MORPHOLOGY OF THE LOWER RESPIRATORY SYSTEM OF THE WHITE PEKING DUCK

Thesis for the Degree of Ph. D.

MICHIGAN STATE UNIVERSITY

Aaldert Mennega

1964

This is to certify that the

thesis entitled

MORPHOLOGY OF THE LOWER RESPIRATORY SYSTEM

OF THE WHITE PEKING DUCK

presented by

Aaldert Mennega

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Anatomy

Lois Calhoun
Major professor

Date August 12, 1964

O-169

ABSTRACT

MORPHOLOGY OF THE LOWER RESPIRATORY SYSTEM OF THE WHITE PEKING DUCK

by Aaldert Mennega

The purpose of this work has been to investigate the morphology of the respiratory system of the White Peking Duck, from the bronchi distad, to establish how the air sacs are supplied with air, and to determine the role played by the diaphragm and pleura. The findings were compared with those of other domestic birds as described by other authors.

Five male and five female White Peking Ducks were used for gross dissection and corrosion, and two males and six females for histologic studies. Sections of the latter were fixed in saturated mercury fixative, dehydrated in a series of alcohols, cleared in xylol, embedded in Paraplast, and stained with Harris' hematoxylin and eosin and with Weigert and Van Gieson's stain. Bone sections were decalcified.

In the White Peking Duck there are eleven air sacs. Of these the cervical, anterior thoracic, posterior thoracic and abdominal sacs are paired, while the interclavicular, dorsal and synsacral sacs are single. Accessory air sacs are located in unusual places on the ventral surface of the lungs of many White Peking Ducks. The cervical air sacs have diverticula nearly all along the neck: the lateral cervical pouches, and the extraneural and intraneural diverticula. The costal diverticulum extends along the first rib. The interclavicular air sac consists of the sac proper and the axillary, postcardiac and sternal diverticula.

The anterior and posterior thoracic air sacs have no diverticula, although the posterior are often split. The only diverticula from the abdominal air sacs are the suprarenal diverticula which partially surround the kidneys. The dorsal air sacs pneumatize thoracic vertebrae 2 through 7 directly, by way of the lateral and dorsal pneumatic fossae. The synsacral air sac arises from the posterior dorsomedial borders of the lungs and pneumatizes the synsacrum.

The trachea has interlocking, bony rings, and a bony _bulla tympaniformis_ at its bifurcation. The extra- and intrapulmonary bronchi have incomplete, hyaline cartilage rings. There are 5 dorsomediobronchi, 3 large laterobronchi, and a number of dorsolaterobronchi and dorsobronchi branching off the primary bronchus. They give rise to the parabronchi which lead to the atria; from the latter air enters into the air capillaries which are surrounded by the blood capillaries.

The cervical air sac is supplied by dorsomediobronchus 1; the interclavicular by saccobronchi; the anterior thoracic by dorsomediobronchus 3 and saccobronchi; the posterior thoracic by laterobronchus 2 and saccobronchi; and the abdominal by a large bronchus which arises from the adjacent parabronchi. The dorsal and synsacral sacs are supplied by the parabronchi of the medial surface and posterior dorsomedial corner of the lung.

There is a firm, tendinous diaphragm stretched across the thorax which inserts on ribs 2 through 9 by means of the _Mm. pulmocostales_. A typical pleura is lacking.

The cervical and thoracic vertebrae, the synsacrum, the sternum and the humerus are pneumatized by the different air sac diverticula.

The extra- and intrapulmonary bronchi are lined with ciliated pseudostratified columnar epithelium, which changes in the secondary bronchi to cuboidal with patches of simple squamous or pseudostratified columnar epithelium. The parabronchi and air sacs have cuboidal and simple squamous epithelium. The lamina propria persists through the air passages and air sacs except in the atria and air capillaries; it has two vascular networks. Elastic fibers form a network enclosing the bronchial rings and are present in the walls of the atria and air capillaries. A bronchial muscle connects the cartilage rings externally. Smooth muscle bands are also present in the posterior part of the intrapulmonary bronchus, the secondary bronchi and parabronchi, all air sac ostia, the septal walls of the parabronchi, and their openings into the air capillaries.

MORPHOLOGY OF THE LOWER RESPIRATORY SYSTEM OF THE WHITE PEKING DUCK

By

Aaldert Mennega

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Anatomy

1964

ACKNOWLEDGMENTS

The author wishes to express his appreciation to all who, in any way, have helped to make this work a reality. Special thanks are due to Dr. M. L. Calhoun for guiding this work as Chairman of the Guidance Committee; to Drs. E. M. Smith, C. W. Titkemeyer and G. J. Wallace for serving on the Guidance Committee and assuming the responsibilities this entails; and to Drs. E. H. Roege, A. M. Lucas, R. E. Brown and T. W. Jenkins for their valuable advice.

For my fellow students who, with advice, criticism and forbearance, have promoted progress in diverse ways, a word of appreciation is in order.

Above all, tribute is due to my wife who has, with patience, understanding and encouragement, done so much to help bring this work to completion.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF FIGURES - Continued

FIGURE | Page

INTRODUCTION

Among the chordates the birds stand out because of their unusual, but highly efficient respiratory system. Since the middle of the 17th century, when Harvey first discovered the air sacs, scientists have been intrigued by the structure and function of the lungs and air sacs of birds and have often speculated on the meaning of their findings. But due to incorrect observation and indiscreet copying, many fallacies have crept into the literature and theories have been built on mere suppositions, some of which still persist to this day.

This work originated in a strong interest in the structure and function of the respiratory system of different groups of animals, and in the conviction that more basic studies are needed to clarify, improve and expand the store of knowledge in this area of scientific investigation.

Although much work has already been done on the chicken, the White Peking Duck, because of its availability, size and economic importance, and because it is representative of the class Aves, is well suited for the study of the avian respiratory system.

LITERATURE REVIEW

In the past, several different names have been used to indicate the same structure in the same birds, or analogous structures in different birds. To avoid confusion and needless repetition of explanation, all terms were converted to the nomenclature used by the Federal Poultry Inspection Service, viz.: the cervical, interclavicular, anterior thoracic, posterior thoracic and abdominal air sacs. In those instances where the author did not indicate which species of birds was involved, the work was reviewed under "Other Birds - Specific and General." The name of the parabronchial connections with the air sacs has been converted from "recurrent bronchi" to "saccobronchi."

A. Gross Anatomy

The Cervical Air Sacs

Duck - In the duck the cervical and interclavicular air sacs fill the anterior portion of the thorax (Rigdon, 1959). Each of the paired cervical sacs has only a single connection with the lungs; no saccobronchi are present (Vos, 1934; Rigdon, 1959; Akester, 1960). Cervical diverticula inside and outside the vertebrae, and lateral pouches are recognized but not carefully described (Rigdon, 1959; Lucas, 1960). Lucas (1963) described dorsal outpocketings from the cervical vertebral diverticula. Rigdon (1959) also stated that the right cervical air sac is larger than the left.

Chicken - Some authors reported a single cervical air sac in the chicken (King, 1956; Akester, 1960), while others (McLeod and Wagers, 1939) called them paired, although they described an oval communication between the right and left sacs. Cervical lateral pouches, intraneural and extraneural diverticula were mentioned by different authors (Kaupp, 1918; McLeod and Wagers, 1939; Cover, 1953; King, 1956; Lucas, 1960). The cervical air sacs connect with the lung by means of the first ventromediobronchus (King, 1956; Akester, 1960; Lucas, 1960).

Turkey - Cover (1953) included the cervical air sac with the interclavicular and anterior thoracic air sacs in what he called the "aggregate sac." He described the cervical diverticula, both inside and outside of the neural canal. Lucas (1960) made similar observations. Cover (1953) stated that the cervical diverticula extend back as far as the fourth coccygeal vertebra, pneumatizing all vertebrae along the spine. He assigned costal and suprarenal diverticula to the cervical sac as well.

Other Birds - Specific and General - There is a variety of observations on the cervical sacs of birds. The common loon has none (Gier, 1952). Wetherbee (1951) and Marshall (1960) described direct communications between the cervical and interclavicular sacs. The cervical air sacs lie outside the thoracic cavity and connect with the lung by means of the first ventrobronchus (Victorow, 1909; Martin and Schauder, 1923; Groebbels, 1932; Marshall, 1960).

The Interclavicular Air Sac

Duck - The interclavicular air sac lies in the anterior part of the thorax, and sends diverticula from its periphery between the adjacent muscles and the subcutaneous tissues. It is not paired, but is fused across the midline (Rigdon, 1959), and extends practically to the posterior end of the keel (Lucas, 1963). Several connections with the lung have been reported (Rigdon, 1959; Akester, 1960).

The humerus is penetrated by the axillary diverticulum of the interclavicular air sac, and enters the bone at the foramen pneumaticum. The sternum, and occasionally some of the ribs, are also pneumatized by the interclavicular air sac (Rigdon, 1959; Akester, 1960; Lucas, 1960).

Chicken - Most authors agreed that the interclavicular air sac is a complicated structure. It consists of extra- and intrathoracic parts which occupy the thoracic inlet and surround the shoulder joints. The connection with the lung is by means of the first and third ventrobronchi. The main diverticula named are the pectoral, the humeral and the subscapular. The interclavicular air sac pneumatizes the sternum, the humerus and the ribs (Chauveau, 1891; Kaupp, 1918; McLeod and Wagers, 1939; King, 1956; Akester, 1960; Bradley and Grahame, 1960; Lucas, 1960).

Turkey - Cover (1953), who grouped the interclavicular air sac with the "aggregate sac," described an extension leaving the aggregate sac, which crosses the axillary space and pneumatizes the humerus through a large foramen on the proximal end of its shaft. He also mentioned a small subscapular diverticulum. Lucas (1960) found the interclavicular air sac especially large and said that it "pushes backward, ventral to the lung and fills the area that in the chicken was occupied by the anterior thoracic air sacs." He stated that the axillary diverticula from the interclavicular air sac form cushions around the bones of the shoulder girdle. Some processes extend between the breast muscles. Rigdon *et al.* (1958a) mentioned an axillary space which has no connection with the respiratory passages. In a later statement (1958b) they explained that the membrane separating this space from the respiratory tract is very thin and may easily be ruptured. These axillary hernias progressively regress as the turkey ages.

Other Birds - Specific and General - Most authors agreed that the interclavicular air sac is unpaired, although Stresemann (1937) made an exception for herons and storks. He also described a broad communication between the interclavicular air sac and the anterior thoracic air sacs. In this point he is supported by the observations of Wetherbee (1951) on the sparrow and of Victorow (1909) on the pigeon. Most authors disagreed, and reported a single interclavicular air sac (Martin and Schauder, 1923; Marshall, 1960). Usually three diverticula have been described: the axillary, the subscapular and the humeral (Victorow, 1909; Stresemann, 1937; Marshall, 1960). Pneumatization of the sternum and the humerus has been mentioned by Gilbert (1939) and Marshall (1960). Victorow (1909) ascribed the pneumatization of the cervical vertebrae to the interclavicular air sac, but Pettingill (1961) agreed with most authors that this is accomplished by the cervical air sacs. The connection with the lung has been indicated as a ventrobronchus (Stresemann, 1937; Marshall, 1960).

The Anterior Thoracic Air Sacs

Duck - The anterior thoracic air sacs are located at the inferior margin of the lung. The right one is larger than the left. There are two communications with the lung (Rigdon, 1959), the same as in the chicken, viz.: dorsomediobronchus 3 and a saccobronchial connection, but the duck has many more saccobronchi entering the sac directly (Akester, 1960). Lucas (1960) stated that the anterior thoracic air sacs of the duck are much smaller than those of the chicken.

Chicken - The anterior thoracic air sacs in the chicken are relatively fixed in shape and position, and cover the ventromedial surfaces of the lungs (King, 1956). They lie between the two diaphragms and are limited laterally by the sternal ribs (McLeod and Wagers, 1939).

They have no diverticula (Lucas, 1960). The connection of the anterior thoracic air sacs with the lung is by means of the third ventromedial bronchus and by several parabronchi (Chauveau, 1891; Kaupp, 1918; McLeod and Wagers, 1939; Cover, 1953; Akester, 1960; Lucas, 1960).

Turkey - According to Lucas (1960) the anterior thoracic air sacs are large in the turkey and overlie the abdominal air sacs. Cover (1953) considered the anterior thoracic air sacs a part of the "aggregate sac." Connections with the lungs are by means of a ventral bronchus and several parabronchi. It appears that the anterior thoracic air sacs described by Lucas (1960) and the posterior thoracic air sacs described by Cover are the same structures.

Other Birds - Specific and General - The anterior thoracic air sacs described by Marshall (1960) are in the anterior chamber of the oblique septum. They extend from the base of the lungs to the edge of the sternum and overlap the posterior air sacs at about the sixth rib. They have no diverticula. Communication with the lungs is by means of ventrobronchi 3 and 4. Groebbels (1932) and Gilbert (1939) gave a similar description. Victorow (1909) stated that the anterior thoracic air sacs of a pigeon are similar to those of other birds but have a median diverticulum, which connects the right and left sacs. He also mentioned a direct connection with the interclavicular air sac.

The Posterior Thoracic Air Sacs

Duck - The posterior thoracic air sacs are large in the duck and have a single major communication with the lungs on each side of the body (Rigdon, 1959; Akester, 1960; Lucas, 1960). No diverticula have been described.

Chicken - In the chicken the posterior thoracic air sacs are much smaller than the abdominal air sacs (Akester, 1960) and also much smaller than the posterior thoracic air sacs of the duck (Lucas, 1960). Chauveau (1891) stated that they lie between the two diaphragms, and Kaupp (1918) agreed. McLeod and Wagers (1939) and King (1956) described their relatively fixed position as dorsal in the coelom, near the middle of the lateral abdominal wall. They are nearly circular in shape, have a diameter of about one inch, are related medially to the abdominal air sacs, and are supplied with air by means of the third laterobronchus (King, 1956; Lucas, 1960) and several saccobronchi (McLeod and Wagers, 1939). According to Lucas (1960) the posterior thoracic air sacs have no diverticula. Akester (1960) reported an air supply by way of a secondary bronchus from the medial side of the primary bronchus.

Turkey - There is disagreement on the presence or absence of the posterior thoracic air sacs in the turkey; both Cover (1953) and Rigdon *et al*. (1958) mentioned them, while Lucas (1960) reported their absence. Cover found them between the body wall and the anterior part of the abdominal air sacs of the same side, connecting with the secondary bronchi at the hilus of the lung by means of two communications. This corresponds to the description of the structure which Lucas (1960) called the anterior thoracic air sacs.

Other Birds - Specific and General - Hazelhoff (1951) made the statement that the posterior thoracic air sacs are the largest sacs in most birds, but did not find any support from other workers. He called special attention to the fact that they are caudally recurrent and have a "guiding dam" at their junction with the primary bronchus. They are unequal in length, the left being larger than the right (Gilbert, 1939; Marshall, 1960). They are in contact with the posterior part of the lung and lie in the posterior chamber of the oblique septum, touching the vertebral ribs and sternum. Medially they are related to the viscera and the abdominal air sacs. According to Victorow (1909) the anterior and posterior thoracic air sacs are connected in the pigeon, but Pettingill (1961) stated they are not. Marshall (1960) described a large branch of the mesobronchus and a number of saccobronchi connecting with the lateral portion of the lung.

The Abdominal Air Sacs

Duck - The abdominal air sacs are the largest sacs in the duck, extending posteriorly the entire length of the abdominal cavity. Diverticula from the abdominal air sac extend from their posterior superior surfaces into the spaces about the head of the femur (Rigdon, 1959). The major communication of the abdominal air sac with the lung is a single duct, which is much larger than a tertiary bronchus (Akester, 1960). Lucas (1960) stated that the left abdominal air sac has a broad, shallow impression, made by the gizzard. Vos (1934) observed that the abdominal air sacs lie dorsally when the duck is in a standing position, while they lie ventrally when the duck is held lying on its back. This indicates that the abdominal air sacs are not fixed in position. Lucas *et al.* (1959) found no suprarenal diverticula.

Chicken - The abdominal air sacs of the chicken are supplied by the terminal end of the mesobronchus (King, 1956; Akester, 1960; Bradley and Grahame, 1960; Lucas, 1960). They are the largest of the air sacs, and are very mobile. They extend the entire length of the abdominal cavity, reaching to the roof of the pelvis dorsally, and reaching almost to the abdominal wall ventrally. The left abdominal air sac is larger than the right, due to the presence of a medial pouch of the left sac, which is not present on the right (McLeod and Wagers, 1939). Chauveau (1891), Kaupp (1918), McLeod and Wagers (1939), Lucas (1960) and Lucas and Stettenheim (1964) all described a suprarenal diverticulum which extends from the abdominal air sacs into the depressions of the pelvic girdle above the kidneys, and two femoral diverticula which form a pouch around the hip joint.

