THE AIR-SAC SYSTEMS AND BUOYANCY OF THE ANHINGA AND DOUBLE-CRESTED CORMORANT

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BOTH the Anhinga, Anhinga anhinga, and the Double-crested Cormorant, Phalacrocorax auritus, secure prey while swimming submerged, but they vary considerably in their buoyancy (Owre 1967: 60-63). Anhingas usually swim at the surface with only the head and part of the neck emergent. Cormorants, when at the surface, always swim with the back and shoulders exposed. Anhingas seem to expend little effort in remaining submerged even when moving at low speed. In fact, the Anhinga may use its feet to overcome a tendency to sink slowly (Owre 1967: 107). In contrast, cormorants must paddle with their feet to remain submerged.

A number of factors may operate in producing this difference in buoyancy. Water absorption by the feathers of the Anhinga and cormorant is considered an adaptation to reduce buoyancy (Owre 1967: 61). The Anhinga's breast feathers are completely void of hooklets for interlocking the barbules. In the cormorant only the distal portions of the barbs are devoid of hooklets (Casler MS). The structure of Anhinga feathers allows water to penetrate any air spaces next to the skin thus reducing buoyancy. As only the distal portions of cormorant feathers are modified to hold water, the feathers apparently enclose some air next to the skin in the thicker layer of down feathers and thereby afford some buoyancy.

In addition, the cormorant's skin is thicker and spongier and appears more pneumatic. Structural differences of the feathers and skin undoubtedly contribute to differences in buoyancy between the two species.

The Anhinga may use ballast in the form of water. Owre (pers. comm.) has often noted what appears to be copious drinking before submerging. This would be helpful, especially as the specific gravity of the bird's body is normally less than that of water.

The air-sac system may also contribute to the differences in buoyancy, but little is known about air-sac systems in diving birds. The Anhinga's air sacs might be permanently and greatly reduced in volume and in extent of bone penetration, thus making the bird less buoyant. Also the Anhinga's aquatic habits, unlike those of the cormorant, suggest that the Anhinga controls its specific gravity; this may be accomplished by regulating the volume of the air-sac system. This paper describes and illustrates the structure of the air-sac systems of the Anhinga and Double-crested Cormorant and correlates modifications of their structure and behavior with differences in buoyancy.

Air sac	Cormorant	Anhinga
Medial interclavicular	Single, no diverticula	Same
Lateral interclavicular A. Medial chamber	Single or paired	Single
D. subcordale B. Lateral chambers	Present	Present
D. subpectorale	Present	Present
D. subscapulare	Present	Present
D. cervicale	Present	Absent
D. propatagiale	Present	Absent
D. suprahumerale	Present	Present (?)
Cervical	Paired, no diverticula	Same
Lateral cervical	Paired, no diverticula	Same
Anterior thoracic	Single, right side only	Paired, no diverticula
Posterior thoracic	Paired, no diverticula	Same
Abdominal	Paired, no diverticula	Same

TABLE 1

PARTS OF THE AIR-SAC SYSTEM IN THE ANHINGA AND DOUBLE-CRESTED CORMORANT

METHODS AND MATERIALS

In past years, various techniques have been developed to study air sacs by injecting them with different materials to form casts that can be handled. This study used the recently improved technique of Hamlet and Fisher (1967). Fully discussed in their paper, this method uses carbon dioxide to absorb the liquid latex as it fills the minute diverticula and passageways of the air-sac system.

Adult specimens were collected in southern Florida in March 1968. Four Anhingas (two of each sex) and three female cormorants were used.

To reduce nomenclatural problems, I have used the terminology of Hamlet and Fisher (1967) who mostly followed that of Ulrich (1904) and Müller (1908). Table 1 lists parts of the air-sac systems in the Anhinga and Double-crested Cormorant.

The air-sac system and lungs of the Anhinga and Cormorant are similar, and the descriptions pertain to both species except as differences are noted. The casts of lungs and air-sacs showed little intraspecific variation except in the diverticulum subcordale.

THE LUNGS

Mesobronchus.—The mesobronchus first gives rise to five ventrobronchi (Figure 1). It then curves posteriorly toward and appears upon the dorsolateral surface, where it gives rise to a variable number of dorsobronchi and laterobronchi (Figure 2). Caudally the diameter of the mesobronchus narrows and, at the posterior edge of the lung, opens into the abdominal air sac (Figures 1 and 5). The main opening is accompanied by secondary ostia (not shown in figures) only in the Anhinga.

