The Anatomy of the Larynx of the Bowhead Whale, *Balaena mysticetus*, and its Sound-producing Functions

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ABSTRACT

This study describes the morphology of the laryngeal apparatus in bowhead whales (*Balaena mysticetus*) with respect to respiration, deglutition, and vocalization. We also examined the intrinsic cricoarytenothyroid muscle (*Musculus (M.) diverticuli laryngei*) which forms the laryngeal diverticulum, to ascertain its interactions with the laryngeal cartilages during respiration and sound production. Five fetal larynges and four from adult whales were studied using noninvasive imaging, as well as macroscopic and microscopic techniques. The larynx extends from the skull base into the thoracic inlet. The dorsally curved laryngeal stalk, supported by epiglottis and the corniculate processes of arytenoid cartilages, is situated within the nasopharynx. The epiglottic cartilage exhibits a prominent medial ridge. The arytenoid cartilages are rod-shaped, and extend through the laryngeal cavity. The thyroid cartilage possesses a prominent caudal horn with a fibrous articulation to the ventrally incomplete cricoid cartilage. The *M. thyroepiglotticus* forms the connection between epiglottic and thyroid cartilages. The *M. cricothyroideus lateralis* connects the caudal horn of the thyroid cartilage with the cricoid cartilage and the *M. cricothyroideus medialis* connects the cricoid and thyroid cartilage. An extensive laryngeal diverticulum *(Diverticulum laryngis)*, formed by the laryngeal mucosa and *M. diverticuli laryngei*, is positioned caudo-ventral to the laryngeal vestibule. The mucosa thickens into a fold medial to the vocal processes of the arytenoid cartilages. Experiments with airflow combined with histological and anatomical evidence strongly suggest a sound producing function for these (vocal) folds. This analysis provides the first account of sound producing structures and function in bowhead whales. Anat Rec, 297:1316–1330, 2014. © 2014 Wiley Periodicals, Inc.

Key words: mysticeti; bowhead whale; laryngeal diverticulum; vocalization; morphology

TABLE 1. Specimens used in this study

Specimen no.	Sex	Length	Specimen preparation	Study methods
ADULT	?	App. 16m	Extirpated larynx	Dissection, histology
87N1F	Female	1.7m	Whole fetus, frozen	Extrinsic structures
88KK1F	Female	1.5m	Whole fetus, frozen	Transverse sections
89B2F	Male	4m	Extirpated larynx	Dissection
90B4F	Female	3.9m	Cranial half of larynx perfused	Extrinsic structures, midsagittal section
91BF	Male	1.2m	Whole fetus perfused	Magnetic resonance imaging (MRI)
93B21	Male	10.9m	Cranial third of larynx, frozen	Extrinsic structures
95B17	Female	7.5m	Extirpated larynx, frozen	Dissection, histology, radiology, sound experiments
02B	?	?	Extirpated larynx	Dissection, MRI, CT scan

The cetacean transition from a terrestrial to an aquatic environment occurred ~50 million years ago (Gingerich et al., 1983; Fordyce, 1980, 1992; Milinkovitch, 1992; Berta, 1994; Gingerich, 1994; Thewissen, 2001). This transition favored adaptations of the larynx to an aquatic environment. Further specialization of the larynx occurred ~35 million years ago when modern cetacean species and suborders evolved from the archaeocete whales (Fordyce and Barnes, 1994). In whales, the perhaps most interestingly skill is to vocalize within an aquatic environment without the loss of air, for example, using nasal sacs and "monkey lips" in odontocetes (Cranford et al., 1996).

Efficient respiration in an aquatic environment was an evolutionary process that resulted in morphological changes to the skull, as exemplified by the position of the nasal aperture and orientation of the nasopharynx, and also to the orientation, musculature, and function of the laryngeal apparatus and trachea (Reidenberg and Laitman, 2007a). Three functional properties for the cetacean larynx have been discussed previously: first, the larynx as a part of the respiratory passage way (Haldiman et al., 1983; Henry et al., 1983, Reeb and Best, 1999; Huggenberger et al., 2008; Reidenberg and Laitman, 2008); second, the larynx as a water excluding device in deglutition (Harrison, 1995; Hosokawa, 1950; Reidenberg and Laitman, 1987); third, the larynx as a sound producing organ while diving (Green et al., 1980; Reeb and Best, 1999; Reidenberg and Laitman, 1988, 2007a, 2008). These properties have not been investigated in detail for the larynx of the bowhead whale, *Balaena mysticetus*, one of the largest cetacean species.

Eschricht and Reinhardt (1866) provided the only available anatomical description of the bowhead whale larynx. Though an important publication, it is hampered by limited study materials and the authors made no attempt to provide a functional analysis of the described structures. In the past, research on bowhead whales had to rely on accounts of respiratory structures in other mysticete whales (Beauregard and Boulart, 1882; Benham, 1901; Schulte, 1916; Hosokawa, 1950; Omura, 1964; Sukhovskaya and Yablokov, 1979; Reeb and Best, 1999; Reidenberg and Laitman, 2007a). For the bowhead whale, gross anatomical descriptions of the respiratory system (Campbell, 1986; Haldiman et al., 1983; Henry et al., 1983) and microscopic descriptions of the lung (Haldiman at al., 1984; Henk and Haldiman, 1990) have been presented. However, a functional analysis of the bowhead whale larynx, based on a detailed evaluation of its anatomical structures, is still lacking.

Sound production in the bowhead whale larynx had been suggested before, but never in the context of a detailed anatomical discussion (e.g., Hosokawa, 1950; Slijper, 1962; Haldiman and Tarpley, 1993). Only one study to date has provided a detailed anatomical account of sound producing structures in other mysticetes whales (Reidenberg and Laitman, 2007a). In contrast, odontocetes have been studied in detail regarding their sound producing mechanisms (Dubois, 1886; Caldwell et al., 1976; Dormer, 1979; Green et al., 1980; Behrmann, 1987; Reidenberg and Laitman, 1987, 1988, 1994, 2008; Cranford et al., 1996). Although sounds of communicating bowhead whales have been recorded and described in the past (Clark and Johnson, 1984) an understanding of the sound-producing system in the bowhead whale is still missing. The purpose of this study was, therefore, to provide a detailed description of the bowhead whale larynx, to investigate its functional properties, and to study potential sound producing structures and mechanisms in the larynx. The large number of bowhead whale specimens included in this study, considering the endangered status of the species, and the diversity of specimens in size, sex, and developmental status, provide a unique opportunity to fully evaluate structural and functional properties of the bowhead whale larynx.

MATERIALS AND METHODS

The larynges of nine bowhead whales were collected for anatomical studies over a period of 15 years from along the North Coast of Alaska (Table 1). Collections were made possible through the courtesy and cooperation of Eskimo subsistence hunters under the authority of the United States National Marine Fisheries Service (Scientific Permits SP 345 and 519 issued to Dr. Thomas F. Albert, Dept. Wildlife & Management, North Slope Borough, Alaska). Bowhead whale subsistence hunts were conducted in accordance with guidelines established by the Alaska Eskimo Whaling Commission (AIWC) and the International Whaling Commission (IWC). The specimens consisted either of whole fetuses with the larynx preserved *in situ* or isolated laryngeal tissues from larger fetuses or adults. Laryngeal tissues represent a wide range of specimens considering the limited availability and the circumstances of the collection. Whale identification number encodes the year of collection (87N1F = 1987), the site of collection (N = Nuiqsut; KK = Kaktovik; B = Barrow), the running number of whales caught in that year, and the developmental status (F = fetus). One specimen lacked an identification

TABLE 2. Measurements obtained from laryngeal specimens used in this study

	Laryngeal length	Length incl. trachea	Largest diameter	Diameter at thyroid	Diverticulum length	Epiglottic length	Arytenoid length	Cricoid length	Thyroid length
Adult	60 cm	67 cm	–	–	35 cm	21.6 cm	54 cm	23 cm	33 cm
88KK1F	7 cm	8.5 cm	–	–	–	2 cm	5.5 cm	–	–
89B2F	30 cm	–	51 cm	36 cm	–	–	–	–	–
90B4F	35 cm	–	–	–	15 cm	12 cm	–	13 cm	16 cm
93B21	–	–	–	–	–	18 cm	–	–	–
95B17 02B	54 cm	66 cm	76 cm	52 cm	25 cm	–	–	–	30 cm

Laryngeal length is measured from tip of epiglottis to end of diverticulum; length including trachea measures to the tracheal bifurcation; – indicates no measurement taken.

code; however, this larynx provided valuable data and was included in this study under the designation ADULT, because of the size of the organ.