Turkey - Cover (1953) stated that in the turkey the abdominal air sacs arise on the most lateral aspect of the posterior extremity of the lungs by the confluence of 20 to 30 parabronchi. He and Lucas (1960) both described suprarenal diverticula, which enter the bones of the back.

Other Birds - Specific and General - The abdominal sacs have usually been described as the largest sacs, and extend the full length of the abdominal cavity. Suprarenal and femoral diverticula have generally been recognized in ducks and chickens (Victorow, 1909; Martin and Schauder, 1923; Gilbert, 1939; Wetherbee, 1951; Marshall, 1960). The communication with the lungs is by means of the terminal end of the mesobronchi. Martin and Schauder (1923) found cartilaginous rings surrounding the ostium. Lucas et al. (1959) found the abdominal air sacs greatly reduced in the great horned owl, due to the enlargement of the interclavicular and anterior and posterior thoracic air sacs. Cowles and Nordstrom (1946) noted that they are in contact with the testes.

Miscellaneous Items Concerning Air Sacs

Ducks - Rigdon (1959) observed that the thoracic vertebrae are diffusely infiltrated with latex in tracheally injected specimens. He also described two latex-filled spaces of moderate size on each side of the midline in the area of the anterior portion of the lumbosacral vertebral mass. Akester (1960) observed thin-walled air sacs with a poor blood supply.

Chicken - Lucas and Denington (1961a, b) stated that diverticula arise only from the cervical, interclavicular and abdominal air sacs, not from the thoracic air sacs. Diverticula in general form air cushions around movable joints and have extensions into adjacent bones.

Taylor et al. (1962) indicated the presence of an extra pair of thoracic sacs in the cockerel, situated posterior to the interclavicular and anterior to the thoracic sacs.

Turkey - Lucas (1960) mentioned numerous small projections penetrating the bones of the back that lie above the lungs.

Other Birds - Specific and General - Pelicans, gannets, toucans and storks have an extensive subcutaneous air sac (Ellenberger and Baum, 1943). The common loon has the simplest set of air sacs (Gier, 1952). Subcutaneous air sacs do not occur in domestic fowls (Martin and Schauder, 1923). All sacs, except the cervicals, have saccobronchi (Sturkie, 1954). The highest development of air sacs has been found in those birds which are the best flyers (Weichert, 1953). Sparrows have no diverticula into the thoracic vertebrae (Wetherbee, 1951).

Air sacs are noticeably thin-walled, have few blood vessels and no respiratory surfaces (Pettingill, 1961). In the kiwi the air sacs are so poorly developed that they do not even enter the abdominal cavity. Martin and Schauder (1923) and Marshall (1960) stated that there is a rich blood supply in the diverticula inside the bone, as contrasted to the avascularity of the main part of the air sacs.

Pneumatization

Duck - Rigdon (1959) described diverticula from the suprarenal diverticulum extending through the sciatic foramen and ending blindly around the head of the femur, along with other diverticula from the abdominal air sac. According to Rigdon the femur is sometimes pneumatized, and diverticula extend into the sacrum from the last dorsal vertebrae. He also made the statement that the cervical and dorsal vertebrae, the sternum and the humerus are always pneumatized in all birds.

Chicken - Bradley and Grahame (1960) made the observation that the cavities of embryonic bones are filled with marrow and are invaded by the air sacs only as a later development. The humerus appears to be the most completely pneumatized bone in the skeleton (McLeod and Wagers, 1939). The vertebrae, from the third cervical to the fifth thoracic, and some ribs, are pneumatized by the cervical air sac (Chauveau, 1891; King, 1956; King and Kelly, 1956; King 1957; Akester, 1960). The sternum, humerus, coracoid, clavicle, scapula and sternal ribs are pneumatized by the interclavicular air sac (Chauveau, 1891; King, 1956; Akester, 1960). The posterior thoracic vertebrae, lumbar vertebrae, coccygeal vertebrae, pelvic bones, ilium and femur are pneumatized by the abdominal air sac (Chauveau, 1891; McLeod and Wagers, 1939; King, 1956; Akester, 1960; Bradley and Grahame, 1960). Lucas (1960) distinguished the chicken from the pheasant by means of a femoral diverticulum, which enters the bone in the latter only. The only bones that are pneumatized in the chicken are the cervical vertebrae, except the atlas and axis; the thoracic vertebrae, except the fifth; the lumbosacral mass; the pelvic girdle; the first two vertebral ribs; the sternum; the humerus and the coracoid (King, 1957; Lucas and Denington, 1961a, b).

Turkey - The infiltration of the bones by the air sacs in the turkey was described by Cover (1953). The interclavicular air sac pneumatizes the sternum and the humerus. The pelvic bones are infiltrated from the abdominal air sacs, which also surround the hip joints, but do not enter the femurs. Other bones, which are pneumatized in the turkey, are the cervical, thoracic, lumbar and sacral vertebrae and the ribs.

Other Birds - Specific and General - The loon, the kiwi and the penguin have no pneumatization of the bones at all (Gier, 1952; Weichert, 1953; Goodrich, 1958). On the other hand, in the frigate-bird all bones are pneumatic, down to the metatarsals (Goodrich, 1958). The anterior and posterior thoracic air sacs do not pneumatize any bones (Martin and Schauder, 1923).

The Lungs and Bronchi

Duck - The lungs of ducks are very large as compared to those of other birds (Lucas, 1960). They are about twice as long as wide (Groebbels, 1932). They are thick, while their lateral edges are flattened, and they do not lie in a pleural cavity (Dobi, 1942). The trachea divides into two primary bronchi, which enter the lungs, traverse the lung parenchyma and terminate in the abdominal air sacs (Akester, 1960). According to Vos (1934) and Delphia (1959) the primary bronchus widens into a vestibulum after entering the lung. Akester (1960) denied this. Posteriorly the primary bronchus diminishes in size, but remains larger than the parabronchi (Akester, 1960). A number of secondary bronchi branch off from the primary bronchus. The anterior and posterior groups of secondary bronchi are separated by a short area which has no connections (Akester, 1960). It is in this area, according to Vos (1934), that "the existence of a muscular valve is fairly evident from the anatomy, and was confirmed by injection experiments." No other author agreed with this. Three groups of secondary bronchi are recognized which are given diverse names. The anteriormost group, called ventrobronchi (Vos, 1934), anterior dorsal secondary bronchi (Akester, 1960) or entobronchi (Delphia, 1959) are four in number and send branches to the medial and ventral surfaces of the lung. Their openings are strengthened by cartilage. The most prominent of the posterior groups is the one called dorsobronchi (Vos, 1934), posterior dorsal secondary bronchi (Akester, 1960) or ectobronchi (Delphia, 1959). The number reported varies between 7 and 9. They send branches to the dorsal, medial and lateral surfaces of the lung. Akester (1960) reported that one of these leads to the ventral surface of the lung. The third group consists of the laterobronchi (Vos, 1934), posterior ventral secondary bronchi (Akester, 1960) or lateroventrobronchi (Delphia, 1959). Their number ranges from three to many. They supply the lateral periphery of the lung. Many parabronchi are said to come off the primary bronchus in its posterior part (Vos, 1934). The secondary bronchi supply air not only to the respiratory surfaces of the lung, but also to the air sacs. The cervical air sac is supplied by ventromedial bronchus 1, the interclavicular by 1 and 2, the anterior thoracic air sac by the third, the posterior thoracic air sac by the third laterobronchus, while the abdominal is supplied by the terminal end of the primary bronchus (Vos, 1934; Delphia, 1958; Akester, 1960). The bulk of each lung is made up of the tertiary bronchial arcades which link together the anterior and posterior groups of secondary bronchi (Akester, 1960).

The saccobronchi, which are small air tubules of the same size as the parabronchi, are secondary connections of the air sacs with the lung parenchyma. Most authors (Locy and Larsell, 1916; Goodrich, 1958) agree that they are outgrowths from the air sacs which have grown into the lung tissue and have then connected with parabronchi. Delphia (1958) disagreed with this and posed that these "auxilliary connections grow from the lungs to the air sacs."

<u>Chicken</u> - The lungs of the chicken are small and are semi-elliptical in shape (Chauveau, 1891). They do not lie in a pleural cavity (Dobi, 1942), but dorsally are firmly attached to the ribs. They lie along the spine, from the second dorsal vertebra to the anterior end of the kidney (Kaupp, 1918), or from rib 1 to 6. The ventral surface relates to the diaphragm. Dorsally four costal grooves are visible (Chauveau, 1891; McLeod and Wagers, 1939; Graham, 1939).

Most authors agreed that there is a vestibule in the primary bronchus of the lung of the chicken (Marcus, 1937; McLeod and Wagers, 1939; Sisson and Grossman, 1953; Bradley and Grahame, 1960). However, Payne and King (1959) concluded from their studies that "the classical vestibule is not present in this species." The primary bronchus enters the ventral surface of the lung, courses through the lung and ends in the abdominal air sac (Zeuthen, 1942; Sisson and Grossman, 1953; Trautmann and Fiebiger, 1952). Lucas and Stettenheim (1964) described it as "S"-shaped. The secondary bronchi have been studied and described by many investigators (Chauveau, 1891; Kaupp, 1918; Marcus, 1937; McLeod and Wagers, 1939; King, 1956; Payne and King, 1960). Their findings agreed in general but not in detail. Usually four groups have been described: 4 ventromedials, which supply the ventral surface of the lung; 6 to 10 dorsomedials, which supply the dorsal surface; 6 to 8 laterals, which supply the lateral margin; and 20 to 40 dorsals, which are very small. Those who do not describe any laterals or dorsals indicate the presence of one tubule (Chauveau, 1891; Kaupp, 1918). This is apparently one of the laterals, described by others, leading to the posterior thoracic air sacs.

The parabronchi have the same function in the chicken as in the duck. Again, saccobronchi have been observed, which do not appear to differ from those in the duck. Each sac, except the cervical, connects with about five saccobronchi to the lung (King, 1956). Graham (1939) reported saccobronchi from all air sacs. Bradley and Grahame (1960) described the parabronchi and the innumerable air capillaries which branch from them. He also noted the air capillaries directly adjacent to the blood capillaries for the establishment of gas exchange between air and blood.

Turkey - Very little research has been done on the anatomy of the lungs and air passages of the turkey. Cover (1953) mentioned that it is much the same as in the chicken. He indicated that the anterior thoracic air sacs are supplied by a ventrobronchus, the posterior thoracic air sacs by a dorsobronchus and the abdominal air sacs by a confluence of 20 to 30 parabronchi. Malewitz and Calhoun (1958) made brief mention of the gross architecture of the lung.

Other Birds - Specific and General - The lungs of birds are inelastic, small, do not fill the thoracic cavity, are fused with the ribs and dorsal wall, and are connected with the thoracic wall by means of connective tissue. They reach from the first rib to the kidney, and ventrally are related to the diaphragm (Grober, 1899; Martin and Schauder, 1923; Goodrich, 1958). The primary bronchus, after entering the lung, is said to widen into a vestibulum, then to constrict posteriorly and to terminate in the abdominal air sac (Victorow, 1909; Groebbels, 1932; Hazelhoff, 1951; Marshall, 1960). Pettingill (1961) stated that a "complicated valvular system" is present, but did not describe it. The secondary bronchi have been described by several authors (Victorow, 1909; Groebbels, 1932; Hazelhoff, 1951; Goodrich, 1958; Marshall, 1960; Delphia, 1961) for different species, and a general pattern was observed by all. Again, the ventrobronchi are 4 to 8, the dorsobronchi 6 to 10, the laterobronchi 6 to 9, and the dorsolaterals 7 to 9.

The cervical air sac is always supplied by ventrobronchus 1, sometimes by 2 and 3 as well. The interclavicular air sac is supplied by the first and third ventrobronchus, and by the second or by dorsobronchus 1. The anterior thoracic air sacs may be supplied by the third and fourth ventrobronchus, and by several others, three connections not being uncommon. The posterior thoracic air sacs are usually supplied by the third laterobronchus. The abdominal air sac is said to be supplied by the primary bronchus and by several saccobronchi (Victorow, 1909; Groebbels, 1932; Hazelhoff, 1951; Marshall, 1960;

Delphia, 1961; Pettingill, 1961). The description of the parabronchi did not differ from that given for the duck or the chicken. Saccobronchi are lacking only in the case of the cervical air sac (Groebbels, 1932; Marshall, 1960; Pettingill, 1961).

The Pleura

Duck - The duck has a thin pleura. The lung is bound to the chest wall by fibrous adhesions and small muscles. The latter are fanshaped and extend from the ribs to the pleura (Rigdon, 1959). The pleura covers the lung surface as a tender membrane, but is lacking at the junction of the lung and the pulmonary diaphragm (Groebbels, 1932).

Chicken - McLeod and Wagers (1939) described a thin membrane, resembling a pleura, which covers the lungs and lines the thoracic cavity. The lung is separated from the diaphragm and the costal wall by alveolar connective tissue, which is very delicate. Bradley and Grahame (1960) only mentioned that the ventral surface of the lung is covered by pleura. Pleura and pleural cavity are completely lacking according to Ellenberger and Baum (1943), and are simply replaced by connective tissue.

Turkey - No mention has been made of a pleura in the studies on turkeys.

Other Birds - General and Specific - The pleura covers only the ventral side of the lungs, according to Pettingill (1961). Marshall (1960) found the whole lung covered by a thin pleura, and attached to the thoracic wall and the pulmonary diaphragm by thin strands of connective tissue. Martin (1923) reported the visceral and parietal pleura fused along the ribs. Hyman (1947) described both pleura and pleural cavity in the pigeon. Krölling and Grau (1960) on the other hand maintained that birds have no pleura, but a connective tissue attachment of the lung parenchyma to the body wall and diaphragm. Makowski (1938) noted that the lung is fused with the thoracic wall.

The Diaphragm

Duck - Ventrally the lung is covered by a frail, transparent membrane, the diaphragm, which has muscle fibers present at its edges (Vos, 1934). Rigdon (1959) stated that "there is no muscular diaphragm separating the lungs from the abdominal viscera only a thin membrane" (sic). He still called this fibrous membrane a diaphragm. Babak (1921) showed a diagram of a thoraco-abdominal diaphragm, separating the thoracic air sacs from the viscera. He did not discuss it.

Chicken - Kaupp (1918) mentioned a diaphragm, which separates the posterior thoracic air sacs from the abdominal air sacs. He also mentioned a "fibrous septum," which in all birds divides the abdominal cavity into an anterior part, containing the liver, and a posterior part, containing the gizzard and intestines. Ellenberger and Baum (1943), Sisson and Grossman (1953), Bradley and Grahame (1960) and Krölling and Grau (1960) mentioned the rudimentary and largely tendinous diaphragm, which covers the ventral surface of the lung. McLeod and Wagers (1939) described two distinct diaphragms: the pulmonary and the thoraco-abdominal. They described the pulmonary diaphragm as a horizontal sheet, dividing the thoracic cavity into dorsal and ventral parts. It has a narrow fleshy belly attaching to the ribs while the remainder is tendinous. Medially it is attached to the ventral crest of the thoracic vertebrae. The thoraco-abdominal diaphragm, also mentioned by Evans (1961), separates the thoracic and abdominal cavities, and encloses the thoracic air sacs. It is attached to the sternum, the ventral part of rib 7, all of rib 6 and the 6th thoracic vertebra, and is firmly fused with the pericardium. The dorsal part is fused with the posterior part of the pulmonary diaphragm. Kadono et al. (1963) stated: "As is well known, chickens lack diaphragm muscles."

Turkey - No description of the diaphragm in the turkey was found in the literature.

