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Reduction of olfactory and respiratory turbinates in the transition of whales from land to sea: the semiaquatic middle Eocene Aegyptocetus tarfa

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Abstract

Ethmoturbinates, nasoturbinates, and maxilloturbinates are well developed in the narial tract of land-dwelling artiodactyls ancestral to whales, but these are greatly reduced or lost entirely in modern whales. Aegyptocetus tarfa is a semiaquatic protocetid from the middle Eocene of Egypt. CT-scans of the skull show that A. tarfa retained all three sets of turbinates like a land mammal. It is intermediate between terrestrial artiodactyls and aquatic whales in reduction of the turbinates. Ethmoturbinates in A. tarfa have 26% of the surface area expected for an artiodactyl. These have an olfactory function and indicate that early whales retained a sense of smell in the transition from land to sea. Maxilloturbinates in A. tarfa have 6% of the surface area expected for an artiodactyl. These have a respiratory function and their markedly reduced size suggests that rapid inhalation and exhalation was already more important compared to warming and humidifying air, in contrast with extant land mammals. Finally, the maxilloturbinates of A. tarfa, although greatly reduced, still show some degree of similarity to those of artiodactyls, supporting the phylogenetic affinity of cetaceans and artiodactyls based on morphological and molecular evidence.

Keywords: Archaeoceti, Protocetidae, Artiodactyla, Eocene, turbinates, CT-scans.

Introduction

The nasal chamber of mammals typically contains three sets of epithelium-covered bony plates or turbinates. Posterior turbinates associated with the ethmoid bones, the ethmoturbinates, have an olfactory function (Van Valkenburgh et al. 2004, 2011; Pihlström, 2008). Anterior turbinates associated with the maxillary bones, the maxilloturbinates, have a respiratory function: they warm and humidify air as it is inspired, and recover heat and water from air as it is expired (Hillenius, 1992, 1994; Van Valkenburgh et al. 2004; Crompton et al. 2015). Dorsal turbinates associated with the nasal bones, the nasoturbinates, are located more centrally in the nasal cavity, above and behind the maxilloturbinates and above and in front of the ethmoturbinates. The function of the nasoturbinates is not fully understood although it seems that they have a predominantly olfactory function (Hillenius, 1982; Van Valkenburgh et al. 2004, 2011; Harkema et al. 2006).

Turbinates are present and important in almost all mammalian groups, but extant aquatic Cetacea are an exception. Modern odontocetes have no turbinates at all and modern mysticetes preserve only rudimentary ethmoturbinates (Godfrey et al. 2012; Godfrey 2013; Berta et al. 2014; Buono et al. 2015). The fossil record shows that whales evolved from terrestrial Artiodactyla (Gingerich et al. 2001; Thewissen et al. 2007; Uhen, 2010) and several genomic studies identify Hippopotamidae as the closest extant relatives of cetaceans (Geisler & Theodor, 2009; Zhou et al. 2011; Hassanin et al. 2012). Gatesy et al. (2013) analysed molecular and paleontological data and reinforced previous molecular studies by recognising Hippopotamus within Artiodactyla as the extant sister group of whales. Artiodactyls all have the three sets of turbinates, ethmoid, nasal, and maxillary, well developed (Hillenius, 1992; Clifford & Witmer, 2004a, 2004b), and

turbinates were clearly reduced and lost as whales evolved to become fully aquatic (Berta et al. 2014).

