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THE DEVELOPMENT OF THE LUNGS OF THE ALLIGATOR

(With Nine Plates)

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(With Nine Plates)

As in the chick, the primordia of the lungs in the alligator are budded off from the ventral side of the pharynx just caudad to the region of the gill clefts. They are first seen in embryos of about thirty somites, slightly younger than the one shown, in outline, in figure 1. (The figures are arranged consecutively on plates at end of paper.)

Figure 7 represents a wax reconstruction of the respiratory tract of an embryo of the stage shown in figure 1. Four gill clefts and about thirty-five somites are present in this embryo; but the buds of the appendages are not yet visible. The allantois is evident, just anterior to the tail, but the yolk stalk was torn away and hence is not shown in the figure.

In the embryo from which this reconstruction was made the right bronchial bud was considerably thicker than the left, but extended only about half as far caudad. It is frequently the case that one bronchial bud pushes caudad faster than the other. The planes of the sections are indicated by the numbers 2 to 6, in figure 7.

Figure 2 represents a section through the pharynx, in the region of the last gill cleft, *c*, of the stage under discussion. As seen in the figure, the epithelium of the cleft is here continuous with that of the pharynx, though there is no opening at this point. This section is at the anterior end of the deep, median depression, *g*, in the floor of the pharynx which extends from this point caudad for a considerable distance, and is called by Lillie the laryngo-tracheal groove. This groove is deep, and is so narrow that its cavity is a mere vertical slit; it is open throughout its length to the trachea above. At its posterior end the groove suddenly becomes less deep and widens out, as shown in figures 3 and 7. The plane, 2, of this section is in the region of the extreme anterior end of the reconstruction, figure 7. The lining of all these cavities consists, at this stage, of a compact, stratified epithelium, six or more cells deep.

The structures surrounding those under discussion are shown, but need no description.

Figure 3 shows a section at the point of separation of the trachea, *t*, from the pharynx or œsophagus, *œ*.

Figure 4, six sections caudad to figure 3, shows the trachea primordium, *t*, distinct from the œsophagus, *œ*. The latter has here a circular outline, while the former is much wider from side to side.

Figure 5 is a few sections caudad to figure 4, and shows the trachea at its point of division into the two bronchial primordia, *b*. The œsophagus, *œ*, has the same appearance as in the preceding figure.

Figure 6 is a few sections caudad to figure 5, and represents the two bronchi, *b*, as widely separated from the œsophagus and from each other. As noted above, the right bronchus is of considerably greater diameter than the left, but, as shown in figure 7, it does not extend so far caudad. The epithelium is of the same character as in the more anterior sections.

The entodermal bronchial primordia are surrounded by a rounded mass of pulmonary mesoblast, *m*, that bulges laterally into the crescentic pleural cœlom, *pl*, on each side.

Figure 8 represents a reconstruction on paper of the pulmonary tract of a slightly later stage. The pharynx, *p*, shows the same deep groove in the post-pharyngeal region that was noted in the preceding stage. It rather suddenly divides into the dorsal œsophagus, *œ*, and the ventral trachea, *t*. The œsophagus gradually enlarges as it passes caudad; the trachea, which now extends through a number of sections, diminishes slightly in caliber to its point of division into the two bronchi, *b*, b^1. Each bronchus is rather irregular in shape, but gradually increases in diameter to form an enlargement near its posterior end. In the embryo here represented the right bronchus, *b*, was of greater caliber but of less length than the left, b^1. At the point of separation from the trachea the bronchi lie at a considerable distance ventrad to the œsophagus, but as they pass caudad they gradually approach the horizontal plane of the œsophagus until they lie practically on each side of it. The histological structures are about the same as in the preceding stage so that no sections of this stage need be figured.

Figure 9 represents, in outline, an embryo of the next stage to be described. The appendages are here well developed and the face is beginning to assume form.

Figure 10 is a camera sketch of a wax reconstruction of the entodermal respiratory tract of the embryo shown in figure 9. The

extreme right of the figure is in the posterior region of the pharynx, where the trachea begins to separate from the œsophagus. As may be seen in cross sections, the pharynx is here of a crescentic outline, convex dorsally, and hence is much smaller in cross section than it seems in the figure under discussion. Projecting caudad and ventrad from the horns of the crescent (figures 10, 11 and 12) are one or more hollow, cylindrical bodies, perhaps the so-called epithelial vestiges. The largest and most posterior of these, on the right side is shown at *e* in figure 10. It is quite a conspicuous projection, somewhat swollen near its distal end, lying laterad and somewhat ventrad to the base of the trachea; its mate of the left side is not shown in figure 10. The other epithelial vestiges are smaller and are not represented in this figure; they may be discussed in a later paper. The trachea, *t*, after separating from the œsophagus, *œ*, extends caudad for some distance before it divides into the two bronchi, *b*, b^1. Its anterior region lies parallel to and fairly close to the œsophagus, but at its point of divergence into the bronchi it bends ventrad, so that the bronchi lie at a considerable distance below the œsophagus.

