CT STUDY OF ACOUSTIC SIGNAL PATHWAY THROUGH THE MIDDLE EAR OF THE SPERM WHALE (*PHYSETER MACROCEPHALUS*)

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ABSTRACT

The ability of marine mammals to adapt to an underwater acoustic environment is a remarkable evolutionary achievement. Of particular interest is how the middle and inner ear structures are modified relative to those of terrestrial mammals. For the large whale species there are very few anatomical descriptions of the ear, in part because of the large and dense bony structures involved. Because the sperm whale (*Physeter macrocephalus*) is listed as an endangered species, legal fresh specimens are rare. However old dry specimens can be found and we are able to present here a study of the periotic-tympanic bone complex of the sperm whale, using high resolution computer tomography (CT) imaging. We discuss the marine adaptations of the middle and inner ear structures.

SOMMAIRE

La capacité des mammifères marins de s'adapter à un environnement acoustique sous-marin est une réalisation évolutif remarquable. D'un intérêt particulier est de savoir comment l'anatomie de l'oreille moyenne et interne sont modifiés par rapport à ceux des mammifères terrestres. Pour les grandes espèces de baleines il y a très peu de descriptions anatomiques de l'oreille, en raison de la grandeur et densité des os impliquées. Parce que le cachalot (*Physeter macrocephalus*), est classé espèce menacée, les spécimens frais sont rares. Toutefois, nous sommes en mesure de présenter ici une étude du labyrinthe osseux temporelle du cachalot, en tomographie haute résolution. Nous discuterons les adaptations de l'anatomie de l'oreille moyenne et interne pour l'environnement marin.

1 INTRODUCTION

Whales are a part of the mammalian order Cetacea, which is subdivided into two suborders, Odontoceti and Mysticeti. Otodontocetes are toothed whales of which the sperm whale (*Physeter macrocephalus*) is the largest. Figure 1 outlines its main characteristics. Sperm whales are particularly vocal mammals and have a highly developed echolocation ability that makes use of broadband click patterns (codas) that pulse through water to locate food, navigate, and socialize (*e.g.* Madsen *et al.* 2002; Rendell and Whitehead, 2003). Click patterns appear to vary according to the group composition and activity. Several different vocalization patterns have been identified: i) vocalization associated with diving and feeding (echolocation clicks, creaks, and trumpet) and ii) vocalization associated with socializing (chirrups and squeals). The importance of echolocation for socialization and survival in the limited visibility in the ocean depths, stresses the need for a highly developed auditory system that can effectively detect and interpret sounds conducted through water.
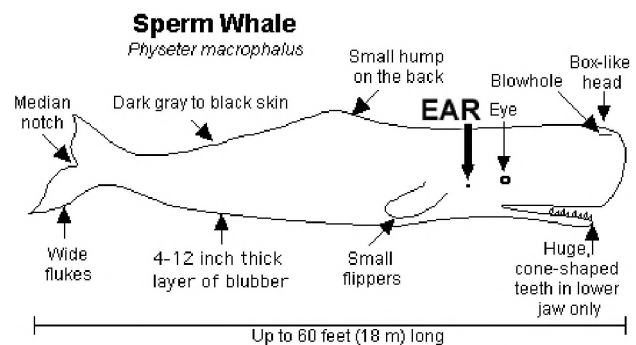

Figure 1. General characteristics of *Physeter macrocephalus*

The auditory systems of whales are thus highly evolved and essentially act as the primary sensory organ of cetaceans. As the whale has evolved from a land to marine mammal, the audio-vestibular system has undergone evolutionary changes to adapt to this new environment (Nummela *et al.* 2004; 2007). Many of these anatomical evolutions have been described for various whale types, however, to date we have not found any descriptions of the middle ear anatomy of *Physeter macrocephalus*. There are CT scan studies in a number of whale species (e.g. Ketten,

1997) including fossil specimens (e.g. Stokstad, 2003) but few have examined the middle ear. There is much interest in the sound transmission within the bulbous nose of the sperm whales (e.g. Cranford, 1999; Mohl 2001), however there are no detailed descriptions or radiological studies of its middle ear as recently noted by Cranford et al. (2010). In the present study we examine the structure and function of the auditory and vestibular system of the sperm whale using high resolution CT imaging of two temporal bone specimens.