Although the turbinates are thin, delicate bone structures that lie within the nasal cavity of a skull, making them difficult to see, they are preserved in some Eocene archaeocetes, the stem group for cetaceans. The first description of turbinates in an archaeocete was by Stromer (Stromer, 1903) in the late Eocene basilosaurid Saghacetus osiris. Ethmoturbinates are preserved in Stromer's specimen as delicate laminae of bone encased in fine sediment filling the nasal capsule. Uhen (2004) observed similarly preserved ethmoturbinates forming a bony labyrinth in another late Eocene basilosaurid, Dorudon atrox, where the ethmoturbinates extend as far anteriorly as the mesethmoid supporting them. Ethmoturbinates were identified in a specimen attributed to the middle Eocene remingtonocetid Andrewsiphius sp. (Pihlström, 2008; Thewissen & Nummela, 2008), and a ridge for possible attachment of maxilloturbinates was identified in Remingtonocetus (Bajpai et al. 2011). Ethmoturbinates have also been reported in the middle Eocene protocetids Artiocetus clavis (Fahlke at al. 2011), Aegyptocetus tarfa (Bianucci & Gingerich, 2011), and a protocetid of unknown genus and species (Godfrey et al. 2012). Neither nasoturbinates nor maxilloturbinates were observed in these specimens.

The purpose of this study is to reconstruct the three-dimensional size and shape of turbinates in the nasal cavity of the holotype of Aegyptocetus tarfa, and to comment on their function and stage of reduction relative to artiodactyls as land mammals and to extant cetaceans as fully aquatic mammals. The holotype of A. tarfa is exceptionally well preserved. It was found in fine-grained marbleized limestone from the middle Eocene of Egypt after it was exported commercially to Italy, where the limestone was cut into slabs of decorative facing stone, revealing the fossil. The specimen, a partial skeleton, is preserved in the Museo di Storia

Naturale dell'Università di Pisa (MSNUP). Bianucci and Gingerich (2011) described ethmoturbinates visible on the surface of one of the limestone slabs. Here we use Computerized Axial Tomography (CT) to study the full set of turbinates in A. tarfa. Nasoturbinates and maxilloturbinates are present in A. tarfa in addition to ethmoturbinates, which enables the first quantitative description of turbinate surface areas within an archaeocete and the first quantitative comparison with artiodactyls as representatives of the land-mammal ancestry of whales.

Materials and methods

We analysed the skull of the holotype of Aegyptocetus tarfa (MSNUP I15459) and, for comparison, skulls of the following five extant artiodactyls in the zoological collections of the MSNUP:

- Alcelaphus buselaphus buselaphus (Bovidae: African hartebeest) (MSNUP C1343)
- Boselphus tragocamelus (Bovidae: Indian nilgai) (MSNUP C1423)
- Camelus dromedarius (Camelidae: Arabian camel) (MSNUP C1435)
- Hippopotamus amphibius (Hippopotamidae: African hippopotamus) (MSNUP C228)
- Sus scrofa (Suidae: Eurasian wild pig) (MSNUP C1418)

Specimens were chosen to represent a range of shape and size variation from turbinates in skulls of artiodactyls comparable in size to A. tarfa. All skulls were CT-scanned in Azienda Ospedaliero-Universitaria di Pisa. The machine used was a GE LightSpeed RT 16, with a slice thickness of 1.25 mm and spacing between slices of 0.625 mm. CT-scans were analysed with open-access Mango software for medical image visualization (Multi-image Analysis GUI; http://rii.uthscsa.edu/mango/). Mango was also used to create virtual 3D models of turbinates

and to calculate their surface area. The skull of *A. tarfa* is weakly asymmetrical due to its clockwise torsion (Bianucci & Gingerich, 2011), so turbinates were mapped on both sides. Artiodactyl skulls are bilaterally symmetrical, and mapping was confined to turbinates of the left side of the skull (Ranslow et al. 2014). Surface area measurements for artiodactyls were then doubled to represent both left and right sides.

There are two sources of uncertainty in measurements of the fossil *A. tarfa*. Differences in bone and sediment density enabled reconstruction of the three-dimensional shape of turbinates when surrounded by calcareous matrix, but the resolution was lower than for skulls of extant artiodactyls with empty nasal cavities. In addition, it was necessary to reconstruct turbinates damaged when the *A. tarfa* skull entombed in matrix was cut into slabs (Bianucci & Gingerich, 2011). Uncertainty of measurements in the extant artiodactyls was due to breakage of the thinnest laminae of bone. All these sources of uncertainty cause turbinate areas to be similarly underestimated, meaning comparisons should still be reliable within and between taxa.