In the region of the ventrobronchi, the mesobronchus has no connecting

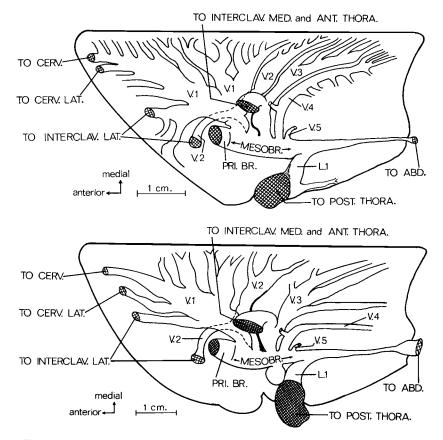


Figure 1. Ventral view of right lung showing relationship between mesobronchus and ventrobronchi. Top, Anhinga; bottom, cormorant. Abbreviations: LUNGS—Br., bronchus; D., dorsobronchi; L., laterobronchi; Mesobr., mesobronchus; Parabr., parabronchus; Pri. br., primary bronchus; V., ventrobronchi. AIR SACS—Abd., abdominal sac; Ant. thora., anterior thoracic sac; Cerv., cervical sac; Cerv. lat., lateral cervical sac; Interclav. lat., lateral interclavicular sac; Interclav. med., medial interclavicular sac; Post. thora., posterior thoracic sac. DIVERTICULA—D. cerv., D. cervicale; D. prop., D. propatagiale; D. subcord, D. subcordale; D. subpect., D. subpectorale; D. subscap., D., subscapulare; D. suprah., D. suprahumerale.

parabronchi, but some small bronchi connect to the mesobronchus in the region of the dorso- and laterobronchi. These may correspond to the caudolateral secondary bronchi of King (1966).

First ventrobronchus.—V. 1 is the largest in diameter and its largest branch extends to the anterior edge of the lung and connects to the cervical sac (Figure 1). The main opening to the cervical sac is accompanied by

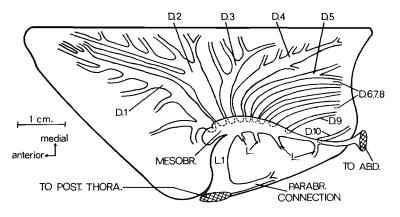


Figure 2. Anhinga. Dorsolateral view of left lung showing relationships between mesobronchus, dorsobronchi and laterobronchi. Abbreviations as in Figure 1.

secondary ostia. Another branch, usually the next lateral one, goes to the lateral cervical sac. The main ostium of this sac is not accompanied by secondary ostia, but parabronchial (also called tertiary bronchial) openings are just inside the lung. The lateromost of the anterior projecting branches of V. 1 is the anterior opening to the lateral interclavicular sac. In one Anhinga two branches opened into this sac anteriorly. Secondary ostia may be present near the major opening, and parabronchi connect to the branch.

The cormorant has no secondary ostia into the three air sacs. Only three anterior projecting branches of V. 1 exist; each opens into an air sac (Figure 1, bottom).

Second ventrobronchus.—V. 2 has two main branches (Figures 1 and 3). A large branch extends medially on the ventral surface of the lung and gives

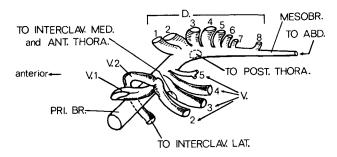


Figure 3. Anhinga. Mediodorsal view of mesobronchus with ventrobronchi and dorsobronchi. Natural size. Abbreviations as in Figure 1.

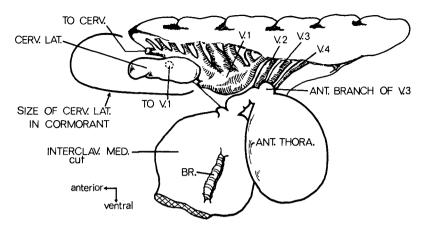


Figure 4. Anhinga. Medioventral view of right lung showing connections between medial interclavicular and anterior thoracic sacs. Natural size. Abbreviations as in Figure 1.

rise to parabronchi. The smaller branch curves dorsal to V. 1 inside the lung and comes to the ventral surface just anterior to the entrance of the primary bronchus. This second branch gives rise to the posterior of the two openings into the lateral interclavicular sac. Only in the Anhinga are secondary ostia present.

