The Development of the Avian Lung.

by.

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INTRODUCTION.

The developmental Anatomy of the Avian Lung, although studied by several authors, is generally accepted as being inadequate, and deficient in many important respects.

On consideration of this it was with pleasure, therefore, at the suggestion of the late Dr. O. Charnock Bradley, Principal of the R.(Dick). V.C., that I undertook the investigation of the subject, giving cognisance to work already done. I have endeavoured to elucidate and enlarge facts therein, which are not now clear and in addition to detail data which has not previously been appreciated.

I have approached the problem with the following as a basis for my research.

(a) The intercommunication of Bronchioles.
(b) The development of air-sacs and recurrent bronchi.
(c) The determining of communications between all parts of the Bronchial Tree.

The structural arrangement of the adult lung in fowl is peculiar to aves, and not readily comparable with the adult lung in any other group of vertebrates.

With developing chick embryos, difficulties are encountered from variation in development occurring in eggs which have been given the same incubation period. (Patten, 1925).
This latter complication may be accounted for as follows:-

(a) The ova may be fertilised by the spermatazoön at varying distances from the commencement of the oviduct, and the segmentation will be most advanced in those eggs which are fertilised earliest.

(b) Segmentation is dependent on the body heat of the hen, and therefore, this process ceases when the temperature falls after laying — i.e. when the egg cools. It recommences only when the optimum temperature is reached during incubation.

Consequent upon these facts it is naturally difficult to estimate accurately, in hours, the age of the embryo.

Lastly, I considered that in spite of the complicated nature of the developing lung in fowl, relative scale reconstruction models would simplify the reading of the text and elucidate and enhance the appreciation of the actual structure. I have no knowledge of such a method being previously attempted and I have therefore completed 4 scale reconstruction models of embryonic lungs of chicks aged 4, 5, 6 and 7 days.

Extensive investigation has been carried out on
on the avian lung and much work published by many authors. One is, therefore, faced with the difficulty of discriminating between those original theories and facts and the more recent work and reviews, for the purpose of references.

In order to prevent the long detailed and comprehensive chronology of those authors, I have decided only to select a condensed review of the results of a few workers, particularly those which have done continuous work on the subject and eliminating such as only mention isolated features, in the latter case, in many instances, simply a reference to the findings of another investigator.

The literature has been repeatedly reviewed (as in Flint's '06, in Juillet '12, in Locy and Larsell, '15,'16, and in many other papers.

The chief contributions of the embryology observations are by:- Rathke,1826, containing the buds of the ecto and endo primary bronchi. Selenka,1887, the development of air sacs. Zumstein, 1900, lung and air sacs. Juillet,1912, Locy and Larsell, 1915-16, the development of the bronchial tree and air sacs. Campana 1875. Huxley, 1882, using the term mesobronchium. F.A.Schulze, 1908-09-10-11., bronchial tree and air sacs. Miller,1893, comparative structure of
of lungs, including birds. G. Fischer, 1905. Brandes, 1924., besides textbooks, as Lillie, Patten, Arey, Etc.

The air sacs have been described in the adult lung of bird by Muller, 1908, pigeon. Schulze, Juillet, and Flint, reviews the literature on vertebrate and on the study of growth in birds. Locy and Larsell, growth of the bronchial tree and air sacs.

Campana's paper of 1873, made analysis of the bronchial tree and its ramifications. Schulze, 1911, published a paper on the comparative anatomy of the air sacs in the adult. Juillet, 1912, published an important paper on the morphology of the avian lung. The most recent and important contribution to the morphology of the avian lung is the paper by Locy and Larsell, 1915-16. This is a comprehensive study of the avian lung. Its most significant fact, is the description of the bronchial tree and air sacs.
5.

**Histological Technique.**

Chick embryos from the second day of incubation up to the hatching time were used in the observation of the development of the lung.

For embedding in paraffin, fresh embryos were first fixed in 5% formalin solution and then dehydrated by the graded alcohol method. All embryos were cut in serial sections 10m. in thickness and parts from different areas of the adult lung were prepared and serial sections made in the same manner.

Attempts were made to inject the blood vascular system of the early embryos with Indian ink but with no material advantage to the reading of the serial sections.

Injections of adult lungs with celluloid and injection of the blood vessels with carmine gelatine. Modification of H.M.Carlton histological technique, 1926, were also made. The carmine method did not prove so successful as anticipated owing to the residual air in the bronchial tree being expanded by the heat of the solution and bursting the walls of the ramification tubules except in small isolated areas.

The technique observed for the celluloid corrosion method was as follows: the fowl was killed and bled
bled then injected through the jugular vein with 5% Aquas formalin solution under pressure introduced by the gravitation method, thus fixing and hardening the lung tissue and preparing the tubules to receive the celluloid solution. It was noticed that the fresh tissues of the lung were not able to withstand the pressure and the weight of the thinnest celluloid solution, the smaller tubules ruptured and a homogeneous mass of celluloid resulted.

The next step was to cut the trachea and drain away the surplus formalin. This usually occupies two days—the drying of the interior of the tubes by injecting alcohol through the trachea assisted in getting rid of the residual air before the injection of celluloid.

Wax models of the developing lung at different stages—4, 5, 6, 7 and 8 days were made in accordance with Karl Peter's (Peter, K. 1906, Die Methoden der Rekonstruktion. Jevd Verlog von Gustav Fischer), modification of Barn's wax-plates method, and these reconstruction models are illustrated by photographs.

The material studied in this investigation was obtained from chick embryos of 16 doz. eggs, 14 adult fowls, 4 geese, 4 swans, 10 pigeons, a penguin and a stork.
Embryo of 2½ Days.

Following the formation of the bronchial cleft from the pharynx, the tube becomes a vertical slit, Fig.1. From the lower portion of this slit-like tube the lateral endodermal lung buds make their appearance, pushing into the mesoderm in a caudo-lateral and somewhat dorsal direction. Fig.2. It would appear as though these pouches (buds) are direct evaginations of the pharynx. There is as yet no evidence of the trachea, Fig. 3 & 3a.

The dorsal continuation of the oesophagus is prolonged above and between these lung buds. The lung buds are at first ventral to the oesophagus and have a diameter similar to that structure, Fig.4. Towards their termination the cul de sacs are distended, and terminate blindly, Fig.5.

Embryo of 3 Days.

At this stage the caudal part of the pharynx elongates, forming the tubular trachea with the lateral lung appendages. Fig.6. From this, it is evident that the trachea is formed after the lung buds have developed. Photographs of serial sections of the 2½ and 3 days old chicks corroborate this fact.
It is interesting to note that the formation of the trachea changes from a vertical, to a horizontal slit, just prior to its division into 2 lung buds.