Other Birds - Specific and General - Although several authors (Soum, 1896; Babak, 1921; Martin and Schauder, 1923; Hazelhoff, 1951; Weichert, 1953; Sturkie, 1954; Pettingill, 1961) cursorily mentioned or incompletely described the diaphragms, a fairly good description has been given by both Groebbels (1932) and Marshall (1960). Marshall's account was particularly eloquent in describing the relative position of the two diaphragms. He likened them to two roofs, one above the other, both having the same ridgepole. The ridgepole is the ventral surface of the vertebral column. The dorsal one is the pulmonary diaphragm, which stretches from the dorsal midline to the lateral walls of the thorax to which they connect by means of the Mm. costopulmonales. The ventral roof is the abdominal diaphragm, which stretches from the same dorsal midline to the lateral margins of the sternum and reaches posteriorly to the synsacrum. This diaphragm represents the "oblique septum," which has split into two layers. Between these two layers lie the anterior and posterior thoracic air sacs which are separated from each other in most species by a septum. The pulmonary and abdominal diaphragms fuse together posteriorly. The pulmonary diaphragm consists of three layers: an outer, connective tissue layer, stemming from the pleura; a middle layer, which is a continuation of the Mm. costopulmonales; and a third layer, which is formed by the dorsal wall of the three adjacent air sacs (Groebbels, 1932). According to Rogers (1961) a rudimentary diaphragm separates the anterior and posterior thoracic air sacs.

B. Histology of the Air Passages and Air Sacs

Duck - Dobi (1942) and Rigdon (1959) described the respiratory passages. The trachea and extrapulmonary bronchi contain a mucosa, under which lie cartilaginous rings and a connective tissue layer containing muscle fibers. Lining the mucosa is a ciliated pseudostratified epithelial layer, containing many goblet cells. The folded, lymphocyte-laden mucosa has no muscularis mucosae. The intrapulmonary bronchus and the secondary bronchi are similar to the extrapulmonary bronchus, but the mucosa loses its folds, and the muscle layer diminishes gradually until it reaches the parabronchi. While the parabronchi are lined with squamous epithelial cells, they have membranous partitions made up of collagenous and elastic connective tissue, with smooth muscle at their edges. The terminal dilatations of the parabronchi at the periphery of the lung show a muscle layer, and an areolar connective tissue stroma. Although lymph channels, a few fibroblasts and small amounts of fat have been found in this area, no lymph nodes have been observed. Air capillaries, which are intimately related to the blood capillaries, extend from the lumen of the parabronchi. They are lined with large, flat, respiratory epithelial cells, under which a very thin elastic network is found. Except for Akester's (1960) indication of the poor blood supply to the air sac walls, no further observations on the latter have been found.

Chicken - The histology of the chicken lungs and air passages has received little attention. Dobi (1942) found many glands surrounding the extrapulmonary bronchus. Bradley and Grahame (1960) found no evidence of elastic fibers in the lung septa. De Groodt et al. (1960), through the use of the electron microscope found a continuous layer of cells lining the alveoli, the cytoplasmic layer of which is so thin as to make it look discontinuous, thus disproving the contention of Trautmann and Fiebiger (1952) that there is no continuous respiratory epithelium.

More attention has been paid to the walls of the chicken air sacs. Many authors have described two layers in the air sac wall; an outer serous and an inner mucous membrane, with a thin connective tissue layer between them (Chauveau, 1891; Kaupp, 1918; McLeod and Wagers, 1939; Cover, 1953; Sisson and Grossman, 1953; Bradley and Grahame, 1960; Angulo, 1961; Lucas and Denington, 1961a, b). Elastic fibers have been noted by some (Chauveau, 1891; Cover, 1953; Lucas and Denington, 1961a, b; Rogers, 1961).

The external epithelium of the air sac wall is a very thin layer of flat cells of the mesothelial type. The internal epithelium is largely a simple flat type but is different from the external eptithelium; the cells are larger, nearly cubical and their cytoplasm contains granular mitochondria. Their nuclei are longer, smaller and more chromatic. Where the epithelium joins the bronchial tree it changes to a ciliated, cylindricated, pseudostratified respiratory type containing mucous cells. This epithelium rests on a delicate basal membrane (Angulo, 1961). Lucas and Denington (1961a, b) noted that in the abdominal sac the cells on the "endodermal" side are smaller than those of the peritoneal side, and that the endodermal derived cells of the thoracic air sacs may be ciliated and include goblet cells. Trautmann and Fiebiger (1952) also indicated simple ciliated columnar or cuboidal epithelium lining the air sacs. According to Rogers (1961) no mucous glands are present.

The air sac walls are poorly vascularized, with long, thin blood vessels which belong to the systemic circulation rather than the pulmonary (Chauveau, 1891; Kaupp, 1918, Cover, 1953). In contrast to the above, Angulo (1961) stated that the membrane of the air sacs has an important vascularization. No lymphatics have been found (Chauveau, 1891; Kaupp, 1918). Lucas and Denington (1961a, b) noted that the abdominal air sacs are vascularized only in part and described the layers in the vascular and avascular parts, both with and without reaction tissue.

Turkey - Cover (1953), Malewitz (1956), and Malewitz and Calhoun (1958) described the air passages and lungs of the turkey. The mesobronchus is lined with ciliated columnar epithelium, below which are areolar connective tissue, elastic fibers and smooth muscle. The lining of the secondary bronchi is similar to that of the mesobronchus, but reduced in height. Cuboidal or simple squamous epithelium lines the parabronchi. As the air passages diminish in size their lining becomes steadily thinner until it becomes indistinguishable.

The air sacs were described by Cover (1953). They consist of three layers: the inner epithelial lining, a connective tissue layer and the outer epithelial covering. Near the lung the epithelial lining is simple ciliated columnar, but distally is simple squamous. The connective tissue is mostly elastic, while the outer epithelial covering is simple squamous.

Other Birds - Specific and General - Marshall (1960) discussed the histology of the air passages and described the epithelial lining of the entire primary bronchus as pseudostratified, with simple alveolar mucous glands and goblet cells. The lamina propria has lymph nodules, and the adventitia consists of connective tissue and longitudinal smooth muscle fibers. The secondary bronchus is much like the primary, but has ciliated simple columnar epithelium, while the smooth muscle fibers are arranged circularly here. Krölling and Grau (1960) found the cartilage rings ending at the vestibulum.

Several authors mentioned the air sac wall, and named the serosa and mucosa as their component parts (Victorow, 1909; Martin and Schauder, 1923; Ellenberger and Baum, 1943). Gilbert (1939) and Marshall

(1960) described a fibrous connective tissue layer in addition to these. Lining the mucosa is the epithelium, which is squamous where the wall is free, but simple columnar where it attaches to surrounding structures. According to Gilbert (1939) cilia are present throughout the air sac, except inside the bones. That the vascularization of the air sacs is insignificant has been mentioned by Victorow (1909), Winterstein (1921), Ellenberger and Baum (1943), Hazelhoff (1951), Weichert (1953) and Marshall (1960). Winterstein, Hazelhoff and Weichert explained that the blood supply of the air sacs is not from pulmonary but from systemic vessels.

METHODS AND MATERIALS

For the gross anatomical studies five male and five female White Peking Ducks were obtained from the Tulip City Duck Farm, Holland, Michigan. They were all nearly one year old, weighed approximately 8 lbs, and were prepared for study as follows:

M1 injected with latex and corroded
M2 injected with latex and corroded
M3 injected with latex and macerated
M4 injected with latex and embalmed
M5 embalmed
F1 mounted skeleton, by boiling
F2 injected with latex and corroded
F3 injected with latex and corroded
F4 injected with latex and corroded
F5 embalmed
M = male, F = female

The ducks were killed by an intramuscular injection of pentobarbital sodium. The latex preparations were made by injecting 650 to 850 ml of latex through the trachea, and immersing the animals in concentrated hydrochloric acid until all tissues were corroded. The resultant casts of the respiratory system were then rinsed, degreased and dried. The embalming was done by injecting 100 to 175 ml of 6% formalin through the carotid artery. To show the relationship of the latex cast of the respiratory system to the skeleton, one of the latexed ducks was immersed in water at room temperature and left until the decomposition of the soft tissues was complete.

For the histologic studies 2 male and 3 female White Peking Ducks were purchased from the same source as above. They were killed with pentobarbital sodium and embalmed with about 200 ml of a saturated mercury fixative. All sections were taken from the left side (fig. 1), unless otherwise indicated, and fixed in saturated mercury fixative for three days. Sections containing bone were decalcified. All sections were rinsed in running tap water for 8 hours and stored in 70% alcohol. They were dehydrated in an ascending series of alcohols, cleared in xylol and imbedded in Paraplast.* Most sections were cut at 7 micra and stained with Harris' hematoxylin and eosin and with Weigert and Van Gieson's stain.

Three female ducks $2\frac{1}{2}$ months of age were used to ascertain the gross and microscopic relationship of the lung parenchyma and the body wall.

The extent of the cartilaginous rings into the lung was confirmed by staining in methyl green, dissecting out the bronchi under the dissecting microscope and clearing in a 1:1 mixture of benzene and benzyl-benzoate.

All gross measurements were made to the nearest millimeter and, because of the relatively low number of specimens, ranges of measurements are given in rounded figures.

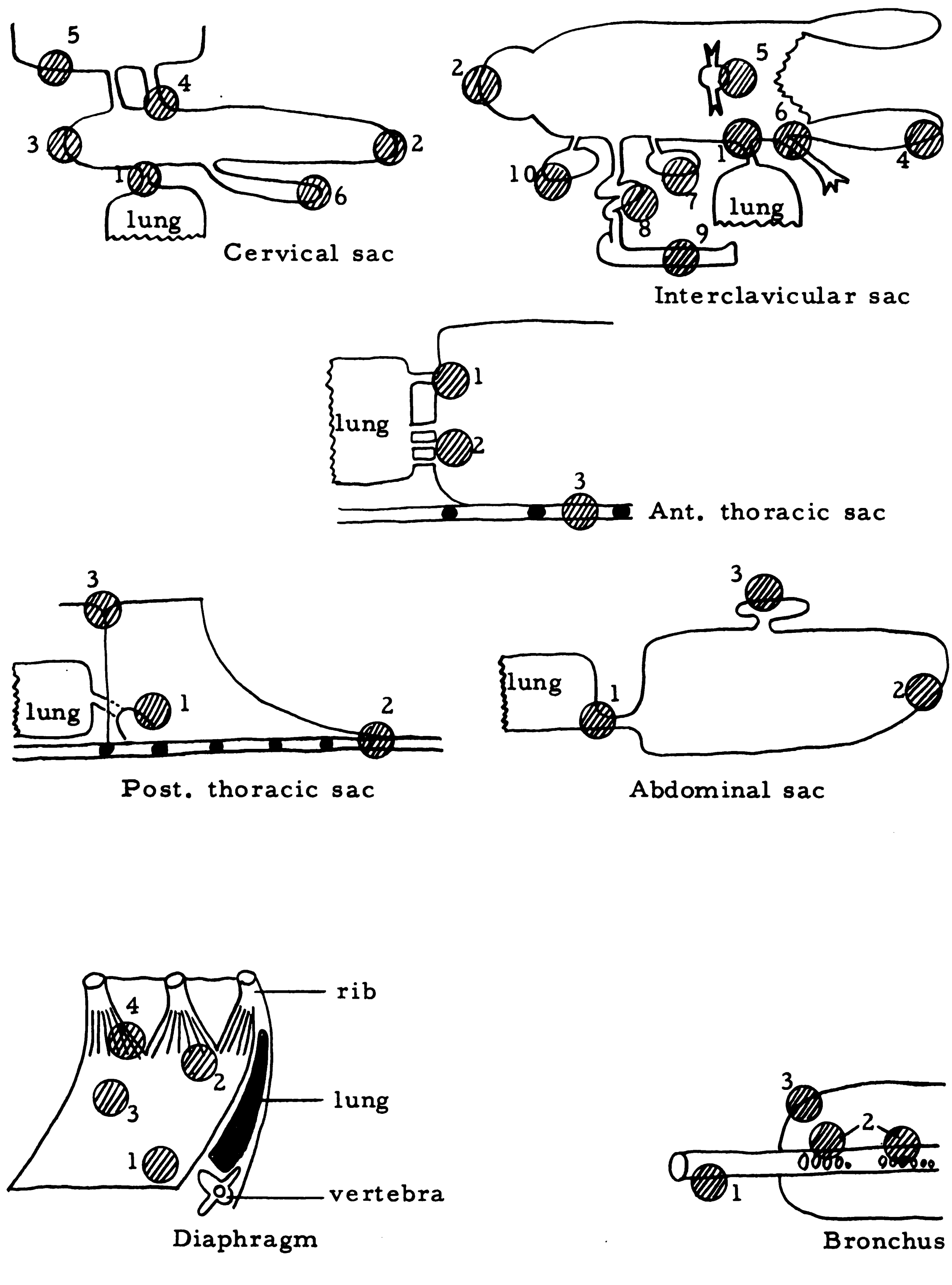
---

*Biological Research, Inc., St. Louis 3, Mo.

Fig. 1.

Section	Location
C1	Cervical sac at or near ostium
C2R	Cervical sac at posterior tip, right side
C2L	Cervical sac at posterior tip, left side
C3	Cervical sac at anterior tip
C4	Cervical sac at ostium of cervical vertebral diverticulum
C5	Cervical sac through lateral cervical pouch
C6	Cervical sac at tip of costal diverticulum
I1	Interclavicular sac at saccobronchial connection with lung
I2	Interclavicular sac at anterior tip, with furcular ligament
I4	Interclavicular sac at posterior tip of postcardiac diverticulum
I5	Interclavicular sac through medial sternal diverticulum
I6	Interclavicular sac through lateral sternal diverticulum
I7	Interclavicular sac through dorsal diverticulum
I8	Interclavicular sac through extrahumeral diverticulum with muscle
I9	Interclavicular sac through central part of humeral shaft
I10	Interclavicular sac at distal end of pectoral pouch
TA1	Ant. thoracic sac at or near ostium of dorsomediobronchus 3
TA2	Ant. thoracic sac at saccobronchial connection
TA3	Ant. thoracic sac with thoracic wall between ribs 4 and 5
TP1	Post. thoracic sac at ostium of laterobronchus 2
TP2	Post. thoracic sac with abdominal wall at rib 9
TP3	Post. thoracic sac at medial TA/TP junction
A1	Abdominal sac at ostium
A2	Abdominal sac at posterior tip
A3	Abdominal sac through suprarenal diverticulum, with kidney
S1	Synsacral sac through intertransverse fossa (not shown)
Z1	Diaphragm at midline
Z2	Diaphragm with *Mm. pulmocostales*
Z3	Diaphragm longitudinal section
Z4	Diaphragm with lung and thoracic wall
P1	Extrapulmonary bronchus, longitudinal and cross-section
P2	Intrapulmonary bronchus, with secondary bronchial connections
P3	Apex of lung, cross-section

Fig. 1. Diagram indicating the location of the histologic sections in each air sac and diverticulum.



RESULTS

A. Gross Anatomy

The Air Sacs

In the White Peking Duck there are eleven air sacs: four paired and three single. The paired ones are, from anterior to posterior, the cervical, the anterior thoracic, the posterior thoracic and the abdominal air sacs; the single, median sacs are the interclavicular, dorsal and synsacral air sacs (fig. 7, 8 and 9).

Near the thoracic inlet are the cervical air sacs which lie dorsally and send extensive diverticula into the cervical vertebrae. The interclavicular air sac lies ventrally near the thoracic inlet and has many diverticula. The latter surround the pectoral muscles and the heart, and penetrate the humerus and the sternum. The anterior thoracic air sacs lie laterally, touching the thoracic wall from the second to the fifth rib. Just behind the anterior thoracic air sacs are the posterior thoracic air sacs which touch the body wall from the fifth rib nearly to the pubic bone. The abdominal air sacs lie in the abdominal cavity between the posterior margin of the lung and the caudal extreme of the abdominal cavity.

For the sake of clarity an air sac must be distinguished from a diverticulum. Whereas an air sac is supplied with air from the lungs directly, a diverticulum receives its air from an air sac. The opening through which the air is supplied is the ostium.