At this stage each endothelial lung rudiment consists of three main lobes, l^1 to l^3, which project dorsad, on each side of the œsophagus, at the region where the latter enlarges and passes ventrad into the stomach, *s*. The mesoderm of the lungs is not lobulated.

Figures 11 to 18 represent transverse section through the respiratory tract in the planes shown on figure 10.

Figure 11 passes through the posterior region of the pharynx, *p*, where it still retains a somewhat crescentic outline, at the point of origin of the trachea, or glottis, *gl*. The epithelium is here comparatively thin and the cavity of the pharynx comparatively spacious. Around the glottis a condensation of mesoblast, *la*, represents the beginning of the larynx. Dorsad and laterad to the pharynx a cylindrical mass is the thymus, *ty*, while one of the epithelial vestiges is shown at *e*. The spinal cord, notochord, etc., may be recognized in this section, but need not be discussed here.

Figure 12 is through the point of separation of the trachea and œsophagus. The deep depression from the floor of the pharynx is here widening to form a tube, *t*, the trachea. The pharynx, *p*, is still of crescentic outline and its cavity is much reduced in extent. The thymus *anlage*, *ty*, appears the same as in the preceding figure, while the epithelial vestige, *e*, here shown is on the right instead of the left side.

Figure 13 is through the region just caudad to the point of separation of trachea, *t*, and œsophagus, *œ*. The former is here a cylindrical tube with a lumen of considerable diameter, while the latter is still crescentic in cross section and has no lumen at all. This solid region of the œsophagus extends through a considerable number of sections, and the fusion of the dorsal and ventral walls is so complete that, even under high power, no indication of the line of fusion is visible. At one side of the trachea is still seen the epithelial vestige, *e*.

Figure 14 represents a section through the middle region of the trachea, *t*, which has here about the same external diameter as in the preceding figure; but, owing to the thicker walls, its lumen is narrower than in the more anterior section. This section is just caudad to the solid region of the œsophagus, *œ*, and shows the reappearance of the lumen as a small, circular opening at each lateral end of the now dumbbell-shaped œsophagus. A very small, irregular space is seen above and below the nearly solid œsophagus, as though it had shrunk away from the surrounding tissue.

Figure 15 shows a section passing through the embryo at the point of division of the trachea into the two bronchi, *b*. At this point the triangular, combined areas of the two bronchi are considerably greater than that of the trachea.

The mesoblast immediately surrounding the bronchi is considerably denser than the general mesoblast of this region. A similar, but less marked, condensation of the mesoblast is seen around the trachea anterior to this region. The œsophagus, *œ*, is here cylindrical and exhibits a large lumen.

Figure 16 represents a section through the bronchi, *b*, just cephalad to the region where they expand to form the first lung lobule, l^1, figure 10. The bronchi here are much larger in diameter than the œsophagus, *œ*, and each is surrounded by a narrow zone of dense mesoblast. In cross section the bronchi are circular, and their walls and that of the œsophagus are composed of a compact epithelium of three or four layers of cells. At this point the œsophagus and two bronchi lie at the angles of a nearly equilateral triangle.

Figure 17 passes through the second pulmonary lobe, l^2, figure 10. That the section does not seem to quite fit the reconstruction is due partly to the angle at which the reconstruction was drawn and partly to a slight falling ventrad of the lungs and trachea, owing to the softening of the wax. The œsophagus, *œ*, is here considerably larger than in the preceding section, is compressed laterally, and lies

immediately between the lungs on either side. The irregular outlines of the lungs and the variation in the thickness of their walls are due, of course, to the plane of the section. The surrounding zone of dense mesoblast is narrower than in the preceding section.

Figure 18 passes through the third and most posterior lobe, l^3, figure 10, of the lung. At this point the œsophagus, *œ*, bends sharply ventrad and rapidly enlarges to form the stomach, *s*. On the right the lung is so cut as to exhibit two cavities, almost at their point of union: a small, dorsal lobule, and a larger, ventral one; on the left the two lobules are cut caudad to their junction, and the upper one is cut through its extreme caudal wall so that its cavity does not appear in the section. The walls are of the same character as in the preceding section, and the dense layer of surrounding mesoblast is even narrower than in the more anterior section.

In this section a small mass of Wolffian tubules, *Wt*, is seen on each side of the aorta and dorsal to the lungs; while both in this and in the preceding two sections the dorsal region of the liver is seen in the lower part of the section, *li*.

