DEVELOPMENT OF THE LUNG OF THE CHICK

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The development of the chick begins primarily from a leaf-like membrane, consisting of three layers, the epiblast, mesoblast and hypoblast. The nervous system is the first part to take definite shape, being formed by a folding together of the epiblast along and above the primitive groove. At an early stage the mesoblast separates into two layers, one of which unites with the epiblast to form the somatopleure or body wall, and the other adheres to the hypoblast, forming the splanchnopleure, or wall of the alimentary canal. Following the appearance of the rudimentary nervous system, the muscular tissue, which properly determines the outline of the future adult, is developed from the mesoblast. Next the tubular heart and the beginnings of the vascular system are formed from the splanchnic mesoblast. Then in order comes the formation of the alimentary canal, first really
determined and described by the German embryologist Wolff, and published in 1768-69. At first a mere furrow, the alimentary canal begins to close up simultaneously from the head-fold backward, and from the tail-fold forward, the enclosing portions coming together in the region of the peduncle of the yolk-sac. Several of the internal organs, such as the lungs, liver, and pancreas, take their origin from the alimentary canal, and hence it is with the latter that one must begin to study the development of the lungs in the chick. The space formed by the separation of the primitive mesoblast is at first called the coelomic space, and later, into this the lungs project from either side the alimentary canal, whence it is known as the pleuro-peritoneal cavity. In the adult fowl, the lungs are closely pressed against and adhere to the anterior ventral surface of the spinal column and ribs, pushing around the former and into between the latter, thus adapting their contour to the irregularities of the surface.

The mass of mesoblast containing and surrounding the alimentary
canal, and the organ developed from the latter, extends along the middle dorsal line of the body cavity, from which it is later suspended by the rudimentary mesentery, (See Plate I, Fig. 4, m.). The pleuroperitoneal cavity begins at a point in the region of the visceral clefts, but the splanchnic mesoblast does not begin to project into this cavity until a point just anterior to the union of the trachea and oesophagus has been reached. Anterior to this point the splanchnic mesoblast may be traced as a rounded core with the alimentary tube as its centre. Posteriorly it appears as a ridge extending downward from the dorsal surface of the body cavity. (See Plate I, Fig. 1). This dorsal projection gradually increases in size with the increasing diameter of the body cavity, and spreading downward and laterally comes to nearly fill the dorsal portion of the latter.

During all the earlier stages of the development of the lungs of the chick, one cannot fail to be struck by the vast discrepancy between the growth of the lungs and of neighboring organs, such as the heart, liver, etc. This is explained by the fact that some organs become
functional earlier than others, and there is therefore a demand for
their earlier development. The heart is in action almost from the
first day, while the lungs do not come into use until the chick
has reached a comparatively full stage of development, prior to which
the allantois acts as the organ of respiration.

The development of the lungs begins about the middle of the third
day of incubation. The time can be given only approximately, since there
is much diversity in the rate of development in individual embryos.
While at this stage, the alimentary canal is not yet entirely enclosed,
the lungs which are primarily buds from the former, have already begun
their development. First the pair of buds, one on each ventral lateral surface,
and directly opposite each other, pushes out from the alimentary wall in the
surrounding mesoblast, and thus simple is the beginning of one of the most
important organs of a typical vertebrate. Following the appearance of the
buds, just back of the visceral clefts the alimentary canal is first lat-
erally compressed, and then longitudinally constricted, so that a cross-
section shows the canal much the shape of an hour-glass, consisting
of two cavities united by a short narrow neck (See Plate I, Fig. 2). The upper or dorsal cavity (al. c.) persists as the oesophagus, while the lower or ventral (t.) goes to form the future trachea. The latter gradually widens (Fig. 3, t.), and the mesoblast pushing inward from the sides and below (Fig. 4), divides the pulmonic tube into two branches (Fig. 5, t.), corresponding to and uniting with the lung-buds, which latter are cut off by the constriction of the same process of constriction which severs the pulmonic from the alimentary tube. So far the description applies only to changes occurring in the hypoblast, which forms the lining of the tube. Meanwhile, the mass of splanchnic mesoblast surrounding the alimentary tract has been gradually changed in conformity with the changes within. The mesoblast greatly thickens in the region of the bifurcation of the pulmonary tube, and adapting its shape to the contour of the outer surface of the hypoblast, forms two rounded lobes which project backward and outward (See Plate II, Fig. 6, l.). Some authorities state that there is a distinctly bilobed appearance from
from the first.

