

MORPHOLOGY OF THE LARYNX OF *CORVUS*
BRACHYRHYNCHOS (PASSERIFORMES:
CORVIDAE)

WALTER J. BOCK

The bones and muscles that support and control the opening of the glottis are among the poorest known parts of the avian skeletomuscular system. These features are either not mentioned in avian anatomical texts (e.g., Beddard 1898), or are described without illustrations (e.g., Gadow 1891:718, George and Berger 1966:264) or are described with inadequate figures (e.g., Schufeldt 1890:45, Edgeworth 1935:175-176, Fisher and Goodman 1955:36). White (1975:1891-1897) summarized the knowledge of the morphology of the larynx in domesticated birds and provided references to the veterinary anatomy literature; however, his descriptions are hard to use because of difficulties in correlating his terminology for the muscles with that used in the zoological avian anatomical literature. In all these cases, the descriptions are so vague or incomplete that it is not possible to visualize the configuration of the structures or to understand how the muscles operate to open and close the glottis. Shufeldt's descriptions, for example, apparently intermingle the 2 muscles of the larynx. None describes the constrictor muscle properly. Knowledge of the morphology of the larynx and of the muscles operating it is essential before the mechanism of this structure during respiration and feeding can be understood. Moreover, opening and closing of the glottis may play a role during calling and singing of birds by regulating the rate of air flow through the trachea. Questions such as the speed of opening or closing of the glottis may be critical in elucidating the production of avian sounds.

MATERIALS AND METHODS

Dissections were made on 6 adult specimens of *Corvus brachyrhynchus* from the avian anatomical collection of the American Museum of Natural History or which were collected especially for this study. The specimens were prepared routinely for gross dissection, i.e., fixed in 10% formalin and stored in 60-70% alcohol. All dissections were done with the aid of a Wild M5 stereo dissecting microscope; I used an iodine solution to stain the muscles. Drawings were made directly from the dissected preparations with the use of a drawing tube (camera lucida) attached to the microscope.

NOMENCLATURE

The names of the several skeletal elements of the larynx and of the associated muscles have been in a state of confusion partly because of the lack

of study of these features and partly because of some variation among different groups of birds. In its attempt to standardize avian anatomical names, the International Committee on Avian Anatomical Nomenclature (ICAAAN) has suggested (not yet published) a set of names based largely on work done on the domestic chicken (*Gallus gallus*). Most, but not all of these names, are reasonable and should be used; my only disagreement lies with the terms recommended for the 2 major laryngeal muscles that open and close the glottis. These and a few other nomenclature problems should be discussed pending publication of the *Nomina Anatomica Avium*.

The larynx of the *Gallus* is comprised of 4 bones, the large cricoid, the small dorsal procricoid, and the paired arytenoids. The cricoid possesses a pair of dorsal wings, and each arytenoid has a long caudodorsal process. In *Corvus*, the wings of the cricoid and the process of the arytenoids are represented by separate skeletal elements which must be designated by distinct terms. I know of none available in the literature and propose to call these structures the dorsal cricoid (homologous to the cricoid wing in *Gallus*) and the dorsal arytenoid (homologous to the caudodorsal process of the arytenoid in *Gallus*). The cricoid in *Corvus* could be referred to as the ventral cricoid and the arytenoid as the ventral arytenoid, but I would oppose such a terminology as unnecessarily cumbersome. Thus the larynx of *Corvus* is comprised of 8 separate skeletal elements as opposed to 4 in *Gallus*.

Names for the muscles pose special problems for 2 reasons. The first stems from the fact that 2 muscles of the larynx have not been described earlier, and the second arises as a nomenclatural question of the names of the 2 main laryngeal muscles.

In an earlier study (Bock 1972:73-75), I described a new muscle lying on the dorsal surface of the major laryngeal muscles and associated with the posterior flaps of the larynx. This muscle was named the M. thyreohyoideus superior. One of the goals of this study was to provide a better description of this muscle; however, 2 muscles were found. These muscles control elevation and depression of the posterior flaps. I know of no earlier descriptions of these muscles aside from my earlier tentative description of the one; hence these muscles must be named. They appear to be part of the M. cricothyoideus system so that appropriate names would be the M. cricothyoideus superior (= M. thyreohyoideus superior of Bock 1972) and the M. cricothyoideus posterior. Many workers have pointed out that birds do not possess a thyroid cartilage, making the name M. thyreohyoideus inappropriate for an avian muscle (e.g. George and Berger 1966:262). A substitute name, the M. cricothyoideus, has been proposed by the ICAAN for the M. thyreohyoideus and I will use it for these parts of this muscle system.