The relative sizes of turbinates in *A. tarfa* were compared to those of artiodactyls in three ways. First, we compared the area of the ethmoturbinate surface (ETS), the area of the nasoturbinate surface (NTS), and the area of the maxilloturbinate surface (MTS), to the total turbinate surface (TTS). In the second comparison we measured the size of the turbinate chamber surface (TCS) within the nasal chamber of *A. tarfa*. This measured value of TCS was then compared to TCS for an animal the skull length, bizygomatic skull width, and body weight of *A. tarfa*, based on TCS measured in the five extant artiodactyls. Turbinates do not fill the whole nasal chamber. The anterior end of the turbinate chamber coincides with the anterior extremity of the maxilloturbinates, and its posterior end coincides with the ethmoidal portion of the cribriform plate (excluding the maxilla). In this comparison the natural logarithm (ln) of the square root of

TCS was regressed on ln cranial length (cm), on ln cranial width (cm), and on ln cube root of body weight (kg) for the artiodactyls. TCS was measured using the same methods as those described above for calculating the surface area of turbinates. Skull length and width were measured on the skulls used for CT-scanning. The body weight for A. tarfa is that estimated by Bianucci & Gingerich (2011). Body weights for the artiodactyls were estimated from a regression of body weight on skull length (Janis, 1990).

Finally, we compared the surface area for each set of turbinates, ETS, NTS, and MTS, to the area expected, based on extant artiodactyl, for the set given the associated TCS. Measured values for ETS, NTS, and MTS in A. tarfa were compared to the values expected from regressions of artiodactyl ETS, NTS, and MTS on TCS.

Results

CT-scans show that the turbinate sets in Eocene A. tarfa are slightly asymmetrical (Fig. 1A,B). This feature is possibly related to the clockwise torsion of the rostrum (Bianucci & Gingerich, 2011), a genuine anatomical feature that has also be observed in other archaeocetes (Fahlke at al. 2011; Fahlke and Hampe, 2015). This hypothesis is supported by the fact that, in A. tarfa, the maxilloturbinates, which extend more anteriorly in the rostrum than ethmoturbinates and nasoturbinates, exhibit the greater degree of asymmetry (i.e., the right maxilloturbinates are slightly wider transversely than the left maxilloturbinates). The ethmoturbinates, like those in other mammals (Hillenius, 1994), are convoluted and densely packed in the olfactory recess. Left and right nasoturbinates are elongated, narrow, and, for most of their length, a single laterally-concave lamina of bone. Posteriorly a second medially-concave plate appears, giving the nasoturbinates in this region a more tubular appearance. Left and right maxilloturbinates are small compared to those of modern artiodactyls (Fig. 1C–H), and the maxilloturbinates occupy a

relatively small portion of the nasal chamber. They do not extend anteriorly beyond the nasoturbinates. Their morphology is simple: the most anterior part of the lamina is hook-shaped and concave dorsally and laterally (Fig. 2A). There is a narrow downward-facing lamina in the middle part, and the posterior part of the lamina is again hook-shaped.

Maxilloturbinates of A. tarfa and the five artiodactyls studied for comparison are illustrated in red in the cross sections of skulls in Fig. 2. All of the artiodactyls have elongated, double (lower and upper) scroll-shaped maxilloturbinates without projecting branches (Fig. 2B–F). The upper scroll is more developed and convoluted than the lower scroll. These features, which have been observed in all specimens, are typical of and exclusive to artiodactyls (Hillenius, 1992). For example, the maxilloturbinates of Equus caballus (Perissodactyla) have a single high and narrow scroll; also, they show a greater thickness than the maxilloturbinates of artiodactyls (Arencibia et al. 2000: figures 7–8, where the maxilloturbinates are named "ventral conchal bulla"). Carnivora have richly-branching double-scroll-shaped maxilloturbinates (Van Vakenburgh et al. 2004). The maxilloturbinates of A. tarfa clearly differ from those of carnivores in lacking the external branches, while they exhibit some affinities with those of artiodactyls. Indeed, the maxilloturbinates of A. tarfa could be considered a simplified version of the artiodactyl double scroll (Fig. 2A). The upper scroll in A. tarfa is reduced to only one half-round. The lower scroll has almost disappeared but there is a small branch at mid- length of the maxilloturbinates suggesting a lower scroll. Similarities to Equus caballus are weaker because the latter has the lower scroll completely missing (Arencibia et al. 2000).

