Discovery of a Low Frequency Sound Source in Mysticeti (Baleen Whales): Anatomical Establishment of a Vocal Fold Homolog

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ABSTRACT

The mechanism of mysticete (baleen whale) vocalization has remained a mystery. Vocal folds (true vocal “cords”), the structures responsible for sound production in terrestrial mammals, were thought to be absent in whales. This study tests the hypothesis that the mysticete larynx possesses structures homologous to vocal folds and that they are capable of sound generation. Laryngeal anatomy was examined in 37 specimens representing 6 mysticete species. Results indicate the presence of a U-shaped fold (U-fold) in the lumen of the larynx. The U-fold is supported by arytenoid cartilages, controlled by skeletal muscles innervated by the recurrent laryngeal nerve, is adjacent to a diverticulum (laryngeal sac) covered with mucosa innervated by the superior laryngeal nerve, and contains a ligament—conditions that also define the vocal folds of terrestrial mammals and, therefore, supports homology. Unlike the vocal folds of terrestrial mammals, which are perpendicular to airflow, the mysticete U-fold is oriented parallel to airflow. U-fold adduction/abduction and elevation/depression may control airflow, and vibration of its edges may generate sounds. The walls of the laryngeal sac can expand and contract, may serve as a resonant space, and may also propagate vibrations generated by movements of the supporting arytenoid cartilages. The extensive musculature surrounding the laryngeal sac may enable rapid and forceful expulsion of air from the lumen of the sac into other respiratory spaces, or maintain a constant sac volume despite the effects of ambient pressure (e.g., changes during diving or ascent). The size and complexity of the mysticete larynx indicates an organ with multiple functions, including protection during breathing/swallowing, regulation of airflow and pressures in the respiratory spaces, and sound generation. The presence of a vocal fold homolog offers a new insight into both the mechanism of sound generation by mysticetes and the divergent evolution of odontocete and mysticete cetaceans. Anat Rec, 290:745–759, 2007. © 2007 Wiley-Liss, Inc.

Key words: whale; larynx; anatomy; mysticete; cetacean; respiratory; sound; communication; vocal

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Received 2 March 2007; Accepted 13 March 2007 DOI 10.1002/ar.20544
Published online in Wiley InterScience (www.interscience.wiley.com).
Mysticete cetacean (baleen whale) vocalizations are related to a variety of behaviors including intraspecific communication, mate attraction, aggression, distress, and feeding (Payne and McVay, 1971; Thompson et al., 1979; Thompson et al., 1986), but probably not echolocation (Beamish, 1978). Vocalizations are produced primarily in the low frequency range (see review in Richardson et al., 1995; see also Thompson et al., 1986, 1992; Cummins and Holliday, 1987; Crane and Lashkari, 1996; Stafford et al., 1999; Mellinger and Clarke, 2003). As low frequency sounds travel farther than high frequencies before attenuating, mysticetes appear to use low frequencies to communicate over long distances and thereby maintain pod cohesion when visual contact is obscured by large separations (Wursig, 1988). While an anatomical mechanism for sound production (specifically biosonar signal production) in odontocete cetaceans (toothed whales, including dolphins and porpoises) has been described (Cranford et al., 1996), the anatomical mechanism of sound generation in mysticetes has not yet been established. Odontocetes have a complex system of nasal air sacs (Mead, 1975) and fatty tissues (Au et al., 2006) that generate and modify sound. As mysticetes do not possess such structures, sound production is thought to occur solely in their larynx (Purves and Pilleri, 1983). Although vocal folds (vocal cords, true vocal cords, or true cords) are the prime generator of initial laryngeal sounds in terrestrial mammals, it is currently widely accepted that mysticetes lack them (Carte and MacAlister, 1867; Turner, 1870; Dubois, 1886; Hosokawa, 1950; Purves and Pilleri, 1983; Quayle, 1991; Paterson et al., 1993; Haldiman and Tarpley, 1995). Thus, other regions of the larynx have been suggested as possible sound sources (Beauregard and Boulart, 1982; Benham, 1901; Hosokawa, 1950; Sukhovskaya and Yablokov, 1979; Henry et al., 1983; Reeb and Best, 1989). While the presence of vocal folds has only been recently discovered in odontocetes (Reidenberg and Laitman, 1988), no one has yet confirmed the existence of vocal folds in mysticetes. As a result, the actual mechanism of mysticete sound generation has remained elusive.

BACKGROUND: INTRINSIC ANATOMY OF THE LARYNX IN TERRESTRIAL MAMMALS

The mammalian larynx is a valve-like structure situated at the beginning of the trachea. It is designed to protect the airway from accidental incursions of food, regulate intrathoracic/abdominal pressures, and generate sound (for review of comparative laryngeal anatomy and evolution, see Reidenberg and Laitman, 2005; Laitman and Reidenberg, 2007; in press). Its skeleton usually contains three unpaired cartilages (epiglottis, thyroid, and cricoid) and three paired cartilages (arytenoid, corniculate, and cuneiform), derived from the third through sixth branchial arches (for review of laryngeal embryology and development, see: Som et al., 2003a,b; Laitman et al., 2005, 2006). The arytenoid cartilages are joined to the corniculate cartilage by a synovial joint, and arytenoid movements about this joint are controlled by several intrinsic laryngeal muscles: posterior cricoarytenoid, lateral cricoarytenoid, oblique arytenoid, transverse arytenoïd, thyroarytenoid, aryepiglotticus, and vocalis. The arytenoid cartilages each possess a vocal process, which supports a vocal ligament that attaches ventrally to the thyroid cartilage. The ligament is covered by tissue that attaches to the lateral wall of the laryngeal lumen. Together, the ligament and its membranes form a shelf-like structure called a vocal fold (plica vocalis). Interestingly, this fold continues to be referred to incorrectly as a vocal “cord,” a term that was first used by Ferrein (1741) as he likened their actions to strings of a violin. His contemporary, Bertin, immediately (1745)—and correctly—noted that the term was totally inappropriate as the structures were unambiguously “folds.” While Bertin was correct, Ferrein’s term vocal “cord” has obviously struck a popular note as its frequent, and continued, usage indicates.