The structure of the M. ch. superior and M. ch. posterior in *Corvus* does

not provide strong clues to their evolutionary origin and possible homology. Fortunately dissection of the larynx of the Rock Dove (*Columba livia*) demonstrated clearly that these muscles are derivatives of the M. cricothyroideus system. In this species, the M. ch. superior arises from the posterior flap of the larynx but inserts on the basihyale with the rest of the M. cricothyroideus (pers. obs.). Dissection of *Plectorhyncha* (Meliphagidae) revealed a condition of the M. cricothyroideus superior that is intermediate to those seen in *Columba* and in *Corvus*. About half of this muscle in *Plectorhyncha* arises from the hyoid skeleton, mainly from the ceratobranchiale, and the rest from the dorsal edge of the cricoid cartilage (pers. obs.).

The names for the dilator and constrictor muscles of the glottis pose a greater problem. These muscles have been called the M. thyroarytenoideus and M. constrictor glottidis by most workers (George and Berger 1966:264), but these names are not the best possible. An alternate set of names, the M. laryngeus superficialis and the M. laryngeus profundus, has been suggested by the compilers of the *Nomina Anatomica Avium*. I prefer not to use these names because they necessitate 2 changes where only 1 is necessary, because they provide only a vague indication as to the position of the muscles, and because they could lead to possible confusion with other laryngeal muscles. The M. cricothyroideus superior lies superficial to the M. laryngeus superficialis, and the M. l. profundus could be interpreted as a muscle lying on the ventral surface of the larynx and hence confused with the main part of the M. cricothyroideus. I propose the names M. dilator glottidis (= M. thyroarytenoideus, M. laryngeus superficialis) and M. constrictor glottidis (= M. laryngeus profundus) for these muscles because these names are descriptive of the major functions of the 2 muscles and because this set of names necessitates only 1 name change from those used by most avian anatomists (e.g., George and Berger 1966). The M. dilator glottidis is similar to the names used for this muscle by Gadow (1891:718) and by Edgeworth (1935:176).

DESCRIPTION

The larynx.—The larynx, when viewed from the oral cavity, is a low mound lying in the floor of the pharynx just posterior to the base of the corneous tongue and immediately anterior to the opening of the esophagus (Fig. 1). The laryngeal mound is covered with a number of posteriorly projecting papillae and terminates in a pair of posterior flaps. The flaps are comprised of a row (sometimes 2 rows) of larger papillae and delimit the anterior end of the esophagus. In many birds, these flaps are distinct projections of the laryngeal mound and are much larger than those present in *Corvus*. The glottis, or opening of the trachea, lies between and just anterior to the paired

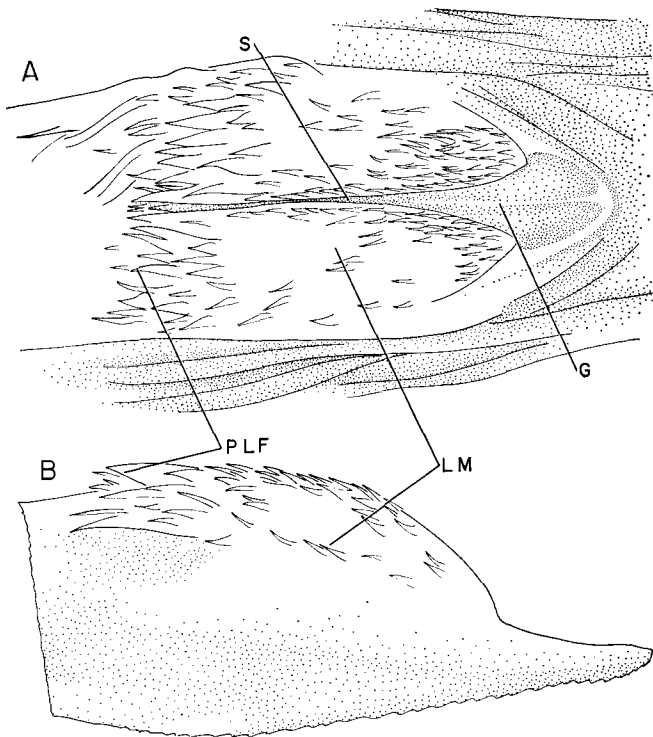


FIG. 1. External view of the larynx of *Corvus*. (A) Dorsal view. (B) Lateral view. Abbr: G—glottis; LM—laryngeal mound; PLF—posterior laryngeal flap; S—sulcus.