2 METHODS

2.1. Materials and DNA sequencing

Sperm whales are protected under the Endangered Species Act and the Marine Mammal Protection Act, thus fresh specimens are rare. We obtained old, left and right petrous temporal bones from the estate of whaling station manager. The transport and importation of the bones for academic study was approved by an officer of Environment Canada (Canadian Wildlife Service). To confirm species identification, DNA matching was carried out. Thus, DNA nucleic acid was extracted from bone powder samples and DNA sequencing information was used to ascertain accurate species information. This was carried out in the Ecology & Evolutionary Biology unit of University of Toronto, based at the Royal Ontario Museum. Ten sequences producing significant alignments were identified, with the closest match being *Physeter macrocephalus.*

2.2. CT Scanning

Computer tomography (CT) was used to identify the structural components of the bones. A General Electric (GE) 1.5 Tesla scanning system was used to examine the bones. The very dense nature of the specimens was a challenge but we could resolve 0.625 mm slices with a spatial image of 512 x 512 (approx. pixel size = 0.04mm). Using Advantage Workstation software, 3-D reformats were created from axial slices and differential bone densities were used to identify large structures housed within the dense bone. In this study the gross specimens and CT images were correlated with anatomy of the whale petrous temporal bone previously described in the literature, as well as in relation to more familiar human temporal bone structures.

3 RESULTS

Photographs of right and left temporal bone specimens of *Physeter macrocephalus* are shown in figure 2, with the periotic and tympanic bones of the T-P complex identified.
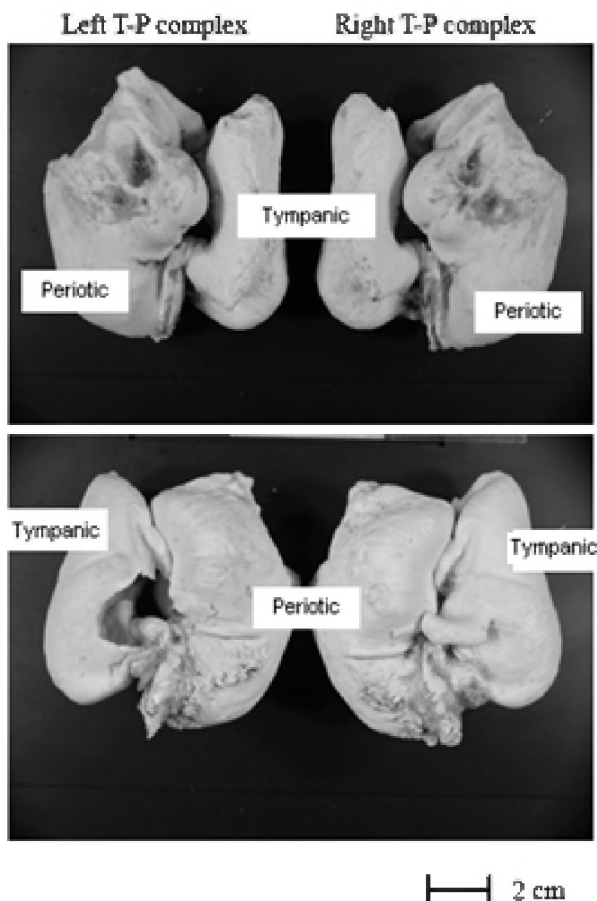

Figure 2. Gross images of the left and right petrous temporal bones of a sperm whale (*physeter macrocephalus)*. Upper panel: Medial view. Lower panel: Lateral view.
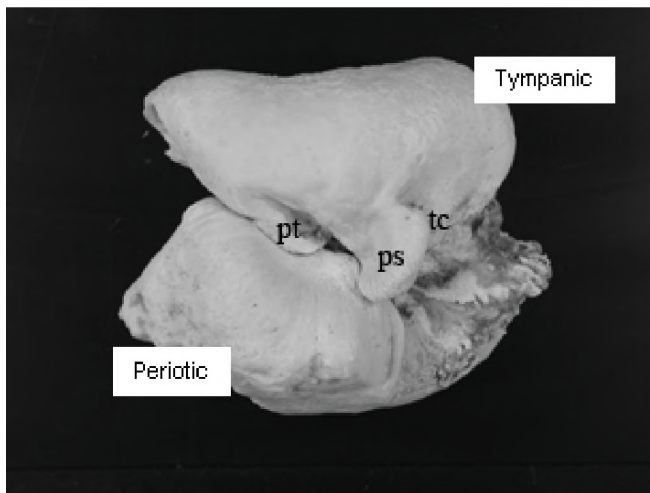