This division is brought about by the lower wall coming up in regular manner to meet the upper wall, about mid way between the lateral extremities. The cleavage is sharply defined, and two more or less symmetrical tubes result, which are soon widely separated by a mass of mesodermal tissue. Fig.7.

The tubes are at this stage lying some distance below the oesophagus. The lumen of each tube is small and inconspicuous, and lined with columnar-like cells, closely packed, similar in appearance to the cells lining the oesophagus.

The tubes diverge, extending caudo-dorsally so that the oesophagus interposes between them. At this point, cul de sacs of the coelomic cavity make their appearance between the lung buds, and shortly after these structures come into view, the lung buds end blindly.

The diameter is at first constant, but this ends near the caudal third. From this point to the blind extremity the tubes show a gradual increase in size. Fig.7.
9.

**Embryo of 4 Days.**

In following the course of the oesophagus and bronchi (lung tubes) it is noticed that the oesophagus curves gently downward to become more ventral to the bronchi. Fig.8.

Caudally the bronchi and oesophagus become parallel and lie in the same plane, and here the coelomic cavities make their appearance on the medial aspect of each bronchus, partially isolating the oesophageal analage.

Each bronchus is attached to the liver by a mesodermal fold, which persists on the right side but soon disappears on the other side. Fig.9 & 9a. In addition, the two bronchi and also the oesophagus are connected above to the dorsal aorta by a moderately thick band of mesoderm.

The lining columnar cells of the bronchi are better defined, and considerable mitotic activity is apparent indicating cellular formation. The basement membrane is clear and homogeneous. Surrounding each tube is a thick mesodermal covering of closely packed cells, each having a large mitotic nucleus.
10.

Embryo of 5 Days.

Examination of the trachea at this stage shows this structure to be for a considerable extent, a single rounded tube. This shape, however, does not persist and changes into the form of a horizontal slit, immediately preceding its division into two small bronchi—the meso-bronchi. These latter structures diverge below and to either side of the oesophagus, each surrounded by condensed mesodermal tissue. Fig.10.

The tubes, i.e. the meso-bronchi, are now large and better developed. The basement membrane and epithelium is more distinct and the lumen is better defined.

As in the previous embryo (4 days) the coelomic cavities appear on the medial aspect of the meso-bronchi. The oesophagus and bronchi are here, in the same horizontal plane. At this plane, there arise from the dorso-medial aspect of each dilated meso-bronchus, the primary bronchi. Fig.11.

The primary bronchi are comparatively large and have a much more defined lumen than the parent structures, the latter factor being early evident and maintained through all their extent. Relative position of the oesophagus to the meso-bronchi and primary bronchi
bronchi changes, the developing lung structures occupy a plane dorsal to the gullet, the primary bronchi lying on the dorso-medial aspect of the meso-bronchi.

Two other primary bronchi appear almost immediately, caudal to the first and parallel to it, one on each meso-bronchus. They are shorter and less dilated than those preceding, like structures.

Immediately following those, a pair of still smaller and narrower primary bronchi evaginate from the mesobronchi. So that now there are three primary bronchi on each meso-bronchus, more or less symmetrical in shape.

From the point of origin of the third primary bronchus the mesobronchus continues for a distance as a large, slightly dorso-ventrally flattened cone, (Embryonic Vestibulum), forming a tube with a blind extremity. Fig.12 & 12a.

Regarding the presence of air sacs, as in interpreted by Bertelli, at this stage of development, photographs of different sections and reconstruction models which I have completed, show conclusively that the presence of the so called "air sacs" is absolutely negative.
Embryo of 6 Days.

As in the preceding embryo the trachea divides, below the oesophagus, into two mesobronchi. No further description of the trachea will be given unless there is some deviation from the course already described.

In this embryo the mesobronchus is considerably more dilated forming the vestibulum. Fig.13 & 13a. This vestibulum corresponds to that of the adult lung and it is homologous to that in the adult. It is from this thin walled structure that the primary bronchi originate. Fig.13 & 13a. The vestibulum of the embryo was described by Selenka in 1866.

Shortly after the appearance of the embryonic vestibulum, the buds of the primary bronchi grow out from the wall, and are designated according to Locy and Larsell — Entobronchi (ventri bronchi — Schulze) ectobronchi (dorsibronchi — Schulze) Laterobronchi and dorsobronchi.

Sappy, in 1847 described two principal kinds of bronchi, the diaphragmatics (bronchus Diaphragmatiques), extending towards the ventral surface, and the costals (Bronchus costales) extending towards the dorsal surface, below the ribs.

Campana, in 1875 designated three kinds of bronchi,
primary, secondary and tertiary. The primary (la bronchi primaire ou souche) he described as the central lung tube, commonly called mesobronchus, and described four groups of secondary bronchi (1) The system of five large divergent bronchi. (2) The system of eight internal bronchi. (3) The system of six external bronchi, latero bronchi (Laterobronchi of Schulze). (4) The system of posterior or dorsal bronchi, dorso-bronchi (Dorsilateribronchi of Schulze). Locy and Larsell, 1916, slightly modified these terms.

Huzley in 1882, introduced the terms mesobronchus for the central lung tube, and ento- and ecto-bronchi for the diaphragmatic and the costal bronchi.

Owing to the multiplicity of the terms describing the bronchi I have adopted a nomenclature, which does not introduce any new terms, and is designed to simplify the reading of the script.

Perhaps it would have been more correct to use primary bronchus for mesobronchus but subsequent work has shown this application to lead to confusion. The term mesobronchus is more generally used by most of the modern authors, and is applied to the tubes which split directly from the trachea. Moreover, the mesobronchus is the source from which the major tubes spring, and its position rightly determines its name.
For purposes of description and on account of the anatomical variation of the mesobronchus, it has been considered most profitable to divide the tube into three portions – (a) anterior part, (b) vestibulum, (c) terminal part.

All tubes arising from the mesobronchus are termed primary bronchi; each is continued by not more than four or five divisions which are still considered primary bronchi. From these tubes the secondary bronchi arise. The air capillaries are numerous small tubes which originate from both primary and secondary bronchi.

The vestibulum in the developing embryo of 6 days lies obliquely and transversely across the lung, from the medial to the lateral side.

From the embryonic vestibulum, two groups of primary bronchi arise, which are separated by a dense mass of mesodermal tissue. From the medial side of the vestibulum two primary bronchi originate which extend cranially. Fig. 14. The one more ventral in position being the larger.

Lateral to the above tubes, two small tubes arise, from the lateral aspect of the vestibulum, and extend in a cranio-dorsal direction. From the caudal medial
15.

medial part of the vestibulum three short tubes take origin, Fig.14. the most caudal of the three being the longest, all three branches extending caudally.

The terminal part of the mesobronchus continues caudally in a lateral and somewhat dorsal direction, showing one or two small evaginations from its surface. Fig.14.