laryngeal mounds. The floor of the glottis has a pair of shallow depressions into which fit the anterior ends of the laryngeal mounds when the glottis is closed completely. A narrow sulcus or groove separates the posterior halves of the 2 mounds; it begins at the level of the pointer in Fig. 1A. The floor of the sulcus is formed by the *M. constrictor glottidis*.

Laryngeal skeleton.—A complex of 8 skeletal elements (cartilage, partly ossified, or completely ossified) constitutes the skeleton of the larynx (Fig. 2). The main bone is the cricoid, which forms the ventral floor and lateral walls of the larynx and supports the other bones. The tracheal rings attach to the posterior edge of the cricoid. One or more tracheal rings may be partly or completely fused with the cricoid in some birds. The cricoid is a trough-like structure, narrowest and lowest at its anterior end. Its sides slope gradually dorsally to reach their maximum height at their posterior end. Articular surfaces for the dorsal cricoids are present on the dorsal rim of the cricoid walls just anterior to their posterior corners.

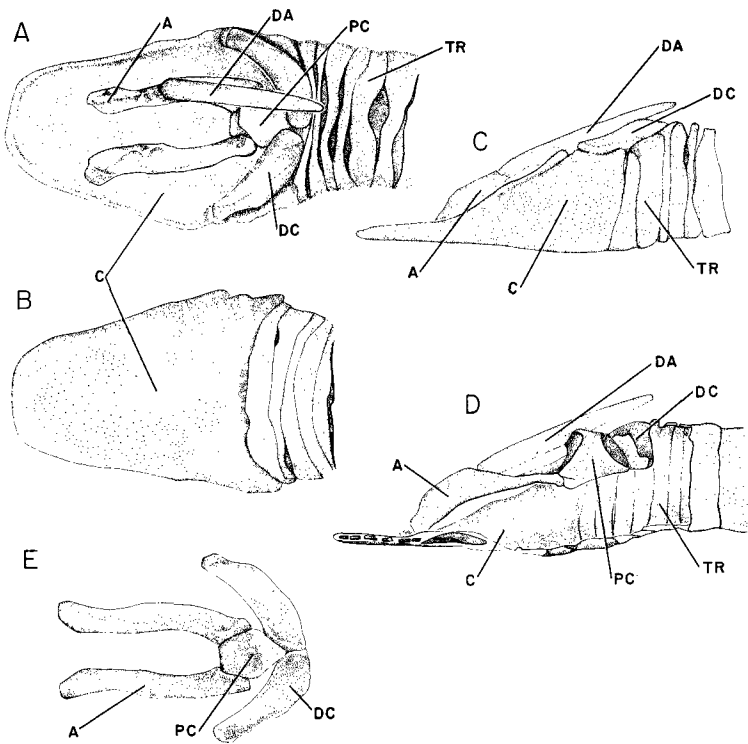


FIG. 2. Laryngeal skeleton of *Corvus*. (A) Dorsal view. (B) Ventral view. (C) Lateral view. (D) Medial view. (E) Ventral view of the main dorsal complex of bones (the dorsal arytenoid is omitted). Abbr: A—arytenoid; C—cricoid; DA—dorsal arytenoid; DC—dorsal cricoid; PC—procricoid; TR—tracheal ring.

The cricoid forms the foundation for the larynx and provides the support for the other laryngeal bones and for the laryngeal muscles. In addition 3 pairs of extrinsic muscles take origin from or insert onto its outer ventral and lateral surfaces; these are the *M. cricothyroideus*, the *M. tracheothyroideus* (not in all birds) and the *M. tracheolateralis*. (The description by Gaunt and Gaunt [1977:5] that the *M. tracheolateralis* of *Gallus* "extends from the glottis caudad along the lateral margins of the trachea" is a terminological slip. They meant to say that this muscle attaches to the larynx or to the cricoid, not to the glottis.) These muscles are parts of the tongue and/or respiratory-vocal systems. The remaining 7 bones of the laryngeal skeleton constitute the movable elements that support and alter the position of the glottal lips.

