm, as shown in Fig. 17*a*. In the neck region where the embryo gains the level of the blastoderm, one is able to recognize distinctly the extra-embryonic cœlomic cavity on each side of the embryo appearing as a vesicle which bulges out the dorsal and ventral surfaces of the blastoderm (Figs. 17 and 17*a*). The level of its posterior limit is the same as that of the posterior limit of the amnion, and the growth backward of the cœlomic cavities progresses hand in hand with the backward growth of the amnion. These two cavities, one on each side of the embryo, are of course the same as Strahl's " Mesoblastische

Schläuche" (Cf. Strahl No. 5). The sections of this embryo show that in the region where the lateral folds of the amnion have not yet united in the median line (Fig. 50 Pl. VI.), the fold is purely epiblastic and solid, and the mesoblast has no share in it at all. In the region where the extra-embryonic body cavity is present (Fig. 51), the mesoblastic folds have already pushed themselves considerably into the epiblastic amniotic sheet, dividing it into two limbs: the amnion proper and the serous envelope. In the embryo of Clemmys given in Fig. 2 (Pl. I.), the mesoblast has as yet no share whatever in the formation of the amnion. It follows therefore that the mesoblastic folds begin to push themselves into the epiblastic amniotic sheet somewhat earlier in Trionyx than in Clemmys. Fig. 52 is from the head region of the embryo given in Fig. 17. The head is surrounded by the proamnion composed for the most part of the epiblast and hypoblast, and appears beneath the blastoderm instead of above it.

Figs. 18 and 19 (Pl. III.) show that the amnion is gradually spreading backward, and with it the extra-embryonic cœlomic cavities are growing larger and larger. In Fig. 18, the cavities of the two sides are still wide apart over the dorsal region of the embryo; in Fig. 19 they almost touch each other along the median dorsal line in the anterior dorsal part of the embryo, but are considerably apart in the posterior region. A section from the anterior region (Fig. 57) shows that they are separated by the sero-amniotic connection which appears, however, still very short in a section.

In the embryo given in Fig. 23 (Pl. IV.) the amnion has covered the embryo entirely and has even extended a short distance behind it. The cœlomic cavites are correspondingly enlarged.

In the stage given in Fig. 24 (Pl. IV.), the posterior amniotic tube has become already quite elongated. Its posterior opening is now just at the edge of the vascular area. The extra-embryonic cœlomic cavities have now extended so much that they are no longer recognizable as vesicles in a surface view. Figs. 53–55 (Pl. VI.) are three sections from different parts of the posterior amniotic tube of this embryo, Figs. 53 being near the posterior opening and others being in front of it. Only the epiblast and somatic mesoblast are represented in these figures, the cœlom, the splanchnic mesoblast and yolk being left out, as a comparison with Figs. 39 and 40 (Pl. V.) will show. Fig. 56 is the median part of the amnion from over the middle region of the body of the embryo and shows the greatest encroachment at this stage of the extra-embryonic cœlomic cavities, reducing the sero-amniotic connection to a mere septum-like partition.

Figs. 21 *a*, *b*, *c*, and *d*. (Pl. III.) show the posterior amniotic tube of four embryos of the stage a little older than that given in Fig. 24. In *a* the tube is still straight, in *b* it is slightly curved, and in *c* and *d* more curved. In *a* the embryo is 6 mm. long, while the posterior amniotic tube is only $3\frac{1}{2}$ mm. As this is no doubt the stage of the highest development of the tube, it follows that the posterior tube in Trionyx is not as long relatively to the body of the embryo as it is in Clemmys.

In Figs. 22 *a* and *b* (Pl. III.) the posterior amniotic tube is becoming very irregularly curved.

In Fig. 27 (Pl. IV.), most of the posterior amniotic tube has already disappeared or at least is unrecognizable. The proximal or basal part of it is, however, very distinct. At this stage, the sero-amniotic connection exists from the neck-region to the tip of the remnant of the posterior amniotic tube.

The manner in which the proamnion consisting only of the epiblast and hypoblast is gradually replaced by the amnion consisting of the epiblast and mesoblast is exactly as in Clemmys.

II. Origin of the Allantois.

Besides Kupffer who derives the allantois from the neurenteric canal, the one who has most carefully studied its origin in Reptilia is Strahl (Nos. 1 and 2). According to this author, the allantois is laid, in Lacerta, as a solid knob at the posterior end of the embryo, subsequently hollows itself out, and only then comes to communicate with the hind-gut by an independently formed allantoic stalk. It then turns round the tail end and comes to lie in front of, and below, the latter.

After Strahl, Hoffmann (Nos. 6 and 7) and Perenyi (No. 16) have studied the origin of the allantois in Reptilia. The views which Hoffmann expresses in his first paper (No. 6) mainly support Strahl's observations, while in his second paper (No. 7) he seems to have somewhat modified his idea. For the exact details in which his later ideas differ from those of Perenyi (No. 16), I must refer the reader to the original papers themselves, as I have to confess my inability to grasp them precisely. Notwithstanding Perenyi's statement that they differ, it appears to me that they are describing substantially the same process. Under the circumstances, I am unable to say whether my results agree with the view of either or both of these authors, although I think we have arrived at nearly the same results. Hoffmann says that the origin of the allantois in Reptilia is throughout the same as in Birds (No. 7. *p.* 189). Such is the conclusion I too have arrived at, after a careful study of Chelonia. In fact, this is so much so that Gasser's figures (Nos. 12 and 13) or Balfour's description (Comp. Embryol. Vol. II.) on the origin of the allantois in Birds might be bodily adopted to describe the same process in Chelonia.

As I have a more complete series of the Trionyx embryos illustrating this point than those of Clemmys, I shall begin with the former species.

Figs. 60–63 (Pl. VII.) and Figs. 87 and 87*a* (Pl. X.) give successive stages in the development of the allantois in Trionyx.

Fig. 60 is from an embryo very similar to the one represented in Fig. 23 with about seventeen mesoblastic somites. The splanchnopleure has not yet been folded under to form the hind-gut. The first trace of the allantois (All.) is, however, already visible as a shallow notch in the posterior part of the tail-lobe. In a surface-view, this notch appears as a shallow transverse slit as represented in Fig. 20. From the first, the posterior wall of the allantois is lined with a distinct epithelium of the hypoblast. Its anterior wall is no doubt also of the hypoblastic nature, but is here fused with the indifferent cell-mass above it.

Figs. 61–63 (Pl. VII.) and Figs. 87 and 87*a* (Pl. X.) speak sufficiently for themselves and need not be minutely explained to those who are already familiar with the corresponding stages in Birds. By the gradual folding of the splanchnopleure on the ventral face, the hind-gut is produced, and on its ventral floor the allantois becomes established as a vesicle at first wide open above (Figs. 62–63) but with its gradual growth constricted at the neck (Fig. 87). Fig. 87*a* represents a cross-section of the allantoic region from an embryo of the same stage as that represented in Fig. 87. It shows that the cavity of the allantois is at this stage two-lobed.

Figs. 64–66 (Pl. VII.) are three successive stages in the development of the allantois in Clemmys. Although these do not give as complete a series as in Trionyx, they are yet sufficient to show that the process in Clemmys is in all essential respects similar to that in Trionyx.

In none of my series of sections can I detect any trace of an independently formed vesicle which afterwards puts itself in communication with the hind-gut by an independently formed stalk. The figures given above sufficiently warrant us in concluding that in Chelonia at least, the allantois arises as a diverticulum of the hind-gut and is from the first continuous with it.

III. Later Stages of the Foetal Membranes.

In the preceding two sections we followed separately the growth of the amnion and of the allantois up to a certain stage. It will be more convenient to treat the later stages of these membranes together. As the development advances, they begin to differ in the two genera Clemmys and Trionyx, until, when completed, they present important differences in their structures. As those in Clemmys present in my opinion more primitive relations, I begin with that species.

a. Clemmys Japonica.

As the allantois pushes itself out as a vesicle into the extra-embryonic cœlomic cavity, the allantoic blood-vessels are soon found distributed in two groups (Compare Fig. 27 Pl. IV.). One (the right) set of arteries and veins is placed in that part of the vesicle facing anteriorly while the other (the left) set is placed on the posterior external aspect of the vesicle. The manner of distribution of the blood-vessels exerts a considerable influence on the future shape of the allantois.

As the allantois spreads itself over the embryo as well as over the yolk in the extra-embryonic cœlomic cavity, it assumes a peculiar shape represented in Fig. 67 (Pl. VIII.). The vesicle now flattened is divided by two peculiar constrictions into two parts of unequal sizes. The larger part is again subdivided into two lobes by the posterior set of blood-vessels. These two lobes of the larger part may be called respectively the right, and the left lobe, while the smaller half of the allantoic vesicle may be called the middle lobe.

The two constrictions that divide the middle lobe from the larger half of the allantoic vesicle are caused in two different ways. The anterior constriction is very easy to explain. It was mentioned above that one set of the allantoic vessels runs on the anterior side of the as yet small allantoic vesicle. Now, in the rapid growth of the vesicle, the lines along which blood-vessels run cannot, on account of their presence, keep up in their growth with the rest of the vesicle, and are necessarily left behind until along these lines there are produced grooves at the bottom of which the blood-vessels run. When the allantoic vesicle is flattened, these grooves necessarily produce notches or bays in the margin of the vesicle, more or less deep according to the size of the blood-vessels. In the case of the anterior set of the allantoic vessels, the groove has become so deep that the right lobe and the middle lobe on the two sides of it have met again and become firmly appressed with each other, so that practically these blood-vessels are supported in their course by a mesentery-like fold of the allantoic vesicle. This explains the origin of the anterior constriction of the allantois. In a similar way the notch that divides the larger part of the allantois into the right and left lobes is produced by the posterior or left set of blood-vessels, although the notch is not as deep as in the anterior constriction and consists of two or three minor indentations.

The posterior constriction of the allantoic vesicle given in Fig. 67 is also not very difficult to explain. There can be no doubt that it is due in the main to the fact that the vesicle finds itself unable to spread freely over the embryo on account of the sero-amniotic connection. The only thing it can do is to grow round the sero-amniotic connection, thus producing a deep incision in its outline. The posterior constriction owes its origin to this circumstance, and thus between the middle, and the left, lobe there is always interposed the sero-amniotic connection. There are some details of this posterior constriction which I am not able to understand. The allantois prepares to meet the sero-amniotic connection, sometime before it reaches in its growth the latter structure (*i. e.*, before there is, so far as I see, any mechanical necessity for a constriction) by folding itself and producing a constriction. Thus in Fig. 67 the apex of the posterior constriction is some distance from the remnant of the posterior tube of the amnion (which marks the posterior end of the sero-amniotic connection), and is marked by folds of the allantois showing themselves as white streaks. The result of this is that in later stages (Fig. 12) the posterior constriction is, near its head, divided into two limbs: one contains the sero-amniotic connection and its termination, the remnant of the posterior tube of the amnion, and the other is simply an incision in the margin of the allantoic vesicle. In still later stages, the latter is much the deeper of the two and becomes quite conspicuous (Figs. 68 and 71, Pl. VIII.). I am unable to see any necessity for the existence of this incision. I can not detect any one large blood-vessel or set of blood-vessels, which might cause it, as the anterior constriction of the allantois is caused by the right set of allantoic vessels. It appears to be a congenitally acquired character.

The nearly circular shape of the middle lobe is produced by the fact that it is necessarily limited in its growth by the sero-amniotic connection which obstructs its front. In fact it is the right and left allantoic lobes that grow to cover the larger part of the yolk-sac.

The right and middle lobes are supplied mostly by the right set of blood-vessels, while the left lobe is supplied by the left set.

The allantois has not yet in this stage entirely covered the amnion and the embryo from above so that the amnion with its sero-amniotic connection, and the anterior dorsal part of the embryo are visible beyond the margin of the middle allantoic lobe. The amnion at these stages does not fit itself tightly over the embryo but leaves a spacious amniotic cavity around the embryo. Especially there is a remarkable snout-like prolongation of the amnion extending in front of the head.

Fig. 68 represents an embryo about forty days old. The allantois has now spread over a large part of the upper half of the yolk, and this extension is due mostly to the right and left lobes and not to the middle lobe. A peculiarly sharp demarcation between the middle and left lobes of this stage is due to the fact that the sero-amniotic connection is placed between them. The remnant of the posterior tube of the amnion appears as a white triangular patch extending to the left at the head of the posterior incision. The long white streak extending from the same point obliquely backward over the back of the embryo is the simple incision of the allantois referred to above in Fig. 12 (Pl. II.). The allantoic vesicle being of some thickness, the walls of the incision which extend from the inner to the outer limb of the allantois are of some depth, and being pressed from above are bent down and show as a white conical streak of peculiar appearance. Note also the deep anterior constriction with the right set of allantoic vessels at its bottom.

It may be remarked in passing that the position of the embryo on the yolk is not necessarily as in Fig. 68. The embryo is formed at any place which happens to be uppermost when the egg is deposited. If an egg happens to stand on its end, the embryo will occupy the end of the oblong yolk.

Fig. 69 (Pl. VIII.) gives a side view of a somewhat older embryo. The allantois has spread over the larger part of the yolk so that, in the figure, the latter shows bare only at the posterior part of the ventral side. The figure shows the left lobe of the allantois, the sero-amniotic connection with peculiar structures at its posterior end, and the left set of allantoic vessels with the corresponding incision in the margin of the allantoic vesicle.

Fig. 70 gives a ventral view of an egg of about the same stage. The three lobes of the allantois have now spread themselves over a part of the lower half and are here very conspicuous. The lobe that appears to the observer's right is the left allantoic lobe. Next to it is the middle lobe and finally at the observer's left is the right allantoic lobe. The incision between the middle and the right lobes is the anterior constriction of Figs. 67 and 68, and at its dorsal end is found the right set of allantoic vessels. The incision between the middle and the left lobes passing over the head of the embryo corresponds to the posterior constriction of the earlier stages, and has the sero-amniotic connection placed in it. While in Figs. 67 and 68 the embryo is confined to the space below the middle lobe, in this figure the head of the embryo appears below the left lobe to the left of the sero-amniotic connection. This is brought about by the following circumstances. In Fig. 67, the embryo lies on its left side and, the sero-amniotic connection being approximately over its dorsal median line, we are viewing it, so to speak, from the side. As the embryo and with it the amnion grow, the embryo comes again to lie on its ventral surface, as in the earliest stages, and the sero-amniotic connection again accompanying the dorsal surface of the embryo is turned toward the observer. The amnion is thus free to grow to the left of it, under the left allantoic lobe. The amnion being spacious, the embryo is able to move within it, and the head may now be seen to the left, or to the right, or directly under, the sero-amniotic connection, although the position shown in Fig. 71 appears to be the most normal.

