

Terrestrial, Semiaquatic, and Fully Aquatic Mammal Sound Production Mechanisms

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Aquatic mammals generate sound underwater but use air-driven systems derived from terrestrial ancestors. How do they do it without drowning?

Terrestrial mammals produce sound in air mainly for communication, while many aquatic mammals can communicate by vocalizing in air or underwater. A subset of aquatic mammals called odontocetes (toothed whales, including dolphins and porpoises) can also use echolocation sounds for navigation and prey tracking. In all cases, mammals use pneumatic (air-driven) mechanisms to generate these sounds, but the sources and transmission pathways differ depending upon whether sounds are emitted into air or water.

Terrestrial Mammals

The voice box, or larynx, is the organ of vocalization used by most terrestrial mammals. It initially evolved from the protective anatomy used to keep water out of a buoyancy organ in fish (the swim bladder). The main function of the larynx remains protection, only now it prevents incursions of foreign material into the “windpipe” (trachea) and lungs of mammals.

The entrance of the larynx is sealed by a pair of vocal “cords” (vocal folds). In addition, there are tall cartilages (epiglottic and corniculate) that act as splashguards to deflect food and water away from the opening. These cartilages overlap in front with the soft palate and behind with the posterior wall of the airspace (pharyngeal wall) to interlock the larynx with the rear of the nasal cavity (Figure 1). This interlock channels airflow through the larynx and isolates it from the swallowing pathway that is now diverted around the interlock. This division of the airspace into two separate pathways allows simultaneous breathing and swallowing, a trait that allows prey to detect the scent of a predator even while constantly feeding (Laitman and Reidenberg, 2016).

Over time, additional roles beyond coordinating swallowing were added to the larynx, including stabilizing the ribcage (for weight lifting or for “bearing down”; Laitman and Reidenberg, 2016). One of the last functions to be added was phonation, producing the initial sound (fundamental frequency) of vocalizations.

The vocal folds attach between the thyroid cartilage in front and the arytenoid cartilage in the rear, and lie across the airway oriented perpendicular to the direction of tracheal airflow (Figure 1). Closed vocal folds protect the opening and elevate internal pressure; opened vocal folds release pressure and allow respiration. The intermediate positions, however, can be used to generate sounds. Air rushing between vocal folds pushes on the free edges, causing them to vibrate (see Video 1, <https://youtu.be/7RV4mBk53kQ>).

The vocal folds are not actually free string-like “cords,” but rather are shelves of tissue (thus the term “folds”). Therefore, as they oscillate, they repeatedly com-

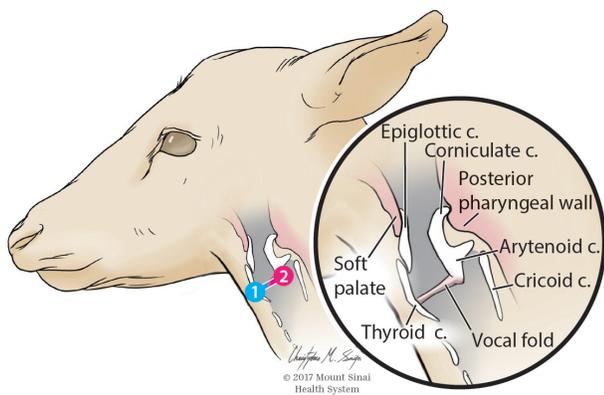


Figure 1. Schematic drawing of the larynx in a deer. Enlargement shows the upper laryngeal cartilages (epiglottic and corniculate) interlocking with the soft tissues surrounding the nasopharynx (soft palate and posterior pharyngeal wall). This interlock divides the airspace into two separate pathways for breathing/vocalizing (shown in gray) and swallowing (not shown because they are lateral to the larynx but then merge in the midline to become the esophagus shown in yellow behind the cricoid cartilage). The right vocal fold is indicated in the inset, spanning between the thyroid and arytenoid cartilages. Vocal fold position is schematized in the whole head as a line spanning from point 1 (blue; at front of larynx) to point 2 (red; at back of larynx). The paired vocal folds lie perpendicular to the long axis of the trachea, a pattern found in most terrestrial mammals. Air flows upward and between the two vocal folds to the supralaryngeal vocal tract, causing vibrations that generate the fundamental frequencies of vocalizations. Printed with permission from © 2017 Mount Sinai Health System. Illustration by Christopher M. Smith.

press air in the space surrounding the folds (vocal tract). These compressions generate the fundamental frequency, i.e., pressure waves in air. The waves propagate along the airspace above the larynx (supralaryngeal vocal tract) toward the nose and/or mouth for release as a vocalization.

