

THE LUNG AND AIR-SAC SYSTEM OF THE COMMON GRACKLE

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THIS paper describes and discusses the anatomy of the lung and air-sac system in the Common Grackle, *Quiscalus quiscula*. Much has been published about air sacs of many birds in many orders, but few detailed studies have been made of single species, especially in the order Passeriformes. The only recent publications known to us are those on the House Sparrow, *Passer domesticus*, by Wetherbee (1951) and Delphia (1961). Wetherbee's study of the adult was brief and gave no details about the lungs and diverticula of the interclavicular sac. Delphia described the origin and location of the secondary bronchi but did not consider the air sacs in the adult. The comparative studies of Baer (1896), Fischer (1905), Schulze (1911), and Juillet (1912) include parts of passeriform lung and air-sac anatomy, but attempt no complete description of any one species.

METHODS AND MATERIALS

Table 1 lists the names of the parts of the air-sac system in the Common Grackle. The terminology of Hamlet and Fisher (1967) is used for the air sacs.

Of the many techniques developed in past years, we consider that of Hamlet and Fisher (1967) the most satisfactory. It was used in this study and is fully described in their paper. Briefly, the air in the respiratory tract of a freshly killed bird is evacuated, carbon dioxide is injected and evacuated several times, and finally liquid latex is injected. The latex and moist tissues absorb the carbon dioxide, allowing the latex to fill the minute passageways and diverticula. The bird is then injected with and immersed in formalin.

We used 8 Common Grackles, and for comparative purposes we also studied 8 Cardinals, *Richmondia cardinalis*, 2 Rufous-sided Towhees, *Pipilo erythrophthalmus*, and 1 Song Sparrow, *Melospiza melodia*. We found no significant differences in structure of the air-sac system in the four species. Specimens were live-trapped and killed with chloroform.

THE LUNGS

Just inside the lung the mesobronchus immediately gives rise to four ventrobronchi (Figure 1):

Ventrobronchus 1 forms the entire portion of the ventral aspect of the lung anterior to the bronchus. It stems dorsally from the mesobronchus and forms two large branches that in turn divide into several, bringing the total number of tubes to approximately 11. Dorsally V. 1 gives rise to parabronchi (also called tertiary bronchi).

Ventrobronchus 2 also originates dorsally from the mesobronchus. It bifurcates just outside the mesobronchus. One branch extends along the ventral surface of the lung to the medial edge and connects to parabronchi on its dorsal surface. The

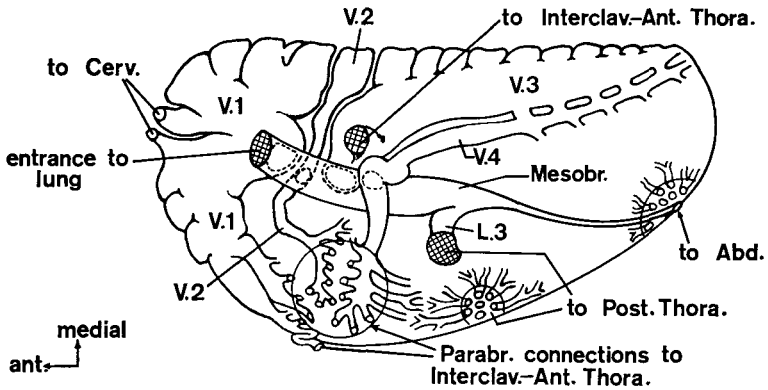


Figure 1. Ventral view of right lung of Common Grackle showing ventrobronchi. Parabronchial connections to mesobronchus and dorso- and laterobronchi are not shown except for laterobronchus 3. Dotted circles represent openings of ventrobronchi to mesobronchus. Length of casts averaged 3 cm. Abbreviations: Abd., abdominal sac; Cerv., cervical sac; Interclav.-Ant. Thora., interclavicular-anterior thoracic sac; L. 3, third laterobronchus; Mesobr., mesobronchus; Parabr., parabronchus; Post. Thora., posterior thoracic sac; V. 1-4, ventrobronchi 1-4.

second branch curves dorsally into the lung, then ventrolaterally toward the ventrolateral edge where it ends in a network of parabronchi posterior to the latero-most branch of V. 1.

Ventrobronchus 3 arises from the dorsomedial surface of the mesobronchus. It also bifurcates: one branch goes to the interclavicular-anterior thoracic sac (Figure 1), the other extends posteriorly along the ventral surface of the lung and connects to parabronchi dorsally.

