THE AIR SACS OF THE LOON

BY H. T. GIER

AT irregular intervals during the past 100 years, there have been reports on the methods of study, general structure, modifications, and functions of the avian respiratory system. Most of the work has been done with the Pigeon, *Columbia livia* (Muller, 1908; Gilbert, 1939) and the Chicken, *Gallus gallus* (Locy and Larsell, 1916; McLeod and Wagers, 1939). These and other references in the literature serve merely as an introduction to the study of functions and variations in structure of avian respiratory systems.

The state of knowledge as to the extent and positions of the air sacs of the Pigeon and the Chicken and the various terminologies used are well-covered by the references listed above, and will not be reviewed.

This report is the first of a series being prepared in an effort to augment and clarify our store of knowledge on the morphology of air sacs so that an overall comparative picture is possible. This work was started under the direction of the late Dr. Will Scott at Indiana University in 1935, was continued at Ohio University from 1938 to 1946, and has been resumed at Kansas State College. After preliminary dissections of specimens from most of the orders of North American birds, the Common Loon, *Gavia immer*, was selected as having the simplest set of air sacs, and for that reason is being used as the type with which other birds will be compared later. Much of the dissection and detailed description recorded here was done by Phyllis Ruhland under supervision of the author.

MATERIALS AND METHODS

The walls of the air sacs are so thin that, in most birds, as soon as the body cavity is opened the sacs collapse, making their extent and connections extremely difficult to determine. In order to overcome this difficulty, some material which will solidify later is injected into the respiratory system through the trachea. Muller (1908) used paraffin or gelatin, and Gilbert (1939) used Wood's metal for injection.

In this study, three Loons were used. Gelatin was injected into the respiratory system of one bird, and paraffin (melting point 45° C.) was used in the other two. Gelatin filled well but became brittle and crumbly in formalin and thus proved to be unsatisfactory.

For injection with a heat-liquified medium, such as paraffin, the body of the bird must be maintained at a temperature slightly above the solidification point of the medium to insure filling of the smaller