Figure 3. Right temporal bone showing structures that link tympanic and periotic segments of the T-P complex. pt: processus tubarius; ps: processus sigmoideus; tc: tympanic conus.
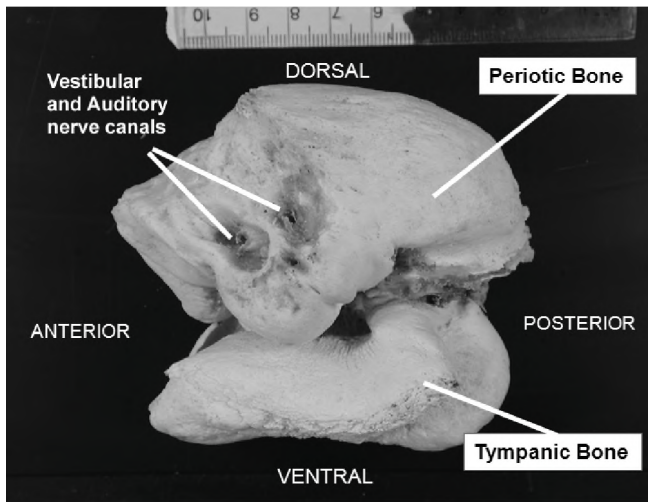
Figure 4. Details the surface anatomy of the right temporal bone as viewed from the intra-cranial side, showing internal auditory and vestibular nerve canals. A mm ruler scale is shown.
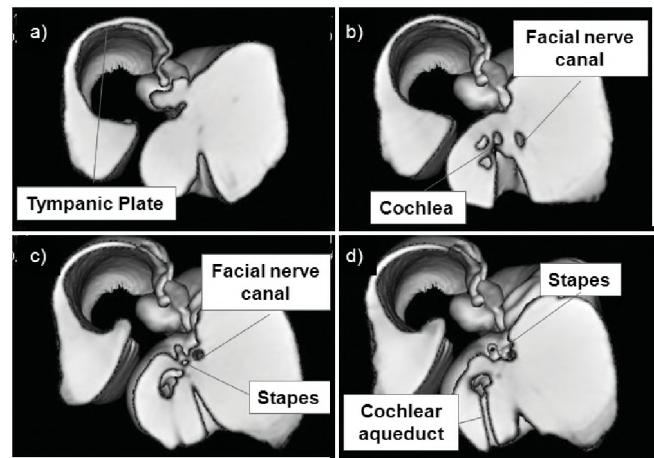

Figure 5. CT sections of the left petrous temporal bone from anterior to posterior. The following features can be noted: In (a) connection of the malleus head via processus gracilis (bony ridge) and tympanic plate (thin portion of ventrolateral wall of tympanic bulla) to the processus tubarius (pt). In (b) connection of the T-P complex via processus petrosus (pp). Cochlea, cochlear canal, and facial nerve canal (VII) can be identified in the periotic bone. In (c) the stapes sits on the oval window, with the facial nerve superior. In (d) note the cochlear aqueduct posterior to cochlear canal.

As shown in fig. 3, there is a connection between the tympanic and periotic bones via the processus tubarius (pt) anteriorly (an accessory ossicle) and more posterior there is the processus petrosus (not clearly visible). In between these processes lies the processus sigmoideus (ps), the very specific anatomical identifier for all whale species. Posterior to this is the tympanic conus, a calcified funnel that has a ligamentous attachment to the malleus. On the lateral aspect of the T-P complex (fig. 4), the large cochleo-vestibular nerve canal is observed.

