

THE DEVELOPMENT OF AIRSACS IN DUCKS

by

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INTRODUCTION

The construction of the lung of the bird is different from that of other vertebrates in that it has four groups of secondary bronchi from a median mesobronchus connected to each other by parabronchi; and that the mesobronchus and certain secondary bronchi extend beyond the lung as airsacs. Significant investigations of the bird lung were made by Rathke, Goette, Selenka and Bertellie (Lillie, 1908; p. 326). Our present conception of the bird lung has been derived from these plus contributions of Lillie (1908) in the "Development of the Chick"; Locy and Larsell (1916) in the "Embryology of the Bird Lung"; and McLeod and Wagers (1939) in the "Respiratory System of the Chicken". Locy and Larsell (1916) gives credit to both Schulze (1909) and Selenka (1866) for contributions toward the understanding of the bird lung.

The airsacs have been known since the 18th century; Muller (1908) gave credit to Harvey (1774) for having distinguished the connection of the interclavicular airsac to the lung in the Ostrich. Locy and Larsell (1916) give credit to Selenka (1866) as the first worker in the field to study the embryology of the airsacs of the chicken. More accurate descriptions of the airsacs in adult birds

has been given by Muller (1908) in the "Airsacs of the Pigeon"; Gilbert (1939) in the "Avian Lung and Airsac System"; and McLeod and Wagers (1939) in the "Respiratory System of the Chicken". The most recent contribution to the embryology of the airsacs was given by Locy and Lar-sell (1916) in the "Embryology of the Bird Lung".

The earlier workers apparently studied the lungs and airsacs by gross dissection, as nothing specific is stated about methods. Muller (1908) developed the first accurate method of injection; he made paraffin and gelatin injections into the respiratory tract of the pigeon after the tract had been hardened by formalin. As the injection mass entered, the airsacs were punctured to permit the escape of air. Lillie (1908) made photomicrographs of embryo chick lungs. Gilbert (1939) injected melted Wood's metal into freshly killed pigeons whose airsacs were punctured to permit escape of air during injection; then the tissues were corroded away, leaving the casts for study. Locy and Lar-sell (1916) studied microscopic sections of embryos through four days incubation and used chloroform and cedar oil fixatives to obtain a metallic cast from the dissected respiratory tract of chicks through eighteen days incubation; from this stage to hatching, Wood's metal injections were performed. McLeod and Wagers (1939) made celloidin injections

of the respiratory system of the chicken and studied the airsacs by dissection.

There are regularly considered to be nine separate airsacs in the adult birds (Plate I; B). As exemplified by the pigeon, the paired cervical airsacs (thoraco-cervical airsac of McLeod) extended anterior to the lung as a lobe on each side which is closely apposed to the ventral and lateral surfaces of the muscles of the neck; and from which, in this form, diverticula penetrate the lateral foramina of the thoracic and cervical vertebrae. The cervical airsac also comes in contact with the subscapular diverticulum of the interclavicular airsac, the trachea, vagus nerves and jugular veins. The interclavicular airsac (anterior thoracic airsac of McLeod) is a single airsac in the adult pigeon; it is located in the anterior portion of the thoracic cavity, and is bordered by the heart, the free ribs, coracoids, clavicles, interclavicular membrane, cervical airsacs, and the anterior portion of the sternum. The intermediate airsac (the posterior thoracic airsac of McLeod) was given by Muller as extending in the pigeon in the area between the pulmonary and abdominal diaphragms along the lateral surface of the heart posterior to the interclavicular airsac; the intermediate airsac is bounded laterally and ventrally by the lungs and ribs. The anterior abdominal

airsac (lesser abdominal airsac of McLeod) extends beyond the last rib into the abdominal cavity; ventrally it is in contact with a small portion of the lungs and the wall of the thoraco-abdominal cavity; it covered the lateral surface of the liver, parts of the intestine, and the stomach. The posterior abdominal airsac (greater abdominal airsac of McLeod) was the largest of the paired airsacs in the pigeon; these airsacs arose from the most posterior tip of the lung and partially enclosed the abdominal viscera (Muller; 1908). Muller also described the diaphragm in the pigeon; the pulmonary portion consisted of the diaphragm tissue adjacent to the lateral surface of the airsacs and the medial surface of the lung while the abdominal diaphragm consisted of the diaphragm tissue between the medial surface of the airsacs and the visceral peritoneum.