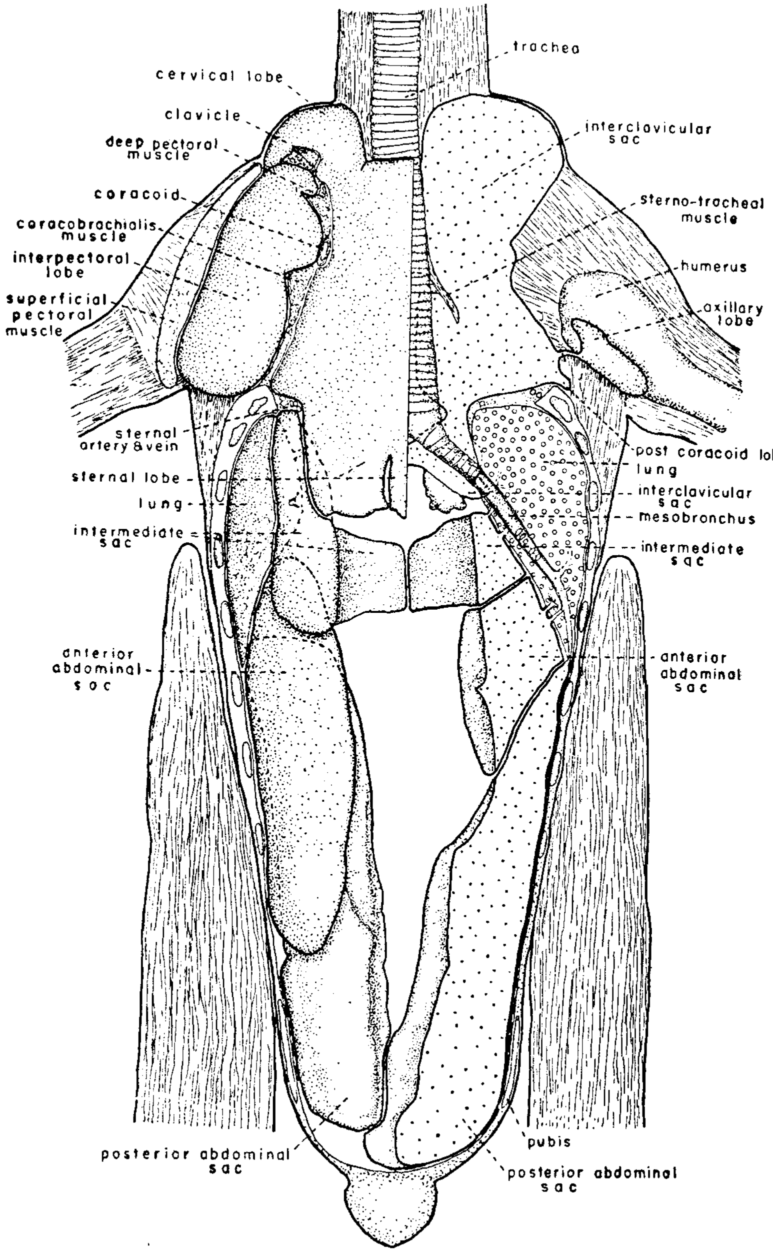


FIGURE 1. Ventral view of respiratory system of Common Loon with body wall removed. The ventral half of left side of respiratory system was removed as shown in Figure 3, B. (2/5 nat. size.)

spaces. This was done effectively by keeping the bird immersed in a water bath of the desired temperature. The injection was accomplished by forcing the injection mass, from a pressure flask held in a hot-water bath, through a canula inserted into the trachea. Controlled air pressure was supplied by a small air pump. An automatic cut-off in the line, adjusted to three pounds pressure for the Loon, prevented over-distention of the sacs. Air was forced from the respiratory system by alternately filling it with paraffin and squeezing out the paraffin-air mixture until no more air bubbles could be expelled. Usually four or five fillings, with proper turning of the bird while the air was being forced out, proved sufficient to remove all air. When injection was considered adequate, the canula was removed from the trachea, excess injection medium allowed to escape under pressure of the normal elasticity of the bird's body, the trachea tied, and the body immersed in formalin or phenol solution until the tissues were fixed thoroughly or, if already fixed, until the injection mass had solidified.

The birds were skinned either before injection or after fixation. Detailed dissections were made to determine the locations of the air sacs and their diverticula in relation especially to the muscles, nerves, and skeletal units. Howell's (1937) terminology was followed. For relationships not covered by Howell, Kaupp (1918) was used as a guide.

Drawings were made life size from a specimen injected with paraffin. Some details were omitted for the sake of clarity. The body wall and skeletal units are shown only to give relationships; viscera other than the respiratory structures were omitted.

THE INTERCLAVICULAR SAC

The interclavicular sac (anterior thoracic of Locy and Larsell, and McLeod and Wagers) is a large, unpaired sac located anterior and ventral to the heart and lungs. In the Loon it fills the position that is occupied by the cervical and interclavicular sacs of the Chicken and Pigeon.

The main part of the interclavicular sac lies posterior to the clavicles and dorsal to the coracoid and sternum. It extends around the cranial end of the heart, dorsally around the bases of the bronchi, and laterally to the cranial tip of the lung.

The paired subclavian, subscapular, and sternal arteries, the sternal veins, and the accompanying nerves pass through the cavity of the sac. The innominate and carotid arteries and the innominate, jugular, and subclavian veins protrude into the wall of the sac, but are not completely surrounded by the air space. Penetration of the air sac by nerves and blood vessels was accomplished embryonically by expansion of the sac around the obstruction, and subsequent fusion and disappearance of walls that became appressed (Gier, unpubl. data).

The posterior half of the part of the trachea within the sac is attached to the esophagus by a fold of mesentery, in the anterior end of which are located the paired tracheal arteries and veins. Anterior to these blood vessels, the trachea is completely surrounded by the interclavicular sac. The sterno-tracheal muscle extends through the sac, cranio-medially, from its origin on the lateral tip of the sternum to its insertion on the side of the trachea at the level of the tracheal arteries and the anterior connection of the tracheo-esophageal mesentery.