The blood-vessels that pass through the umbilicus at these later stages, are arranged as in Fig. 75 (Pl. IX.). The most anterior is the vitelline vein, then comes the vitelline artery, after it the allantoic artery and last of all the allantoic vein. The last three divide into two, the right and left branches, soon after their exit from the umbilicus. The vitelline artery is distributed over the surface of the yolk, but the vitelline vein is somewhat peculiar: it is much larger than the vitelline artery and while it receives branches from the surface of the yolk, the main bulk of it enters right into the substance of the yolk. This no doubt makes the acquisition of nutriment from the yolk much easier.

I may now proceed to describe the relations of the embryo, the fœtal membranes and the yolk shortly before hatching. (Figs. 71 and 71*a* Pl. VIII. and Diag. VI. Pl. X.).

The yolk sac (Fig. 71*a*) is now reduced considerably in size and the three lobes of the allantois have entirely enclosed it. These three lobes never fuse with one another, but are permanently separate. The seams that separate them are roughly speaking tri-radiate, the center being at the anterior end of the yolk-sac slightly to the left (to our right as we view it from the ventral surface) of the median ventral line. The seam that extends transversely from the center towards the right (to the left of the observer) separates the middle (placed in front of it) from the right allantoic lobe (placed behind it) and corresponds to the anterior constriction in Fig. 67. Hence, at its distal end, is found the right set of the allantoic arteries and veins. The seam that runs back from the center nearly parallel with the median ventral line separates the left lobe (placed to its left or to the observer's right) from the right lobe, and corresponds to the shallow notch produced by the posterior (the left) set of blood-vessels in Fig. 67, or to the incision in Fig. 69. Hence, at its distal end the posterior or left set of allantoic vessels is found. The seam that separates the middle from the left allantoic lobe is different from the other two, for here the two lobes of the allantois cannot come into contact, being separated by the sero-amniotic connection. It passes over to the dorsal side of the embryo (Fig. 71), and its dorsal end has the triangular remnant of the posterior tube of the amnion, and the peculiar conical white streak caused by the simple incision of the allantois. (Compare Figs. 68, Pl. VIII., and 12, Pl. II.).

There is one feature in an egg thus advanced which deserves special notice. The white of the egg which disappeared very early from over the embryo continues to grow smaller and smaller in quantity. But it persists up to a very late date, if it ever disappears entirely. There is always, even in very much advanced eggs, a small mass of the white just at the point where the three lobes of the allantois meet at the lower pole. This mass seems to have undergone some change in its chemical composition for it is now much denser, slightly yellowish in color and sticky. To receive this mass the membranes are often shallowly depressed. Into the center of this mass of the white a thick low process of the membranes penetrates (shown in Fig. 71*a* on the left allantoic lobe, just to the right of the sero-amniotic seam), so that when the membranes are removed, the mass of the white with the central part hollowed out appears like a bowl. The cells of the serous envelope on the surface of this process are peculiarly modified. They are more columnar than in other parts (Fig. 29, Pl. IV.). Their nuclei are larger, irregular in shape, and stained deeper. In these cells are found many large vacuoles which remain unstained. There can be no doubt that these cells are absorbing albuminous particles from the mass of the white. It seems to me that here we have in a very primitive condition the structure described by Duval (No. 10) as the placenta in Birds.

The amnion in these later stages seems to envelope the embryo tolerably closely, and its cavity is no longer spacious.

In hatching, the yolk-sac passes into the interior of the body where it lies for a long time—in fact for several months, for I found it in young tortoises late in the spring of the year following that in which they were hatched. The amnion is torn into shreds, but the allantois seems to be split open by the anterior limbs of the emerging embryo along the sero-amniotic seam—if not always, at least in some cases, for I have specimens in which the allantois has been cast away in this manner and is uninjured. The outer shell which has become very brittle is easily broken through and the young tortoise emerges into the world.

We may now examine the microscopic structures of these membranes. We left the sero-amniotic connection in the condition represented in Fig. 49 (Pl. VI.). After that stage, as the distance between the amnion and the serous envelope increases and the connection becomes accordingly elongated in its vertical extension, the epiblast cells in it become flattened in the direction perpendicular to the plane of the connection. Fig. 76 (Pl. IX.) represents a part of a section of the sero-amniotic connection from the same embryo as that from which Fig. 86 (Pl. X.) is taken. The cells show decidedly the flattening referred to above.

This flattening goes on more and more, but I omit the intermediate stages and proceed to the description of the sero-amniotic connection in the finished fœtal membranes (Fig. 71, Pl. VIII.) Figs. 78–80 (Pl. IX.) are selected sections from an embryo of the same stage as that represented in Figs. 71 and 71*a* (Pl. VIII.). All three are from the region of the remnant of the posterior tube of the amnion, Fig. 78 being the most anterior, and in order to facilitate the understanding of these sections, I have introduced a diagram of this region in Fig. 77. In this diagram, the serous envelope is represented as spread over all the structures; the amnion is below it and is indicated only by the line from which the sero-amniotic connection arises. The remnant of the posterior tube of the amnion has before this stage been modified into a solid compressed string of cells and is shown by the heaviest dark line which stretches from the amnion to the serous envelope. The sero-amniotic connection is represented shaded by parallel dotted lines. Throughout the largest part of its length (from its anterior end to near its posterior end) this structure lies in one plane and is simply a membrane stretching between the amnion and the serous envelope. But on coming to the region of the posterior tube of the amnion, it makes a sudden turn of over 90° to the left and goes to the serous termination of the posterior tube, which latter structure it connects on its way with the serous envelope. It will of course be understood that the sero-amniotic connection from its anterior to its posterior end was originally in one straight line and that its peculiar bent termination at this stage was brought about by its accompanying the posterior amniotic tube in all its changes of relative position. It is this peculiar bent part of the sero-amniotic connection which is seen as the triangular white patch at the dorsal end of the sero-amniotic seam. (Figs. 68, 69, 71, Pl. VIII.).

Fig. 78 is from the region of the simple sero-amniotic connection (the line 1–1 in Fig. 77). In such a section, the sero-amniotic connection is really a striking structure, forming a broad and conspicuous connection between the serous envelope and the amnion. The epiblast cells in it are now very flat and closely packed. The allantoic lobes become closely applied against the mesoblast of the connection but are permanently separate from each other. The epiblast of both the amnion and the serous envelope consists of two layers of cells. The inner layer of the former and the outer layer of the latter consist of very much flattened cells with large nuclei—which, in the case of the serous envelope at least, are much larger and stained deeper than those of the second layer. It is the cells of the outer layer which become specially large in the region of the placenta. The second or underlying layer consists of cubical cells which in some places may be present in more than one layer. It is this inner second layer alone that forms the sero-amniotic connection, the outer taking no part in it. As regards the allantois, the outer limb is generally much thicker than the inner limb and has many more blood-vessels distributed in it. The thickness of the allantoic walls is crossed in all directions by slender spindle-shaped cells.

Fig. 79 corresponds to the line 2–2 in Fig. 77 just through the angle of the bend which the sero-amniotic connection makes. The sero-amniotic connection goes here on one side to the amnion and on the other to the remnant of the posterior tube of the amnion, which, being now reduced to a thick compressed and somewhat convoluted string of cells, shows in section as lobated cell-masses.

Fig. 80 corresponds to the line 3–3 in Fig. 77. The sero-amniotic connection is no longer continuous with the serous envelope but goes to the remnant of the posterior tube of the amnion. To the right of the sero-amniotic connection, the two lobes of the allantois meet but are not fused. This is the section of the conical white streak that stretches over the dorsal region of the embryo and corresponds to the simple incision of the allantois given in Fig. 12 (Pl. II.).

In a few more sections, the sero-amniotic connection disappears. The two lobes of the allantois, however, keep separate and meet in a seam for many more sections, as the simple incision of the allantois extends considerably further posteriorly than the most posterior point of the sero-amniotic connection. Finally, however, the allantoic cavity is continued across. As the incision is deeper in the inner limb of the allantois than in the outer, the allantoic cavity first becomes continuous near the external surface and then gradually extends toward the inner surface.

b. *Trionyx Japonicus.*

As in Clemmys, the allantoic blood-vessels group themselves into two sets : the anterior (or the right) and the posterior (or the left), while the allantois is still a small vesicle (Fig. 27 Pl. IV.). When the allantois has advanced somewhat in its development, it presents the shape represented in Fig. 72 (Pl. VIII.). This corresponds to Fig. 67 of Clemmys but presents some important differences. The allantois consists here of two lobes marked off from each other by two constrictions. One of these is just behind the eye and the other is directly opposite the first on the opposite side of the vesicle. Unlike Clemmys, both these constrictions are produced in the same way. That is, the line along which each set of blood-vessels passes from the inner to the outer limb of the allantoic vesicle is left behind in its growth, and the parts on each side of the same line growing faster and meeting each other soon produce a mesentery-like fold slinging these blood-vessels. In other words, both the constrictions of Trionyx are of the same nature as the anterior constriction of Clemmys (Fig. 67). The posterior constriction of Trionyx is not well-marked in Clemmys: it corresponds to the shallow notch caused by the posterior or left set of blood-vessels. On the contrary, that corresponding to the posterior constriction of *Clemmys*—to that caused by the presence of the sero-amniotic connection—is never produced in *Trionyx*, although at the spot where it ought to be produced, viz., opposite the remnant of the posterior tube of the amnion, the allantois is drawn out to a peculiarly shaped point as if it were trying to go round the sero-amniotic connection. From these considerations, it follows that that part of the *Trionyx* allantois in front of the anterior constriction corresponds to the right lobe of *Clemmys*, the part from the anterior constriction to the point opposite the remnant of the posterior tube of the amnion to the middle lobe, and the part from the same point to the posterior constriction to the left lobe. The middle lobe faces, as in *Clemmys*, the sero-amniotic connection.

Unlike Clemmys, however, the growth of the middle lobe pushes, so to speak, the sero-amniotic connection before it, so that the amnion comes gradually to assume the shape of a bag of which the sero-amniotic connection forms the puckered mouth. Reference to Figs. 25 and 26 (Pl. IV.) will make these processes clear.

In Fig. 25, the sero-amniotic connection is still directly over the dorsal side of the embryo and it is still straight. The allantois is pressing on it.

In Fig. 26, the growth of the amnion has removed the main portion of it from the sero-amniotic connection. The whole amnion has now assumed the shape of a bag hanging pendant by the sero-amniotic connection. The allantois is still pressing on the sero-amniotic connection, and its pressure, so to speak, has bent the hitherto straight sero-amniotic connection like the letter V. Moreover the general axis of the sero-amniotic connection which has hitherto been parallel with the axis of the embryo is now at right angle with the latter. The general appearance of the egg at this stage as seen from the ventral side is given in Fig. 73 (Pl. VIII.). The allantois has covered a larger part of the yolk sac, leaving only an oval space at the lower pole uncovered. This oval space is bounded anteriorly by the sero-amniotic connection bent like the letter V, and from this is seen stretching forward the anterior prolongation of the amnion which unites the main portion of the latter with the sero-amniotic connection (Comp. Diag. VII., Pl. X.). The two constrictions or mesentery-like folds of the allantois caused by the two sets of blood-vessels are also seen distinctly in the figure.

The final shape of the fœtal membranes is seen in Fig. 74 (Pl. VIII. Comp. Diag. VII., Pl. X.), and that part of the ventral surface where the lobes of the allantois finally meet is represented in a more enlarged scale in Fig. 81 (Pl. IX.). The space left uncovered by the allantois in Fig. 73 is now mostly grown over by the growth from the posterior side. There is however a small space still left uncovered by the allantois. It is triangular in shape; the apex of this triangle is bounded anteriorly by the sero-amniotic connection, now compressed to an irregular horse-shoe shaped opaque streak. On two sides of the triangle is the anterior allantoic lobe (which equals the middle and left lobes): posteriorly, it is limited by the posterior allantoic lobe (which equals the right lobe). From the lateral angles of this triangle the mesentery-like fold of the allantois stretches on each side to each set of the allantoic vessels. These correspond to the two notches in Fig. 72. The view from inside of this region is given in Fig. 81*a*. In this there is a ridge across the middle of the triangular area. This is the line of junction of the yolk-sac and the amnion, as will become clear from the sections to be described directly. It appears in the external view as an opaque line across the horse-shoe shaped sero-amniotic connection (Fig. 81). The anterior prolongation of the amnion connecting the main body of the latter with the sero-amniotic connection is now so disproportionately small compared with the amnion itself that it appears as a small irregularly triangular white patch (Fig. 81*a*, Ant. Prolong. Amn., and Fig. 81). Its cavity, now almost obliterated by the appression of its two walls, is still continuous with the amniotic cavity through a narrow slit (see Fig. 81*a* and Diag. VII.). It leads to the sero-amniotic connection. Figs. 82–85 (Pl. IX.) are a series of sections of this region, the plane of sections being in the antero-posterior direction. Fig. 82 is from the left side of the triangular uncovered area in Fig. 81*a* (or from the right side in Fig. 81). The two allantoic lobes, the anterior and posterior, are only slightly apart from each other. Attention is called specially to the section of a part of the anterior prolongation. Figs. 83 and 84 are from the triangular area itself. Here the two allantoic lobes are wide apart. The interspace is filled up mostly by the growth of the somatic mesoblast of the serous envelope. The sero-amniotic connection in Fig. 83 is of a very complicated figure. This arises from two reasons. In the first place, the section being taken in the antero-posterior direction, it cuts one limb of the horse-shoe shaped sero-amniotic connection more or less longitudinally. In the second place, the sero-amniotic connection is not in a simple straight line as in Clemmys, but being compressed and ruffled, appears as of an irregular pattern in a section. In Fig. 84, the sero-amniotic connection is cut more directly across. To give an idea of the structure of this region, I have given a part of Fig. 84 on a more enlarged scale in Fig. 84*a*. In Fig. 85, which was broken by accident, the two allantoic lobes have again approached each other, the section being out of the triangular area. They are, however, distinct and continue distinct until the sections reach the allantoic vessels.

In Trionyx, the remnant of the posterior tube of the allantois is not to be clearly distinguished. The place where it should be present is drawn out to a point (Fig. 26, Pl. IV.): that seems to be all the indication remaining in later stages of the posterior tube of the amnion.