Characteristics of the fundamental frequency are determined by variable parameters such as the size of the gap between the folds and the tension, elongation, and stiffness of vocal fold tissue (Dickson and Maue-Dickson, 1982). The fundamental frequency is then modified by the geometry of the supralaryngeal vocal tract. This results in a complex sound (e.g., fundamental frequency plus harmonics) emitted from the mouth and/or nose. The vocal folds are the “source” of the vibrations that generate the fundamental frequency, and the supralaryngeal vocal tract is the “filter” that modifies the emitted sounds.

Semiaquatic Mammals

Mammals that spend a considerable amount of time both on land and in water are termed “semiaquatic” (e.g., hippopotamus, seal, fur seal, sea lion, walrus, polar bear, various otters, various aquatic rodents). Performing underwater open-

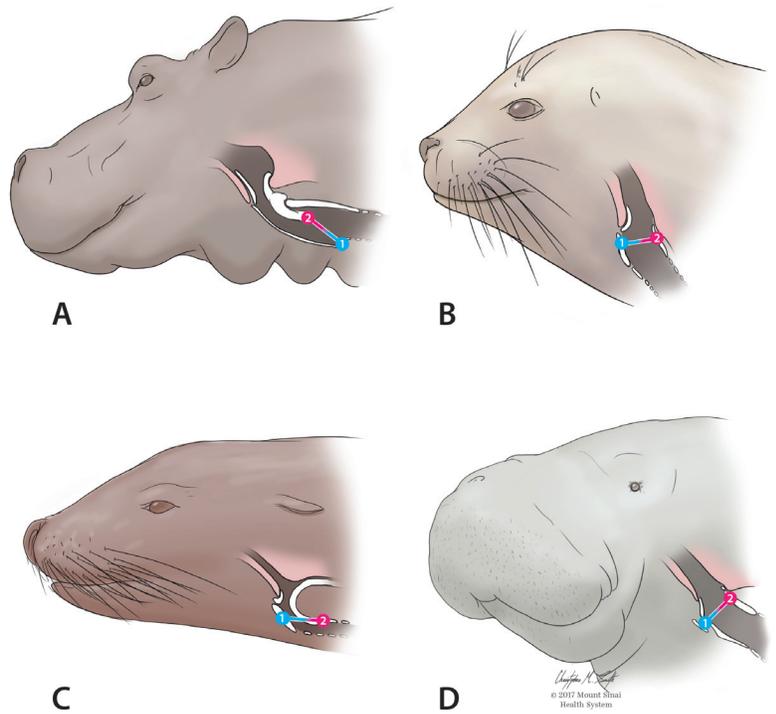


Figure 2. Schematic drawing of the larynx in a hippopotamus (A), seal (B), sea lion (C), and manatee (D). Note that the epiglottis overlaps with the soft palate. This provides protection from swallowed water or food, diverting it away from the laryngeal opening. In the rear of the larynx, the corniculate cartilage is opposed to the posterior wall of the pharynx. It provides good protection in the hippo (A) but does not have enough overlap to provide protection for pinnipeds (B and C) or the manatee (D). Vocal fold orientation is indicated by a line connecting points 1 (blue; attached to thyroid cartilage) and 2 (red; attached to arytenoid cartilage). In hippos (A), the folds are reoriented (counterclockwise or anticlockwise, as viewed from the left side of the animal) to be approximately parallel to tracheal airflow. The thyroid cartilage attachment is extended inferiorly. This pattern is very similar to that in mysticete whales (see Figure 3A). Note that the vocal folds are oriented perpendicular to tracheal airflow in the seal (B) and manatee (D), showing a pattern similar to that found in terrestrial mammals (see Figure 1). The vocal folds are also reoriented nearly parallel to airflow in the sea lion (C) due to elongation of the arytenoid cartilage. This pattern is very similar to that in odontocete whales (see Figure 3B). Printed with permission from © 2017 Mount Sinai Health System. Illustration by Christopher M. Smith.

mouthed/open-nosed behaviors (e.g., sucking in water) can risk drowning. However, as long as the larynx is closed, the respiratory tract is protected. However, this will also prevent sound production underwater because the vocal folds are sealed against each other. Accordingly, these semiaquatic mammals vocalize in air as terrestrial mammals do. Vocalizations in the air can be emitted nasally (e.g., whining, whistling) or orally (e.g., barks, growls, and roars). Regardless of the transmission path, it involves the same pneumatic mechanism of generating vibrations of the vocal folds in the larynx, filtering sounds in the supralaryngeal vocal tract, and emitting them in air from the nose or mouth (Reidenberg and Laitman, 2010).