The interclavicular sac connects to both lungs through one or two tubes on each side located medio-dorsal to the bronchus and the pulmonary vein. These tubes break up into parabronchi before they enter the mesobronchi. In one specimen, a second connection was found, ventral to the bronchus, from the lateral margin of the sac to the medio-ventral edge of the lung.

Diverticula of the interclavicular sac.—The interclavicular sac in the Loon has six secondary lobes or diverticula: cervical, sternal, postcoracoid, subscapular, axillary, and interpectoral. The humerus is not hollow and, therefore, no humeral diverticulum exists in the Loon.

The cervical lobes of the interclavicular sac lie anterior to the clavicles, fill the space between the clavicles and the neck, and are separated medially by the trachea and esophagus. They are limited dorso-laterally by the anterior tip of the scapula and the anterior portions of the rhomboid muscles. Whether these "cervical lobes" have any homologies with the cervical sacs is doubtful. This point can be cleared only by an extensive comparative study or by study of the embryonic development.

The sternal diverticulum is a broad, triangular, posterior projection of the interclavicular sac between the heart and the sternum and extends laterally almost to the margin of the sternum. In two specimens there were a median and two lateral divisions of the posterior tip, as shown in Figures 1–3. In the third specimen, the posterior margin was serrate but not divided.

The postcoracoid diverticulum appears in the Loon only as a slight ridge-like protrusion from the interclavicular sac between the coracoid and the first rib.

The subscapular diverticulum is a caudal extension from the cervical lobe of the interclavicular sac and is secondarily connected medioventrally to the dorsal end of the postcoracoid diverticulum (Fig. 1).

It is limited from the main sac both antero-dorsally and postero-ventrally by a slight infolding of the wall, caused by the projection into the sac of the nerves and blood vessels which supply the pectoral girdle. The subscapular diverticulum lies medial to the anterior one-fourth of the scapula.

The axillary diverticulum is connected by a thin tube to the lateral surface of the postcoracoid diverticulum. It is located in the angle between the scapula and humerus.

The interpectoral diverticulum arises from the postcoracoid diverticulum and is separated from the more dorsal connection of the axillary diverticulum by the coracobrachialis muscle. The interpectoral diverticulum lies in the angle between the humerus and the coracoid and extends ventro-medially between the superficial and deep pectoral (supracoracoid) muscles. It is divided into two broadly-joined lobes by the projection into its posterior wall of the large nerve, artery, and vein which attend the superficial pectoral muscle. The interpectoral and axillary lobes are separated partially by the biceps muscle and the insertion of the scapulohumeralis muscle. Ventro-laterally, the interpectoral diverticulum is covered by the superficial pectoral muscle. The axillary and interpectoral diverticula form a cushion around three sides of the head of the humerus.

THE INTERMEDIATE SACS

The intermediate sacs (anterior intermediate of Locy and Larsell; posterior thoracic of McLeod and Wagers) are paired, almost symmetrical, and located medio-ventral to the lungs and lateral to the heart, proventriculus, and liver (Figs. 1–3). The anterior margin is in contact with the lateral margin of the sternal lobe, and the posterior portion lies ventro-lateral to the anterior end of the anterior abdominal sac. The ventral wall is limited by the ribs and intercostal muscles. A medial projection of each sac extends dorsally around the proventriculus where the membranes are contiguous along the mid-dorsal line. The sacs are separated from the lungs by the pulmonary diaphragm. Ventral to the lung, part of the outer wall of the sac is fused with the parietal peritoneum.

Two or three ostia pierce the pulmonary diaphragm and enter the lung from each intermediate sac. One is located dorsal and posterior to the point of exit of the pulmonary vein from the lung. The other ostia are located near the medial tip of the lung, ventral to the bronchus and pulmonary vein. Location of these ostia varies individually.

