Chapter 3
Anatomy of Sound Production and Reception

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Abstract Mysticetes (baleen whales) have an amazing array of adaptations of mammalian traits and functions enhanced for aquatic submersion. In this chapter, special emphasis is placed on anatomy and physiology of adaptions that enable communication (sound production and reception) in water, including during diving. Whenever possible, data revealing anatomical differences will be pointed out at the family level for balaenids (bowhead whale *Balaena mysticetus*, and right whales *Eubalaena glacialis, E. japonica, E. australis*), neobalaenid (pygmy right whale, *Caperea marginata*), eschrichtiid (gray whale *Eschrichtius robustus*), and balaenopterids (rorqual whales, i.e., whales with throat pleats, including humpback *Megaptera novaeangliae*, and the many species of the genus *Balaenoptera*, including minke whale *B. acutorostrata*, Antarctic minke whale *B. bonaerensis*, blue whale *B. musculus*, fin whale *B. physalus*, sei whale *B. borealis*, Bryde's whale *B. edeni*, and Omura's whale *B. omurai*). Some species groupings (e.g., the various right whales) or subspecies groupings (e.g., subspecies of blue whales) will not be addressed if there is no literature to indicate a difference, and the assumption is made that their anatomy is similar enough to be generalized for the whole group. In many cases, an anatomical feature may be discussed in generalities because it is present in all mysticetes.

Keyword Anatomy · Mysticete · Sound · Production · Generation · Hearing · Diving · Adaptations

3.1 Overview of Mysticete Aquatic Adaptations

Mysticetes are grouped into families based largely on the morphology of the mouth. The parvorder name Mysticeti (literally "mustached" + "whales") refers to the brushy appearance of baleen plates in the whale's mouth that resemble a mustache.

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Mysticetes do not erupt teeth, although remnant tooth buds can be seen in the upper jaw of fetal whales (Deméré et al. 2008; Thewissen et al. 2017). Instead, they sport baleen plates made of keratin that are attached to the upper jaw. The baleen frames the gape on either side of the oral cavity and is used to separate prey from water in a process called filter-feeding using a mechanism of cross-flow filtration (Pinto 2011). Balaenids (bowhead and right whales), and presumably also the neobalaenid (pygmy right whale), feed using a strategy called "skim feeding" or "ram feeding" in which water flows through the mouth and prey is trapped on long baleen plates as the whale continuously swims (Chap. 5). The eschrichtiid (gray whale) can employ a benthic feeding strategy called "suction feeding" that involves sucking in and sifting muddy substrate to catch prey on the baleen. Balaenopterids (rorqual whales) use a different feeding strategy called "lunge feeding" or "gulp feeding." This batch-loading technique involves seeking (or actively corralling) prey in a tight cluster (bait ball), swimming directly at the cluster, opening the mouth, stretching the pleated throat region (engulfing prey-laden water), closing the mouth, and squeezing water out while retaining prey caught on the baleen.

All mysticetes have a very large head that can be up to one-third of the length of the whole body. Most of the head is comprised of the large mouth. Balaenids have a highly arched upper jaw. The blunted front of a balaenid is not a very streamlined shape, and this is associated with their relatively slow swimming speeds compared with the sleeker arrowhead shape of the balaenopterids. The only neobalaenid, the pygmy right whale, has many head features that resemble the balaenids (narrow rostrum, baleen covered by raised lips). However, it is unknown whether their swimming or feeding style is similar to balaenids. Balaenopterids, on the other hand, have a very wide, V-shaped head. The tip of the rostrum is pointed, and the top of the head is broad and flat. The only eschrichtiid, the gray whale, has head features that appear somewhat intermediate between balaenids and balaenopterids. The gray whale rostrum is only mildly arched, but the face is more streamlined because it is relatively narrow and conical. Unlike balaenids, the gray whale lower jaw lips are not raised and the baleen is short, and unlike balaenopterids, there are only a few deep throat grooves (usually only three).

Mysticete species can also be distinguished by unique shapes and color patterns of their caudal (tail) flukes. Each fluke contains no bones and is approximately a triangular shape with a gentle swept-back curve along the leading edge. The trailing edge is highly variable in texture, but there is always a notch that separates where the left and right flukes meet in the midline. The sleeker, swept-back flukes of balaenopterids appear related to hydrodynamic efficiency at higher speeds, compared with the broader flukes of the slower balaenids. Humpback whales have the most distinct flukes. The trailing edge is highly corrugated and may impart an advantage in maneuverability (van Nierop et al. 2008). Flukes often bear unique features, such as scars or notches from injuries (e.g., killer whale rake marks or bites, encounters with fishing gear entanglement, propeller cuts), distributions of parasites such as barnacles and pigmentation variations (e.g., complex black and white patterns of humpback whales). These specific features help identify individual whales.

Pectoral flippers also exhibit species-specific variations in shape. The most distinctive are the extremely elongated and lumpy flippers of humpback whale. Flipper shapes vary, including highly swept-back (balaenopterids), paddle-shaped (gray whale, pygmy right whale), or squarish (balaenids). The swept-back shape of balaenopterids may impart wing-like functions for improved maneuverability for prey capture. The squarish flippers of balaenids may relate to stable, straight-line swimming during ram feeding. Flippers contain nearly all the bones homologous to the forelimb bones of other vertebrates, but are often missing only one digital ray (Cooper et al. 2007a, 2007b).

The mysticete body is a fusiform shape that allows the whale to slip through the high friction aquatic environment with reduced resistance. The body is covered with very smooth and flexible integument (skin) that helps to reduce drag. Cutaneous ridges may sense flowing water (Shoemaker and Ridgway 1991). The skin readily deforms and recoils, channeling water across the body in the most efficient flow directions to reduce drag (Pavlov 2006). A subdermal connective tissue layer of fibers provides support for dermal projections (dorsal fin, caudal peduncle) and adds spring-action that stores and releases energy to aid locomotion (Pabst 1996).

Mysticetes have the mammalian trait of hairs, but these are sparse and found mainly on the head. These whisker-like hairs may be homologous to vibrissae (Bauer et al. 2018; Berta et al. 2015). Pits may remain in adults where the hairs fall out (especially visible on the rostrum of gray whales), but their function in receiving sensation is still not well understood. Many mysticetes retain hairs into adulthood on top of the head or the chin (Reeb et al. 2007). Chin hairs may transmit information about prey density and water flow during feeding (Drake et al. 2015; Nakai and Shida 1948). Sensory receptors are also suspected in what look like vibrissal pits on either side of the tip of the lower lip (Pyenson et al. 2012). Hairs are also found in the callosities of right whales and may also mediate feeding-associated sensations (Reeb et al. 2007). Adult humpback whales have a single hair in each raised bump (tubercle) on the dorsum of the head and the front and lateral surfaces of the lower jaw. Bending these hairs or stimulating the nerve endings in the tubercles could deliver a host of mechanical or electrical sensory information, such as detecting swimming speed, water currents, water's surface, contact with another whale, vibrations or electrical fields of prey, or sound pressures (Mercado 2014). The tubercles may also cushion impacts during aggressive encounters or disrupt the whale's outline (camouflage) deterring detection by echolocation.