Measurements for each set of turbinates are given in Table 1. When we compare the ETS, NTS, and MTS areas for artiodactyls to their sum, TTS, we find modal proportions of 0.42, 0.14, and 0.41, respectively. These proportions are 0.61, 0.20, and 0.15 in A. tarfa, indicating that A. tarfa

has more of its turbinate area devoted to ethmoturbinates than expected from comparison to artiodactyls, and less devoted to maxilloturbinates.

We can compare turbinate size in a different way by asking how the area of TCS compares to body size measured by skull length, skull width, or body weight. A. tarfa has a skull length of 68 cm (table 1). Regression of ln √TCS on skull length for artiodactyls (Fig. 3A) yields an expected TCS for A. tarfa of 195604 mm^2, corresponding to ln square-root value of about 6.092. The observed TCS for A. tarfa is 64953 mm^2, corresponding to ln square-root value of 5.541. Thus, the residual for length (observed-minus-expected) is calculated to be −0.549 and the corresponding proportion 0.333. In the previous paragraph we found that TCS of A. tarfa is about 33% as large as expected for an artiodactyl of the same skull length.

Similar calculations show that TCS for A. tarfa is about 57% as large as expected for an artiodactyl of the same skull width, and about 63% as large as expected for an artiodactyl of the same body weight. Variation in the residuals and proportions observed here are probably related to differences in skull shape for the species compared. Taking the median, we conclude that the area of TCS is about 57% as large as expected in an artiodactyl of the same size.

Another way to compare turbinate size is to compare the turbinate area observed in A. tarfa with the turbinate area expected for an artiodactyl of the same TCS. The comparison for ethmoturbinates is shown in Fig. 3B, where the observed-minus-expected residual for ln ETS is −0.76, and ETS itself is 0.47 the size expected for TCS observed in A. tarfa. Similar calculations for nasoturbinates and maxilloturbinates are shown in Fig. 3C–D, where the residuals are −0.78 and −2.30, respectively, and the corresponding proportions for NTS and MTS are 0.46 and 0.10 the size expected for TCS observed in A. tarfa. Combining all observations in Fig. 3 by multiplying each proportion in Fig. 3b-d by 0.566 from Fig. 3A, ETS and NTS for A. tarfa are

each about 26% of the size expected for an artiodactyl, and MTS for A. tarfa is about 6% of the size expected for an artiodactyl.

Discussion

Morphofunctional considerations

The general trend of reduction of turbinate size from artiodactyls to extant cetaceans (Berta et al. 2014) is supported by three-dimensional reconstruction of the turbinates of A. tarfa and comparison of their size and shape to the turbinates of extant artiodactyls. Ethmoturbinates, nasoturbinates, and maxilloturbinates are all retained in A. tarfa, but all are reduced in size compared to expectation based on artiodactyls. As calculated above, ETS and NTS are each about 26% of the area expected for an artiodactyl, and MTS is about 6% of the expected size. This atrophy in A. tarfa cannot have been caused by post-mortem breakage because observations made on cross sections of the skull before reassembly showed excellent preservation of the turbinates (Bianucci & Gingerich, 2011: figures 4-5). Further, three-dimensional reconstruction of the A. tarfa turbinates shows a close correspondence of turbinates on the left and right sides of the skull. Thus, we consider the turbinates of A. tarfa, to be complete (except for the parts destroyed by the cuts) and regard the reconstruction shown in Fig. 1A–B as reliable.