Figure 19 represents a reconstruction, on paper, of the endodermal lung of the right side (together with the trachea and œsophagus), of a later stage than the preceding. While the endodermal lung here shows this comparatively complicated series of lobules, the surrounding mesoderm (not shown in figure 19) is still smooth in outline and free from lobules as might be expected from the smooth, unlobulated condition of the adult lung. The extreme right of the figure begins just anterior to the lung and shows the œsophagus, *œ*, and trachea, *t*, the latter being now of much smaller diameter than the former; in the preceding stage they were of about the same caliber. In relation to the size of the lungs the trachea is now of much smaller diameter than before; it is of considerably greater length, though only its posterior part is shown in the figure. The point of division into the two bronchi is at the plane of the line 21, but only one bronchus is shown in the figure. The point of emergence of the bronchus into the lung is in the plane of line 22. At the left of the figure the œsophagus, *œ*, is of much greater caliber than at the more anterior end, but the difference is not so great as is apparent in figure 19, because at the anterior end the long axis of the cross section is horizontal, while at the posterior end it is nearly vertical. Projecting cephalad are seen seven or eight larger lobules of various sizes and shapes, some of which bear secondary lobules; projecting caudad are only five or six lobules, most of which

are smaller than those of the anterior end. Some of the very small secondary lobules are not shown in this figure.

Figure 20 represents a transverse section through line 20 of figure 19; only the respiratory tract and immediately surrounding structures are shown. In the center of the figure is seen the very large œsophagus, *œ*, below which is the relatively narrow trachea, *t;* the epithelium of the former consists of only two or three layers of cells; that of the trachea consists of about four or five layers. Surrounding both tubes is a fairly thick layer of condensed mesoblast; that surrounding the œsophageal epithelium consists of more or less elongated or spindle-shaped cells; that around the tracheal epithelium consists of closely arranged spherical cells. Projecting dorsad and laterad from the undifferentiated mesoblast that surrounds the œsophagus and trachea are two rounded masses, the mesodermal lung primordia, *m*. The mass on the left of the figure is the one shown in figure 19; it is larger than the one on the right and exhibits two lobules of the entodermal lung primordia, *l,* while on the right only the anterior end of a single entodermal lobule is shown. The entoderm of these lobules usually consists of a single layer of rounded cells, but immediately surrounding this entoderm is a thin, dense layer of somewhat flattened mesoderm cells. With the low power, under which the figures are drawn, the entodermal and mesodermal cells cannot be distinguished from each other. In the mesoderm surrounding the layers just described may be seen many small dark areas, *c;* these are the *anlagen* of the pulmonary blood vessels.

Figure 21 shows a section through the point of division of the trachea into the two bronchi, *b* (line 21 of figure 19); each bronchus is of as great diameter as the trachea of the preceding figure. The œsophagus, *œ*, has the same general appearance as in the preceding figure, but has increased somewhat in cross section. The mesodermal lung primordia, *m,* are here much larger than in the preceding section and that on the left is again larger than the one on the right; neither shows any division into lobes. On the left are seen three large and several smaller entodermal primordia, $l^{1\,2}$, while on the right two large and one small entodermal cavities, l^{2}, are seen.

Figure 22 represents a section through line 22 of figure 19; it passes through the point of emergence of the bronchi, *b*, into the lungs. On the left the bronchus is seen opening into the most ventrally located entodermal cavity, l^{1}. On the right the section is just cephalad to the corresponding opening. The œsophagus, *œ*, is

somewhat larger in cross section than in the preceding figure, and the lungs have a greater area than in any other section; they extend from the level of the lower side of the œsophagus to nearly the level of the ventral side of the notochord, *n*. Each lung shows several small and two large entodermal cavities; the mesoderm is still without lobules, and is continuous mesially and ventrally with the mesoderm that surrounds the œsophagus. The entire lung of the right side is not shown in the figure; it has the same general outline as that of the left side.

The wall of the œsophagus at this stage is seen, under higher power, to consist of a thin lining epithelium and a dense layer of surrounding mesoblast, the latter being, on an average, about four times as thick as the former. The epithelium, *ep*, consists of one or two layers of cubical cells; the basal cells are usually the larger. The surrounding mesoblastic layer, *ml*, consists of flattened cells that are evidently turning into fibers, and lie with their long axes parallel to the epithelial layer.

The walls of the trachea and bronchi consist of the same two layers, but the epithelium is much thicker than that of the œsophagus, and consists of three or four layers of cells, the basal cells being again much larger than those nearer the lumen.

The mesoblastic layer is of about the same thickness as that of the œsophagus but consists of closely packed spherical cells instead of the elongated cells seen in the former place.