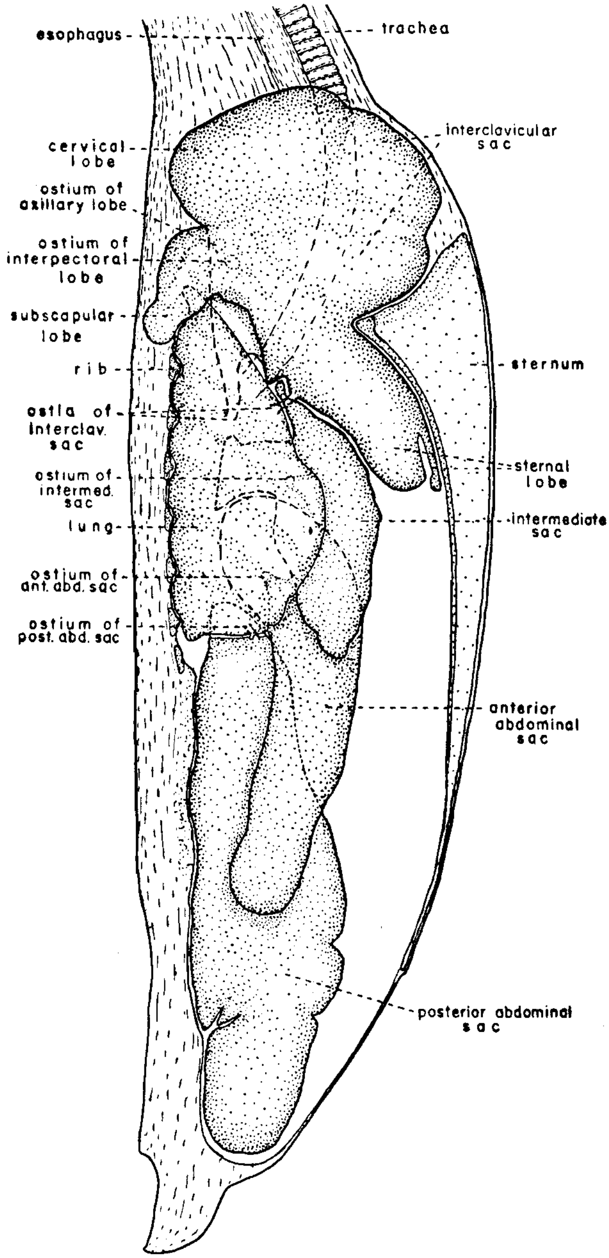


FIGURE 2. Respiratory system of Common Loon from left side. The body wall was removed by sagittal cut along left margin of carina and to left of vertebral column. Diverticula of interclavicular sac are omitted. The most lateral sacs are drawn as if transparent to show outlines of deeper sacs. (⅖ nat. size.)

THE ANTERIOR ABDOMINAL SACS

The anterior abdominal sacs (posterior intermediate of Locy and Larsell; lesser abdominal of McLeod and Wagers) are large, asymmetrical sacs, located along the ventro-lateral abdominal wall (Figs. 1 and 2). Each sac extends anteriorly to the cranial tip of the liver and presses against the posterior margin of the intermediate sac. Posteriorly, the sac reaches slightly beyond the last rib; dorsally it is limited by the pulmonary diaphragm and posterior abdominal air sac, ventro-laterally by the body wall, and medially by the viscera. The anterior abdominal sac is separated from the posterior abdominal sac by the parietal peritoneum covering of both sacs.

Three separate ostia from each sac were noted in one Loon. Two small openings were located on the postero-ventral margin of the lung, and a large one was slightly anterior and medial to these. Numerous parabronchi extended from the lung into the wall of this larger ostium. A second Loon was found to have only two ostia from the anterior abdominal sac to the lung—the smaller, marginal ostium being absent. All ostia pierce the muscular pulmonary diaphragm which lies between the lung and the air sac.