The most significant contributions to the early embryology of the bird lung and airsacs was given by Locy and Larzell (1916). These workers described in detail the origin and further development of the airsacs in the chick. The paired cervical airsacs arose on each side from an anterior continuation of the most medial secondary bronchus on the ninth day of incubation. The interclavicular airsac, single in the adult, had on each side a medial portion continuing from a secondary bronchus posterior to the entrance of the bronchus into the lung and arising on the ninth day of

incubation; a lateral portion arising on the tenth day of incubation developed from a median anterior secondary bronchus (Plate I, B). The median and lateral branches on each side come together to form the single interclavicular airsac. The intermediate airsac was shown to arise from the same secondary bronchus as does the medial portion of the interclavicular airsac. The anterior abdominal airsac was shown to arise from a lateral secondary bronchus posteriorly and laterally to the origin of the intermediate airsac. The posterior abdominal airsac arose as a direct continuation of the mesobronchus (Locy and Larsell; 1916). These men recognized Schulze (1909) as having described the establishment of secondary communications of the airsac to the tissue of the lung. These secondary communications were termed recurrent bronchi because the early workers had interpreted their material to indicate that these secondary connections grew from the airsac toward the lung and were later connected to the endoderm of the lung.

MATERIALS AND METHODS

Review of the literature and preliminary work indicated that the early development of the airsacs could be determined best by preparation and study of serial sections, and that later stages could be studied by means of injection and

dissection. A survey of the respiratory systems of adult birds showed that ducks have the simplest airsacs of all birds whose eggs are readily available.

Eggs of white Pekin ducks were obtained from a commercial duck farm. The eggs were incubated at 101 degrees Fahrenheit and embryos were removed at desired intervals for study. Embryos from three and one-half days through eighteen days incubation were fixed in Bouin's fluid, and the bodies were partially dissected after hardening in alcohol. Seventy per cent alcohol with one per cent acetic acid was used to decalcify embryos from eight to thirteen days incubation. Embryos from fourteen to eighteen days were decalcified and softened in seventy per cent alcohol with five per cent hydrochloric acid. The embryos were cleared with carbolxytol and embedded in 52-54 degree paraffin. Serial sections were studied under low power magnification and drawings were traced from a projection microscope. Photographs of serial sections were made regularly at a total magnification of 15x or 25x and enlarged to the desired size with printing. Drawings were photographed and printed to correspond with the photomicrographs.

Embryos of more than 18 days incubation could not be sectioned successfully. The respiratory tracts of embryos from eighteen to twenty-one days were injected with india ink, hardened in alcohol, and dissected. Careful removal of

the body wall and the organs adjacent to the lungs and airsacs revealed the respiratory tract to be outlined in a dark, smoky color. Details of airsac development in the stages succeeding the serial sections were obtained by dissection and outline drawings of the airsacs and adjacent tissues. Embryos of approximately twelve days incubation contained mucous in the respiratory tract. This mucous accumulation hindered injections prior to the eighteen day stage, at which time the respiratory tract had been cleared sufficiently to allow entrance of the injection media.

At least one embryo each day from twenty-one days incubation to hatching was injected with liquid latex. The injected embryos were either fixed in formalin for dissection or immersed in one per cent hydrochloric acid to harden the latex and begin tissue digestion; after forty-eight hours in this solution, the specimens were placed in a one-tenth solution of hydrochloric acid with pepsin at 37 degrees centigrade. When all the tissues had been digested off, there remained a rubber cast of the ramifications of the airsacs. Liquid latex was used as an injection medium in embryos of sufficient development to allow the passage of the medium through the entirety of the respiratory system. Both the latex and india ink injections were performed with sufficient pressure to insure complete penetration and maintain the normal distention of the airsacs. Test cases were performed

on a sufficient number to determine the exact amount of pressure that could be handled by the respiratory tract. Slight palpation aided penetration.

The apparatus for the injection of india ink and latex was the same (Plate I; A). A large flask (3) with a siphon tube for pressure was elevated to a position two feet above the level of the specimen. The pressure tube was connected to a second flask (2) by means of glass and rubber tubing. This flask was connected to the flask containing the injection media. From the flask (1), the injection medium was carried by tubing, via a hypodermic needle, to the trachea of the specimen. With this apparatus, water was let run through the tube from flask (3) into flask (2) where it caused an increase in air pressure which could be conveyed to the flask containing the injection media and thus force the latex or india ink in the trachea of the specimen.

OBSERVATIONS

The Lung

The lung of the white Pekin duck first appeared on the fourth day of incubation (Plate IV; A). It was composed of a single endodermal tube, the mesobronchus, surrounded by splanchnic mesoderm. The pulmonary artery and vein entered

the lung dorsal to the bronchus. The medial posterior surface of each lung is covered by diaphragmatic tissue which is continuous with the mesesophagus but does not yet connect to the body wall.