The paired dorsal cricoid bones articulate with the dorsal rim of the cricoid

close to its posterior corner. These bones curve posterodorsally and then somewhat ventrally just before their articulation with the lateroposterior surfaces of the procricoid. The 2 dorsal cricoids approach one another at the midline but do not meet. The procricoid is a cuboidal structure lying in the dorsal midline of the larynx. It usually lies at or slightly above the level of the dorsal edge of the cricoid. The procricoid has 4 articular surfaces, 2 at its lateroposterior corners for the paired dorsal cricoids and 2 at its lateroanterior corners for the paired arytenoids. The paired arytenoids extend anteriorly from the procricoid, first at the same level and then curving ventrally to approach the floor of the cricoid. Their free anterior ends are generally curved slightly laterally, usually more than shown in the illustrated specimen. (The free tips of the arytenoids in this specimen may have been eroded away during preparation.) An articular surface lies on the dorsal surface of the arytenoid midway between its anterior and posterior ends; the rod-like dorsal arytenoid articulates at this point. The 2 arytenoids support the glottal lips, while the dorsal arytenoids form the edges of the sulcus.

Movement of the entire dorsal complex relative to the cricoid is permitted by the articulations between it and the paired dorsal cricoids. The arytenoids can swing lateromedially as well as ventrodorsally about their articulations with the procricoid, and the dorsal arytenoids are free to move relative to the arytenoids. Opening and closing of the glottis is accomplished largely by movement of the arytenoids relative to the procricoid, but some movement of the dorsal cricoids and of the procricoid probably also contributes to glottal action.

Laryngeal muscles.—Four sets of intrinsic muscles are found in the *Corvus* larynx, 2 operating the posterior flaps and 2 controlling the opening of the glottis. The extrinsic muscles attaching to the larynx will not be considered herein; these are usually considered part of the tongue apparatus and/or of the respiratory-vocal system.

M. cricothyroideus superior: The origin of the *M. ch. superior* is from the dorsal rim of the cricoid (Fig. 3) just at the point where the rim slopes ventrally. The fibers of the *M. ch. superior* originate contiguously with the dorsal head of origin of the *M. cricothyroideus* (= *M. thyrohyoideus*); separation of these 2 origins must be done with care. Insertion of this muscle is into the mucosa underlying the large papillae of the posterior flap. The *M. ch. superior* is a thin, parallel-fibered muscle overlying the posterolateral corner of the *M. dilator glottidis*. The fibers are 5–6 mm long and the muscle cross-sectional area is about 0.2 mm² (2 mm wide and about 0.1 mm thick). The *M. ch. superior* elevates the posterior flap.

The *M. ch. superior* is a very thin muscle closely associated with the mucosa

covering the laryngeal mound. It is easily destroyed when removing the epithelium and mucosa in preparation to dissect the main laryngeal muscles and hence has escaped the notice of morphologists. Moreover, this muscle is so closely appressed to the surface of the *M. dilator glottidis* that it would escape detection in histological sections, especially as the fibers of the two muscles run in the same direction. Its discovery in *Ciridops* (Bock 1972) was by good fortune because the epithelium covering the larynx peeled away easily without damage to the muscle.

M. cricothyoideus posterior: The origin of the *M. ch. posterior* is from the dorsal rim of the cricoid at its dorsoposterior corner (Fig. 3). The muscle is a thin band that runs along the ventral edge of the posterior flaps from one side of the cricoid to the other. Possibly the fibers from the right and left sides of the larynx meet in a medial raphe, but no sign of a midsagittal connective tissue line could be seen. The parallel fibers of the *M. ch. posterior* are about 10–12 mm long (from one origin to the other) and form a thin band with a cross-sectional area of 0.1–0.2 mm² (width 1 mm and thickness 0.1 to 0.2 mm). The muscle acts like a sphincter and serves to depress the posterior flaps.

The *M. ch. posterior* is buried within the mucosa forming the ventral half of the posterior flaps and is easily destroyed when removing the epithelium and connective tissue to expose the muscles. Its discovery was the result of a search for a muscle antagonistic to the *M. ch. superior*.