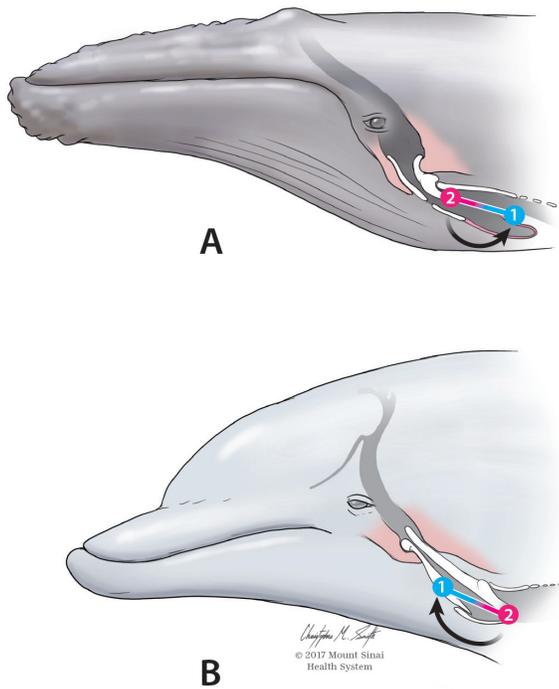


Figure 3. Schematic drawing of laryngeal position in a baleen (mysticete) whale (A) and an toothed (odontocete) whale (B). Note that the epiglottic and corniculate cartilages provide protection to the laryngeal entrance by interlocking into the nasal region through overlap with the soft palate and posterior pharyngeal wall. This interlock enables function of the vocal folds during open-mouthed behaviors that would otherwise risk drowning. Vocal fold position is indicated by a line spanning from point 1 (blue) to point 2 (red). In mysticetes (A), the folds are rotated approximately 90° (counterclockwise or anticlockwise, if viewed from the left side of the animal) from the terrestrial position (Figure 1) to be approximately parallel to the long axis of the trachea. The front attachment point has left the thyroid cartilage and been extended rearward, all the way to the trachea. This may be related to expansion of the laryngeal sac (the pouch located under the larynx). In odontocetes (B), the fold is rotated in the exact opposite direction (clockwise). The front attachment has left the thyroid cartilage and is extended further forward along the epiglottis. In both mysticetes and odontocetes, the rear attachment is placed more inferiorly due to elongation of the arytenoid cartilage. The cetacean patterns involve rotations in opposite directions, but both place the vocal folds parallel to the long axis of the trachea. Printed with permission from © 2017 Mount Sinai Health System. Illustration by Christopher M. Smith.

Hippopotamuses have adapted to produce sounds in air, underwater, or simultaneously both above and below water (Barklow, 2004). Interestingly, the vocal folds are oriented parallel to the tracheal airflow (Figure 2A), a condition seen again in their close relatives the cetaceans (whales, including dolphins and porpoises; Figure 3). As in other semiaquatic mammals, hippos use a terrestrial mechanism to transmit sound to air: they vibrate the vocal folds to generate a fundamental frequency and modify it in the supralaryngeal vocal

tract. The larynx is protected by tall cartilages that interlock the larynx with the nasal cavity (Figure 2A). This ensures that air is directed into the larynx while food is swallowed laterally around the interlock. This protection also enables hippos to vocalize during underwater open-mouthed behaviors. Underwater sound emission likely involves the transfer of vibrations through the overlying throat tissues of the ventral neck (see Video 2, <https://youtu.be/VqxHMDIfxkk>).

Pinnipeds (seals, fur seals, sea lions, walruses) also produce sounds with the larynx (Poulter, 1965) both in air and underwater. These sounds can be in the form of songs, pulses, sliding chords, and bell-like sounds (see review in Ballard, 1993). (Readers interested in hearing recordings can go to <http://acousticstoday.org/pinni> where many of these sounds can be found. For more information on how marine mammals use sound for communication, see the article by Peter Tyack in this issue of *Acoustics Today*.)