CT imaging of the T-P complex from anterior to posterior is shown in figs. 5a-d. The tympanic plate (tp) is the thin portion of the ventrolateral wall of the tympanic bone which is connected via the processus gracilis (pg), a bony ridge, to the malleus (anterior portion of pg). The 'fixed' malleus is then connected to the oval window via the ossicular chain (not pictured here in continuity). The anterior (processus tubarius) and posterior (processus petrosus) T-P connections are again visualized in these serial CT sections (surface cuts through 3D images). The cochlea and the cochleo-vestibular nerve canal are noted within the periotic bone, as are the facial nerve canal and the cochlear aqueduct.

Using this CT imaging of the T-P complex, direct and indirect connections via the processus tubarius, processus petrosus, and processus gracillus could be identified. In addition the tympanic plate and tympanic conus (an evolutionary substitute for the tympanic membrane) were identified in their attachments to the malleus. Unfortunately our specimens were both lacking in a complete ossicular chain, and therefore we are unable to comment on the extent of fusion of the ossicular chain, or its connections to the periotic bulla. However, as shown in Figure 6 (particularly in the enlargement inset) we were able to identify the stapes superstructure positioned on the oval window.

By making a 3-D reconstruction of the CT images we were able to picture (figure 7) the cochlea and its related structures deep within the dense periotic bone. The spiral cochlear structure is clearly seen as is the large cochleo-vestibular nerve canal, the cochlear aqueduct and facial nerve canal. Interestingly the cochlear apex points down with the round window posterior and medial to the oval window, as found in some other whale species (e.g. Ketten, 1997; Whitlow and Ketten, 2000).

With the CT image resolution of the present study we were able to identify the distinct grouping of vestibular organs (otoliths and semicircular canals). The size of the semicircular canals in cetaceans is considerably reduced compared with most other mammals, and this was the case in our sperm whale specimens. We found the diametric extent of the semi-circular canals to be approximately 10 mm. This is consistent with the small sized vestibular apparatus seen in other cetacean species and supports the evolutionary adaption of cetaceans to marine activity. The vestibular contribution of this organ is to provide gravity and linear acceleration cues, but with limited input for rotation and 3-D acceleration (e.g. Van Bergeijk, 1967; Ketten, 1997). There were no obvious aberrant structures identified in our petrous temporal bone specimens.

4 DISCUSSION

4.1 Transmission of acoustic signals to the tympano-periotic complex

One of the obvious evolutionary changes of the odontocete auditory system in the move from land to marine mammal is the loss of the external pinna and external auditory canal,

with only a dimple or residual canal remaining that has no contact with the middle ear (Whitlow and Ketten, 2000). Sound is therefore transmitted to the middle ear via a large mandibular fat pad and is then received by the lateral wall of the temporal bone, known (and as described in this paper) as the tympano-periotic (T-P) complex. The T-P complex is composed of two connected bones: 1) the dorsal periotic bone, which encloses the inner ear and functionally connects to the brain via the vestibulo-cochlear nerve and 2) the ventral, bowl shaped, tympanic bone. This is often described as the tympanic bulla. It encloses the middle ear space and ossicular chain, and is in direct contact with the surrounding soft tissues. The T-P complex is isolated from the rest of the skull by surrounding air sinuses in a peri-bullar cavity and is suspended from the walls by ligamentous attachments (Ketten, 1997).
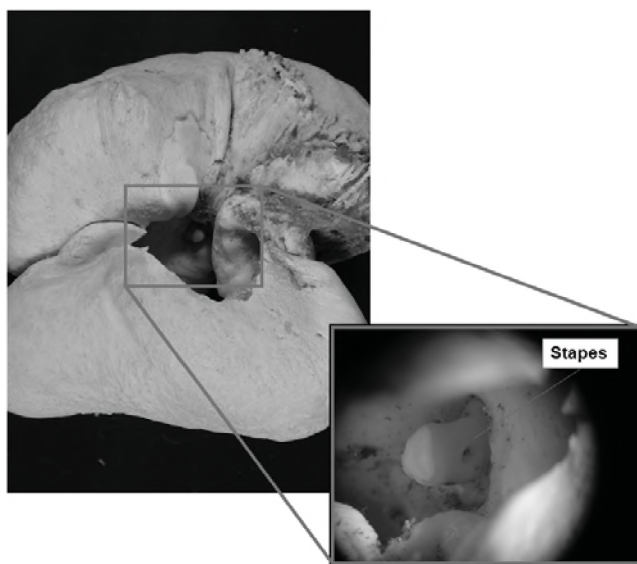

Figure 6. Photographic imaging of the T-P complex with an enlargement showing the stapes present on the stapes footplate and oval window of the periotic bone.