The white remains to the last in Trionyx as in Clemmys, and is found opposite the triangular area of the ventral pole left uncovered by the allantois. This part is generally more or less depressed to receive the mass which is sticky and yellowish. The outermost cells of the serous envelope in this area undergo modifications similar to those of the corresponding spot in Clemmys. They become taller and larger and contain large vacuoles, their nuclei become larger and irregular in shape and stained deeper (Fig. 84*a*., Comp. Fig. 29, Pl. IV.). In Trionyx however, there appears to be no process that penetrates into the white as in Clemmys.

The yolk passes inside the embryo in hatching.

Of the completed fœtal membranes of Clemmys and Trionyx above described, there can be no doubt that Clemmys has retained more primitive relations. The main ground for this conclusion is that, starting from the same point, different structures (above all, the sero-amniotic connection) retain in Clemmys their original position and arrangement, while in Trionyx various structures are disturbed from their first arrangement, the sero-amniotic connection being pushed forward, bent and compressed into a secondary shape. If the process begun in Trionyx were to go one step further, no spot would be left uncovered by the allantois, the sero-amniotic connection might be pressed out of existence, the two allantoic lobes might come in contact with each other, and then the condition hitherto accepted as occurring in Birds would be the result.

General Considerations.

The noteworthy features in the history of the fœtal membranes of Chelonia as given above are :—

1. The presence of the Proamnion and the manner in which it is replaced by the permanent Amnion.
2. The presence of a peculiar tube stretching posteriorly from the posterior end of the Amnion connecting the cavity of the latter with the exterior—the Posterior Tube of the Amnion.
3. The permanence of the Sero-Amniotic Connection.
4. The differences in the fate of the Sero-Amniotic Connection in Trionyx and Clemmys.
5. The presence of the rudimentary "Placenta."

Of these, the first point has been noticed in nearly all the amniota whose development has been carefully studied within recent years. The only new feature is the fact that the dorsal part of the proamnion consists at first solely of a solid sheet of epiblast cells. The second, third, and fourth points are, so far as I am aware, brought out for the first time in the course of the present investigation. They certainly are very remarkable features, and, so far as our present knowledge goes, might be looked on as distinctive of the Chelonian fœtal membranes. I think it, however, highly probable that if other groups of Reptilia and Birds are carefully gone over again, many structures which are highly significant in the light of the facts now obtained will be found to have hitherto escaped notice or been laid aside as unimportant. For instance, in the sections of Lacerta given by several anthors, the sero-amniotic connection is distinctively figured even up to comparatively late stages. Being possessed with the idea obtained from the study of Birds that it is soon to disappear, different writers have not thought it worth their while to follow its history further. Nevertheless I can not but think that the sero-amniotic connection runs a similar course in other groups of Reptilia as described now for Chelonia. I also think that the posterior tube of the amnion is not such an unique structure as it appears to be at present.

The fifth point, the presence of the rudimentary placenta, is certainly very interesting. If the depression into which the white is received should become deeper, and the allantoic folds should be produced to enclose it, we shall have exactly the same structure as "the placenta" described by Duval in Birds.

The Reptilia, being the lowest group of the Amniota, are of great importance in the comparative study of the fœtal membranes. What light does the history of the Chelonian fœtal membranes as given above throw on the phylogeny of those membranes in the Vertebrata? Without going into a general discussion of this difficult problem, I think I might offer here a few suggestions which have presented themselves to me in the course of the present investigation. I strongly incline to the view that the amnion was originally developed by mechanical causes. In Chelonia, when the head fold is produced, there are two reasons why it should sink into the yolk below. In the first place, the yolk is very large and liquid, especially just beneath the blastoderm, so that a slight weight is enough to sink any structure into it. In the second place, the white rapidly disappears from over the blastoderm, which adheres then firmly to the shell-membrane: hence there is no space for the head-fold to grow except towards below. Without asserting that these are the very same causes that produced the anterior fold of the amnion, I think it reasonable to assume that it was produced by some such mechanical means. In this relation, I think, those inconstant adventitious folds as given in Figs. 1 and 2 (Pl. I.) are highly significant. These undoubtedly arise by the neighboring parts sinking below. We might suppose that in the earlier stages of development many such folds are produced, different in different embryos according to their individual idiosyncracies, and the anterior fold of the amnion may be looked upon merely as one of these. Only the cause that produces it being present in all the embryos and acting permanently and augmenting steadily, finally gave rise to the structure which we call the amnion, heredity of course helping a great deal.

The anterior fold of the amnion, when produced, consists only of the hypoblast and epiblast, and is called the Proamnion. We now know that this is found in all the groups of the Amniota, and I think we ought to add the stage of the proamnion as of normal occurrence n the development of the amnion. In Chelonia, the dorsal part of the proamnion is for some time entirely epiblastic. Should this be looked upon as a primitive feature or as a secondary one? I am inclined to adopt the former view for two reasons :—

(1). The inconstant adventitions folds are, as previously stated, always purely epiblastic and exactly like the lateral folds of the proamnion (Fig. 30*a*, Pl. V.): hence, it is reasonable to conclude that all such folds produced on the surface of the blastoderm are at first always purely epiblastic, and the solid epiblastic dorsal sheet of the Proamnion produced by the coalescence of the lateral folds of two sides have reason to be simply epiblastic.

(2). In Clemmys, whose development is certainly more primitive than that of Trionyx, the solid dorsal sheet persists for a longer time than in the latter genus, and there is a considerable interval of time before the mesoblastic folds insinuate themselves into the epiblastic sheet. I think, however, that although these folds are solid and without any cavity, they ought to be regarded as consisting of two limbs, the inner and outer, which are firmly appressed against each other: otherwise there is no reason why the sero-amniotic connection, which ought to be regarded as the seam along which the folds of the two sides have met, should remain permanently and separate the mesoblastic folds of the two sides to the end.

If the dorsal part of the proamnion consisted primarily of the epiblast alone, why should the mesoblastic folds afterward insinuate themselves between the two limbs of that part, thus extending the extra-embryonic cœlomic cavity into that region? For the explanation of that process, I adopt Balfour's view. To give efficacy to the allantois as a respiratory organ, it is desirable that it should be spread as extensively as possible close under the surface of the egg; hence the extra-embryonic cœlomic cavity must have spread *pari-passu* with the gradual growth of the allantois. The extension of the folds of the somatic mesoblast into the epiblastic folds of the proamnion is, I think, due primarily to this cause. That the mesoblast spreads itself at present long before the allantois, is to be explained as a case of precocious development.

The sero-amniotic connection is, in my opinion, decidedly a primitive structure. The manner in which the allantois spreads itself in Clemmys by rounding the sero-amniotic connection can also be explained only on phylogenetic grounds. The manner in which the allantoic blood-vessels are slung on mesentery-like folds of the allantois, is, I think, also a primitive feature. The manner in which the sero-amniotic connection in Trionyx is pushed forward, bent and compressed, points out, I think, the way in which that structure historically disappeared in higher forms. As I have stated above, if the process begun in Trionyx is carried just one step further, the sero-amniotic connection would cease to exist. What is the cause which brought about this disappearance? So far as I can see, the sero-amniotic connection serves no practical purpose in Clemmys and its presence is only to be accounted for phylogenetically. If such is the case, it would be undoubtedly economical to skip over the roundabout manner by which the allantois spreads itself in Clemmys round the sero-amniotic connection. Hence its disappearance at last in higher forms. Whether the immediate agent of its forward shifting is the force exerted solely by the growing edge of the allantois I cannot tell. It is no doubt partly due to that, but in addition I offer the following as a suggestion. In Trionyx, the allantoic vessels come out symmetrically on each side; in Clemmys, the symmetry is disturbed, the right set is found more anteriorly than the left. As I have often remarked, Clemmys presents on the whole more primitive relations, but I cannot regard this asymmetry of the allantoic blood-vessels as a primitive condition: something being present in Clemmys has disturbed the original symmetry and being absent in Trionyx no longer intereferes with it and this something I think is the presence of the sero-amniotic connection. May not the tendency of the blood-vessels to assume a symmetrical arrangement help to push the sero-amniotic connection forward in Trionyx?

List of Works referred to.

1. H. Strahl :—Ueber die Entwicklung des Canalis Myeloentericus u. d. Allantois der Eidechse. Arch. f. Anat. u. Physiol. 1881. Anat. Abth.
2. ———— :—Beiträge zur Entwicklung von Lacerta agilis. Ibid. 1882.
3. ———— :—Beiträge zur Entwicklung der Reptilien. Ibid. 1883.
4. ———— :—Ueber Canalis neurentericus u. Allantois bei Lacerta viridis. Ibid. 1883.
5. ———— :—Ueber Entwicklungsvorgänge am Vorderende des Embryos von Locerta agilis. Ibid. 1884.
6. C. K. Hoffmann :—Beiträge zur Entwicklungsgeschichte der Reptilien. Zeit. für Wiss. Zoöl. Bd. 40. 1884.
7. ———— :—Weitere Untersuchungen zur Entwicklungsgeschichte der Reptilien. Morph. Jahrb. Bd. 11. 1886.
8. Ed. Ravn :—Ueber die mesodermfreie Stelle in der Keimscheibe des Hühnerembryos. Arch. f. Anat. u. Entwickl. 1886.
9. ———— :—Bemerk. ueber die mesodermfreie Zone in der Keimscheibe der Eidechse. Anat. Anz. IV. 1887 No. 5.
10. M. Duval :—Etudes histologiques et morphologiques sur les Annexes des Embryons d'Oiseau. Journ. de l'Anat. et de la Physiol., XX. 1884.
11. E. Van Beneden et C. Julin :—Recherches sur la Formation des Annexes fœtals chez les Mammifères (Lapin et Cheiroptères) Arch de Biol. V. 1884.
12. E. Gasser :—Beiträge zur Entwicklungsgesch. der Allantois der

Müller'schen gänge u. des Afters. Fraukfurt 1874.

13. ———:—Der Primitivstreifen bei Vogelembryonen (Huhn u. Gaus) Cassel. 1879.

14. K. Mitsukuri and C. Ishikawa:—On the formation of the Germinal Layers in Chelonia. Quart. Jour. of Micros. Sci. 1886. Also Jour. of Science College. Imp. Univ. Tokyo, Japan. Vol. I.

15. A. Ostroumoff:—Zur Entwicklungsgeschichte der Eidechsen Zoöl. Anz. Nr. 292.

16. Jv. Perenyi:—Entwicklung des Amnion, Wolff'schen Gauges u. der Allantois bei den Reptilien. Zoöl. Anz. Nr. 274.

17. A. A. W. Hubrecht:—The Placentation of Erinaceus Europeus, with Remarks on the Phylogeny of the Placenta. Quart. Jour. Micros. Sci. Vol. XXX. 1889.

18. J. A. Ryder:—The Origin of the Amnion. Amer. Natur. 1886.

19. A. Fleischmann:—Mittelblatt und Amnion der Katze. Erlangen. 1887.

Explanation of Figures in Plates I—X.

List of Reference Letters.

a. (Fig. 2) inconstant adventitious folds. *a. l. f.* anterior limiting furrow= vordere Grenzfurche. *All.* Allantois. *Amn.* Amnion. *b.v.* blood-vessels. *Coel.* coelom within the embryo. *Coel'.* extraembryonic coelom. *ch.* notochord. *Epi.* Epiblast. *H. F.* head-fold. *Hyp.* hypoblast. *Lat. f. Amn.* Lateral fold of Amnion. *Mes.* mesoblast. *N. E. Can.* neurenteric canal. *Post. Tu. Amn.* Posterior tube of Amnion. *prox. pt.* proximal part of posterior tube of Amnion. *Proam.* Proamnion. *Remnant. Post. Tu. Amn.* Renmant of posterior tube of Amnion. *Ser. Env.* Serous envelope. *Sero-Amn-Conn.* Sero-Amniotic connection. *v. v. a.* anterior vitelline vein. *yk.* yolk.

In colored figures of sections, the epiblast is always colored red, the mesoblast blue, and the hypoblast yellow. In Pl. IX. blue stands for the somatic mesoblast, and green for the splanchnic mesoblast.

Plate. I.

Fig. *1.* Dorsal view of a Clemmys embryo 2 days old. Zeiss *aa* × 2. (LIV.)

Fig. *1a.* Ventral view of the same. *aa* × 2.

Fig. *2.* Dorsal view of a Clemmys embryo 4 ½ days old, with 2–3 mesoblastic somites. *aa* × 2. (XXXXIX.)

Fig. *2a.* Ventral view of the same.

Fig. *3.* Dorsal view of a Clemmys embryo 4 days old, with 6–7 mesoblastic somites. Extra-embryonic cœlomic cavities of two sides distinctly seen almost touching each other over the median dorsal line of the embryo. *aa* × 2. (LV.)

Fig. *3a.* Ventral view of the same. *aa* × 2.

Fig. *4.* Dorsal view of a Clemmys embryo 7 days old. *aa* × 2. (XXXXI.)

Fig. *5.* " " " 8 " " *aa* × 2. (XXXXIII.)

Fig. *6.* " " " 9 " " *aa* × 2. (XXXIX.)

Fig. *7.* " " " 4 ½ " " *aa* × 2. (LIII.)

Plate. II.

Fig. *8.* Clemmys embryo slightly older than Fig. 7. Enlarged. (L.)

Fig. *9.* Clemmys embryo 13 days old. *aa* × 2. (XXVIII.)

Fig. 10. Posterior tube of the Amnion highly convoluted, from a Clemmys embryo 14 days old. *aa* × 2. (LVIII.)

Fig. 11. Dorsal view of a Clemmys embryo, 10 days old, 6 ½ mm. long. Enlarged about 17 times. (LVII.)

Fig. 11a. Ventral View of another embryo from the same deposit. Enlarged about 17 times.

Fig. 12. Semi-diagramatic view of the posterior constriction of the Allantois in a Clemmys embryo 31 days old, seen from outside the serous envelope. *ca* × 7. (LVI.)

Fig. 13. Two Clemmys embryos 18 days old. Slightly enlarged. (XXXXV.)

Fig. 14. Dorsal view of a Clemmys embryo whose amnion is open toward the left. (XXXVIII.)

Fig. 15. Posterior tube of the Amnion disappearing. From a Clemmys embryo 13 days old, 8 mm. long.

Plate. III.

Fig. 16. Dorsal view of a Trionyx embryo 3½ days old. *aa* × 2. (126.)

Fig. 17. Dorsal view of a Trionyx embryo 5½ days old, 3 mm. long, with 5–6 mesobl. somites. *aa* × 2. (128.)

Fig. 17a. Ventral view of the same.

Fig. 18. Dorsal view of a Trionyx embryo 7½ days old, 3½ mm. long, with 7–8 mesoblastic somites. *aa* × 2. (141.)