M. dilator glottidis: The *M. d. glottidis* is the superficial glottal muscle and almost completely obscures the *M. constrictor glottidis* (Figs. 3, 4, and 6). It originates from the posterior and dorsal surfaces of the dorsal cricoid (Fig. 6); none of the fibers originate from the cricoid in *Corvus*. Note that in some other birds, e.g. *Gallus* and *Columba*, in which a distinct cricoid does not exist, the *M. d. glottidis* arises from the cricoid, that is, from the dorsal wing of the cricoid. Its description in *Ciridops* (Bock 1972) is not quite correct as it most likely does not originate from the cricoid cartilage. Insertion of the *M. d. glottidis* is along the laterodorsal surface of the anterior end of the arytenoid (up to its articulation with the dorsal arytenoid) and along the lateroventral surface of the anterior 1/3 of the dorsal arytenoid. Most of the fibers originate from the posterior surface of the dorsal cricoid and curve around the dorsal surface of that bone before extending to their insertion. The *M. d. glottidis* is parallel-fibered with the fibers varying in length from 8–9 mm (lateral-most) to 3–4 mm (medial-most). The cross-sectional area is about 3 mm² (width is 4 mm and thickness is 0.5 to 1 mm with an average of 0.75 mm).

Upon contraction, the *M. d. glottidis* rotates the arytenoid laterally about its articulation with the procricoid as well as elevating it. Moreover, the

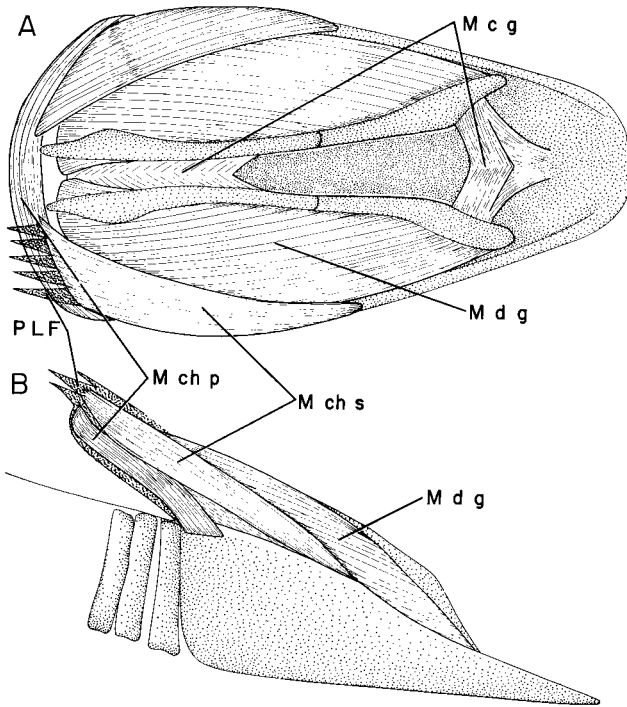


FIG. 3. Superficial muscles of the larynx of *Corvus*, showing the muscles regulating the posterior flap. (A) Dorsal view. (B) Lateral view. Abbr: M ch p—M. crico-hyoideus posterior; M ch s—M. crico-hyoideus superior; M c g—M. constrictor glottidis; M d g—M. dilator glottidis; PLF—posterior laryngeal flap.

dorsal cricoid would be rotated about its longitudinal axis, i.e., the bone rotates about its articulations with the cricoid and the procricoid. Because of the shape of the dorsal cricoids, this longitudinal rotation would raise the posterior ends of the bones and hence elevate the procricoid and with it, the paired arytenoids. Thus the entire dorsal complex of bones and the lips of the glottis are elevated with respect to the cricoid. This action increases the maximum possible opening of the glottis.

M. constrictor glottidis: The M. c. glottidis lies deep to the M. d. glottidis (Figs. 3, 4, 5, and 6) and is a much more complex muscle with respect to its origins and insertions. For clarity of description the muscle will be divided into 3 parts: A, B, and C, but these subdivisions merge into one another without any sign of a break. These parts were not distinguished in *Cirridops* (Bock 1972) as the muscle was incompletely described.