As most of the intrinsic muscles of the larynx have some attachment to the arytenoid cartilages, there is a wide range of possible movements that can affect the position and tension of the vocal folds. Movements (mostly abduction and adduction) of the vocal fold are controlled by the intrinsic laryngeal muscles, which act directly on the arytenoid cartilage or its attached vocal fold. These muscles are innervated by branchiomeric motor fibers derived from the cranial portion of the accessory nerve (cranial nerve XI) but carried in the recurrent laryngeal nerve branch of the vagus nerve (cranial nerve X). Tension of the vocal folds can also be controlled by contraction of the cricothyroid muscle, due to movement of the thyroid cartilage to which the vocal folds attach ventrally. The cricothyroid muscle is the only laryngeal muscle innervated by branchiomeric motor fibers derived from the vagus nerve (cranial nerve X), by means of the external branch of the vagus’ superior laryngeal nerve. Sensory innervation of the mucosa above the glottis (i.e., the level of the vocal folds) is also carried by the superior laryngeal nerve (by means of the internal branch), while sensory innervation below the glottis is carried by the recurrent laryngeal nerve.

The paired vocal folds of a typical mammalian larynx each contain a fibrous ligament (vocal ligament) that attaches dorsally to a cartilaginous appendage of the arytenoid (vocal process) and ventrally to the thyroid cartilage. Within the vocal fold are two skeletal muscles: the thyroarytenoid spans dorsoventrally between the arytenoid and thyroid cartilages, and the vocalis spans mediolaterally between the vocal ligament and the lateral cricothyroid ligament. Rostral to the vocal fold is a diverticulum that projects laterally from the laryngeal lumen (laryngeal ventricle). The vocal folds are positioned perpendicular to the long axis of the trachea so that, when opposed across the transverse plane in the midline, they occlude the laryngeal lumen, thereby restricting airflow. (While we realize that the gases within the respiratory tract are not technically “air,” we will use that term as well as “airflow” to describe them as this is the more familiar and classically used descriptor.)

MATERIALS AND METHODS

Specimens

Larynges were examined post mortem from 37 baleen whale (suborder Mysticeti) specimens representing two families: Balaenidae (right whales) and Balaenopteridae (rorqual whales) (Table 1). Specimens are derived from six species, including North Atlantic (northern) right whale (Eubalaena glacialis), humpback whale (Megaptera novaeangliae), minke whale (Balaenoptera acutorostris), and fin whale (Balaenoptera physalus) (Table 1).
ostrata), sei whale (*B. borealis*), fin whale (*B. physalus*), and blue whale (*B. musculus*). This is a very large sample, considering mysticete specimens are difficult to obtain as they are protected in the United States and most are listed as endangered species.

All specimens were donated through the National Marine Mammal Stranding Network and were collected under a letter of authorization (issued to J.R.) by the National Marine Fisheries Service, National Oceanic and Atmospheric Administration, United States (U.S.). Specimens derive from U.S. waters of the northwest Atlantic Ocean, except for one fin whale recovered from the northeast Pacific Ocean. No whales were killed for this study; all specimens were obtained post mortem from carcasses.

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The information listed below was derived from the U.S. National Marine Mammal Stranding Network “Level A” data sheets. When information was not available, N/A is listed. Sex was determined by examination of external genital slit and/or examination of reproductive tract. No attempt was made to assign sex to a partial specimen missing the reproductive tract. Lengths were measured as straight line distance from tip of rostrum to midline notch between flukes. Measurements originally made in feet or inches were converted to metric measurement in centimeters. All lengths are rounded to nearest centimeter. Two partial lengths (indicated by asterisks) are given for specimens missing the tail (caudal peduncle and flukes). Age was either recorded by stranding network or determined by authors based upon total length of whale or size of larynx. When available, information from examination of reproductive tract or stomach contents (pre- vs. post-weaning status) was used. C = calf, J = juvenile, A = adult. Specimen Identification numbers were assigned by regional stranding network members, and usually identify the stranding organization or state, year of stranding, and sometimes other information (e.g., sex, species, sequential tally of stranding order). Two specimens did not have ID numbers, thus the institution and year (NEA 1998) or state and year (NY 1999) of specimen recovery is indicated. **CCSN** = Cape Cod Stranding Network, Massachusetts; **MDDNR** = Maryland Department of Natural Resources, Maryland (including Delaware); **MMA** = Mystic MarineLife Aquarium (Mystic Aquarium), Connecticut (including Rhode Island); **MMSC** = Marine Mammal Stranding Center, New Jersey; **NEA** = New England Aquarium, Massachusetts; **NY** = Okeanos Ocean Research Foundation, or Riverhead Foundation, New York; **USNM** = United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.; **VMSM** = Virginia Marine Science Museum (Virginia Marine Science Center), Virginia; **VN** = Humboldt State University, California; **WAM** = University of North Carolina, Wilmington, Marine Mammal Stranding Program. **Specimen condition made it difficult to determine species. Originally identified as a fin whale, but assigned as a sei whale after genotyping biopsy sample.**
that were discovered floating, brought into port by large ships that had accidentally struck them, or found naturally washed ashore on beaches (often subsequent to a ship strike).

**Method of Laryngeal Retrieval**

Mysticetes are very difficult to dissect due to their large size, making access to laryngeal specimens limited in certain field necropsy situations. Beached carcasses were dissected in the "field" (i.e., at the shore site where they were discovered) or moved when necessary (e.g., posing a public health hazard) by means of crane and flatbed truck to a more suitable location (e.g., wildlife sanctuary), for further dissection and burial. Floating carcasses were towed to a shore-based facility (e.g., beach or dry dock) by the U.S. Coast Guard or the U.S. Army Corps of Engineers. The condition of the carcass dictated the necropsy technique relative to soft palate, hyoid, tongue, and skull base was noted.

