Sisters of the Sinuses: Cetacean Air Sacs

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ABSTRACT

This overview assesses some distinguishing features of the cetacean (whale, dolphin, porpoise) air sac system that may relate to the anatomy and function of the paranasal sinuses in terrestrial mammals. The cetacean respiratory tract has been modified through evolution to accommodate living in water. Lack of paranasal sinuses in modern cetaceans may be a diving adaptation. Bone-enclosed air chambers are detrimental, as their rigid walls may fracture during descent/ascent due to contracting/re-expanding air volumes. Flexible-walled "sinuses" (extracranial diverticula) are a logical adaptation to diving. Odontocetes (toothed whales) exhibit several pairs of paranasal air sacs. Although fossil evidence indicates that paranasal sinuses occur in archaeocetes (ancestors/relatives of living cetaceans), it is not known whether the paranasal sacs derive from these sinuses. Sac pigmentation indicates that they derived from invaginations of the integument. Unlike sinuses, paranasal sacs are not circumferentially enclosed in bone, and therefore can accommodate air volume changes that accompany diving pressure changes. Paired pterygoid sacs, located ventrally along the cetacean skull, connect the pharynx and middle ear cavities. Mysticetes (baleen whales) have a large midline laryngeal sac. Although cetacean air sacs do not appear to be homologous to paranasal sinuses, they may serve some analogous respiratory, vocal, or structural functions. For example, these sacs may participate in gas exchange, thermoregulation, resonance, and skeletal pneumatization. In addition, they may subserve unique aquatic functions, such as increasing inspiratory volume, mitigating pressure-induced volume change, air shunting to reduce respiratory dead space, and facilitating underwater sound production and transmission. Anat Rec, 291:1389–1396, 2008. © 2008 Wiley-Liss, Inc.

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Life in a liquid environment poses many challenges, particularly for air-breathing mammals whose ancestors were originally adapted for life on land (see reviews in Reidenberg, 2007; Uhen, 2007). One system in particular, the respiratory, has undergone extensive evolutionary modifications to accommodate functions during repeated or prolonged submersion. These uniquely derived adaptations include: protection from drowning while foraging, converting sound production in air to sound transmission in water, accommodating changing buoyancy at varying depths, minimizing damage from

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diving pressure changes, and maximizing a limited air supply at depth.

Anatomic adaptations of the soft tissues of the respiratory tract are seen beginning at the nostrils. Although many aquatic species such as pinnipeds (seal, sea lion, walrus) and sirenians (manatee, dugong) maintain the double external nairal openings of land mammals, the surrounding tissues have been modified through evolution into mobile valves that can close the nostrils and exclude water while submerged. The external nares of cetaceans (whales, including dolphins and porpoises) are sealed by valvular structures called nasal plugs. Although mysticetes (baleen whales) maintain a pair of nostrils (blowholes), they have been modified into one blowhole opening in odontocetes (toothed whales). Cetacean nostrils have also migrated during evolution from an anterior (rostral) location to a dorsal position. This position ideally places the nostrils where they can be exposed at the water’s surface during swimming, without the energy expenditure associated with lifting the head to get them clear of the water’s surface.

Further respiratory tract modifications are seen in the laryngeal region of marine mammals that relate to the need to protect the airway from incursions during feeding. For example, the larynx of odontocetes has evolved into a tubular structure that can be circumferentially “gripped” by a powerful soft palate literally locking it into a permanently intranarial position (Reidenberg and Laitman, 1987). This arrangement separates the respiratory tract from the digestive tract, thereby protecting the animal from drowning while swallowing or vocalizing.

Diving presents additional risks to the respiratory tract, as ambient pressure rises with increasing depth. Air spaces in marine mammals are subjected to dramatic changes in pressure during diving. Boyle’s Law states that the product of the pressure and volume for a gas is a constant for a fixed amount of gas at a fixed temperature. Therefore, as a marine mammal dives, the increasing ambient pressure (encountered at increasing depth on descent) will cause a decrease in the volume of air held in a closed chamber (e.g., paranasal sinuses, air cells, middle ear, air sacs, nasal cavity, larynx, trachea, lung). Some marine mammals, particularly deep diving seals and whales, encounter rapid changes in pressures during diving and ascent back to the surface. These pressure changes pose a challenge to maintaining the structural integrity of air-filled chambers, particularly those with rigid walls (such as the paranasal sinuses).