Third ventrobronchus.—V. 3 divides into two branches (Figure 1). A large branch extending caudomedially on the ventral surface gives rise to parabronchi only. Close to the mesobronchus, at the ventral surface, a short branch turns sharply and bifurcates just outside the lung. The

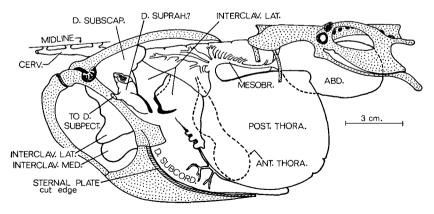


Figure 5. Anhinga. Lateral view showing relationships of air sacs and skeleton. D. subpectorale not shown. Abbreviations as in Figure 1.

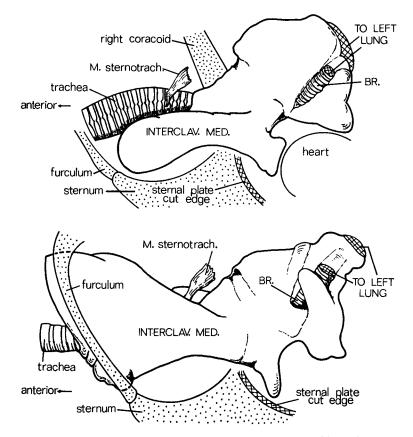


Figure 6. Lateral view of medial interclavicular sac. Top, Anhinga; bottom, cormorant. Natural size. Abbreviations as in Figure 1.

branch opens anteriorly into the medial interclavicular sac and posteriorly into the anterior thoracic sac (Figure 4). Secondary bronchi may connect to the medial interclavicular sac.

In the left lung of the cormorant, the short anterior branch of V. 3 opens into the medial interclavicular sac only. The left anterior thoracic sac is absent and there are no secondary bronchi.

Fourth ventrobronchus.—V. 4 extends posteriorly on the ventral surface, connecting to parabronchi only (Figure 1).

Fifth ventrobronchus.—V. 5 is much smaller than the others, connects to parabronchi only, and is not seen on the ventral surface (Figure 1).

Dorsobronchi.—The mesobronchus gives rise to 8 to 10 dorsobronchi (Figures 2 and 3). They connect to parabronchi only.

Laterobronchi.---Most laterobronchi are smaller than the other secondary

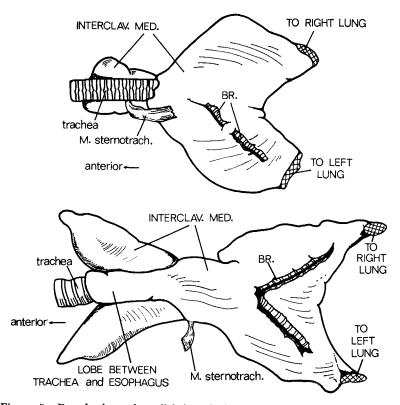


Figure 7. Dorsal view of medial interclavicular sac. Top, Anhinga; bottom, cormorant. Natural size. Abbreviations as in Figure 1.

bronchi, but laterobronchus 1, which opens into the posterior thoracic sac, is as large or larger in diameter than the primary bronchus (Figure 2). The homologies of the laterobronchi are unknown. In the chicken, *Gallus domesticus* (Locy and Larsell 1916a, 1916b) and House Sparrow, *Passer domesticus* (Delphia 1961) the posterior thoracic sac arises from laterobronchus 3. This same laterobronchus appears to be number 1 in the adult Anhinga and cormorant. Parabronchial connections with laterobronchus 1 are absent except for one (in *Anhinga* only) from the ventral edge where many parabronchi converge (Figure 2).

Posterior to laterobronchus 1, five small laterobronchi are usually present on the dorsal surface (Figure 2).