Some specimens (87N1F, 88KK1F, 93B21, 95B17, 02B) were frozen immediately after collection and remained in this condition until dissection. Other larynges (ADULT, 89B2F, 90B4F, 91BF) were detached on site and immediately perfused with formalin fixative. After the initial dissection most specimens were immersed and stored in an embalming solution of 6% formalin and 1% phenol. Specimen 02B was shipped frozen to the School of Veterinary Medicine, Louisiana State University (Louisiana/USA), and stored in this condition until shortly before dissections commenced. Several days prior to the dissection, the specimen was placed in Jore's solution, that is, aqueous solution of sodium chlorate, sodium sulfate, sodium bicarbonate, chloral hydrate, and formaldehyde, as a fixative (Waters, 2009). Jore's solution was chosen because it preserves tissues without the noxious fumes of typical formaldehyde fixatives while maintaining pliability and coloration. After 36 hours in Jore's solution the larynx was sagittally sectioned and the left portion was used for dissection.

Tissue samples for histological preparation were removed from the specimen 95B17 and fixed in 10% buffered formalin. Tissues were dehydrated through a graded series of ethanol and xylene before being embedded in paraffin. After sectioning tissues were stained using a standard hematoxylin and eosin staining protocol (e.g., Gabe, 1976).

Radiographs of bowhead whale fetuses and isolated larynges (91BF, 02B) were produced in the Radiology Section of the Veterinary Clinic and Teaching Hospital, School of Veterinary Medicine, Louisiana State University, Baton Rouge, Louisiana/USA. The magnetic resonance imaging (MRI) for this study was performed through the generosity of the Baton Rouge General Hospital, Baton Rouge, Louisiana/USA.

Morphological measurements from all cartilages (except 87N1F, 91BF, 02B) were taken (Table 2). Because of the nature of the collection, it was possible to observe only the attachment of the hyoid suspension to the larynx in fetus 90B4F, which comprised the head and larynx *in situ*. Additional information came from the isolated larynges from the bowhead whales 89B2F, and 93B21, which had part of the hyoid suspension still attached after extirpation.

The nomenclature of all structures identified and described in the text followed the guidelines established by the International Committee on Veterinary Gross Anatomical Nomenclature and are described in the fifth edition of the "Nomina Anatomica Veterinaria" (2012). For ease of reading, common names are used throughout the text if appropriate with scientific names following in italics in parenthesis after the first mentioning of a structure.

For simulations of sound production in the larynx of the bowhead whale, airflow experiments were conducted on specimen 95B17 (the only large larynx that was not perfused at the time of the study). The end of a 15-mm diameter pressure hose was inserted in the fundus of the laryngeal diverticle. The other end of the hose was attached to a pressure-monitoring gage, which was connected to the outlet for pressurized air. A range of air pressures ($\sim$20–350 kPa) were applied to the specimen to assess its sound-producing capability. Multiple successive attempts of producing sound were made over the course of an hour.

RESULTS
Topography of the Larynx

The bowhead whale larynx is situated ventral to the base of the skull and in the short cervical region of the animal (Fig. 1). The most rostral portion of the larynx, the laryngeal stalk, extends through the intrapharyngeal orifice (*Ostium intrapharyngeum*) and opens into the nasopharynx (*Pars nasalis pharyngis*) (Figs. 1 and 2). The opening of the laryngeal stalk (*Aditus laryngis*) can be effectively sealed off from the laryngopharynx with a strong pharyngeal muscle (*Musculus [M.] palatopharyngeus*). The thyroid cartilage rests on the *Musculi [Mm.] sternothyroideus* and *sternohyoideus* forming the most ventral extension of the laryngeal structures. The most caudal extension of the larynx curves dorsally and comes to rest in the thoracic inlet, dorsal to the great vessels of the heart. The larynx in an adult (ADULT) bowhead whale measured $\sim$60 cm in length from the rostral end of the epiglottis to the caudal end of the cartilaginous cricoid plate. Immature and fetal specimens had correspondingly shorter larynges, which were well developed even in fetal specimens (Table 2).

Laryngeal Cartilages

Epiglottic cartilage. The epiglottic cartilage (*Cartilago epiglottica*) is a single cartilage that is most rostral in position relative to the other laryngeal cartilages
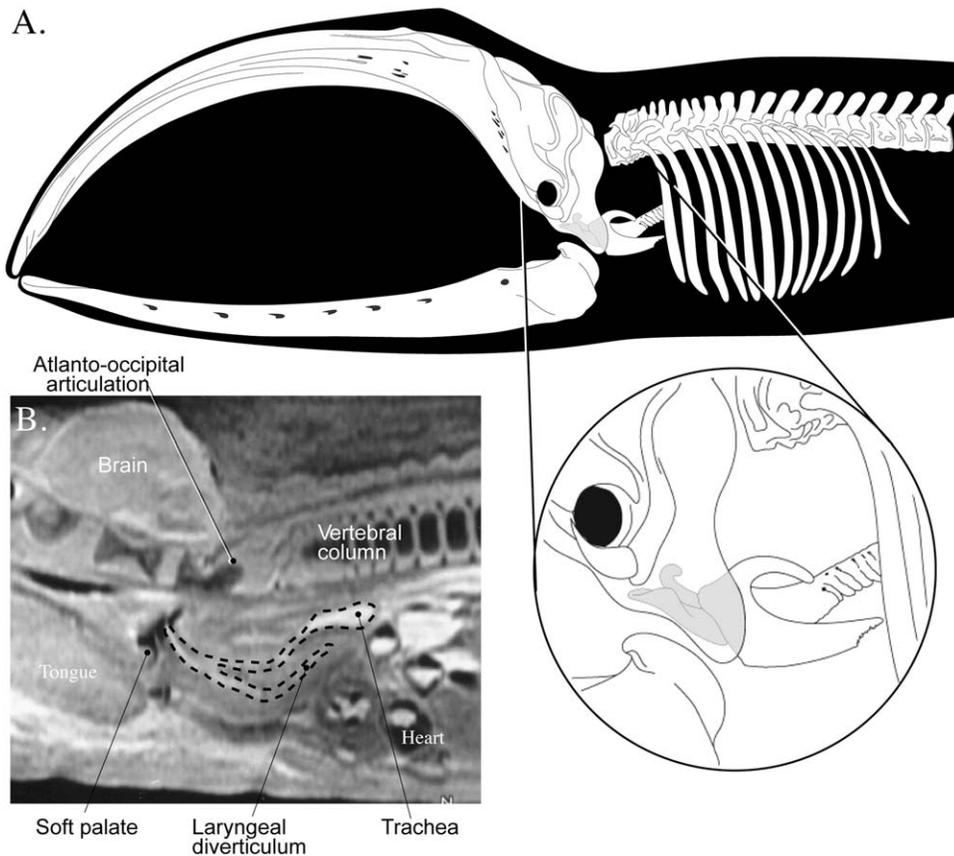
Fig. 1. Bowhead whale larynx *in situ* (paramedian section). **A**: Skeletal drawing with call-out of an adult bowhead whale. **B**: MRI of respective post-cranial area (specimen 91BF). The air conducting structures through the larynx are indicated by broken lines. Illustrations by D.J. Hillmann.

(Figs. 3 and 4). It is positioned rostroventral to the arytenoid cartilages, rostral to the thyroid cartilage, and extends in a rostrodorsal direction, paralleling the corniculate processes of the arytenoid cartilages (Fig. 4). The epiglottic cartilage is concave with a prominent medial ridge on the dorsal surface extending from the apex of the cartilage caudally, along approximately two thirds of the length of the cartilage (Fig. 3). The medial ridge on the dorsal surface of the epiglottic cartilage divides the cartilage into two troughs, each accommodating a corniculate process of the arytenoid cartilages. The lateral wings of the epiglottis are closely apposed to the rostral portion of the arytenoid cartilages. *In vivo*, the cartilage is oriented in a rostrodorsal to caudoventral direction with the apex oriented at a 40° angle to the dorsal plane, and a 110° angle to the longitudinal axis of the cricoid cartilage plate of the larynx (Fig. 4). Thus, the rostral end of the epiglottic cartilage extends through the intrapharyngeal orifice into the nasopharynx (Fig. 2). Based on manual manipulations of the available laryngeal specimens, it appears as if the laryngeal stalk is permanently situated in the nasopharynx and cannot be retracted into the laryngopharynx (*Pars laryngis pharyngis*).

The base of the epiglottic cartilage is deeply serrated for the attachment of the *M. thyroepiglotticus* (Fig. 3A). The surface of the caudal end of the epiglottic cartilage

is concave and caudally elongated, giving it a spoon-shaped appearance. There is no cartilaginous connection between the epiglottic and thyroid cartilages, but a broad and thick ligament (*Ligamentum thyroepiglotticum*) connects the base of the epiglottic cartilage to the rostral margin of the thyroid cartilage.