Pinniped vocal folds may be oriented perpendicular relative to tracheal airflow (e.g., seal; Figure 2B) in a terrestrial pattern (e.g., deer; Figure 1) or parallel (e.g., sea lion; Figure 2C) in a cetacean pattern (e.g., dolphin; Figure 3B). The pinniped larynx is not well protected from flooding with water because the protective cartilages surrounding the opening are very short, particularly in the rear of the larynx (Figure 2B,C). Therefore, open-mouthed behaviors with open vocal folds could result in the animal drowning. It follows that underwater laryngeal sound production is risky and occurs primarily when the mouth is closed. Some pinnipeds evolved a clever “work-around” solution involving pharyngeal or tracheal membranes, valves, or diverticulae (see review in Reidenberg and Laitman, 2010). These secondary vibrators enable sound production during open-mouthed behaviors without risking drowning because the vocal folds of the larynx can remain closed. The transmission route into water, however, is still unknown because pinniped vocal anatomy is not well understood. It is likely that pharyngeal/tracheal vibrations are transmitted through adjoining neck tissues. This ability may differ between the sexes because males often have thicker necks than females.

Fully Aquatic Mammals

Fully aquatic mammals are restricted to living in water only and include sirenians (manatees and dugongs) and cetaceans (mysticetes or baleen whales and odontocetes). Fully aquatic mammals emit sounds nearly exclusively underwater; however, they still generate them with a pneumatic mechanism.

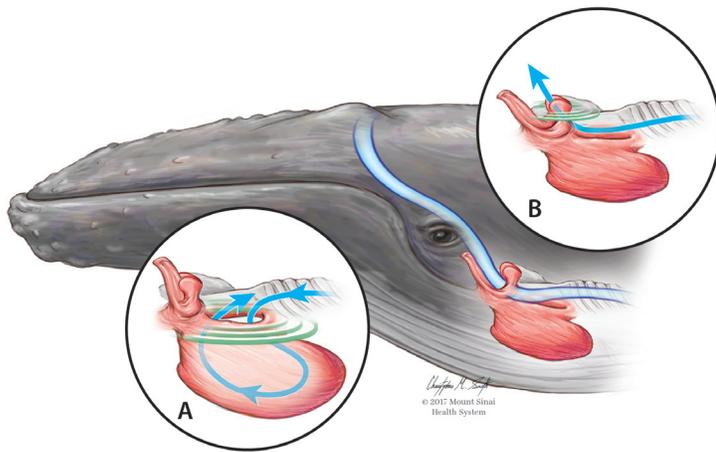


Figure 4. Schematic drawing of the larynx (red) and the vocal tract (blue) in a mysticete whale. **A:** close-up of the larynx, indicating the U-shaped pair of vocal folds guarding the opening into the laryngeal sac and oriented parallel to the trachea. The front of the larynx is closed by opposition of the epiglottic and corniculate cartilages, causing diversion of airflow (blue arrow) from the trachea into the laryngeal sac. This airflow causes fold vibrations, generating low-frequency sounds (larger green arcs). Air in the laryngeal sac may be recycled back to the lungs to be used in the next vocalization (curved blue arrow). **B:** closed vocal folds and airflow passing above the epiglottis and between the paired flaps of the corniculate cartilage. These flaps may clap together to produce pulsed sounds (smaller green arcs). Printed with permission from © 2017 Mount Sinai Health System. Illustration by Christopher M. Smith.