The Cervical Air Sacs

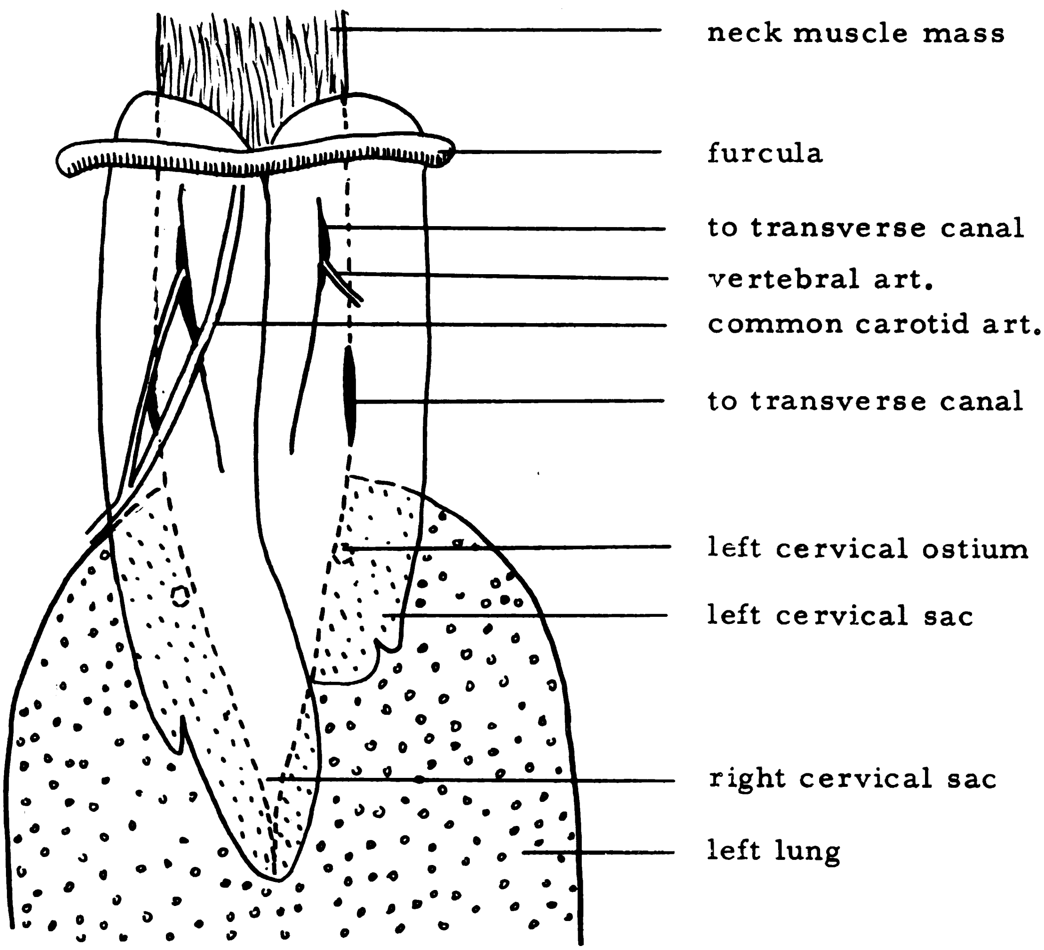
The cervical air sacs lie ventral to the neck muscle mass and the anterior half of the lung (fig. 2). The longer right cervical air sac is 110 mm long, and the left one 80 mm. Their anterior limit is 10 mm anterior to the furcula. The posterior limit of the right cervical air sac is at the point where the *Mm. longus colli* attach to the ventral spine of the fifth thoracic vertebra, 25 mm caudal to the hilus of the lung. That of the left cervical air sac is 10 mm anterior to the hilus. The right and left cervical sacs meet and interlock along the midline from the furcula to the anterior border of the lung. Posterior to this point the right one crosses the midline and lies about 8 mm to the left of the median plane (fig. 11).

The cervical air sacs are bounded ventrally by the interclavicular air sac and by the esophagus and laterally by the skin of the neck. The cervical ostium is located in the middle of the caudal one third of the dorsal surface of each sac, about 4.5 mm from the apex of the lungs. The left cervical ostium lies a few millimeters more anterior than the right.

The cervical air sacs are traversed by two arteries (Adams, 1958). The common carotid arteries enter the lumen of the air sacs from the lateral side and immediately give off the vertebral arteries. The common carotids course anteriorly, and, as they leave the cervical air sac and enter the neck muscle mass along the ventral surface of the cervical vertebrae, are separated from each other by a few millimeters. The vertebral arteries enter the neck muscle mass laterally alongside the brachial plexus and vertebral diverticulum of the cervical air sacs.

The cervical air sacs on each side give rise to the cervical vertebral diverticula, which enter the vertebral column between the 14th and 15th cervical vertebrae, and between the latter and the 1st thoracic vertebra. From these cervical diverticula all cervical

Fig. 2. Sketch of cervical air sacs - ventral view.

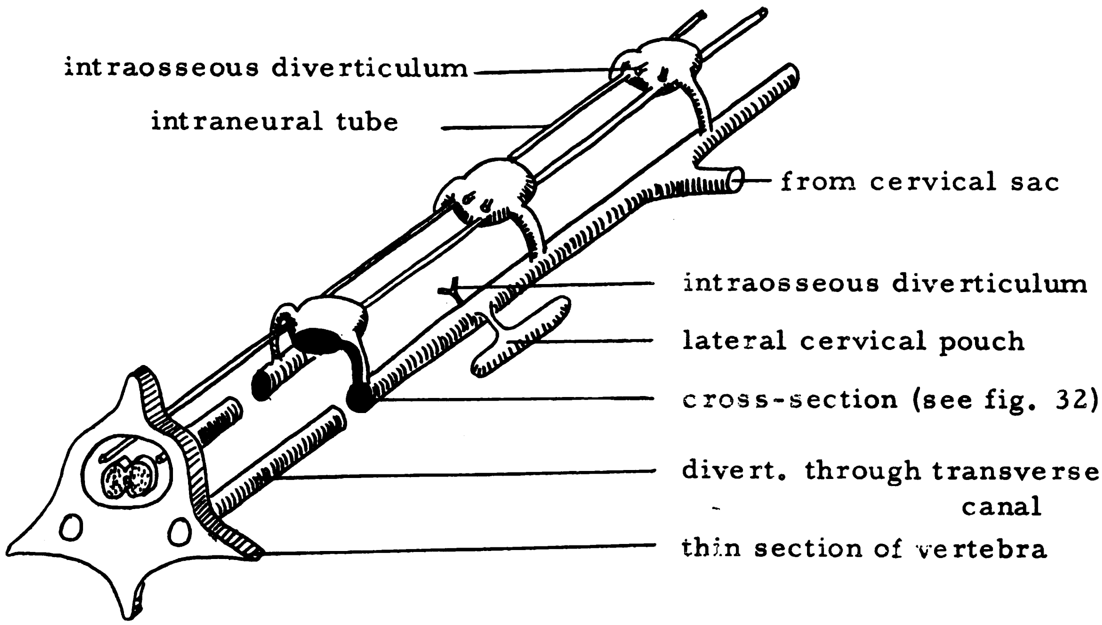


vertebrae, from the 3rd to the 15th, are pneumatized. The first thoracic vertebra is pneumatized directly from the cervical air sacs. At the 14th and 15th cervical vertebrae the cervical diverticulum enters the transverse canal and courses through the latter anteriorly to the 3rd or 4th cervical vertebra. From the transverse canal three groups of diverticula are supplied: the lateral cervical pouches, the intraneural diverticula and the intraosseous diverticula (fig. 3).

The lateral cervical pouches are supplied through a lateral foramen in the middle of the transverse processes (fig. 22) of the 3rd through the 13th cervical vertebrae. Although there is no lateral foramen in the transverse process of the 14th cervical vertebra, a lateral pouch does come off the transverse canal at the intervertebral foramen. After the lateral cervical pouches leave the transverse canal they extend laterally and dorsally. Whereas most of the pouches are only a few millimeters long, usually two large ones, which may reach a length of 60 mm and a width of 20 mm, are present between the 9th and the 12th cervical vertebrae. They lie between the *Mm. biventer* and *semispinalis* (Chamberlain, 1943), and come to lie subcutaneously (fig. 3). They may meet each other dorsally at the median plane (fig. 20).

At each intervertebral foramen a branch of the cervical diverticulum enters from the transverse canal into the vertebral canal, to form the intraneural diverticula. As it does so, it forms a cushion around the intervertebral foramen. The extensions from the transverse canal from each side widen and meet to form a flat rounded space (fig. 3). This space lies immediately ventral to the dorsal membranous ligament, which spans the space between the vertebrae. These rounded spaces of successive vertebrae are connected with each other on both sides of the spinal cord by narrow communications, the intraneural tubes.

Fig. 3. Diagram of cervical vertebral diverticula.



The intraosseous diverticula invade the bone substance of the cervical vertebrae in three places. From the medial side of the transverse canal and from the vertebral canal the centrum and ventral spine are pneumatized through small foramina. These are evident from the 5th cervical vertebra to the 15th. Posteriorly the infiltration of both the centrum and the ventral spine becomes progressively more complete. The ventral spine of the 13th cervical vertebra is largest and shows the greatest amount of infiltration. The 13th, 14th and 15th cervical vertebrae have large lateral pneumatic fossae, posterior to the transverse processes. From these fossae a number of small foramina extend into the centra (fig. 4, 22).

The neural arch is pneumatized from the intraneural diverticulum. The posterior border of the neural arch has ventrally, on each side, a small fossa (fig. 4), which has several small foramina, through which the intraneural diverticulum enters the bone substance.

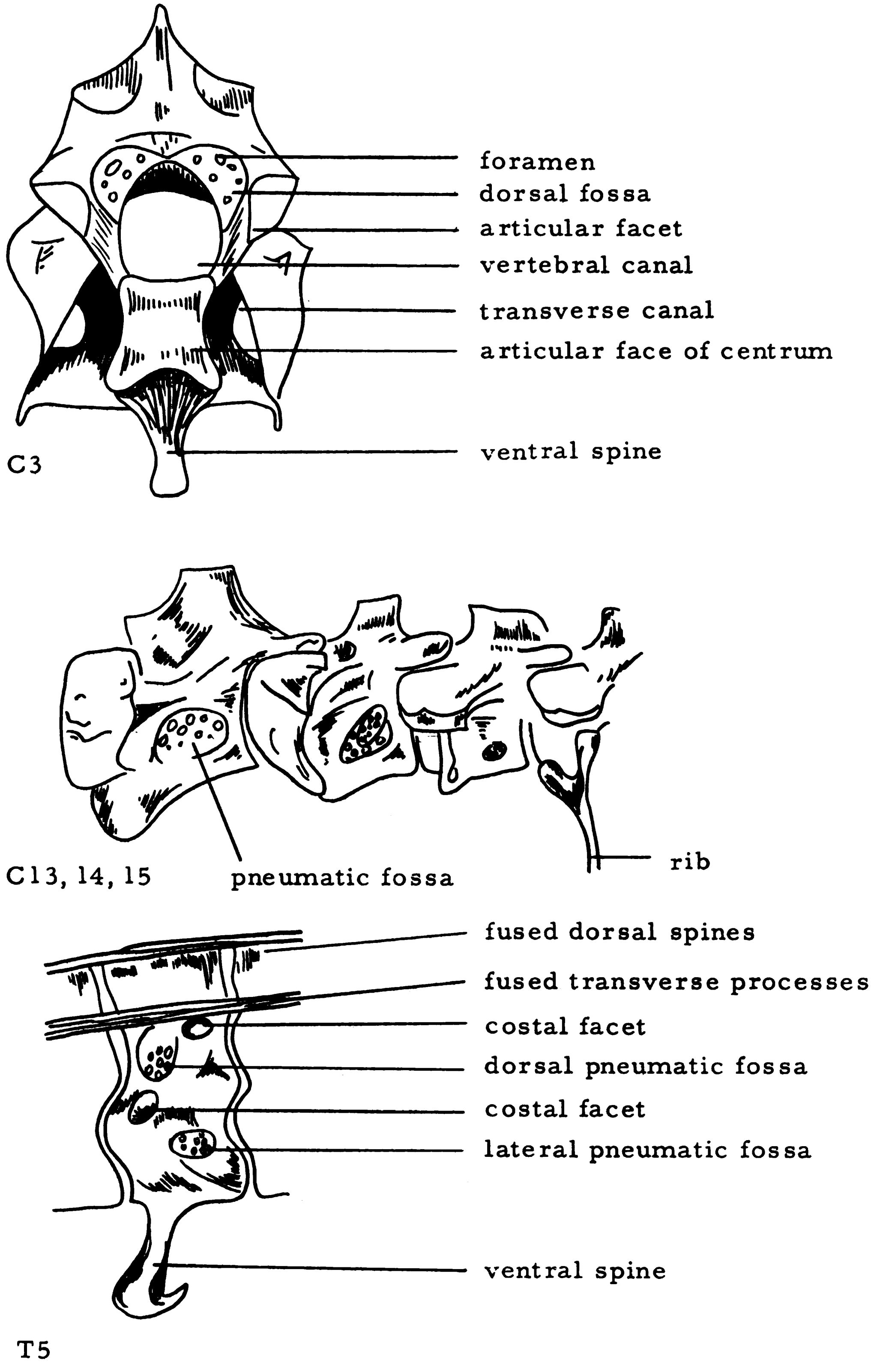
The costal diverticulum is given off from the cervical sac along the anterolateral border of the first vertebral rib. Its length ranges from 20 to 40 mm. It originates just caudal to the entrance of the cervical diverticula into the neck muscle mass.

The Interclavicular Air Sac

The interclavicular air sac is a single median structure, which has many diverticula extending between the surrounding structures and entering the adjacent bones. Its main divisions are the sac proper, the axillary diverticula, the postcardiac diverticula and the sternal diverticula.

The interclavicular sac proper extends from the furcula to the heart (fig. 10). Its anterior limit is the furcular ligament, which is found between the two clavicles and the neck muscle mass and may bulge

Fig. 4. Sketch indicating the pneumatic fossae of cervical vertebrae 3 and 13, 14, 15, and thoracic vertebra 5.



craniad up to 2 cm anterior to the furcula. Posteriorly it is limited by the atria of the heart, and reaches to the sterno-vertebral junction of rib 2. Dorsally it touches the esophagus and the cervical air sacs, sometimes partly enveloping the latter laterally. It extends to the axillae. Ventrally it is related to the coracoid bones, the sterno-coraco-clavicular ligament, and the sternum. Between the furcula and the sternum the interclavicular air sac is very flat and thin. Just ventral to the neck muscle mass it completely encloses the trachea, and in males the bulla tympaniformis as well. The caudalmost part of the interclavicular air sac proper lies dorsal to the sternum and anterior to the heart, surrounding the large blood vessels which enter and leave the heart. It is covered caudolaterally by part of the sternal ribs and surrounds the heads of sternal ribs 2 through 6 (fig. 9). Ventrally it is firmly attached to the sternum by means of connective tissue. It connects the interclavicular air sac with the lung passages at the lateral margin of the lung at the level of vertebral rib 2.

The axillary diverticulum is that section of the interclavicular air sac which is located in each axilla and surrounds the shoulder joint. It lies lateral to the coracoid bone and medioventral to the *M. pectoralis superficialis*. It is connected to the interclavicular air sac proper by means of a flat opening, which stretches from a few millimeters caudal to the point where the brachiocephalic artery leaves the thorax to a point about 30 mm anterior to it. In general it follows the lateral border of the coracoid bone. The axillary diverticulum consists of three major parts: the pectoral pouch, the humeral diverticulum and the dorsal division.

The pectoral pouch is easily located by severing the *M. pectoralis superficialis* from its origin and deflecting it laterally which exposes its ventral surface. Its ostium is located between the tendon of the *M. pectoralis profundus minor* and the coracoid bone where the latter is narrowest. Anteriorly it reaches to the anterior tip of the coracoid bone where the coraco-humeral ligament attaches. Its posterior limit is at the point where the brachial plexus and the subclavian artery leave the thorax. Laterally it is related to the coraco-humeral ligament and the M. pectoralis superficialis; medially to the M. pectoralis profundus minor and the coracoid bone. And dorsally it is limited by the humeral head, coraco-humeral joint and M. pectoralis profundus minor; ventrally by the M. pectoralis superficialis. The ventral limit does not extend past the coracoid bone. In transverse section the pectoral pouch is triangular. Its length ranges from approximately 40 to 60 mm.

The humeral diverticulum (fig. 7) lies between the body wall and the head of the humerus. It receives its air supply through an opening 13 to 15 mm wide, which lies medial to the center of the humeral head. Extrahumeral and intrahumeral parts can be distinguished. The extrahumeral part consists of a few "leaves" of diverticulum which fit between the muscles, medial to the head of the humerus. The most medial leaf folds around the outside of the scapula. Their greatest length ranges between 25 and 35 mm. From here a cylindrically shaped passage enters the pneumatic foramen of the humerus. From the pneumatic foramen many small foramina penetrate the bone. The intrahumeral diverticulum passes through these foramina and fills the spaces around the bony spicules of both epiphyseal ends of the humerus and the large spaces of the humeral shaft. The humerus is pneumatized completely from one end to the other (fig. 23).

The dorsal division branches off the interclavicular air sac just caudal to the humeral diverticulum. Its ostium is about 15 mm long. This diverticulum consists of several non-descript "leaves," with a total length of 25 to 40 mm. The caudal part may wrap partly around the subclavian artery. In some specimens another small, separate diverticulum comes off the interclavicular air sac, directly caudal to the dorsal division. It, too, may partly envelop the subclavian artery. Measurements of their lengths range from 15 to 25 mm.