In its rostral third, the lateral margins of the epiglottis are connected to the corniculate processes of the arytenoid cartilages by the aryepiglottic folds (*Plicae aryepiglotticae*), thus establishing the lateral parameters of the laryngeal stalk. The laryngeal stalk terminates rostrodorsally in the entrance to the laryngeal cavity *(Aditus laryngis)*, the anchor-shaped opening of the laryngeal cavity.

Arytenoid cartilage. The paired arytenoid cartilage (*Cartilago arytenoidea*) is the most medial of the four cartilages and extends caudally from the nasopharynx to approximately two-thirds into the laryngeal cavity medial to the incomplete cricoid ring (Figs. 3B and 4). Its rostral portion is formed by the corniculate process *(Processus corniculatus)* that apposes the lateral wings of the epiglottis. The apices of both corniculate processes possess a distinct hooked feature (Fig. 3B) and are tightly connected by the *Ligamentum arycorniculatum* (Fig. 2). The transept of the corniculate process of
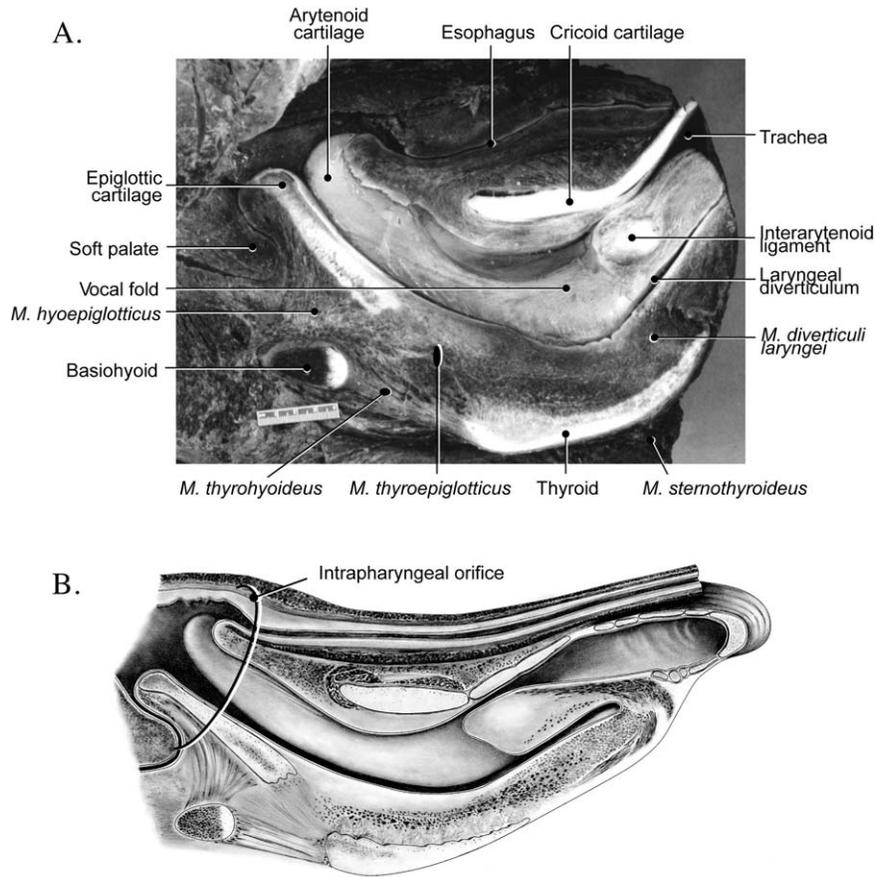
Fig. 2. The bowhead whale larynx *in situ*. **A**: Mid-sagittal section through the larynx of fetus 90B4F. The caudal one-third of the specimen is distorted dorsally due to long-term storage. **B**: Schematic drawing (D.J. Hillmann) of same structures.

an arytenoid cartilage is oval in shape with the greater curvature situated rostrally. Approximately half the distance caudally is the body of the arytenoid with a distinct muscular process. The vocal process (*Processus vocalis*) of the arytenoid cartilage extends caudoventrally, medial to the cricoid ring, and ends juxtaposed to its counterpart at the level of approximately two-thirds the length of the cricoid cartilage.

Caudal to the aryepiglottic fold, the body of the arytenoid cartilage widens considerably to accommodate a synovial articulation *(Articulatio cricoarytenoidea)* with the cricoid cartilage. The articular surface is positioned on the dorsomedial aspect of the body of the arytenoid cartilage. It consists of a shallow groove situated obliquely to the longitudinal axis of the larynx from caudoventral to rostromedial. The synovial cricoarytenoid joint allows limited rotational and abductional movement of the arytenoid cartilages in relation to the cricoid plate. A tight synovial capsule (*Capsula articularis cricoarytenoidea*) provides for the articulation between these two cartilages and is supported by a number of short collateral ligaments. The bodies of the arytenoid cartilages are tightly connected by the *Ligamentum interarytenoideum* (Fig. 2A) caudal to the position of the joint capsule. Caudal to the insertion of this interarytenoideal ligament, the arytenoid cartilage regains its rod-

shaped character and forms the caudoventrally directed vocal process (Fig. 3B). The cutaneous mucosal membrane covering the surface of the arytenoid cartilages is uniformly thin except for the area along the medial aspect of the body and vocal process where it thickens considerably with a massive layer of connective and adipose tissue in the adventitia beneath the epithelium (Fig. 5). This connective tissue layer becomes 18-mm thick at its widest extension and has been identified functionally through airflow experiments (see below) as a vocal fold (*Plica vocalis*).

Histological analysis of these vocal folds in specimen 95B17 revealed their microscopic anatomy (Fig. 5A). The vocal folds are covered by a stratified squamous epithelium (Fig. 5B). The epithelium is thin and a *Stratum granulosum* is missing. Prominent papillae of the *Lamina propria mucosae* extend close to the surface of the epithelium. There are numerous nerve fibers and nerve endings visible within the connective tissue of the Lamina propria. The connective tissue of the *Tela submucosa* constitutes approximately three-quarters of the thickness of the vocal folds. This loose connective tissue consists mainly of adipose tissue and collagen fibers, which are poorly organized and extend in all directions throughout the vocal folds (Fig. 5C). Few elastic fibers are interspersed and provide some elasticity to the vocal
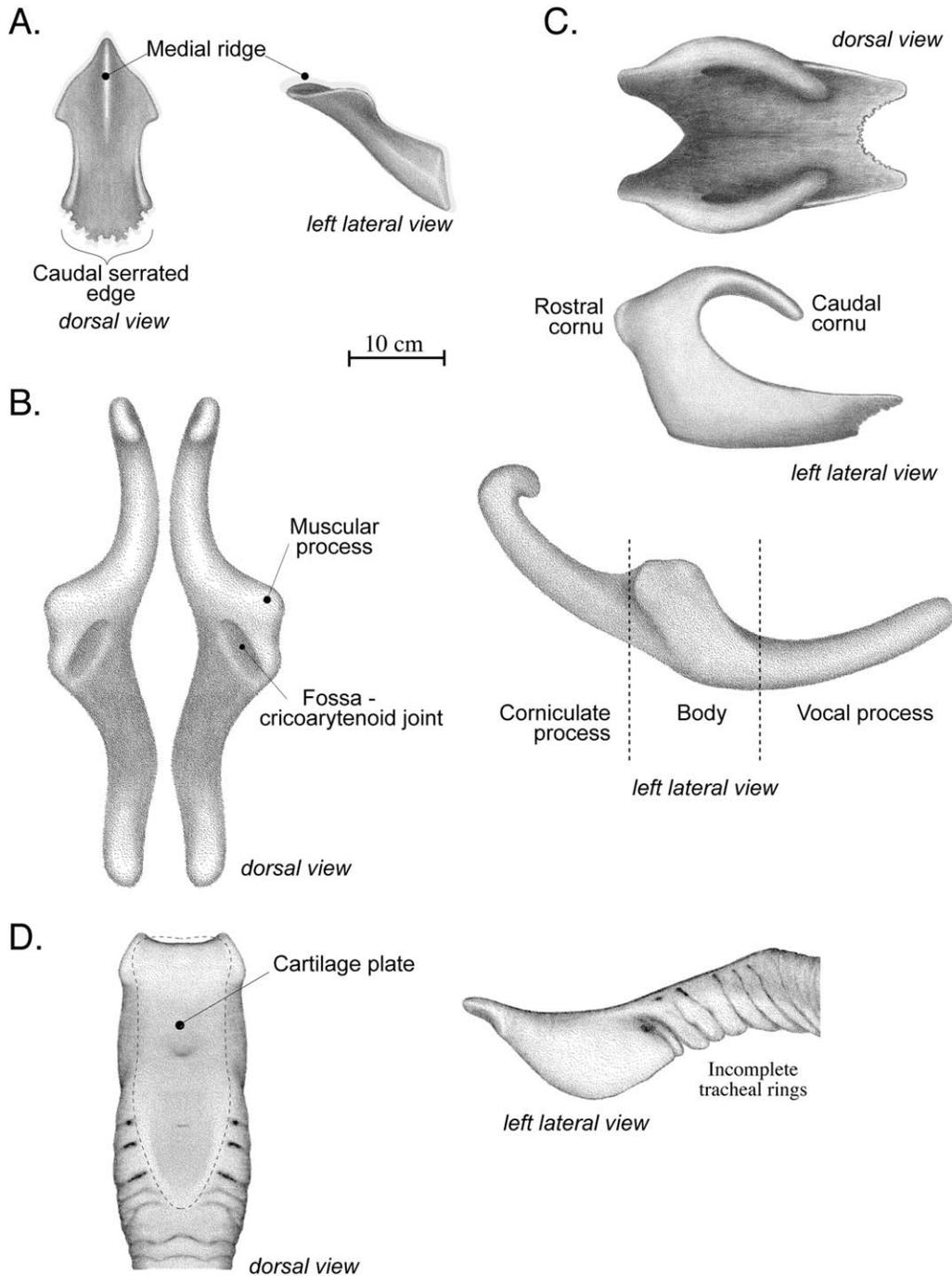
Fig. 3. Laryngeal cartilages in the bowhead whale. **A**: Epiglottic cartilage. **B**: Arytenoid cartilage. C: Thyroid cartilage. **D**: Cricoid cartilage. Dashed line indicates extend of continuous cartilage plate. All cartilage plates are drawn to scale, following the dimensions measured in the ADULT specimen. Illustrations by D.J. Hillmann.