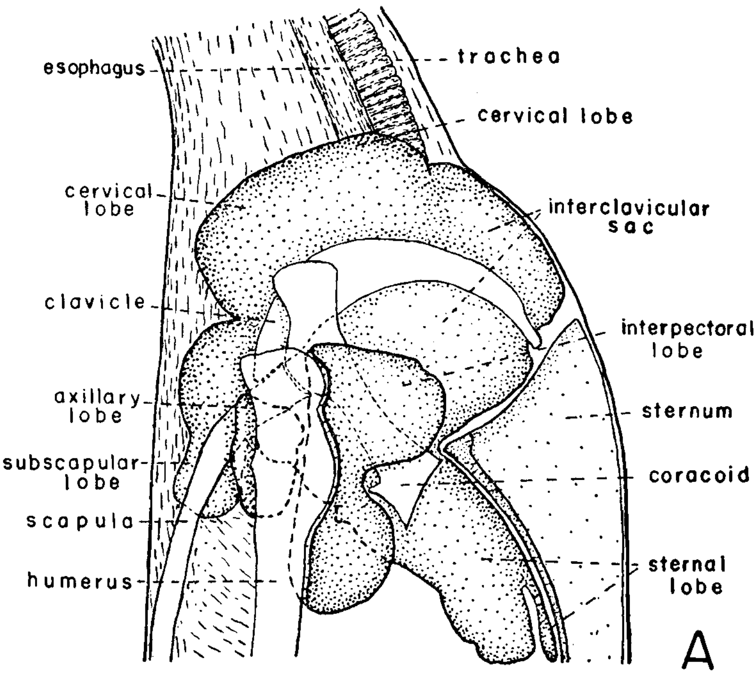
THE POSTERIOR ABDOMINAL SACS

The posterior abdominal sacs (abdominal of Locy and Larsell; greater abdominal of McLeod and Wagers) are the largest, most asymmetrical air sacs in the Loon and extend from the tip of the lung to the posterior limit of the abdominal cavity (Figs. 1 and 2). Dorsally and laterally, they are limited by the body wall with which they are fused; ventrally and medially, they adjust their shape to the digestive viscera. The left abdominal, which was observed to be the larger of the two sacs in the three Loons examined, is much broader posterior to the gizzard. The enlarged portion of this sac crosses the midline of the body and extends around the tip of the smaller and more uniform right abdominal. These sacs have no diverticula in the Loon. Variations of the general contour of the posterior abdominal sacs were found in all specimens examined.

Connection of the posterior abdominal sac with the posterior tip of the lung occurs regularly by a single broad tube which is a direct continuation of the mesobronchus. In one specimen, a second, smaller connection was found lying parallel to the regular connection.

DISCUSSION

No injection material which is entirely satisfactory has been used thus far in the study of air sacs. Paraffin, which must be heated before injection, is apt to solidify before all the sacs are filled. Any



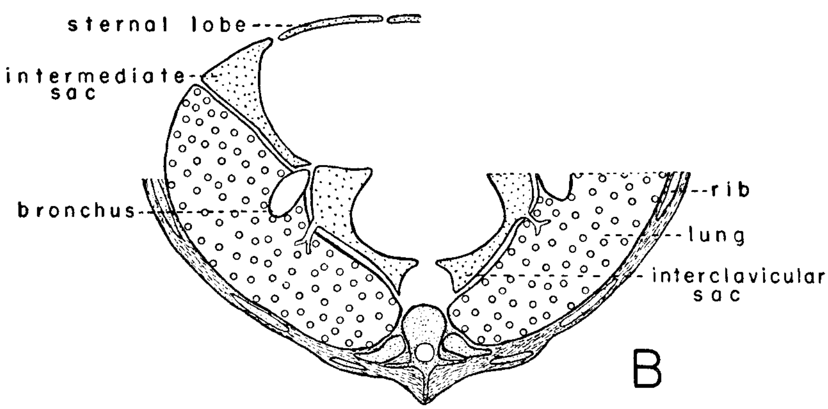


FIGURE 3. *A*. Lateral view of pectoral region of Common Loon to show relationships of interclavicular diverticula and pectoral girdle. *B*. Transverse section through body of Loon, at level of guide line for "interclavicular sac" on Figure 1, to show the dissection made to obtain the view represented in that drawing. (Both ⅖ nat. size.)

fluid which might be in the sacs is a hindrance to proper filling of the system. Paraffin with a low melting point must be used so that the body of the bird is not heated to a high degree, which would weaken the tissues and increase the danger of rupture. Paraffin that melts at 45° C. is too pliable, and the shape of the air sacs becomes distorted during dissection. Paraffins of higher melting points require too much heat and are too brittle to maintain slender connections.