The lung cavities are lined by a thin epithelium which consists, in most places, of a single layer of cuboidal cells; in many places, however, are seen cresentic thickenings which consist in their thickest part, of four or five layers of cells. These crescents are usually seen in the bottoms of the smaller diverticula from the main lung cavities. Surrounding the epithelial lining is a thin, indistinct layer of slightly condensed mesoblast, scarcely discernible under the low power used in drawing this series of figures.

Figure 23 shows the conditions that are to be seen at a plane about half way between the openings of the bronchi and the posterior ends of the lungs, line 23, figure 19. The œsophagus, *œ*, is very large in this region and might, perhaps, be called the stomach, since, ventrad to it, is seen the liver, *li*. In the upper part of the figure are seen two masses of Wolffian tubules, *Wt*, attached to the mesentery on either side of the dorsal aorta, *a*.

The two lungs are of somewhat smaller area than in the preceding section and that on the right shows an indication of a division into a mesodermal lobe at l^3. Part of the lung on the right side is not

included in this figure. The main entodermal cavity on the right side is very irregular in outline and is surrounded by several smaller lobules which are not indicated in the reconstruction.

Figure 24 represents a hasty reconstruction of the mesodermal lung on the right side of an embryo of about seven centimeters length. The lung, *m,* it will be seen, is without division into lobes and is very deep dorso-ventrally, in proportion to its length. The bronchus, *b,* enters it slightly caudad to its middle region. The point of division of the trachea, *t,* into the two main bronchi is in the plane of figure 25. The œsophagus, *œ,* is of large diameter, but its apparently unusual size is partly due to its being laterally compressed.

Figure 25 represents a section through the body of this embryo at the point of division of the trachea, *t,* into the two bronchi, line 25 in figure 24. The skeleton, *aa, ce, r,* is now well outlined in cartilage, and the lungs are approaching their adult condition. The lung on the right side of the figure is somewhat larger than that on the left and exhibits six or eight large endodermal cavities, *l,* l^1, etc., and numerous smaller ones.

Just ventrad to the œsophagus is the trachea, *t,* with thick walls in which several condensations indicate the formation of the tracheal cartilages, as noted below. Surrounding the trachea are several large pulmonary blood vessels, *bv.*

Figure 26, through line 26 of figure 24, represents a section through the region where the bronchi, *b,* enter the lungs. On the right the bronchus is shown opening directly into the endodermal diverticulum, l^2. Ventrad to the œsophagus, *œ,* and bronchi are several large blood vessels, *bv,* five of which are grouped in a dense mass of mesoblast.

At this stage there has been but little change, histologically, from what was noted in connection with figure 22, though the poor fixation of the material at hand makes it difficult to determine minute details. In the œsophagus the epithelium is about as before, but the surrounding, dense layer of mesoblast now exhibits a faint division into a granular layer, next the epithelium and a more fibrous layer outside of this; the former may represent the submucosa; the latter, the muscular layer, though this point has not been worked out. In the trachea and bronchi the epithelium is thinner than in the preceding stage and consists of only one or two layers of cells. In the surrounding condensed layer of mesoblast may be seen a number of small, darkly stained areas, *ca;* these, under a higher magnification, are seen to consist of a closely-packed

mass of cells, and doubtless represent the *anlagen* of the cartilaginous rings, as noted above. The lung cavities, l^1—l^3, have about the same appearance as described in connection with figure 22, though the epithelium is, perhaps, somewhat thinner, and the crescents are not quite so marked. No attempt has been made to show these details with the low power used in this figure.

Figure 27 represents a ventral view of the body of an alligator of about 15 cm. length, dissected to show the respiratory organs and the neighboring structures.

The trachea, *t,* is seen lying against the ventral wall of the large œsophagus, *œ*; its numerous cartilaginous rings are easily seen. At the anterior end of the trunchus, *tr,* the trachea disappears beneath (dorsad to) the thyroid gland, *tg,* and its division into the two bronchi cannot be seen in this figure. The lungs, *l,* are elongated bodies, lying on each side of and mostly anterior to the heart. Their medial borders are covered by the auricles, *au,* and the thymus glands, *ty,* while the posterior end of each lies beneath (dorsad to) the corresponding lobe of the liver, *li.* The alveolar appearance of the lungs is easily seen with the naked eye. A thymus gland, *ty,* is seen on either side of the posterior region of the trachea; it consists of a lobulated mass posteriorly and of an anteriorly directed cylindrical portion extending forwards into the neck. The heart and liver need not be described here. In the cut surface of the neck may be seen the spinal cord, *sp,* and the notochord, *n,* surrounded by the now cartilaginous vertebral column. The yolk or umbilical stalk, *u,* is shown, somewhat diagrammatically, just caudad to the opened body cavity.

Figure 28 represents, in outline, the respiratory organs of an alligator of about 75 cm. length; this animal was probably two years old and its lungs should have reached approximately their adult condition.