Fig. 19. Dorsal view of a Trionyx embryo 8½ days old, 4 mm. long. *aa* × 2. (142.)

Fig. 19a. Ventral view of the same. *aa* × 2.

Fig. 20. Ventral view of the posterior part of a Trionyx embryo

8 days old, showing the beginning of the Allantois. *AA* × 2. (112.)

Fig. 21. Posterior tube of the Amnion in four Trionyx embryos 13 days old. Slightly enlarged. (162.)

Fig. 22. Posterior tube of the Amnion in two Trionyx embryos 16 days old. *aa* × 2. (167.)

Plate. IV.

Fig. 23. Dorsal view of a Trionyx embryo 10½ days old. *aa* × 2. (157.)

Fig. 24. Dorsal view of a Trionyx embryo 11½ days old, 5½ mm. long. Posterior Tube 2 + mm. long. 161.

Fig. 25. Trionyx embryo 38 days old, seen from the side of the yolk-sac which has however been removed. (175.)

Fig. 26. Trionyx embryo 53 days old. The yolk-sac removed and the embryo seen from the ventral or yolk-sac side. × 3. (179.)

Fig. 27. Trionyx embryo 10½ days old. (176.)

Fig. 28. Same embryo seen from its dorsal aspect, with the serous envelope lifted up, showing the sero-amniotic connection and the remnant of the posterior tube of the Amnion.

Fig. 29. Cells of the serous envelope in the region of the "placenta" in the Clemmys embryo represented in Figs. 71 and 71*a*. *DD* × 4.

Plate. V.

Fig. 30–33. *(5–8)*. Selected transverse sections from the Clemmys embryo represented in Figs. 2 and 2*a*. *CC* × 1.

Fig. 30. From the region of the lateral limbs of the Amnion.

Fig. 31. From the region where the two lateral limbs have just united.

Fig. 32. From the region where the head is partly sunk below the level of the blastoderm.

Fig. 33. From the region of the head which is wholly sunk below the level of the blastoderm.

Fig. 30a. Region of the left amniotic limb in Fig. 30. under a higher power. *DD* × 4.

Fig. 31a. Left half of the amnion in Fig. 31. *DD* × 4.

Figs. 34–38. Selected transverse sections from the Clemmys embryo represented in Fig. 3 and *3a.* *CC* × 1.

Fig. 34. From the region of the lateral limbs of the Amnion.

Figs. 35–36. From the dorsal region.

Fig. 37. From the region of the heart.

Fig. 38. From the region of the head.

Fig. 35a. Median dorsal part of the Amnion in Fig. 35. under a higher power. *DD* × 4.

Fig. 36a. Median dorsal part of the Amnion in Fig. 36. under a higher power. *DD* × 4.

Fig. 36b. The same region a few sections in front of Fig. 36. *DD* × 4.

Fig. 37a. Median dorsal part of the Amnion in Fig. 37. under a higher power. *DD* × 4.

Fig. 39. Transverse section of the posterior tube of the Amnion from the embryo given in Fig. 5. near its proximal end. *CC* × 1.

Fig. 40. Do. from about its middle. *CC* × 1.

Fig. 41. Longitudinal Section, slightly out of the median line, of a Clemmys embryo from the same stage as that represented in Fig. 3. *BB* × 2.

Fig. 41a. Diagrammatic longitudinal section of a Clemmys embryo somewhat older than that given in Fig. 41.

Plate. VI.

Figs. 42–47. Selected transverse sections from a Clemmys embryo 6 days old with 20 mesoblastic somites. *CC* × 1. (XXXII.)

Figs. 44a. Median dorsal part of the Amnion in Fig. 44. under a higher power. *DD* × 4.

Figs. 48–49. Selected transverse sections from a Clemmys embryo 9 days old. *CC* × 1.

Fig. 48. From the tail-region.

Fig. 49. From the dorsal region.

Fig. 48a. Median dorsal part of the Amnion in Fig. 48. under a higher power. *DD* × 4.

Fig. 49a. Median dorsal part of the Amnion in Fig. 49. under a higher power. *DD* × 4.

Figs. 50–52. Selected transverse sections from the embryo represented in Fig. 17. *CC* × 1.

Fig. 50. From the region of the lateral limbs of the Amnion.

Fig. 51. From the dorsal region of the Amnion.

Fig. 52. From the region when the head is sunk almost entirely below the level of the blastodem.

Figs. 53–55. Selected transverse sections from the posterior tube of the Amnion in the embryo represented in Fig. 24. Only the epiblast and somatopleuric mesoblast are represented, the hypoblast and splanchnopleuric mesoblast being omitted. *DD* × 4.

Fig. 53. Near the posterior opening of the tube.

Figs. 54–55. At various distances in front of Fig. 53.

Fig. 56. Median dorsal part of the Amnion in a section from the middle dorsal region of the Trionyx embryo represented in Fig. 24. *DD* × 4.

Fig. 57. Median dorsal part of the Amnion in a section from the dorsal region of Trionyx embryo represented in Fig. 19. *DD* × 4.

Plate. VII.

Fig. 58. Longitudinal section of an embryo from the same stage as that represented in Fig. 1. *DD* × 2.

Fig. 59. Transverse section of the embryo represented in Fig. 1. *DD* × 2.

Fig. 60. Longitudinal section of the Trionyx embryo shown in Fig. 20. *CC* × 2.

Fig. 61. Longitudinal section of a Trionyx embryo $10\frac{1}{2}$ days old. *CC* × 2. (157.)

Fig. 62. Longitudinal section of a Trionyx embryo 9 days old. *CC* × 2. (115.)

Fig. 63. Longitudinal section of a Trionyx embryo $11\frac{1}{2}$ days old. *CC* × 2. (116.)

Fig. 64. Longitudinal section of a Clemmys embryo 4 days old with 16 mesoblastic somites. *BB* × 2. (XXX.)

Fig. 65. Longitudinal section of a Clemmys embryo 6 days old with about 20 mesoblastic somites. *BB* × 2. (XXXII.)

Fig. 66. Longitudinal section of a Clemmys embryo 9 days old. *BB* × 2. (XXIX.)

Plate. VIII.

Fig. 67. Surface view of a Clemmys embryo 28 days old. Seen from outside the serous envelope. $\times 4\frac{1}{2}$. (LXXI.)

The upper transparent membrane is the *serous envelope*. The lower opaque membrane with blood-vessels is the *yolk-membrane*. Between these two membranes are placed the *embryo*, *the allantois* &c. Different divisions of the allantois are sufficiently explained in the text. The white line close to and parallel with the median dorsal line of the embryo is *the sero-amniotic connection:* traced posteriosly, it bends sharply to the left, this short limb being the *remnant* or *proximal part* of the posterior tube of the amnion. Over the posterior part of the embryo, is a delicate, irregularly curved white tube: this is the distal part of the posterior tube of the amnion with its horse-shoe shaped posterior opening. It has no connection with the *proximal part.*

Fig. 68. Dorsal view of a Clemmys egg, with the embryo, the fœtal membranes, and the yolk-sac. About 40 days old. $\times 2$. (LXXII.)

Fig. 69. Side view of a Clemmys egg with the embryo, the fœtal membranes, and the yolk-sac. 51 days old. Nat. size. (LXXIII.)

Fig. 70. Ventral view of a Clemmys egg with the embryo, the fœtal membranes and the yolk-sac. 55 days old. Blood-vessels on the yolk-sac omitted. Nat. size. (LXXV.)

Fig. 71. Dorsal view of a Clemmys embryo, shortly before hatching with the fœtal membranes. 45 days old. (LXIV.)

Fig. 71a. Ventral view of the same.

A low lobate process of the membranes situated close to the left of the tri-radiate allantoic seams penetrates into the mass of the white.

Fig. 72. Surface view of a Trionyx embryo $15\frac{1}{2}$ days old. $\times 5\frac{1}{2}$.
(177.)

This corresponds to Fig. 67. of Clemmys, and the explanation of the latter is applicable to this. The white line stretching from the neck of the embryo to its posterior end is the *sero-amniotic connection.* Its slight posterior expansion marks the *remnant* of *the posterior tube of the amnion.*

Fig. 73. Embryo represented in Fig. 26. with the yolk-sac and the fœtal membranes. Blood-vessels on the yolk-sac omitted. Slightly enlarged. (179.)

Fig. 74. Ventral view of a Trionyx embryo 42 days old, with the yolk-sac and the fœtal membranes. Slightly enlarged.
(181.)

Plate. IX.

Fig. 75. Blood-vessels that pass through the umbilicus.

Fig. 76. Part of a transverse section through the sero-amniotic connection of a Clemmys embryo 13 days old. *DD* × 4.
(LIX.)

Fig. 77. Diagram of the region of the posterior tube of the Amnion.

Figs. 78–80. Selected transverse sections through the posterior part of the sero-amniotic connection and the remnant of the posterior tube of the Amnion in the Clemmys embryo represented in Fig. 71. *CC* × 2.

Fig. 78. Through the line 1–1 in Fig. 77.

Fig. 79. „ „ „ 2–2 in Fig. 77.

Fig. 80. „ „ „ 3–3 in Fig. 77.

Fig. 81. Region on the non-embryonic pole of the yolk-sac where the allantoic lobes meet. From a Trionyx embryo similar to Fig. 74. Seen from outside the serous envelope. × 3. (182.)

Fig. 81a. The same region seen from inside.

Figs. 82–85. Selected sagittal sections through the region represented in Figs. 81 and 81*a*. *aa* × 2.

Fig. 82. is to the extreme left of Fig. 81*a*. and the sections gradually proceed toward the right.

Fig. 84a. Region of the sero-amniotic connection in Fig. 84. more highly magnified. *DD* × 2.

Plate. X.

Fig. 85. Transverse section from the head-region of the Clemmys embryo represented in Fig. 11. *aa* × 2.

Fig. 86. Similar section from the head-region of a Clemmys embryo 13 days old. *aa* × 2. (LIX.)

Fig. 87. Longitudinal section of a Trionyx embryo 16 days old (the same embryo as that given in Fig. 22). *CC* × 1. (167.)

Fig. 87a. Transverse section through the allantoic vesicle of an embryo of the same stage. *CC* × 1.

Diags. I–VII. Give a summary of the development of the fœtal membranes in Chelonia.

Diags. I–V. Applicable to both Clemmys and Trionyx.

Diag. I. Corresponds to Fig. I. (Pl. I.) and to Fig.

58 (Pl. VII.). The head-fold of the embryo is sunk below the level of the blastoderm and enveloping it is the proamnion as yet only slightly developed.

Diag. II and II'. Correspond to Fig. 2 (Pl. I.). The amniotic hood proceeding backward has covered the anterior half of the embryo. Its cephalic portion consists of the hypoblast and epiblast; its dorsal portion of the epiblast alone. II' represents a cross-section of the dorsal region. It shows clearly that the mesoblast has as yet no share whatever in any part of the amnion (or more properly proamnion).

Diag. III and III'. Correspond to Fig. 3. (Pl. I.). The amniotic hood has extended nearly to the posterior end of the embryo. The extra-embryonic cœlomic cavities of two sides are united across in the head-region. The mesoblastic folds have also insinuated themselves into the hitherto solid epiblastic dorsal part of the amnion (III'.) A partition—*the sero-amniotic connection*—in the median line, however keeps the cœlomic cavities of two sides separate in the dorsal region.

Diag. IV and IV'. Represent the stage when the posterior tube of the amnion is fully developed. The sero-amniotic connection in a cross-section (IV'.) is now closely invested on each side by the mesoblastic fold, and is longer than in III'. The mesoblastic fold is peeling the hypoblast off the proamnion covering the head. (IV.).

Diag. V. All but a small proximal part of the posterior tube has now disappeared. The sero-amniotic connection is more developed. The mesoblastic fold has now entirely peeled the hypoblast off the proamnion, and the head is now enclosed in the amniotic cap consisting of the *epiblast* and *mesoblast*. Although these diagrams (III, IV and V) show the encroachment of the mesoblast on the proamnion as taking place from before backward, it in reality takes place mostly from two sides. In Diags. IV and V, the gradual development of the allantois is shown.

Diag. VI. Shows the fœtal membranes of Clemmys as completed.

Diag. VII. Shows the fœtal membranes of Trionyx as completed.

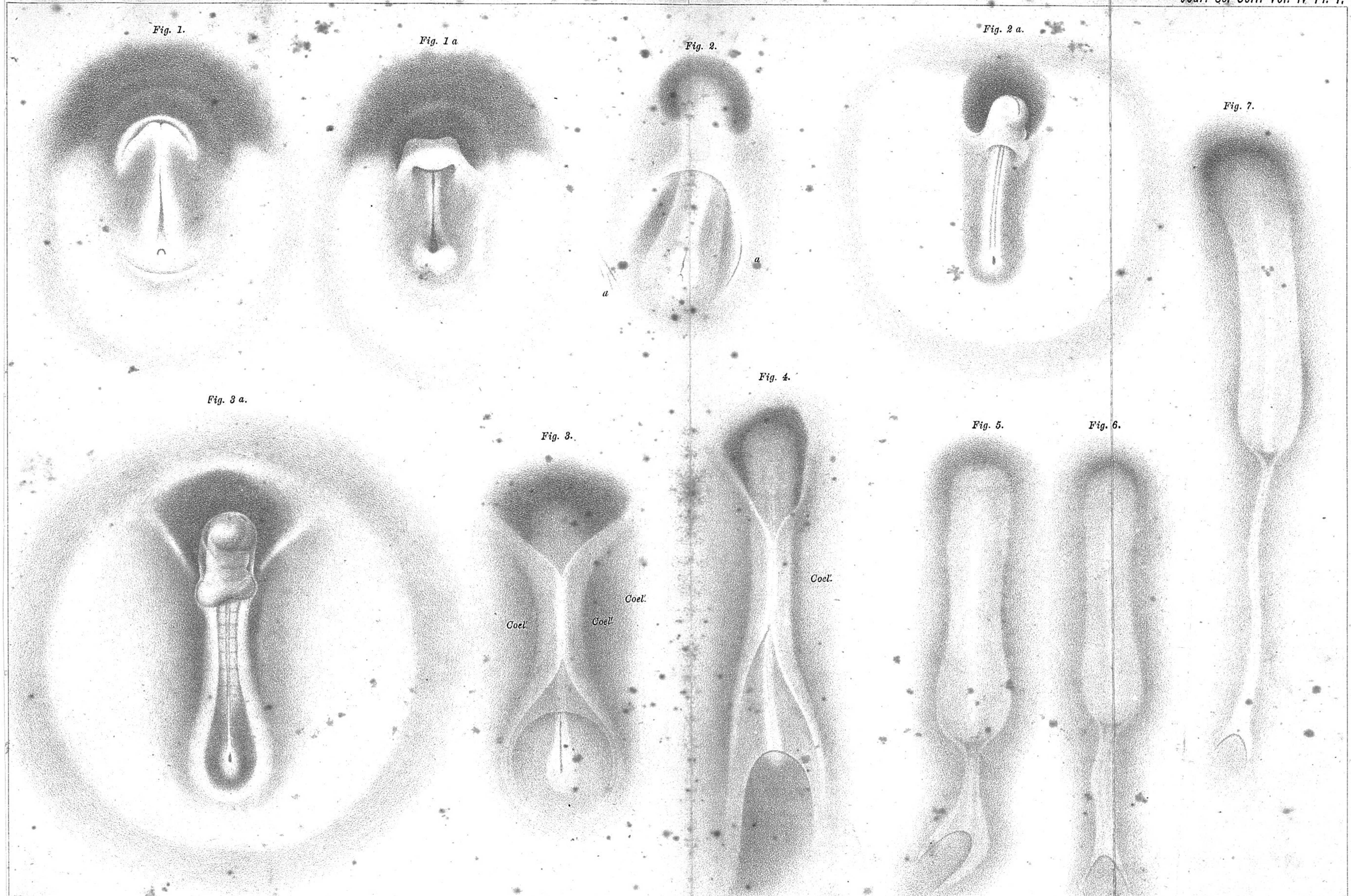

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Fig. 9.