As most beached carcasses naturally lie with the ventral surface exposed (due to the weight of the skull dorsally, counteracted by the gas build-up from bacterial fermentation that usually accumulates under the distensible ventral throat pleats of the oral cavity), a ventral necropsy approach was usually used. The superficial layers of skin, blubber, and muscle were removed in the midline region extending between the mandibular condyles and the sternum, approximately ventral to the eyes and rostral to the flippers. The hyoid bone (fused basihyal and thyrohyals) was identified by means of palpation under the ventral musculature. The thyroid cartilage of the larynx was usually palpable between the hyoid and the sternum, and the trachea was positioned completely within the thorax. The trachea, lingual, and pharyngeal tissues were cut, and tension was applied to the hyoid to assist with removal of the larynx.

**Method of Laryngeal Dissection**

Excised larynges retrieved from the field were stored frozen or formalin fixed for further subsequent laboratory examination. Detailed dissections of larynges were performed at our laboratory at the Mount Sinai School of Medicine, or at those of the Woods Hole Oceanographic Institution and the Osteoanatomy Laboratory of the National Museum of Natural History (Smithsonian Institution). The method of preservation and the condition of the larynges dictated the dissection protocol. Twenty-seven whole larynges were opened to view their internal anatomy. The cricoid cartilage was incised in the dorsal midline, and each portion reflected laterally. This method afforded the best view of the internal arrangement of the ventral aspect of the larynx, particularly the extensions of the arytenoid cartilages into the laryngeal lumen. Most of these larynges were subsequently bisected along the midsagittal plane. One sei whale larynx was bisected into dorsal and ventral halves, and one minke whale larynx was cut transversely to the long axis into multiple sections. In eight severely decomposed specimens (two right whales, four humpback whales, one sei whale, one fin whale), the whole larynx was defleshed and disarticulated to examine ligamentous connections and the morphology of individual cartilages. All larynges were photographed, and then either stored frozen or preserved by immersion in 10% formalin.

Internal laryngeal anatomy was examined to determine whether the there were structures that are homologous to the vocal folds of terrestrial mammals. Candidate tissues were evaluated for their (1) orientation, (2) cartilaginous attachments, (3) potential cartilage movements and mechanism of control, (4) presence/absence of ligaments, (5) innervation of associated musculature and mucosa, and (6) relationships to adjacent structures. These structures were also assessed for their ability to vibrate, and thereby generate a fundamental frequency for sound production. Potential resonating spaces and sound transmission pathways through adjoining tissues were also considered.

Additional methods that would be of value in comparing material to terrestrial forms, such as histology or muscle fiber typing, could not be attempted due to the preservation and condition of recovered material. Fresh tissues were frozen (thereby introducing freeze artifact). Decomposing specimens, although formalin fixed, showed signs of tissue autolysis and bubble formation from bacterial fermentation.

**RESULTS**

The mysticete larynx resembles the terrestrial mammalian laryngeal configuration in both position and overall structure. It is positioned in the midline with the epiglottis overlapping the soft palate, forming a bridge connecting the air passageways of the nasal and laryngeal regions (Fig. 1). The rostral portion of the mysticete larynx is relatively wide compared with odontocetes, and has a large opening (laryngeal aditus) between the epiglottis and corniculate cartilages that leads into the laryngeal lumen. The aditus faces dorsally, and is positioned within the nasopharynx, directly below the posterior choanae. The laryngeal skeleton is pictured in Figure 2. No cuneiform cartilages were found. The thyroid cartilage covers the midline ventrally and extends laterally on either side as a thin cartilage bar curved into an arch that attaches dorsolaterally to the cricoid cartilage. The cricoid cartilage is fused dorsally and laterally to the rostral tracheal rings, and is incomplete ventrally. The arytenoids are fused rostrally to the corniculate cartilages. A U-shaped laryngeal fold (see below) is attached to extensions of the arytenoid cartilages within the laryngeal lumen. The larynx expands ventrally into a single, midline diverticulum (see below). The larynx attaches rostrally to the hyoid apparatus, which in turn is suspended dorsally from the skull base. The hyoid (basihyal and thyrohyals) and the rostral portion of the larynx lie under the skull base, approximately between the two condylar swellings of the mandible at the temporomandibular joint. The caudal aspect of the larynx is located at the thoracic inlet; the trachea begins immediately dorsal to the sternum. The abrupt transition in position from subcranial to intrathoracic is related to the highly compressed cervical vertebrae, and, therefore, the lack of a neck in mysticetes.

**U-Fold**

The internal arrangement of the mysticete larynx contains a prominent U-shaped structure that borders the
opening between the laryngeal lumen and the ventral laryngeal sac. The left and right extensions of this structure are joined ventrocaudally in the midline, forming a continuous, U-shape, and, therefore, will be referred to as the “U-fold.” The U-fold is oriented in the coronal plane, with the curve of the U directed caudally and the opening between the parallel extensions of the U directed rostrally. When viewed from its dorsal (laryngeal luminal) surface, the U-fold appears as a raised, thick ridge of tissue that spans between the arytenoid cartilages (Fig. 3). Its thickness varies with different species, being thickest in *Eubalaena* (northern right whale) (Fig. 3e). The right and left extensions of the U-fold are each supported by cartilage bars that taper caudally to a point. The cartilage bars are extensions of the arytenoid and likely homologous to the vocal processes of terrestrial mammals. The curved portion of the fold (i.e., the bottom of the U) contains a ligament that spans between the caudal tips of the vocal processes (Fig. 2b). As the ligament tethers the tips together in the midline, it causes the U-fold to take

![Figure 1](image)
on a V-shaped appearance when the arytenoids are abducted. The U-fold surrounds the slit-like ostium of a diverticulum (laryngeal sac) located ventral to the larynx. When the lateral walls of the U-fold are approximated during adduction of the arytenoids, they resemble two opposed lips that seal the laryngeal sac ostium closed. The surface of the U-fold in most specimens exhibits numerous closely packed folds separated by narrow and often deep, irregular grooves. These grooves indicate a folded mucosa that provides flexibility of the tissue and an increased surface area.