The postcardiac diverticulum is the caudalmost extension of the interclavicular air sac on each side (fig. 8, 9). It lies between the sternum and the anterior thoracic air sac, the interclavicular air sac proper and the posterior thoracic air sac, the thoracic wall and the viscera. Covering the entire ventral surface of the anterior thoracic air sac, and extending under the ventral surface of the posterior air sac for about 25 mm, its caudal tip is visible through the ligament of the caudal sternal incision. Anteriorly it lies ventral to the caudal part of the interclavicular air sac proper. Ventrally it adheres closely to the sternum by means of connective tissue. Laterally it is related to the thoracic wall between vertebral ribs 3 and 5. And medially it is fused to the pericardium. Deep impressions of the sternocostal junctions of ribs 7 and 8 are visible on the lateral surface of the post-cardiac diverticulum. In transverse section the postcardiac diverticulum is triangular in shape, and its ostium lies anterodorsally, at the costosternal junction of rib 7. When well developed, the total length of the postcardiac diverticulum varies from 50 to 65 mm, and its width from 20 to 30 mm.

The sternal diverticula enter the sternum in three places: at the anterior end of the keel, and, on each side, at the costo-sternal junctions. The keel is pneumatized through a large pneumatic fossa (5-7 mm wide) on the dorsal surface of the sternum near its anterior tip (fig. 21). From this fossa many small foramina extend ventrally, laterally and anteriorly, through which the keel and the anterior margin of the sternum proper are pneumatized. The infiltrations extend about 20 mm into the bone. The sternum is invaded laterally by diverticula from the interclavicular air sac at the sterno-costal articulations. They may measure up to 45 mm.

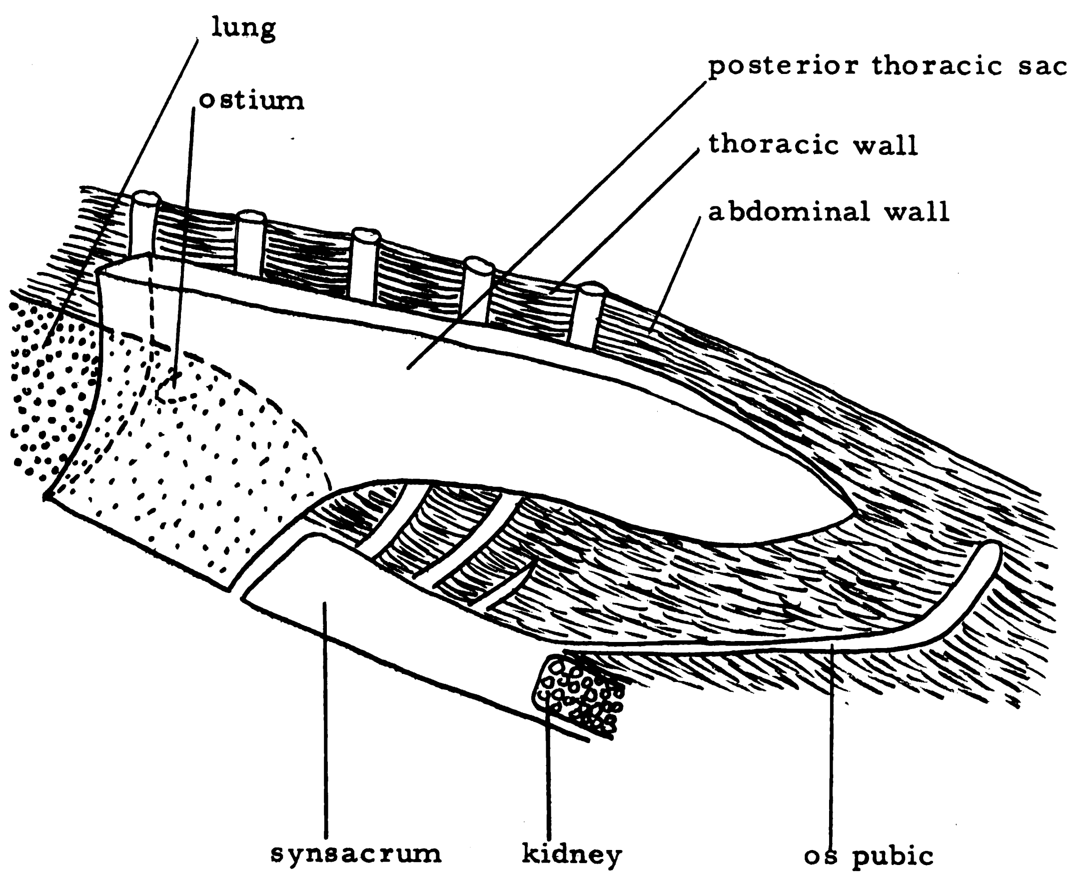
The Anterior Thoracic Air Sacs

The anterior thoracic air sacs lie against the thoracic wall, between vertebral ribs 2 and 5 (fig. 6, 9). Their anterior surfaces are related to the heart and to the interclavicular air sac. The posterior surfaces are related to the anterior surfaces of the posterior thoracic air sacs. Medially they touch the liver, heart and esophagus; dorsolaterally the lungs; laterally the ribs and the thoracic wall. Ventrally they are completely covered by the postcardiac diverticula of the interclavicular air sac, while dorsally they almost reach the median plane. At their anterodorsal border the anterior thoracic air sacs have two or more ostia, just caudal to the hilus of the lung. Occasionally a small diverticulum arises on the anterodorsomedial corner of the right anterior thoracic air sac.

The Posterior Thoracic Air Sacs

The posterior thoracic air sacs lie against the thoracic wall, between the anterior thoracic air sacs and the abdominal air sacs (fig. 9). Ventrally they border the sternum and part of them can be seen through the ligament of the caudal sternal incision; anteriorly, however, the postcardiac diverticula of the interclavicular air sac intervene between the sternum and the posterior thoracic air sacs. Dorsally they are related to the posterior part of the lungs where they nearly reach the median plane between vertebral ribs 5 and 7. Posterior to this they diverge up to 35 mm from the midline (fig. 5). Laterally they touch the thoracic wall from vertebral ribs 5 to 9, and the abdominal wall from the last rib to within 10 mm of the pubic bone.

Fig. 5. Diagram of left posterior thoracic air sac <u>in</u> <u>situ</u> - caudoventrolateral view.



At their caudal ends they taper to a point. Caudomedially they overlap the abdominal air sacs. Anteromedially they are related to the testes or left ovary. Their anterior surfaces match the posterior surfaces of the anterior thoracic air sacs. The left posterior thoracic air sac covers the lateral surface of the gizzard, and separates it from the body wall.

The ostia of the posterior thoracic air sacs are located at their anterolateral borders (fig. 5, 16), just medial to vertebral ribs 5 and connect to the lateral margins of the lungs.

Occasionally the posterior thoracic air sacs are double on one side, together assuming the same shape and relations as the single sacs in other specimens (fig. 8). Instead of a single ostium, medial to vertebral rib 5, there is an additional ostium, medial to vertebral rib 6, which supplies the posterior part of the split sac. There is no direct communication between the two halves.

The Abdominal Air Sacs

The abdominal air sacs lie mainly in the abdominal cavity and surround the intestinal mass. They reach anteriorly to the heart, sweeping around the testes or the left ovary. Posteriorly they extend to the very end of the abdominal cavity, the right sac being longer than the left. Dorsally they are related to the kidney and the vertebral column. Ventrally they lie against the abdominal wall. Laterally they lie against the abdominal wall and the anterior and posterior thoracic air sacs; medially against the testes of left ovary, and the intestines. They also touch each other medially but do not fuse (fig. 7, 8, 19). The gizzard makes a deep impression on the left abdominal air sac ventrolaterally. The ostia of the abdominal air sacs are at the caudolateral corners of the lungs, medial to ribs 7 (fig. 16). Just ventral to the ostia is the taut edge of the posterior thoracic air sacs.

The only diverticula from the abdominal air sacs are the suprarenal diverticula, which lie dorsal to the air sacs and partially surround the kidneys (fig. 7, 27). Their length ranges from 20 to 55 mm.

The Dorsal Air Sac

The dorsal vertebrae are pneumatized from the medial surfaces of the lungs (fig. 4, 7). Thoracic vertebrae 2 through 7 have lateral pneumatic fossae, similar to those described for cervical vertebrae 13 through 15, through which the air sacs enter and send diverticula into the centra of the vertebrae. In addition, thoracic vertebrae 3 through 7 have a dorsal pneumatic fossa, located anteriorly in the vertebra between the transverse process and the tubercular costal fovea. From the dorsal pneumatic fossa many small foramina penetrate the bone substance, and pneumatize the neural arch.

The Synsacral Air Sac

From the posterior dorsomedial corners of the lungs the synsacral air sac extends caudally, protrudes through the intertransverse foramina of the synsacrym and penetrates its bone substance. It extends back to the fifth intertransverse foramina (fig. 19, 20). Dorsally the synsacral sac gives rise to the iliac diverticulum which pneumatizes the ilium anteriorly.

Accessory Air Sacs

Extra sacs appear in unusual places in many of the ducks used in this study. In one specimen a sac was located between the left anterior thoracic air sac and the left cervical air sac. It measured 30 x 14 mm. Another, measuring 14 x 20 x 7 mm, lay between the right anterior and posterior thoracic air sacs. Frequently small sacs arise just medial to the hilus of the lungs, measuring up to 20 x 10 mm. These may be paired or unilateral.

The Air Passages

The trachea has thin, bony rings 3 mm wide and 12 to 14 mm in diameter, which interlock middorsally and midventrally. At the apex of the lung it bifurcates into two bronchi. At the bifurcation of the male trachea a 30 x 20 mm dilatation, the bulla tympaniformis, is located on the left side. Before entering the lung ventrally at the level of thoracic vertebra 5 the bronchi reach a length of 40 to 50 mm, and a diameter of about 9 mm. The cartilaginous rings of the extrapulmonary bronchi continue inside the lung past the opening of the last dorsomediobronchus.

Lying between vertebral ribs 1 and 8, the lungs present three surfaces: the dorsal, which lies against the costal wall and has deep impressions where it fits around the ribs (fig. 16); the ventral, which is covered by the diaphragm; and the medial, which lies against the lateral side of the thoracic vertebrae (fig. 15). From their apex to the ostium of the abdominal air sac the lungs measure 80 to 100 mm; at their greatest width they are 55 to 65 mm; and medially they are 15 to 20 mm thick.

After entering the lung substance, the primary bronchus courses posteriorly, giving rise to many secondary bronchi. Two major groups of secondary bronchi can be recognized: an anterior and a posterior, which are separated by a distance of about 10 mm.

The anterior group consists of five dorsomediobronchi, which in embalmed specimens have oval openings of 2 x 5 mm. The first dorsomediobronchus branches off the primary bronchus dorsomedially and immediately turns craniad and, through its many branches, supplies air to the ventral surface of the lung anterior to the hilus. From an anterior

branch (fig. 17) the cervical air sac is supplied. The second dorsomediobronchus branches off the primary bronchus dorsally and immediately turns mediad to supply the medial surface of the lung.
It sends a branch laterad to supply part of the lateral margin of the lung. The third arises dorsomedially from the primary bronchus and immediately turns ventromedial and bifurcates. Whereas its lateral branch arises near the hilus of the lung and supplies air to the anterior thoracic air sac, the medial branch supplies air to a triangular area caudomedial to the hilus. The fourth one arises dorsally, and turns caudad to supply air to the ventral surface of the lung in an area just lateral to that supplied by the third dorsomediobronchus. The fifth one is very small or sometimes lacking.

The posterior group consists of three groups of secondary bronchi: the laterobronchi, the dorsolaterobronchi and the dorsobronchi.

There are three large laterobronchi which arise on the lateral side of the primary bronchus (fig. 17). The first one supplies the lateral margin of the lung. The second extends caudolaterad and supplies air to the posterior thoracic air sac directly. And the third laterobronchus extends caudad, ventral to, and paralled with, the primary bronchus. It gives rise to many parabronchi which supply the caudolateral margin of the lung. Some of these form saccobronchial connections with the abdominal air sac.

The dorsolaterobronchi are smaller than the foregoing secondary bronchi. The first one has an opening of 1 x 2 mm, the second of 2 x 4 mm; from the third one on they gradually diminish in size until the seventh measures only 1 x 1 mm. Directed craniad the first connects with the first dorsomediobronchus to supply air to the ventral surface of the lung. All other dorsolaterobronchi open on the dorsal surface. Of these, the third and fourth supply the anteromedial part, and the fifth one a section medial to the hilus (fig. 16). The remaining ones supply the caudodorsal part of the lung. Their total number was not established.

The small dorsobronchi branch off the primary bronchus dorsally. No further study was made of them.

Branching off the secondary bronchi are the parabronchi, which constitute the bulk of the pulmonary parenchyma. Their lumina measure 0,5 mm or less. Small atria extend from the wall of the parabronchi and communicate with the air capillaries (fig. 28). The latter are small, dead-end passages which are interwoven with blood capillaries. Some secondary and many tertiary bronchi open into the parabronchial dilatations which cover the surfaces of the lungs. Proximally their lining is continuous with that of the bronchial tubes, while distally their outer surfaces become contiguous to resemble a membrane surrounding the lung (fig. 24). The saccobronchi connect the air sacs with the lung parenchyma.

The Connections With The Air Sacs

The cervical air sacs are supplied by means of an anterior branch of dorsomediobronchus 1 which leaves the lung substance about 10 mm from the apex of the lungs (fig. 17). There is no saccobronchial connection to these air sacs.

The interclavicular air sac is connected to the lungs only by means of a group of saccobronchi, which arise from an area immediately caudal to the caudalmost branch of dorsomediobronchus 1, and probably are supplied by dorsomediobronchus 1, the large lateral branch of dorsomediobronchus 2 and dorsolaterobronchus 2.

Just caudomedial to the hilus the lateral branch of dorsomediobronchus 3 brings air to the anterior thoracic air sacs. Caudolateral to the hilus is also a saccobronchial connection which penetrates the diaphragm in one or more location. This connection arises from the large lateral branch of dorsomediobronchus 2, dorsolaterobronchus 2 and a large lateral branch of dorsomediobronchus 4, immediately posterior to the saccobronchial connection of the interclavicular air sac.

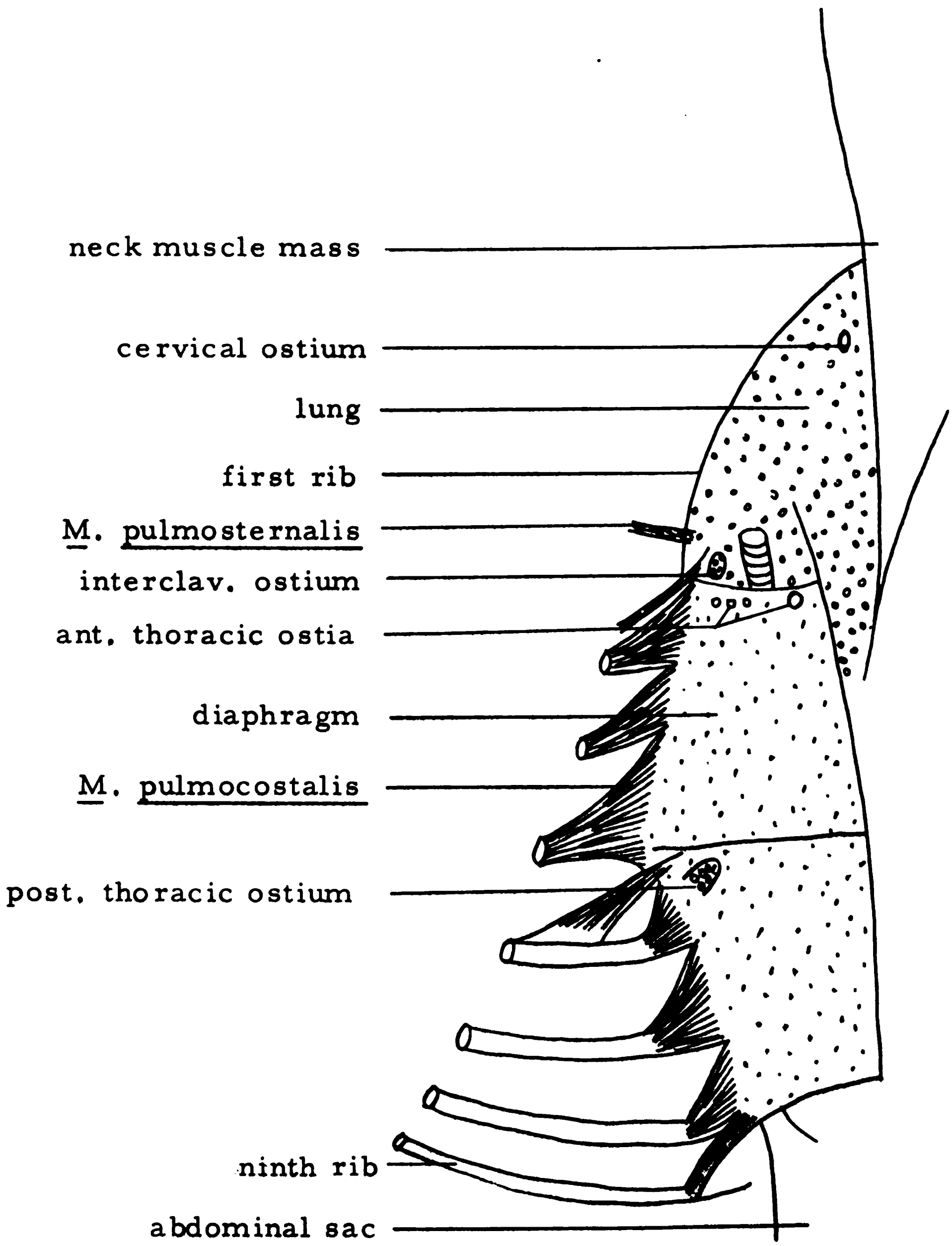
The posterior thoracic air sacs receive air from the second large laterobronchus and have a saccobronchial connection at the ostium of the laterobronchus.