Mysticetes migrate from productive high-/low-latitude feeding grounds to mid-latitude locations where they give birth away from predators (Corkeron and Connor 1999, Chap. 4). A recent study posits that whale migrations to warmer water increase metabolic rate, promoting shedding and rejuvenation of skin (Pitman et al. 2020). The large mysticete body has a higher surface-to-volume ratio that conserves heat. The blubber provides insulation and stores extra energy used during migration. Whales also use some of this fat as an energy source for behaviors relevant to reproduction (e.g., fighting, chasing, fleeing, singing). For females, gestation followed by lactation are additional long-term strains that require extra fat reserves. In humpback whales, larger females can produce larger calves and are suggested to be preferred by males for mating (Pack et al. 2009).

Mysticete brains are among the largest of any animal's, but are less impressive when measured relative to head size or body size. Mysticetes have unusually large heads adapted to hold their enormous feeding apparatus, skewing the brain-to-body size ratio. This ratio and other similar measures such as encephalization quotient appear to be poor methods for assessing intelligence in large whales (Marino 2009). Size is irrelevant to social complexity, and large bodies do not require much more brain tissue than small bodies to coordinate muscle and organ functions. Another method to assess complexity is the degree of gyrification (convolutions). Mysticete brains are highly convoluted, providing more surface area for gray matter (for processing signals), as opposed to white matter (for transmission of signals). Complexity of convolutions does not always equal intelligence, as some regions are specialized for other functions (e.g., sound production and reception). However, sound production and hearing are necessary not only for navigation-orienting and foraging, but also for complex social communication, and thus indicate a high level of cortical brain function. Mysticetes (specifically humpback and fin whales) have been documented to have spindle (*von economo*) neurons (Hof and VanDer Gucht 2007). These neurons are associated with complex social skills and emotions (Butti et al. 2013), but are not restricted to highly encephalized species (Raghanti et al. 2015).

3.2 Anatomy of Sound Production: Respiratory Tract

The respiratory tract begins at the crown of the head, where paired blowholes regulate the passage of air.[1] They are guarded by a chevron-shaped ridge that acts as a splashguard, diverting water away from the blowholes. This location on top of the head reduces the energetic cost of swimming, as the whole head does not need to be lifted out of the water to enable breathing. Opening and closing the blowholes are regulated by moving cartilage plates located at the lateral aspect of the openings (alar cartilages) (Buono et al. 2015). Immediately below the opening(s) are the paired nasal plugs, which obstruct the nasal lumen to protect the respiratory tract from incursions of water while submerged (Fig. 3.1). The paired nasal plugs are covered by pigmented epithelium, indicating they are derived from invaginations of the external skin—most likely the tissue that was previously the upper lip. These bulbous structures are largely comprised of fat, with strands of skeletal muscle inserted into them that contract to retract the plugs rostrally (Gil et al. 2020). Muscle action is only required for the momentary opening of the blowholes, while excluding water from the respiratory tract (the position for the majority of time) does not require energy

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[1] Note the use of the colloquial term "air" to refer to the gas inside the respiratory tract, even though it may have a different mix of chemical concentrations compared with the ambient air at 1 atmosphere of pressure (sea level).

Fig. 3.1 Oblique caudal-cranial view of the nasal plugs being dissected away from the dorsum of a deceased neonate fin whale (*Balaenoptera physalus*). Note the paired nasal plugs have a black pigmented epithelium that matches the outer black skin (visible on the whale's left side). The lower right region of the image shows the cranial cavity (brain has been removed)

(Maust-Mohl et al. 2019). Nasal plug geometry appears to be species-specific and likely contributes to determining the unique shapes of the blow in each species.

Below the paired nasal plugs, the paired nasal passageways continue along a diagonal slope leading caudo-inferiorly through the skull (Fig. 3.2; Chap. 2, Fig. 3.3). These passageways exit the skull at the posterior choanae, where the two tubes are united into a common space called the nasopharynx. The nasopharynx is a soft-walled chamber and can be contracted by the surrounding skeletal muscle (superior pharyngeal constrictor). The nasopharynx has a pitted surface lined with glands that secrete mucus and may also expel excess salt. The bottom of this chamber is regulated by a muscular ring called the palatopharyngeal sphincter comprised of the palatal skeletal muscles. The top of the larynx (voice box) overlaps the palatopharyngeal sphincter. When the sphincter contracts, it closes the narrow gap through which the larynx is inserted, ensuring a tighter seal around the larynx and thus separating the respiratory tract from the digestive tract (Reidenberg and Laitman 2007a).

Lateral diverticulae emerge off the respiratory tract in the region of the nasopharynx. They are called pterygoid sacs (or sinuses). These are paired, air-filled chambers located under, but outside, the skull. Unlike true sinuses, the pterygoid sacs are not completely encased in bone, thus allowing flexibility to respond to ambient

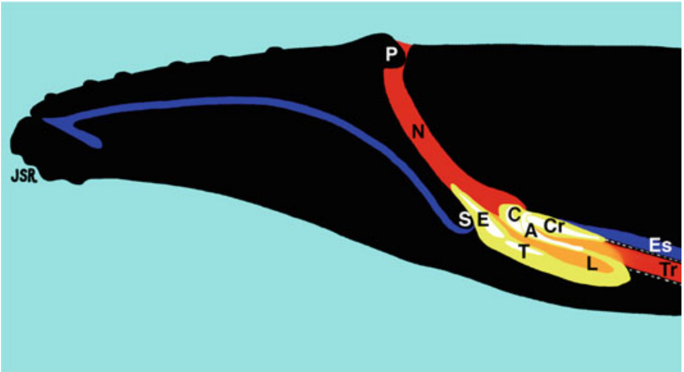

Fig. 3.2 Diagram of midsagittal anatomy of the upper respiratory system in a typical mysticete. Yellow = larynx, Red = respiratory passageways, Blue = digestive passageways. A = arytenoid cartilage, C = corniculate cartilage, Cr = cricoid cartilage, E = epiglottic cartilage, Es = esophagus, L = laryngeal sac, N = nasal passageways (paired), P = nasal plugs (paired), S = soft palate (palatopharyngeal sphincter), T = thyroid cartilage, Tr = trachea

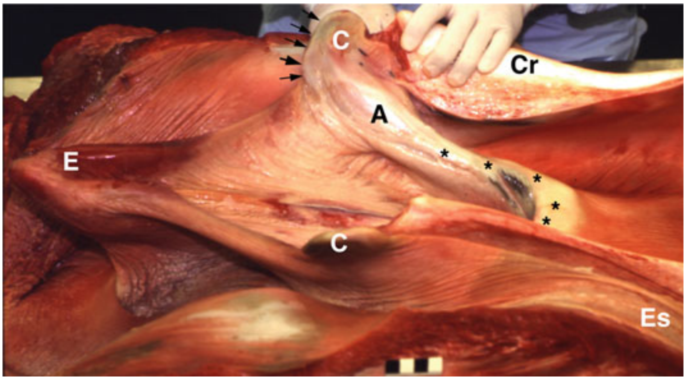

Fig. 3.3 Left latero-dorsal view of the larynx of a juvenile humpback whale (*Megaptera novaeangliae*) that has been cut along the dorsal midline and pulled open (note hand at top of figure). A = arytenoid (paired, only right is visible), C = corniculate (paired, left is projecting toward viewer), Cr = cricoid (unpaired, cut in midline), E = epiglottis (unpaired), Es = esophagus, arrows = corniculate flap, asterisks (*) = U-shaped vocal fold (only right side is visible). Scale bar: 1 square = 1 cm

pressure changes. They appear to be expansions of the Eustachian (pharyngotympanic) tubes connecting the respiratory tract to the middle ear. Similarly to terrestrial mammals, they are used for equilibrating pressure changes in the airspace of the middle ears. In mysticetes, this is a critical function for hearing, as ossicles in the middle ear must have space to vibrate in order to transmit sounds to the inner ears at depth. The sacs hold excess air that can be sacrificed to collapse at depth, thus protecting the remaining small but critical volume of residual air in the middle ear.