The marine mammal respiratory tract is adapted for withstanding changes in pressure related to diving. Modifications are seen, for example, in the bony nasal cavity, which is lined with pliable soft tissues in cetaceans. These nasal wall tissues may swell to occupy the collapsing air volume of the nasal cavity at depth. Trabeculated tissue at the base of the larynx and trachea, which has been described as a reservoir of lymphoid tissue (Smith et al., 1999) may also enable partial collapse of the lumen without risking fracture of the laryngeal and tracheal cartilages (Reidenberg and Laitman, 1988). Laryngeal, tracheal, and bronchial airways are further reinforced from permanent collapse with circular rings of cartilage that may partially deform at depth and reopen on ascent (Reidenberg and Laitman, 1987; Cozzi et al., 2005). Air is trapped in collapsing alveolar spaces of the lungs at depth, but the small muscles surrounding the alveoli and the elasticity of cartilage-reinforced tertiary bronchi may help re-open these air spaces on ascent (Ninomiya et al., 2005). A joined and collapsible rib cage (differing from the condition of terrestrial mammals) enables thoracic compression, which accommodates diminishing lung volumes at depth (Boyd, 1978; Falke et al., 1985; Ridgway and Heward, 1979).

Skeletal changes evolved in concert with respiratory changes in marine mammals to create a dynamic control of buoyancy, which is regulated by a balance between the different densities of fixed volume tissues (e.g., bone, fat) and the variable amount of air in the respiratory system (Gray et al., 2007). The marine mammal skull exhibits a number of modifications related to the respiratory tract commensurate with aquatic life. For example, the walls of the bony nasal cavity have become smooth in cetaceans, eliminating the projecting turbinates and ethmoid air cells. This allows rapid exchange of a large volume of air during a brief encounter with the surface, with very little frictional resistance to airflow. The anterior nasal apertures (“bony nares,” Cranford et al., 1996; Heyning and Mead, 1990; “external nares,” Rommel et al., 2002; “choanae (internal nasal openings),” Rauschmann et al., 2006), located at the distal extremity of the rostrum in terrestrial mammals, have changed their position through evolution to a more posterior and dorsal position adjacent to the cranial vault in living cetaceans. Intermediate stages of anterior nasal aperture position are seen in the skulls of fossil archaeocetes (cetacean ancestors/relatives) (Kellogg, 1936). The cetacean skull is described as having “telescoped” through evolution, with facial and vault bones flattening and overlapping each other (Miller, 1923; Kellogg, 1928; Rommel, 1990; Rommel et al., 2002). Repositoning of the cetacean anterior nasal apertures is associated with the rostral (e.g., maxilla and premaxilla) and caudal (e.g., occipital) cranial bones approximating each other near the dorsum of the skull. Evolutionarily, in the process of telescoping, the cetacean maxillary and frontal bones have become so flattened that they no longer contain the hollow chambers of the maxillary and frontal paranasal sinuses of archaeocetes.

Perhaps one of the most dramatic changes in the respiratory tract configuration is the reduction or absence of paranasal sinuses in marine mammals. Terrestrial mammals, which exist in a near-constant ambient pressure of 1 atmosphere, do not need to contend with contracting or expanding paranasal sinus volumes. A bony-walled sinus, however, presents a structural risk to the skull of marine mammals that encounter high pressures while diving to deep depths. If the rigid-walled cavity cannot contract or expand, the skull may fracture. Some marine mammals (e.g., cetaceans, sirenians) have therefore evolved a skull devoid of bony-walled paranasal sinuses. Perhaps to compensate for the loss of these sinuses, these marine mammals have developed air sacs that appear to have similar functions. This article will focus on the air sacs in cetaceans, with a particular
emphasis on whether they exhibit homology or analogy to the paranasal sinuses of terrestrial mammals.