The abdominal air sacs are supplied mainly by a large bronchus which extends along the dorsal surface of the lung (fig. 16). It appears to arise from parabronchi of the lateral margin of the lung and receives many other parabronchi before it reaches the abdominal air sac. As it enters the abdominal air sac this large bronchus is joined by a medium-sized bronchus which arises from parabronchi of dorsomediobronchus 4 at the lung's posterior margin. The primary bronchus probably contributes to this parabronchial mass.

The Diaphragm

The diaphragm stretches across the thorax in a frontal plane, covering the lungs ventrally from the hilus to the ninth rib. Medially it attaches to the ventral spines of the thoracic vertebrae. Laterally the small, fan-shaped *Mm. pulmocostales* attach the diaphragm to vertebral ribs 2 through 9 (fig. 6, 12). The one attached to rib 2 is very small and inserts just anterior to the ostium of the interclavicular air sac. Those attaching to vertebral ribs 3, 4 and 5 are the largest, reaching ventrad to the sternovertebral junction of the ribs. The *M. pulmocostalis* to vertebral rib 6 is divided into two parts. Its anterior part originates at the sternovertebral junction and inserts anterior to the ostium of the posterior thoracic air sac. The posterior part originates about 20 mm dorsal to the sternovertebral junction and has a broad insertion

Fig. 6. Sketch of diaphragm, indicating the <u>Mm</u>. <u>pulmocostales</u> - ventral view.



posterior to the ostium of the posterior thoracic air sac. The muscles which attach to vertebral ribs 7, 8 and 9 attach dorsal to the sterno-vertebral junction and diminish sharply in size, the last one being very small. The insertions of all _Mm. pulmocostales_ on the diaphragm are contiguous.

The small _M. pulmosternalis_ originates on the anterolateral corner of the sternum and inserts on the diaphragm just lateral to the insertion of the first _M. pulmocostalis_. It has a diameter of 4 mm and is about 14 mm long.

B. Histology

The Air Passages and Air Sacs

From the extrapulmonary bronchus to the proximal end of the secondary bronchi the epithelium is ciliated pseudostratified columnar, with goblet cells (fig. 25). In the secondary bronchi it changes from ciliated pseudostratified columnar near the primary bronchus to cuboidal with simple squamous or pseudostratified columnar patches at the ostia of the air sacs (fig. 26), and continues into and throughout the air sacs as chiefly simple squamous with some cuboidal epithelium (fig. 27). The saccobronchial ostia have cuboidal and squamous epithelium. Lining the parabronchi is a very thin, simple squamous epithelium, which also lines the atria and parabronchial dilatations (fig. 28).

The lamina propria consists of elastic and collagenous fibers which, though gradually diminishing in size, persist throughout the secondary and tertiary bronchial and air sac walls, but is not evident in the air capillaries or atria. It contains two vascular beds (fig. 25), the smaller of which lies directly under the epithelium, and extends from the extrapulmonary bronchus into the air sacs, although in the latter they are very sparse. The other network lies central to the elastic membrane as far as the last bronchial rings, and then continues central to the smooth muscle bands.

External to the lamina propria is an elastic connective tissue membrane in which the bronchial rings are enclosed (fig. 29). In addition there is an elastic connective tissue network in the walls of the parabronchial atria and air capillaries. The ventromedially incomplete rings are made of hyaline cartilage. A bronchial muscle connects their free ends, inserting on the outside of the elastic membrane, and also connects successive rings (fig. 29). The rings extend from the trachael carina to the first laterobronchus, and into the thin partitions separating the dorsomediobronchi where the latter branch off the intrapulmonary bronchus. Besides connecting the bronchial rings, smooth muscle bands also surround the walls of the posterior part of the intrapulmonary bronchus, the secondary bronchi and parabronchi, all air sac ostia, the parabronchial atria and their openings into the air capillaries, and the paràbronchial dilatations (fig. 28, 30). Sections from some specimens showed smooth muscle bands inside the air sac wall (fig. 31).

The adventitia of the extrapulmonary bronchus consists of areolar and adipose connective tissue.

The inside of the pneumatized bones is spongy, and those spaces between the trabeculae not filled with bone marrow are occupied by air spaces which connect with each other and with the air sacs (fig. 32, 33). Bridging the distance between trabeculae is a thin membrane which is continuous with the air sac outside the bone. Usually it hugs the bone closely, but sometimes is separated from it by connective tissue, fat or receding bone marrow. The membrane consists of thin, simple squamous epithelium, supported by a thin layer of elastic or collagenous connective tissue fibers, and is separated from the bone by the endosteum. Wherever the epithelium stretches between two trabeculae several blood vessels are present; alongside the bone they are fewer.

Bone marrow replacement is almost complete in the humerus. In the sternal diverticula, both lateral and medial, the pneumatization is greater proximally. Pneumatic foramina penetrate the carina and the horizontal lamina of the sternum. The lateral sternal diverticula are less extensive than the medial, and show more bone marrow in the trabecular spaces. The synsacral air sac pneumatizes the vertebral part of the synsacrum more completely than the ilia, and lines the intertransverse fossae.

The Diaphragm and Pleura

The tendinous part of the diaphragm consists of a strong collagenous tissue sheet, which ventrally is covered by air sac epithelium and dorsally adheres to the subjacent lung parenchyma by means of a few collagenous and elastic connective tissue fibers (fig. 30). Along the costal margin the striated *Mm. pulmocostales* insert on this tendinous sheet. Medially the diaphragm attaches to the ventral spine of the thoracic vertebrae by means of collagenous and elastic connective tissue fibers, which also anchor the aorta.

The lung parenchyma attaches to the diaphragm and to the body wall by means of connective tissue, without interpolation of a pleura or pleural cavity (fig. 34).

DISCUSSION AND CONCLUSIONS

Usually the White Peking Duck is considered to have nine air sacs, but since the dorsal and synsacral sacs are supplied directly by the lungs this brings the total to eleven, not counting the accessory sacs. In the domestic birds all cervical vertebrae, from the third caudad, are pneumatized but their caudal limit varies. Whereas in the chicken the cervical vertebral diverticula extend through the fifth thoracic, and in the turkey to the fourth coccygeal vertebra, in the duck they enter only the first thoracic, which is supplied directly from the air sac, not from the diverticula of the cervical vertebrae. The cervical vertebral pneumatization is extensive in many birds, but none appears as complicated as that of the White Peking Duck. The turkey has very large expansions at each intervertebral space, which cover most of the lateral surface of the vertebrae; these are restricted to a small expansion in the duck, immediately surrounding the intervertebral foramen. Only in the duck, so far as is known, is there a costal diverticulum extending along the first rib.

Although the interclavicular air sacs of birds differ in many details, partly due to their differences in size and structure, their general plan is strikingly similar. Although others have reported pneumatization of the ribs, in the duck as well as the chicken, the latex casts of these ducks showed only the heads of the ribs to be surrounded by latex. The subscapular diverticulum, described by many authors for different birds, is not very prominent in the White Peking Duck, but merely consists of a leaf from the extrahumeral diverticulum. The sternal diverticula are very prominent in the latex casts of the White Peking Duck, although they do not reach the same proportions as in the pigeon, where the entire sternum may be pneumatized. The pneumatization of the duck's humerus is quite complete in the one-year-olds, but in the three young females of $2\frac{1}{2}$ months they were filled with fatty marrow.

Repeatedly the statement has been made that the anterior thoracic air sacs have no diverticula. In the White Peking Duck, however, a small diverticulum occasionally arises; but no bones are ever pneumatized from this air sac. And the pigeon is said to have a diverticulum connecting the right and left sacs. The posterior thoracic air sacs are interesting in that they sometimes split and have separate connections with the lung for each compartment. A report of this phenomenon does not appear in the literature on any bird.

Rigdon (1959) described diverticula from the abdominal air sacs surrounding the head of the femur and entering the substance of this bone in the White Peking Duck. This was not evident from the present study. Akester observed a single duct as a major connection with the lung, at least three times as big as the parabronchi. Present observations, on the contrary, indicate that the primary bronchus diminishes in size until it is part of the parabronchial mass. From these and other parabronchi a new duct is then formed which corresponds to the one described by Akester, but is not a direct continuation of the primary bronchus. The latter relationship does seem to hold true for the chicken, however. Cover (1953) attests to the fact that in the turkey, too, this connection is not by the primary bronchus but by 20 - 30 parabronchi. The turkey is the only domestic bird which has diverticula from the abdominal sac supplying the vertebrae.

Although Rigdon (1959) noted that the thoracic vertebrae are infiltrated with latex in injected specimens, he did not point to the fact that they communicate directly with the medial parabronchi of the lung, in contrast to the chicken and the turkey where they are connected with the cervical vertebral diverticula. What he described as two latex-filled spaces of moderate size on each side of the midline in the area of the anterior portion of the lumbosacral vertebral mass, seems to correspond to the synsacral sac.

Rigdon's (1959) statement that the cervical and dorsal vertebrae, the sternum and the humerus are always pneumatized in all birds has at least some exceptions: the Swainson's thrush and robin do not show any pneumatization of the sternum or the humerus, and the common loon, kiwi and penguin have no pneumatization of any bones.

Akester (1960) rightly refuted the idea of Vos (1934) and Delphia (1959) that the primary bronchus has a widened part, the vestibule, for no widening occurs. Instead, the primary bronchus remains of equal diameter until caudally it sharply decreases in size and is lost in the caudal parabronchial mass. The secondary bronchi are separated into anterior and posterior groups by an area which has no connections, but the muscular valve which Vos said is located here, could not be shown. The anterior group is analogous to the ventro-mediobronchi in the chicken and turkey but, unlike them, arises from the primary bronchus dorsomedially, and therefore should be called dorsomediobronchi. Although usually four are described, a fifth one, much smaller than the other four, is often present caudally. Of the posterior groups only three laterobronchi and the first few dorsolatero-bronchi are prominent, the remaining ones being indistinguishable from the parabronchi, and therefore a detailed study of them is unprofitable. The pattern of distribution of the secondary bronchi is similar in most birds, the anterior group supplying air to the ventral surface of the lung, the posterior group to the lateral and dorsal surfaces.

Most difficulties in regard to the diaphragm of birds appear to revolve around the definition of the term. To compare all findings on a common basis, a diaphragm should be defined as "a musculo-membranous partition separating the lungs from the other viscera." These White Peking Ducks have a definite, strong diaphragm, membranous in the center and muscular at the edge. It is not nearly as frail as Vos (1934) indicated. Although Rigdon (1959) made the statement that there is no muscular diaphragm, but only a thin membrane, his ducks probably did have a good diaphragm, since he described small, fan-shaped muscles, extending from the ribs to the pleura. These seem to be identical to the *Mm. pulmocostales*, except that the latter do not insert on the pleura but on the tendinous diaphragm. The diaphragm in chickens is largely tendinous, but should not be called rudimentary, since it has developed completely and is functional. Even though Kadono *et al.* (1963) maintain that chickens lack diaphragm muscles, they can easily be shown to be present.

The question of whether or not a second diaphragm is present in birds is, again, largely a matter of definition of terms. The so-called thoraco-abdominal diaphragm, also called the oblique septum, is said to separate the thoracic from the abdominal cavity and to extend from the ventral spine of the thoracic vertebrae to the lateral edge of the sternum. It is said to be split into two layers, containing the anterior and posterior thoracic air sacs which are usually separated by a septum. This seems to indicate that the air sac structures are present in addition to the oblique septum. If this were true both should be demonstrable histologically. In the White Peking Duck this is not so: only the medial wall of the anterior and posterior thoracic air sacs separate the viscera from the air sac lumina. Since, then, only the thoracic air sacs intervene between the viscera and the thoracic wall, an abdominal diaphragm cannot be considered to be present.

Another confusion of terminology centers around the problem of the presence or absence of a pleura. Hyman's (1947) description of the pigeon's pleura and pleural cavity strongly resembles that of the morphology of the anterior and posterior thoracic air sacs. Usually a pleura is described as either partially or completely surrounding the lungs, which is connected to the diaphragm and thoracic wall by means of delicate connective tissue strands. On gross examination the White Peking Ducks seemed to confirm this, but careful examination of the histological sections showed this impression to be incorrect. What initially looked like a pleura surrounding the whole lung proved to be the outer surface of the adjoining parabronchial dilatations, which are an essential part of the pulmonary parenchyma. Between the dilatations and the diaphragm or body wall nothing but connective tissue obtains. From these observations the conclusion that there is no pleura or pleural cavity in the adult White Peking Duck is inevitable. In conformance with this are the findings of Ellenberger and Baum (1943) in the chicken where the pleura and pleural cavity are lacking and the lung itself attaches to the diaphragm and body wall directly by means of connective tissue fibers. In mammals, adherence of the lung to the thoracic wall is encountered in the elephant as the exception to the rule (Engel, 1963).

The histological features of the air passages of the domestic birds are strikingly uniform and deviate little from the findings of this study. The air sac lining is a mixture of simple squamous and low cuboidal epithelium throughout the air sacs, in contrast to that of the turkey, which proximally is simple ciliated columnar but distally is simple squamous. There is no evidence that the epithelium differs where the air sacs attach to other structures. No mucous cells or cilia were found within the air sac in this study, although several instances have been reported in the literature concerning the chicken.

It is not within the scope of this work to determine the nature of the air capillary lining, since an electron microscope is needed to establish the continuity of the epithelial cells, as De Groodt et al. (1960) did in the chicken.

It is true that, through contraction of the skeletal muscles, the air sacs passively assist in respiration. There are, however, some smooth muscle bands in the air sac walls of some ducks (fig. 31), indicating some ability of the air sac to contract on its own. To determine the exact significance and function of these muscle bands, further investigations are needed. From present evidence it appears that the contraction of the surrounding skeletal muscles has the greater effect on the movement of air out of the air sacs.

From this work it appears that the air sacs are fairly vascular; whole mounts and cross-sections show an abundance of capillaries. Insufficient evidence is present to determine their contribution to gas exchange.

The question of saccobronchi needs some elucidation. Whereas only one sac, the cervical, has a single communication with the lung, the others have more complicated connections. The interclavicular air sac has a few parabronchi opening directly into it. The anterior thoracic sac has, besides a large bronchial connection, also some parabronchial ones, which may anastomose and open into the air sac by means of one to three ostia. The second laterobronchus, as it approaches the posterior thoracic air sac, gives rise to many parabronchi, and continues to do so at its ostium. Those arising at the ostium do not appear to differ from more proximal parabronchi, although the last few do connect directly with the air sac lumen. At the abdominal sac the arrangement is still different; the parabronchi at the caudal border of the lung give rise to two medium-sized bronchi, which, after anastomosing, connect with the air sac. From this evidence it appears that, although direct connections exist between parabronchi and air sacs, only the anterior thoracic air sac could possibly be considered to have a separate entrance and exit for the air, thus rendering the entire concept of "recurrent flow" or "recurrent bronchi" of questionable value in the duck.