Ventrobronchus 4 arises on the medial side of the mesobronchus. It branches once, sending one branch parallel to V. 3 and the other to the lateral edge of the lung where it ends in a system of parabronchi near the lateral branch of V. 2 and the

TABLE 1
PARTS OF THE AIR-SAC SYSTEM IN THE COMMON GRACKLE

Sac	Diverticula
Cervical (single)	D. intervertebrale
Interclavicular-anterior thoracic (single)	D. subscapulare D. suprahumerales D. axillares D. propatagiales D. subcordales
Posterior thoracic (paired)	None
Abdominal (paired)	D. dorsales and two secondary diverticula

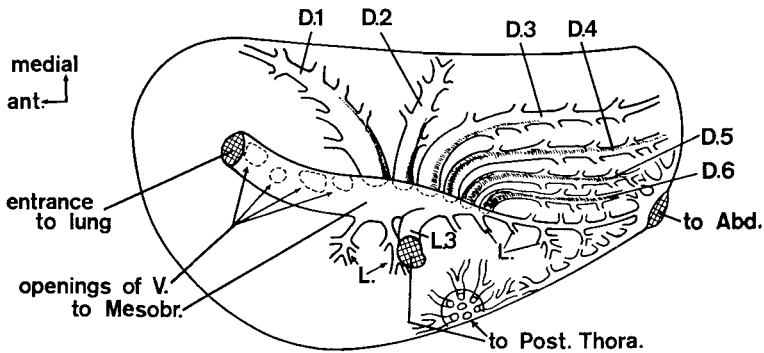


Figure 2. Ventral view of right lung of Common Grackle showing dorsobronchi. Abbreviations: D. 1-6, dorsobronchi 1-6; L., laterobronchi; others as in Figure 1. and laterobronchi. Ventrobronchi are not shown. Length of casts averaged 3 cm.

posterolateral branch of V. 1. Both portions connect to parabronchi and branch within the parabronchial system.

Posterior to V. 4, the mesobronchus, which remains close to the ventral surface in the anterior portion of the lung, constricts and turns dorsally to curve toward the posterolateral edge. The posterior half of the mesobronchus, reduced to a fraction of its original diameter, passes beneath the dorsal surface of the lung and enters the abdominal sac (Figure 1).

DORSOBRONCHI

Posterior to V. 4, where the mesobronchus curves posteriorly, six dorsobronchi branch from the medial side of the mesobronchus (Figure 2). Often they are not visible on the lateral surface of the lung because of an overlying network of parabronchi. In some lung casts the tubes may be traced to the dorsomedial edge.

LATEROBRONCHI

The thin posteroventral portion of the lung is subtended with parabronchial-size laterobronchi (Figure 2). Locy and Larsell (1916a, 1916b), in the Domestic Fowl, *Gallus gallus*, and Delphia (1961), in the House Sparrow, found the laterobronchi as discrete secondary branches of the mesobronchus, which branched in a predictable manner. We found a variable system of tubules. In one specimen four main bundles of tubules came off the mesobronchus and gave rise immediately to parabronchial-like tubules. In other specimens as many as seven branches, some slightly larger than parabronchi and some as large as parabronchi, came off the mesobronchus randomly. There seems to be no orderly arrangement of branching in the laterobronchi.

The largest laterobronchus (L. 3) comes off the ventral surface of the mesobronchus anteriorly (Figure 1). It then curves posteriorly and enters the posterior thoracic sac.