**ANATOMY OF CETACEAN AIR SACs**

Cetaceans possess soft-walled diverticula, frequently referred to as air sacs, that are attached to the airway but remain outside the skull. Cetaceans have three types of such sacs: nasal sacs located paranasally and dorsal to the skull, parapharyngeal pterygoid sacs located ventral to the skull, and laryngeal sacs located at the ventral aspect of the larynx (Figs. 1 and 2). The nasal air sacs are of particular interest as they are "paranasal" in location, occupying positions against the skull near the regions of the paranasal sinuses of terrestrial mammals.

Nasal sacs are only present in odontocetes, and usually consist of three to four paired sacs (vestibular, anterior and posterior nasofrontal, and premaxillary) and several connected unpaired smaller sacs (e.g., accessory and caudal) that are present only in some species (Fig. 1). The sacs exhibit left-right directional asymmetry, and species-specific shapes/numbers of sac pairs (Mead, 1975; Heyning and Mead, 1990). The nasal sacs are paranasal out-pouchings off the spiracular passage and are located between the dorsal aspect of the skull and the blowhole. This portion of the respiratory tract is homologous to the external nose (nasal vestibule and atrium) of terrestrial mammals. Most of the surrounding facial musculature has been adapted to regulate sac dimensions. As these sacs are outside the skull, they can expand into the surrounding layers of muscle, fat, and connective tissue of the facial region. Only the premaxillary sacs are adherent to the dorsal surface of the skull's rostrum, overlying the caudal portion of the premaxilla. This attachment may limit their ability to expand. It is interesting to note that nasal sac epithelium contains black pigment and the portion adjacent to the sound generating structures is keratinized (Cranford et al., 1996).

Fig. 1. Schematic illustration of an odontocete head (dolphin) showing the positions of the air sacs (black) relative to the respiratory tract (blue) and skull (individual bones indicated by various shades of yellow). Only the left pairs of air sacs are shown. The dashed outline through the skull indicates bony nasal passageway of left side. A posterior portion of the mandible has been removed to reveal the sacs and larynx under the skull. B, blowhole; L, laryngeal sacs; N, nasofrontal sac; PM, premaxillary sac; PT, pterygoid sac; V, vestibular sac. The nasal sacs (black) are shown in their epicranial position overlapping the skull. Each sac has a separate opening into the single, external nasal passageway. The opening of the nasofrontal sac is not shown, as it lies under the vestibular sac. The pterygoid sac is visible (black) where it emerges from under the pterygoid bone. However, the rostral aspect is largely enclosed within the pterygoid bone and extends both superiorly (under the palatine, maxillary, and frontal bones) and caudally (under the occipital and temporal bones, to surround the ear region). These bone-enclosed extensions are indicated with a dotted gray outline and are shaded dark gray. The laryngeal sacs are positioned on either side of the midline laryngeal fold.
An additional pair of air-filled diverticula, called pterygoid sacs (Fig. 1), can be found on the ventral aspect of the skull in both odontocetes and mysticetes. These sacs are extensions of the pharyngotympanic tube and are comprised of several air sacs connected to the middle ear cavity (Rauschmann et al., 2006). They extend caudally to form the peribullar space surrounding the ear. The pterygoid sacs are bounded medially by the contours of the pterygoid plates of the sphenoid bone. In many species, there is no bone surrounding portions of the ventral and lateral aspects of the sacs. Even though they are not fully enclosed by bone, the pterygoid sacs are sometimes referred to as "sinuses" (e.g., Rauschmann et al., 2006; Cranford et al., 2008a). These sacs are very large, particularly in deep diving whales (e.g., Ziphiidae, the beaked whale family), and appear to be lined with a complex network of vessels or blood sinuses that most likely fill with blood under increased ambient pressure to accommodate the decrease in air sac volume (Cranford et al., 2008b).