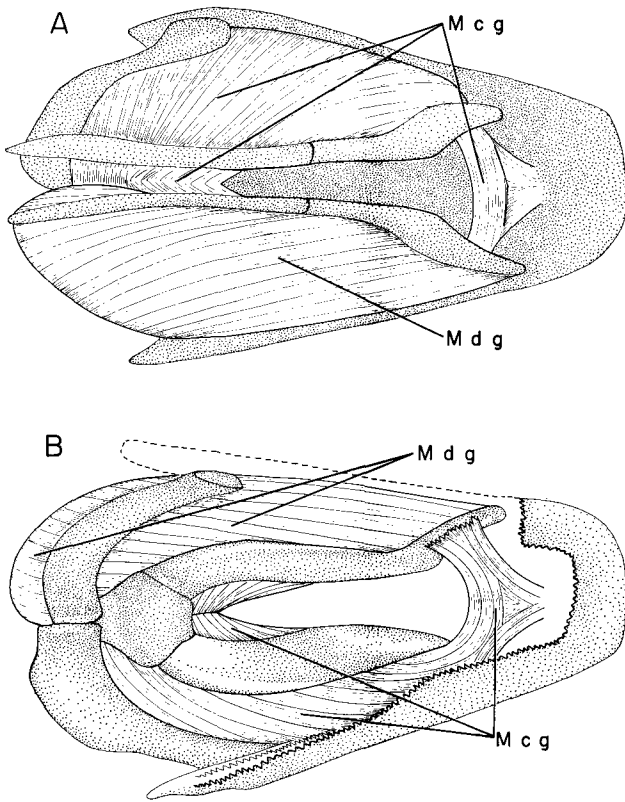


FIG. 4. Main laryngeal muscles of *Corvus*. (A) Dorsal view with the M. dilator glottidis removed from the left side. (B) Ventral view with most of the cricoid and much of the right M. constrictor glottidis removed. Abbr: M c g—M. constrictor glottidis; M d g—M. dilator glottidis.

The origin of the M. c. glottidis is from a midsagittal raphe dorsal and anterior to the procricoid and the adjacent arytenoid (parts A and C), and from the lateral surface of the arytenoid anterior to its articulation with the dorsal arytenoid (part B). Fibers run laterally and anteriorly to several areas of insertion; these will be described separately. Part A inserts along a thin line along the medial surface of the cricoid just below its dorsal rim and along the medial surface of the dorsal cricoid. Fibers of part A vary from 9 mm long (anterior fibers) to 2–3 mm long (posterior fibers); this part is 7 mm wide and 0.25 to 0.5 mm thick for a cross-sectional area of about 2–3 mm². Part B inserts on the floor of the cricoid anterior to the opening of the glottis, but at least half of the fibers are continuous with

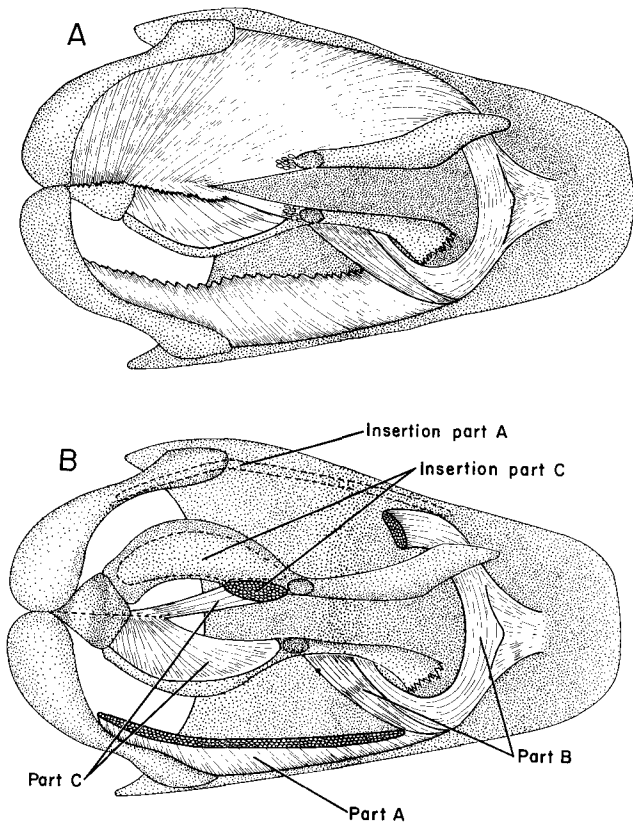


FIG. 5. The *M. constrictor glottidis* of *Corvus* seen in dorsal view. (A) Overview of the muscle with a portion of part A removed on the right side. (B) Deeper and more detailed view showing parts B and C and the areas of insertion. See text for a more detailed description of this muscle.