Again there is as yet no evidence of the formation of any air sac at this stage. (see figure and photograph. Figs.13a,14,15 & 15a.)

**Embryo of 7 Days.**

Now the trachea becomes dilated. For a short distance the mesobronchus describes a course almost parallel to the oesophagus. Gradually inclining dorsal -ly above the oesophagus, it maintains this plane to approximately the centre of the lung, where the lumen of the tube dilates forming the large embryonic vestibulum.Fig.16. The vestibulum, which is relatively small in the embryo passes almost transversely across the lung from the medial to the lateral side. The vestibulum narrows and is continued on the lateral aspect of the lung as the terminal part of the mesobronchus. Fig.17.
From the vestibulum four distinct branches run cranially, and three run caudally. These are the primary bronchi and are designated as follow:

(1) Those which run cranially or the cranial branches:
   (a) Two medial primary bronchi. Fig.16.
   (b) Two lateral primary bronchi. Fig.17.

(2) Those which run caudally or the caudal branches:
   Three medial primary bronchi. Fig.18.

The cranial branches:
(a) The first medial cranial primary bronchus, Fig.22, extends in a cranial, lateral and dorsal directions and gives off 3 branches dorsally and two ventrally to be considered part of the primary bronchus. These divisions are slightly dilated and laterally flattened. The branches arising from the ventral side of the primary bronchus extend in a lateral ventral direction. The dorsal divisions extend in a latero-dorsal direction.

The second medial cranial primary bronchus, originates slightly caudal to the first. It extends cranieo-dorsally and presents one or two small divisions.
(b) The lateral primary bronchi. These extend cranio-dorsally from the vestibulum, side by side near the lateral surface of the lung. One arises at a more
17.

more dorsal point than the other. The upper one gives off two or three branches which extend ventrally.

At this stage of development there is no indication of the primordia of the cervical or abdominal air sacs as interpreted by Locy and Larsell, 1915-16.

The Caudal Branches:

The Medial Primary Bronchi.

1. Ventral.
2. Intermediate.
3. Dorsal.

The ventral bronchus is a very small tube, the intermediate and the dorsal are elongated, single tubes, larger than the ventral.

From the terminal part of the mesobronchus, primary bronchi arise, four from the dorsal aspect, which are flattened and extend dorsally, and five from the ventral part, which are tubular and extend ventrally. Fig. 17.

From the medial side of the caudal aspect of the terminal part of the mesobronchus, a single primary bronchus grows out, which almost immediately splits into two parts. The larger dilated portion runs cranially, and the small inconspicuous portion caudally, both ending blindly. Fig. 19.

There is no evidence of the abdominal air sacs as
as yet, but in the 7½ days old embryo there is concrete evidence that the shorter tubule projects beyond the wall of the lung and in my opinion this forms the primordia of this air sac.

The abdominal air sac develops very rapidly, resulting in the short tube being further shortened and the entrance into it widened so that eventually the larger cranial portion opens directly into the air sac along with the mesobronchus.

From the medial side of the commencement of the vestibulum and near the origin of the medial caudal primary bronchus, the primordia of the cranial thoracic and the medial primordia of the interclavicular air sac take their origin. Fig. 16. The primordia of the latter passes along the medial side of the mesobronchus.

**Embryo of 8 Days.**

At this stage the bronchial tree continues to grow, with a large increase in those branches which are most profuse in their ramifications (secondary bronchi).

The embryonic vestibulum is commencing to disappear. Fig. 20.

Cranial branches of the vestibulum:

The first primary bronchus, originating from its dorso-medial aspect, Fig. 21, extends forward to near
near the cranial end of the lung. The secondary bronchi which arise from the lateral aspect of this primary bronchus, extend in a cranial and dorsal direction. They curve slightly, and incline caudally. The most cranial curve round the lateral surface of the lung, the remainder are within the lung parenchyma. The whole of the cranial medial aspect of the lung is occupied by this primary bronchus and its branches, i.e. the secondary bronchi.

Two of the divisions of the primary bronchus occupy the ventral aspect of the cranial part of the lung, and the other three divisions occupy the dorsal aspect of the cranial part of the lung.

Near the tip of the primary bronchus the cervical air sac originates, which is situated medial to the bronchus, and extends a little beyond the wall of the lung.

The second medial primary bronchus arising a short distance caudal to the first, Fig. 21, is smaller, but in this stage it shows two small divisions. Several secondary bronchi arise from it, extending towards the dorso-lateral surface of the lung.

Originating from the simple embryonic vestibulum are two lateral primary bronchi which extend cranially. Fig. 22. The ventral is the larger of the two
two and gives three divisions which with the secondary bronchi from it, occupy the whole of the ventro-lateral border of the lung. The dorsal bronchus is smaller. It has no divisions but gives rise to secondary bronchi as usual. It and some of its branches occupy the caudo-lateral part of the lung. Both of these primary bronchi give rise to many other secondary bronchi which extend towards the medial border of the lung inclining slightly cranially.

The Caudal Branches of Vestibulum:-

(1) The dorsal primary bronchus, is the largest of the three and is the most medially situated. It gives off many secondary bronchi which run towards the lateral aspect of the lung. Fig.23.

From the ventral side of this primary bronchus, a secondary bronchus originates, and extends in a caudo-ventral direction. Opening from this secondary bronchus is the cranial thoracic air sac, and the medial primordia of the interclavicular air sac. These two air sacs are connected by a single tube. Fig.23. The medial primordia of the interclavicular air sac follows the medial aspect of the mesobronchus.

The intermediate primary bronchus, which is situated between the dorsal and the ventral primary bronchi is the second in size. It gives off a few secondary
secondary bronchi which extend towards the lateral border of the lung. These two primary bronchi (the dorsal and the intermediate) run parallel to each other for a distance and then the dorsal primary bronchus becomes dorsal to the intermediate. Fig. 23.

The ventral primary bronchus, which is the smallest of the three, bifurcates after it leaves the vestibulum. One of the divisions extends somewhat cranially and the other caudally. This bronchus, gives off many secondary bronchi which run in the direction of the medial aspect of the lung.

The terminal part of the mesobronchus continues on the lateral aspect of the lung, following the termination of the embryonic vestibulum, and during its course it gives off many primary bronchi. From the ventral side many arise, and each extends ventrally as a single tubular bronchus. Most of them are short cul de sacs.

From the dorsal side of the terminal part of the mesobronchus many primary bronchi originate. These are larger than the ventral and divide, giving many secondary bronchi.

