THE AVIAN LUNG AND AIR-SAC SYSTEM

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Plate 4

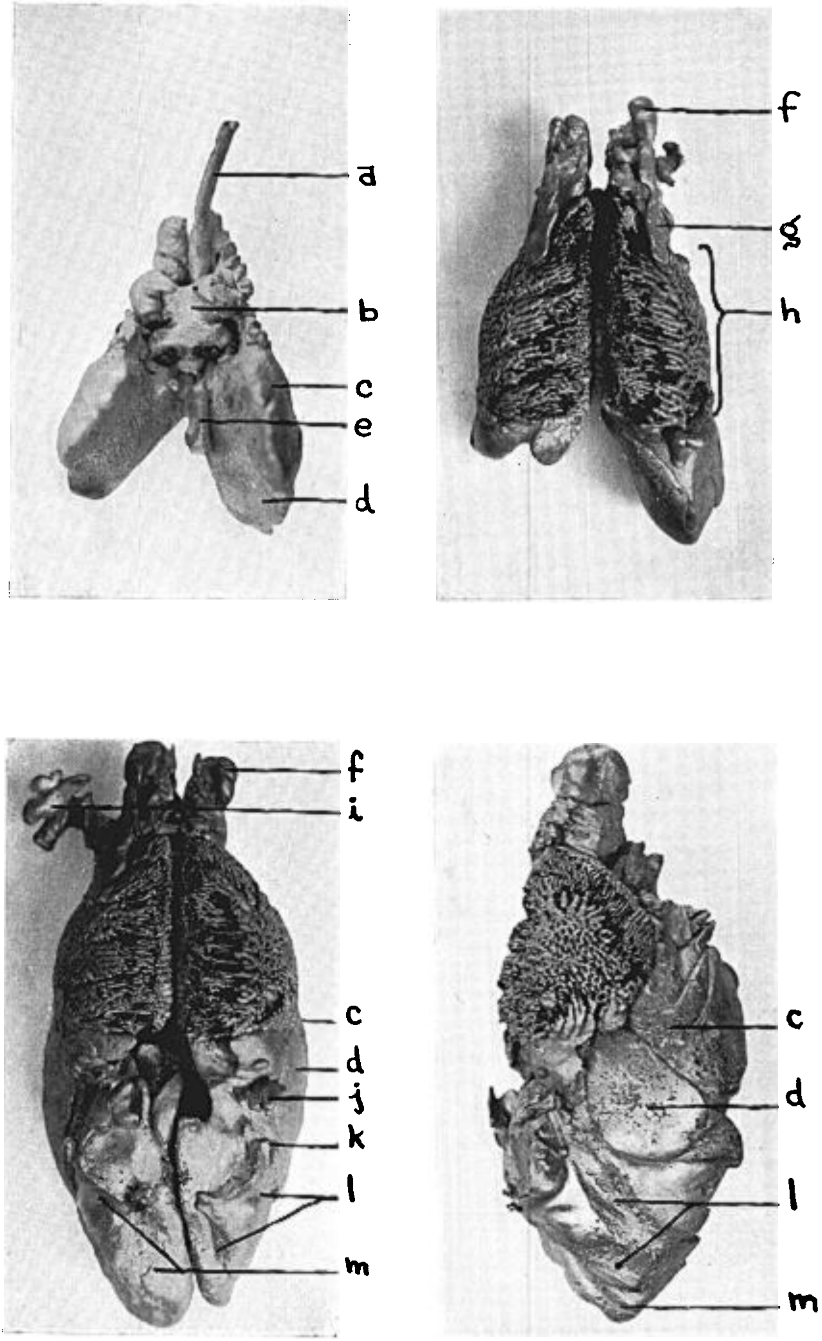
IN the following pages the author has attempted to review briefly the main contributions pertinent to an understanding of the avian lung and air-sac system. Supplementing this review is a description of a method for casting the system using Woods Alloy. Casts were made of the lungs and air sacs of the Domesticated Pigeon (*Columba livia*). This bird was chosen because considerable work had already been done on its respiratory system.

I am indebted to the Department of Zoology at Dartmouth College for furnishing me the necessary equipment with which to pursue the experimental aspect of this problem. I also wish to thank Dr. N. K. Arnold and Dr. W. W. Ballard for their encouraging enthusiasm and assistance.