4.2 Ossicular transmission of acoustic signals from the tympanic plate to the cochlea

Once sound is transmitted via the mandibular fat pad, it vibrates the tympanic plate which is found on the ventrolateral wall of the tympanic bone. The acoustic signal is then transmitted by the ossicular chain, perhaps via the unusual impedance matching model proposed by Hemila et al. (1999). This transmission scheme suggests that increases in both signal amplitude and velocity occur as it travels from the tympanic plate, along the ossicular chain, to the oval window. The malleus is connected to the tympanic plate by an anterior bony ridge known as the processus gracilis which transmits sound vibration to the malleus-incus complex. The head of the malleus rests against the periotic bone while the other end connects to the incus and stapes. Vibration of the malleus causes the malleus to rotate around an axis that directs sound down the malleus-incus

complex to the stapes supra-structure and footplate. The acoustic signal is then transmitted from the footplate across to the cochlea housed in the periotic bone (Hemila et al., 1999; Nummela et al., 2004). The cetacean cochlea has the same fundamental organization as other mammalian inner ears and is connected to the brain via the large cochleo-vestibular nerve.
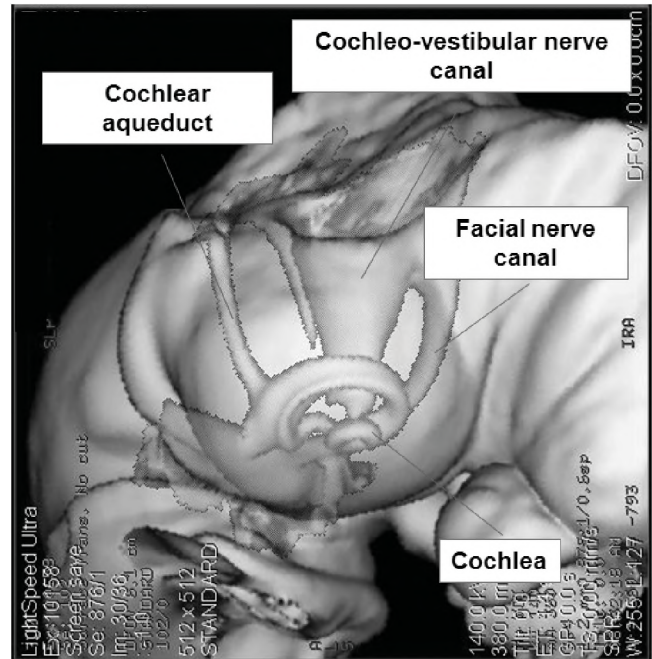

Figure 7. Three dimensional CT reformat of the periotic bone showing the cochlea and associated cochlea-vestibular nerve canal. The cochlear aqueduct and facial nerve canal are clearly resolved.

4.3 Vestibular function

The vestibular system of cetaceans has also undergone significant evolutionary changes with the conversion from land to marine mammal. These alterations result from changes in head movement, body movement, and gravitational forces. In an aquatic environment, cetaceans were freed from gravitational forces and increased their acrobatic abilities. In addition to this, their streamlined bodies, with fused cervical vertebrae and limited neck mobility, limited the need for reflex stabilization of the head. There is also likely a reduced need for vestibulo-ocular reflexes. Therefore, over time the size of the semi-circular canals of cetaceans has drastically decreased. In fact, their semi-circular canal size (corrected for body mass) is three times smaller than in other mammals. In addition to the reduced vestibular reflex requirements out lined above, it is also widely assumed that the small canal size acts to reduce the sensitivity of cetacean vestibular responses to high levels of uncompensated angular motion, thereby preventing overstimulation (Spoor et al. 2002).

5 SUMMARY

The anatomy of the middle ear has been well described for many cetacean species, however few specific descriptions exist for the sperm whale (*Physeter macrocephalus*). We were fortunate to acquire dry, left and right temporal bone specimens and confirm species by DNA analysis. Using modern CT scan technology we were able to identify and describe important anatomical features.

ACKNOWLEDGEMENT

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