By the seventh day of incubation the mesobronchus projects dorsally and posteriorly to the posterior tip of the lung and secondary bronchi make appearance as three short branches from the mesobronchus: anteriorly and dorsally; dorsally and laterally; and dorsally and posteriorly (Plate IV; A). By the end of the ninth day the secondary bronchi have developed as two main groups; one series along the dorsal surface of the mesobronchus and continuing dorsally to the margin of the lung and another series along the ventral surface of the mesobronchus, supplying branches for the medial, posterior portion of the lung (Plate IV; C). The dorsal series of secondary bronchi consistently extend dorsally and laterally from the mesobronchus to the dorsal-lateral margin of the lung. The most anterior of this group of secondary bronchi travelled dorsally and laterally along the median-anterior surface of the lung. The secondary bronchi at this period of incubation are not connected to each other on the periphery.

During the tenth day of incubation the secondary bronchi were found to give rise to irregular subdivisions which developed into a series of small tubules (parabronchi)

interconnecting the branches of the secondary bronchi along the margin of the lung wall (Plate IV; D). The interior of the lungs were void of parabronchi until near the end of the eleventh day of incubation, at which time parabronchi formed a complete circuit of anastomosing tubules (Plate V; A).

The tracheal cartilages were first distinguished during the twelfth day of incubation. The cartilaginous rings developed posteriorly along the mesobronchus so that by the eighteenth day of incubation they were visible along the anterior half of the mesobronchus and became complete throughout the length of the mesobronchus by the time of hatching.

During the fourteenth day of incubation the diaphragm established its association dorso-laterally between the pleural and peritoneal cavities by making contact with the support of the mesonephric duct. At this time, the posterior tip of the lung extends posteriorly into the angle formed by the association of the diaphragm with the lateral body wall. The medial edge of the lung mesoderm appears less dense than the rest of the lung mesoderm but it is much more dense than in the diaphragm with which it is continuous. Muscle fibers are evident within the diaphragm tissue as a narrow border along the medial edge of the lung (Plate V; D).

The lung gradually filled the pleural cavity until by the end of the thirteenth day the lung surface contacted the

ridge-like prominences of the ribs, folding around them, and conforming with the body wall by the eighteenth day.

Posterior Abdominal Airsac

The posterior abdominal airsac was first identifiable during the ninth day of incubation as a tubular extension of the mesobronchus from the posterior tip of the lung into the tissue of the diaphragm near its free end anterior and ventral to the connection of the diaphragm to the body wall (Plate II; B--Plate IV; C). The posterior abdominal airsac is composed of four layers of tissue: the inner endodermal lining; a thin layer of lung mesoderm; a layer of diaphragmatic tissue, and the parietal peritoneum (Plate II; D--Plate V; A). The airsac continues posteriorly within the limits of the diaphragmatic tissue to the body wall, then pushes into the peritoneal cavity ventrally and medially, pressing the face of the diaphragm out as its cover (Plate VI; B). By the twenty-first day of development, the posterior-medial surface of the airsac bulges into the spaces between the coils of the intestine. The anterior, medial, and dorsal surface of the airsac in the region where it bulged into the peritoneal cavity become associated with the posterior surface of the anterior abdominal airsac (Plate VII; E).

The Parabronchi appear as outgrowths from the secondary bronchi into the surrounding lung mesoderm during the tenth day of incubation (Plate IV; D). As secondary bronchi protrude beyond the normal limits of the lung, parabronchi continue to develop along their margins as far out as there is surrounding lung mesoderm to accommodate them. The secondary bronchi appear to actually migrate out from the lung, increasing the airsac from its base, thus carrying the peripheral parabronchi outward until some of them connect from the wall of the airsac rather than from the ostium. These parabronchi are interpreted to be the "recurrent bronchi" of previous authors (Plate V; A).

The size of the airsacs varied with the individual at any given stage. The left posterior abdominal airsac, normally, is slightly larger than the right. Occasionally one of the posterior abdominal airsacs was found to be absent; this was observed both in embryos studied by serial sections and in latex-injected specimens.

Anterior Abdominal Airsac

The anterior abdominal airsac originates from a ventral secondary bronchus on the medial side of the mesobronchus approximately halfway between the entrance of the bronchus and the tip of the lung. During the ninth day of incubation

this secondary bronchus pushes ventrally and medially for a short distance and then turns ventrally and posteriorly; as it enters the diaphragm it becomes cone-shaped. The secondary bronchus, normally, enters the diaphragm tissue midway between the anterior connection of the lung to the mesesophagus and the free end of the diaphragm (Plate II; B--Plate IV; C--Plate V; A).