Two or three small primary bronchi originate from the lateral aspect of the terminal part of the mesobronchus.
Two primary bronchi arise from the caudal end of the termination of the mesobronchus. Fig. 24. One of those arise from the lateral aspect, and is very short, extending laterally and ending blindly. The second primary bronchus (recurrent primary bronchus) arises from the ventro-medial aspect of the termination. This tube has two extremities, as can be seen in the 7 days old embryo. One of the extremities, which is large and dilated, extends cranially and gives origin to a few secondary bronchi. The other extremity, which is a short tubular branch, runs caudally extending beyond the wall of the lung to form the abdominal air sac which is comparatively small. Fig. 25.

**Embryo of 9 Days.**

On the sixth day of development the vestibule presented a sac-like appearance. From that time onwards, there is gradual change in the form of the vestibule to a tubular structure, which transformation is finally completed by this stage, i.e. the ninth day.

The mesobronchus in this embryo, presents a shape comparable to an elongated S, the posterior bend of which is the more pronounced. In the previous embryo there were two short primary bronchi originating from the caudal end of the mesobronchus. The most caudal
caudal of these is now very much enlarged and forms a cranially directed tube forming another recurrent primary bronchus.

The terminal end of the mesobronchus along with these two recurrent primary bronchi open freely into the abdominal air sac by a common orifice.

The bronchial tree from this stage onwards, continues to grow with a large increase in the number of those branches which present the most profuse ramifications. Consequently, for the sake of clearness, I have deemed it necessary to describe its subsequent development under separate headings.

Because of the above facts, I also, consider it necessary to classify the main primary bronchi under two separate groups, viz.

A. The ecto-primary bronchi, those which run along the medial surface of the lung.

B. The endo-primary bronchi, those which are within the lung mesenchyme.

With regard to the latter groups, I wish to explain now, that innumerable small endo primary bronchi arise from all sides of the mesobronchus. Those endo-primary bronchi which I intend to describe fully, are much larger and arise from the dorsal and ventral parts of the mesobronchus.
The appellation of the ecto- and endo-primary bronchi is based on their site of origin as from the cranial extremity of the mesobronchus.

On the ninth day of development the first ecto-primary bronchus which is very large and important exhibits 5 divisions, each of which give off secondary branches. This primary bronchus arises from the dorsal side of the mesobronchus. Fig.26. Three of its divisions run dorsally with an inclination cranially, and two divisions extend ventro-cranially.

At the cranial part of the lung and along its dorsal and ventral surfaces, the majority of the secondary bronchi, which arise from the 5 divisions, curve round the border of the lung towards its lateral surface and continue caudally for a considerable distance. These secondary bronchi supply the cranial aspect of the lung, and also give rise to the lateral primordia of the interclavicular air sac, Fig.28.

The cervical air sac originates from the tip of the first primary bronchus, Fig. 27 & 27a., and is slightly enlarged at this stage.

The second ecto-primary bronchus has a similar origin to the previous, i.e. from the dorsal surface of the lung and its secondary bronchi extend dorso-laterally. Fig.28.
Near the middle of the medial surface of the lung the third ecto-primary bronchus originates. Fig. 29. It arises caudal to the second ecto-primary bronchus, and runs caudally. It divides into four parts which extend dorsally, and gives off many secondary bronchi.

This ecto-primary bronchus which gives origin to the medial primordia of the interclavicular air sac and the cranial thoracic air sac, is connected to them, as before, by a single orifice. These air sacs have increased in size at this stage. Fig. 30 & 30a.

The fourth ecto-primary bronchus arises from the dorsal aspect of the mesobronchus slightly behind the third. It runs caudally, more or less, parallel to the previous one and gives rise to numerous secondary bronchi, Fig. 30, which run in caudal and lateral directions. This primary bronchus gives off one, laterally and cranially directed division.

The first endo-primary bronchus arises from the dorso-lateral part of the mesobronchus, Fig. 30a and lies near the lateral surface of the lung. It extends dorso-cranially and gives rise to many secondary bronchi which run cranially, dorsally and medially.

The second endo-primary bronchus originates from the dorsal side of the mesobronchus Fig. 32 and extending cranio-dorsally, and giving off many secondary
secondary bronchi which run dorsally, medially and cranially.

The third endo-primary bronchus arises from the ventral side of the mesobronchus, Fig.32 corresponding to the third "latero bronchus" of Locy and "bronches secondaires externes" of Campana. It is situated near the lateral border of the lung and extends caudally in a ventro-medial direction.

This endo-primary bronchus projects beyond the wall of the lung and forms the primordia of the caudal thoracic air sac. The cranial part of this air sac remains within the lung and from here two or three buds may be seen extending cranially. This air sac makes its first appearance in the embryo of 9 days, Fig.33.

The fourth endo-primary bronchus arises from the dorsal side of the mesobronchus, Fig.32 and extends dorsally. It lies near the lateral surface of the lung and has many secondary bronchi some of which run medially and some laterally.

After the fifth endo-primary bronchus, the mesobronchus gives rise to 7 or 8 short primary bronchi, before it gives origin to the sixth endo-primary bronchus.

The sixth endo-primary bronchus arises from the dorsal side of the mesobronchus. Fig.34. It is larger.
larger than the previous one and extends caudally, its secondary bronchi running dorso-medially.

The subsequent endo-primary bronchi have a practically similar origin to the previous ones. It is sufficient to note that each has a more caudal origin than its preceding one. These endo-primary bronchi give rise to many secondary bronchi some of which in later stages of development anastamose with the deeper lying secondary primary bronchus.

Finally, the end of the mesobronchus opens along with the two recurrent primary bronchi which extend cranially. Each of these primary bronchi give off 2 secondary bronchi which run cranially on the lateral surface of the lung. Fig.33a.

There are however, numerous other bronchi which originate from the mesobronchus. They are smaller and their point of origin is variable, viz. "Bronches posterieurs ou dorseles" of Campana, "dorselateri bronchi" of Schulze.

The abdominal air sac Fig.35. opens into a common orifice which is formed by the gradual enlargement of the caudal extremity of the recurrent primary bronchus and caudal end of the mesobronchus.
Embryo of 10 Days.

The interesting feature at this stage of development is the appearance of cartilage. Fig. 36. This cartilage extends as an incomplete ring round the mesobronchus but does not penetrate very far into the substance of the lung. The lung parenchyma and the blood vessels, beginning at this stage, become arranged, around the divisions of the primary bronchi and secondary bronchi, into prismatic columns which on cross section are (quintagonal or hexagonal) lobules. Fig. 37. In the middle of these lobules lie the circular primary or secondary bronchi.

The first ecto-primary bronchus originates from the dorsal aspect of the mesobronchus. It is situated on the medial side of the lung and practically occupies the medial cranial part of the lung. It has five divisions. Three divisions arise from the dorsal side of this ecto-primary bronchus and two divisions from the ventral side.