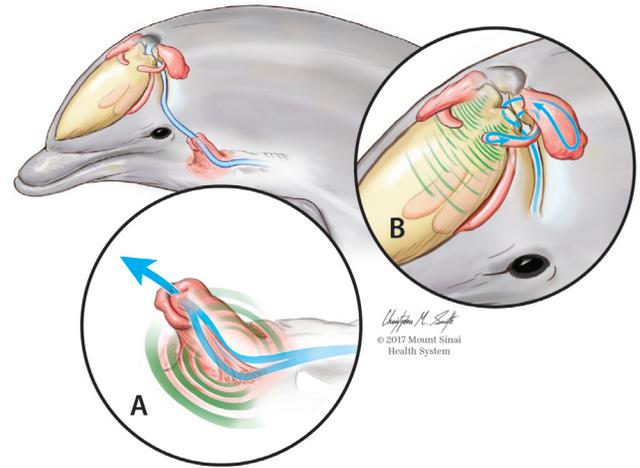


Figure 5. Schematic drawing of the larynx (red), nasal region (red and yellow), and vocal tract (blue) in an odontocete whale. **A:** close-up of the larynx, indicating a single vocal fold in the midline of the larynx. It is oriented parallel to the direction of airflow (blue arrow). The airstream (double blue lines) is divided to flow along either side of the fold. Sounds are hypothesized to arise from fold vibrations (larger green arcs). **B:** the nasal region where echolocation clicks and whistles are produced. Elevating the larynx pushes air toward the closed blowhole (crescent mark at the top of the head). Airflow (blue arrow) passes between the two pairs of phonic lips and causes high-frequency vibrations (smaller green arcs). These pulses pass into the adjacent melon (yellow oblong body) where they are focused into a beam to be transmitted out of the forehead. Air used in this process (curved blue arrows) is collected in the nasal air sacs (red) and may be recycled back to be used again in the next phonation. Printed with permission from © 2017 Mount Sinai Health System. Illustration by Christopher M. Smith.

Sirenians vocalize only underwater (Schevill and Watkins, 1965) and, as in most other semiaquatic and terrestrial mammals, the sound source appears to be the larynx (Reynolds and Odell, 1991). Although sirenian vocal folds are thick and don't have a sharp edge, they lie perpendicular to tracheal airflow (Figure 2D) and can still oppose each other and regulate airflow to cause sound-generating vibrations (Landrau-Giovannetti et al., 2014). Sirenian sounds are not complex (listen to audio recording at <http://acousticstoday.org/manatee>) and the simple squeaks are probably used only for communication. The larynx is not well protected from water incursions (Figure 2D), thus risking drowning through parted vocal folds if the animal opens the mouth to vocalize. Therefore, sound production probably occurs only when the mouth is closed. The sound transmission pathway is not known but may involve transferring vibrations through the fat of the neck or the thin membrane covering the bony nasal aperture (an opening of the skull just behind the nostrils; Landrau-Giovannetti et al., 2014).

The evolutionary transition from a terrestrial life to a fully aquatic one appears to have had little effect on the mechanism of sound production in sirenians. Vocalizing still involves airflow, just as it did in their terrestrial ancestors. The

vocal folds have returned to their original role of providing protection from incursions (particularly during swallowing) while keeping the new role of producing sound (although not simultaneously with swallowing; Reidenberg and Laitman, 2010).

Cetaceans are also fully aquatic mammals that vocalize underwater. Unlike sirenians, cetaceans make complex sounds including clicks and whistles (see the review in Tyack and Clark, 2000; listen to audio recordings at <http://acousticstoday.org/mmammals>). As in other terrestrial and aquatic mammals, cetaceans also use a pneumatic mechanism to generate sound. However, their respiratory tract is exquisitely protected from incursions of water (Figure 3). Therefore, simultaneous vocalizing and underwater open-mouthed behaviors (e.g., sucking in water during prey capture) do not risk the animal drowning.

Cetaceans use airflow to cause respiratory tissues to vibrate, generating pressure waves in both the surrounding tissues and air in the supralaryngeal vocal tract. Unlike terrestrial mammals, it is the vibrations in the tissues rather than in

the supralaryngeal vocal tract air column that are propagated through the cetacean head or neck and emitted into the water. These tissues have a density close to seawater, thus enabling the efficient transfer of sound (i.e., acting as a transducer with minimal transmission loss at the density interface). The mechanism of sound generation, while still pneumatic, differs between mysticetes and odontocetes. These two taxa have evolved along different trajectories (**Figure 3**) using different sources within the respiratory tract (**Figures 4** and **5**) that produce sounds on opposite ends of the frequency spectrum (mysticetes generate infrasound, odontocetes generate ultrasound).

Mysticetes (Baleen Whales)

Mysticetes are well-known for their ability to sing underwater (listen to audio recordings at <http://acousticstoday.org/baleen>). Because low-frequency sounds travel farther than high frequencies before attenuating, mysticetes generally use low frequencies (infrasound) to communicate over long distances. Their sounds can thus be heard many miles away. Mysticetes, similar to other mammals, produce these sounds laryngeally.