SUMMARY

To investigate the respiratory system of the White Peking Duck, 18 ducks were obtained. Ten of these were studied by means of gross dissection and latex casts, while histological preparations were made of the remaining eight. The literature was reviewed and compared with the present findings.

The White Peking Duck has eleven air sacs: paired cervicals, anterior thoracic, posterior thoracic and abdominals, and a single interclavicular, dorsal and synsacral. By definition an air sac connects directly to the lungs, while diverticula arise from air sacs. The cervical air sacs lie at the thoracic inlet below the neck muscles and the anterior half of the lung. The right sac is longer than the left, extending about 30 mm further caudal than the latter. The cervical vertebral diverticula enter the vertebral column between the last two cervical vertebrae and the first thoracic vertebrae, and pneumatize all but the first two cervical vertebrae. The diverticula are continuous through the transverse canal, and supply the lateral cervical pouches, and intraneural and intraosseous diverticula. The first thoracic vertebra is supplied directly from the cervical sac. A costal diverticulum extends along the first rib. The interclavicular sac lies between the cervicals and the sternum, and extends laterad into the surrounding tissues. Its main divisions are the sac proper, and the axillary, postcardiac and sternal diverticula. The axillary diverticulum consists of the pectoral pouch, humeral diverticulum and dorsal division; the sternal diverticula are medial and lateral. The anterior thoracic air sacs lie ventral to the lungs between ribs 2 and 5; sometimes the right one has a small diverticulum anterodorsomedially. The posterior

thoracic air sacs extend caudal to the anteriors from rib 5 to the pubic bone, where they taper to a point. They frequently are split, the individual parts together assuming the shape and relations of the single sac in other specimens. Extending the full length of the abdominal cavity are the abdominal air sacs, which surround the intestinal mass. The suprarenal diverticula arise from the dorsal part of the air sac and partially surround the kidneys. The dorsal air sacs are supplied from the medial surface of the lungs and penetrate thoracic vertebrae 2 through 7 via the lateral and dorsal pneumatic fossae. The synsacral air sac extends caudad from the posterior margin of the lung, protrudes through the intertransverse foramina, penetrates its bone substance and pneumatizes the ilium dorsally. Accessory sacs sometimes appear in other places, usually medial to the hilus of the lung.

At the bifurcation of the trachea, marked in the male by the <u>bulla tympaniformis</u>, the two extrapulmonary bronchi arise which course caudad and enter the lungs ventrally. The intrapulmonary bronchus gives rise anteriorly to 5 dorsomediobronchi which supply the ventral surfaces of the lung, and posteriorly to 3 laterobronchi and a number of dorsolaterobronchi and dorsobronchi which supply the dorsal and medial surfaces and the lateral margins. Caudally the primary bronchus sharply diminishes in size and loses its identity among the parabronchi. Parabronchi arise from the secondary bronchi and connect the anterior and posterior groups and communicate with the air sacs as saccobronchi. Many parabronchi and some secondary bronchi open into the parabronchial dilatations at the surfaces of the lung.

The cervical air sacs are connected to the lungs by an anterior branch of dorsomediobronchus 1. The interclavicular sac is supplied by saccobronchi arising from dorsomediobronchi 1 and 2 and dorsolaterobronchus 2. The anterior thoracic air sacs are supplied by dorsomediobronchus 3 as well as saccobronchial connections from dorsomediobronchi 2 and 4 and dorsolaterobronchus 2. Laterobronchus 2 supplies the posterior thoracic sacs. The abdominal air sacs are supplied by a bronchus which arises from anastomosing parabronchi of the lateral margin of the lung and from parabronchi from the primary bronchus and dorsomediobronchus 4.

The diaphragm covers the lungs ventrally from the hilus of the lung to the ninth rib, attaching medially to the ventral spines of the thoracic vertebrae and laterally to the ribs by means of the Mm. pulmocostales. It consists of a strong collagenous tissue sheet, which attaches to the lung substance by means of a few collagenous and elastic fibers. The M. pulmosternalis originates on the sternun and inserts just lateral to the first M. pulmocostalis.

The lining of the primary bronchi is ciliated pseudostratified columnar epithelium which has many goblet cells; it changes in the secondary bronchi to simple cuboidal with patches of simple squamous or pseudostratified columnar cells. In the air sacs it is simple squamous with some cuboidal. The parabronchi and their atria, and the parabronchial dilatations are lined with simple squamous epithelium. The submucosa has collagenous and elastic fibers, which persist throughout the secondary and tertiary bronchial and air sac walls, but are not evident in the air capillaries or atria. It contains two vascular networks. External to the submucosa is an elastic connective tissue membrane which encloses the bronchial rings; it is also found in the parabronchial atria and air capillaries. The ventromedially incomplete, hyaline cartilage rings are connected externally by a bronchial muscle, and extend from the tracheal carina to the first laterobronchus and into the thin partitions between the dorsomediobronchi. Smooth muscle also surrounds the walls of the posterior part of the primary bronchus, the secondary bronchi and parabronchi, all air sac ostia, the parabronchial atria and their openings into the air capillaries. Occasionally it occurs in an air sac wall. The air sac lining is continuous with that of the air spaces of the pneumatized bones, where it is thin, simple squamous epithelium. It spans the distance between trabeculae and is supported by a thin layer of connective tissue.

Cervical vertebral pneumatization appears greater in the White Peking Duck than in other domestic birds. Whereas the primary bronchus of the duck and the turkey terminate in the posterior parabronchial mass, that of the chicken continues into the abdominal air sac. There is no evidence of a vestibule in the primary bronchus, nor of any valves. Ducks have a strong diaphragm which is membranous in the center and muscular at the edge, and is neither incomplete nor nonfunctional. The anterior and posterior air sacs are the only structures separating the thoracic wall from the viscera, so that a thoracoabdominal diaphragm cannot be considered to be present. What appears as a pleura covering the lung is actually the outer surface of the adjoining parabronchial dilatations, which is connected directly to the diaphragm and body wall by connective tissue, without interposition of pleura or pleural cavity. Although some smooth muscles are present in the air sac walls, the skeletal muscles of the thoracic and abdominal wall and the diaphragm have the greater effect on air movement. The concept of recurrent air flow is of questionable value in the duck.

LITERATURE CITED

Adams, W. E. 1958. The Comparative Morphology of the Carotid Body and Carotid Sinus. C. C. Thomas, Publ., Springfield, Ill.

Akester, A. R. 1960. The comparative anatomy of the respiratory pathways in the domestic fowl (Gallus domesticus), pigeon (Columba livia) and domestic duck (Anas platyrhyncha). J. Anat. 94:487-505.

Angulo, E. 1961. Structure histologique des sacs aeriens des Gallines. Rec. Med. Vet. 34:951-961.

Babak, E. 1921. Handbuch der Vergleichenden Physiologie, I, Part II. Gustav Fisher, Jena.

Bradley, O. C. and T. Grahame. 1960. The Structure of the Fowl. Oliver and Boyd, London.

Chamberlain, F. W. 1943. Atlas of Avian Anatomy. Michigan Agricultural Experimental Station Memoir Bulletin 5. Mich. State Univ., East Lansing, Mich.

Chauveau, A. 1891. The Comparative Anatomy of the Domesticated Animals. Appleton and Co., New York.

Cover, M. S. 1953. Gross and microscopic anatomy of the respiratory system of the turkey. II. The larynx, trachea, syrinx, bronchi and lungs. III. The air sacs. Am. J. Vet. Res. 14:230-238, 239-245.

Cowles, R. B. and A. Nordstrom. 1946. A possible avian analogue of the scrotum. Sci. 104:586.

De Groodt, M., M. Sebruyns and A. Lagasse. 1960. De ultrastruktuur van de bloed-luchtbarriere in the long van vogels. Vlaams Diergeneesk. Tijdschr. 29:313-317.

Delphia, J. M. 1958. The origin of the air sacs in the white Peking duck: Anas platyrhynchos, L. Proc. N. Dakota Acad. Sci. 12:86-92.

Delphia, J. M. 1959. Establishment of the secondary bronchi in the white Peking duck: Anas platyrhynchos, L. Proc. N. Dakota Acad. Sci. 13: (pages not numbered).

Delphia, J. M. 1961. Early development of the secondary bronchi in the house sparrow Passer domesticus L. Am. Midland Naturalist 65:44-59.

Dobi, E. 1942. Über den Bau der Hühner- und Entenlunge. Ph. D. Thesis, Budapest. Abst. in Jahrb. Vet. Med. 70:514, 1943.

Ellenberger, W. and H. Baum. 1943. Handbuch der Vergleichenden Anatomie. Edited by O. Zietzschmann et al. Springer, Berlin.

Engel, S. 1963. The respiratory tissue of the elephant (Elephas indicus. Acta Anat. 55:105-111.

Evans, H. E. 1961. Guide to the Study and Dissection of the Chicken. Mimeographed material, Cornell Univ., Ithaca, N. Y.

Gier, H. T. 1952. The air sacs of the loon. Auk 69:40-49.

Gilbert, P. W. 1939. The avian lung and air-sac system. Auk 56: 57-63.

Goodrich, E. S. 1958. Studies on the Structure and Development of Vertebrates. Dover Publ., Inc., New York.

Graham, J. D. P. 1939. The air stream in the lung of the fowl. J. Physiol. 97:133-137.

Grober, J. A. 1899. Ueber die Atmungsinnervation der Vögel. Pfluegers Arch. Ges. Physiol. 76:427-469.

Groebbels, F. 1932. Der Vogel. Erster Band: Atmungswelt und Nahrungswelt. Borntraeger, Berlin.

Hazelhoff, E. H. 1951. Structure and function of the lung of birds. Poultry Sci. 30:3-10.

Hyman, L. H. 1947. Comparative Vertebrate Anatomy. Univ. of Chicago Press, Chicago.

Kadono, H., T, Okada and K. Ono. 1963. Electromyographic studies on the respiratory muscles of the chicken. Poultry Sci. 42:121-128.

Kaupp, B. F. 1918. The Anatomy of the Domestic Fowl. W. B. Saunders Co., Philadelphia.

King, A. S. 1956. The structure and function of the respiratory pathways of Gallus domesticus. Vet. Rec. 68:544-547.

King, A. S. 1957. The aerated bones of Gallus domesticus. Acta Anat. 31:220-230.

King, A. S. and D. F. Kelly. 1956. The aerated bones of Gallus domesticus: the fifth thoracic vertebra and sternal ribs. Brit. Vet. J. 112:279-283.

Krölling, O. and H. Grau. 1960. Lehrbuch der Histologie und Vergleichenden Microscopischen Anatomie der Haustiere. Parey, Berlin.

Locy, W. A. and O. Larsell. 1916. The embryology of the bird's lung. I and II. Am. J. Anat. 19:447-504, 20:1-44.

Lucas, A. M. 1960. The respiratory system and processing procedures in relation to shelf-life of poultry. Unpublished mimeographed material available from author at U. S. Department of Agriculture, Avian Anatomy Project, Department of Poultry Science, Mich. State Univ., East Lansing, Mich.

Lucas, A. M. 1963. The gross and microscopic structure of the avian respiratory system and its reactivity to stimuli. Abstract of lecture during Poultry Disease Training Program, National Animal Disease Laboratory, Ames, Iowa.

Lucas, A. M. and E. M. Denington. 1961a. A brief report on anatomy, histology, and reactivity of air sacs in the fowl. Avian Diseases 5:460-461.

Lucas, A. M. and E. M. Denington. 1961b. Disease, environmental, and management factors related to poultry health. Symposium, March 1961, Jefferson Auditorium, U. S. D. A., Washington, D. C.

Lucas, A. M., R. J. Keeran and C. F. Coussens. 1959. Air sacs of chicken, turkey, duck and owl. Anat. Record 133:452.

Lucas, A. M. and P. R. Stettenheim. 1964. Avian Anatomy. In Diseases of Poultry. Edited by H. E. Biester and L. M. Schwarte. Iowa State Univ. Press, Ames, Iowa.

Makowski, J. 1938. Beitrag zur Klärung des Atmungmechanismus der Vögel. Pfluegers Arch. Ges. Physiol. 240:407-418.

Malewitz, T. D. 1956. The normal histology and hematology of the turkey and the pathology due to Histomonas meleagridis. Ph. D. Thesis, Mich. State Univ., East Lansing, Mich.

Malewitz, T. D. and M. L. Calhoun. 1958. The gross and microscopic anatomy of the digestive tract, spleen, kidney, lungs and heart of the turkey. Poultry Sci. 37:388-398.

Marcus, H. 1937. Lungen. In Handbuch der Vergleichenden Anatomie der Wirbeltiere, III. Edited by L. Bolk, et al.:909-988. Urban und Schwarzenberg, Berlin.

Marshall, A. J. 1960. Biology and Comparative Physiology of Birds. Vol. I. Academic Press, New York.

Martin, P. and W. Schauder. 1923. Lehrbuch der Anatomie der Haustiere. Vol. IV. Schickhardt und Ebner, Stuttgart.

McLeod, W. M. and R. P. Wagers. 1939. The respiratory system of the chicken. J. Am. Vet. Med. Assoc. 95:59-70.

Payne, D. C. and A. S. King. 1959. Is there a vestibule in the lung of Gallus domesticus? J. Anat. 93:577.

Payne, D. C. and A. S. King. 1960. The lung of Gallus domesticus: secondary bronchi. J. Anat. 94:292-293.

Pettingill, O. S. Jr. 1961. A Laboratory and Field Manual of Ornithology. Burgess Publ. Co., Minneapolis, Minn.

Rigdon, R. H. 1959. The respiratory system in the normal white Peking duck. Poultry Sci. 38:196-210.

Rigdon, R. H., T. M. Ferguson, G. L. Feldman and J. R. Couch. 1958a. Air sacs in the turkey. Poultry Sci. 37:53-60.

Rigdon, R. H., T. M. Ferguson, G. L. Feldman, H. D. Stelzner and J. R. Couch. 1958b. Spontaneous hernias in the axilla of the turkey. Poultry Sci. 37:169-173.

Rogers, A. N. Jr. 1961. The demonstration of air sacs in the chicken. Southeast. Vet. 12:59-62.

Sisson, S. and J. D. Grossman. 1953. The Anatomy of the Domestic Animals. W. B. Saunders Co., Philadelphia.

Soum, J. M. 1896. Recherches physiologiques sur l'appareil respiratoir des oiseaux. Ann. Univ. Lyon 28:1-126.

Stresemann, E. 1937. Syrinx. In Handbuch der Vergleichenden Anatomie der Wirbeltiere, III. Edited by L. Bolk, et al.:867-882. Urban und Schwarzenberg, Berlin.

Sturkie, P. D. 1954. Avian Physiology. Comstock Publ. Assoc., Ithaca, N. Y.

Taylor, R. Q., M. A. Boone and B. D. Barnett. 1962. Plastic infusion and casting of the avian air sacs. Poultry Sci. 41:1940-1943.

Trautmann, A. and J. Fiebiger. 1952. Fundamentals of the Histology of Domestic Animals. Comstock Publ. Assoc., Ithaca, N. Y.

Victorow, C. 1909. Die kühlende Wirkung der Luftsäcke bei Vögeln. Pfluegers Arch. Ges. Physiol. 126:300-322.

Vos, H. J. 1934. Ueber den Weg der Atemluft in der Entenlunge. Z. Vergleich. Physiol. 21:552-578.

Weichert, C. K. 1953. Elements of Chordate Anatomy. McGraw-Hill Book Comp., Inc., New York.

Wetherbee, D. K. 1951. Air sacs in the English sparrow. Auk 68: 242-244.

Winterstein, H. 1921. Handbuch der Vergleichenden Physiologie I, Part II. Gustav Fisher, Jena.

Zeuthen, E. 1942. The ventilation of the respiratory tract in birds. K. Danske Videnskab. Selskab Biol. Meddelel. 17:1-50.

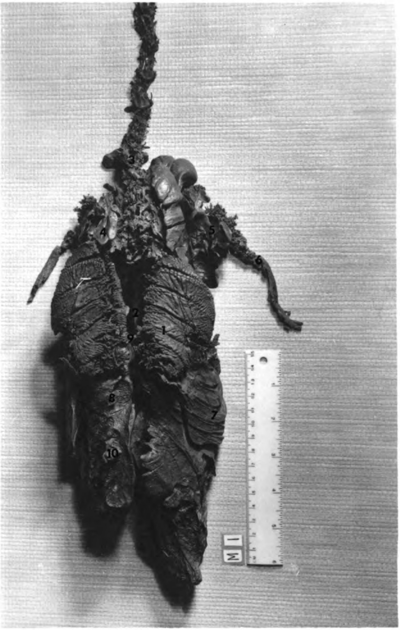


Fig. 7. Latex cast of lungs and air sacs - dorsal view. 1. lungs; 2. cervical sac; 3. cervical vertebral diverticula; 4. interclavicular sac; 5. axillary diverticulum; 6. humeral diverticulum; 7. posterior thoracic sac; 8. abdominal sac; 9. dorsal sac; 10. suprarenal diverticulum.