Gelatin requires little heat and mixes with water. However, in either alcohol or formaldehyde, the gelatin becomes extremely brittle so that it crumbles within the sacs, and interconnections are difficult to follow.

Wood's alloy, which has a specific gravity of 9.5 and a melting point of 70° C., gives an excellent injection of the lungs. For a bird as large as a Loon, however, the mass of Wood's alloy necessary to fill the respiratory system is so great that it would rupture the air sacs. Also, it seems from Gilbert's discussion (1939) that it is nearly impossible to get a complete injection in a single specimen.

Liquid latex is an excellent injection medium, since it is elastic, holds its shape, and fills connections so that they do not break when dissected. However, it was not available at the time this work was done. Details of its use will be given in subsequent reports.

Muller (1908) injected formalin through the trachea before filling the air sacs with an injection mass. Sacs fixed in formalin, chromic acid, or other fixatives are toughened enough to withstand considerable extra pressure, but they are shrunken by such treatment and thus normal distention is prevented. On the other hand, fresh sacs are so soft that there is no question about full, and sometimes abnormal, distention; however, possibilities of rupture of free-walled sacs are much greater than when the walls are properly fixed. Birds as large as a Loon usually have firm enough air sacs that any reasonable pressure (up to four or five pounds per square inch) will not cause a rupture, unless the walls are already weakened by bacterial decomposition or excessive heat.

The air sacs of the Loon are simple and smooth in outline, compared to those of other birds. The large smooth diverticula have no intricate connections or delicate tubes such as have been found in most of the orders of birds. Ostia connecting the air sacs with the lung of the Loon are in approximately the same position as those described in the Pigeon by Muller (1908). Muller, however, does not point out variations of the locations of the ostia, which are noticeable in the three Loons examined. Absence of the cervical air sacs, of pneumatized bones, and of small secondary diverticula in the Loon constitutes the essential difference between the air sacs of the Loon and those of most of the other orders of birds that have been examined.

SUMMARY

Air sacs of several orders of birds have been studied. The Common Loon was selected as showing the simplest set of air sacs. Specimens were prepared by injection of the respiratory system with paraffin, followed by fixation in formalin. The animals were dissected to establish relationships of air sacs to other structures.

The air sacs of the Loon consist of an unpaired interclavicular sac anterior to the lungs and the paired intermediate, anterior abdominal, and posterior abdominal sacs posterior to the pulmonary diaphragm. The interclavicular air sac occupies much of the space anterior to the heart. It has five pairs of diverticula, namely the cervical, sternal, subscapular, axillary, and interpectoral. The intermediate sacs are almost symmetrical, are located medio-ventral to the lungs, and nearly surround the heart. The large asymmetrical anterior abdominal sacs are ventro-lateral to the liver. The posterior abdominal sacs are the largest and most asymmetrical and are dorso-lateral to the abdominal viscera.

In the Common Loon there is no penetration of any bone by any air sac.

LITERATURE CITED

GILBERT, PERRY W. 1939. The avian lung and air-sac system. Auk, 56: 57–63, 1 pl.

HOWELL, A. B. 1937. Morphogenesis of the shoulder architecture: Aves. Auk, 54: 364–375, 3 figs., 1 table.

KAUPP, B. F. 1918. The anatomy of the domestic fowl. (W. B. Saunders Co., Phila.), 11–373 pp., illus., col. pl.

LOCY, W. A., AND O. LARSELL. 1916. The embryology of the bird's lung. Part I. Amer. Journ. Anat., 19: 447–504, 46 figs.

LOCY, W. A., AND O. LARSELL. 1916. The embryology of the bird's lung. Part II. Amer. Journ. Anat., 20: 1–44, 22 figs.

MCLEOD, W. M., AND R. P. WAGERS. 1939. The respiratory system of the chicken. Journ. Amer. Vet. Med. Assoc., 95 (748): 59–70, 12 figs., 1 table.

MULLER, B. 1908. The air sacs of the pigeon. Smiths. Misc. Coll., 50: 365–414, 12 figs., 5 pls.

Contribution No. 231, Department of Zoology, Agricultural Experiment Station, Kansas State College, Manhattan, Kansas, March 8, 1951.