At the end of the fourth day considerable advance has been made. The alimentary tube in the region of its union with the trachea shows a beginning differentiation in the mesoblast preparatory to formation of the muscular coats, but this appearance grows gradually less distinct as we proceed posteriorly. The mesoblast of the pulmonary tube at this time shows no such internal changes, but the cells of that portion next the hypoblast are closely applied, and this condition can be traced for a considerable distance along the trachea and bronchi, but gradually disappears as the lung tissue proper is reached. At this stage, the bronchial cavities have penetrated in a straight line almost to the lowest point of the lung tissue, and now the first change within the lung itself after the bronchial penetration takes place. While the bronchial cavity proper extends downward, a branch, is given off at a point somewhat above the middle transverse line, and penetrates upward and backward into the dorsal portion of the lung tissue (See Plate IV, Fig. 19).
This branch together with the main trunk later forms the general cavity of the lung, and from these other branches will be given off in turn. In general at this stage the lung lobes have assumed a more definite form, and are further advanced in their separation from the mesoblast of the rudimentary oesophagus and mesentery. At the point where the trachea divides into the bronchi, the cavity of the alimentary canal is dorsal to a plane passing horizontally through the bronchi (See Plate III, Fig 12), but the canal gradually inclines downward and the bronchi upward, until the respective positions are reversed (Plate III, Fig 15). All changes of this date described are those of the hypoblast, the mesoblastic tissue proper of the lungs being still homogeneous, no internal changes being visible.

At the end of the fifth day, the development of the muscular coats of the intestine has advanced considerably. One marked feature in this and closely preceding stages is the peculiar gathering of the mesoblast about the outer lateral and lower surfaces of the bronchi. It would
seem as if the bronchi in their divergence and downward growth pressed against the mesoblastic cells in their course, and thus crowded them together in those regions. The constriction of the lung-lobes from the splanchnic mesoblast still continues. This separation began posteriorly, and at this stage the posterior third of the lobes is free, but the remaining anterior portion is united along its ventral surface to the hepatic mesoblast, from which it is gradually separated from behind forward as the constriction of the lobes continues. Beyond this description of this day's events, with the exception of an expected large increase in the size of the lobes, there are no greatly marked changes.

In other ways, however, the fifth day may be remembered. It really marks the beginning of the histological differentiation of the various cell-layers. While the cells in different parts of the embryo still have somewhat their original similarity, yet the changes which have occurred are comparatively small, to the great modification which follow. Hitherto the cells have been generally of a
size, with large rounded nuclei, and in shape, spherical, elongated, or columnar, according to their position. The mesoblast, especially, which undergoes far more changes than either of the other layers, up to now has consisted of little more than indifferent tissue.

There are as yet no characteristic tissues, and the various parts and organs are simply marked out by a greater or less condensation of the mesoblast. From now on, histological differentiation goes on rapidly, and it becomes possible to say that this or that part is composed of muscular, cartilaginous, or connective tissue, as the case may be. The hypoblastic lining of the alimentary canal, trachea and bronchi now consists of several layers of columnar cells, containing elongated nuclei, while the mesoblast surrounding these tubes, is composed of rather smaller oval cells, with rounded nuclei. Small blood vessels containing large blood corpuscles appear in the lower and outer portions of the pulmonic mesoblast.

On the sixth day the development of the muscular coats of the alimentary canal in the pulmonic tract, and a similar change
may be seen in the mesoblast surrounding the trachea at the point
of its union with the oesophagus. The lung lobes exhibit a special
development of their dorsal parts, and now nearly fill their respective
portions of the pleuro-peritoneal space. The great enlargement of
the liver at this stage causes an encroachment upon the
lung cavity, and the lobes are thereby pressed upward. The
process of constriction has rapidly continued, and now the lungs
are attached by less than half their anterior ventral edges to
the hepatic mesoblast, and along the middle longitudinal line
on the respective sides next to the alimentary canal by a short
thick mesentery-like structure. The general cavity of the lungs has
been greatly enlarged by the branching and widening of the pene-
trating bronchi, and forms a considerable space within the lung
tissue (See Plate V, Fig. 20). A transverse section (Plate V, Fig. 21) above
the middle line shows the lobes somewhat kidney-shaped, plump,
and rounded, as if the fullness were due to the expansion of
the general cavity. This cavity is everywhere lined with an ex-
tension of the same hypoblastic lining of the bronchi and trachea.