Mysticetes have evolved enhanced protection of the larynx from water incursions (**Figure 3A**). Although all mammals protect the larynx from the front using the epiglottic cartilage, mysticetes have evolved tall corniculate cartilages that also protect the larynx from behind (Reidenberg and Laitman, 2007). This creates circumferential protection around the larynx, keeping its opening completely interlocked with the nasal region. The cartilages are sandwiched between the soft palate and the posterior pharyngeal wall. Thus, food and water are swallowed past the larynx but cannot slip through the interlock and end up accidentally inhaled.

The mysticete larynx is both absolutely and relatively large, being larger than either one of the whale's lungs (Reidenberg and Laitman, 2010). The increased size is correlated with loud and low-frequency sounds; bigger vocal folds and larger resonant volumes correspond with longer wavelengths and increased amplification (Aroyan et al., 2000; Cazau et al., 2013).

Mysticetes have vocal folds that make a U-shape (Reidenberg and Laitman, 2007). Interestingly, the vocal folds do not lie in the typical terrestrial position perpendicular to tracheal airflow (**Figure 1**). Instead, they are rotated approximately 90° (counterclockwise or anticlockwise, if viewed from the left side of the animal) to lie parallel to the long axis of the

trachea (**Figure 3A**). The ventral (inferior) attachment has moved caudally (rearward) from the thyroid cartilage to the base of the trachea, and the dorsal (superior) attachment has moved ventrally (inferiorly) and caudally with elongation of the arytenoid cartilage. Air can still flow through the gap between the vocal folds and into the laryngeal sac (a pouch located just below the larynx; **Figure 4A**).

Parted vocal folds allow air to flow between the lungs and the laryngeal sac. Vocal folds are controlled by cartilages that are moved by muscle contractions, similar to those of other mammals. Regulating vocal fold opening, orientation, thickness, and tension can control airflow volume and rate, setting the whale's folds in motion to produce the fundamental frequency (Adam et al., 2013; Cazau et al., 2013, 2016).

The laryngeal sac is very stretchy, but its volume can be compressed by a thick surrounding muscle layer (Reidenberg and Laitman, 2008). The sac provides an important reservoir for increasing total air volume available during diving for use in both respiratory and buoyancy control (Gandilhon et al., 2014). The laryngeal sac expands as air is used during vocalization, and on contraction it recirculates the air back to the lungs to be used again in the next vocalization (**Figure 4A**). The inflated air sac and contiguous nasal passageways may also serve as resonant spaces because larger volumes mean that the whale can project longer, louder, and lower sounds. This ability can advertise the whale's size and strength particularly in diving whales, where the air volume is severely constrained by deep depths. Laryngeal sac walls may act as a pulsing drumhead to transfer vocal fold vibrations through the overlying throat muscles, blubber, and skin and into the water (Reidenberg and Laitman, 2007).

The mysticete larynx also has a second, perhaps unique, site that may also generate sound: a pair of broad tissue flaps supported by the corniculate cartilages (**Figure 4B**). These flaps lie in opposition across the laryngeal opening and may clap together to generate pulsed sounds (Reidenberg and Laitman, 2007). Mysticetes have been documented to produce pulses (e.g., Thompson et al., 1992). This is intriguing because it supports the idea that mysticetes may echolocate, an idea originally proposed by Norris (1969). Infrasonic frequencies have long wavelengths and therefore may only be useful in conveying the presence of large or distant objects, e.g., seamounts or schooling prey. Bowhead whales, for example, may navigate around ice obstacles using cues from the echoes of their vocalizations (George et al., 1989; see **Video 3**, <https://youtu.be/rysR5SNwrn8>).

Odontocetes (Toothed Whales, Including Dolphins and Porpoises)

Odontocetes generate high frequencies (ultrasound) that they use for navigation and finding prey, as well as other sounds used for communication (listen to audio recordings at <http://acousticstoday.org/twhales>). Controlled experiments with hydrophones and blindfolded dolphins proved they emit clicks while navigating and finding targets (Kellogg, 1958; Norris et al., 1961). The mechanism of sound production, however, was controversial. At first, it seemed logical to assume that the larynx was the source (Purves, 1966; Purves and Pilleri, 1983) because this was the origin of sound in other ultrasonic vocalizers such as bats, rodents, and shrews. However, the complexity of the nasal region begged an explanation, and many researchers proposed that it functions in generating sound (reviewed in Cranford, 2000). Controlled experiments on live dolphins and detailed dissections (reviewed in Cranford and Amundin, 2003) proved that odontocetes use the nasal region to generate these clicks (see below).