Extending from the glottis, *gl,* at the base of the tongue, *to,* is the fairly wide trachea, *t;* between the lungs it divides symmetrically into the two bronchi, *b,* which enter their respective lungs a little cephalad to the middle region of these organs. The pulmonary veins, *pv,* are shown at the posterior edge of the bronchi; the corresponding arteries are not shown in this figure.

The internal structure of the adult lung has been described by Miller (3) and others and need not be noted here.

The thyroid gland, *tg,* is shown against the trachea just cephalad to the origin of the bronchi.

The material upon which the foregoing work was done was collected by the author in central Florida with the aid of a grant from the Smithsonian Institution.

The embryos were removed from the eggs, in the field, and fixed in various ways. They were sectioned chiefly in the transverse and sagittal planes and were stained, in most cases, with borax carmine and Lyon's blue.

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LETTERING

a, aorta.
aa, anterior appendage.
au, auricle.
b, b', bronchi.
bv, blood vessel.
c, last gill cleft.
ca, cartilage rings of trachea and bronchi.
ce, centrum.
co, cœlom.
e, epithelial vestige.
ep, epithelium.
g, laryngo-tracheal groove.
gl, glottis.
h, heart.
l'—l,[3] lung or lung diverticula.
la, larynx.
li, liver.
m, mesoblastic lung primordium.
ml, mesoblastic layer.
n, notochord.
œ, œsophagus.
p, pharynx.
pl, pleural cœlom.
pv, pulmonary veins.
r, rib.
s, stomach.
sp, spinal cord.
t, trachea.
tg, thyroid gland.
to, tongue.
tr, trunchus arteriosus.
ty, thymus gland.
u, umbilical cord.
v, ventricle.
Wt, Wolffian tubules.

DESCRIPTION OF FIGURES

Fig. 1.—An outline of an alligator embryo at the beginning of the formation of the lungs.

Figs. 2 to 6.—Transverse section through an embryo of the stage shown in figure 1. The planes of these sections are shown in the reconstruction, figure 7.

FIG. 7.—A wax reconstruction of the respiratory tract of the embryo shown in figure 1.

FIG. 8.—A reconstruction, on paper, of the respiratory tract of an embryo of slightly later development than the one shown in figure 1.

FIG. 9.—An outline of an embryo somewhat older than the one represented in figure 8.

FIG. 10.—A camera sketch of a wax reconstruction of the entodermal respiratory tract of the stage shown in figure 9. The extreme right of the figure is in the region of the pharynx, where the trachea begins to separate from the œsophagus.

FIGS. 11 to 18.—Transverse sections through the respiratory tract in the planes shown on figure 10.

FIG. 19.—A reconstruction, on paper, of the entodermal lung of the right side (together with the trachea and œsophagus) of a later stage than the one represented in figures 10 to 18.

FIGS. 20 to 23.—Transverse sections through the embryo represented in figure 19, in the planes of lines 20 to 23 of that figure.

FIG. 24.—A reconstruction, on paper, of the mesodermal lung on the right side of an embryo of about 7 cm. length.

FIGS. 25, 26.—Transverse sections through the embryo represented in figure 24, in the planes of lines 25 and 26.

FIG. 27.—A ventral view of a dissected embryo of about 15 cm. length, showing the respiratory and other organs.

FIG. 28.—An outline of the respiratory organs of an alligator of about 75 cm. length.

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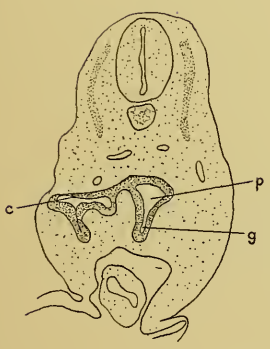

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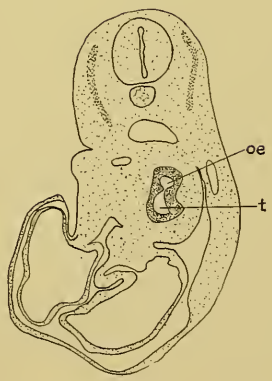

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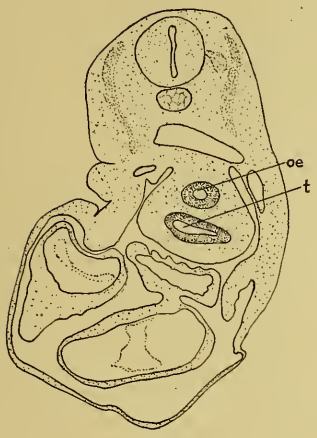
DEVELOPMENT OF LUNGS OF ALLIGATOR