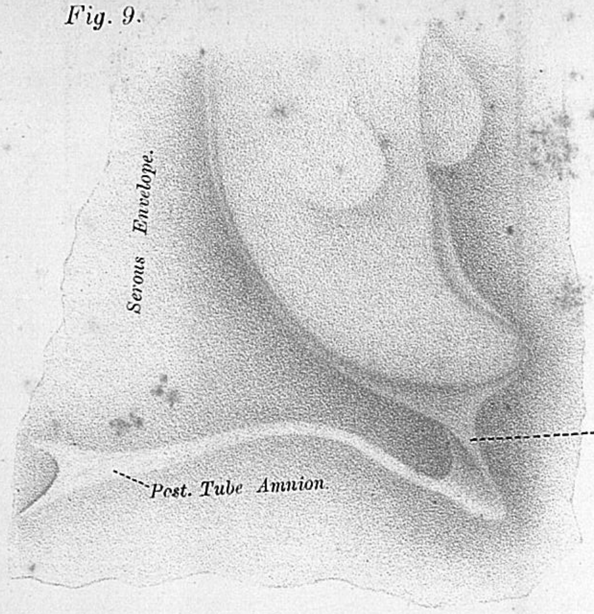


Fig. 8.

Fig. 11.

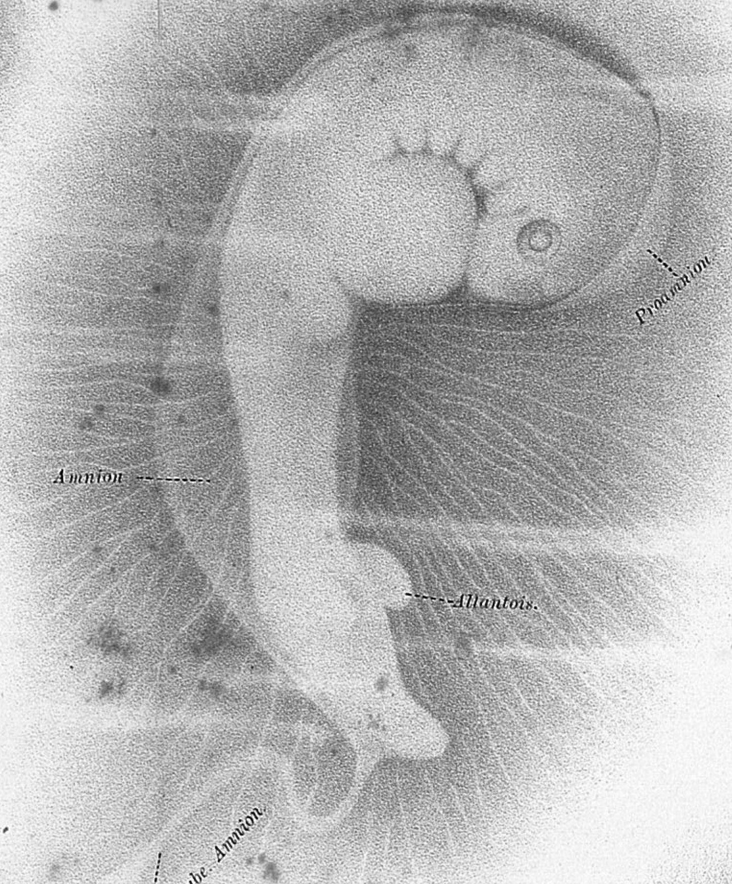
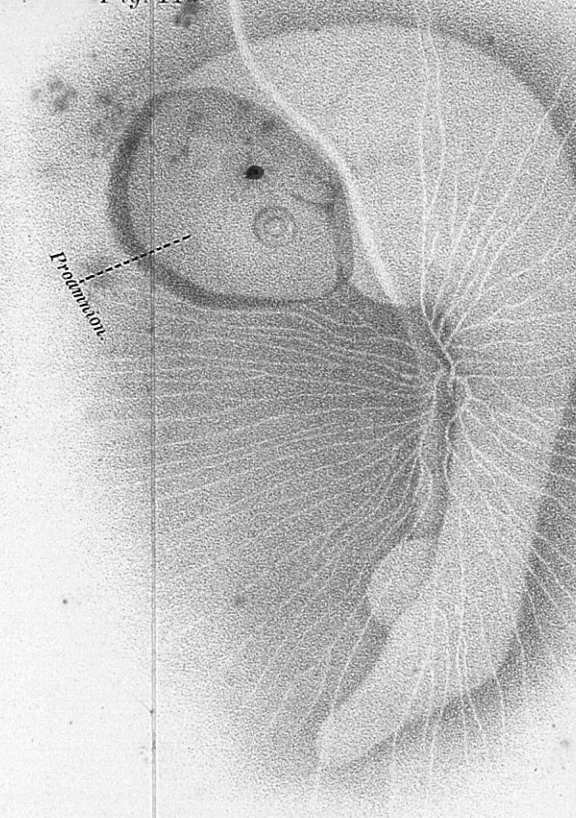


Fig. 11a.



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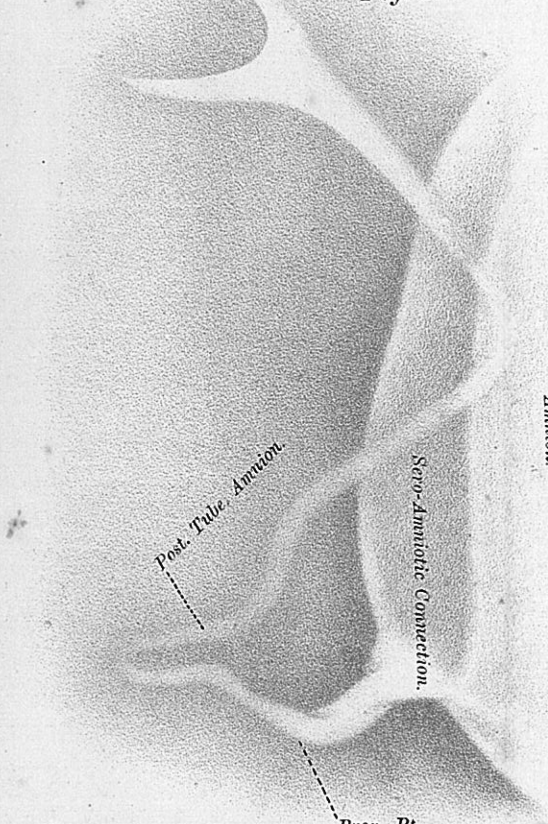

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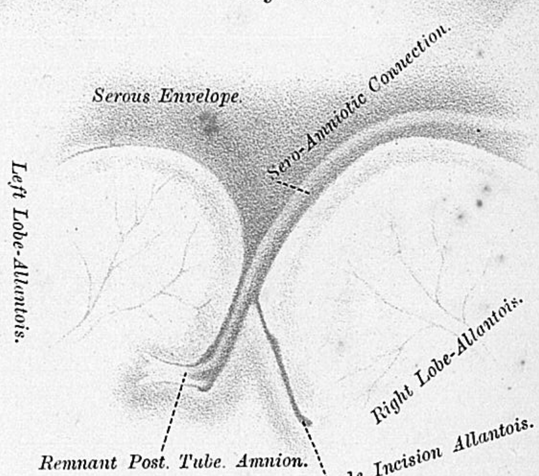


Fig. 13.

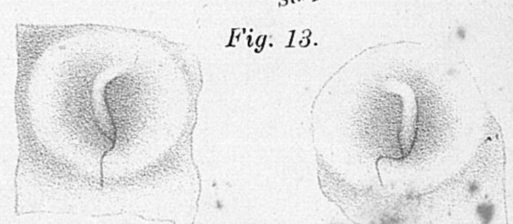


Fig. 14.

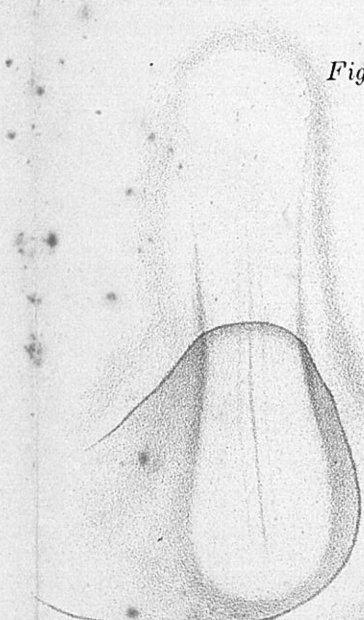


Fig. 15.

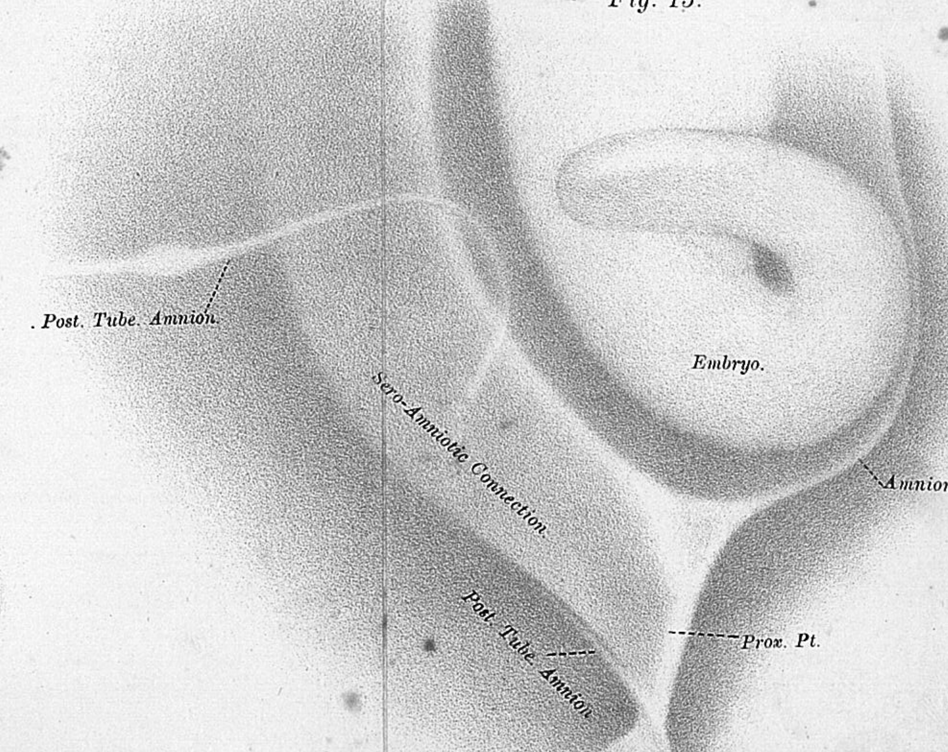
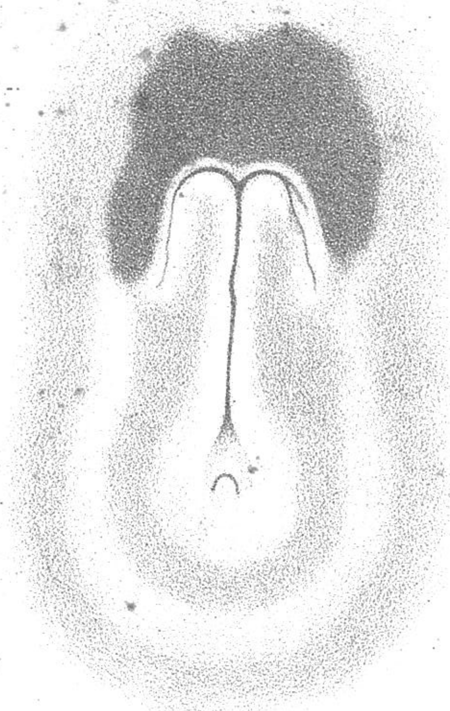


Fig. 16.