those of the contralateral muscle, forming a ring-like sphincter about the anterior ends of the paired arytenoids. The parallel fibers of part B are 8–9 mm long and form a band 1.0 mm wide and 1.0 mm thick, which results in a cross-sectional area of 1.0 mm². Part C inserts onto most of the mediodorsal surface of the arytenoid between its articulations with the procricoid and the dorsal arytenoids and onto the ventral surface of the dorsal arytenoid for a short distance posterior to its articulation with the arytenoid. This part is fan-shaped in appearance, but its fibers are essentially parallel. The fibers are only 2–5 mm long (from posterior to anterior) and are 3 mm wide and 1 mm thick giving a cross-sectional area of 3 mm².

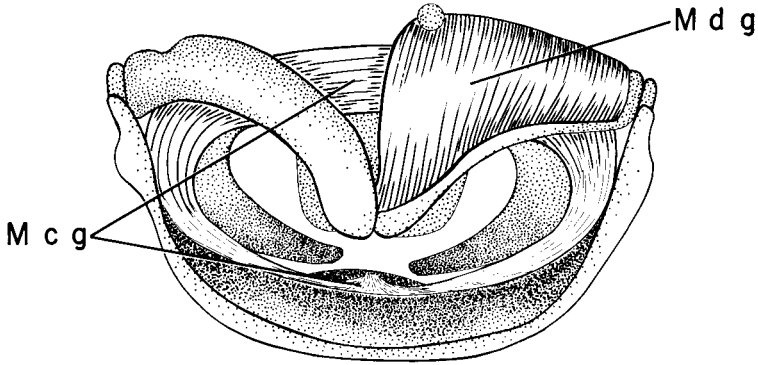


FIG. 6. Main laryngeal muscles of *Corvus* seen in posterior view. The origin of the M. dilator glottidis (M d g) from the posterior surface of the dorsal cricoid and the sphincter like structure of part B of the M. constrictor glottidis (M c g) are emphasized.

Because of its complex fiber arrangement, the action of the M. c. glottidis to close the glottis is more complicated than the opening by the M. d. glottidis. Contraction of part C serves to draw the 2 arytenoids toward the midline in a simple closing action. However because this muscle part lies close to the articulation of the arytenoid with the procricoid, its moment arm is short and hence its torque development is relatively low. Part B acts like a simple sphincter muscle to draw the tips of the arytenoids toward the midline. Moreover, it draws the tips of the arytenoids to the floor of the cricoid because of the insertion of approximately half of the fibers to the cricoid cartilage anterior to the opening of the glottis. It is the combined action of parts B and C that closes the glottis and depresses the tips of the glottal lips. Part A has no role in closing the glottis. Rather, contraction of this part serves to lower the entire dorsal complex of bones relative to the cricoid, an action that is antagonistic to the elevating action of the M. d. glottidis.

The operation of the 2 glottal muscles is thus (a) to open and elevate the glottal lips and (b) to close and depress them, and the arrangements of fibers in the 2 muscles permit full antagonistic actions.

DISCUSSION

A comparison of the description of the skeletomuscular system of the *Corvus* larynx with those presented earlier suggests that the passerine larynx had never been described properly and that the glottal muscles in birds had

never been described correctly. (This includes the description of Bock 1972, which can, however, be corrected in light of the redescription of the glottal muscles presented above.) Indeed from an examination of the text and figures of earlier descriptions of these muscles, it is not possible to understand how these muscles, especially the *M. constrictor glottidis*, operate. A description of part C has never been presented clearly; the descriptions of Gadow (1891:817) Edgeworth (1935:176), and White (1965:1894) are suggestive at best. Shufeldt (1890) shows most of the laryngeal bones (the dorsal arytenoids are lacking) but his indications of the attachments of the muscles as well as his text description and figure of the *M. d. glottidis* (= his thyreoarytenoideus, Fig. 18, p. 46) are confusing. The description of the glottal muscles by Fisher and Goodman (1955:36), which is followed by George and Berger (1966:264), does not appear to be correct (although I have not been able to check it by dissections on *Grus*), but more importantly it is impossible to see how the *M. c. glottidis* can close the glottis.