The ventral lumen of the odontocete larynx has a number of small diverticula called laryngeal air sacs (Fig. 1). In odontocetes, these small air pockets extend ventrally as blind sacs on either side of the midline laryngeal fold (Reidenberg and Laitman, 1988). They are divided from each other by thin, fleshy, occasionally fenestrated, walls of varying heights that may allow some communication between adjacent sacs. The blind ends of the sacs stop at the thyroid cartilage, thus limiting their expansion.

Mysticetes differ from odontocetes in that they possess a single, large, diverticulum located ventrally in the midline of the larynx (Fig. 2) (Reidenberg and Laitman, 2007). The laryngeal sac surrounds a space that may be expanded with air from the laryngeal lumen. A very thick layer of muscle runs circumferentially around the sac in the transverse plane, leaving a dorsal gap in perimeter coverage only where it meets the laryngeal lumen. The sac tapers caudally in a cone shape to a blunt cul-de-sac. The lumenal surface of the sac exhibits many folds that provide additional surface area for expansion/contraction of the sac's volume.

**CETACEAN AIR SACS: HOMOLOGY WITH PARANASAL SINUSES?**

The position of an air-filled chamber in or near the skull is not a sufficiently strong character by itself to establish homology with the cranial sinuses in general, much less with any particular paranasal sinus of terrestrial mammals. For example, the pneumatized antorbital cavity of archosaurs (including living groups such as birds and crocodilians) occupies a similar location to the paranasal sinuses of terrestrial mammals, but is not considered a homologous structure due to the absence of definitive embryological patterns of formation (Witmer, 2005). Therefore, the simple attachment of odontocete nasal air sacs to the nasal passageway, or their proximity to the nasal cavity itself, are not sufficient evidence to assume that they are derived from the paranasal sinuses.

Unfortunately, anatomical examination of the skulls of archaeocetes does not clearly answer the question of whether cetacean nasal sacs are or are not derived from paranasal sinuses. Interestingly, fossil specimens of *Dorado* (an archaeocete close to the emergence of the modern cetacean suborders Odontoceti and Mysticeti), possessed paranasal sinuses. Indeed, fossil specimens of
Dorodon skulls revealed the presence of both frontal and maxillary sinuses (Kellogg, 1936), and a CT examination of a Dorodon skull revealed the presence of a frontal sinus (Uhen, 2004). It is not clear whether any epicranial nasal air sacs were simultaneously present in Dorodon.

Developmental studies of cetaceans are few, and those that have offered some data on this area unfortunately cannot shed much light on the homology question. For example, a study of head development in early fetal odontocetes did not demonstrate the presence of any paranasal sinuses but, interestingly, did show the presence of premaxillary and nasofrontal sacs (Rauschmann et al., 2006). The absence of co-temporaneous sacs and sinuses in these fetuses is intriguing, yet cannot offer any substantive evidence to either support or refute homology.

Although a possible relationship between nasal sacs/sinus in archaeocete fossils or early odontocete fetuses remains unclear, homology has been proposed between the nasal air sacs of odontocetes and lateral diverticula of the external nares found in many ungulates (reviewed in Kellogg, 1936). The observations that the nasal sacs are pigmented black and some regions have keratinized epithelium (Mead, 1975; Cranford et al., 1996) support an epidermal origin. As melanin is useless in a structure never exposed to light, the presence of this pigment may indicate that the epithelium invaginated from the external skin of the facial region. This may have occurred during evolution as the nasal region underwent changes associated with protection from water incursion. A mobile upper “lip” that could curl dorsally over the nostrils may have provided an initial closure mechanism in ancestral odontocetes. Upward curling of the lip upon the philtrum could form a pocket trapping air. If this ability helped early odontocetes exclude water, the selection for individuals with extended and mobile lips could eventually lead to the evolution of the nasal plugs. This concept is supported by the observation that the inferior surface of the nasal plugs is continuous with the dorsal surface of one pair of nasal sacs (the premaxillary sacs). Additional lateral extensions through evolution of the nasal vestibule could have given rise to the lateral nasal sacs (vestibular and nasofrontal sacs).