The first dorsal division extends dorsally inclining a little towards the cranial aspect of the lung. The second and third dorsal divisions extend obliquely in a cranio-dorsal direction. The fourth and fifth divisions which are ventral extend in a ventro-cranial direction.
The third dorsal and the fourth and fifth, which are ventral, curve round the cranio-ventral aspect of the lung and run along the lateral border, caudal wards, for a considerable distance. The three dorsal divisions also curve round the cranio-dorsal border of the lung and extend caudally.

This ecto-primary bronchus gives rise to the cervical air sac, which extends cranial wards on the medial side of the lung, Fig.38. This air sac now shows a slight expansion of the distal end, Fig.38a.

The fourth division of this primary bronchus opens into the lateral primordia of the interclavicular air sac, Fig.39 which extends slightly beyond the lung wall.

The first ecto-primary bronchus gives rise to many secondary bronchi which extend in a latero-cranial direction and curve round the lateral border of the lung to extend caudal wards for a considerable distance.

Caudal to the first ecto-primary bronchus, the mesobronchus gives rise to the second ecto-primary bronchus. This primary bronchus is situated on the medial surface of the lung and extends in a dorsal direction, the most caudal part of it runs slightly backwards. This tube has many secondary bronchi which run in a dorso-lateral direction.

The third ecto-primary bronchus takes origin behind the previous one from the dorsal side of the
the mesobronchus. It is situated on the medial surface of the lung and runs in a caudal direction with an inclination towards the dorsal aspect. It is a very large branch and has many divisions which extend in a dorso-caudal and lateral direction.

This primary bronchus gives rise to the cranial thoracic air sac and the medial primordia of the interclavicular air sac. The medial primordia of the interclavicular air sac is divided into two parts which extend along the medial aspect of the mesobronchus. Fig. 40. This primordia, at this stage of development is much larger and has many pouches projecting from it. The cranial thoracic air sac has also increased in size, and both connected by a single tube.

Immediately following the third, the mesobronchus gives rise to the fourth ecto-primary bronchus from its dorsal aspect. This ecto-primary bronchus runs caudal wards parallel to the third. It is more ventral in position now, to the latter, with many secondary bronchi arising from it.

Following the origin of the fourth ecto-primary bronchus the mesobronchus gives rise to the first endo-primary bronchus which arises from the dorso-lateral side. It is situated near the lateral border
border of the lung and runs cranio-dorsally, and has two divisions, one extends laterally and the other extends dorso-cranially.

Caudal to the latter, the mesobronchus gives origin to the second endo-primary bronchus from its dorso-lateral aspect. This endo-primary bronchus runs cranio-dorsally near the lateral border of the lung, parallel to the first. Both first and second have few main divisions but many secondary bronchi, which extend latero-dorsally and some of them medio-dorsally towards the cranial aspect of the lung.

Following the above, the mesobronchus gives rise to the third endo-primary bronchus from its ventral side. This runs in a caudo-ventral direction and has few divisions but many secondary bronchi which run in all directions.

The fourth endo-primary bronchus originates from the dorsal side of the mesobronchus and runs dorsally. It gives off many small divisions and secondary bronchi, most of the latter bronchi run medially and some laterally.

The fifth endo-primary bronchus originating caudal to the preceding one from the medial side of the mesobronchus, runs in a medio-caudal direction where it extends beyond the wall of the lung, to form
form the caudal thoracic air sac. Fig. 41. This air sac at this stage is increased in size.

More caudal to the above, the mesobronchus gives rise to a sixth endo-primary bronchus from its dorsal aspect. This bronchus is situated near the lateral surface of the lung and extends dorso-caudally. It possesses many secondary bronchi some of which run in a medio-dorsal direction, and the others in a lateral direction.

Immediately after the preceding one, the mesobronchus gives rise to a small primary bronchus from its ventro-medial side, this gives off a few secondary bronchi which extend ventrally.

Following the above, the mesobronchus gives origin to the seventh endo-primary bronchus from its dorsal side. This bronchus is situated laterally, and runs in a dorso-caudal direction. It has a few divisions and secondary bronchi which extend in a medio-dorsal direction.

At the same time as the seventh endo-primary bronchus arises, the mesobronchus gives rise to three or four small primary bronchi from its lateral, ventral and medial sides. These primary bronchi each have one or two secondary bronchi. Behind the above primary bronchi, other similar structures originate from the dorsal aspect of the mesobronchus and run in
in a caudo-dorsal direction.

The embryonic history of the remaining three or four endo-primary bronchi is so similar, that it is sufficient to note, only that in the adult lung they supply the caudo-medial and part of the caudo-lateral regions of that organ.

At the caudal end of the lung, the mesobronchus along with the cranially extending endo-primary bronchi (recurrent cranial primary bronchi) opens into the abdominal air sac. This latter structure has in this stage greatly increased in size. Each of these primary bronchi gives two or three secondary bronchi, which travel cranially along the lateral border of the lung.

Embryo of 11 Days.

The obvious external feature of the lung of the 11 days old embryo, is the impression of the ribs on the dorsal and lateral borders of this structure.

The air sacs are enlarged and all bronchi are also much more developed. Fig. 42.

The development of a fine muscularis mucosa round each primary and secondary bronchus is another feature of this stage. The lobular structure of the divisions of the primary bronchi and secondary bronchi is more pronounced.
The secondary bronchi grow larger and many have come into contact with each other. Figs. 43, 43a, 43b, 43c.

The first ecto-primary bronchus is better developed now. The cervical air sac and the lateral moiety of the interclavicular air sac which originates from this bronchus, is well shown in Figs. 44 & 45. The bronchi which lead into the lateral primordia of the interclavicular air sac is shown in Fig. 45. Both air sacs have enlarged greatly.

It is important to note that the second ecto-primary bronchus does not communicate with any air sac.

The third ecto-primary bronchus, is much larger than that of the 10th day. It opens into the cranial thoracic air sac and the medial primordia of the interclavicular air sac. Fig. 46.

The fourth ecto-primary bronchus is also better developed. It gives origin to many secondary bronchi which extend caudally and laterally. It gives off many small divisions from the medial side, the latter extends in a lateral direction.

The endo-primary bronchi are also greatly increased in size, and some of the small evaginations (cul de sacs) — i.e. Those which in the 10 days old embryo were simply mentioned as being formed and not
not designated as primary bronchi -- now become much bigger and thus are classified as endo-primary bronchi.

This phenomenon results in a large increase in the number of these structures in this phase of development.

At the caudal end of the lung the mesobronchus opens by a common orifice with the recurrent primary bronchi, into the abdominal air sac. These latter bronchi have been termed "recurrent" -- recurrent bronchi of Locy and Larsell, this term being applied to them as their origin was reckoned to be from the air sac, and also because of their cranial ward direction. It is my opinion, however, from the number of embryos I have examined, that these bronchi do not originate from the air sac but from the terminal part of the mesobronchus.