The hyoid apparatus is comprised of an unpaired basihyal in the midline and laterally projecting paired thyrohyals (the "greater horns"), and paired stylohyals that connect them to the skull. They provide a large surface area for the attachment of several robust skeletal muscles that can cause it to be elevated/depressed, or protracted/retracted. Depression/retraction lowers (opens) the mandibles and depresses the floor of the mouth, while elevation/protraction lifts the floor of the mouth and assists closing the gape. The hyoid apparatus also supports movements of attached lingual (tongue) muscles (Kienle et al. 2015). The hyoid apparatus also protects the airway during swallowing by elevating the larynx and opening the lateral food channels of the pharynx (Reidenberg and Laitman 1994, and Werth 2007 for detailed descriptions of the hyoid apparatus and associated skeletal muscles). Asymmetric placement of the hyoid apparatus in odontocetes assists with engulfing large prey (Reidenberg and Laitman 1994; MacLeod et al. 2007), but mysticetes do not appear to have any asymmetry of the hyoid apparatus or associated lateral food channels for swallowing prey.

The larynx is comprised of the epiglottic, thyroid, cricoid, and fused arytenoid–corniculate cartilages (the latter being paired cartilages). The larynx is positioned under the skull base and maintains an intranarial position through its interlock of the epiglottis and corniculates being positioned above the palatopharyngeal sphincter (Fig. 3.2). This ensures that the opening of the larynx is contiguous with the space of the nasopharynx, maintaining an interrupted connection between the nasal tract above and the trachea and lungs below. There are differences in the shapes of the laryngeal cartilages among the various species (Reidenberg and Laitman 2007a for details).

Balaenopterid whales have a slender and elongated epiglottis, with a pointy tip (Fig. 3.3). The epiglottis is deeply concave, having a trough-shaped channel for its entire length. It resembles a canoe, with the concavity facing the lumen of the larynx. In the rest position, the epiglottis lies over the soft palate, creating a bridge that channels air in this concavity in either direction. If the epiglottis is inserted into the oral cavity, the concavity faces the palate and together they form a half-cylinder tube. This position enables shunting air into the mouth (for bubble cloud production). Water in the mouth may be excluded if the epiglottis is forced dorsally against the ventral aspect of the soft palate, sealing the edges and allowing air to exit only at the epiglottic tip (Reidenberg and Laitman 2007b).

The corniculate portion of the arytenoid–corniculate complex in balaenopterids curls dorso-caudally away from the epiglottis to interlock with the posterior edge of the palatopharyngeal sphincter (Fig. 3.2). These paired cartilages are not able to oppose the epiglottis tightly to close the larynx. Rather, the epiglottis can be lifted dorsally to oppose the leading edges of the corniculates. Each corniculate has a flap of tissue (corniculate flap) on the rostral edge that extends toward the epiglottis (Fig. 3.3). It is unknown whether the flaps rest inside the concavity of the epiglottis, or only approach it to form a lateral boundary that helps enclose the air passageway. The size of the flap is species-specific, with humpback whales having the smallest flaps and minke whales having the largest flaps (relative to the size of the whole larynx). The function of these flaps is unknown, but as they are opposed against each other it may be possible for them to clap together and passively create pulse-like vibrations with airflow, with species-specific frequency characteristics related to their geometry (Damien et al. 2019).

The neobalaenid has an unusual appearance of the epiglottic and arytenoid–corniculate cartilages (Fig. 3.4). While it has a similar shape to balaenopterid laryngeal cartilages, the mucosal surface is unusually pitted (Reeb and Best 1999). The function of these pits is still unknown.

In balaenids, the epiglottis is shorter, thicker, has a rounded tip, and a ridge in the midline of the luminal surface (Reidenberg and Laitman 2007a) (Fig. 3.5). The epiglottis appears less mobile compared with balaenopterids. It is directed superiorly toward the skull, rather than forward on a diagonal as in balaenopterids. The arytenoid–corniculate cartilages are straight cartilages that extend in the same direction as the epiglottis, and slightly curl caudally only at the very tip. The corniculates are very thick and do not have any flaps of tissue extending from the leading edge, as in balaenopterid whales (Reidenberg and Laitman 2007a).

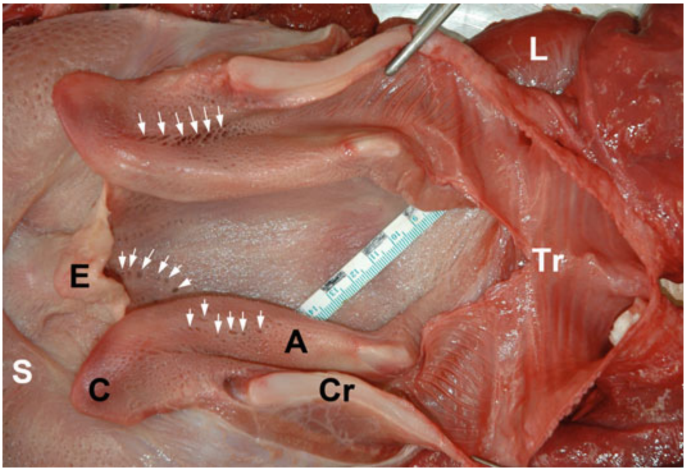

Fig. 3.4 Dorsal view of the larynx of a pygmy right whale (*Caperea marginata*) that has been cut along the dorsal midline and opened laterally to reveal the lumen. Note the many pits in the mucosa (some indicated by arrows). A = arytenoid cartilage (paired) supporting the U-shaped vocal fold (cut caudally), C = corniculate cartilage (paired) supporting the corniculate flap, Cr = cricoid cartilage (unpaired, but cut in the midline), E = epiglottis (unpaired, curled caudally and projecting dorsally), L = laryngeal sac (deviated to the right), S = soft palate (palatopharyngeal sphincter), Tr = trachea (just above the bifurcation or carina). Note the vocal fold is cut caudally in the midline to reveal passageway to laryngeal sac. The laryngeal sac begins where the scalebar ruler lies and deviates to the right side. The ruler is placed diagonally so that it is inserted fully into the sac. Note white paper towels were placed in the left main bronchus and under the carina to absorb fluids and hold those spaces open