The more complex system of bones in the *Corvus* larynx as compared to that of *Gallus* and *Columba* raises several interesting questions. The first is what is the arrangement of laryngeal bones in the different orders of birds? Next is whether the morphology of the *M. dilator glottidis* and *M. constrictor glottidis* alters with change in the laryngeal skeleton. Most interesting is the mechanism of evolutionary change whereby the cricoid wing separated from the body of the cricoid and became a distinct bone with a diarthrosis between it and the cricoid; a similar question can be asked about the evolution of the dorsal arytenoid. And lastly is the question of whether the evolution of the more complex larynx in *Corvus* and presumably other passerine birds is associated with the evolution of the most complex syringeal muscles and more complex song in these birds.

The cross-sectional areas (and presumed force developments) of these muscles are larger than expected if these muscles simply opened and closed the glottis during respiration. An explanation may lie in one or a combination of possible glottal actions. The first is that the glottis may have to be opened and closed very rapidly; rapid movement requires high acceleration which necessitates large force development. Second is that the glottis may have to be opened and closed many times in rapid succession over a period of time. Or it may be necessary to hold the glottis fully opened or tightly closed against some resistance for a long period of time. Both actions would require a muscle with a large cross-sectional area to provide enough fibers to permit recruitment of fresh fibers as the contracting fibers become fatigued. A subsequent question would be the possible functions of such muscle actions in the role of the glottis in respiration, swallowing, or sound production.

Although movement of the glottal lips is a simple scissorlike opening and closing, the morphology of the underlying skeletomuscular system proved to be more complex than expected. Comprehension of the mechanics of glottal action is not possible without a detailed knowledge of the structure of the laryngeal skeleton and muscles. In closing, I would like to emphasize the need and importance of thorough, careful dissection and description as the foundation of avian morphology and all other studies, e.g. functional and evolutionary analyses, based upon it.

ACKNOWLEDGMENTS

I would like to thank Mr. John Morony for supplying me with several specimens of crows used in the dissections for this study and Miss Dorothea Goldys for drawing the illustrations which are the core of any anatomical study. Dr. Abbot Gaunt provided many helpful criticisms and suggestions which are much appreciated. This study was done with the support of grant BMS-73-06818 from the National Science Foundation which is gratefully acknowledged.

LITERATURE CITED

- BEDDARD, F. E. 1898. The structure and classification of birds. Longmans Green and Co., London.
- BOCK, W. J. 1972. Morphology of the tongue apparatus of *Ciridops anna* (Drepanididae). *Ibis* 114:61-78.
- EDGEWORTH, F. H. 1935. The cranial muscles of vertebrates. Cambridge Univ. Press, Cambridge, England.
- FISHER, H. I. AND D. C. GOODMAN. 1955. The myology of the Whooping Crane, *Grus americana*. III. Biol. Monogr. 24:1-127.
- GADOW, H. 1891. Vögel. In Bromm's Klassen und Ordnungen des Thierreichs. Vol. 6, div. 4, part I. Anat. Theil. Leipzig.
- GAUNT, A. S. AND S. L. L. GAUNT. 1977. Mechanics of the syrinx in *Gallus gallus*. II. Electromyographic studies of *ad libitum* vocalizations. *J. Morph.* 152:1-20.
- GEORGE, J. C. AND A. J. BERGER. 1966. Avian myology. Academic Press, New York.
- SHUFELDT, R. W. 1890. The myology of the Raven (*Corvus corax sinuatus*). Macmillan, London.
- WHITE, S. S. 1975. The Larynx. In Sisson and Grossman, "The Anatomy of the Domestic Animals," R. Getty (ed.), W. B. Saunders Co., Philadelphia, Vol. 2:1891-1897.

DEPT. OF BIOLOGICAL SCIENCES, COLUMBIA UNIV., NEW YORK, NY 10027, AND
DEPT. OF ORNITHOLOGY, AMERICAN MUSEUM OF NATURAL HISTORY, NEW
YORK, NY 10024.