As with the nasal air sacs, there is no evidence to support homology between the other remaining cetacean air sacs and the paranasal sinuses. Homology has been proposed, however, between the pterygoid air sacs and the lateral diverticula of the pharynx (e.g., guttural sac/pouches) found in many ungulates (summarized in Kellogg, 1936). This homology is based partly on the infra-cranial location as well as the connection to the pharyngotympanic tube.

The midline laryngeal sac of mysticetes may derive from ventro-caudal expansion of the supraglottic laryngeal lumen. It may be homologous to the unpaired laryngeal air sac found in some artiodactyls. In the reindeer, the diverticulum emerges ventrally between the epiglottis and the thyroid cartilage (Frey et al., 2007), whereas in the takin it is contained within a thyroid cartilage bulla (Frey and Hofmann, 2000). Although the mysticete sac is also a midline, ventral, and unpaired diverticulum, it differs from the artiodactyl sac in that it emerges caudal to the thyroid cartilage (Fig. 2). It is possible that the mysticete condition follows the pattern of the takin, having a caudally expanded laryngeal vestibulum that lost its covering by the thyroid cartilage (Frey personal communication, 2008). An alternative homology has also been proposed between the mysticete laryngeal sac and the laryngeal ventricles (Reidenberg and Laitman, 2007), which are lateral air pockets located between the vestibular and vocal folds (“cords”) of most terrestrial mammals. In mysticetes, evidence of a line of fusion between the left and right sides is visible as a midline ridge, or raphe, along the ventral surface of the sac’s lumen. Interestingly, the laryngeal air sacs of odontocetes are found ventrally on either side of the midline laryngeal vocal fold, indicating that they too are likely derived from laryngeal ventricles displaced ventrally (Reidenberg and Laitman, 1988). The laryngeal sac of mysticetes and the laryngeal sacs of odontocetes may be homologous to each other.

**AIR SAC AND PARANASAL SINUS FUNCTIONS: ANALOGOUS OR UNIQUE?**

The cetacean air sacs do not appear to be homologous to the paranasal sinuses of terrestrial mammals; however, they may have analogous roles in supporting respiratory, vocal, and structural functions.

**Respiratory Functions**

Respiratory functions of paranasal sinuses include regulating both the movement and conditioning of air. Cetacean air sacs may have an analogous role to paranasal sinuses in the regulation of gas concentrations in the respiratory tract. Although terrestrial mammals may regulate gas concentrations (e.g., nitrous oxide production) locally in the tissues lining the walls of the paranasal sinuses (Lundberg, 2008), it is not known whether the walls of cetacean air sacs can perform this function. It should be noted, however, that the pterygoid sacs have both an abundant vascular supply and an increased surface area because of their trabeculated surface, both of which may facilitate gas exchange.

Although terrestrial mammals may regulate gas concentrations in the upper respiratory tract (i.e., in the paranasal sinus walls), cetacean air sacs may have an analogous function in regulating gas concentrations—but in the lower respiratory tract. They appear to use the air sacs as a pump and/or reservoir to effectuate air movement, thereby increasing oxygenation in the lungs. Most mammals do not efficiently use inspired air, as only the oxygen that comes in contact with the alveolar tissue of the lungs can be extracted. Oxygen trapped in the respiratory dead space of the upper respiratory tract (nose, pharynx, larynx), trachea, and bronchi cannot reach the gas-exchanging thin epithelium of the alveoli, and therefore cannot be used to oxygenate blood. Interestingly, birds are one of the few animals that have optimized their respiratory system by connecting several accessory lungs in series and parallel, creating multiple pathways of air circulation (Bretz and Schmidt-Nielsen, 1971). This ensures that more oxygen is extracted with each breath, compared to using the traditional single pair of lungs with a shared entrance/exit. Cetaceans retain the traditional mammalian pattern of a single pair of lungs with a common entrance/exit for inspiration/expiration. However, like birds, they have changed...
the flow of air through the system to reduce respiratory dead space. Cetacean respiratory muscles (including muscles covering the air sacs) may act as a bellows, drawing and pumping air back and forth between the lungs and the various air sacs, creating turbulence, and mixing the oxygen-depleted air from the lungs with the oxygen-rich air that was trapped in the respiratory dead spaces of the air sacs and the upper respiratory tract, trachea, and bronchi. This activity would make more oxygen available to the lungs during breath-hold diving. This closed-circuit sequence of movements between the lungs and the air sacs allows the whale to conserve and recycle (shunt, capture, and reuse) air.