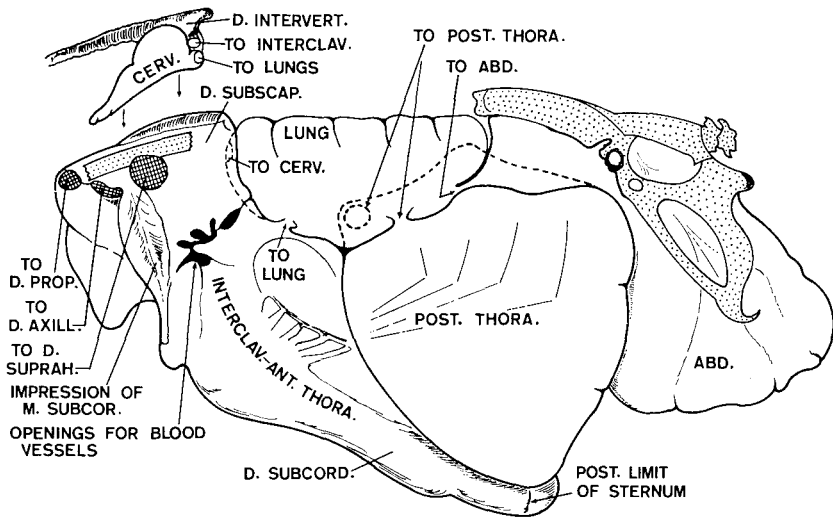


Figure 3. Lateral view of air sacs and lung of the Common Grackle. The cervical sac lies medial to D. subscapulare. All muscles and bones, except the scapula and synsacrum, have been removed. Abbreviations: D. axill., D. axillare; Interclav., interclavicular-anterior thoracic sac; D. intervert., D. intervertebrale; D. prop., D. propatagiale; M. subcor., M. subcoracoideus; D. subcord., D. subcordale; D. subscap., D. subscapulare; D. suprah., D. suprahumale; others as in Figure 1.

THE AIR SACS

CERVICAL SAC

The cervical sac arises from the anterior edge of each lung and wraps around the ventral portion of the neck musculature dorsal to and within a depression formed by the interclavicular-anterior thoracic sac (Figure 3). The shape and size vary, but generally the cervical sac extends anteriorly along the last one or two cervical vertebrae. D. intervertebrale arises from the cervical sac proper, passes anteriorly through the vertebral arterial canals, and surrounds the lateral and ventral surfaces of the centra in the spaces between the dia- and pleurapophyses. There are also diverticula in the fossae lateral to the neural spines and within the neural canal, dorsal and lateral to the nerve cord. In one specimen diverticula extended nearly to the axis.

INTERCLAVICULAR-ANTERIOR THORACIC SAC

Anteriorly the interclavicular-anterior thoracic sac lies between the coracoids and sternofurcular membranes (Figure 3). Posteriorly it fits against the ventral surfaces of the posterior thoracic sacs, the lungs, and heart.

We believe the anterior thoracic sacs are fused to the interclavicular sac to form one aggregate sac, because all comparable tubes connecting to the interclavicular and anterior thoracic sacs in other birds connect to the single aggregate sac in the grackle. A branch of V. 3 and lateral branches of V. 1, 2, and 4 enter the aggregate

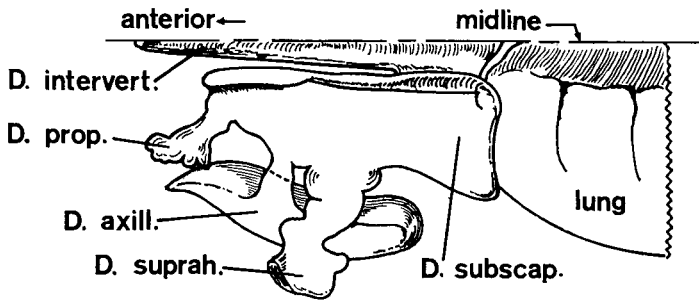


Figure 4. Dorsal view of the left half of a cast of the interclavicular-anterior thoracic sac of the Common Grackle showing lateral diverticula. Abbreviations as in Figure 3.

sac (Figure 5). The anterior branch of V. 3 bifurcates and opens anteriorly into the interclavicular sac and posteriorly into the anterior thoracic sac in many species (Juillet, 1912; Locy and Larsell, 1916a; Akester, 1960; Delphia, 1961; King, 1966). The above studies indicated that a branch of V. 1 formed the lateral moiety of the interclavicular sac. In the Domestic Fowl, King (1966: 183) showed portions of V. 1 entering the interclavicular and anterior thoracic sacs, and portions of V. 4 entering the anterior and posterior thoracic sacs. Other studies did not reveal as many parabronchial connections between the ventrobronchi and the air sacs, but all of them showed branching of the ventrobronchi on the lateral aspect of the lung. In the White Pekin Duck, *Anas platyrhynchos*, the lateral ramus of V. 2 develops into the lateral moiety of the interclavicular sac (Delphia, 1958).