To determine whether the U-fold is homologous to the vocal folds of terrestrial mammals, we examined it for the presence of specific traits that define mammalian vocal folds, specifically: (1) orientation, (2) cartilaginous attachments, (3) potential cartilage movements and mechanism.
Fig. 3. Dorsally opened larynges from five representative mysticete species. Ventral luminal surface of larynx was visualized by cutting the cricoid cartilage dorsally in the midline and reflecting each half laterally. Asterisks indicate location of U-shaped fold. a: *Balaenoptera acutorostrata*, minke whale. b: *Balaenoptera borealis*, sei whale. c: *Megaptera novaeangliae*, humpback whale (note retractor pole on left and dissector's gloved hands on right, overlying cut edges of cricoid cartilage). d: *Balaenoptera physalus*, fin whale. e: *Eubalaena glacialis*, northern right whale.
of control, (4) presence/absence of ligaments, (5) innervation of associated musculature and mucosa, and (6) relationships to adjacent structures.

**Orientation.** The U-fold is oriented parallel to the long axis of the larynx and trachea (Fig. 4). The caudal edge of the U-fold is usually positioned below the cricoid cartilage in the midline, near the level where the cricoid becomes fused with the tracheal cartilages laterally. There is a longitudinal gap in the midline between the parallel extensions of the U-fold. This gap enables communication between the spaces of the laryngeal lumen dorsally and the laryngeal sac ventrally. The U-fold can be positioned diagonally so that the rostral portion is located dorsally and the caudal portion terminates ventrally. The U-fold can be positioned diagonally so that the rostral portion is located dorsally and the caudal portion terminates ventrally. This orientation creates a ventral boundary to the space contained between the trachea and the laryngeal lumen, narrowing it to a cone-shape with the apex directed dorsorostrally. Adduction of the corniculate and arytenoid cartilages seals the cone-shaped space ventrally so that air in the laryngeal sac cannot communicate with air in the caudal larynx, trachea, or lungs. However, slight abduction of the corniculates and rostral portions of the arytenoids creates a passageway for air to flow dorsostrally between flaps of tissue on the corniculate cartilages. The caudal portion of the U-fold can also be elevated dorsally to approximate the midline luminal aspect of the cricoid cartilage, which is correspondingly thickened in this region. This action divides off the rostral laryngeal lumen and laryngeal sac from the caudal laryngeal lumen (under the caudal part of the cricoid cartilage) and trachea. Unlike the former depressed position, this elevated orientation prevents air from flowing to or from the trachea and lungs. However, if the arytenoids are abducted while the U-fold is elevated, then a communication for airflow is established between the laryngeal sac, the laryngeal aditus and laryngopharynx (space between and surrounding the epiglottis and corniculate cartilages), and the nasal passageways.

**Cartilaginous attachments.** The mysticete larynx is composed of three unpaired cartilages (epiglottis, thyroid, and cricoid) and two paired cartilages (arytenoid and corniculate). Unlike many terrestrial mammals, but similar to the odontocete condition, there was no pair of cuneiform cartilages, the cricoid cartilage is incomplete ventrally, and the arytenoid cartilage is fused dorsorostrally to the corniculate cartilage forming an arytenocorniculate complex (Fig. 2). It is possible that the corniculate cartilage is actually the cuneiform cartilage, but based upon its similarities in position and attachment to the corniculate cartilage of odontocetes (Reidenberg and Laitman, 1987, 1988), it is assumed that this is the homologous cartilage.
The arytenoid cartilage has three features: a curved articular joint facet on the caudal aspect, a muscular process on the lateral aspect, and an extension projecting ventrocaudally into the lumen of the larynx. We will refer to this extension as the “vocal process” due to similarities in position and attachment to the vocal process of the arytenoid in other mammals. The interarytenoid, posterior cricoarytenoid, and lateral cricoarytenoid muscles attach to the muscular process. The arytenoid has a concave joint facet that opposes a convex joint facet on the leading edge (dorsorostral) of the cricoid cartilage (Fig. 2a). The diarthrodial joint between the arytenoid and the cricoid contains fluid (assumed to be synovial fluid), and the curved joint surface indicates movements in at least two planes: rostrocaudal rocking, rostrocaudal sliding, and lateromedial sliding. The latter two pairs of movements likely occur in tandem, as the cricoid’s joint surface is a diagonal face with the medial aspect positioned further rostrally than the more caudally placed lateral aspect (Fig. 2b).

The vocal process of the arytenoid begins immediately ventral to the cricoarytenoid joint, and extends far into the lumen of the larynx. It projects caudoventrally, beginning at the dorsal aspect of the lumen and terminating ventrally just before the beginning of the trachea. The vocal process narrows to a point, and curves medially to meet the opposing vocal process in the midline. They are connected across the midline by a short but thick elastic ligament. The vocal processes are covered by a layer of soft tissue (mucosa) that is devoid of any grossly observable muscle. The vocal process cartilage, connecting ligament, and overlying tissue, collectively form the U-fold (Fig. 3).

The U-fold is most prominent as a ridge of tissue along the distal extremities of the vocal processes (i.e., ventrocaudally, away from the arytenocorniculate joint), and becomes flattened against the glottis as it approaches the lateral aspect. The U-fold mucosa of some specimens is folded into a series of parallel, shallow wrinkles along the caudal portion of the dorsal aspect of the vocal processes. These wrinkles are oriented perpendicular to the long axis of each vocal process, crossing from the laryngeal lumen into the gap between the two processes. The lateral and ventral laryngeal lumen walls have a series of parallel raised folds of thin mucosa that are aligned with these grooves. Medially, the left and right extensions of the U-fold join in the midline. Unlike the condition in most other mammals, the midline (ventral portion) of the U-fold is not attached directly to the thyroid cartilage. Rather, the U-fold indirectly attaches to the thyroid cartilage through its connection to fibers of the midline raphe of the ventrally located laryngeal sac. Fibers of this raphe, in turn, run rostrally along the ventral surface of the laryngeal sac to attach along the midline of the luminal aspect of the thyroid cartilage.