Odontocetes also have a larynx (**Figures 3B** and **5**), but it is not clear what sounds, if any, it can make. Although it is not the generator of echolocation ultrasounds, it too is a complex structure with an undetermined function. This complexity suggests that it may have a role in producing some sounds, most likely for communication (Reidenberg and Laitman, 1988).

The odontocete larynx can remain open while still protecting the respiratory tract. Its unique shape is reminiscent of a snorkel, allowing air to flow from the lungs to the nasal region while blocking off incursions of water from the mouth (**Figure 3B**). The epiglottic and corniculate cartilages are elongated into a tubular shape and sealed by the tissues of the soft palate and posterior pharyngeal wall (that are formed into an encircling sphincter; Reidenberg and Laitman, 1987). This interlock fully protects the larynx by separating the respiratory passageway (inside the lumen) from the digestive tract (that loops around it), thereby allowing both systems to function simultaneously. This higher level of protection indicates that the larynx must have an essential, and nearly constant, role for airflow (Reidenberg and Laitman, 1994). Otherwise, simply closing the vocal folds would be sufficient to protect the larynx underwater, as likely occurs during feeding in other aquatic mammals. This level of protection is even better than that seen in mysticetes (**Figure 3A**).

Why would odontocetes need to use the respiratory tract while underwater? Clearly, they are not breathing while submerged, so the logical answer is that airflow is necessary for sound production. There are three possible scenarios for such acoustic respiratory function. One is that air flows through the larynx and causes vibrations of laryngeal tissue to generate sound. Another is that air is simply channeled uninterrupted to the nasal region so it can be used to generate sounds there. Finally, elevating the larynx may increase pressure in the nasal cavity, driving air upward through sound-generating tissues located there. This piston-like movement was observed through video endoscopy in a live dolphin while it produced click sounds (Cranford et al., 2011). In all three scenarios, water can surround the larynx without causing drowning. Even swimming upside-down, open-mouthed, while chasing a fish would not cause drowning or compromise the flow of air needed to generate echolocation clicks.

The odontocete larynx contains vocal folds, but they are usually fused into a single midline fold (Reidenberg and Laitman, 1988). The vocal fold can be tensed, relaxed, and erected into the airstream where it may vibrate passively as air rushes along either side (**Figure 5A**), similar to how the reed of a woodwind instrument works. The vocal fold attachment points have migrated during the reshaping of the larynx. The ventral (inferior) attachment has moved rostrally (forward) from the thyroid cartilage to the epiglottic cartilage, and the dorsal (superior) attachment has moved caudally (rearward) and ventrally with elongation of the arytenoid cartilage. The result is a fold rotated approximately 90° (clockwise if viewed from the left side of the animal; **Figure 3B**) compared with that of a typical terrestrial mammal (**Figure 1**). This places the fold parallel to the trachea and therefore parallel to the airflow, rather than perpendicular to it as in other mammals. Curiously, vocal folds are rotated in the opposite direction in mysticetes (**Figure 3A**). Although mysticetes and odontocetes both have vocal folds lying parallel to the trachea, they are oriented nearly 180° apart! This indicates an evolutionary divergence between odontocetes and mysticetes from the basic mammalian pattern.

The pathway for sound transmission from the larynx is not known. Vibrations may travel up through the skull to the forehead or rostrum, or ventrally through the throat tissues in a pattern similar to the sound conduction path proposed for mysticetes, hippos, pinnipeds, and sirenians. Interesting

ly, a path for conducting incoming sounds has been modeled for the throat region of deep-diving odontocetes (Cranford et al., 2008). Perhaps the same tissue properties that channel sounds into the head may allow sound to travel out as well.

Although laryngeal sound generation (and transmission) is anatomically possible, this has not yet been demonstrated in living odontocetes. The overwhelming evidence from studies of captive dolphins and other odontocetes indicates that the laryngeal region remains quiescent during sound generation while the nasal region is active (reviewed in Cranford and Amundin, 2003). Therefore, the main functions of the larynx appear to be limited to protecting the respiratory tract while feeding and channeling air to, or pressurizing the air in, the nasal region during sound production.