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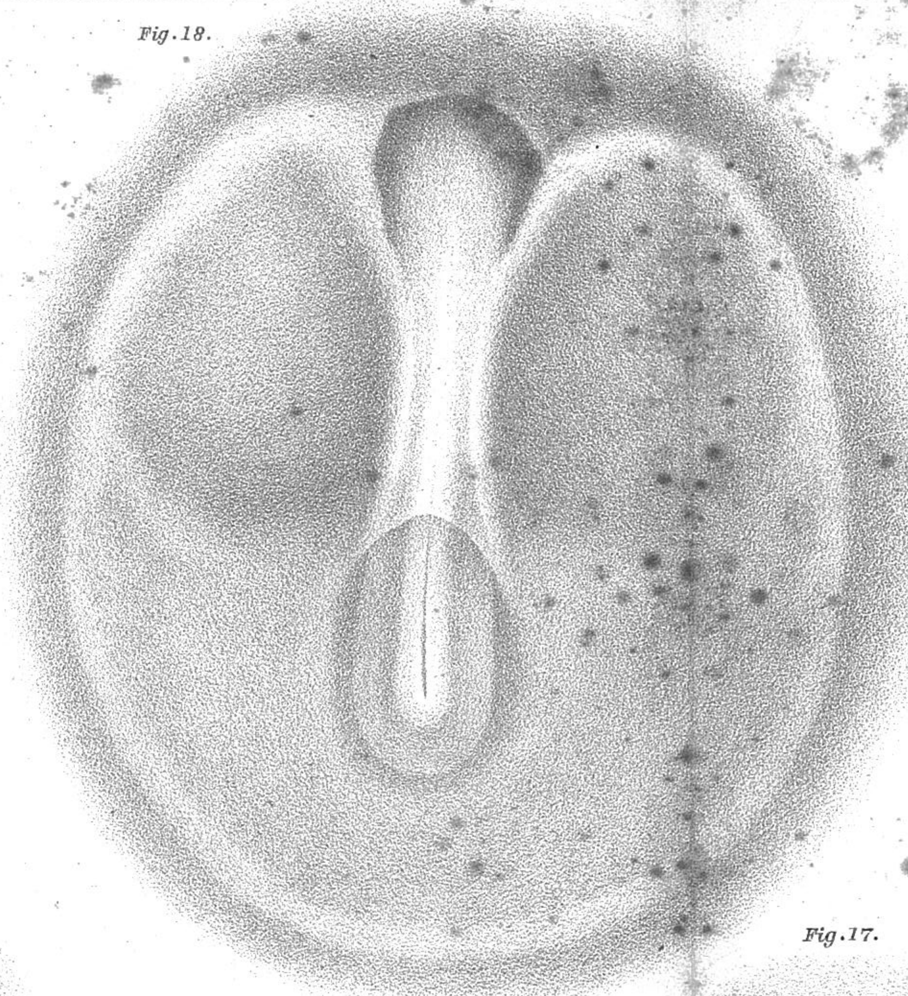


Fig. 19.

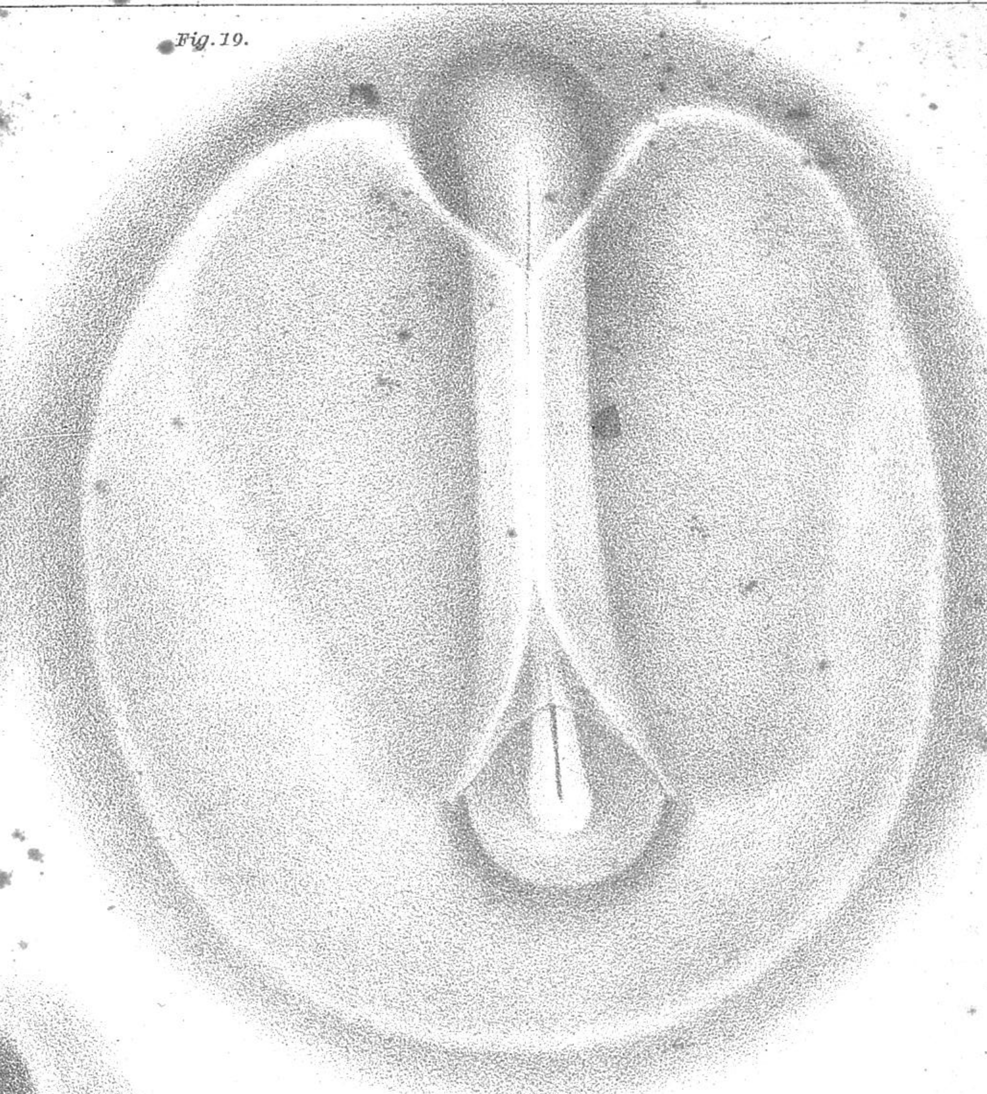


Fig. 19 a

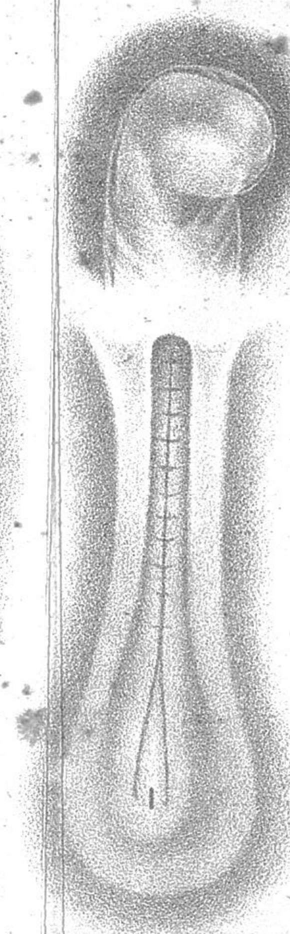
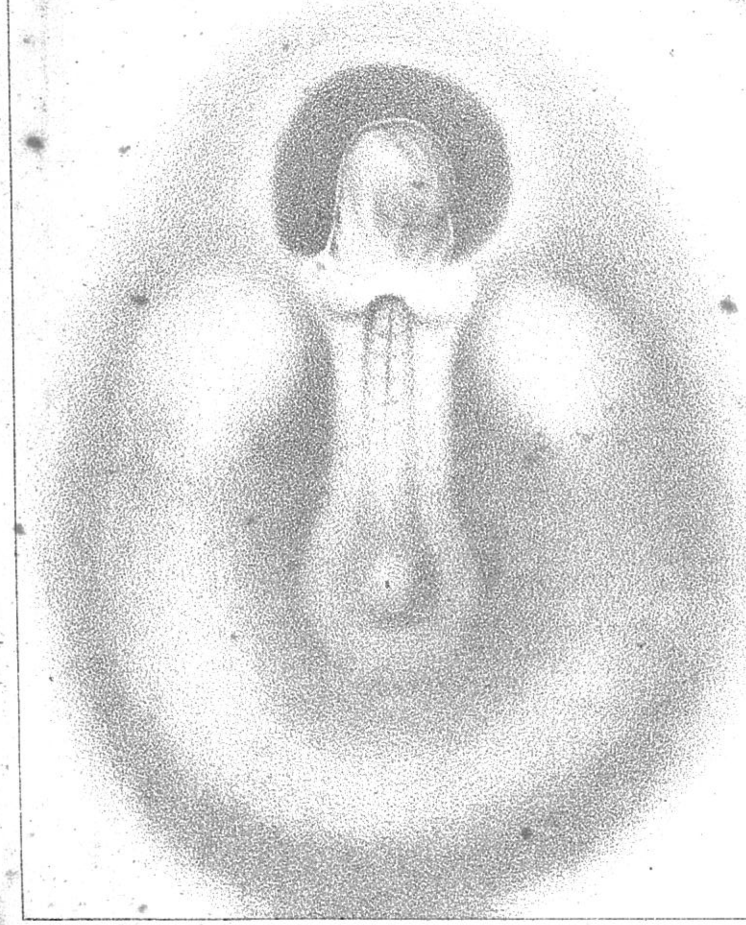


Fig. 17 a



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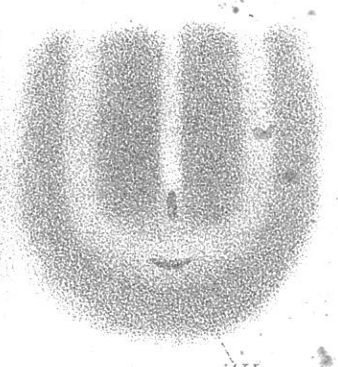

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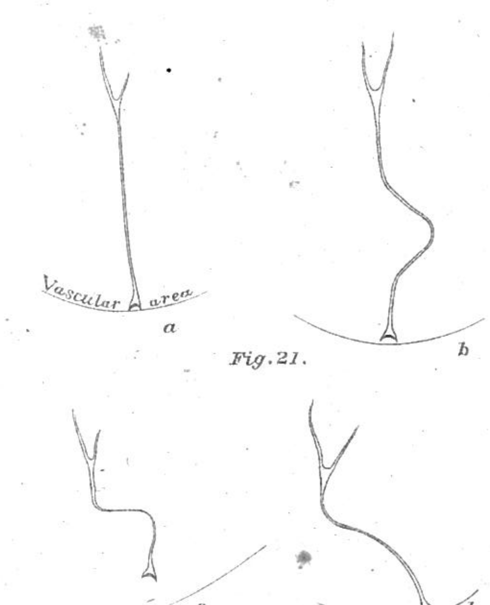

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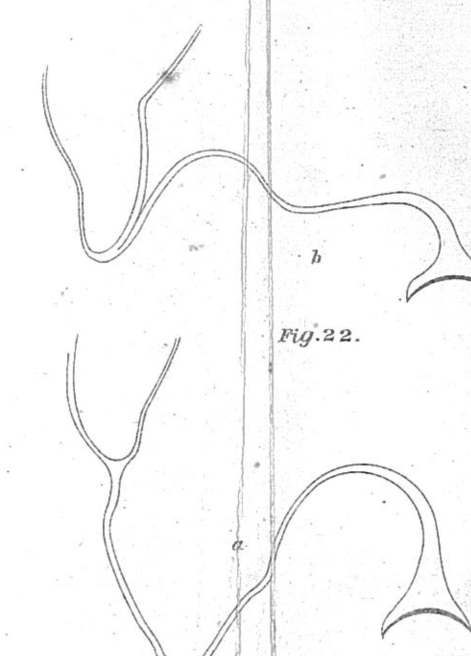

Fig. 22.

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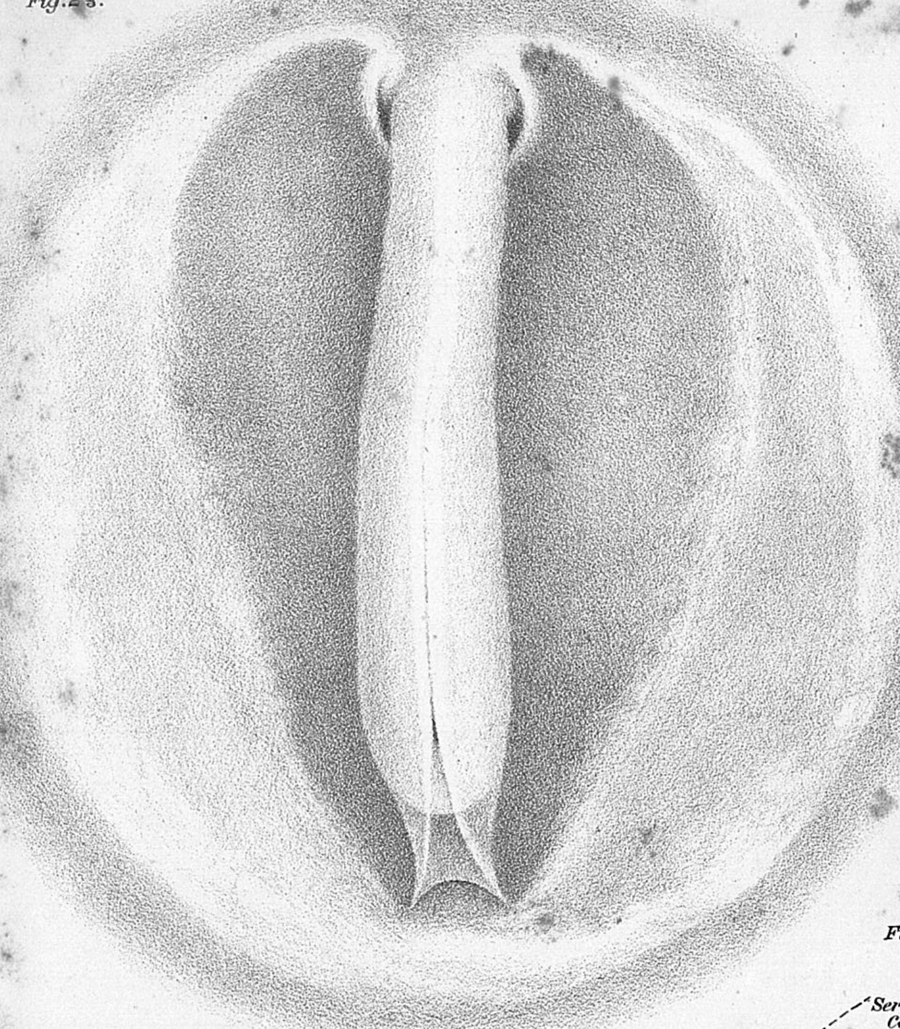
Fig. 23.