An ethmoturbinate and nasoturbinate reduction to 26% of expected value in A. tarfa is relatively easy to explain. Terrestrial mammals use olfaction to locate food and to communicate in social interactions (Hillenius, 1992, 1994; Van Valkenburgh et al. 2011). A. tarfa was a semiaquatic predator, hunting in water like other protocetids (Gingerich, 2003; Bianucci & Gingerich, 2011). Mammalian olfactory receptors differ from those of fishes and amphibians and do not work well in water (Pihlström, 2012), so olfaction would have had limited use for locating prey. A. tarfa,

like other protocetids, was considered able to hear high sonic frequencies, facilitating predation on sound-producing fish (Bianucci & Gingerich, 2011; Fahlke et al. 2011), although a recent study based on the cochlear morphology questioned specialization for ultrasonic hearing among archaeocetes (Mourlam & Orliac, 2017).

Reduction of ethmoturbinates is also observed in pinnipeds. Van Valkenburgh et al. (2011), citing Laska (2005), interpreted ethmoturbinate reduction in pinnipeds to reflect a reduction in olfactory acuity, the range of smells that can be detected, but not olfactory sensitivity or discrimination within a narrower range. Based on this reasoning, *A. tarfa* was probably able to detect and distinguish a restricted range of smells when on land or on the sea surface. This would be important for mate identification and calf recognition.

Near complete atrophy of maxilloturbinates in *A. tarfa* is more difficult to explain. Maxilloturbinates play an important role in heat and water retention in modern mammals. Van Valkenburgh et al. (2011) found the surface area of ethmoidal or olfactory turbinates to be about three times greater than the surface area of maxillary or respiratory turbinates in terrestrial carnivores, and the opposite to be true in aquatic carnivores. Pinnipeds, with marine adaptations paralleling those of protocetids, have maxilloturbinates with a greater surface area than their ethmoturbinates (Van Valkenburgh et al. 2011), which is the opposite of what we see in comparing *A. tarfa* to artiodactyls or to terrestrial carnivores (Van Valkenburgh et al. 2011). Modern cetaceans have a smooth-walled narial tract lacking respiratory turbinates, which Reidenberg & Laitman (2008) consider an advantage for rapid friction-free exchange of large volumes of air during brief breathing events at the sea surface. Rapid transfer of air during breathing may have been important for protocetids like *A. tarfa*. Middle Eocene oceans were 6–8 °C warmer than oceans today (Zachos, 2001) and the relatively constant humidity of an

evaporative environment at the sea surface would reduce the need for both heat and water retention. The extreme reduction of maxilloturbinates could also be a consequence of the moderate posterior shift of the position of the external bony nares observed in A. tarfa and other protocetids. In fact, such a shift reduced the length of the nasal passage. The retention of reduced turbinates in some archaic odontocetes displaying limited telescopy and external bony nares that still do not reach the vertex of the skull (Churchill et al. 2018) lends some support to this hypothesis.

Phylogenetic considerations

The comparison of turbinate cross sections in Fig. 2 shows that maxilloturbinates of A. tarfa, although greatly reduced, still show some similarity to those of artiodactyls, supporting the phylogenetic affinity of cetaceans and artiodactyls based on other evidence (Gingerich et al. 2001; Thewissen et al. 2007; Uhen, 2010). Morphological differences between the maxilloturbinates of cetaceans and artiodactyls (both having the typical double scroll morphology) compared to perissodactyls (with only an upper scroll) and carnivores (where branching turbinates replace scrolls) are consistent with the phylogenetic distance between these three mammalian clades.