Several workers contend that the early dilation of the mesobronchus is the developing air sac. Bertelli, Locy, etc. From my observations and as mentioned in embryos of 7 days of incubation, I maintain that the abdominal air sac is developed from the caudal extremity of the recurrent primary bronchi, which originate from the caudal end of the mesobronchus.

The caudal thoracic and the abdominal air sacs lying at the caudal part of the lung have greatly increased in size, in this embryo.
Embryo of 12 Days.

The lung of the embryo of the 12 days, is in the intermediate stage, or one of transition between the "bronchial tree" stage of the earlier embryos, and the "bronchial circuit" stage of this and the subsequent embryos and the adult.

In the "bronchial tree" stage there is no anastomosis between any of the tubes of the lung. The bronchi divide and end blindly. In the "bronchial circuit" stage a very important structural arrangement has taken place — most of the secondary bronchi bifurcate and have united to form a complete circuit. This stage of development shows that many of the secondary bronchi which were in apposition at their blind extremities in the 11 days old embryos, now unite after bifurcation, to form a complete circuit. Some of the secondary bronchi, however, do not complete the "circuit" until the 14 or 15 days old embryo.

There is also an important change in the appearance of the epithelial lung tubes. In previous embryos, the epithelium is stratified columnar, forming a simple plain lining. At the 12th. day the epithelium expands and is thrown in folds and has a corrugated appearance in cross section. Fig. 47.
Structural alterations have been gradually taking place throughout the past few stages — changes in the lung mesenchyma and modifications in the muscular and vascular tissue.

By this stage of development an obvious change in the lung mesenchyma is evident, the lobules have assumed a quintagonal or hexagonal form. The vascular tissues have increased to a great degree, and the muscular elements are more distinct. Fig. 48.

The ecto-primary bronchi, the endo-primary bronchi, including the small endo-primary bronchi and all the air sacs, especially the abdominal, all show a marked increase in their development.

The ecto-primary bronchi are better developed, Fig. 49 shows the first ecto-primary bronchus and the bronchi of the medial primordia of the interclavicular air sac. It also shows the bifurcations of the secondary bronchi. Fig. 50., shows the second ecto-primary bronchus and Fig. 51., shows the third ecto-primary bronchus and the medial primordia of the interclavicular air sac. Fig. 52., shows the fourth ecto-primary bronchus. The first endo-primary bronchus is seen in Fig. 53. Fig. 54., shows the communication between the third ecto-primary bronchus and the cranial thoracic air sac, it also shows the medial
medial primordia of the interclavicular air sac. Fig. 55., shows the medial ventral division of the first ecto-primary bronchus communicating with the lateral interclavicular air sac. The endo-primary bronchus is seen communicating with the caudal thoracic air sac. Fig. 56. Fig. 57. shows the recurrent primary bronchi.

It is very important to note that the epithelium of the primary and secondary bronchi begins to evaginate somewhat in this stage. (shown in all sections)

Subsequent observations of the air sacs presents little difficulty except in the case of the interclavicular air sac of the adult which is formed by the union of its lateral and medial primordiae. At the 12th. day of incubation the medial primordia of the interclavicular air sac have greatly increased in size and run cranially on the medial aspect of the mesobronchus. The lateral primordia of this air sac is relatively larger than in the earlier stages.

**Embryo of 13 Days.**

The lung of the 13 days old embryo is large enough to dissect. It is applied to the lateral aspect of the thoracic cavity and is marked along its dorsal lateral border by deep indentations shown from the ribs.

The air sacs are larger but are difficult to
to dissect even with the aid of a dissecting microscope, mainly on account of their delicate nature. Four pairs of air sacs may be recognised in the serial sections of the dissected lung. viz. 2 cervical, 2 cranial thoracic, 2 caudal thoracic and 2 abdominal. There are also two other pairs of the interclavicular air sac, 2 medial and 2 lateral primordia. The medial primordia comes into contact with the wall of the corresponding primordia of the interclavicular air sac of the opposite lung, on the fifteenth day of incubation. In later stages, the walls fuse to form a single medial primordia, subsequently the lateral primordia fuses with the medial primordia to form a single interclavicular air sac. (Locy and Larsell).

The modifications which appeared in the epithelium of the primary and secondary bronchi in the previous embryo, is now more pronounced. At irregular intervals, the evagination of the epithelium extends through the surrounding muscularis mucosa of the tube. Fig.58,58a. These extensions of the lining membrane of the bronchi, which project into the loose mesoderm, are the first steps in the formation of the air alveoli. The epithelium is still thick and stratified, the surface cells having a columnar appearance.

Simultaneous with the evolution of the air alveoli, additional small endo-primary bronchi appear in rapid
rapid succession from the wall of the mesobronchus in the spaces between the main larger primary bronchi.

The significance of this feature is the homology of these structures with the air alveoli of mammalian lung. The epithelial lining is not quite similar, there is no evidence in the avian lung of the loose non-nucleated cells or plastid as described for mammalian lung. (Schafer).

The secondary bronchi bifurcate and the diameter of the divisions is reduced, further reduction in the diameter may be considered the tertiary bronchi (tertiaries of Locy). It is these cylindrical tubes which form the anastomosis which is so characteristic of the avian lung in the establishment of the bronchial circuit (Campana).

The process of evolution of the lung in the 14 days old chick is not very striking, except for the increase of length of the tubes, and the gradual increase in dimension of the lung on a whole. The air alveoli are larger and deeper, the epithelium is thinner and the mesodermal tissue is more richly supplied with blood vessels. The air capillaries are very numerous and in consequence, the blood supply to the lobulated areas is improved. Each bronchus surrounded by the mesodermal mass has now a very definite lobulated appearance. Figs. 59, 59a.
Subsequent development of the avian lung from this stage to hatching (21 days old chick) is merely a gradual exaggeration of the preceding. The air alveoli become deeper. The epithelial lining thins to one flattened cell in thickness. Figs. 60,60a,61, 61a,62,62a. The air capillaries become very numerous and it is only with great difficulty that one is able to differentiate between the capillaries and the epithelium of the air alveoli. Fig.63.

The "lobules" are quite independent of one another and are in this state in the adult.

The air sacs do not alter except in size, especially the abdominal sac.

The Bronchial Circuit of the Adult Lung.

After the fourteenth or fifteenth day of incubation, the anastomosis of the secondary bronchi goes on very rapidly, resulting in a profuse intercommunication of the air passages.

Campana's and Locy's detailed account of the bronchial connection is impressive, but owing to the great space required for the description of each branch, I have undertaken to give a condensed account based on my studies of the celluloid cast.