HISTORICAL

For over two and one-half centuries it has been known that there are certain structures accessory to the bird's lung—the air sacs. Harvey (1651) was the first to describe them carefully. For the next century and a half investigators speculated widely as to the function of the sacs but it was not until 1828 that any marked scientific information was obtained concerning them. From this time on, we find the investigators falling into four main groups—embryological, histological, morphological and physiological.

As to the embryological observations, the earliest contribution is by Rathke (1828) in which we find the first figures of the buds of ecto- and entobronchi. Selenka (1866) wrote concerning the development of the air sacs and His, two years later, on the laryngo-tracheal groove and trachea. Zumstein in 1900 explained the nature of the bronchial tree and the air sacs. The sacs and their method of growth were further described by Moser (1902). Juillet (1911) published a comprehensive treatise embracing the anatomical, embryological, histological, and comparative study of the bird's lung. He emphasized the important fact that the branches of the bronchi in the lung never end in 'cul-de-sacs,' but are all in intercommunication, forming circuits which can be traversed by pure air, from one end or the other, according to whether the air comes from the air sacs or the trachea. Thus the lung consists of a labyrinth of air-containing branches interpenetrated by a labyrinth of blood capillaries, each of which is surrounded on all sides by air. The latest investigations of an embryological nature were carried out by William Locy and Olof Larsell (1916). These investigators have attached much importance to the 'recurrent bronchi,' recognized by Schulze and Juillet, which spring from the air sacs and grow



CASTS OF AIR-SAC SYSTEM OF THE PIGEON

back into the lungs where they establish numerous connections with the bronchial branches. We will have occasion to refer to the work of these men later.

The main histological contributions have been advanced by F. E. Schulze (1871); M. J. Ross (1899); and Oppel (1905).

Campana (1875) was the first to make a careful analysis of the anatomy of the bronchial passages. His investigations brought to light the bronchial circuits which unite the various divisions of the bronchi into a plexus of intercommunicating passages. He also noticed recurrent bronchi without understanding their significance. Huxley (1882) brought the terms mesobronchium, ecto-, ento-, and parabronchi into common use. The air sacs in the adult bird have been further described by Bruno Müller (1908) who worked on the pigeon. In his treatise 'On the Air Sacs of the Pigeon' he gives a most detailed and careful description of the sacs themselves without involving the anatomy of the lungs. Some of his methods and results obtained will be referred to below. F. E. Schulze (1911) published an excellent paper on the comparative anatomy of the air sacs in the adult. Here, for the first time, the recurrent bronchi were fully described and their physiological office was pointed out. The most recent observations on the morphology of the bird's lung are contained in the paper of Juillet mentioned above. Here also may be found a review of previous work done on the avian lung and air sacs.

Little work has been done thus far pertaining to the physiology of the air sacs. Campana's paper on the 'Physiology and Respiration of Birds' is of chief importance anatomically. Since the time of Harvey the function of the air sacs has proved fertile soil for speculation. The following functions have been attributed to them: aid in raising feathers; act as resonatory organs; lessen specific gravity of bird; regulate the body temperature; fix wings in a distended position; have a function analogous to that of a swim bladder; have a respiratory function. Müller (1908) rejected all these ideas and made the following statement: "I do not consider the air sacs, including the air cavities of bones, as organs having a positive and special function, but rather as a system of empty interspaces. Their value lies in their emptiness—that is, in their containing nothing that offers resistance or has appreciable weight."

Present Status of Avian Lung and Air-Sac System

It is through the careful investigations of Schulze (1911), Juillet (1911), and Locy and Larsell (1916) that we arrive finally at our present conception of the avian lung and accessory air sacs. Breathing in birds is specialized in relation to flight, to song, and to intense activity in general. The lungs, though relatively small and hardly distensible, have a large internal surface for gaseous exchange. The driving out of air is assisted by strokes of the wings. Expiration is the active part of the respiratory process, not inspiration as in mammals.