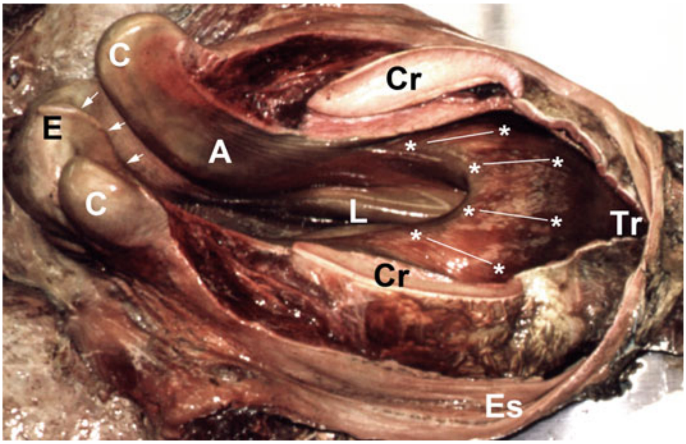

Fig. 3.5 Left latero-dorsal view of the larynx of a North Atlantic right whale (*Eubalaena glacialis*) that has been cut along the dorsal midline and opened laterally to reveal the lumen. A = arytenoid cartilage (paired but only right is visible) supporting the U-shaped vocal fold (asterisks), C = corniculate cartilage (paired) supporting thick “flap” tissue, Cr = cricoid cartilage (unpaired, but split in half in midline), E = epiglottis (unpaired) with a midline ridge (arrows), Es = esophagus (unpaired, but split in the midline), L = laryngeal sac (the lateral walls are collapsing medially), Tr = trachea. Note the depth of the very thick U-shaped vocal fold, indicated by the paired asterisks with connecting lines

Two shallow, concave channels lie on either side of the midline ridge of the balaenid epiglottis (Fig. 3.5). These channels are opposed by the corniculate cartilages (located at the rostral end of the paired arytenoid–corniculate complex cartilages). The three cartilages (epiglottis and paired corniculates) are more rigid and can nest into each other. The midline ridge helps form a seal in its position inserted between the two corniculate cartilages, obstructing any remaining lumen. Unlike the balaenopterid condition, the balaenid larynx appears capable of being tightly close at the tip.

The arytenoid–corniculate cartilages support the vocal folds of the mysticete larynx (note: the lay term “vocal cords” for these folds is erroneous, because they are not string-like cords, but rather, shelves of tissue that project into the laryngeal cavity). The paired vocal folds form a U-shape when viewed dorsally (Figs. 3.3 and 3.5). The vocal fold begins rostrally at the free edge of the corniculate flap and extends caudally to where it meets its pair in the midline. Here, the cartilages are anchored together by a strong ligament, together forming the U-shaped fold. The vocal fold has different characteristics along its length, each capable of vibrating at a different frequency (Damien et al. 2019). At rest, two vocal folds lie in opposition to each other. In balaenopterids, the opposing surfaces are rounded caudally, crinkled where they meet in the middle of the vocal fold’s length, and become flatter toward the rostral end, terminating at a lip-like thickening at the base of each opposed corniculate flap (Reidenberg and Laitman 2007a; Damien et al. 2019). The vocal fold is very elongated in balaenopterids (Damien et al. 2019), but is shorter in balaenids (Schoenfuss et al. 2014). The arms of the U-shaped fold are also much thicker in balaenid whales (bowhead whales, Schoenfuss et al. 2014; North Atlantic right whales, Reidenberg and Laitman 2007a) compared with neobalaenid, eschrichtiid, and balaenopterid whales (Fig. 3.5). As the U-shaped fold appears to be the source of sounds, these differences likely determine the types of sounds each group can make.

In all mysticetes, the arytenoid cartilage is attached to the cricoid cartilage at a large synovial joint, indicating this is a highly mobile cartilage (Reidenberg and Laitman 2007a). Several intrinsic laryngeal skeletal muscles, all attached to the arytenoid cartilage, are responsible for these movements. Regulating how much and where air flows over or between the vocal folds can cause vibrations at different points along the tissue and is likely the reason whales can generate such a large repertoire of sounds (Damien et al. 2019).

Immediately ventral to the vocal folds is a large muscular diverticulum, called the laryngeal sac (Figs. 3.5 and 3.6). It lies in the midline, with its rostral end beginning at the base of the epiglottis, immediately dorsal to the thyroid cartilage of the larynx. It extends out from underneath the caudal edge of the thyroid cartilage and terminates caudally as far as the beginning of the trachea. It is unprotected by the thyroid cartilage for much of its length, allowing it to expand ventrally. Interestingly, the pygmy right whale's laryngeal sac is asymmetrically placed on the right side (Reeb and Best 1999) (Fig. 3.4). The reason for this neobalaenid asymmetry is unknown. It is particularly unusual because mysticete anatomy is otherwise symmetrical.

The opening into the laryngeal sac is regulated by movements of the vocal folds, controlled by muscular action on the arytenoid cartilages (Fig. 3.6). It is not known whether the sac itself can generate or propagate sounds, possibly through muscular

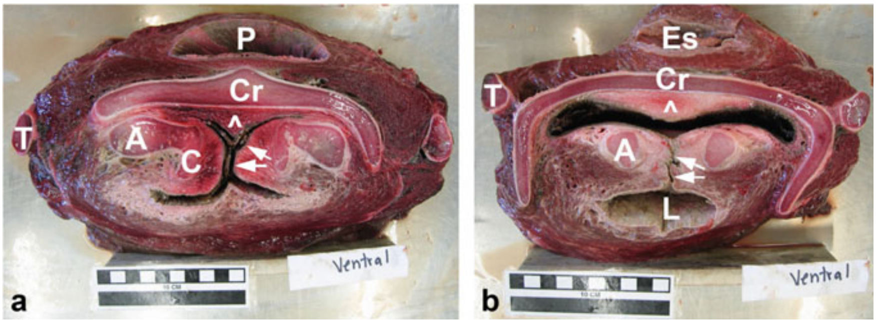

Fig. 3.6 Cross sections of the larynx of a minke whale (*Balaenoptera acutorostrata*), viewed from caudal to cranial. a, more rostral section taken at the junction between the arytenoid and corniculate cartilages and before the enlargement of the laryngeal sac. b, more caudal section taken from the region where the two "arms" of the U-shaped vocal folds meet and regulate the opening to the laryngeal sac. A = arytenoid cartilage (paired), C = corniculate cartilage (paired), Cr = cricoid cartilage (unpaired), Es = esophagus, L = laryngeal sac, P = pharynx, T = thyroid cartilage (unpaired, but two paired projecting caudal horns are visible laterally), arrows = surfaces of a vocal fold (note the rostral region is smooth, while the caudal region is corrugated), ˆ = "cushion" of tissue under the cricoid cartilage that may seal the gap between he vocal folds

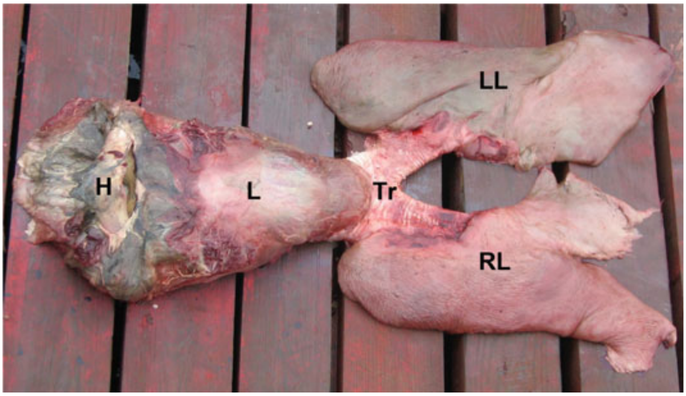

Fig. 3.7 Ventral view of the lower respiratory tract of a minke whale (*Balaenoptera acutorostrata*). H = hyoid bone (basihyal and thyrohyals), L = laryngeal sac immediately ventral to the larynx, LL = left lung, RL = right lung, Tr = trachea. Note that the laryngeal sac (L) is as long as the lungs (LL and RL)

movements along its walls or vibrations transferred to it from movements of the attached vocal folds at the sac's entrance. The sac volume is proportionately larger in balaenopterids compared to balaenids, but the sac walls are proportionately thicker in balaenids compared with balaenopterids. Differences in relative size and thickness of the sac may contribute to the species-specific characteristics of sounds produced.