Unlike the paranasal sinuses, cetacean air sacs appear to have only a limited role in conditioning air (regulating humidity and temperature). As there are no turbinated bones to increase the surface area of the nasal cavity, it is unlikely that the cetacean air sacs contribute greatly to humidification or warming. Indeed, humidification is largely irrelevant for whales, as the air inhaled at the surface of the water is already humid. Warming during inspiration is also unlikely, as inhaled air is channeled quickly to the lungs. However, the volume of air retained in the sacs during submersion may become warmed by contact with the vasculature of the sac walls. It should be noted that warming is a relative phenomenon; the atmospheric air at the water’s surface is often warmer than the ambient water temperature.

**Vocal Functions**

Cetaceans’ air sacs may be used to increase vocal resonance in a manner similar to that often suggested for the paranasal sinuses of terrestrial mammals. Unlike the paranasal sinuses of terrestrial mammals, however, the cetacean air sacs may assist in actually generating underwater vocalizations, a function that may be unique to them. In order to generate sounds underwater, unique conditions must be accommodated, including maintaining airflow in a sealed space, utilizing a limited quantity of air, accounting for air volume changes related to changes in depth, and transferring sound generated in air to water.

Maintaining airflow for sound production is problematic while submerged because the respiratory tract must be closed to prevent drowning. Sound duration, which is dependent upon the movement of air causing structures to vibrate, would be quickly arrested in a closed system of fixed volume with rigid walls as this arrangement provides little or no air movement. Unlike the rigid paranasal sinus walls, the flexible walls of the air sacs can allow air to flow from a high pressure zone in the compressing lungs to a low pressure zone in the expanding sacs. However, when the pressure gradient between the lungs and sacs equalizes, air ceases to flow and sound production stops. A quick reversal of airflow may enable sound production to continue nearly uninterrupted, if sounds could be made during both ingressive (towards the lungs) and egressive (towards the nose/blowhole) air-flows.

Cetaceans are restricted to utilizing a limited quantity of air while vocalizing, as this precious resource cannot be readily replenished at depth. The cetacean air sacs appear to have a unique role in conserving air. Unlike the rigid walled paranasal sinuses, the flexible-walled air sacs can expand and contract (air capturing and recycling, previously described for optimizing respiratory function). Pumping air between the sacs and the lungs allows the same volume of air to be used repeatedly, allowing multiple vocalizations while submerged.

Air volume changes are related to changes in depth, and therefore ambient pressure, during diving. Thus, the limited volume of air available for sound production is further reduced while diving, as pressure increases with depth. The air sacs appear to have a unique function in compensating for this effect. They may provide cetaceans with an additional reservoir of air that is added to the diminished volume in the rest of the respiratory tract, ensuring that a sufficient amount remains for use in sound production at depth.

Transferring sound generated in air to sound propagated in water is a problem unique to an aquatic existence. Cetacean sounds are generated by pneumatically driven vibrations of upper respiratory tract structures (Cranford et al., 1996; Cranford, 1999; Aroyan et al., 2000; Reidenberg and Laitman, 2007). Although movement of air drives the system, it is the energy in the vibration of the adjacent tissues that must be transferred to water. The cetacean air sacs may function similarly to the laryngeal ventricles of terrestrial mammals by providing an air space adjacent to phonic tissues, allowing frictionless vibration of these structures. The sounds generated by these vibrations are directed through the head and out of the body into water. Air sacs, like paranasal sinuses, may resonate and help transmit sound vibrations through the cetacean head. For example, the mysticete laryngeal sac appears to serve as a transducer, transferring sound vibrations to and through the ventral throat skin to water (Reidenberg and Laitman, 2007). However, unlike paranasal sinuses, the specific shapes and positions of the air sacs may also serve to direct sound transmission via reflection at the density interface between air and tissue. For example, the concave shapes of premaxillary nasal air sacs enable reflection and direction of nasally generated sounds, while the position of the pterygoid nasal air sacs create an insulating barrier between sound generating and sound conducting structures (Cranford, 1999; Cranford et al., 2008a,b).