folds. Few blood vessels, mostly of venous nature, are located in the *Tela submucosa*. It is densely populated by nerve fibers, which can be observed throughout the layer. Deep to the reticular tissue is a thick perichondrium, which covers the medial aspect of the vocal process of the arytenoid cartilage (Fig. 5D).

Thyroid cartilage. The thyroid cartilage (*Cartilago thyroidea*) forms the U-shaped base of the laryngeal cavity and encloses the lateral and ventral aspects of the cricoid, arytenoid, and epiglottic cartilages (Figs. 3C and 4). The unpaired thyroid cartilage is the result of the fusion of the paired thyroid laminae, which are
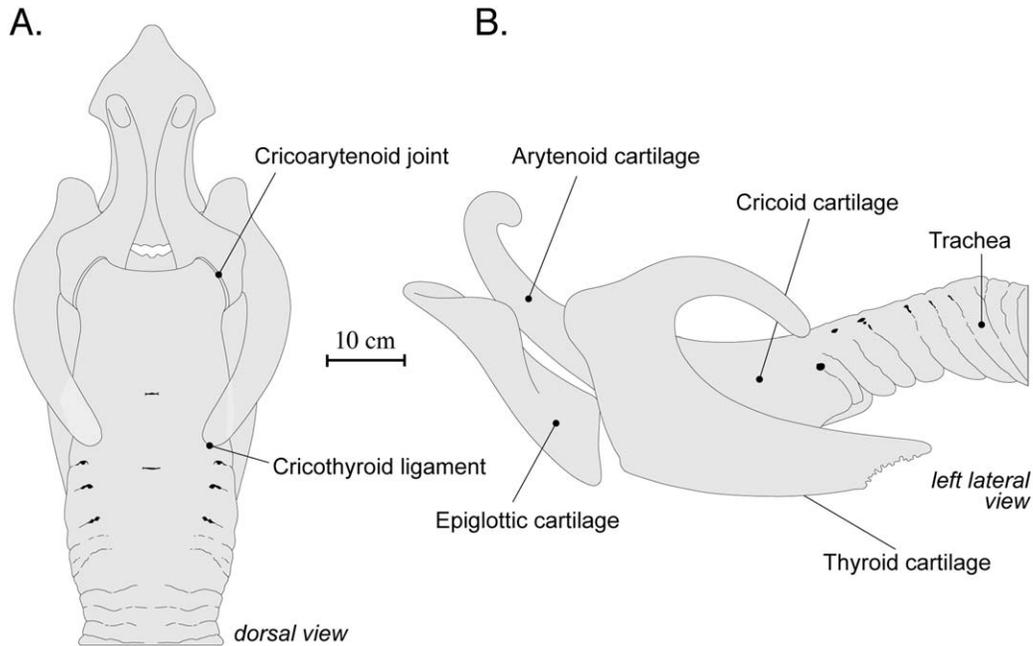
Fig. 4. Composite drawing of laryngeal cartilages *in situ* drawn to scale. **A**: Dorsal view. **B**: Left lateral view. Illustrations by D.J. Hillmann.

connected along the midventral line of the cartilage body. The transept of the thyroid cartilage is "V"-shaped in its rostral portion and becomes increasingly "U"-shaped further caudally. The cartilage extends from just caudal to the epiglottis to just rostral and ventral to the trachea. Its rostral horns *(Cornua rostralia)* are small protuberances at the rostral edge of the laminae of the cartilage, situated in a dorsal position approximately two-thirds of the distance from the most ventral extent of the cartilage. In contrast, the caudal horns *(Cornua caudalia)* are prominent and sweep caudally in an arch to articulate with the dorsal aspect of the plate of the cricoid cartilage (Fig. 3D) forming the *Articulatio cricothyroidea* (Fig. 4A) via a strong fibroelastic cricothyroid ligament *(Ligamentum cricothyroideum*, Fig. 4B). The caudal horn is a projection of the lamina along its caudodorsal edge and curves dorsally in a tight arch, which turns the horn back to the lateral aspect of the laryngeal cavity. The tip of the caudal horn of the thyroid cartilage extends lateral and dorsal to the caudal margin of the thyroid cartilage's body. The cricothyroid articulation allows limited rotation of the thyroid cartilage relative to the cricoid cartilage.

The caudal portion of the body of the thyroid cartilage tapers out into two, wedge-shaped, ventrolateral processes, creating a concave caudal edge (Fig. 3C). The tips of these processes become thinner towards their caudal ends until they are grossly indistinguishable from the surrounding connective tissue. The caudal edge of the thyroid cartilage is serrated, which permits extensive interdigitation with the attached muscle of the laryngeal diverticulum *(M. diverticuli laryngei)*.

The thyroid cartilage is the largest cartilage and forms—in combination with the cricoid cartilage—the main support of the cavity of the larynx. Most of the extrinsic musculature attach to the thyroid cartilage (Fig. 2A), which helps to maintain the position of the larynx in relation to the surrounding respiratory and digestive organs.