THE AIR SACS

The Anhinga and cormorant appear to have two interclavicular sacs, contrary to the situation in other birds studied. I refer to the sac on the

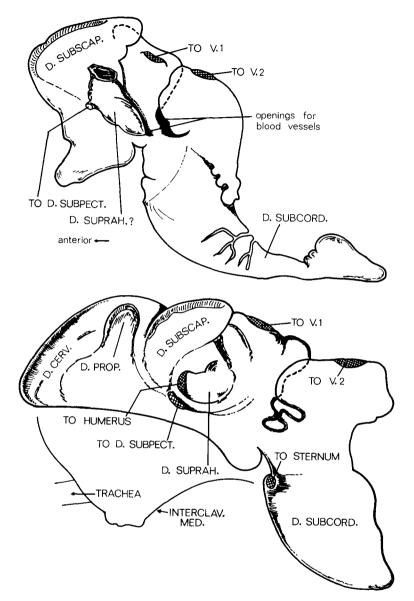


Figure 8. Lateral view of lateral interclavicular sac. Top, Anhinga; bottom, cormorant. Natural size. Abbreviations as in Figure 1.

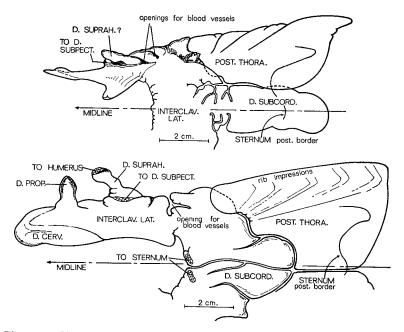


Figure 9. Ventral view of lateral interclavicular sac. Top, Anhinga; bottom, cormorant: D. subcordale shown unfused at the midline. D. subscapulare not shown. Abbreviations as in Figure 1.

midline (enclosing the syrinx) as the medial interclavicular sac and the other (possessing diverticulum subcordale) as the lateral interclavicular sac (Figure 5).

In the Anhinga the air-sac system does not penetrate any bones. Only the humerus, sternum, and centra of a few cervical vertebrae (nos. 15-17) of the cormorant are penetrated. In both species only the lateral interclavicular sac has diverticula.

Medial interclavicular sac.—The medial interclavicular sac is unpaired and centrally located immediately ventral to the esophagus (Figures 6 and 7). The sac consists of two flattened lateral lobes that arise from the lungs via V. 3. The lobes partially envelop the bronchi and join dorsally at the midline to form a central chamber (Figure 7). This central chamber encloses the syrinx and extends anteriorly between the coracoids and into the interclavicular fossa (Figure 6). Laterally the sac is surrounded by the lateral interclavicular sac.

Anteriorly the central chamber is greatly widened and V-shaped in the cormorant (Figures 6 and 7, bottom) and within the V, a small median lobe lies dorsal to the trachea (Figure 7, bottom).

Lateral interclavicular sac.—The lateral interclavicular sac connects to each lung via V. 1 and V. 2 (Figure 8). From each lung, laterally flattened lobes extend ventrally and anteriorly and join at the midline, giving rise to a median diverticulum—D. subcordale (Figures 5, 8, 9). The anterior portion of the sac consisting of D. subscapulare, D. suprahumerale (?), and D. subpectorale lies lateral to the ribs and posterior to the coracoid. The caudal edge of the sac fits tightly against the posterior thoracic sac (Figure 5). Anteriorly M. supracoracoideus and M. subscapularis are lateral to the sac. External to the midportion of the sac are M. coracobrachialis posterior, M. serratus anterior, and M. sternocoracoideus. Posteriorly cervical ribs 1 and 2 are lateral to the sac. The sac lies external to the medial interclavicular sac, heart, neck muscles, and esophagus. Blood vessels connecting to M. pectoralis superficialis are surrounded by this sac.

The lateral interclavicular sac of the cormorant is larger in relation to body size and extends anterior to the furculum (Figures 8 and 9, bottom). It has two additional diverticula—D. cervicale and D. propatagiale.

Diverticulum subcordale.—D. subcordale is a medium lobe extending posteriorly from the junction of the paired portions of the lateral interclavicular sac (Figures 5, 8, 9). It lies between the heart and sternum with the posterior apex sometimes surrounding the caudal tip of the heart. Anteriorly lies a series of small, tightly fitting lobes (esp. in Anhinga); the folds between them may cause the diverticulum to be greatly constricted in certain areas (Figures 8 and 9, top).

In the cormorant, D. subcordale covers only the anterior half of the sternum, but extends posteriorly to cover part of the ventral surface of the heart (Figures 8 and 9, bottom). The diverticulum at its anterior edge pneumatizes the sternum but not extensively. In two cormorants D. sub-cordale was not fused at the midline (Figure 9, bottom), producing a paired rather than a single lateral interclavicular sac.