The sac can distend to a volume that rivals the total volume of one fully inflated lung, and the circumferential skeletal muscle in the walls can contract to expel air from the sac (Reidenberg and Laitman 2008) (Fig. 3.7). The sac may also be used for buoyancy compensation (see below, Diving Adaptations), or to provide excess air volume to accommodate for the volume collapse that occurs when diving (Reidenberg 2018).

It is possible that this sac serves as a sound transducer, sending vibrations from its walls to the overlying blubber and skin, and then into the water (Reidenberg 2017). It is also likely that the sac is an air recycling chamber, catching air used in generating sounds at the vocal folds and then sending it back to be used again for another cycle of sound production (Reidenberg 2018; Damien et al. 2019). This recycling of air lets the whale make multiple sounds in series without having to return to the surface for more air, thus allowing it to stay submerged longer to continue singing. It has been hypothesized that some faint very low-frequency sounds (<10–12 Hz), that have been recorded in between song units from blue and fin whales, may be caused by air movement during air recycling from the sac back to the lungs (C. Clark, pers. comm. 2021).

The laryngeal sac may have multiple roles in all of the above functions. If so, the impact of one function on another may introduce limitations depending upon sac volume as related to depth. For example, as the sac compresses with higher dive pressures it contributes to negative buoyancy, but provides less air volume to be used for sound production. This may explain the observation of balaenopterids producing most sounds in the shallow phases of their dives (depths of only <30–50 m) (Lewis et al. 2018, Chap. 9). Compression or decompression of the laryngeal sac during descent or ascent may oscillate air through the vocal folds to generate sound, thus explaining the long-duration "B"-type calls blue whales make as they descend or ascend (Aroyan et al. 2000). Note that calls are not made below 90 m, the depth at which total lung collapse is predicted and thus airflow between the sac and lungs ceases.

The respiratory passageway continues caudally inside the lumen of the larynx. A thick cushion of fat bulges into the lumen dorsally (Fig. 3.6). It is attached to the ventral aspect of the cricoid cartilage of the larynx. This cricoid cushion is positioned immediately above the vocal folds and is shaped to fit directly into the slight gap between the folds that leads into the laryngeal sac (Damien et al. 2019). This cricoid cushion may function as a valve to help seal the gap between the U-shaped vocal folds, preventing airflow between the sac and the lungs.

Progressing caudally, the larynx transitions into the trachea. This transition is not clearly demarcated, as the cricoid cartilage often breaks into segmented, C-shaped extensions caudally that resemble tracheal rings (Reidenberg and Laitman 2007a). In this region, the C-shaped cartilages are incomplete ventrally, possibly allowing the laryngeal sac to inflate into this soft area and help collapse the trachea (Damien et al. 2019). There is a bifurcation of the trachea (carina), but also an accessory bronchus (epibronchus or eparterial bronchus) above the carina on the right side. Cartilage "rings" may be incomplete C-shapes (proximally near the larynx), complete O-shapes (mid-trachea), or spiraling interlocking shapes (distally in lung). Cartilage is found supporting the airways to the level of the tertiary bronchi. The various cartilage shapes contribute to airway compliance (Moore et al. 2014). The tracheobronchial tree will collapse under extreme pressure from diving, beginning caudally and progressing cranially (Denk et al. 2020).

The lungs are paired, smooth-surfaced organs, bilaterally positioned in the dorsal region of the thorax. Their anatomy is unusual because the lungs are not divided into lobes (Fig. 3.7). The function of this feature is unknown, but perhaps it enables rapid ventilation with less obstruction from angled bronchial branches. This may be related to the adaptive advantage of exchanging all the air in the lungs in one short sneeze-like breath as the whale approaches and briefly breaks the water's surface. The lungs have anatomy that supports pressure-induced collapse and re-expansion (Piscitelli et al 2013). Microscopic examination shows a large number of smooth muscles, particularly around the alveolar openings. Their function is also a puzzle, but perhaps relates to re-expansion of collapsed lungs after a deep dive.

3.3 Sound Generation

All mysticetes studied to date generate underwater sounds. Some sounds are infrasonic (<20 Hz) or in the very low-frequency range (ca. <100 Hz), such as the songs and calls of blue and fin whale singers (Chap. 9). Many sounds are in the low-frequency band (<1000 Hz), such as the songs and calls of humpback, bowhead, right, minke, and Omura's whales (Chaps. 10–15). Mysticetes are specialists in generating low-frequency sounds. These sounds have long wavelengths, suffer little to no attenuation due to frequency-dependent absorption, and can be refracted into pathways with cylindrical, not spherical spreading loss, such that they can travel great distances before attenuating below detection levels (Payne and Webb 1971). In some ways, this long-distance sound transmission phenomenon is similar to that experienced when hearing only the bass beat from the sound system of a distant car or the aggregate noise from a distant highway. Only the low frequencies are perceptible as they travel more efficiently between the distant sound system or highway, while the higher treble frequencies of the song or the collective whines of traffic attenuate before reaching your ears.

The physics of sound propagation in the ocean, from shallow waters along continental shelves or abyssal regions in open ocean environs, has demonstrated the mechanisms by which sounds of different frequency content can travel different distances (Jensen and Kuperman 1983; Jensen et al. 2000). Thus, in the deep ocean, the infrasonic songs of blue and fin whales can be detected on seafloor hydrophones at ranges of many thousands of kilometers, and the very low-frequency portions of humpback songs can be detected at many hundreds of kilometers. In contrast, in relatively shallow waters of a continental shelf, the higher-frequency (> 1 kHz) portions of humpback songs are only detectible out to many tens of kilometers (Clark and Clapham 2004).

All blue, fin, and humpback singers that have been sexed have been males (Glockner 1983; Croll et al. 2002; Oleson et al. 2007; Lewis et al. 2018). Male singing is thought to be important for mate selection and/or male competition (Smith et al. 2008; Herman 2017). Humpback whales are particularly famous for their songs because of their complexity, as well as the social exchange and learning of song components between groups, allowing for song evolution (Chaps. 8, 10 and 11). There are some remarkable species-specific differences in the types of sounds produced by mysticetes. This includes the ability of blue whales to produce intense long sequences of very low-frequency units lasting tens of seconds (>180 dB, Chap. 9), the complex songs of humpback whales (Chap. 10), the "megapclicks" of humpback whales (Stimpert et al. 2007), the "boing" and "star-wars" sounds of minke whales (Rankin and Barlow 2005, Chap. 14), the suggested simultaneous production of two sounds by humpback whales (Jeff Jacobsen, pers. comm.) or bowhead whales (Chap. 12), and the unusual "gunshot" sound of right whales (Crance et al. 2017, Chap. 13).

There are several unique features of mysticete larynges that may support the generation of their unique sounds (Chaps. 6, 9–15). As the air flows out from the lungs and trachea, it passes between the arytenoid–corniculate complexes, crossing over the freely mobile tissue of the vocal folds. This causes them to vibrate, generating variations in pressure at the vibration rate. There are differences in the size and shape of the vocal folds between balaenopterid and balaenid whales. Balaenopterids have long vocal folds with regionally specialized tissues that may generate many different types of sounds as air is directed in different paths across the vocal folds (Damien et al.