Cricoid cartilage. The cricoid cartilage (*Cartilago cricoidea*) has a plate with a flat dorsal surface forming a slight dorsal curve as it transitions to the tracheal cartilages and an incomplete ring. The plate forms the roof of the laryngeal cavity (Figs. 2–4). It is trough-shaped with the concave surface facing ventrally and towards the thyroid cartilage and its dorsorostrolateral aspect articulates with the arytenoid cartilages. The cricoid cartilage is similar in length to the thyroid cartilage and parallels it. In the bowhead whale larynx, the ring of the cricoid cartilage is ventrally incomplete in contrast to the cricoid cartilage of most mammals. Thus, the term "cricoid," or "ring-like," does not accurately describe the shape of the cricoid cartilage in the bowhead whale. The plate of the cricoid cartilage has a rostrodorsal protuberance, which carries the articular surface for the synovial joint it shares with the arytenoid cartilage (*Facies articularis arytenoidea*). Further caudally, on its lateral surface, the plate of the cricoid cartilage is connected to the caudal horn of the thyroid cartilage by means of the *Ligamentum cricothyroideum*. The lateral and ventral extent of the ring of the cricoid cartilage varies and resembles overall a sigmoid curve. Rostrally, the lateral aspect of the cricoid cartilage descends steeply and reaches its most ventral extension caudal to the level of the cricoarytenoid joint. Caudal to the cricoarytenoid joint, the ventral free margin ascents caudally, thus leaving the laterocaudal aspect of the laryngeal cavity devoid of cartilaginous support. The cricoid cartilage is intimately connected with the tracheal cartilages (Figs. 3D and 4B). Segmentation of the cricoid cartilage was
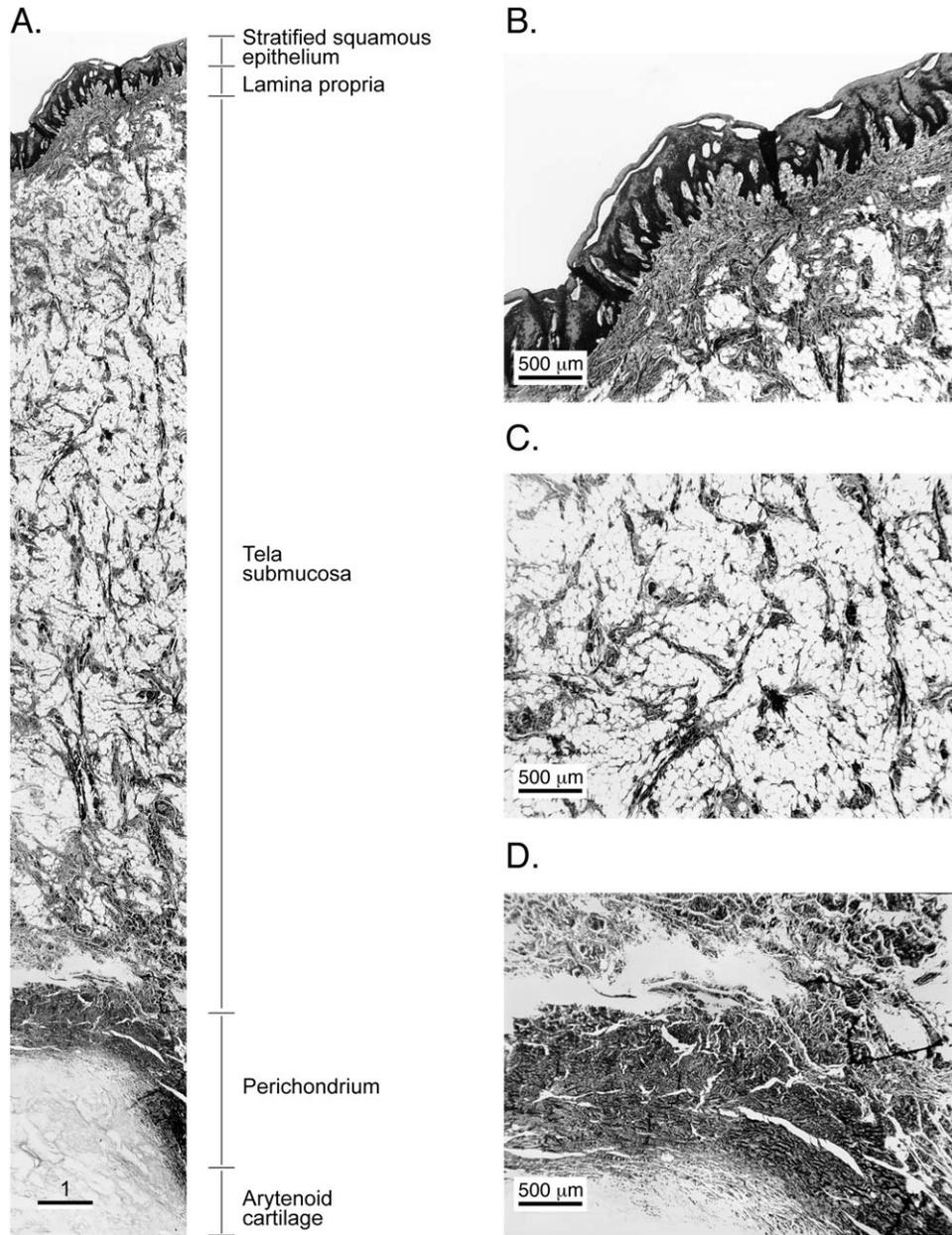
Fig. 5. Histological section through vocal fold and medial aspect of vocal process of the arytenoid cartilage of specimen 95B17. **A**: Section of the entire vocal fold. **B**. Epithelium and Lamina propria. **C**. Tela submucosa. **D**. Perichondrium and cartilage.

present in fetal as well as in adult specimens and appears to be the normal condition in the bowhead whale. Neither a *Ligamentum cricotracheale* nor a *Ligamentum cricothyroideum* were present.

The dorsal surface of the cricoid cartilage plate serves as attachment site for the extrinsic musculature, for example, *M. cricopharyngeus*, connecting the cartilage to the pharynx and esophagus (Fig. 6A). Internally, the cricoid cartilage is covered by a smooth mucosal membrane. The external surface of the cricoid cartilage is occupied by attachments for intrinsic (*M. cricothyreoideus medialis* and *lateralis)* and extrinsic (*M. cricothyro-*

pharyngeus) muscles. Based on gross anatomical observations and the pliability of the cartilages, neither the thyroid nor cricoid cartilage present any sign of ossification in any of the specimens dissected in this study.

Laryngeal Musculature

Extrinsic muscles of the larynx. The *M. sternothyroideus* originates at the cranial edge of the sternal plate (*Manubrium sterni*) and inserts on the ventral surface of the thyroid cartilage (Fig. 2A). This muscle is short, due to the proximity of the sternal plate and the
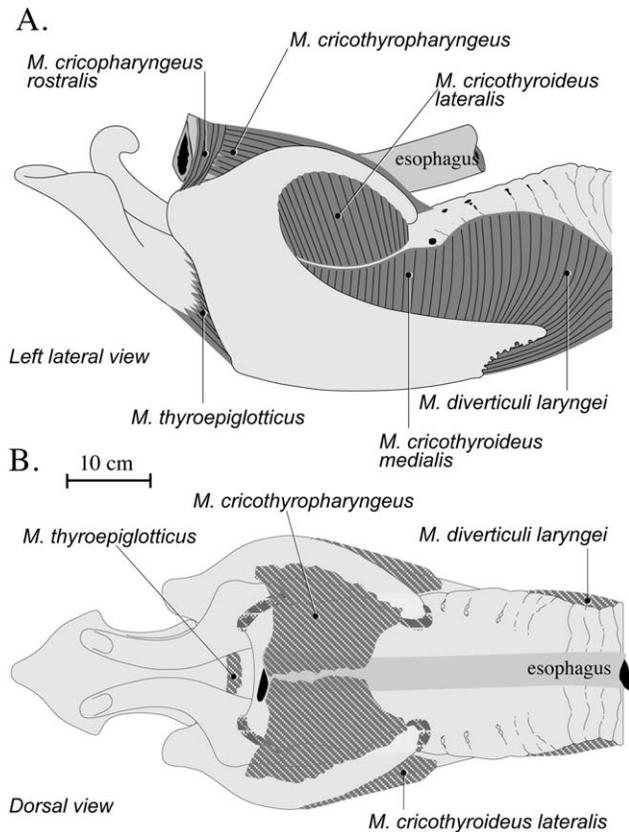
Fig. 6. Extrinsic and intrinsic musculature of the bowhead whale larynx (specimen 95B17). **A**: Left lateral view. **B**: Dorsal view. Illustrations by D.J. Hillmann.

larynx, and is thick, suggesting a powerful retractor function. Immediately rostral to the attachment of the *M. sternothyroideus* is the insertion of the *M. thyrohyoideus*, which connects the larynx with the basihyoid bone (Fig. 2A). This muscle is well developed and anchors the larynx to the hyoid suspension. The *M. hyoepiglotticus*, a depressor of the epiglottis, originates on the basihyoid and interdigitates with the intrinsic *M. thyroepiglotticus* (Fig. 2A). The *M. cricothyropharyngeus*, a combination of the cricopharyngeus caudalis and thyropharyngeus muscles, which originate on the dorsal surface of the cricoid cartilage and the caudal horn of the thyroid cartilage, respectively, blends in with the muscular coat (*Tunica muscularis*) of the esophagus (Fig. 6). This muscle appears to act as a constrictor for the esophagus and the esophageal opening. The synergistic *M. cricopharyngeus rostralis* likely aids the *M. cricothyropharyngeus* in constricting the *Limen pharyngeoesophageum* (Fig. 6). The *M. cricopharyngeus rostralis* originates at the most rostrodorsal extension of the cricoid cartilage and extends in a caudomedial direction to insert in the dorsal portion of the *Tunica muscularis* of the esophagus. When contracting, this muscle is assumed to depress the esophagus and forces it to flatten out against the underlying dorsal surface of the plate of the cricoid cartilage.

Intrinsic muscles of the larynx. The intrinsic musculature of the larynx can be divided into three functional groups. The *M. thyroepiglotticus* (Figs. 2A and 6A) is a likely depressor of the epiglottis and thus opens the laryngeal air passage. The *Mm. cricothyroideus lateralis* and *medialis* (Fig. 6A) may constrict the laryngeal cavity, thus closing the laryngeal passage. Contraction of the *M. diverticuli laryngei* (Fig. 6) appears to compress the air in the laryngeal diverticulum.

The *M. thyroepiglotticus* originates from the rostral and ventral edge of the thyroid cartilage and extends rostrodorsally to meet the serrated caudal edge of the epiglottic cartilage (Fig. 6). On its course this muscle is joined by the *M. hyoepiglotticus*, which also inserts on the caudal edge of the epiglottic cartilage. The two muscles together appear to act as powerful depressors of the epiglottis during the opening of the air passage.