The anterior abdominal airsac is completely surrounded by diaphragmatic tissue throughout its posterior extension, and thus has the same make-up as the posterior abdominal airsac (Plate VI; A). By the sixteenth day of incubation this airsac has extended into the peritoneal cavity and is separated from the liver by this cavity. The diaphragmatic tissue around the dorsal portion of this airsac, posterior to the tip of the lung, presses against the body wall. This airsac, posterior to the tip of the lung, presses against the body wall. This airsac reaches its definitive position by the sixteenth day of incubation. It had changed from an elongated, tubular sac to the form characteristic of the adult airsac: a smooth-surfaced airsac having greatest extension dorso-ventrally, as shown in the twenty-one day stage (Plate VII; D). During this period, the sac extends to the posterior tip of the liver. Later, it extends to the medial-ventral bulge of the posterior abdominal sac (Plate VII; B, C).

During the twenty-fourth day of incubation the posterior-medial surface of the anterior abdominal airsac bulges slightly into the peritoneal cavity. The parabronchi grow from the mesobronchus at the ostium proximally into the lung mesoderm producing "recurrent bronchi" (Plate V; A) in the same pattern as described for the posterior abdominal airsac.

Intermediate Airsac

This airsac arises on the ninth day of incubation as a ventral, secondary bronchus immediately posterior to the entrance of the bronchus into the lung (Plate II; A--Plate IV; B). The secondary bronchus which gives rise to this airsac extends from the ventral surface of the mesobronchus transversely and ventrally to the medial margin of the lung (Plate I; C); thence it enters the diaphragm and bends sharply posteriorly, occupying a position within the diaphragm ventral and anterior to the origin of the anterior abdominal airsac (Plate II; C--Plate IV; D, E). By sixteen days, the anterior margin of the sac has pressed anteriorly and medially and the main part of the airsac extends both dorsally and ventrally as well as medially, pressing the peritoneal side of the diaphragm before it. By the twenty-first day the sac extends both ventrally and dorsally to nearly surround the anterior

portion of the ventricles of the heart (Plate VII; E, F). The intermediate airsac is bounded dorsally and laterally by the lung; medially by the pericardial sac; posteriorly by the anterior abdominal airsac; and anteriorly by the auricular lobe of the interclavicular airsac (Plate VII; A, D).

This airsac occasionally may have two connections to the lung. The typical connection, described above, may be followed by a ventro-lateral connection resulting from a parabronchus. The parabronchi surrounding the ostium of this airsac arose in the same manner as described for the posterior abdominal airsac.

Interclavicular Airsac

The main portion of the interclavicular airsac was first identifiable between the ninth and tenth days of incubation as a projection of the most median-anterior secondary bronchus immediately anterior to the entrance of the bronchus into the lung. The airsac pushes into the thoracic mesenchyme medially to the bronchus (Plate I; D--Plate IV; F), extending anteriorly along the ventral side of the bronchus (Plate II; A--Plate IV; B); it lies adjacent to the lateral surface of the esophagus. It continued posteriorly along the lateral surface of the esophagus to the level of

the entrance of the bronchus into the lung by the fifteenth day of incubation. By the eighteenth day the medio-ventral extensions nearly surround the esophagus (Plate VI; D); and by the twenty-first day the interclavicular airsacs are in contact along the midline ventral to the esophagus, showing evidence of fusion (Plate VII; F).

As in the other airsacs, the lung mesoderm of the airsac was thickest near the connection of the airsac to the lung. Numerous parabronchi were found to arise around the ostium and penetrate into the lung mesoderm in the same manner as parabronchi arise at other points along the secondary bronchus.

The sternal diverticulum was first distinguished in embryos of eighteen days incubation, originating as a posterior continuation from the ventral tip of the paired interclavicular airsacs. As the sternal diverticulae press posteriorly, they contact each other along the median line and by the twenty-first day appear as a single, broad diverticulum (Plate VII; D, F). No sternal penetration was observed in the specimens studied.

The interpectoral diverticulum appeared during the twenty-first day on each side, projecting ventrally between the large pectoral muscles. This diverticulum was connected broadly to the lateral extension of the primary interclavicular airsac.