We believe only the anterolateral region of D. subcordale represents the fused anterior thoracic sacs in the grackle. In the House Sparrow the interclavicular and anterior thoracic sacs are fused, but Wetherbee (1951) assumed that all of D. subcordale constituted the fused anterior thoracic sacs. In other birds with separate anterior thoracic sacs, the interclavicular sac still possesses a subcordale diverticulum.

Diverticulum subscapulare.—This diverticulum is actually the thin anterodorsal portion of the interclavicular-anterior thoracic sac (Figure 4). Appearing as a flattened lobe, it lies medial to the scapula under M. dorsalis scapulae. The interclavicular-anterior thoracic sac connects to the cervical sac via two flattened tubes. One tube arises from the posteromedial edge of each D. subscapulare (Figure 5).

Diverticulum suprahumeral.—D. suprahumeral arises from the lateral side of D. subscapulare just ventral to the scapula and dorsal to the inserting head of M. subcoracoideus (Figures 3, 4). The diverticulum extends between the scapula and M. dorsalis scapulae and expands such that, with the long head of M. deltoideus major and the scapular head of M. triceps reflected, the diverticulum is exposed deep to M. proscapulohumeralis and dorsal to M. dorsalis scapulae. This sac also extends into the pneumatic fossa of the humerus, but there is no penetration of the humerus, which lacks even the pneumatic foramen.

Diverticulum axillare.—D. axillare is dorsoventrally flattened (Figure 4). It arises from the lateral side of the interclavicular-anterior thoracic sac, just anterior to the insertion of M. subcoracoideus (Figure 3). D. axillare passes ventral to D.

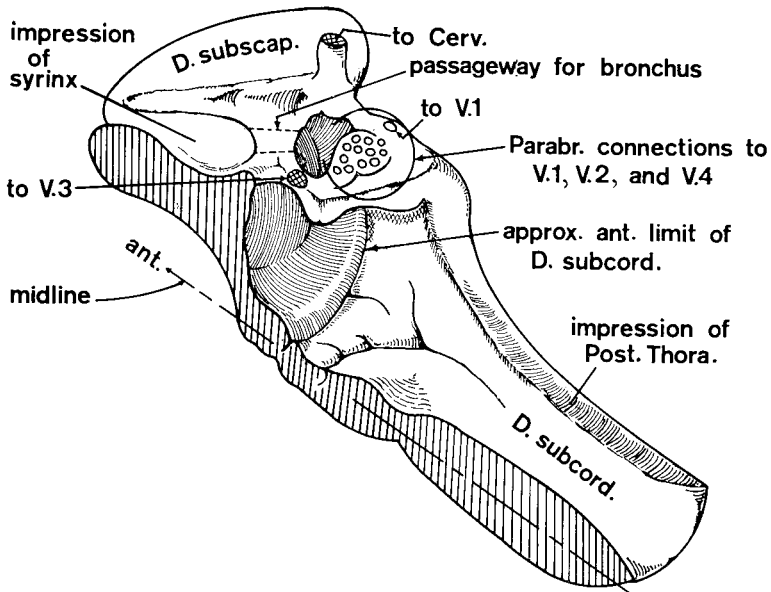


Figure 5. Posteromedial view of the right half of a cast of the interclavicular-anterior thoracic sac and its connections to the lung of a Common Grackle. Abbreviations as in Figures 1 and 3.

suprahumerale and close to the angle formed by the humerus and the coracoid to expand in the space formed between *M. coracobrachialis* medially, the insertion of *M. dorsalis scapulae* dorsally, and *M. pectoralis major* laterally and ventrally. The diverticulum also passes anteriorly, between the coracoid and *M. pectoralis major*, to the anterolateral portion of the coracoid head.

Diverticulum proptagiale.—*D. proptagiale* arises from the anterior edge of *D. subscapulare* medial to the head of the clavicle (Figures 3, 4). It passes through the sternofurcular membrane and forms a pocket under the trisoseum. This pocket lies near the anterior edge of, but does not communicate with, *D. axillare* in this region. In some specimens it communicates with *D. suprahumeralis* through the trisoseal canal.

Diverticulum subcordale.—*D. subcordale* is a broad, median lobe of the interclavicular-anterior thoracic sac extending posteriorly between the heart and the sternum to the caudal edge of the sternum and it separates the ventral edges of the posterior thoracic sacs. It passes anteriorly to the ventral edges of the lungs (Figures 3, 5).