Molecular analyses place Hippopotamidae, within extant Artiodactyla, as the closest living relative of Cetacea (Geisler & Theodor, 2009; Zhou et al. 2011; Hassanin et al. 2012; Gatesy et al. 2013), with the divergence time of hippos and cetaceans estimated at 52.4 Ma (Orliac et al. 2010). Maxilloturbinates of Hippopotamus amphibius are most similar to those of other artiodactyls and do not show any special similarity to maxilloturbinates of A. tarfa (Fig. 2). This is not surprising considering the great reduction of maxilloturbinates in A. tarfa.

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Author contributions

EP and GA analysed and processed the CT-scan images, EP, GB, and PDG, wrote the paper, GB supervised the project, all authors discussed the paper and gave the final approval for publication.

Competing interests

We declare we have no competing interests.

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Figure captions

Figure 1 Three-dimensional CT-scan reconstruction of skulls and related turbinates in dorsal and lateral view. (A,B) Aegyptocetus tarfa, MSNUP I15459. (C,D) Alcelaphus buselaphus, MSNUP C1343. (E,F) Camelus dromedarius, MSNUP C1435. (G,H) Boselaphus tragocamelus, MSNUP C1423. Scale bar is 10 cm.

Figure 2 Left and right maxilloturbinates (red) and nasoturbinates (blue) in CT-scan cross sections of skulls studied here. (A) Aegyptocetus tarfa, MSNUP I15459. (B) Alcelaphus buselaphus, MSNUP C1343. (C) Sus scrofa, MSNUP C1418. (D) Hippopotamus amphibious, MSNUP C228. (E) Camelus dromedarius, MSNUP C1435. (F) Boselaphus tragocamelus, MSNUP C1423. All sections were taken at the anteroposterior midpoint of the maxilloturbinates and all sections are reduced to the same height. Note the small size and simple structure of maxilloturbinates in A. tarfa compared to those of artiodactyls.

Figure 3 Turbinate size observed in middle Eocene Aegyptocetus tarfa (solid symbols) compared to turbinate size in five species of extant artiodactyls (open symbols). (A) allometric scaling of TCS with length, width, and the cube-root of body weight. (B) allometric scaling of ETS with TCS. (C) allometric scaling of NTS with TCS. (D) allometric scaling of MTS with TCS. Dashed lines are projections showing the distance between observation and expectation. 'Proportion' is the residual expressed as a ratio of observation to expectation. 'Combined' is the median proportion in (A) multiplied by the proportion in (B), (C), or (D). Measurements plotted here are listed in Table 1. (Online version in colour.)

Table 1 Measurements of body size, turbinate chamber surface area, and ethmoturbinate, nasoturbinate, and maxilloturbinate surface areas in comparative Artiodactyla and the middle Eocene archaeocete Aegyptocetus tarfa. Right-hand columns list ETS, NTS, and MTS as a proportion of TTS. Medians are in bold-face type.

Genus and species	Cranial length (cm)	Cranial width (cm)	Body weight (kg)	TCS (mm^2)	ETS (mm^2)	NTS (mm^2)	MTS (mm^2)	TTS (mm^2)	ETS/TTS	NTS/TTS	MTS/TTS
ARTIODACTYLA											
Boselphus tragocamelus	38.0	15.4	227	63813	25262	12532	53745	91540	0.28	0.14	0.59
Alcelaphus buselaphus	34.6	11.5	309	63355	30424	19355	44117	93896	0.32	0.21	0.47
Hippopotamus amphibius	63.6	37.4	1532	177606	114138	32039	102397	248574	0.46	0.13	0.41
Camelus dromedarius	34.0	15.0	260	51298	55753	11232	42677	109662	0.51	0.10	0.39
Sus scofa	30.9	15.6	122	52376	22274	11011	19513	52798	0.42	0.21	0.37
Medians:	**34.6**	**15.4**	**260**	**63355**	**30424**	**12532**	**44117**	**93896**	**0.42**	**0.14**	**0.41**
ARCHAEOCETI											
Aegyptocetus tarfa	**68.0**	**27.0**	**650**	**64953**	**17010**	**6638**	**4158**	**27806**	**0.61**	**0.24**	**0.15**