**Structural Functions**

Sinuses in terrestrial species occupy large areas of the skull that would otherwise be solid bone, thereby reducing skull weight. The air sacs of cetaceans may play a similar role, in that they also affect the overall density of the head. Air sacs may aid in buoyancy of the head, as their density is far less than that of bone. Static buoyancy control is accomplished by a balance between the negative buoyancy (high density) of bone and the positive buoyancy (low density) of the surrounding fatty tissues (e.g., blubber, melon, spermaceti organ, jaw fats). The ability to regulate buoyancy dynamically depends upon controlling a variable structure. Air sacs are ideally suited to perform this dynamic function due to their variable volumes. However, the ability to counter the weight of bone would be reduced at depth with air sac collapse. At depth, fat is a better substance than air for counteracting the weight of bone in maintaining neutral buoyancy because its volume is not affected by changes in pressure during diving and ascent. Therefore, cetacean
air sacs may have greatest buoyancy effect in facilitating ascent, as they will expand with decreasing pressure. In addition, their cranio-cervical locations would assist in a head-first orientation upon ascent, and maintaining a rest position that keeps the head, and therefore the blowhole, near the surface.

Diving Function

Acquisition of diving behavior was probably the greatest factor in both the disappearance of cranial sinuses and the appearance of extracrani al air sacs in cetacean evolution. The involvement of cetacean air sacs in protection from pressure changes during diving represents a unique function not found in terrestrial mammalian paranasal sinuses. The extracrani al sacs add more volume to the respiratory tract without increasing lung size or stressing rigid bony spaces under pressure. These pliable sacs provide expendable chambers that can be preferentially evacuated of air in order to maintain the changing pressure gradient during diving while preserving a needed volume of air elsewhere. As ambient pressure rises, air may be shunted out of the collapsing sacs and into connected essential spaces (e.g., middle ear), which might otherwise be reduced below a minimum critical volume for function at depth. The locations of the various air sacs appear related to the region they assist. As the nasal sacs are connected to the bony nares, their collapse may help preserve the integrity of the paired nasal cavities as they pass through the skull. Likewise, reduction of pterygoid sac volume may enable protection of the associated ear region, enabling the ossicles to vibrate within a middle ear air space maintained even at high pressures. Compression of the laryngeal sac(s) may prevent fracture of adjacent laryngeal and tracheal cartilages.

CONCLUSION

The paranasal sinuses are, as the title of this special issue so aptly highlights, the last frontier of craniofacial biology. Although their functions and evolutionary trajectory in terrestrial or avian forms remains both elusive and debated, their disappearance and eventual demise in aquatic mammals is even more unclear. The history of the sinuses in relation to both living cetaceans as well as the primitive fossil archaeocetes is perhaps most shrouded in mystery, because of our relative lack of information on their anatomy in general and of their embryology (and thus potential clues to homology) in particular. Although the disappearance—either gradual or rapid—of the paranasal sinuses in cetaceans and their relatives will assuredly continue to be a topic for investigation, this brief review has sought to focus upon the analogous functional relationships of the air sac system in cetaceans with terrestrial paranasal sinuses. While clearly not homologous to bony sinuses— at least from a dead-first orientation upon ascent—the cetacean sacs have incorporated functions subserved by paranasal sinuses, albeit in ways distinctive to the pressures and requirements of aquatic life. As with much of cetacean biology, our knowledge of function is limited to assumptions based upon our morphological deductions. So too is the case with the riveting and varied anatomy of this complex systems of sacs. Nevertheless, these “sisters of the sinuses,” by their location and structure, clearly play an integral role in cetacean anatomy and function. Just how integral, future research will be left to uncover.

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LITERATURE CITED