The formation and distribution of the primary and secondary bronchi has been sufficiently described at
at eight, nine, ten and eleven days old embryo. It is now, therefore, necessary only to point out their distribution in the adult lung of fowl. The ecto-primary bronchi: It is evident the four ecto-primary bronchi have a wide distribution, as the air passages arising from them occupy substantially one half of the lung, Fig.64 and they also give rise to three air sacs.

The first ecto primary bronchus is situated on the medial surface of the lung. It presents 5 divisions, 3 dorsal and 2 ventral, of the three divisions the first run upwards, the second and third divisions incline dorso-cranially. Their secondary bronchi run dorso-laterally and somewhat caudally. Fig.64.

The two ventral divisions, which are the fourth and fifth divisions of the primary bronchus extend ventrally; part of the fourth division runs caudo-ventrally and gives rise to the lateral primordia of the interclavicular air sac. The other part of this division runs cranio-ventrally and its branches curve round the ventral border, extending on the lateral surface of the lung in a caudo and somewhat dorsal direction. Fig.64 & 65. The fifth division extends cranio-ventrally, and by curving round the border of the lung, its branches run caudally. Fig.65.
The second ecto-primary bronchus lies on the medial surface of the lung, extending dorsally, its branches curve round the dorsal border of the lung and run laterally. Fig. 66.

The third ecto-primary bronchus likewise lies medially, Fig. 66, extending in a caudo-dorsal direction. Its branches, by curving round the dorsal border of the lung, run in a lateral and somewhat caudal direction. This primary bronchus gives rise to the cranial thoracic air sac and the interclavicular air sac.

The fourth ecto-primary bronchus also lies to the medial aspect of the lung, Fig. 67, extending caudo-dorsally, parallel to the third ecto-primary bronchus and ventral to it. Some of its branches run dorso-laterally and some from its ventral aspect, run caudally. This primary bronchus has a large division which runs in a ventral direction giving many branches from its cranial and caudal aspect. Fig. 67.

The endo-primary bronchi:— There are six or seven of these bronchi arising from the dorso-lateral aspect of the mesobronchus.

The first two run towards the lateral surface of the lung with a gentle bend towards the cranio-dorsal aspect, Fig. 68. The third and fourth direct themselves from their origin in the same manner as the first two, but they run in a dorso-lateral direction, Fig. 68.
The fifth and sixth extend likewise but they run in a dorsal and somewhat caudal direction. Fig. 68. The seventh endo-primary bronchus is the recurrent primary bronchus which runs in a cranio-dorsal direction. Fig. 68.

There are many secondary bronchi originating from the medial aspect of these endo-primary bronchi, which extend dorso-medially, cranially and many also, from their lateral aspect which run laterally, Fig. 69.

The dorsal aspect of the lung is formed by the joining of the secondary bronchi of the three dorsal divisions of the first ecto-primary bronchus, with the dorso-medio directed secondary bronchi coming from the first endo-primary bronchus. The remainder of the secondary bronchi of this latter tube run cranially. Fig. 70.

There are 3 or 4 endo-primary bronchi originating from the ventral aspect of the mesobronchus, extending ventrally and giving off many secondary bronchi; some of those run cranio-medially, others laterally and cranio-laterally, Fig. 68. The first ventral endo-primary bronchus, gives branches extending cranio-ventrally, Fig. 69.

The secondary bronchi of the two ventral divisions of the first ecto-primary bronchus, join with those cranially directed secondary bronchi from the first
dorsal and ventral endo-primary bronchus. Fig. 65. The anastomosis of these secondary bronchi form the cranial and ventral aspect of the lateral surface of the lung. Fig. 65. The caudal aspect of the lateral surface of the lung is formed by the terminal bifurcation of the branches of the endo-primary bronchi, Fig. 65, anastomosing with each other giving a sponge-like appearance.

The medial surface of the lung is principally formed by the ecto-primary bronchi and some of their divisions, Fig. 67.

The caudal aspect of the medial surface of the lung is made up by the caudal branches of the fourth ecto-primary bronchus and some branches of the ventral endo-primary bronchi and branches of recurrent bronchi, Fig. 67.

The small endo-primary bronchi are very short, arising from different points on the mesobronchus. They join the adjacent secondary or primary bronchi, Fig. 68.

The secondary branches in each aspect on the lung, run practically parallel to each other, except, as noticed before, at the caudo-lateral aspect of the lung.

Collateral primary and secondary bronchi join each other at different points, Fig. 69 & 71.
The first signs of development in the chick embryos is noticed at the 2½ days old stage, as evaginations of the endoderm into the surrounding mesenchyma. Fig. 3, 3a. show the beginning of the lung pouches. They push out into the mesenchyma which is bordered by a very pronounced mesothelium. At their beginning, therefore, the primitive lungs are paired, and consist of two shallow pouches, which open into the floor of the pharynx.

The surrounding mesoderm is also a part of the lung analage, and increases correspondingly with the growth of the endodermal part. The endoderm, by branching, gives rise to the lining membrane of the bronchial tree, the mesoderm provides material for blood vessels, muscles, connective tissue, etc. The ectoderm provides the nerve elements.

Immediately the lung pouches begin to elongate, by growth of the endoderm, in a caudo-lateral and somewhat dorsal direction, their divergent distal ends become separated from the oesophagus. Fig. 4 & 5 shows the lung primordia diverging from the caudal end of the trachea in an embryo of 3½ days old.

At three days of incubation the lungs are small. Fig. 6. shows the first appearance of the trachea.
47.

At the four days of incubation the lungs are larger than they are at three days, and the trachea is well defined. The lung pouches are smooth, extending caudo-dorsally along each side of the oesophagus and terminate dorsal to it. Figs. 8. & 9. represent the frontal and the lateral views of the lung of 4 days old embryo. The pouches are divergent and their distal portions end caudo-laterally and somewhat dorsally. Their cavities are lined by endodermal diverticula from the pharynx, and these are surrounded by mesoderm. The wall of the lung primordia does not as yet show any surface irregularities.

At the posterior third of the lung tube is a slight enlargement, that foreshadows the embryonic vestibulum and not the abdominal air sac, as interpreted by "Locy and Larsell". The oesophagus makes a gentle curvature continuing caudally, bending ventrally, passing between the lung pouches.

During the fifth day of incubation the lung grows larger and begins to show surface irregularities. Figs. 10 & 11 show buds of 3 primary bronchi originating from the wall of the small embryonic vestibulum. The vestibulum continues caudally as a cone shaped structure, ending blindly.
On the sixth day of development there is a great change in the appearance of the lung; the embryonic vestibulum is large, extending across the lung from the medial to the lateral surface. Many branches (primary bronchi) arise during this stage of development. Fig. 13. shows the large embryonic vestibulum and the primary bronchi which originate from it.

The development of the lung in the 7 days old embryo is greatly advanced by this stage, and the primary bronchi are large, showing signs of division.