**Anatomy underlying potential movements of U-fold.** The arytenoid’s vocal processes support the extensions of the U-fold. The shape of the joint surface allows the arytenoid to move relative to the cricoid in several directions. Manipulation of the arytenoid cartilages’ muscular process caused the following movements: rostral tilt resulting in dorsal elevation of the vocal processes, caudal tilt resulting in ventral depression of the vocal processes, midline approximation (adduction), and lateral separation (abduction). Arytenoid approximation areas resulted in a rostral advance of the cartilages and attached U-fold, while arytenoid separation resulted in a caudal retreat of the cartilages and U-fold away from the aditus. This is because the joint surface on the cricoid presents a diagonal face, with the medial aspect located more rostrally and the lateral aspect located more caudally. The arytenoids can slide simultaneously medially and rostrally, or simultaneously laterally and caudally.

Arytenoid adduction/abduction allows both the vocal processes and the fused corniculate cartilages to likewise approximate or separate, respectively. The likely synovial joint between the arytenoid and the cricoid is oriented at an angle that slopes from dorsorostrally near the midline to ventrocaudally as it approaches the lateral aspect. Thus, both the vocal processes and fused corniculates can slide medially and laterally along this joint, thereby expanding or narrowing the entire length of the gap between the extensions of the U-fold or the contiguous flat surfaces of the corniculate cartilages. When this is closed, the U-fold separates the laryngeal space into two compartments: the dorsal laryngeal lumen and the ventral laryngeal sac. The vocal processes and the fused corniculates can also be rocked forward and backward, pivoting at the attachment in the middle of the fused arytenocorniculate complex. A rostroventral movement of the corniculate simultaneously allows the vocal process of the arytenoid to move dorsally. Rocking the corniculate dorsocaudally causes the vocal process to pivot ventrally. These movements cause the U-fold to either approximate the dorsal surface of the laryngeal lumen (thereby narrowing it), or retract away ventrally (thereby widening the vertical dimension of the lumen). Dorsal approximation of the U-fold separates the laryngeal lumen into two compartments: the rostral laryngeal lumen including the laryngeal sac, and the caudal laryngeal lumen (under the caudal part of the cricoid cartilage) and trachea.

The muscular process of the arytenoid cartilage supports the attachments of several intrinsic muscles that control its movements. The posterior cricoarytenoid, which arises from the dorsal surface of the corniculate cartilage, is a large muscle attaching to the arytenoid. It inserts on the lateral aspect of the arytenoid’s muscular process. The angle of its attachment indicates that it can cause the dorsal portion of the arytenoid and fused corniculate to rock caudally, while simultaneously pivoting the ventral portion (vocal process) rostrally. The lateral cricoarytenoid muscle is larger than the posterior cricoarytenoid. It has two bellies: dorsal and lateral. It can be seen attaching along the dorsal and lateral aspects of the corniculate cartilage and inserting into the dorsolateral and ventrolateral aspects of the muscular process of the arytenoid cartilage. The angle of attachment indicates that the dorsolateral head pulls the arytenoids laterally along the leading edge of the cricoid cartilage, thereby separating the arytenoids and widening the gap between the lateral extensions of the U-fold. The ventrolateral head’s angle of attachment indicates that it counters the action of the posterior cricoarytenoid muscle, causing the arytenoid–corniculate process to tilt rostroventrally and simultaneously pivoting the vocal processes to be elevated dorsally within the laryngeal lumen toward the cricoid cartilage. The interarytenoid is attached between the medial edges of the paired arytenoids. Its position and orientation indi-
cate that it causes approximation (adduction) of the arytenoids, thereby narrowing or closing the slit between the extensions of the U-fold.

Ligaments. There is a large ligament that joins the extensions of the arytenoid cartilages at the midline of the U-fold. In badly decomposed specimens, this interarytenoid ligament remained even though all other soft tissues sloughed off the cartilages (Fig. 2b). A ventral extension of the interarytenoid ligament is observed as a fibrous band of (presumed) connective tissue running along the ventral aspect of the laryngeal sac lumen (see below). This fibrous band is visible in the sac mucosa as a median raphe. The raphe represents the line of fusion between the right and left sides of the sac, and appears as a raised ridge that extends the entire length of the sac ventrally from the base of the epiglottis to the caudal cul-de-sac, and then curves dorsally to meet the midline of the U-fold in the region of its interarytenoid ligament. This ridge thus attaches the U-fold to the thyroid cartilage.

Innervation. The superior and recurrent laryngeal nerves were dissected from a lateral approach in two specimens (one fin whale, one sei whale). The branches of the superior laryngeal nerve terminate in the region of the U-fold. These branches likely provide sensory and perhaps secretomotor innervation, as they are found just under the mucosa. They continue into the laryngeal sac, but do not cross dorsally over the U-fold to innervate the mucosa of the laryngeal lumen or the trachea. The recurrent laryngeal nerve travels along the dorsal aspect of the larynx, turns to run ventrally at the rostral edge of the cricoid, and then curves to run caudally along the lateral aspect of the full length of the laryngeal sac. Branches were found to innervate the posterior and lateral cricoarytenoid muscles and then penetrate the laryngeal sac muscles. The terminal branches of the recurrent laryngeal nerve in this region do not extend to the mucosa of the sac. This finding indicates that the recurrent laryngeal nerve likely provides primarily motor, rather than sensory, innervation to the laryngeal sac.