The *M. cricothyroideus lateralis* originates from the lateral surface of the cricoid cartilage and inserts on the ventrolateral edge of the caudal horn of the thyroid cartilage. The muscle is short and has an extensive cross-sectional area (Fig. 6). The *M. cricothyroideus medialis* also originates from the lateral surface of the cricoid cartilage plate. It inserts on the dorsomedial surface of the lamina of the thyroid cartilage. Together these two muscles are assumed to restrict the diameter of the laryngeal cavity.

The *M. diverticuli laryngei* extends from one ventrolateral edge of the cricoid cartilage to the other, thus forming a sling-like structure in the caudoventral aspect of the laryngeal cavity. The dorsal portion of the muscle extends horizontally connecting the ventrolateral edges of the cricoid cartilage, creating a sac-like space between the dorsal and ventral portions of the muscle. The laryngeal mucosal membrane extends between the two portions, thus defining the laryngeal diverticulum. The volume of the laryngeal diverticulum is extensive even when deflated, for example, ~2 L in the larynx of the adult bowhead whale, specimen 95B17. Caudally, the muscle fibers of both portions unite, and therefore limit the caudal extension of the diverticulum. The *M. diverticuli laryngei* is extensive and has numerous attachment sites. Some muscle fibers attach to the serrated caudal edge of the laminae of the thyroid cartilage. Others extend from the lateral edges of the cricoid cartilage and the first few incomplete cartilage rings of the trachea to the caudal edge of the thyroid cartilage. The laryngeal diverticulum splits rostroventrally from the main laryngeal air passage, which continues along the dorsomedial aspect of the laryngeal cavity. The *Ligamentum interarytenoideum* forms a horizontal septum between the laryngeal passage into the trachea and the laryngeal diverticulum. The vocalis, ventricularis, arytenoideus dorsalis, and arytaenoideus lateralis muscles were missing in the larynx of the bowhead whale.

Trachea

Although the trachea is not part of the larynx, it is still an integral part of the respiratory structures investigated in this study, and thus becomes important in the evaluation of the functional anatomy of the larynx (see Figs. 2B, 3D, and 4). The trachea also serves as an anchor for caudal muscle fibers of the *M. diverticuli laryngei*, thus becoming part of the functional unit of the larynx.

The trachea is very short and does not exceed a length of ~150 mm even in adult specimens. The first six tracheal cartilage rings (*Cartilagines tracheales*) are incomplete. These c-shaped cartilages are intimately connected to the cricoid cartilage and partially fused with each other, especially in their dorsal aspect. It was not possible to distinguish between the caudal extension of the cricoid cartilage and the first few incomplete cartilages of the trachea. Most tracheal cartilages are not situated in a vertical plane but are oblique in direction, extending from craniodorsal to caudoventral. The plane of the tracheal cartilages approaches a vertical plane further caudally with the last ring being positioned vertically. A conspicuous change in direction of the trachea was noted just cranial to the tracheal bifurcation (*Bifurcatio tracheae*), where the trachea changes its dorsal direction and begins to parallel the longitudinal axis of the body. The last five tracheal cartilages are complete rings. Caudal to the last complete tracheal cartilage ring, the trachea bifurcates into the two primary bronchi. The internal surface of the trachea is covered by a thin, smooth mucosal membrane. A *M. trachealis* is missing in the wall of the trachea.

Airflow Patterns

In the Bowhead whale, the airflow through the laryngeal cavity follows a complex pattern. The air in the nasopharynx enters the laryngeal stalk with the opening of the laryngeal cavity, the *Aditus laryngis*, followed by the vestibule of the laryngeal cavity. On the ventral surface of the vestibule of the laryngeal cavity, immediately caudal to the level of the *Articulatio cricoarytenoidea*, a caudoventral passage opens into the blind laryngeal diverticulum. Air flowing into the diverticulum passes between two parallel folds of connective tissue, which are part of the respective medial surfaces of the vocal processes of the arytenoid cartilages. Air flowing through the main air passage ascends caudodorsally to the diversion of the laryngeal diverticulum and enters the trachea above the level of the great vessels of the heart.

DISCUSSION

As a mammal, a whale must breathe atmospheric air and can do so only by surfacing the dorsal aspect of its head, hence the ventilation of the lungs must be rapid—a process facilitated by a streamlined and short respiratory passage. The functional relationship between the upper airway, the cartilages and the intrinsic muscles of the larynx, and the short trachea are expected to facilitate the rapid expulsion and inhalation of a significant volume of air within a respiratory cycle driven by the action of the respiratory musculature. Furthermore, creating sound while underwater without the loss of air poses the challenge of moving air within the nasalpharyngeal-laryngeal cavity (Reidenberg and Laitman, 2007a, 2008). The examinations of the sagittally sectioned adult larynx, the MRI data from an intact fetal specimen, and a sagittally sectioned fetal head and cervical region provided specific information about the species-specific anatomy and topography of the bowhead whale larynx and suggests three functions. First, the larynx is the air-conducting passageway connecting the nasopharynx with the trachea and the lungs. Second, the laryngeal stalk projecting into the nasopharynx is surrounded by the palatopharyngeal muscle and together both function to separate the respiratory from the digestive tracts during feeding. Finally, the larynx is the site of sound production in the bowhead whale.

The paucity of detailed anatomical studies of cetacean respiratory structures limits the ability to assess the anatomy of the bowhead whale larynx in a comparative context. However, the bowhead whale larynx shares several broad similarities with larynges of other mysticete and odontocete whales. These include (i) the extreme rostral position of the larynx with epiglottis and arytenoid cartilages firmly situated in the nasal cavity; (ii) the dorsal-curved laryngeal stalk; (iii) the incompleteness of cricoid cartilage (in contrast to those of terrestrial mammals); (iv) the presence of a diverticulum extending ventro-posteriorly from the main laryngeal passage; and (v) the use of laryngeal structures for phonation. Overall, the bowhead whale larynx appears to share many commonalities with that of other mysticeti whales and more broadly with odontocete whales. These similarities and some of the distinct differences when compared to terrestrial mammals suggest that secondary adaptation to life in water have placed common selective pressures on this structure across cetacean taxa.

The position of the larynx is crucial for its function in the bowhead whale and differs in comparison to terrestrial and semiaquatic mammals. By extending into, and being permanently situated in the nasopharynx, the larynx creates separate passages for the respiratory and the digestive systems. The laryngeal extent into the nasal cavity in cetaceans has been noted previously (Racovitza, 1904; Reidenberg and Laitman, 1987) and has been associated with the ability of whales to swallow prey while under water (Turner, 1872; Racovitza, 1904). Hunter (1787) noted the elongation of the arytenoid cartilages in the minke whale and described their connection with the epiglottis as a "single tube." Interestingly, evidence in humpback whales suggests that the epiglottis in this species may reach into the oral cavity during a species-specific foraging behavior (Reidenberg and Laitman, 2007b). When the bowhead whale larynx is opened for respiration, the epiglottis is likely depressed by the combined action of the *Mm. thyroepiglotticus* and *hyoepiglotticus*. At the same time, the corniculate processes of the arytenoids are rotated laterally, possibly as a passive consequence of the contraction of the *Mm. cricothyropharyngeus*, which appears to generate a rotational movement at the cricoarytenoid joint to further widen the air passage, therefore greatly increasing its cross-sectional area. Finally, the corniculate processes meet the margins and seal off the intrapharyngeal opening. These movements of the arytenoid cartilages appear to match closely those described for several species of mysticete whales (Reidenberg and Laitman, 2007) and suggest a common mode of action in phonation among mysticete whales.

Aiding in the separation of nasopharynx and laryngopharynx is a synergistic group of muscles, for example, the palatopharyngeal and pterygopharyngeal muscles, which surround the intrapharyngeal opening. Once the intrapharyngeal opening is closed, the air passage is completely separated from the food passage and the bowhead whale can feed and breathe simultaneously (this

separation also is noted for cetaceans in general by Racovitz, 1904). This dual action accommodates the feeding mode of bowhead whales, which skim the ocean surface and collect prey. As a "continuous ram feeder" (Tomilin, 1967; Nemoto, 1970; Reeves and Leatherwood, 1985; Würsig et al., 1985; Werth, 2007) the oral cavity of the bowhead whale (and many other whale species) is often open for minutes and the oropharynx is subjected to the water pressures present in the oral cavity (for a review see Sanderson and Wassersug, 1993). Feeding efficiency is vital since bowhead whales are opportunistic feeders that rely on a food resource with a patchy distribution. Although Balanopterids are also reliant on food with patchy distribution, their feeding technique usually involves brief lunges through schools of prey (Reeb and Best, 1999) and should be much shorter in duration than in the bowhead whale. During the evolution of whales, the position of the nostrils has shifted dorsally thereby shortening and streamlining the nasal cavity, likely representing an adaptation to the aquatic environment (Berta and Sumich, 1999). By extending the laryngeal stalk into the nasopharynx, the efficiency of breathing increases even further by shortening the upper airway.