The axillary diverticulum, during the twenty-first day, connected distally from the lateral region of the main interclavicular airsac dorsal to the interpectoral diverticulum. It begins as a narrow tube extending into the axillary region, then spreads to surround the proximal tip of the humerus and trisosseus junction. The axillary diverticulum did not penetrate the humerus.

The subscapular diverticulum appeared between the twenty-second and twenty-fourth day of incubation as a lateral continuation from the connection of the axillary diverticulum. It extends beyond the axillary region between the proximal one-fourth to one-third of the scapula and the ribs.

The auricular lobe of the interclavicular airsac had a separate origin by means of parabronchi deep in the lung pushing out from the ventral surface of the lung between the main connection of the interclavicular airsac and the connection of the intermediate airsac to the lung. This sac first appears as a wide projection into the pleural cavity on the eleventh day of incubation (Plate III; B). It pushes into the thoracic mesenchyme on the thirteenth day of incubation (Plate V; B), extending anteriorly from its connection, and by the seventeenth day of incubation has expanded posteriorly along the anterior surface of the auricles, cushioning this region of the heart, and extending posteriorly to the intermediate airsacs (Plate VI; E). By the eighteenth day, the anterior

projection of this sac reaches to a point posterior to the origin of the thoracic diverticulum of the cervical airsac. By the twenty-fourth day the tubular anterior extension of this sac makes a joint-like articulation with the posterio-lateral surface of the main interclavicular airsac. The auricular lobe on the left side has a shorter anterior extension than its mate on the right side. Occasionally, the auricular lobes were not found in specimens studied. The time of origin varied from the eleventh to the fifteenth day of incubation.

Cervical Airsac

This pair of airsacs was first observed in the nine day duck as a thumb-like projection of the secondary bronchus at the anterior tip of the lung. This secondary bronchus arose from the mesobronchus immediately posterior to the entrance of the bronchus into the lung. The main root of the interclavicular airsac arises from this same secondary bronchus (Plate II; A). The cervical airsac establishes itself within the thoracic mesenchyme along the medial, anterior border of the lung during the thirteenth day of incubation (Plate III; A--Plate V; C). Continued growth of the lung anteriorly in the pleural cavity accounts for the gradual posterior shift of the connection of the cervical airsac along the median ventral surface of the lung (Plate VI; C).

Parabronchi appear in the lung mesoderm around the ostium of this airsac shortly after the parabronchi are established along the periphery of the lung. The parabronchi around the cervical ostium anastomose freely and make direct and indirect connections to the secondary bronchus as do other parabronchi of the lung.

The thoracic diverticulum arises as a ventral, posterior continuation of the cervical airsac between the lung and the mesesophagus. It extends posteriorly as a tubular projection, to become associated with the dorsal, anterior surface of the intermediate airsac. No tertiary diverticulae were observed from this diverticulum.

The vertebral diverticulae on each side begin as three finger-like projections from the dorsal surface of the cervical airsac between the last two cervical and the first thoracic vertebral joints during the seventeenth day of incubation. These projections curve medially and anteriorly within the neural canal to surround the spinal cord. The vertebral diverticulae from both sides make contact along the median line ventral to the vertebral column. The vertebral cushions, thus formed, continue anteriorly to cushion the last four cervical vertebrae by the time of hatching.

The primary cervical airsac on the right side of the embryo tends to be slightly larger medio-laterally than its mate on the left side. The main airsac was observed to cross

the median line dorsal to the esophagus; however, it did not connect to the cervical airsac of the left side.

DISCUSSION

The presence of airsacs as extensions of tubules from the lungs in all members of the Class Aves has been generally accepted by most workers in comparative anatomy and by all those concerned directly with Avian anatomy. It is not generally known, however, that the birds which have been most commonly studied, namely, the domestic chicken and the pigeon, have extremely complex airsac systems, surpassed in complexity only by that of the Falconiformes; and that some of the more primitive groups of birds, as the loons and grebes, have extremely simple airsacs. The airsacs of the ducks, as shown by dissections and macerations of injected adult birds, is intermediate, and possibly also transitory between the simple type of the loons and the complex type of the hawks. An accumulation of mucus within the lung tubules throughout most of the second week of incubation made injection of any kind impossible before the eighteenth day. It is not known whether other birds have a similar accumulation of mucus at a corresponding time in their development; but preliminary work with chicks of twelve to fifteen days showed no indication of it.

The simplicity of the pattern of the airsacs in the white Pekin ducks proved advantageous in this work, making possible the establishment of a general pattern of development without the added complexities of numerous diverticulae and pneumatization of bones. The embryos were very little larger than chick embryos of comparable ages; decalcification of bone proved of little consequence and proper staining was readily achieved with standard techniques.