2019). This could account for the complex sounds of some species (e.g., humpback whales, Chap. 11). The longer folds also hold the possibility of generating much lower frequencies compared with those produced by shorter vocal folds.

Balaenids have shorter, thicker vocal folds, with a smooth surface that does not appear to have regional specializations, and lack corniculate flaps (Reidenberg and Laitman 2007a) (Fig. 3.5). Thicker folds may vibrate at a slower rate (producing lower-frequency sounds), but this is tempered by a short vocal fold length (limiting fold excursion during vibration). This anatomy is predicted to correlate with a more restricted vocal range in right whales (Chap. 13), but does not explain the great variety of sounds produced by singing bowhead whales (Chap. 12).

There is great variation in corniculate flap sizes among mysticetes. Flaps are very small in humpbacks whales and very large in minke whales. These flaps may generate pulses as they clap together, or fluttering sounds ("thrums," "purrs") as they passively vibrate (as a flag does in the wind). Larger flaps are presumed to have a greater role in contributing to the repertoire of sounds. One could speculate that they are perhaps responsible for the unique "boing" sounds of North Pacific minke whales and "star-wars" sounds of dwarf minke whales (Chap. 14).

Balaenids have a unique structure at the tip of the larynx (Fig. 3.5). The epiglottic and corniculate cartilages are much thicker than in other mysticetes, and they can be opposed against each other to form a complete seal of the laryngeal aditus (the opening connecting the larynx and pharynx). In the closed position, the epiglottis and paired corniculates may act together as one unit, completely plugging the opening of the nasopharynx. The trio of epiglottis and corniculates can be elevated into, or lowered out of, the nasopharyngeal space—acting as a piston. Lowering the larynx expands the nasopharyngeal lumen, in turn lowering the pressure in that space. If the larynx is withdrawn to the point of disconnecting from the nasopharynx, the seal of the soft palate tissues (palatopharyngeal sphincter) would be broken. This could create a sudden "pop" sound from air rushing into the space to equalize the pressure (similar to the sounds made when humans click the tongue or finger pop the mouth). This unique laryngeal feature may underlie the ability of balaenids to make unusual sounds, such as the "gunshot" sounds of right whales (Chap. 13) and "two-voiced singing" by bowhead whales (Würsig and Clark 1990, Chap. 12).

Vocal fold and/or corniculate flap vibrations generate sound energy that radiates out from the whale into the surrounding water. The pathway by which sound propagates through and radiates out of the whale's body is not known. One pathway could involve vibrations transferred along the rostral laryngeal cartilages to the skull. Vibrations from both/either the arytenoid-supported vocal folds and/or the corniculate-supported flaps could pass to the opposed epiglottis. When the larynx is elevated, the epiglottis contacts the vomer, a bone in the skull that cradles the mesorostral cartilage. The vomer is very thin, and often has a hole in this region, exposing the cartilage. This cartilage (homologous to the cartilaginous nasal septum) runs a straight path in balaenopterids (Fig. 3.8), a strongly curved path in balaenids, and a moderately curved path in neobalaenid and eschrichtiid whales. If sounds are transmitted along this cartilage, it could serve as a waveguide to send vibrations in a narrow path with no energy loss. The vibrations may travel directly to water

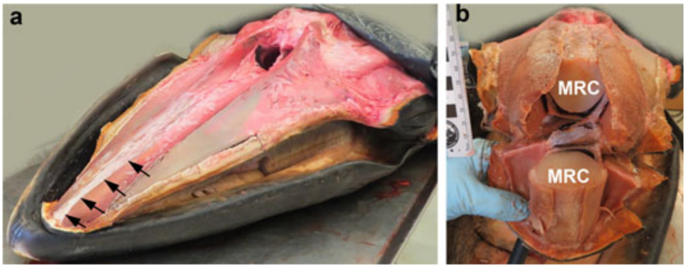

Fig. 3.8 a Left latero-rostro-dorsal view of a deceased juvenile fin whale (*Balaenoptera physalus*) head, dissected to show the mesorostral cartilage (arrows). **b** Same fin whale, rostral view, with the mesorostral cartilage (MRC) cut in cross section and the distal tip reflected inferiorly (ventrally)

at the rostral tip or through the dorsal gap where it is incompletely covered by the premaxillae, both being places where the cartilage meets a thin layer of overlying blubber. As cartilage is mostly comprised of water, there should be very little transmission loss as the energy is transferred to water. There could be great differences in the type of sound emitted, though, as the bowed cartilage should have different resonance properties compared to the straight cartilage rod. In addition, the balaenid whales should have the best coupling of the laryngeal cartilages to the mesorostral cartilage due to higher stiffness of the cartilages and tighter opposition between the epiglottis and corniculate cartilages. This topic needs further investigation, but it is predicted that the two types of mesorostral cartilage geometries will correlate with vocal differences between the balaenopterids and balaenids, while neobalaenid and eschrichtiid whales may possess characteristics shared with both groups.

Another sound path may utilize tissue vibrations from the arytenoid cartilages supporting the vocal folds, to the attached laryngeal sac, and from there to the overlying tissues of the throat including the blubber, and eventually into water. If this throat transmission pathway is used, there should be great diversity in the types of sounds that can be transmitted, as the overlying tissues are quite different between the groups of whales. Balaenopterids have very pliable throat grooves, so the sound vibration would have to pass through highly elastic, expandable tissues of the throat pouch. Perhaps this anatomy is correlated with singing talent, as balaenopterids are hypothesized to seek singing locations where they take advantage of ocean features to broadcast their sounds over greater areas (e.g., use vertical walls to reflect sounds in the manner of a band shell, or sing along the edge of the continental shelf where sound is refracted downward, reflects on the shelf and enters the deep sound channel; Chap. 2). Balaenids, on the other hand, may send their sounds a short distance to nearby whales, and thus may not utilize an elaborate sound transfer mechanism. Balaenid, neobalaenid, and eschrichtiid throats are less pliable, having at most only three short throat grooves. Balaenids have a much thicker blubber layer, and the tissues between the throat grooves do not expand to the same degree as in balaenopterids. If the throat transmission pathway is used, the sounds are likely to be dampened in the balaenid, neobalaenid, and eschrichtiid whales compared with balaenopterid whales, therein consistent with the expectation that sound source levels in balaenids would be lower than those in balaenopterids. The purpose of the neobalaenid's asymmetrically placed laryngeal sac is unclear. Perhaps the position is lateralized due to the absence of highly flexible throat pleats, instead channeling vibrations in a different pathway along the side of the head or neck to minimize dampening.

Another factor influencing sound generation and transmission is the degree of laryngeal sac expansion. As the sac enlarges, the walls become tighter, changing its resonance properties (the sac walls may vibrate as a drum does, with variations in resonance correlated to drum barrel shape and size and drumhead tension). The laryngeal sac of balaenopterids is larger than the sac of balaenids. Differences in laryngeal sac size, shape, and tension are expected to contribute to the qualities of the generated and transmitted sound.