The two pulmonic veins can be seen (Plate V, Fig 21. p.v.) proceeding from the left side of the auricular division of the heart to their respective lungs, entering the latter at a point on the inner ventral surface, and above the transverse middle line. These veins are very large, and each can be traced from the point of entrance for some distance parallel to the inner lateral margin to a point where it turns downward. The pulmonic veins are formed from within and from the mesoblastic tissue, and have no connection with the mesoblastic lining of the general cavity.

At the end of the seventh day the oesophagus has considerably separated from the surrounding mesoblast. The cavity of the trachea in comparison with that of the oesophagus is very small, and where it enters the latter is reduced to a narrow slit. The tracheal cavity gradually increases in size posteriorly, but at no time approaches the diameter of the oesophagus. The angle of the divergence of the bronchi has been changed by an inward elbowing of the tubes at
a point about midway between their union and where they enter their respective lungs. They first diverge at about thirty degrees, and at the point above mentioned suddenly increase the angle to about one hundred degrees (See Plate IV, Fig. 12). The bronchi have also become relatively shortened because of the dorsal development of the lung lobes, which they penetrate for some distance before branching. The lobes have begun to assume their characteristic form and appearance, and to adapt their contour to the varying form of their respective cavities. The lobes rest closely upon the liver below, and press loosely against the oesophagus, which passes downward between them, but are free as to their dorsal and lateral surfaces. The general cavity now occupies fully half of the bulk of the lobes, and while extending to almost the extreme depth of the lung, yet the greater development has occurred in the dorsal portions, as is evidenced by the presence of the greater number of bronchial tubes in those parts. The tubes decrease in diameter with each sub-division, much like the branching of a tree, and the smaller branches are
given off from each successive larger branch. The hypoblastic lining which is several layers in thickness in the oesophagus, branch, and bronchi, diminishes in relative proportion to the decreasing diameters of the bronchial sub-divisions. Each of the pulmonary veins which enter its lung at a point a little below the entrance, after proceeding a short distance separates into two main branches, one passing to the left, and the other to the right side of the general cavity. Beyond this the main branches give rise to further divisions.

Coming to the end of the penultimate day, we find that as the lungs increase in size, there is a corresponding increase in the growth of the pectoral region, and of the body of the chick in general, whereas before the head has been most conspicuous in its development. The neck now increases somewhat in length, while its transverse diameter is relatively shortened. The oesophagus and trachea have developed proportionally with the neck, but between the point of union of the trachea and oesophagus, and the bifurcation of the former, there is, for some reason to one unknown, a
strange flexure (not observable in preceding stages) of both the trachea and oesophagus to the right of the median dorsal-ventral line; while above and below the region of the flexure, the normal position, in which both are situated directly in the line, the trachea in front of the oesophagus, is assumed by both. In this flexure the oesophagus is deflected much farther to the right than the trachea. Both these tubes are now without the general muscular coat of the neck, situated within the substance of the connective tissue cylinder which lies between the muscles and the skin.

The mucous layer (hypoblast) of the trachea is seen surrounded by the submucous which at this stage consists of a homogeneous ring of closely applied mesoblastic cells, and in which small blood-vessels occasionally appear. The muscular layer without the submucous is very small and inconspicuous. Still without this may be seen the cartilaginous rings of the trachea in process of development. Each ring as seen in transverse section at first consists a pair of semi-lunar, dense mesoblastic masses lying opposite the extremities of the median
lateral line. These masses gradually grow together behind and in front, thus forming a complete ring. These rudimentary rings may be traced downward along the bronchi for some distance.