Relationships to Adjacent Structures

Laryngeal sac. The U-fold defines the edges of the opening between the laryngeal lumen and the laryngeal sac (Fig. 4). This position enables the U-fold to regulate airflow between the laryngeal lumen and the laryngeal sac. The laryngeal sac is a single, large, diverticulum located ventrally in the midline of the larynx. The ventral midline of the lumen exhibits a raphe (described above). Its luminal surface exhibits many folds. The folds provide additional surface area that can facilitate expansion and contraction of the sac's volume. The walls are supported by muscles that run circumferentially around the sac in the transverse plane, leaving a dorsal gap in their perimeter coverage only between the extensions of the U-fold. The lumen of the sac is wider cranially, and tapers caudally in a cone shape to a blunt cul-de-sac. The rostral portion is continuous ventrally with the luminal surface of the epiglottis. The laryngeal sac muscles appear to be arranged in two concentric layers. The superficial muscle layer spans between the thyroid cartilage (ventrally) and the cricoid cartilage or trachea (dorsally), and may represent either a second belly of the cricothyroid muscle, or the thyroarytenoid muscle displaced caudally onto the cricoid cartilage. The deep muscle layer, which lies immediately below the mucosa of the laryngeal sac, attaches between the thyroid cartilage (ventrally) and the arytenoid cartilage (dorsi-ally) and likely represents the vocalis muscle. At the caudal portion of the laryngeal sac, immediately ventral to the trachea, this deep layer forms a circumferential cone of muscle encircling the entire perimeter of the sac without attaching to any cartilages or the trachea. Laryngeal sac muscles are innervated by branches of the recurrent laryngeal nerve, while sac mucosa is innervated by branches of the superior laryngeal nerve (see innervation, above).

Cricoid and trachea. The caudal aspect of the U-fold (the bottom of the “U”) is located under the cricoid cartilage and just cranial to the bifurcation of the trachea. Most of the lumen is a combined space, as the dorsal aspect is bounded by cricoid while the lateral aspects are defined by tracheal rings that have fused to the cricoid cartilage (Fig. 2b). The tracheal lumen (i.e., the space not bounded by any portion of the cricoid cartilage) is very short—bounded only by approximately two to four separate tracheal cartilage rings. A forward rocking motion of the arytenoids causes the bottom of the “U” to approximate the undersurface of the dorsal aspect of the cricoid cartilage, just before the beginning of the combined caudal laryngeal/tracheal lumen. This U-fold position isolates the cranial laryngeal lumen and laryngeal sac from the caudal laryngeal lumen and trachea.

DISCUSSION

Homology With Terrestrial Mammals

The mysticete larynx is largely composed of the same cartilages as the larynx of a typical terrestrial mammal, with the notable exception of the cuneiform cartilage. The mysticete's U-fold appears to be homologous to the vocal folds of terrestrial mammals based upon similarities of orientation, attachment, cartilage movements, presence of an interarytenoid (vocal) ligament, innervation pattern, and relationships with adjacent structures. The U-fold's orientation in the laryngeal lumen allows it to serve as a valve to narrow or seal the passageway for airflow between the upper and lower respiratory tracts. The U-fold is supported along each lateral wall by a ventrocaudally directed extension of the arytenoid cartilage that appears to be homologous to the vocal process (Fig. 1). The caudal tip of each vocal process curves medially so that the left and right sides approximate each other in the midline. As in terrestrial mammals, the vocal process originates from the arytenoid base, which in turn articulates at a likely synovial joint to the rostral edge of the cricoid cartilage. Unlike terrestrial mammals, however, the mysticete vocal process does not traverse the laryngeal lumen perpendicular to the long axis of the trachea, and larynx (see below).

A thick interarytenoid ligament is contained within the U-fold and is attached between the cartilaginous terminations of the two vocal processes at the bottom of the curvature of the “U” (Fig. 2b). This ligament appears homologous to the vocal ligament that, in terrestrial mammals, arises from the arytenoid's vocal process and is contained within the vocal fold.
In many mammals, particularly herbivores, the arytenoid's vocal process occupies most of the structure traversing the laryngeal lumen, and the flexible tissue of the vocal fold itself (including the underlying vocal ligament) is reduced to a small section near the ventral aspect of the larynx (Negus, 1929, 1949). This is very close to the arrangement in mysticetes, in which each side of the U-fold is also supported by the vocal process of the arytenoid and only a small interarytenoid ligament is present at its caudal termination. Unlike terrestrial mammals, however, the interarytenoid (vocal) ligament does not attach directly to the thyroid cartilage in mysticetes. Rather, the attachment from the caudal aspect of the U-fold to the thyroid cartilage appears to be by means of a raphe (containing a fibrous band) running as a ridge along the midline of the laryngeal sac lumen (Fig. 5). This extended attachment leaves the caudal tip of the U-fold ''free-floating'' between the laryngeal lumen dorsally and the laryngeal sac ventrally. The ventral portions of the vocal folds thus appear to be fused together caudally into one midline connective tissue ridge (the raphe), which is elongated in relation to the growth and development of the laryngeal sac. The attachments between the vocal processes and the thyroid cartilage supports homology between the mysticete's interarytenoid ligament (and its midline ventral extension) and the vocal ligaments of terrestrial mammals.

While paired laryngeal sacs develop in some terrestrial mammals by laterally extending each laryngeal ventricle, mysticetes have only a midline, unpaired laryngeal sac. The laryngeal sac's position cranial to the vocal processes and caudal to the aditus between the epiglottis and corniculate cartilages, indicates it is likely homologous to the laryngeal ventricles of terrestrial mammals. It appears to be derived from midline fusion of the two lateral ventricles. Evidence of a line of fusion between the left and right sides is visible as a midline ridge, or raphe. The midline out-pocketing of the laryngeal sac appears related to the caudoventral elongation of the vocal folds' fused attachment to the thyroid cartilage (described above).

The inner layer of laryngeal sac musculature attaches between the arytenoid and thyroid cartilages. The attachments and fiber directions of this layer indicate homology with the thyroarytenoid or vocalis muscles. As these muscles underlie the vocal folds of terrestrial mammals, this further supports homology between the U-fold of mysticetes and the vocal folds of terrestrial mammals.
The outer layer of sac musculature attaches between the thyroid and cricoid cartilages rostrally, and thus may be homologous to one of the cricothyroid muscle bellies.