Diverticulum subpectorale.—D. subpectorale arises by one small connection (1-3 mm diameter) from the lateral interclavicular sac immediately posterior to the coracoid and just ventral to the suprahumeral lobe (Figure 5). Removal of M. pectoralis superficialis exposes the sac laterally (Figure 10). The air-sac wall adheres to M. triceps, external head, as well as to other muscles. Thus configuration of the sac is changed as the humerus is moved in flight. A constriction where blood vessels extend laterally divides D. subpectorale into anterior and posterior parts. The anterior portion is laterally flattened and usually borders the furculum. Its medial wall is against M. supracoracoideus and M. coracobrachialis posterior. The opening of the diverticulum is next to the insertion of the latter muscle. The posterior portion ends as a blunt apex dorsal to the

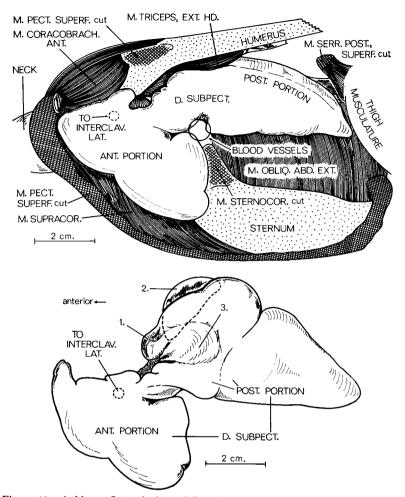


Figure 10. Anhinga. Lateral view of D. subpectorale. Top: M. pectoralis superficialis removed. Bottom: shows dorsal lobes of posterior portion; ostium to Interclav. lat. is on medial wall. Abbreviations: l, lobe between M. dorsalis scapulae and M. triceps external head; 2, lobe medial to M. dorsalis scapulae; 3, impression of humerus. Other abbreviations as in Figure 1.

caudal edge of M. pectoralis superficialis, sometimes just under the skin. M. serratus posterior, superficial layer, lies along the posterodorsal surface of the sac. Dorsally, the posterior portion is revealed lateral to M. dorsalis scapulae by removing M. latissimus dorsi anterior and posterior (Figure 11, top).

Diverticulum subscapulare.—D. subscapulare is a flattened lobe ventral and medial to the scapula (Figures 5 and 8, top). The caudal edge lies

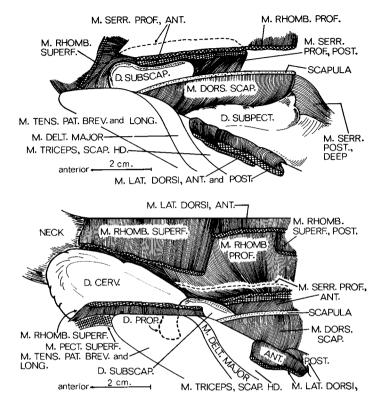


Figure 11. Dorsolateral view. Top, Anhinga: shows D. subscapulare and D. subpectorale; muscles attaching to the medial side of the scapula are cut; M. subscapularis not shown. Bottom, cormorant: shows D. cervicale, D. subscapulare, and D. propatagiale; D. subpectorale not shown. Abbreviations as in Figure 1.

lateral to cervical rib 1. M. subscapularis (not shown in Figure 11, top) lies lateral to the diverticulum, and M. serratus profundus anterior is medial and dorsal (Figure 11, top).

In the cormorant D. subscapulare does not form the anterodorsal border of the lateral interclavicular sac but lies posterior to D. cervicale (Figures 8 and 11, bottom).

Diverticulum cervicale.—It is absent in Anhinga (Figure 8, top). In the cormorant D. cervicale is a broad lobe forming the anterior portion of the lateral interclavicular sac (Figure 8, bottom). It is medial to the junction of the coracoid and furculum and extends anterior to the furculum. The medial wall lies next to the neck muscles. Dorsally D. cervicale is exposed by removing M. rhomboideus superficialis, but anterior to this muscle the sac lies just beneath the skin (Figure 11, bottom).

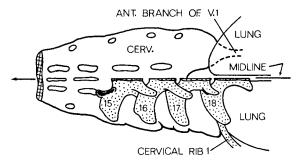


Figure 12. Cormorant. Dorsal view of cervical sacs. Penetration of centra of vertebrae 15-17 not shown. Natural size. Abbreviations as in Figure 1.