Posterior thoracic sacs.—The anterior and ventral walls of the paired, posterior thoracic sacs lie against the interclavicular-anterior thoracic sac (Figure 3). Laterally, the sac is bordered by the ribs and abdominal muscles. Most of the posterior edge and posteromedial surface lie against the abdominal sac. The antermost surface projects medially and lies against the posteroventral surface of the lung.

Abdominal sacs

The paired abdominal sacs lie dorsal and lateral to and often among the viscera in the abdominal cavity (Figure 3).

A small diverticulum (D. dorsale) arises dorsally from the anterior portion of the sac just posterior to the lung, courses caudally in the dorsal part of the body cavity, and extends into the pelvis. A secondary diverticulum in the region of the pectineal process extends over the dorsal surface of the ilium to the acetabulum. The femur is not pneumatized. Small lobes surround the neck of the femur and also protrude from the obturator foramen. Part of the abdominal sac fills the ilio-ischiatic fenestrum but extends from the fenestrum toward the femur only at the anterior edge.

Injection of a gravid female forced the egg partly out of the cloaca, indicating that an egg or a full gut displaces some of the volume of these sacs.

CONNECTIONS BETWEEN LUNGS AND AIR SACS

The cervical sac connects directly with the antermost branches of V. 1 (Figure 1). Two, sometimes three, tubes make this connection. The cervical sac also connects to the interclavicular-anterior thoracic sac.

The interclavicular-anterior thoracic sac has two primary connections to the lung, one via a branch of V. 3 (Figure 1), and another via several parabronchi from V. 1, 2, and 4 at the lateral edge of the lung (Figures 1, 3, 5). The connection originating from V. 3 branches just before entering this sac, sending one extension anteriorly into the interclavicular sac proper and the other into what appears to be the fused anterior thoracic sac (Figure 5).

The posterior thoracic sac connects to the lung in two places, directly from one of the laterobronchi (Figure 2) and indirectly via several parabronchi along the posterolateral edge of the lung (Figures 1, 2, 3). In most species studied, laterobronchus 2 or 3 leads directly into this sac. In the adult grackle, it was generally laterobronchus 3. Some of the parabronchi communicating with the posterior thoracic sac come from ramifications of V. 4 and from some of the laterobronchi.

The abdominal sacs, too, have direct and indirect connections to the lungs. The sacs connect to the posterolateral portion of the lungs via an extensive coalescence of parabronchi; the mesobronchial connection is the same diameter as a parabronchus. The parabronchial connections come from ramifications of the more posterior laterobronchi.

DISCUSSION

While we found no significant differences in comparing the Common Grackle with the Cardinal, Rufous-sided Towhee, and Song Sparrow, the lungs of the three smaller species tended to have fewer laterobronchi. These four species are considered to be in New World families. The air-sac system in some Old World song birds is essentially the same, especially in the amount of fusion of the interclavicular with the anterior thoracic sacs. Schulze (1911) mentioned that these sacs were fused in some European song birds, and Wetherbee (1951) reported the condition in the House Sparrow. The connections between the lung

and air sacs in the Jay, *Garrulus glandarius*, Chaffinch, *Fringilla coelebs*, Greenfinch, *Carduelis chloris*, *Emberiza sp.*, *Saxicola sp.* (Juillet, 1912) and House Sparrow (Delphia, 1961) are also similar to what we found.

At this time it is unknown whether or not the fusion of the interclavicular with the anterior thoracic sacs is primarily a passeriform characteristic. To date, only the Turkey, *Meleagris gallopavo* (Cover, 1953; Rigdon et al., 1958); Red-tailed Tropic-bird, *Phaethon rubricauda* (Casler, MS); and some Apodiformes (Stanislaus, 1938) are known to have these same sacs completely fused.

ACKNOWLEDGMENTS

We thank Harvey I. Fisher for reading the manuscript and suggesting improvements.

SUMMARY

The lungs of the Common Grackle, Cardinal, Rufous-sided Towhee, and Song Sparrow have four ventrobronchi, six dorsobronchi, and a variable number of laterobronchi. The abdominal, posterior thoracic, and cervical sacs are similar to those described for other birds. The interclavicular and anterior thoracic sacs are fused into one unpaired sac. All sacs except the cervical have several parabronchial connections to the lung and one direct connection with either the mesobronchus or a major branch of it.

Existing literature, although still scanty, suggests a great amount of similarity in the air-sac systems of passeriforms.

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