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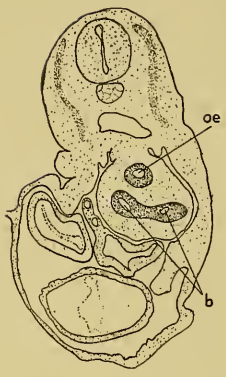

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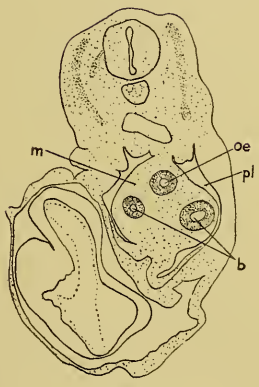

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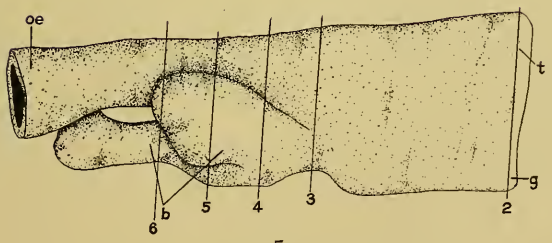

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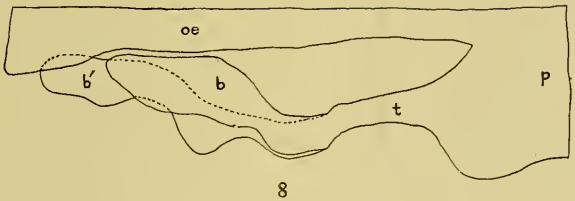
DEVELOPMENT OF LUNGS OF ALLIGATOR



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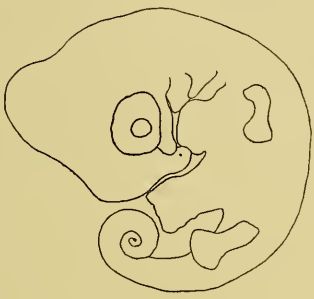

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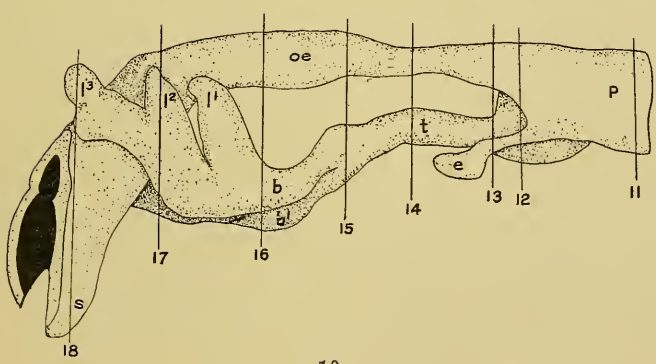

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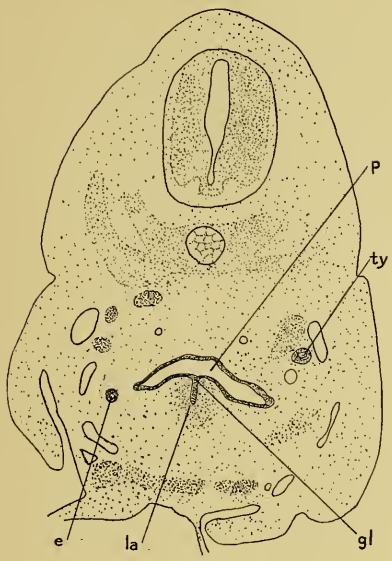
DEVELOPMENT OF LUNGS OF ALLIGATOR



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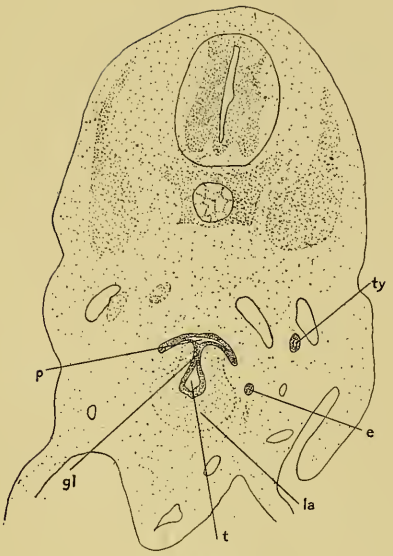

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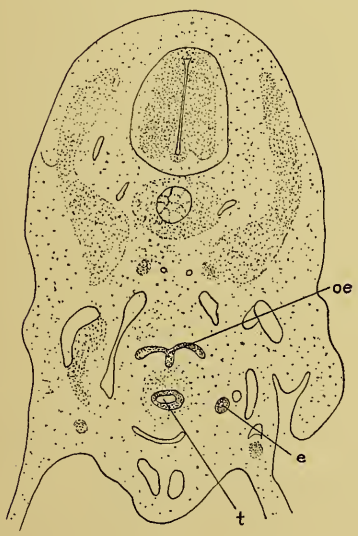