The muscles that attach to and move the muscular process of the arytenoid in mysticetes are the same as those in terrestrial mammals. The innervation patterns are also consistent, with the recurrent laryngeal nerve providing motor supply to all of these muscles. The sensory innervation patterns also support the homology of the laryngeal sac of mysticetes with the laryngeal ventricles of terrestrial mammals. The recurrent laryngeal nerve innervates only the mucosa of the U-fold, and the superior laryngeal nerve innervates the mucosa of the laryngeal sac in mysticetes. In terrestrial mammals, the superior laryngeal nerve only provides sensory fibers to regions rostral to the vocal folds, and the recurrent laryngeal nerve supplies sensation to regions caudal to the vocal folds. The absence of recurrent laryngeal nerve fibers and presence only of superior laryngeal nerve fibers in the mysticete laryngeal sac mucosa supports that this tissue is derived from the laryngeal ventricle—a region that is rostral to the vocal folds in terrestrial mammals. Similarly, the recurrent laryngeal innervation of the mysticete U-fold indicates homology with the undersurface of the vocal folds of terrestrial mammals. These similarities of U-fold and laryngeal sac orientation, cartilage support, attached ligaments, cartilage movements, innervation, and relationships to adjacent structures indicate homology with the vocal folds and laryngeal ventricles of terrestrial mammals.

**Comparison with Odontocetes**

The mysticete larynx shares some unique characteristics with odontocetes, particularly the ventrally incomplete cricoid cartilage, the rostrally elongated corniculate cartilages, and the ventrocaudally elongated vocal processes of the arytenoid cartilages. There are, however, several gross structural differences that distinguish it from the odontocete configuration. While the rostral portion of the odontocete larynx is narrow and elongated into a tubular arrangement (Reidenberg and Laitman, 1987, 1994), the rostral portion of the mysticete larynx is relatively wide and has a large opening between the epiglottis and corniculate cartilages that lead into the laryngeal lumen (Reidenberg and Laitman, 2007, this issue). The ventral luminal surface of the odontocete larynx usually has a trabeculated appearance with numerous small ventral diverticulae and a midline laryngeal fold (Reidenberg and Laitman, 1988), while the mysticete larynx has only one large ventral diverticulum (laryngeal sac) and no midline laryngeal fold.

The mysticete U-fold differs in appearance from the midline laryngeal fold of odontocetes. The odontocete laryngeal fold is homologous to the vocal folds of terrestrial mammals (Reidenberg and Laitman, 1988), and is largely devoid of hard support, attaching to cartilage only at the cranial and caudal aspects. Each lateral portion of the mysticete U-fold, however, is fully supported by cartilage (the vocal process of the arytenoid cartilage). The odontocete laryngeal fold is thin and usually unpaired, while the mysticete U-fold is thick and consists of a pair of parallel extensions. Small laryngeal sacs surround the odontocete laryngeal fold laterally, while one large sac lies between the mysticete U-fold in the midline.

**Differences in Cetacean Vocal Fold Orientation**

While the basic terrestrial mammalian plan is a pair of vocal folds that are oriented perpendicular to the long axis of the larynx and trachea (Laitman and Reidenberg, 2007), cetaceans have evolved vocal folds that lie parallel to the long axis of the larynx and trachea (Fig. 5). However, there are great differences in the direction of vocal fold (odontocete laryngeal fold, mysticete U-fold) re-orientation between the two cetacean suborders.

The evolution of re-oriented vocal folds proceeded along two divergent paths in the two cetacean suborders (Fig. 5). In odontocetes, the ventral aspect of the vocal fold has moved rostrally relative to its homologous attachment in terrestrial mammals, while the dorsal attachment has moved to a ventral location. This is a 90-degree shift from the terrestrial pattern. In mysticetes, however, the ventral aspect of the vocal fold has moved caudally relative to its homologous attachment in terrestrial mammals, while the dorsal attachment has moved to a rostral location. This is also a 90-degree rotation relative to the vocal fold orientation in terrestrial mammals, but it is in the opposite direction from the odontocete shift. Mysticetes are, thus, 180 degrees rotated compared with odontocetes.

Mysticetes and odontocetes have taken two very different trajectories from the common ancestral condition, each rotating their vocal folds in the opposite direction. The two very different laryngeal phenotypes provide anatomical support of the evolutionary divergence of cetaceans into the two suborders: mysticetes and odontocetes. Although there are no fossilized larynges of archaeocetes, we hypothesize that the common ancestor of odontocetes and mysticetes likely retained a vocal fold orientation similar to the nonspecialized pattern seen in modern terrestrial mammals.

**Functional Implications**

While it is recognized that postmortem anatomy is a reflection of, rather than a direct window into, the function of an organism, considerable insights can be gained when no in vivo experimentation is possible. We offer some functional scenarios below.

**U-fold movements.** The mysticete arytenoid cartilage is fused to the corniculate cartilage superiorly, and at its midpoint is attached caudally to the cricoid cartilage by a curved, apparently synovial joint. Movement of the arytenocorniculate complex at this joint may occur in multiple planes. These movements appear to control the size of the opening between the laryngeal lumen and the laryngeal sac, thus regulating airflow. For example, lateral rocking of the corniculate tip may cause medial movement (adduction) of the arytenoid vocal process and, thus, bring only the caudal tips of the U-fold together in the midline. Partial occlusion between the trachea and nasal region may occur through opposition of the arytenoid bases (i.e., the main body of the arytenoid where it attaches to the cricoid cartilage). Rostrocaudal rocking or sliding movements of the arytenoids can pivot and elongate/shorten the U-fold, in turn causing changes in U-fold length or tension or changes in laryngeal sac volume. Pivoting the arytenoids in this manner may move the U-fold in an arc, and per-
are necessary to achieve different pitches. Thus, U-fold vocal fold stretch/recoil (length, tension, and thickness) with a structure that generates sounds, as changes in recoil back to the folded shape. This movement is consistent, they resemble two opposed lips. Airflow through the sac's wall (see below). U-fold vibrations may also be the result of airflow from the laryngeal sac passing through the fold and vibrating its lateral edges (Fig. 6). The laryngeal sac surrounds a space that may be expanded with air from the trachea channeled through the U-fold into the laryngeal lumen. Its muscular wall may function to compress and collapse the enclosed space, forcing air out rostrally through the space between the epiglottis and the paired corniculate cartilages, or back to the laryngeal lumen though the gap surrounded by the U-fold. This latter mechanism may provide the pressurization necessary for vocalizations generated by U-fold vibrations. U-fold vibrations may generate pulsatile sound waves in the airspace of the laryngeal sac, or the physical vibrations of the U-fold itself may be directly translated to the laryngeal sac walls as the U-fold tissue is continuous with the dorsal aspect of the laryngeal sac.