It is noteworthy that no previous studies have described sexual dimorphism in the bowhead whale larynx as would be the case in many terrestrial mammals and Quayle (1991) specifically stated that there were no differences between male and female bowhead whales. Furthermore, overall shape and relative dimensions of the bowhead whale larynx and its cartilages did not differ noticeably among specimens analyzed in this study despite the 13-fold difference in the absolute size of the animals (ADULT vs. 91BF). However, the relative size (length) of the larynx when normalized for the length of the animal (Table 1; [length of larynx $\times$ 100/length of animal]) was noticeably larger in the young females (89B2F and 90B4F) at ∼8% body length when compared to the ADULT specimen with only 4% body length. The large size of the larynx even in immature animals likely relates to the significance of phonation in these highly social animals. Social interactions among bowhead whales are different from those of humpback whales where males have larger larynges. Depending on the mating behavior, in humpback whales the males compete by singing and by fighting in polygynous mating behavior, and are therefore bigger than females; in bowhead whales and in right whales, the females mate with several males (promiscuous or polyandrous mating behavior) and are slightly bigger than the males, which can explain the larger size of the larynx. In bowhead whales females sing to attract males, while males sing for competition (Tervo et al., 2009).

The nostrils are accompanied by musculature closing the nasal openings during diving, but the laryngeal and palatopharyngeal mechanisms also prevent influx of water into the respiratory system. Water could enter the nasopharynx during feeding when the oral cavity and oropharynx is submerged and filled with water, especially if the intrapharyngeal opening is either incompletely sealed or compromised. However, the two corniculate processes of the arytenoid cartilages fit tightly into the shallow grooves of the epiglottic cartilage and form a more complete seal on the laryngeal stalk. The *Mm. cricothyroideus lateralis* and *medialis* act to

further restrict the diameter of the laryngeal cavity, thus closing the laryngeal passage. The fibrous articulation of the caudal horn of the thyroid cartilage with the lateral aspect of the cricoid cartilage acts as a hinge joint with the two cartilages rotating against each other during contraction of the cricothyroid musculature. The greatest extent of this rotational movement occurs in the rostral portion of the laryngeal cavity, which subsequently increases pressure on the arytenoid cartilages against the epiglottic cartilage and further closes the laryngeal passage.

Food, which has been trapped in the baleen plates of the whale, is collected on the tongue and then swallowed into the short oropharynx. The food then passes around the base of the laryngeal stalk in the laryngopharynx (piriform recesses) ventral to the palatopharyngeal folds and enters the funnel-shaped opening of the esophagus. The esophageal opening is situated caudal to the laryngeal stalk, marked by the *Limen pharyngeoesophageum*. The esophagus is extremely narrow with a diameter of only a few centimeters when relaxed, even in an adult bowhead whale. The *M. cricothyropharyngeus* relaxes during feeding, which enables dilatation of the esophageal passage.

Air passing through the nostrils and the nasopharynx into the laryngeal stalk is uninhibited and can be exchanged in large amounts in a short period of time. Air is expelled forcefully by the bowhead whale with velocities likely high in the laryngeal passage as it is one of the narrowest portion of the respiratory tract. The main air passage through the larynx is lined by a smooth mucosal membrane and does not exhibit structural differentiation as was already pointed out by Kükenthal (1900). During exhalation, when air is forced through the laryngeal passage at high velocities, a backflow of air could occur where the passage widens at the rostral end of the laryngeal stalk. Airflow could become turbulent in this area and decrease the volume of air per time passed through the laryngeal passage. "Twisting" of the airflow through the laryngeal tube might reduce turbulent flow and increases the efficiency of flow (comparable to "rifling" in a gun barrel). The negative pressure at the rostral opening of the laryngeal cavity then prevents the formation of "eddies" in the area where the airflow leaves the narrow passage of the larynx.

The most challenging muscle for which to ascertain a function is the muscle forming the laryngeal diverticulum. This muscle takes origin from the cricoid and thyroid cartilages. It spans the length of the larynx from its most rostral position caudal to the epiglottis and extends caudally to a position immediately rostral to the tracheal bifurcation. The dorsal aspect of the caudal portion of this muscle completes the cricotracheal lumen and also creates a laryngeal diverticulum ventrally. We hypothesize that this muscle is involved in the third function of the larynx, that is, to produce sound. Functions of the laryngeal apparatus in sound production are not a novel idea and researchers have debated a function of the cricoarytenothyroid muscle forming a laryngeal diverticulum in this context since at least the mid-1800s (Eschricht and Reinhardt, 1866). The hypothesis that the laryngeal morphology is directly responsible for sound production in mysticetes whales has steadily gained support in numerous publications (Dubois, 1886;

Kükenthal, 1900; Hosokawa, 1950; Slipjer, 1962; Haldiman and Tarpley, 1993; Schoenfuss and Hillmann, 1996; Reeb and Best, 1999; Reidenberg and Laitman, 2007a). Reeb (1999) reported that most underwater sounds by cetaceans are produced without the obvious release of air from the nostrils or the mouth. This evolutionary adaptation to phonate underwater without the release of air requires an ability to alternately move air back and forth in the respiratory passageway. Hosokawa (1950) hypothesized that the alternating movement by mysticete whales involves recycling inspired air using the laryngeal sacs and that these sacs may possibly be involved in sound production (Quayle, 1991; Reeb, 1999; Reidenberg and Laitman, 2008). Reidenberg and Laitman (2007a) have provided extensive evidence for the role of the laryngeal diverticulum in phonation in other species of mysticetes whales; however, their study did not include bowhead whale specimens.

We propose that the laryngeal diverticulum together with the vocal folds of the arytenoid cartilages form the sound-producing organ of the bowhead whale larynx. Although the bowhead whale larynx was mentioned as the possible sound producing structure by authors before (e.g., Haldiman and Tarpley, 1993; Reidenberg and Laitman, 2007a), it has never been examined in detail regarding sound producing mechanisms. The diverticulum extends caudally from the ventral aspect of the laryngeal cavity as an unpaired median structure, occupying the area caudoventral to the body of the thyroid cartilage and ventral to the incomplete cricoid cartilage. The proposed term *M. diverticuli laryngei* was coined because it is unique to the laryngeal diverticulum in mysticetes whales. Reidenberg and Laitman (2007a) suggested that the musculature surrounding the diverticulum is either a second belly of the cricothyroid muscle or the result of the caudal displacement of the thyroarytenoid muscle along with the elongation of the vocal processes. Given the distinct nature of the bowhead whale laryngeal diverticulum and its overall extent, we opted to propose the term *M. diverticuli laryngei* for this structure to reflect its uniqueness and resultant diagnostic nature in mysticete whales. This muscle forms a large caudoventral extension of the larynx and encloses the laryngeal diverticulum, which is lined by a thin and smooth mucosal membrane. It is similar in length to the laryngeal body and follows it parallel to the respiratory air passage.

The laryngeal diverticulum is connected to the main air passage by a narrow longitudinal slit along the ventral aspect of the laryngeal cavity. The two vocal folds are situated along the sides of this slit, which is supported by the two paralleling vocal processes of the arytenoid cartilages. In contrast to the descriptions for other mysticete larynges (Reidenberg and Laitman, 2007a), the vocal folds in the bowhead whale's larynx appear to lack the distinct "U"-shaped component of the fold across the midline of the larynx from one arytenoid cartilage to the other. Instead, the vocal folds are mostly prominent along the medial margin of each vocal process and have only a thin continuation across the midline. However, despite these differences, the vocal folds in the bowhead whale are likely homologous to those described by Reidenberg and Laitman (2007a) for other mysticete whales and homologous also to vocal folds in terrestrial and semiaquatic mammals (Kükenthal, 1900).

We propose that vocalization may occur as a function of the temporary interruption of airflow as it is manipulated back and forth within the entire nasal and laryngeal passage. After a respiratory cycle has been completed and the animal dives, a column of air (dead space air) remains from the nares to the lumen of the laryngeal diverticulum and into the trachea and bronchi. Air movement within this space may be facilitated by the *M. diverticuli laryngei* in either of two ways.

1. With the infraglottic entrance to the trachea "closed," the muscle of the laryngeal diverticulum may push air into the nasal cavity past the vocal folds resulting in the vibration of these structures with the sound possibly transmitted through the body wall. Higher pressure in the nasal cavity may push the air back into the diverticulum as the muscle of the laryngeal diverticulum relaxes, allowing for repeated cycles of vocalization. In the context of air movement and contraction of the muscle of the laryngeal diverticulum Ravitz (1900) hypothesized that the laryngeal diverticulum during contraction may serve to seal the entrance to the trachea supporting our first functional hypothesis for air flow.