Just posterior to the tongue is the glottis, the opening into the trachea. The upper part of the trachea is known as the larynx, which, unlike that of mammals, possesses no vocal cords. It is supported by cartilages which are transformed representatives of the branchial arches. The trachea is supported by bony rings which usually form a complete circuit around the wind pipe. It is moved by two sternotracheal muscles attached to the anterior part of the sternum. The base of the trachea is enlarged to form the syrinx or voice-box, an organ found in most birds though absent in ostriches, storks and some vultures. The three upper rings of the two bronchial tubes also aid in the formation of the syrinx. The short bronchi divide in a unique fashion to form the lung. A main stem passes right through as the mesobronchus and leads into the abdominal air sac. The greater part of the mesobronchus appears to be dilated. From this enlarged portion secondary bronchi arise, some of which lead directly into the air sacs, while others merge into the highly branched parabronchi (tertiary bronchi) supplying the lung. These parabronchi are continuous, thus forming a network of air capillaries—the bronchial circuit. Budding off from the air sacs are the 'recurrent bronchi' which lead into the lung parenchyma and merge with various parabronchial air capillaries. "By means of the recurrent bronchi and their anastomoses with other branches of the bronchial circuits the air-sacs are brought into communication with all parts of the lung. They have direct communication with bronchus and central lung tube through their 'direct orifices' and a recurrent communication through the recurrent bronchi" (Locy and Larsell, 1916, part 2, p. 21). Thus the air sacs are not to be thought of altogether, at least, as terminal sacs; "they may be regarded as expanded reservoirs on the course of the bronchial circuits" (Thomson, 1923, p. 129).

It is now generally accepted that there are nine sacs accessory to the avian lung. Four paired sacs and one single sac can be distinguished as follows:

(1) Cervical sacs (paired)—in region of the nape of the neck.

(2) Interclavicular sac (single)—adherent to syrinx and situated ventrally, laterally, and proximally to it. Numerous diverticula arise from this sac including the subscapulare, axillare, suprahumerale, and sternale.

(3) Anterior intermediate sacs (paired)—separated from lung by pulmonary diaphragm.

(4) Posterior intermediate sacs (paired)—asymmetrical, left sac reaching farther posteriorly and larger than right. Left sac extends beyond last rib into abdominal cavity. Right sac extends but little or not at all beyond last rib.

(5) Abdominal sacs (paired)—largest of all sacs; enter abdominal cavity dorsally and partially enclose viscera; have several accessory diverticula. One may find further detail as to the relative size and location of the sacs in Müller's (1908) treatise on the 'Air Sacs of the Pigeon.'

The sacs appear as thin transparent membranes, with more or less of a fibrous connective-tissue basement. All the sacs, with the exception of the interclavicular, can be freed of connections with adjacent tissues. The sacs are lined with pavement epithelium. Where the sac is attached to surrounding tissue the lining cells become columnar. Cilia are present over the entire surface of the sacs contained within the body cavity. They are absent, however, in the prolongations of the sacs into the joints and in the cavities of the bones. The function of the cilia is not definitely known but is believed to be that of removing exfoliated epithelium and foreign substances from the sacs. Brief histological reviews of the air-sac system have been set forth by M. J. Ross (1899) and by Oppel (1905).

The excellent treatise on 'The Embryology of the Bird's Lung' by W. A. Locy and Olof Larsell (1916) has shed much light upon the development of the avian lung and air-sac system. They succeeded in tracing the development of the lung and air-sac system in the chick embryo from the time the egg was laid up through time of hatching. The following are some of their interesting observations. The lung became definable near the close of the third day of incubation. The abdominal and cervical sacs were the first to appear at the end of the seventh day. These were followed shortly by the anterior and posterior intermediates, the interclavicular being the last to appear. At the end of the ninth day all sacs had projected beyond the periphery of the lung. The recurrent bronchi made their first appearance after ten and one-half days of incubation. All the sacs except the cervical possessed these recurrent branches.

As to the present conceptions concerning the functions of the sacs, much may be said. Locy and Larsell state: "The lung of birds is not large in extent, but it is highly vascular and the continuous air current from the air sacs through the recurrent bronchi makes it an effective apparatus for aëration of the blood." The air sacs are also believed to promote internal perspiration, thus aiding in regulating the high temperature of the avian body. "Most birds take much water, but there is little water in their urine, which is semi-solid, and they have no sweat glands like mammals. Hence, the advantage of the internal surfaces of the air sacs, for water-vapour diffuses from the blood into the cavities and passes out by the lungs" (Thomson, 1923, p. 128). Thus the theory of Müller that the air sacs have no definite function but are valuable because of their emptiness, tends to overemphasize one aspect.