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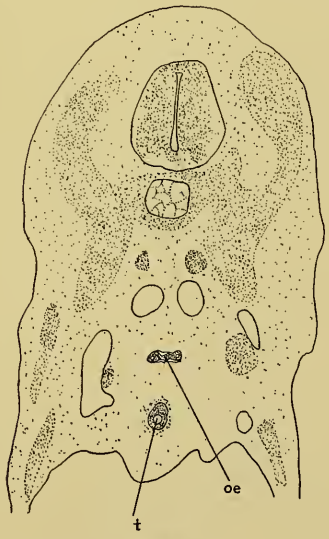

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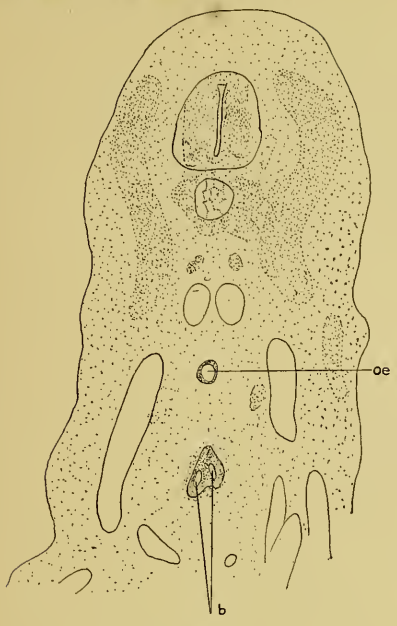
DEVELOPMENT OF LUNGS OF ALLIGATOR



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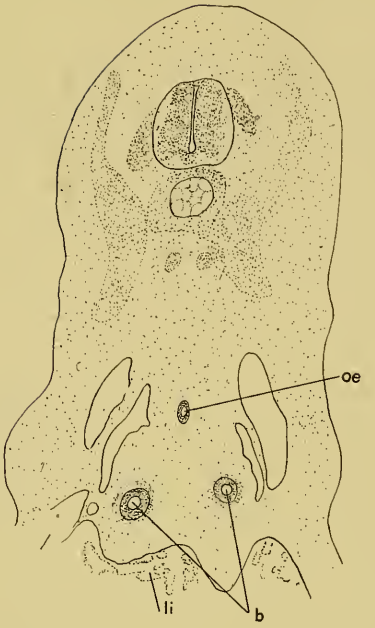

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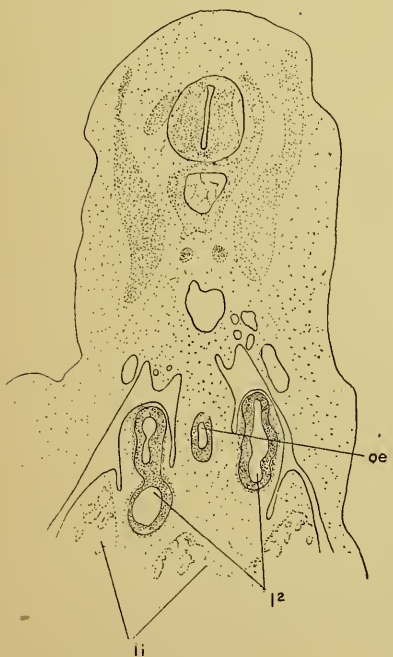

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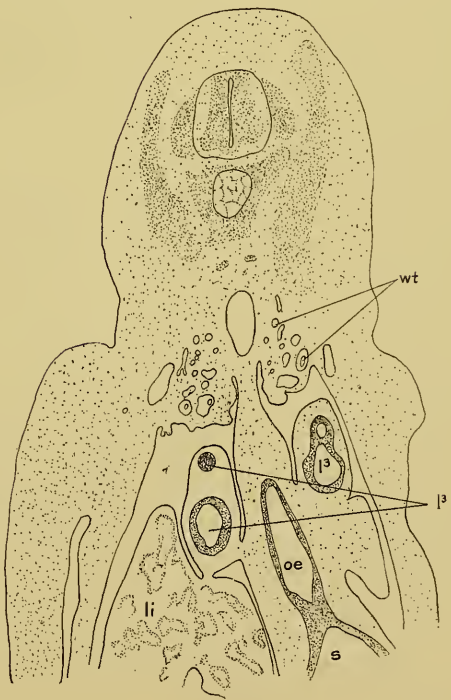

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DEVELOPMENT OF LUNGS OF ALLIGATOR