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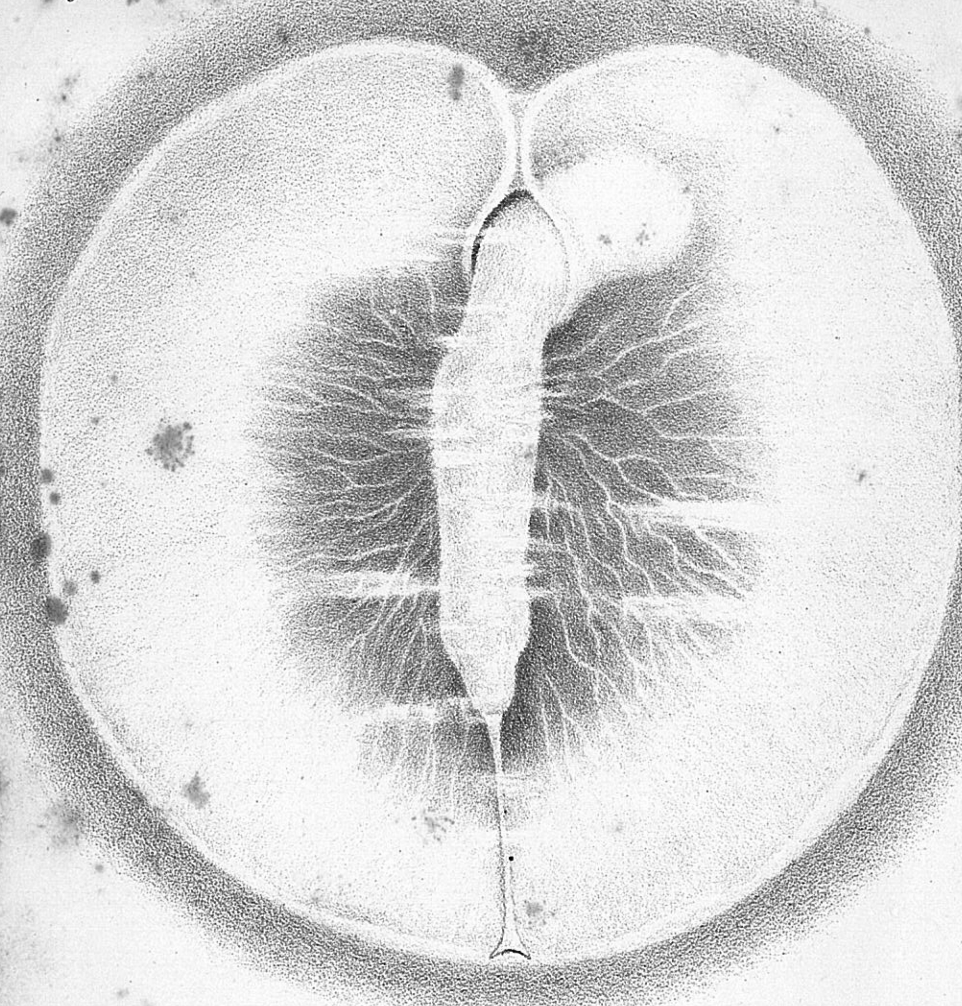

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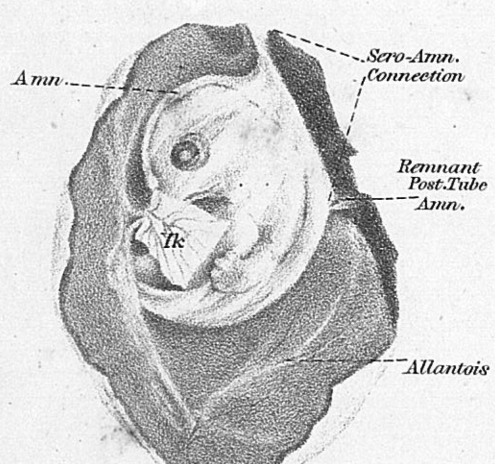

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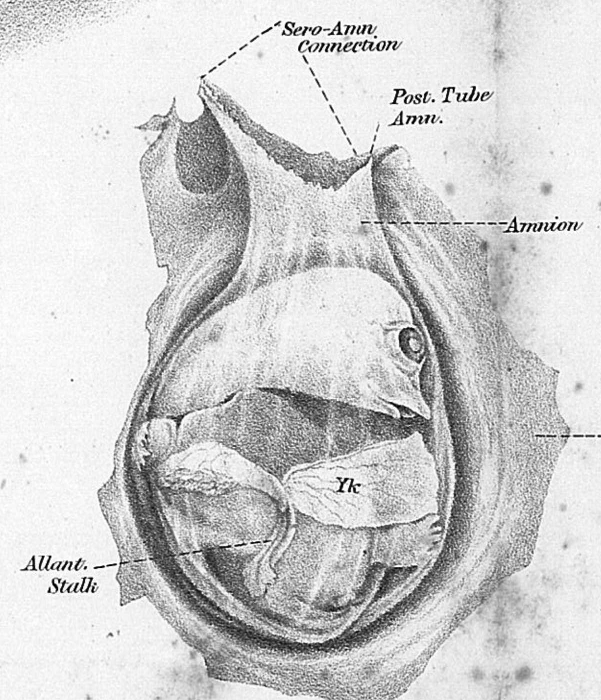

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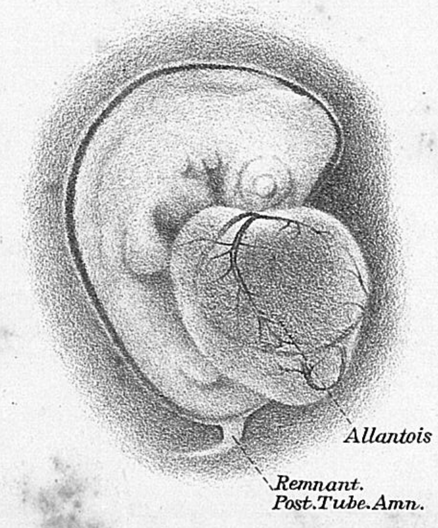

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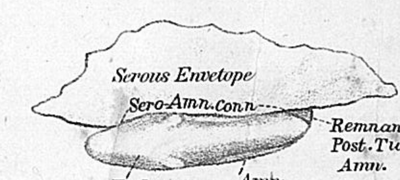

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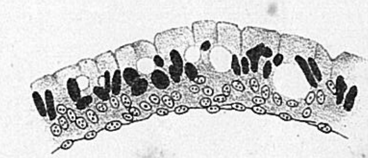

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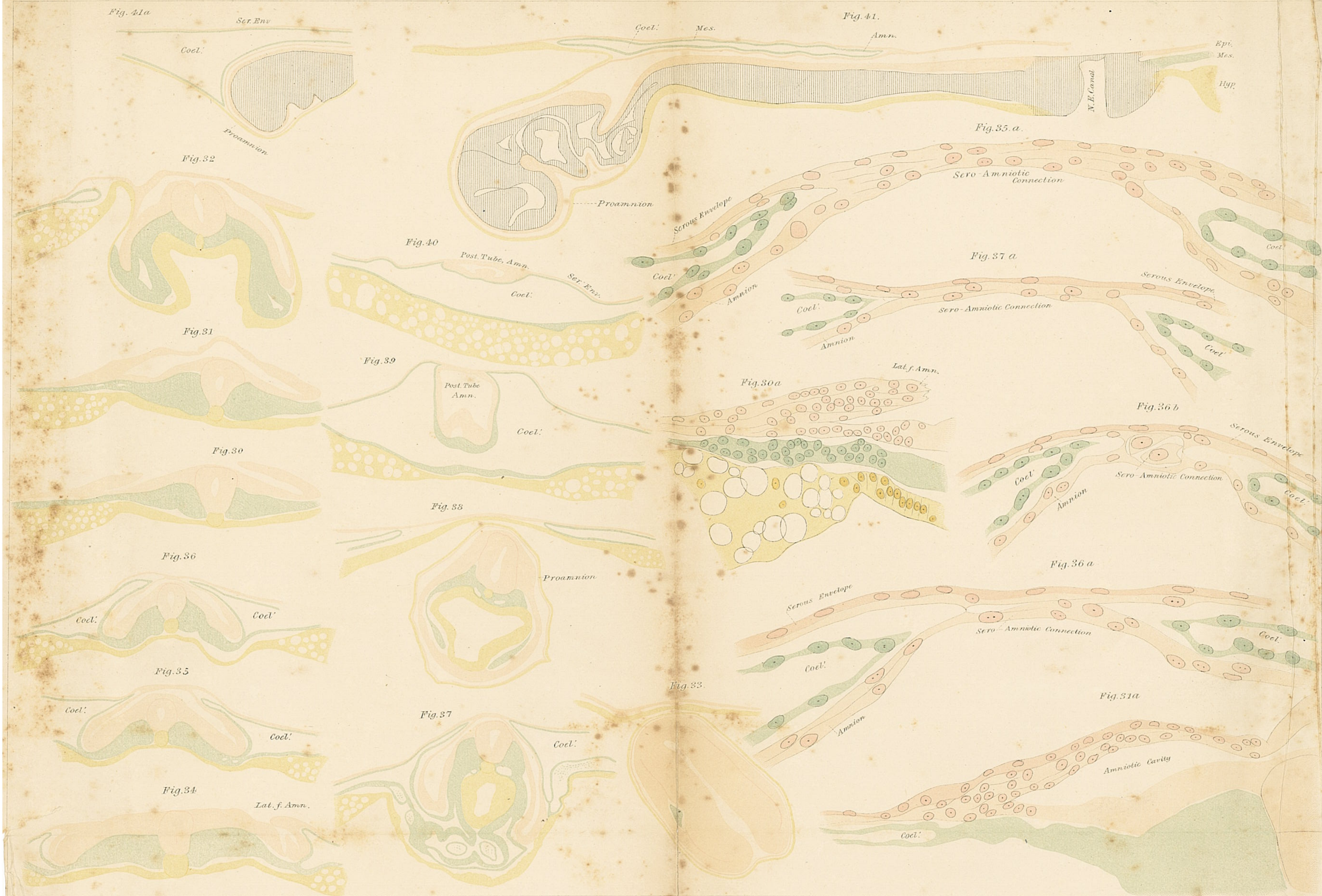

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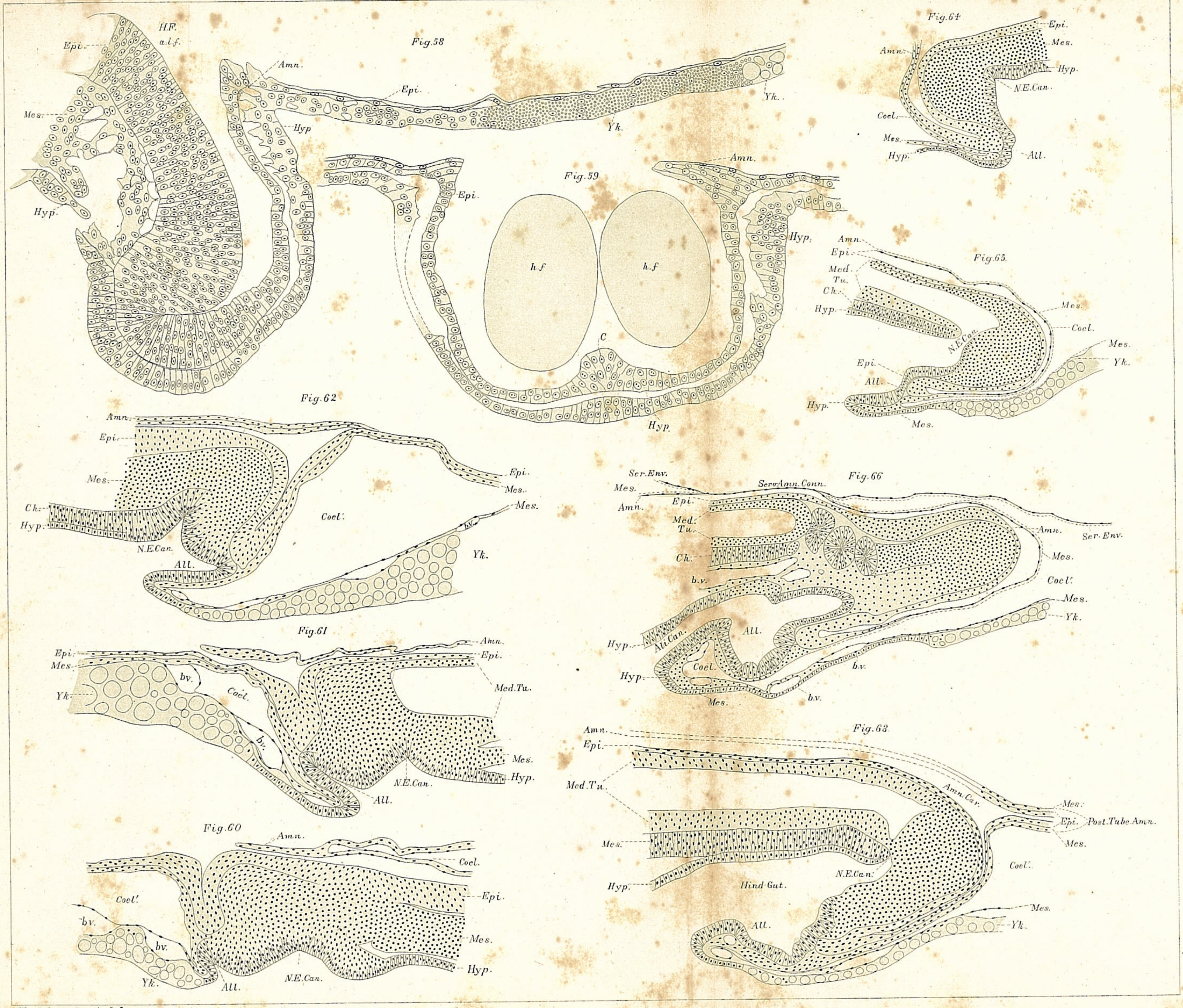

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Fig. 67

Fig. 72.