The lung lobes are gradually filling up the dorsal and anterior portions of the pleuro-peritoneal cavity, and are beginning to conform their outer surfaces preparatory to filling up the space in between the ribs and around the ventral surface of the dorsal vertebrae, a noticeable avian characteristic. The formation of the bronchial tubes has now reached a fifth division, as evidenced by the graduated series of five sizes of tubes which are found in marked uniformity throughout the lung tissue. These branches, as has been before stated, are given off at right angles, and generally run parallel to each other (See Plate VII. Fig. 24.) The mucous membrane of these tubes consists of two or three layers of columnar cells, as yet unciliated. This living epithelium is generally of a uniform thickness throughout these branches, except at the penetrating ends of the smallest tubes, where it seems abnormally developed.
The pulmonic veins divide and subdivide, sending minute vessels in between the ultimate ramifications of the bronchi. Already there is seen a differentiation of the mesoblast composing the walls of these pulmonary veins preparing to the formation of a definite lining.

We have seen what great advances have been made in the development of the lungs of the chick up to the tenth day, but as yet there are no indications of the development of the infundibula, and their alveoli, which must be sought for in later stages.
**Explanations of Plates**

**Plate I.** Fig. 1. Transverse section of 48-hour chick, through the pulmonary tract just prior to the lung formation.
- f.a. - false amnion
- t.a. - true amnion
- m.c. - medullary canal
- m.p. - muscle plate
- n.c.h. - notochord
- d.a. - dorsal aorta
- c.v. - cardinal vein
- d.c. - alimentary canal
- s.p.p. - splanchnopleure
- s.o.p. - somatopleure
- c. - somatic cavity
- y.s. - yolk-sac
- h. - heart

Fig. 2, 3, 4, and 5, sections of 66hr. chick, showing successively sections which exhibit formation of trachea and bronchi.
- a. - aorta
- d.c. - alimentary canal
- t. - tracheal cavity (trachea and bronchi)

**Plate II.** Fig. 6. Longitudinal section of 72-hour chick, for showing formation of primitive lung-bud.
- d.c. - alimentary canal
- t.b. - lung-bud
- h. - liver
- s. - stomach
- p. - pancreas

Figs. 7, 8, 9, 10, and 11. Successive transverse sections through (1) anterior portion of alimentary canal,
(2) union of trachea and oesophagus,
(3) just back of the union,
(10) union of bronchi,
(11) back of union of bronchi.
Plate III. Successive sections transversely through pulmonic region of 90 hr. chick. Figs. 12, 13, 14, 15, 16, and 17. al.c. alimentary canal; b.c. body cavity.

Plate IV. Vertical longitudinal section of 84 hour chick, showing relative positions of trachea, esophagus, and lung lobes. al.c. alimentary canal; 3. stomach; ph. pharynx; t. trachea; b. bronchus; l. lung lobe; b.c. body cavity.

Fig. 19. Section transversely through 96 hr. chick, showing bronchi and bronchus. al.c. alimentary canal; b.c. body cavity; d.b. dorsal branch of bronchus; m.b. main branch.

Plate V. Fig. 20. Horizontal longitudinal section of 6 day chick, showing development of lung cavity. t. trachea; b.r. bronchi; l.l. lung lobes; b.c. lung cavity; b.c. body cavity.

Fig. 21. Transverse section of lung of chick of same age, showing pulmonic veins. al.c. alimentary canal; l.l. lung lobes; a. aorta; d.b. dorsal branch of bronchus, and m.b. main branch; b.c. body cavity; p.v. pulmonic veins.
Plate VI. Fig. 22. Horizontal longitudinal section of 7 day chick, showing elbowing of bronchi, and increase in number of bronchial tubes. t.—trachea; b.—bronchi; b.c.—body cavity; l.c.—lung cavity (bronchial tubes; s.m.—splanchnic mesoblast.

Fig. 23. Transverse section of lung of same date, showing pulmonic veins and general lung cavity. s.m.—splanchnic mesoblast; b.c.—body cavity; l.c.—general lung cavity; a.l.c.(o.c.).—alimentary canal (oesophagus); l.t.—lung tissue; p.v.—pulmonic vein.

Plate VII. Transverse section of lung of 10 day chick, showing pulmonic veins and general internal development. a.l.c.—alimentary canal (oesophagus); b.c.—body cavity; p.v.—pulmonic vein; b.—bronchial tubes, both in transverse and longitudinal section.

II. 13. All drawings were drawn from pencil sketches made with camera lucida, and are somewhat diagrammatic. All are magnified about 35 diameters.