After eighteen days the entire respiratory system was substantial enough to withstand pressure necessary for injection with india ink; and by twenty-one days liquid latex could be injected without rupture or overdistention of the airsacs.

The results of this study clarified a number of facts about the airsacs and their development. The general pattern of development of the respiratory system in white Pekin ducks has been determined to be quite comparable to that described by Locy and Larsell for the chicken (1916) as also are the relationships of the individual airsacs to the other organs of the body. It seems that the bronchial system of the chicken and pigeon are much more complex than that of the duck; also, it was found that the references in the literature to recurrent bronchi were attempts to describe the parabronchi which were found connecting the lung periphery to the airsac adjacent to the original ostium. These

parabronchi develop, consistently, as outgrowths of the secondary bronchi into the lung mesoderm. As the secondary bronchi or mesobronchus grows outward from the lung and enlarge into the airsacs, they carry with them a thin layer of lung mesoderm, thickest near the ostium. This thin layer of lung mesoderm contains the distal parabronchi which anastomose in a normal manner within the lung proper but along the ostium become elongated, and enlarge both in the lung mesoderm adjacent to the airsac ostium and in the lung mesoderm proper, thus producing the secondary connections from the airsac to the lung.

The diaphragmatic support of the lung in the duck conforms generally with earlier descriptions of this tissue. The distinction between pulmonary and abdominal diaphragms, however, must be considered simply as a matter of orientation. The diaphragm arose as a single mass from the dorsal mesentery extending laterally between the lung and the liver; later it connected to the body wall in the region of the mesonephric duct. A muscular sheath developed in the diaphragmatic tissue between the lung tissue proper and the airsacs. This muscle layer continued to the posterior tip of the lung in embryos prior to hatching, and constitutes the essential part of the diaphragm of the adult. The intermediate, anterior abdominal, and posterior abdominal airsacs, in the pre-hatched bird, lie within the diaphragm in such a way

that they separate the diaphragm into two layers: the muscular layer that is regularly known as the pulmonary or respiratory diaphragm and the posterior-medial surface of the sacs that are frequently termed the abdominal diaphragm.

Some clarification of the construction of the airsac walls has been accomplished. The inner layer consisting of lung endoderm is completely surrounded by a thin layer of lung mesoderm; this is totally invested by the diaphragmatic tissue in the case of the intermediate, anterior abdominal and posterior abdominal airsacs. In the later stages of development these airsacs bulge into the peritoneal cavity, thus causing their medial borders to be covered by an outer layer of parietal peritoneum. As they protude farther into the peritoneal cavity, the peritoneum cuts in between the aidsac and the diaphragm to some extent, so that the sacs are almost completely covered by peritoneum. The interclavicular and cervical sacs have the endodermal tube surrounded by the thin layer of lung mesoderm; this is surrounded by the thoracic mesenchyme. In the case of the auricular lobe of the interclavicular airsac, its posterior face is separated from the intermediate airsac by the anterior end of the diaphragm, so it is nowhere in contact with the peritoneum. It does, however, replace a considerable mass of mesenchyme around the anterior part of the heart, and comes into the same relationship with the parietal pericardeum over part of

its surface as the intermediate airsac does with the parietal peritoneum.

The time of origin of each airsac was observed to be within a period of four days. The interclavicular airsac gives rise to interpectoral, axillary, subscapular, and sternal diverticulae. The auricular lobe of this airsac arose independently from parabronchi along the ventral surface of the lung; it has been considered a diverticulum of the interclavicular airsac because of the relation of the auricular lobe to the primary interclavicular airsac in the stages subsequent to the development of the other interclavicular diverticulae, and because it is unknown as a separate sac in any adult bird. In the duck, all of the major airsacs have developed to near final proportions before hatching. The vertebral diverticulae of the cervical sacs have not yet penetrated as far anteriorly or posteriorly as they were found in the adult duck. In this form, no bone penetration has been demonstrated in the adult; and none was found in the embryo.

SUMMARY

A review of the literature was made.

The embryos of white Pekin ducks were studied by serial sections and injections.

The origin, time of development and ramifications of the airsacs were established to be comparable to that previously reported for the chicken.

The posterior abdominal airsac arose on the ninth day as a direct continuation of the mesobronchus within the diaphragm and expanded into the abdominal cavity.

The anterior abdominal airsac arose on the ninth day as a continuation of a ventral secondary bronchus extending posteriorly into the diaphragmatic tissue to the posterior limit of the liver.