METHOD FOR CASTING

Since the author was especially interested in the relative positions of the sacs and their accessory diverticula, the most satisfactory approach to the problem was by means of casts. Several types of injection masses were considered including Fol's metagelatin vehicle, celloidin, gelatin, paraffine, Woods Alloy and Darcet's metal. Finally it was resolved to use Woods Alloy. This fusible alloy is made up of bismuth, lead, tin and cadmium, has a specific gravity of 9.5 and a melting point at 70° C.

Rather than go through the long formalin-hardening process of Müller and injecting individual sacs, it was decided to inject directly into the trachea of a pigeon freshly killed with ether. About 600 grams of Woods Alloy were melted in a beaker placed in boiling water. The melted metal was then transferred into the chamber of the syringe which was heated further. Simultaneously the pigeon was heated a few minutes in a water bath at a temperature of approximately 65° C. The bird was then removed from the water bath and the trachea quickly exposed and slit for the reception of the syringe canula. The posterior end of each abdominal sac was punctured so that air in the lungs and sacs might escape and be replaced by Woods Alloy. The injection time lasted forty-five seconds. During this process the bird was held with the left hand while the syringe was manipulated with the right. A glove was used to insulate the right hand. The Woods Alloy remained fluid approximately a minute and a half. This gave time to massage and turn the bird in various positions so that the metal might be uniformly distributed throughout the system. The metal was allowed to set for half an hour before the casts were dissected out. In the case of the lung and smaller diverticula where dissection was difficult, artificial gastric juice proved a useful agent in digesting away neighboring tissue.

The anterior and posterior intermediate sacs cast well consistently. To obtain the remaining sacs it was necessary to place the bird in various positions while injecting the metal and then to hold the bird head downward, closing the trachea to prevent back flow. The cast of the interclavicular sac and diverticulum sternale was obtained by allowing the bird to rest on its ventral surface. The best lung detail was obtained when the bird rested on its dorsal surface. The abdominal sacs were the most difficult to cast. This was probably due to the fact that they were farthest from the point of injection and the metal began to cool before reaching their orifices from the mesobronchi. Thus it was necessary to place the posterior and middle portions of the bird in a hot bath and inject while the long axis of the bird was vertical. The subscapulare, axillare, and suprahumerale diverticula were obtained by puncturing the pneumatized humerus.

DISCUSSION

The casts obtained agree rather closely with those of Müller (1908) who used wax as an injection mass. The advantage of Woods Alloy over wax lies in the fact that the former is more permanent and less likely to be secondarily distorted. By injecting directly into a warm, freshly killed bird the long formalin-hardening process of Müller and the alcohol-distension process of Locy and Larsell are eliminated. Because of the pressure with which the metal was forced into the sacs, the complete casts obtained probably represent the sacs at their maximum distension. By regulating the amount of metal injected and the position of the bird during the injection it is possible to cast only a desired part of the system (see Plate 4). Duplicate and unsatisfactory casts may be melted and the metal injected into another bird. Casts of the lung and air sacs have proved useful as teaching demonstrations and it is hoped will be of service in making a comparative morphological study of this remarkable avian system.

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DESCRIPTION OF PLATE 4

Upper left: Ventral view of partial cast, approximately two-thirds natural size. Note: trachea (*a*); single interclavicular sac (*b*); left anterior intermediate sac (*c*); left posterior intermediate sac (*d*) with accessory diverticulum (*e*).

Upper right: Dorsal view of partial cast, approximately two-thirds natural size. Note: right cervical sac (*f*); right subscapular diverticulum (*g*); right lung (*h*).

Lower left: Dorsal view of nearly complete cast, approximately two-thirds natural size. Note: right cervical sac (*f*); left suprahumeral diverticulum (*i*); right anterior intermediate sac (*c*); right posterior intermediate sac (*d*); right anterior femoral diverticulum (*j*); right posterior femoral diverticulum (*k*); right and left abdominal sacs (*l* and *m*). Observe asymmetry of abdominal sacs.

Lower right: Right lateral view of same cast, approximately two-thirds natural size. Note: right anterior intermediate sac (*c*); right posterior intermediate sac (*d*); right abdominal sac (*l*); left abdominal sac (*m*).

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