2. Alternatively, with the entrance of the larynx closed, the muscle of the laryngeal diverticulum may push air into the trachea and bronchial tree past the vocal folds. Once the *M. diverticuli laryngei* relaxes, contraction of the thorax may raise the pressure in the bronchi and trachea (presumably smooth musculature along the bronchioles would prevent air from reaching respiratory alveoli; Henk and Haldiman, 1990). It is even possible that both mechanisms of air movement are used during phonation and result in the "simultaneous dual frequency sound production" described in bowhead whales by Tervo et al. (2011). The function of the laryngeal diverticulum in either of the two ways described above may be impacted by the condition of the diverticulum itself during diving. Should the respiratory system collapse during diving as has been proposed for other cetaceans (Ridgeway and Howard, 1979; Berta and Sumich 1999), then the *M. diverticuli laryngei* may be forced dorsally resulting in the blockage of the tracheal passage. However, in contrast to other cetaceans (especially some odontocete), bowhead whales are not known for deep dives limiting the pressure exerted on the thoracic cavity that may result in the dorsal displacement of the laryngeal diverticulum.

The *in situ* position of the laryngeal diverticulum was recorded by magnetic resonance imaging in specimen 91BF (Fig. 1B). During exhalation the diverticulum is deflated due to contraction of the M. diverticuli laryngei (Fig. 7A). Inflation of the diverticulum could occur during inhalation or through back flow of air from the nasopharynx or bronchi as suggested above (Fig. 7B–D). When the *M. diverticuli laryngei* contracts, air is forced into the primary laryngeal passage (Fig. 7E). While passing by the two folds of connective tissue, the air stream causes pressure differences on either side of the vocal fold. An area of low pressure forms on the side of each fold where the air speed is higher, and an area of high pressure on the opposite site of the fold (Bernoulli's principle). Pressure differences will cause the folds to oscillate in dorsoventral direction (Fig. 7E, F). The result

A. B. C. D. E. F.

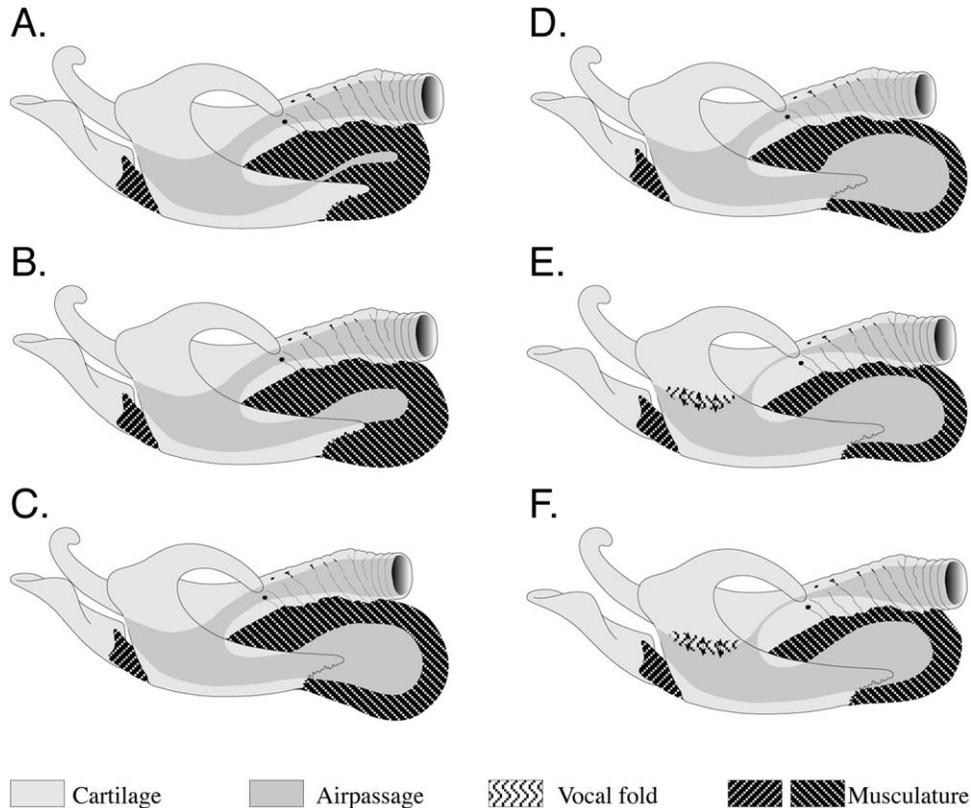Cartilage | Airpassage | Vocal fold | Musculature

Fig. 7. Sequence depicting the hypothesized stages of inflation and deflation of the laryngeal diverticulum during phonation (based on compressed air experiments conducted with specimen 95B17). **A**: Complete deflation of the laryngeal diverticulum. **B**: Beginning inflation. **C**: Continued inflation. **D**: Maximum inflation. **E**: Beginning defla-tion, vibration of the vocal folds, and phonation. Note the opening of the laryngeal aditus through the rostro-inferior rotation of the epiglottis and the closure of the tracheal passage due to the extension of the *M. diverticuli laryngei*. **F**: Continued deflation and phonation. Illustrations by D.J. Hillmann.

of the oscillation is a high pitch sound resembling the higher frequency sounds (500 Hz–4 kHz) ascribed to several whale species including bowhead (Ljungblad et al., 1982), humpback and right whales (Bass and Clark, 2003). Manipulation of the arytenoid cartilages along their anatomically normal range of movement causes changes in frequency of the vibration and thus a change in sound level. While contracting, the *M. diverticuli laryngei* bulges dorsally into the main laryngeal air passage and prevents the reflux of air into the lower respiratory system (Fig. 7E, F). The laryngeal diverticulum may also act as a resonance chamber, whereby at maximum air capacity the frequency is low providing a basal tone and while the diverticulum volume decreases through constriction the frequency increases providing a more treble tone. An analogy is the different tonal qualities that can be achieved when blowing into a jug filled to different levels with a fluid. However, it needs to be noted the sound propagation through air differs from that through fluids and assessing the final sounds emitted by bowhead whales was beyond the scope of the current anatomical study.

It is difficult to investigate sound production in an extirpated larynx, but it is even more difficult to attempt the same task in a living animal, which motivated us to choose the first option. By conducting experiments using compressed air, which was injected into the fundus of the laryngeal diverticulum, we were able to produce oscillating sounds not dissimilar from those recorded from bowhead whales. The lateral rotation and adduction of the arytenoid cartilages proved to be the decisive factor in changing frequency of the sound produced. These experiments are simplistic, but should not be dismissed as evidence of sound production as they simulate closely the airflow through the laryngeal diverticulum. It should be noted that similar experiments conducted by Fabricius in 1600 with human laryngeal specimens led to the discovery of the functional significance of the laryngeal structures today known as vocal folds (Fabricius, 1600, as cited by Harrison, 1995). More recently, similar experiments have been conducted in an extirpated elephant larynx to study infrasonic vocalization (Herbst et al., 2012).

While these findings are preliminary, they fit the reports of communication among bowhead whales. Bowhead whales produce sounds and are able to create a range of different sounds. Communication in the bowhead whale might not be as sophisticated as in the humpback whale (although band-width and internote intervals match closely in these two species), but it is well established that bowhead whales can change amplitude and sound intensity (Bass and Clark, 2002). These changes are possible in our model of sound production

via the manipulation of the arytenoid cartilages, which support the vocal folds of the laryngeal diverticulum. We also know that bowhead whales communicate while diving. The laryngeal diverticulum is an ideal place to hold air in a non-respiratory environment. While it is unclear how whales avoid the negative effects of gas exchange during deep diving, we can assume that it would be disadvantageous to circulate oxygenated air into the respiratory system during diving. The bulging *M. diverticuli laryngei* constitutes a valve that closes the laryngeal air passage caudal to the connection with the laryngeal diverticulum (also noted by Ravitz, 1900). Air passing into the nasopharynx after oscillating the vocal folds will not enter the lower respiratory system (see also Henk and Haldiman, 1999 for further microscopic evidence of bronchi occlusion). Interestingly, a convergent function for air sacs in apes and large gibbons was hypothesized by Hewitt et al., (2002), who suggested that air sacs are used to avoid hyperventilation during prolonged vocalization events. Finally, the expulsion of air after a dive is rapid, almost complete, and extremely forceful. Any vocal structure in the main air passage would be, under best circumstances, an obstacle for a fast airflow. The evolution of vocal structures separated from the primary laryngeal passage favor a rapid gas exchange as these structures would not block the airflow. Furthermore, vocal structures not exposed to the force created by rapid exhalation would be protected better and less prone to structural damage.

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