The intermediate airsac originated on the ninth day from a ventral secondary bronchus into the diaphragm, partially surrounding the ventricles of the heart.

The interclavicular airsac arose on the ninth day as a continuation of the anterior medial secondary bronchus into the thoracic mesenchyme. The auricular lobe arose independently on the eleventh day of incubation and fused secondarily with the interclavicular airsac.

The cervical airsac continued from the anterior medial secondary bronchus on the thirteenth day into the thoracic mesenchyme anteriorly along the vertebrae.

Recurrent bronchi were determined to be normal parabronchi that had been carried outward from their origin by the expansion of the airsacs.

ACKNOWLEDGMENTS

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LITERATURE CITED

- Gier, H. T.
Airsacs in the loon. Unpublished manuscript.
- Gilbert, W. P.
Avian lung and airsac system. *Auk*. 56:59-63. 1939.
- Howell, A. B.
Morphogenesis of the shoulder structure of Aves.
Auk. 43(3): 364-375. 1937.
- Lillie, F. R.
The development of the chick. New York: Henry Holt
& Co. 325-347. 1908.
- Locy, W. A. and O Larsell.
The embryology of the bird's lung.
Part 1. *Amer. Jour. Anat.* 19: 447-504. 1916.
Part 2. *Amer. Jour. Anat.* 20: 1-44. 1916.
- McLeod, W. M. and R. P. Wagers.
The respiratory system of the chicken.
Amer. Vet. Med. Assoc., Jour. XCV (748): 59-70.
1939.
- Muller, B.
The airsacs of the pigeon. *Smithsonian Misc. Coll.*
50: 365-414. 1908.

APPENDIX

EXPLANATION OF PLATES

Drawings are composites made by projecting twenty consecutive sections on the same drawing outline. Drawings were inked and shaded with pencil. Surrounding organs were blocked in to show position and not structure. Photographs were made of the drawings; magnification of the photographs reached 20x. Photographs of sections were taken at fifteen to twenty-five x; by printing, the magnification was increased to twenty-five x or thirty-seven x as designated in specific figures. Rubber casts were photographed at a magnification of 3 x. Drawings are found on plates I, II, and III. Photomicrographs are shown on plates IV, V, and VI. Plate VII contains photographs of rubber casts.

The following key was used in labelling photographs:

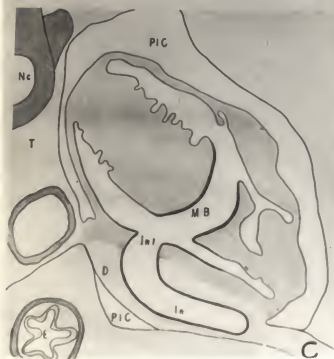
Anterior abdominal airsac	A A
Anterior abdominal secondary bronchus	A A 1
Auricular lobe	A L
Bronchus	B
Cervical Airsac	C
Diaphragm	D
Esophagus	E
Interclavicular airsac	I c
Interclavicular secondary bronchus	I c 1
Intermediate airsac	I n
Intermediate secondary bronchus	I n 1
Interpectoral diverticulum	I D
Kidney	K
Liver	L
Lung	Lung
Mesobronchus	M B
Notochord	N c
Pericardial cavity	P C
Peritoneal cavity	P e C
Pleural cavity	P l C

Posterior abdominal airsac	P	A
Pulmonary artery	P	u A
Pulmonary vein	P	u V
Rib	R	
Sternal diverticulum	S	D
Stomach	S	
Thoracic mesenchyme	T	m
Trachea	T	
Vertebral diverticulum	V	D

EXPLANATION OF PLATE I

- A. Line drawing of pressure apparatus.
 - 1. injection media.
 - 2. pressure flask.
 - 3. flask from which pressure was derived.
- B. Lung and airsacs of thirteen day duck; ventral-lateral view.
- C. Transverse sections of ten day duck.
- D. Transverse sections of ten day duck.

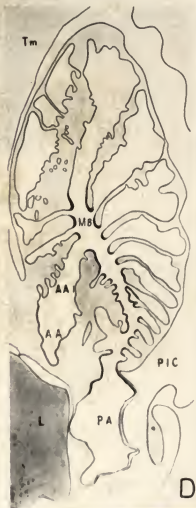
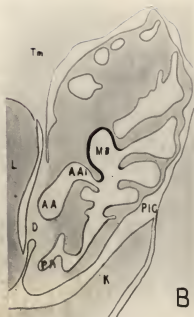
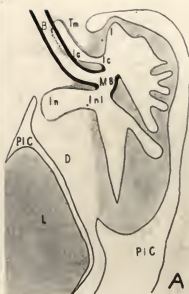
PLATE I



EXPLANATION OF PLATE II

- A. Sagittal sections of nine day duck.
- B. Sagittal sections of nine day duck.
- C. Sagittal sections of ten day duck.
- D. Sagittal sections of eleven day duck.