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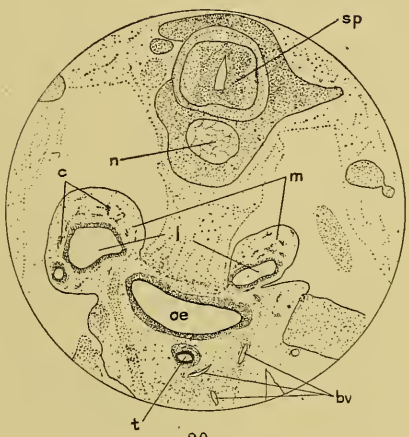

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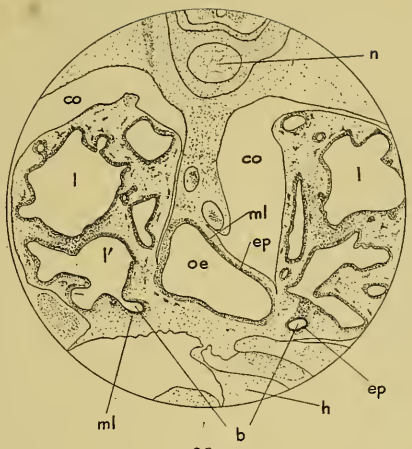

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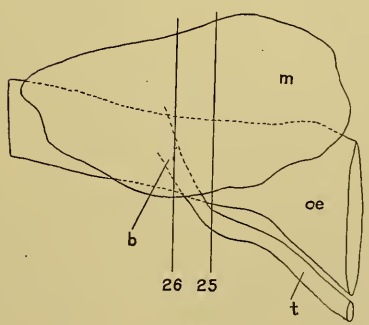

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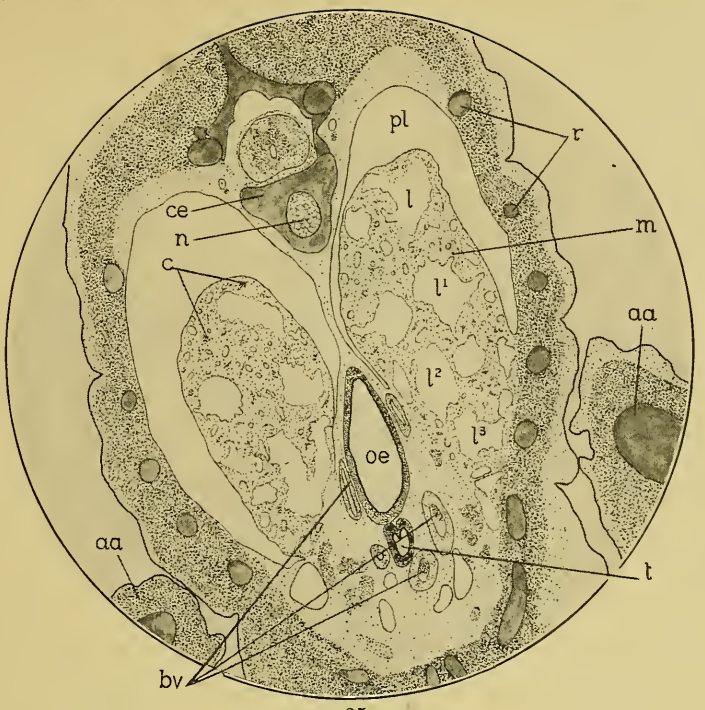
DEVELOPMENT OF LUNGS OF ALLIGATOR



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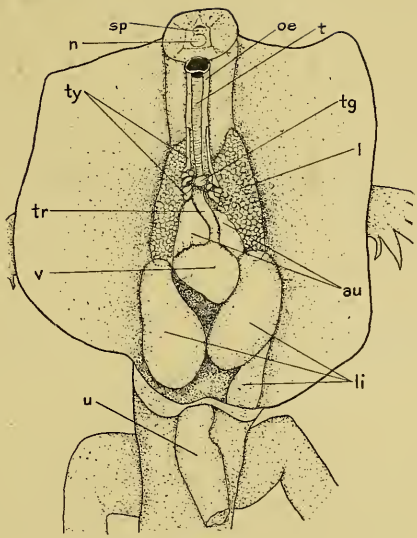

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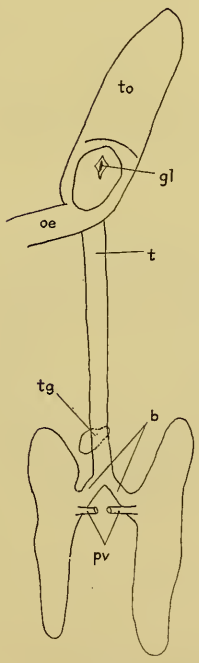

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DEVELOPMENT OF LUNGS OF ALLIGATOR