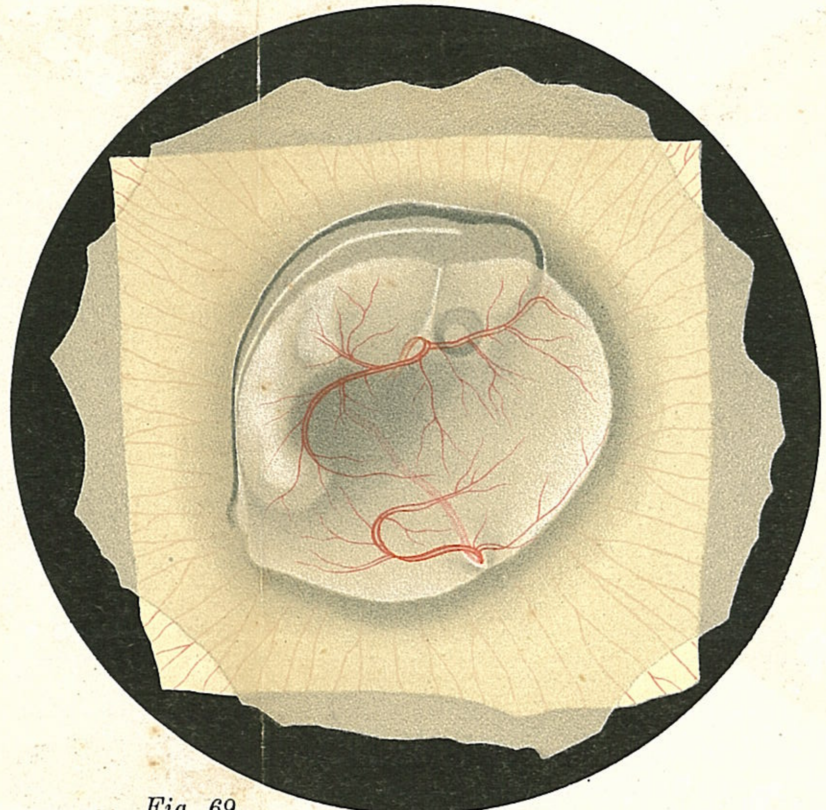


Fig. 71b

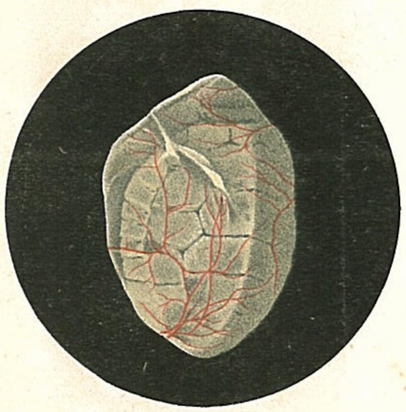


Fig. 70

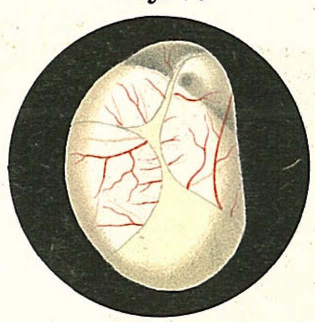


Fig. 69

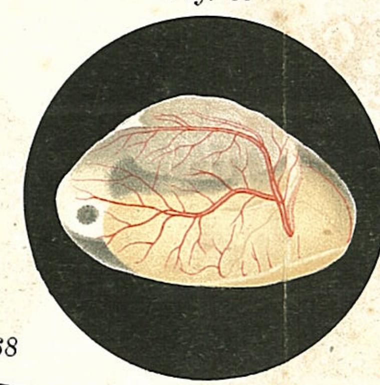


Fig. 73

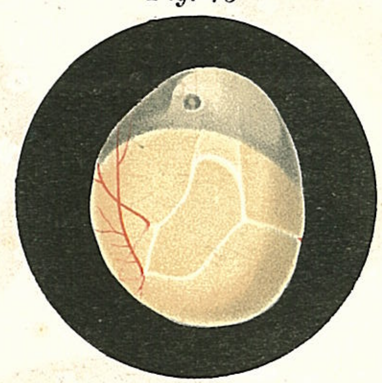


Fig. 68

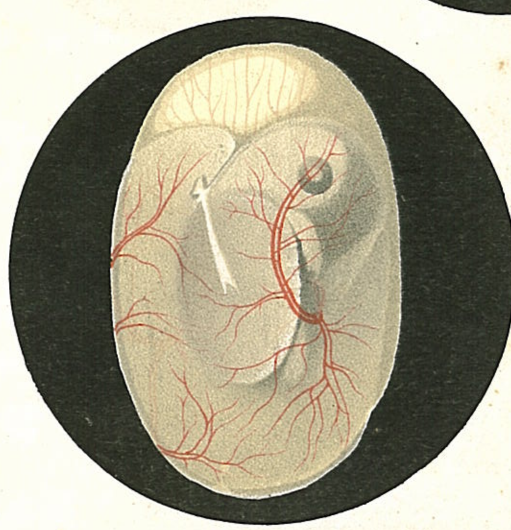


Fig. 71a

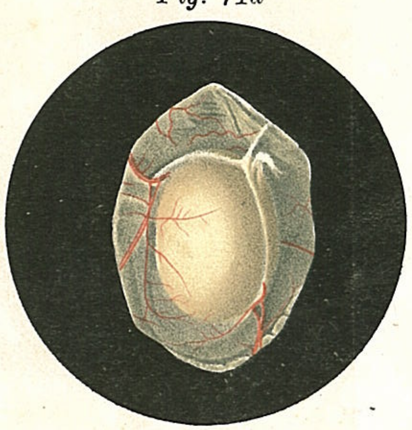
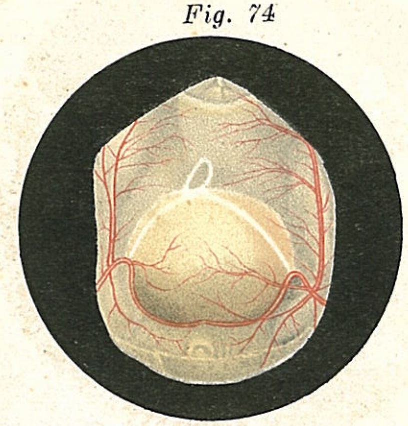


Fig. 74



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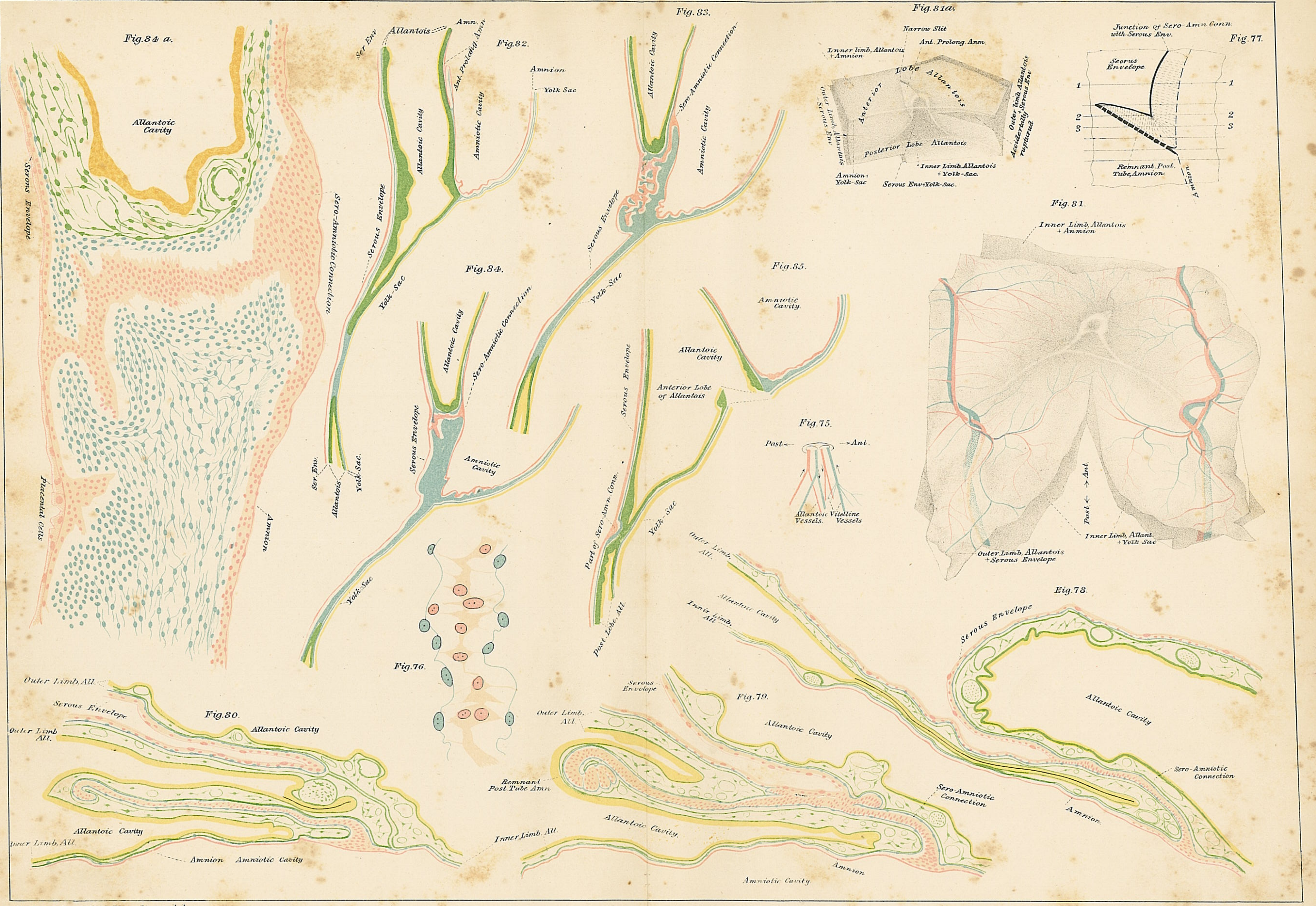

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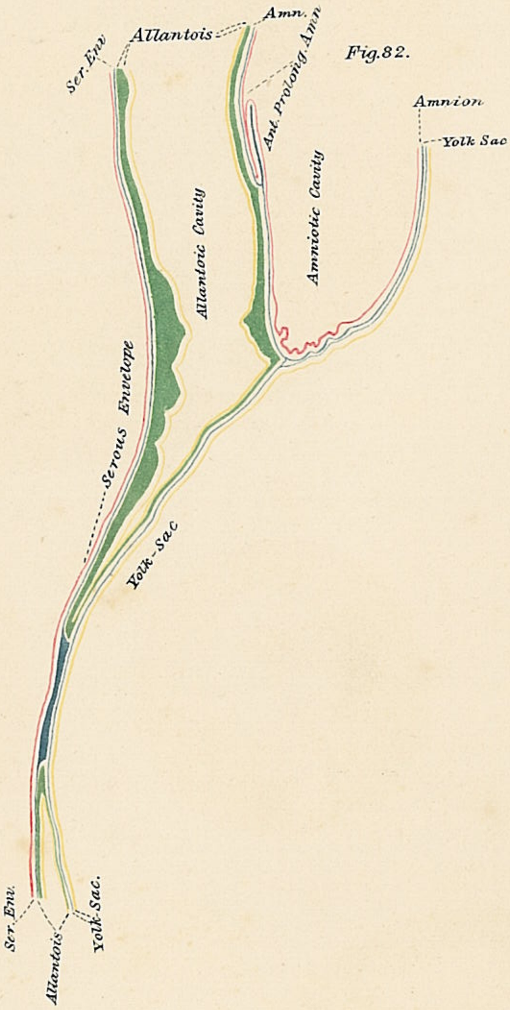
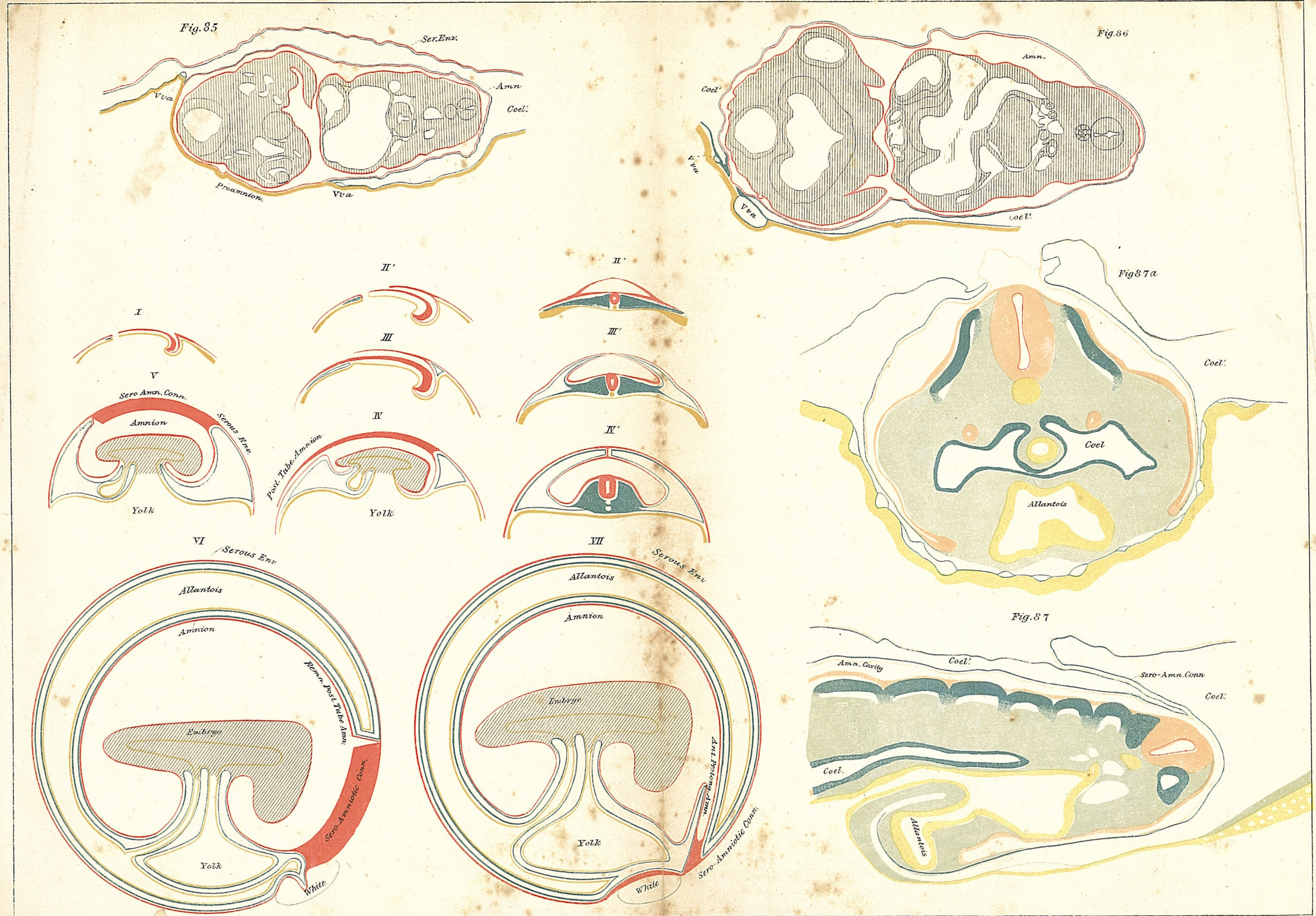
Erratum.

Fig. 82.





K. Mitsukuri & K. Nagahara del.