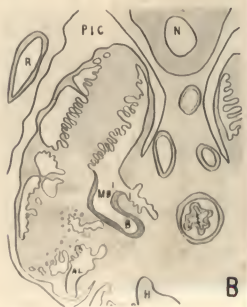
PLATE II



EXPLANATION OF PLATE III

- A. Sagittal sections of thirteen day duck.
- B. Transverse sections of eleven day duck.

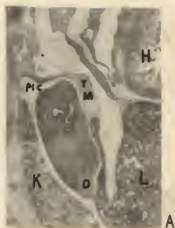
PLATE III



EXPLANATION OF PLATE IV

- A. Seven day duck; sagittal section; 28x magnification.
- B. Nine day duck; sagittal section; 28x magnification.
- C. Nine day duck; sagittal section; 28x magnification.
- D. Ten day duck; sagittal section; 28x magnification.
This individual was extremely large considering its
age and degree of development.
- E. Ten day duck; transverse section; 28 x magnification.
- F. Ten day duck; transverse section; 28x magnification.

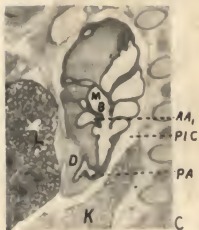
PLATE IV



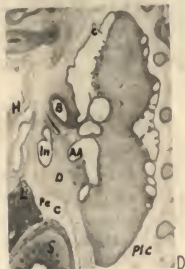
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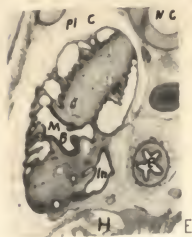
B



C



D



E

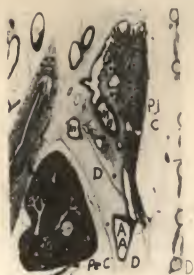
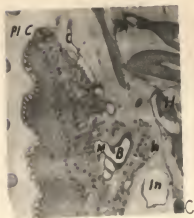
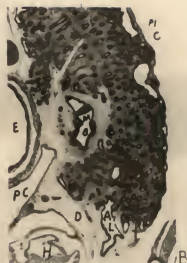
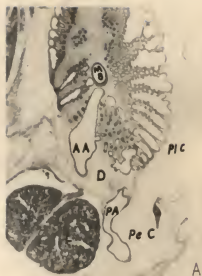


F

EXPLANATION OF PLATE V

- A. Eleven day duck; sagittal section; 28x magnification.
- B. Thirteen day duck; sagittal section; 28x magnification.
- C. Thirteen day duck; transverse section; 28x magnification.
- D. Fourteen day duck; frontal section; 20x magnification.

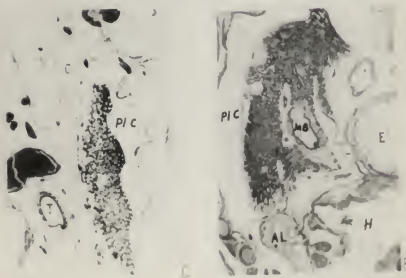
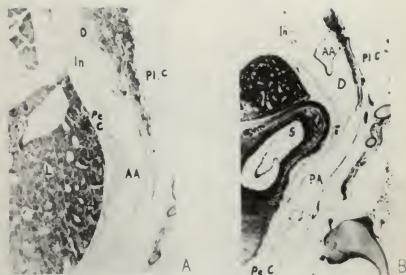
PLATE V



EXPLANATION OF PLATE VI

- A. Sixteen day duck; sagittal section; 20X magnification.
- B. Fifteen day duck; sagittal section; 20X magnification.
- C. Sixteen day duck; sagittal section; 20X magnification.
- D. Eighteen day duck; transverse section; 20x magnification.
- E. Eighteen day duck; transverse section; 20x magnification.

PLATE VI



EXPLANATION OF PLATE VII

- A. Twenty-four day duck; right side; ventral view.
- B. Twenty-four day duck; left side; medial view.
- C. Twenty-four day duck; right side; lateral view.
- D. Twenty-one day duck; right side; lateral view.
- E. Twenty-one day duck; ventral view.
- F. Twenty-one day duck; right side; median view.

PLATE VII