Before continuing further, the parts of the main bronchus and the mesobronchus should be described. The mesobronchus continues caudally soon after it leaves the trachea as a round tube, where near the middle of the lung it dilates forming the "vestibulum" which has been previously described. This vestibulum continues posteriorly along the lateral surface of the lung as the terminal part of the mesobronchus.

Many primary bronchi, in the lung of the 7 days old embryo, arise from the terminal part of the mesobronchus. Fig. 19. The mesobronchus ends by giving origin to a primary bronchus which extends cranially. (recurrent primary bronchi). Fig. 17. The latter primary bronchus, which will be described below is of great importance in respect to the "recurrent bronchi".
There is no indication of either the abdominal air sac or the primordia of the cervical air sac in this stage of development. Fig. 17 of the reconstruction model of this stage proves my statement. However, the primordia of the cranial thoracic air sac and the medial primordia of the interclavicular air sac are present as seen in Fig. 16.

It is important to note that the latter two air sacs appear before any others and not, as stated by previous workers; Bertelli, Locy, etc. that the abdominal air sac, is the first to be seen in this stage.

In the 8 days old embryo, the bronchial tree is very much larger and the embryonic vestibulum about to disappear. The appearance of the secondary bronchi indicates progressive development.

The cervical air sac and the medial primordia of the interclavicular air sac originate together from the third lateral primary bronchi.

The recurrent primary bronchi are larger.

At 7 days this bronchus presented two extremities, the larger, the above recurrent primary bronchus, extending cranially, and the smaller, which is inconspicuous but slightly dilated, extending caudally. This latter division projects beyond the wall of the lung at 7\(\frac{1}{2}\) days and is well seen at 8 days of development, forming
forming the primordia of the abdominal air sac. Fig. 25.

This fact concerning the abdominal air sac is a direct contradiction to the statements of Locy and Larsell, who assert that this air sac originates from the caudal extremity of the mesobronchus, and moreover state that this is evidenced at 7 days.

Between the 8th. and 9th. day the abdominal air sac opens directly into the large cranial division of the recurrent bronchus and into the caudal end of the mesobronchus. (see diagram).

The ninth day stage is distinctive in the embryonic development of the lung, the feature being the disappearance of the vestihulum.

By the disappearance of the embryonic vestibulum, the mesobronchus resembles somewhat that in the adult lung, and those primary bronchi which originate from the vestibule, now assume a different position. Therefore, the nomenclature of the primary bronchi, hence-
henceforth, is changed to ecto- and endo-primary bronchi, the name indicating their position.

The secondary bronchi are more numerous than those of the first ecto-primary bronchus and curve round the cranial, dorsal and ventral borders of the lung to extend caudally.

The lateral primordia of the interclavicular air sac appears in this stage, originating from the fourth ventral division of the first ecto-primary bronchus.

The cranial thoracic air sac and the medial primordia of the interclavicular air sac, arise from the third ecto-primary bronchus and are well developed, and the caudal thoracic appears, arising from the fourth endo-primary bronchus.

At a later period "fifteen days of incubation" the medial primordiae of the interclavicular air sac come into contact with that of the opposite lung and subsequently fuse into one sac. In later stages the medial primordia fuses with the lateral one to form the single interclavicular air sac. Locy and Larsell.

The abdominal air sac is greatly elongated and is connected to the mesobronchus and two recurrent bronchi.

The second recurrent bronchus develops at this stage immediately above the first, by a single orifice.
Juillet studied the recurrent bronchi but he did not give a detailed account of their development.

Locy and Larsell made an extensive study of the recurrent bronchi, but by study of their sketches, it seems that they, too, arrived at the wrong conclusion.

I have already defined my findings with regard to this important detail, and re-affirm my assertion that the first recurrent primary bronchus appears before the abdominal air sac and that the air sac, in fact, develops from the caudal extremity of this bronchus.

Scale reconstruction models, and serial sections are my corroboration.

In the tenth day of development the lung has grown larger and shows indentations of the ribs on its lateral surface.

The air sacs are enlarged, especially the abdominal air sac which surrounds the abdominal viscera in the adult bird.

The prismatic shaped lobules are seen, with circular primary, or secondary bronchi, in the middle.

The interesting feature of the 11th. day stage is the appearance of the muscularis mucosa round each primary and secondary bronchus.

The approaching secondary bronchi come into
Both recurrent primary bronchi give origin to a few secondary bronchi which run cranially.

The cranial recurrent bronchi "recurrent bronchi" of Locy and Larsell, was regarded by them as branches developing from the abdominal air sac. Apparently they did not appreciate the fundamental features which are present in the lung of the 7 days old embryo.

In this respect, Campana, described the air sacs and bronchial tree. He also made a careful analysis of the orifices connecting the lung and the air sacs, and considered the recurrent primary bronchi the result of a reconstitution of several secondary bronchi into a single trunk, without recognising their true origin.

G. Fischer makes reference to the cellulodin cast, calls attention to a bronchial trunk larger than the other, which extends dorsally. This bronchial trunk, he says, directs itself towards the abdominal air sac. It seems, however, that Fischer had the wrong conception of this bronchus.

Schulze 1909, 1910, recognised these bronchi as coming from the air sacs and called them "Ruchlaufigen Bronchen", and (Bronchi recurrentus sur Saccobronchi). He, also, considered them as originating from the air sacs.
into contact and the lung has increased in size. The air sacs are well developed.

The 12th day of development of the lung, is an intermediate stage between the embryonic bronchial tree and the bronchial circuit of the adult lung. The approaching secondary bronchi join together, and by the fifteenth day a complete circuit of the bronchial tree is established.

There are 4 pairs of air sacs and a single one in the adult lung of the fowl, 2 abdominal, 2 caudal thoracic, 2 cranial thoracic, 2 cervical and an interclavicular air sac. Figs. 72. & 73. From the celluloid corrosion cast, show all the air sacs, and Figs. 74. 75. & 76. from the dissected fowl, swan, and pigeon, show these air sacs.
CONCLUSION.

I conclude my observations as follows:

1. The recurrent primary bronchi are off-shoots from the mesobronchus, and the air sacs, are the projections and expansion of the terminal end of the primary or secondary bronchi.

2. The air sacs are brought into communication with all parts of the bronchial circuit by the anastomosis of the bronchial branches. The abdominal air sac has direct communication with the mesobronchus and the recurrent primary bronchi.

3. The interclavicular air sac of the adult lung, is the fusion of four primordiae; two primordia from each lung, to form the single interclavicular air sac. Lacy and Larsell.

4. The cranial thoracic air sac and the medial primordia of the interclavicular air sac are the first to appear.

5. The air capillaries are formed by the evagination of the bronchial epithelium, and are cul de sacs.

6. The first appearance of air sacs, is in the embryo of 7 days development.
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