While the U-fold may generate the fundamental frequency, the laryngeal sac appears responsible for further sound modification and transmission. The laryngeal sac may affect frequency or amplitude through variations in the volume or shape of the resonant air space or tension of the walls. For example, sac expansion may decrease the frequency, as larger volumes resonate with longer wavelengths.

Alternatively, the sac may be a temporary air reservoir. The extensive musculature surrounding the laryngeal sac may enable rapid and forceful expulsion of air from the lumen of the sac into other respiratory spaces, or maintain a constant sac volume despite the effects of ambient pressure (e.g., changes during diving or ascent). Compression of the sac can force the air through the U-fold gap back to the larynx, trachea and lungs, thus returning it for use in the next set of vocalizations. This air recycling conserves the original volume, and would free a submerged vocalizing whale from needing to inhale repeatedly at the surface for each vocalization.

The laryngeal sac musculature may also serve as a secondary source of pressurization for vocalizations if the U-fold can generate vibrations during back flow of air from the laryngeal sac into the larynx, trachea, and lungs. Coupling such “ingressive” vocalizations (i.e., airflow from the laryngeal sac to the lungs driven by contraction of laryngeal sac musculature) with “egressive” vocalizations (i.e., airflow from the lungs to the laryngeal sac driven by diaphragm contraction) would enable the whale to vocalize nearly continuously. It is not clear, however, whether ingressive vocalizations are consistent with sound transmission by means of laryngeal sac walls, as pressurizing the laryngeal sac requires either an elevation of ambient pressure (as occurs during diving) (Aroyan et al., 2000) or contraction of sac wall musculature, in turn dampening sound wave transmissions through the sac’s wall (see below).

Once the mysticete generates pneumatically driven pulsations of the U-fold internally, these pulses must be transferred externally to the water for sound propagation. A pneumatic sound generating mechanism, however, presents a problem for underwater existence. How can sounds generated by such a system be transferred to water? To avoid transmission loss, sound waves must ideally travel through media of similar densities, other-
wise the energy will attenuate as the waves are reflected or refracted at different density interfaces. Mysticetes may have solved this by developing a transducer—a structure that can transfer the pneumatically generated vibrations to the water. This transducer may be the laryngeal sac.

Movements of the U-fold may create pressure waves both in the air of the laryngeal sac lumen as well as along the attached laryngeal sac walls. These pressure waves may cause pulsations in laryngeal sac air volume and wall vibration. The pulses are probably directly translated from the laryngeal sac walls to the surrounding soft tissues, including the expandable ventral throat pleats that are in contact with the water externally (Fig. 6). If the throat pleats are capable of expanding and contracting with the same displacement and frequency as the laryngeal sac wall pulsations, sound may be transferred to the water at this point with very little distortion or attenuation. Furthermore, as the density of the throat pleats is a closer match to the density of water than the density of air in the respiratory tract, it is ideally suited to aid the laryngeal sac as a transducer in transferring sound waves to the water with no reflective transmission loss. The sac may also be used as a transducer for vibrations generated by pulsations at the U-fold that then spread through the sac tissues. Pulsatile contractions of the muscular walls of the sac itself may also generate sound. As the sac is relatively superficially positioned and is covered externally by the ventral throat pleats, sac vibrations or inflations and deflations by any mechanism could vibrate or expand and contract these pleats, thus transferring sound waves into the surrounding water.

**CONCLUSION**

Despite previous claims that mysticetes have no vocal folds, data from this study indicate that the mysticete U-fold does appear to be homologous to the vocal folds of terrestrial mammals based upon position, attachments, and composition. Although the mysticete U-fold is oriented parallel to airflow (compared with the perpendicular vocal folds of terrestrial mammals), it nevertheless appears to have a similar function in airflow regulation and pneumatic sound generation. These findings suggest that the mechanism of low frequency sound production in mysticete whales involves generating the fundamental frequencies through U-fold vibration, followed by sound quality modification through variation of laryngeal parameters (by means of muscle contractions), and then sound transduction by means of laryngeal sac wall vibration to ventral throat pleat pulsations impinging on water.

**ACKNOWLEDGMENTS**

We thank the Northeast Regional Stranding Network (U.S.A.) for permission to dissect cetacean specimens, particularly: Cape Cod Stranding Network, Massachusetts; Humboldt State University, California; Maryland Department of Natural Resources, Maryland; Mystic (Marinlefe) Aquarium, Connecticut; Marine Mammal Stranding Center, New Jersey; New England Aquarium, Massachusetts; Riverhead Foundation (formerly Okeanos Ocean Research Foundation), New York; United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.; University of North Carolina, Wilmington, Marine Mammal Stranding Program; Virginia Marine Science Center (Museum & Aquarium), Virginia. We also express our sincere appreciation for the assistance of the skilled crews of the United States Coast Guard and the Army Corps of Engineers (Point Caven, NJ) for recovering whale carcases and facilitating dissections. Thanks are also given to Dr. Samuel Márquez, Dr. Douglas Broadfield, Dr. Armand Balboni, Dr. Michael Lipan, Dr. Reginald Miller, Mr. Calvin Keys, Mr. Jason Klein, and many student members of the Mount Sinai School of Medicine for technical and dissection assistance. We would also like to thank Dr. Robert Gisiner (Office of Naval Research) and Dr. Teri Rowles (National Marine Fisheries Service, National Oceanic and Atmospheric Administration) for their ongoing encouragement and support of our research.

**LITERATURE CITED**