Odontocete Nose

The odontocete nose is highly modified from the typical terrestrial nose. As in all whales, it is located on the top of the head, enabling efficient breathing at the surface without having to lift the head out of the water. The nostrils (blowholes) are paired in mysticetes, but they have become fused into only one opening (blowhole) in odontocetes.

Immediately below this nostril are two nasal passageways and a complex arrangement of air sacs, nasal plugs, and fatty structures (**Figure 5**). These epicranial structures are homologous to the facial tissues (e.g., lips, nasal cartilages, facial muscles) of terrestrial mammals, as evidenced by their pigmented surfaces (indicating that they derive from tissues whose skin coverings were located on the outside of the face in an ancestor). Some of this tissue comprises the muscular nasal plugs that close the nasal passageways to protect them from water while submerged or that can retract to expose them for breathing. The remainder of these tissues are involved in sound generation, including bilaterally paired sets of air sacs, a large fatty structure called the melon, and two sets of paired fat bodies called “phonic lips” that are the sonar sources (Cranford, 1999; **Figure 5B**).

Each phonic lip opposes its pair and, as air passes between them, they can either clap against each other to create clicks or channel air along ridges of their surface to generate whistles (**Figure 5B**). There is only one pair of these phonic lips in sperm whales (see **Video 4**, <https://youtu.be/sW7o5IC2io0>). High-speed video endoscopy on live dolphins shows that phonic lip vibrations correlate with produced sounds, and the two sets of paired phonic lips can operate independently (Cranford et al., 2011; see **Video 5**, which is on the linked

page <http://acousticstoday.org/bdolphin>). This confirms that dolphins can use both pairs of phonic lips to produce two different frequency click trains simultaneously or emit whistles while clicking).

Air is next directed into (usually) three pairs of air sacs located underneath the blowhole (Mead, 1975; Rodionov, 2001; **Figure 5B**). The blowhole is closed during sound production, thus preventing water flooding in or air escaping out. As in mysticetes, inflating air sacs delays system pressurization (thus allowing continued airflow for sound production) while capturing air for reuse. Muscles covering the nasal sacs contract, sending air back to the lungs. The air is recycled, producing more sounds as it flows again through the phonic lips and into the nasal sacs.

The phonic lips vibrate very quickly, generating ultrasonic click trains that are then transmitted as vibrations to attached fat bodies called dorsal bursae. Vibrations are transferred through the anterior dorsal bursa to a contiguous, but larger, fat body in the forehead area called the “melon” (Harper et al., 2008; McKenna et al., 2012; **Figure 5B**).

The melon is a biconvex shaped organ, comprised largely of isovaleric acid (Koopman et al., 2003) that is of similar density to seawater. It can therefore transfer sound waves to water with minimal transmission loss (from reflection, refraction, impedance mismatch, or attenuation). The chemical structure of the melon may modify the sounds, perhaps filtering out certain frequencies (Koopman et al., 2003). The shape of the melon may be altered through facial muscle contractions to act as a lens that focuses the width and direction of the sound beam.

Odontocetes use these sounds to explore their environment. The emitted sound travels forward and reflects from objects in the path. The returning echoes are used to understand surface characteristics, composition, and location/movement of nearby objects, thus allowing navigation or prey capture (Tyack and Clark, 2000).

Conclusion/Summary

The transition from a terrestrial to a semiaquatic lifestyle did not result in substantial changes in vocalizations mechanisms because semiaquatic mammals continue to vocalize largely in air. Underwater sound production in semiaquatic mammals involved redirecting the sound transmission pathway through overlying tissues without radical changes to the larynx. Even the transition to a fully aquatic life was

conservative in the case of sirenians. However, for whales, this transition resulted in great changes in the respiratory tract. Sound production abilities are highly divergent in cetaceans. Mysticetes generate low-frequency sounds with a highly modified larynx, whereas odontocetes generate high-frequency sounds with a highly modified nasal region. This highlights an important step in the evolution of whales, indicating two vastly different trajectories for baleen and toothed whales. Perhaps the pressures to communicate, navigate, and find food in the open ocean allowed selection for respiratory tract traits that enhanced underwater sound production and transmission. The divergence into opposite ends of the frequency spectrum highlights how these two taxa, although related, pursued very different niches for their acoustic abilities.

Biosketch



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