During sound production, the mouth and nose are closed, and air does not escape from those openings. Instead, air flows through the gap between the free edges of each vocal fold into the ventrally placed laryngeal sac. As the sac expands, it captures the air used to generate sound. Then the sac contracts and sends the air back to be reused. This recycling of air is the mechanism by which whales can produce multiple sequential or a continual series of sounds over long periods without having to return to the surface for more air. Balaenopterids have the largest laryngeal sac volume, relative to the size of the larynx. Studies are ongoing to determine whether this difference is sexually dimorphic. A relatively large laryngeal sac may correlate with longer song cycles performed on a single breath.

3.4 Sound Reception

Mysticetes do not have external ears (pinnae), giving a streamlined contour. The external ear canals are filled with a wax plug, avoiding a cavity that would otherwise retain air that dampens underwater sound transmission, or could become a reservoir for developing an infection. In addition the Eustachian tubes are wide, allowing an easy mechanism for regulating diving-related pressure changes in the middle ear. Despite these aquatic adaptations, the anatomy of the mysticete inner ear (e.g., low basilar membrane thickness: width ratios, large organ of Corti mass) indicates they hear particularly well in the low-frequency range (Wartzok and Ketten 1999, Chap. 2). Although hearing ranges are often correlated with the sound production frequency ranges, one does not always predict the other. Rather, hearing ranges can be estimated through measurements of the cochlea's basilar membrane or reconstructed through physiologic measurements of brainstem responses to auditory evoked potentials (Auditory Brainstem Response, ABR). The ABR method has been applied successfully on odontocetes and is only applicable to temporarily restrained, very small mysticetes (e.g., it was attempted on a gray whale calf in a captive rehabilitation situation with equivocal results, Ridgway and Carder 2001). It cannot be performed on free-swimming wild mysticetes.

The ear has many of the same components as that of land mammals including a highly modified tympanic membrane, tympano-periotic complex (sometimes called the petrotympanic complex, comprised of the tympanic bulla, petrosal bone, and the ossicles of the middle ear), and a fluid-filled labyrinth system consisting of semicircular canals (for balance) and a cochlea (for hearing). The middle ear chamber is air-filled and maintained as such even at depth due to the adjacent pterygoid air sac that can collapse at depth and shunt all remaining air to the middle ear. The semicircular canals are very small relative to the whole labyrinth system. It has been proposed that this reduction may be related to decreased head rotation, particularly as mysticetes filter feed rather than pursue highly mobile individual prey (Ekdale and Racicot 2015). Head movements are restricted due to the flattened cervical vertebrae that compress the neck region and greatly curb its flexibility. This, in turn, stabilizes the head and neck from lateral movements (and thus undue friction), particularly at high speeds (VanBuren and Evans 2017).

Unlike the semicircular canals, the cochlea is hypertrophied, perhaps as an adaptation for high background noise (Ketten 2012). Cochlear apical width is greater than odontocetes, and similar to elephants that are also known to hear in the infrasonic range (Payne et al 1986). Unlike odontocetes, mysticetes do not have extensive outer bony laminae (a feature associated with high frequency hearing). Inside the cochlea, mysticetes have a broad, flaccid basilar membrane—an adaptation that responds well to infrasonics (Ketten 1997). The innervation densities of auditory ganglion cells are three times higher than that of humans, likely enabling the central nervous system to process multiple response sets in parallel. Interestingly, both odontocetes and mysticetes have similar high ratios of ganglion cells to hair cells, indicating both groups have equally complex signal processing even though the perceived sounds are on opposite ends of the frequency spectrum (Wartzok and Ketten 1999).

The petrotympanic bone is unusual because it is very large and extremely dense—more so than the petrous bone, or any other bone, in any other mammal (Cozzi, et al. 2009). It likely functions as a lever, bringing force (pressure) amplification of low amplitude sounds to the ossicular chain (Tsur et al. 2019). Both bone and tissue conduction of sound to the ear are likely (Ketten 2012). Modeling has shown that low-frequency sound transmission primarily occurs through bony conduction in the fin whale, and likely in all mysticetes (Cranford and Krysl 2015). Bone conduction enhances hearing at lower frequencies, and this mechanism is more sensitive than pressure transmission through soft tissues (Cranford and Krysl 2015). However, bone conduction transfers vibrations to both ears simultaneously and thus limits localization and discrimination of the sound source (Tubelli et al. 2018). The tympano-periotic complexes are attached to the skull at the pedicles, enabling bone conduction, but most of the complex is actually detached from the skull. Perhaps this detachment limits bone conduction or directs the sound in specific pathways to increase auditory localization processes. The bony conduction pathway has merit because the receiver is so large (the whole skull) that it may be ideal for perceiving the longer wavelengths of the low-frequency sounds. These sounds are generally used for communication, but have been suggested by some to serve also as coarse sonar for navigating around large underwater obstacles or using them as navigational aids (e.g., ice keels, George et al. 1989; seamounts or canyons, Clark and Ellison 2004). Precise localization is probably unnecessary when the target is so large, and thus bony conduction reaching both ears at approximately the same time may not be a serious detriment. Alternatively, the brain may be tuned to detect microsecond differences in arrival times between the bony conduction to each ear, enabling directional hearing.

The evolutionary retention of an ossicular chain implies it is also used for sound transfer. If bone conduction is the preferred mechanism for low-frequency sound transfer, perhaps tissue transfer is the mechanism for higher frequencies. Two mechanisms have been proposed for transferring sounds to the ossicular chain. Vibrations may be transferred by the tympanic membrane, although not from the external ear canal as in terrestrial mammals. This is because the tympanic membrane is not in contact with an air-filled external acoustic meatus. Rather, it is a highly modified structure (also called the “glove finger” due to its invagination into an elongated sac-like structure) that lies in a fluid-filled chamber adjacent to a large wax earplug. Modeling and experimental studies in humpback and minke whale ears predict the apex of the tympanic membrane receives vibrations passing through tissues in this region and regulates the vibration transfer to the ossicles of the middle ear (Tubelli and Zosuls 2012; Tubelli et al. 2018). In minke whales, sound may be received by the fat bodies located adjacent to the lower jaw and directly transferred through their connection to the middle ear ossicles (Yamato et al. 2012). Conversely, these fat pads were not found in the bowhead whale (unpublished data, pers. comm. D. Hillmann, Louisiana State University), although this may be because the specimens were only fetal.

3.5 Diving Adaptations

Fluids such as blood are relatively incompressible and may be used to compensate for pressure-related volume changes of air-containing spaces during diving. Blood may be shunted into these spaces to occupy volumes (that were expanded with air before diving compression) to prevent damage to structural tissues surrounding these spaces. There are two major regions where blood-filled tissue expands adjacent to collapsing air-filled spaces: the lungs and the pterygoid sacs.

As the lungs shrink during diving, the vacated negative space is filled by an expanding vascular tissue called the retia mirabilia thoracica that swells with blood (Moore et al. 2011). This is not a simple erectile tissue comprised of blood sinuses, but rather, a complex network of blood vessels in the thoracic cavity located on the dorsal, paraspinal region. These vessels may also function to trap bubbles that might form in the blood on ascent, preventing the bubbles from circulating to vital organs and thus mitigating for decompression sickness (Reidenberg and Laitman 2015).