Fig. 8. Latex cast of lungs and air sacs - ventral view. 1. cervical sac; 2. cervical vertebral diverticula; 3. large lateral cervical pouch; 4. interclavicular sac proper; 5. pectoral pouch; 6. postcardiac diverticulum; 7. anterior thoracic sac; 8. right posterior thoracic sac (split); 9. abdominal sac.

Fig. 9. Latex cast of lungs and air sacs - lateral view. 1. lung; 2. cervical sac; 3. cervical vertebral diverticula; 4. trachea; 5. interclavicular sac; 6. medial sternal diverticulum; 7. humeral diverticulum; 8. postcardiac diverticulum; 9. anterior thoracic sac; 10. posterior thoracic sac; 11. synsacral sac; 12. abdominal sac.

Fig. 10. Latexed specimen, with abdominal wall and sternum removed.
1. heart; 2. liver; 3. small intestine; 4. interclavicular sac proper; 5. furcula; 6. postcardiac diverticulum; 7. posterior thoracic sac; 8. pubic bone.

Fig. 11. Latexed cervical sacs - ventral view.
1. furcula; 2. right cervical sac; 3. left cervical sac; 4. right extrapulmonary bronchus; 5. common carotid artery; 6. neck muscle mass.

Fig. 12. Diaphragm over latexed lung - ventromedial view. 1. tendinous part of diaphragm; 2. Mm. pulmocostales; 3. anterior thoracic sac at ostium; 4. posterior thoracic sac at ostium; 5. abdominal sac at ostium; 6. common wall of anterior and posterior thoracic sacs.

Fig. 13. Latexed lungs <u>in situ</u> - ventral view.
1. cervical ostium; 2. interclavicular ostium; 3. anterior thoracic ostium; 4. posterior thoracic ostium; 5. abdominal ostium; 6. neck muscle mass; 7. ventral spine of thoracic vertebra 5; 8. dorsomediobronchus 3; 9. dorsomediobronchus 4.

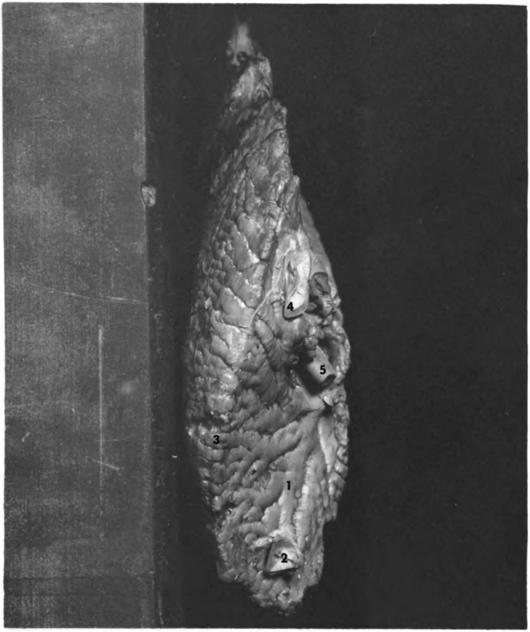


Fig. 14. Latexed lung - lateral view.
1. dorsomediobronchus 1; 2. cervical ostium; 3. parabronchi at lateral margin; 4. interclavicular ostium; 5. extrapulmonary bronchus.

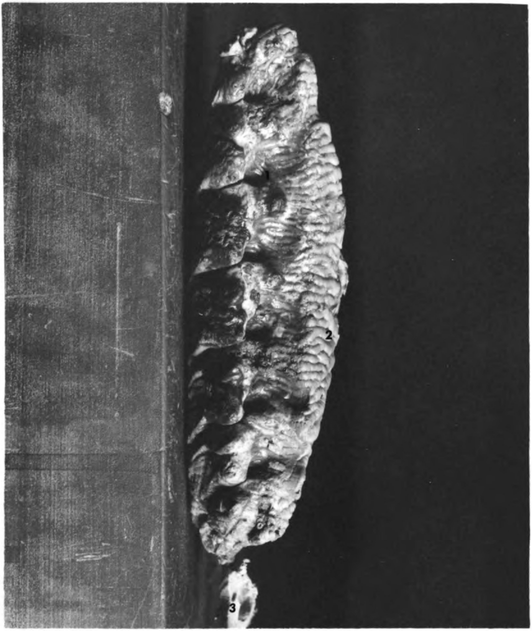


Fig. 15. Latexed lung - medial view.
1. costal space; 2. parabronchi; 3. abdominal sac at ostium.

Fig. 16. Latexed lung - dorsal view.
1. bronchus, leading to abdominal sac; 2. abdominal sac; 3. posterior thoracic sac, at ostium; 4. dorsolaterobronchus 2; 5. dorsolaterobronchus 3; 6. dorsolaterobronchus 4; 7. dorsolaterobronchus 5; 8. costal groove.

Fig. 17. Dissected latexed lung, showing main air passages to air sacs - ventral view.
1. extrapulmonary bronchus; 2. dorsomediobronchus 1; 3. cervical ostium; 4. interclavicular ostium; 5. dorsomediobronchus 3; 6. parabronchial mass supplying anterior thoracic saccobronchial ostia; 7. laterobronchus 2; 8. posterior thoracic ostium; 9. laterobronchus 3; 10. bronchus leading to abdominal sac; 11. abdominal ostium.

Fig. 18. Pectoral girdle - ventral view.
1. coracoid; 2. furcula; 3. scapula; 4. humerus;
5. humeral pneumatic foramen.

Fig. 19. Latex cast of lungs and air sacs, with left posterior thoracic and abdominal sacs removed to show synsacral sac - ventral view.
1. synsacral sac; 2. left postcardiac diverticulum;
3. right abdominal sac; 4. right posterior thoracic sac.

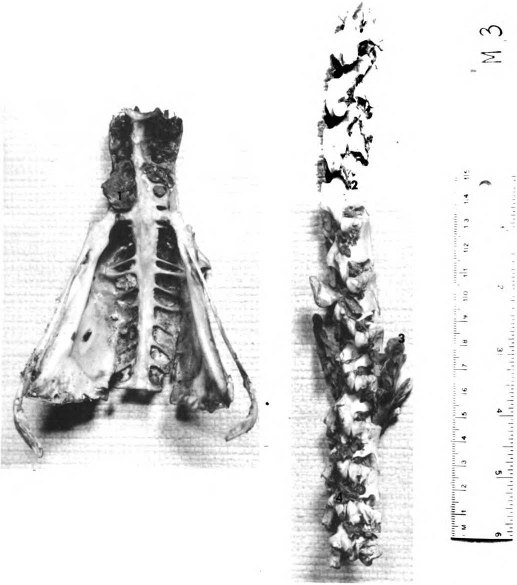


Fig. 20. Diverticula of the synsacral and cervical sacs. 1. synsacral sac protruding through intertransverse foramina of synsacrum; 2. small lateral cervical pouch; 3. large lateral cervical pouch; 4. circular pouch under dorsal ligament.

Fig. 21. Sternum - dorsal view.
1. sternal pneumatic fossa; 2. costal facet.

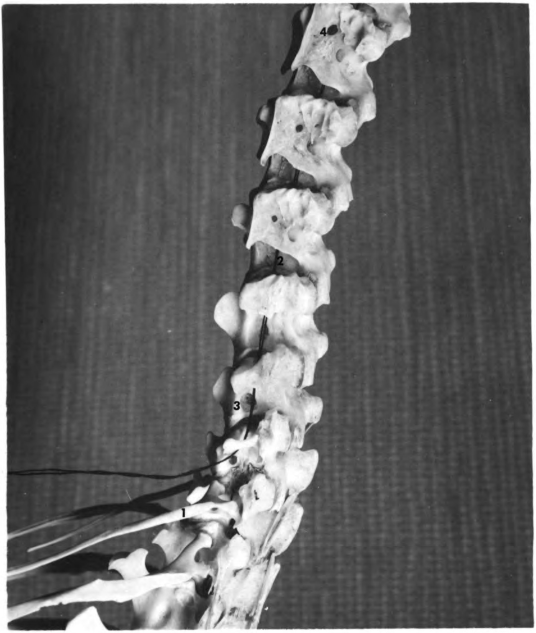


Fig. 22. Cervical vertebrae - lateral view.
1. rib 1; 2. thread in transverse canal; 3. lateral pneumatic fossa; 4. foramen through transverse processes, leading to lateral cervical pouch.

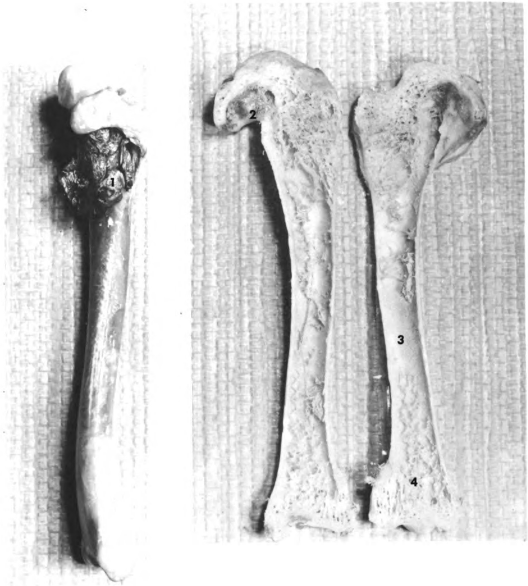


Fig. 23. Humerus showing air passages in bone.
1. latex mass at pneumatic foramen; 2. entrance into bone substance; 3. humeral diverticulum at center of shaft; 4. distal bone trabeculae surrounded by humeral diverticular air spaces.

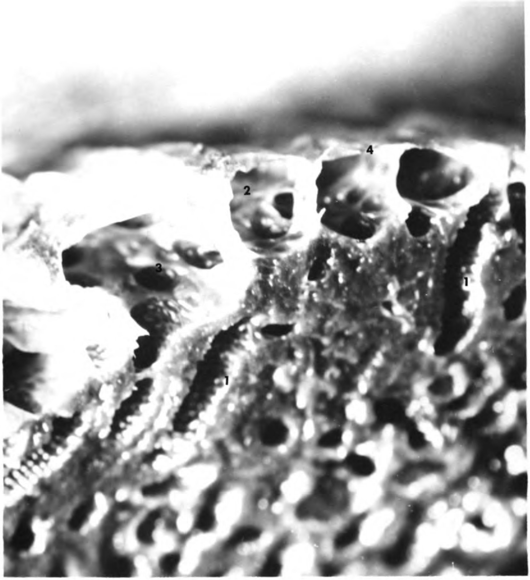


Fig. 24. Parabronchial dilatations at lung surface - cross-section. 1. parabronchus; 2. parabronchial dilatation; 3. opening of parabronchus into dilatation; 4. external surface of parabronchial dilatation. 14 X.

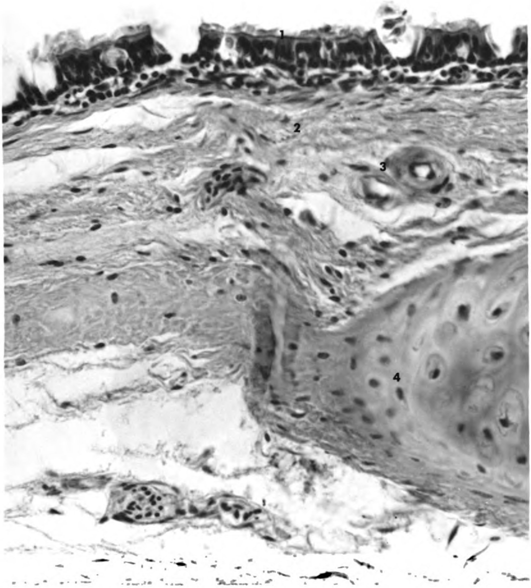


Fig. 25. Primary bronchus - longitudinal section.
1. ciliated pseudostratified columnar epithelium;
2. lamina propria; 3. blood vessels; 4. hyaline cartilage.
Hematoxylin - eosin. 445X.

Fig. 26. Secondary bronchus at ostium - longitudinal section. 1. simple squamous epithelium; 2. parabronchial dilatation; 3. air capillaries; 4. secondary bronchus. Hematoxylin - eosin. 260X.

Fig. 27. Suprarenal diverticulum.
1. simple squamous epithelium; 2. low cuboidal epithelium; 3. connective tissue; 4. renal parenchyma.
Hematoxylin - eosin. 185X.

Fig. 28. Lung parenchyma with parabronchial dilatations. 1. parabronchus; 2. air capillary; 3. parabronchial dilatation; 4. smooth muscle band; 5. simple squamous epithelium. Weigert's - Van Gieson's. 165X.

Fig. 29. Primary bronchus - cross-section.
1. bronchial muscle; 2. hyaline cartilage; 3. perichondrium; 4. lamina propria. Weigert's - Van Gieson's. 170X.

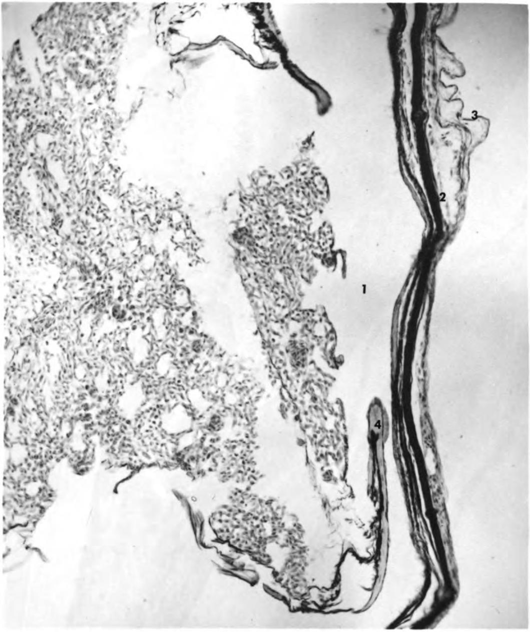


Fig. 30. Diaphragm and lung.
1. parabronchial dilatation; 2. diaphragm; 3. air sac epithelium; 4. smooth muscle band. Weigert's - Van Gieson's. 155X.

Fig. 31. Junction of medial walls of anterior and posterior thoracic air sacs.
1. air sac lumina; 2. low cuboidal epithelium; 3. connective tissue; 4. smooth muscle band. Hematoxylin - eosin. 410X.

Fig. 32. Neck - cross-section.
1. centrum; 2. spinal cord; 3. intervertebral foramen; 4. transverse canal; 5. dorsal ligament; 6. extraneural diverticulum; 7. intraneural diverticulum connecting with extraneural diverticulum. Hematoxylin - eosin. 9X.

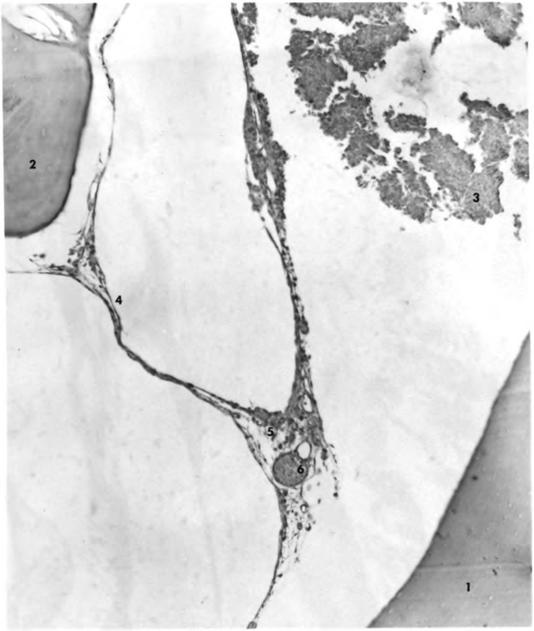


Fig. 33. Humerus - cross-section.
1. shaft; 2. trabecula; 3. bone marrow; 4. diverticulum, showing simple squamous epithelial lining; 5. connective tissue; 6. blood vessel. Hematoxylin - eosin. 165X.

Fig. 34. Body wall and lung.
1. parabronchial dilatation; 2. connective tissue;
3. intercostal muscle; 4. lung parenchyma. Weigert's - Van Gieson's. 175X.