Diverticulum propatagiale.—D. propatagiale is absent in Anhinga. In the cormorant (Figure 11, bottom) it arises from D. cervicale. It is a small lobe about 15 mm in length and fills the triosseal canal (Figures 8 and 9, bottom).

Diverticulum suprahumerale.—The existence of D. suprahumerale in the Anhinga is questionable. A small lobe is present that corresponds in location to D. suprahumerale in the cormorant, but it does not pneumatize the humerus or even reach the pneumatic fossa (Figures 8 and 9, top).

In the cormorant D. suprahumerale arises from the lateral interclavicular sac slightly posterior to the coracoid (Figures 8 and 9, bottom). It pneumatizes the humerus via the foramen in the pneumatic fossa.

Cervical sacs.—The paired cervical sacs arise from V. 1 near cervical vertebra 18 and extend cranially through only five or six vertebrae (Figures 5 and 12). These small, tubular sacs penetrate the vertebrarterial canals, the intervertebral spaces (where left and right sacs fuse), and the neural canal. The sacs are most extensive near cervicals 17 and 18, but immediately diminish in diameter anteriorly and lie only in the neural canal. A septum separates the sacs from the nerve cord. The septum is especially distinct in the cormorant where it divides the diameter of the neural canal into three sections. The most veneral section contains the nerve cord, and the two dorsal sections the left and right cervical sacs.

In the cormorant the cervical sacs extend anteriorly to approximately cervical number 7. The centra of vertebrae 15–17 are penetrated.

Lateral cervical sacs.—The paired, lateral cervical sacs arise from V. 1 just lateral to the connection with but are not fused with the cervical sacs (Figure 4). These are small sacs in the Anhinga; in the cormorant they are larger in relation to body size and lie medial to D. cervicale. The sacs vary in size from bird to bird but not in number and origin. The terminology of Juillet (1912: 350) is applied to these sacs.

Anterior thoracic sacs.—A small anterior thoracic sac arises from each lung via V. 3. Each sac extends ventrally around the esophagus and may cover the side of the heart. Each is medial to the posterior thoracic sac and variable in volume (Figure 5). Usually the sac is laterally flattened with the distal end thicker, but sometimes is flattened into a thin slip lateral to the esophagus (Figure 4). A distended esophagus seems to prevent filling of these sacs.

In the cormorant only the right anterior thoracic sac exists. It extends from the right lung to the midline where it lies between the esophagus and posterior thoracic sacs. The enlarged distal end partly covers the caudal end of the heart.

Posterior thoracic sacs.—The paired posterior thoracic sacs are the largest. Each communicates with the lung by a single ostium—laterobronchus 1 (Figure 5). The sacs are just ventral to the lungs and almost meet at the midline. Anteriorly they fit against the lateral interclavicular sac, laterally against the ribs and sternum, and medially against the heart, anterior thoracic sacs, the liver and/or esophagus, and sometimes the abdominal sacs. D. subcordale lies between the ventral edges of this pair of sacs (Figure 9, top). Thus the esophagus and part of the liver are encircled. The sacs are laterally and differentially compressed, depending upon the degree of distention of the esophagus.

In the cormorant the connection with the lung is farther posterior on the lateral side, and D. subcordale (Figure 9, bottom) separates only the anteroventral edges of the sacs.

Abdominal sacs.—The paired abdominal sacs arise from the posterior end of the mesobronchus and lie against the dorsal wall of the abdominal cavity (Figure 5). The ventral surface fits tightly against the intestine on the right side of the body and the stomach on the left side. The sacs partially envelop the testes; in females the left abdominal sac is ventral to the ovary.

Abdominal sacs vary in volume. When the stomach and intestine are distended with food, the sacs are greatly compressed and may have less volume than the lungs. In one cormorant with esophagus and stomach completely contracted, the large left sac was 43 ml whereas the right sac was only 6 ml in volume. There seems to be little space for expansion even though the sacs are capable of it.