The pterygoid sacs have a complex network of vessels running through and along pterygoid sac walls. The arterial system of this region has a considerable surface area in contact with both the fat of the mandibular region and the air in the pterygoid sacs. This may facilitate nitrogen gas exchange to prevent decompression sickness

(Costidis and Rommel 2016a). There are also thin-walled, venous lakes (large open blood sinuses through which arteries pass) in the pterygoid sac that may participate in nitrogen exchange (Costidis and Rommel 2016b). The pterygoid sacs are soft-walled and respond to ambient pressure changes by collapsing during a dive and re-expanding upon ascent. Filling the sacs with air before diving ensures that there is extra volume associated with the middle ear, thus mitigating the effect of volume collapse at depth. As the soft-walled pterygoid sacs deflate, the residual air volume is preferentially preserved in the rigid space of the middle ear (surrounded by bone). This arrangement preserves hearing at depth because it ensures that the ossicles have a space in which to vibrate so they can transmit sounds to the inner ear.

While diving, whales, particularly balaenopterids, approach neutral buoyancy as the positive buoyancy of blubber is countered by the negative buoyancy of the relatively incompressible tissues (bones, muscles, and organs) (Gray et al. 2007; George et al. 2016). These factors cannot be changed, and thus comprise the static component of buoyancy. Dynamic buoyancy, however, is regulated by the air spaces of the respiratory tract (lungs, laryngeal sac, trachea, larynx, pharynx, sinuses, nasal passageways), as they can contain variable amounts of air. During inhalation, a fully inflated respiratory tract makes the whale positively buoyant. However, as the whale begins its dive, and ambient pressure increases, the air in the respiratory tract begins to compress. As these air spaces collapse, the whale's body becomes denser and its buoyancy becomes negative, thus aiding descent. The whale's head would be pointing down during descent, so air will naturally rise to the highest point in the respiratory tract: the lungs. Evacuating air out of the nasal passageways, nasopharynx, pterygoid air sacs, larynx, and laryngeal sac should make the head heavier (particularly since it is mostly comprised of dense skull bone), and this would help the whale maintain a head-down orientation. After a few initial beats of the tail to begin the descent, the negatively buoyant whale could now save energy and glide the rest of the way down (Williams et al. 2000)—following its own heavy head as if following a sinking stone. Balaenopterids spend more energy swimming during ascent to overcome negative buoyancy. Achieving negative buoyancy is more difficult in balaenids, as they tend to float at the surface due to the thicker blubber layer. They must exert more energy in powerful tail strokes when initiating a dive until lung collapse contributes to achieving negative buoyancy, enabling continued descent with less effort.

Whales appear able to vocalize at any depth, but there can be advantages to emitting sound during deep dives. However, the collapse of air spaces should make vocalizing nearly impossible at extreme depths. The laryngeal sac may be just the diving adaptation necessary for sound production to proceed. Extra air carried in this sac can be added to the air volume available for generating sounds. As the whale descends, the lungs would only have a fraction of the original volume they contained at one atmosphere of pressure, according to Boyle's law (i.e., for a fixed amount of gas kept at steady temperature, pressure and volume are inversely proportional—that is, when one doubles, the other is reduced by half). The nasal region will also collapse its volume in the same proportion, sucking in the nasal plugs down the tubular nasal passageway's length and shrinking the walls of the nasopharynx and pterygoid sacs. The larynx and trachea would similarly collapse, squeezing the epiglottis toward the corniculates and contracting the tracheal rings similarly to a compressed accordion. These spaces may not be able to contract any further, or may be insulated from doing so in order to maintain some air in the pterygoid sac to preserve a space for ossicular vibration for hearing.

The laryngeal sac can inflate to approximately the volume of one lung at the surface. This is an expendable space that would have a lot of extra volume available if inflated before descent, although it would be reduced by the same percentage at depth. Contraction of the laryngeal sac muscles could evacuate this air to the lungs. Perhaps it would be enough to increase the lung volume to initiate sound production. The flattened rib cage that accommodated the lung collapse at depth would now partially re-expand. Contraction of the intercostal muscles would re-flatten the ribs, compressing the thorax, and drive air from the lungs into the trachea, larynx, and through the vocal folds. This should vibrate the folds and generate the fundamental frequency needed to create sounds. This small amount of air would be captured by the expanding laryngeal sac. The muscular walls of the sac could then compress this air volume and expel it back to the lungs to be recycled for repeated rounds of sound production.

As the whale ascends, the whole process reverses. Contraction of the intercostal muscles would compress the thorax and shunt lung air cranially to the trachea, larynx, laryngeal sac, pterygoid sacs, nasopharynx, and nasal passageways. This makes the head lighter than the rest of the body, and the whale now follows the head up, as if following a rising balloon. After a few initial tail strokes to begin the upward ascent, the whale could save energy and simply glide effortlessly to the surface. This is particularly true for balaenids, as the positively buoyant effect of the blubber becomes greater during ascent, helping to power their rapid glides back to the surface (Nowacek et al. 2001).

Whales are champion breath-holders, but this means less oxygen in the blood is delivered to the tissues during diving. There are many adaptations that accommodate for this, including the previously mentioned energy conservation during descent and ascent, and the slowed metabolism evidenced by the very low heart rate while diving. This means their bodies use less oxygen, so the muscle contractions can last longer before building up oxygen debt. Another adaptation lies in the skeletal muscles themselves. They contain high levels of myoglobin, the substance that makes the muscle appear very dark. Myoglobin helps bind extra oxygen where it is needed most for muscle contractions, thus compensating for the lack of circulating oxygenated blood during the dive. Myoglobin concentrations appear to correlate with average duration and depth of dives, thus enhancing dive capacity (Helbo and Fago 2012).

The bones have also evolved to be adapted for buoyancy control with anatomy specific to diving behavior. The skull is devoid of any bony paranasal air sinuses, likely as an adaptation for diving. Rigid-walled sinuses would crack under pressure as the contained volume of air shrinks during a dive. Bowhead whales (and presumably all balaenids) have dense bones as calves, but lose this density with age (George et al. 2016). The heavy bones impart ballast (negative buoyancy) that helps counter-balance flotation (positive buoyancy) caused by the fat tissues (e.g., blubber). Balaenids have comparatively more blubber (compared with other mysticetes), and there is proportionally more in calves. Thus, despite dense bones, balaenids tend to be positively buoyant near the surface. This causes them to spend more energy as they begin a dive (compared with non-balaenids) to overcome the positive buoyancy provided by the thicker blubber layer (Nowacek et al. 2001). In contrast, most other cetaceans have osteoporotic (less dense) bones in the ribs and flippers that balance the buoyancy of the thinner blubber layer, thus contributing to an overall neutral buoyancy (Gray et al. 2007). This enables dynamic buoyancy regulation, achieved by controlling the amount of air in the respiratory tract.

3.6 Conclusion

Mysticetes are a very diverse group of whales. Major differences are found between the anatomy and physiology of balaenopterids versus balaenids, with the neobalaenid and eschrichtiid whales often exhibiting an intermediate morphology and function between these two extremes. Unique features of balaenopterids describe a faster, more agile, and deeper diving whale, with a gulping feeding style, and (in some species) lower frequency calls/songs. Unique features of balaenids describe a slower swimming, shallower diving, less agile whale, with a continuous flow feeding style, and a broader vocal range with some unique sound production abilities (e.g., bowhead two-voiced singing, Chap. 12). Less well understood are the intermediate morphologies exhibited by the neobalaenid and eschrichtiid whales. Further research is needed to relate the variations in laryngeal anatomy to the species-specific sounds produced by the four different mysticete families.

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