DISCUSSION

DIFFERENCES IN BUOYANCY

Regulation of volume of air sacs.—Behavioral differences between the Anhinga and cormorant may affect the regulation of the volume of the air-sac system. As mentioned earlier, certain of the Anhinga's habits suggest it may to a degree control its specific gravity. Unlike the cormorant, the Anhinga may increase its specific gravity by expelling air before it dives. The Anhinga may regulate the air content of the subpectoral diverticula. These diverticula are large and each is connected to the lateral interclavicular sac via one small tube that lies in a narrow passageway between the coracoid and the insertion of M. coracobrachialis posterior. Wing position (flexion) or muscle contraction may affect the size of the opening or even close it. The Anhinga's peculiar habit of holding its wings slightly extended during submergence is noteworthy (Owre 1967: 61). If the opening is closed, two "buoyancy tanks" are separated from the remainder of the respiratory system. Increased volume of the diverticula could compensate for an increased specific gravity. This may explain the Anhinga's ability to remain submerged, even after feeding, with only the head and neck (or just the head) emergent. Because the wings and flight muscles are not used while the bird is underwater, the diverticula may not be needed for possible respiratory functions.

Speculation about this behavior stems from Richardson's (1939) study of the inflation of sacs in the California Brown Pelican, *Pelecanus occidentalis californicus*. Pelicans can inflate the large superficial air system, which may be modified subpectoral diverticula. This is considered an adaptation for diving, to lessen the force of impact with the water. When artificially inflated, air soon leaves the superficial air system when pressure forcing air in is reduced. Richardson attempted to explain why air does not rush out when the bird strikes the water. He proposed that tight and strong closure of the glottis kept air from escaping. I believe the pelican may close off the subpectoral diverticula where they connect to the interclavicular sac, as suggested for the Anhinga. Thus the D. subpectorale, not the entire respiratory system, would absorb most of the shock of impact with the water.

Air-sac volume and bone pneumaticity.—Compared to nondiving species, the air-sac systems of the Anhinga and cormorant exhibit few diverticula; those from the lateral interclavicular sac being exceptions. However the systems are not greatly reduced in volume.

Structural differences between the Anhinga and cormorant air-sac systems are not striking, but the Anhinga's air-sac volume is less in relation to body size. The medial interclavicular (Figure 6) and lateral cervical sacs (Figure 4) are smaller; and D. cervicale and D. propatagiale are absent from the lateral interclavicular sac (see figures 8 and 11).

The air sacs in the Anhinga penetrate no bones. The bones are heavy and have small central cavities (especially in the humerus) filled with marrow. Bones of the cormorant are pneumatic and air sacs penetrate the humerus, sternum, and the centra of a few cervical vertebrae. The humerus has a large central cavity.

Pneumatic bones, of course, increase buoyancy by reducing density in relation to total body volume. However I think the effect of differences in bone pneumaticity, combined with the differences in volume of the air sacs, may be overshadowed by the effect of the degree of distention of the digestive system. If the ingestion of food is not correlated with a proportional increase in total body volume, the distended digestive tract must displace some of the air in the air sacs, and thus increase the bird's specific gravity. This apparently happens in the Anhinga and cormorant. Specimens with stomachs distended had small abdominal sacs. The anterior and posterior thoracic sacs in some were also reduced in volume, mostly by esophageal expansion. In both species fish taken into the stomach may extend well up into the esophagus and be carried there for some length of time (Owre, pers. comm.).

Owre (1967: 129) discussed the size, quantity, and kinds of fishes eaten by the Anhinga and cormorant. Stomach contents of one Anhinga constituted more than 7 percent of the bird's total weight. A daily requirement for *Phalacrocorax auritus* is 27 percent of the body weight (Wetmore 1927) and 20 percent for *P. carbo sinensis* (Van Dobben 1952: 23). A cormorant with a distended esophagus and stomach still floats, even though it may have less total volume in its air sacs in relation to body size than an Anhinga with an empty digestive system. In my opinion, static differences in volume of the air-sac systems and bones are not significant factors in determining differences in buoyancy between the two species.

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SUMMARY

The Anhinga and Double-crested Cormorant vary considerably in their buoyancy but static differences in volume of the air-sac systems and bones are not regarded as significant factors in determining interspecific differences in buoyancy. The Anhinga's air-sac volume is less in relation to body size but the difference is not striking. The differences in air-sac volume between the two species may be overshadowed by the effect of degree of distention of the digestive system. If the digestive system is distended with food, the abdominal sacs are greatly compressed and may have less volume than the lungs. The anterior and posterior thoracic sacs are also reduced in volume. A cormorant with a full digestive system still floats, even though it may have less total volume in its air sacs in relation to body size than the Anhinga with an empty digestive system.

The air-sac system and lungs of the Anhinga and cormorant are similar except for one significant difference—the cormorant has only one anterior thoracic sac. Two separate sacs occur where the single interclavicular sac is found in most species.

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