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Low-frequency hearing preceded the evolution of giant body size and filter feeding in baleen whales

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Living baleen whales (mysticetes) produce and hear the lowest-frequency (infrasonic) sounds among mammals. There is currently debate over whether the ancestor of crown cetaceans (Neoceti) was able to detect low frequencies. However, the lack of information on the most archaic fossil mysticetes has prevented us from determining the earliest evolution of their extreme acoustic biology. Here, we report the first anatomical analyses and frequency range estimation of the inner ear in Oligocene (34–23 Ma) fossils of archaic toothed mysticetes from Australia and the USA. The cochlear anatomy of these small fossil mysticetes resembles basilosaurid archaeocetes, but is also similar to that of today's baleen whales, indicating that even the earliest mysticetes detected low-frequency sounds, and lacked ultrasonic hearing and echolocation. This suggests that, in contrast to recent research, the plesiomorphic hearing condition for Neoceti was low frequency, which was retained by toothed mysticetes, and the high-frequency hearing of odontocetes is derived. Therefore, the low-frequency hearing of baleen whales has remained relatively unchanged over the last approximately 34 Myr, being present before the evolution of other signature mysticete traits, including filter feeding, baleen and giant body size.

1. Introduction

The monophyletic living cetacean groups Odontoceti (toothed whales and dolphins) and Mysticeti (baleen whales) display a clear dichotomy in their acoustic biology, with odontocetes hearing and producing ultrasonic signals (more than 20 000 Hz) for echolocation, and mysticetes possessing low-frequency or infrasonic (less than 20 Hz) hearing and vocalizations [1,2].

Although it is debated whether the earliest cetaceans (archaeocetes) were low- or high-frequency specialists [3–5], archaic odontocetes have been shown to use high-frequency echolocation [5–7]. However, no descriptions of the cochlear anatomy of early mysticetes have been published, which included the critical transition from predation using teeth to filtering with baleen [8]. Because of this, we have not been able to establish whether the earliest mysticetes retained the primitive low-frequency hearing of archaeocetes, or initially evolved high-frequency hearing like odontocetes, which was subsequently lost. The latter has been suggested by studies based on the presence of a large mandibular foramen, asymmetry in basilosaurid skulls, analyses of basilosaurid cochlear morphology and ancestral state reconstructions from molecular phylogenies [5,9–11]. For the first time, we describe the cochlear anatomy of toothed archaic mysticetes using micro-computed tomography (microCT) of periotic bones representing Mammalodontidae (Museums

Victoria NMV P173220, P199986) and Aetiocetidae (NMV P229119), early-diverging clades pivotal to understanding the origin of baleen whales [12–16].

2. Material and methods

Three toothed mysticete periotics were scanned using the Zeiss Xradia 520Versa microCT at the Monash University X-ray Microscopy Facility for Imaging Geo-materials (XMFIG). The raw data from these scans were used to create three-dimensional digital models of the periotics using the visualization software package Avizo (v. 9.0.1 Standard) [17]. From these models, digital endocasts of the cochleae were segmented using Avizo. The same process was carried out for a comparative sample of one extant odontocete species, five extant mysticete species and one species of basilosaurid archaeocete (*Zygorhiza kochii*; table 1). Owing to their larger size, the five extant mysticete specimens were scanned using a Siemens 128-slice PET-CT scanner at the Melbourne Brain Centre Imaging Unit. Multiple linear morphometrics were measured, with several ratios calculated from them: basal ratio (cochlear height divided by cochlear width), axial pitch (cochlear height divided by number of turns) and radii ratio (basal cochlear radius divided by apical cochlear radius). Both maximum and minimum frequency limits were estimated. Estimates of the low-frequency hearing limit for the toothed mysticetes were calculated from the linear regression of low-frequency hearing limit and radii ratio for other mammals performed by Manoussaki *et al.* [18]. Estimates of the maximum frequency limit for the toothed mysticetes (except NMV P229119) and other fossil cetaceans were made using a new equation derived in this study from a linear regression of basal basilar membrane width and maximum frequency limit for a 14 species of terrestrial mammal and 14 species of cetacean. Basilar membrane width was either taken from previously published measurements or estimated from laminar gap width measurements, corrected for the overestimate reported by Ketten [1], using the slice tool in Avizo. Detailed methods can be found in the electronic supplementary material.

3. Descriptions of cochlear anatomy

(a) Mammalodontidae

The description of mammalodontid cochlear morphology is based on *Mammalodon colliveri* (NMV P199986; figure 1) and a mammalodontid of indeterminate species (NMV P173220; figure 1), with values for the former specimen given first and the latter given in parentheses where different. The cochlea completes approximately 2.25 turns (2.5 turns). The scala tympani is inflated radially along the first quarter turn only, lacking a distinct tympanal recess like that seen in some mysticetes and odontocetes [3–6,19–21]. The cochlear canal retains its width for the first turn, before tapering in the second turn, becoming narrowest at the apex. The fenestra cochleae is large and opens posteriorly to the cochlear canal, with the canaliculus cochleae for the membranous perilymphatic duct (only the base of which is shown) extending dorsomedially (dorsally), dorsal to the fenestra cochleae.

In vestibular view, the first quarter of the basal turn of the cochlea is separated from the apical turns, similar to *Zygorhiza kochii*. The apical turns are, however, tightly coiled, with a small open space enclosed by the apical turn (apex essentially completely closed). There is a high degree of overlap of the turns, with well over half of the apical-most turn

overlapping the section of the cochlear canal below it. The basal ratio is 0.55 (0.58), indicating that the cochlea is approximately twice as wide as it is high. The axial pitch and slope values are 2.57 (2.23) and 0.08, respectively. The radii ratio of the cochlea is 6.77 (6.44), a value within the range of those calculated for living mysticetes previously [3]. In cross section, the bone separating the basal turn from the apical turn is thin, similar to living mysticetes.

The spiral laminae are represented on these digital endocast models as grooves. The primary spiral lamina extends for almost the entire length of the cochlea, being widest at the base. The secondary spiral lamina extends along the radial wall of the cochlear canal for less than half of the basal turn (approx. 33% (42%) of the total length of the cochlear canal), a value similar to extant mysticetes. Using the equation from Manoussaki *et al.* [18], the estimated low-frequency hearing limits are 53.81 Hz (65.07 Hz). The basal basilar membrane width (bmw) was related to the maximum frequency limit (f_{max}) as: $\log(f_{max}) = -1.3090 \log(bmw) + 4.1316$, with an R^2 of 0.78. Using this equation, the estimated maximum frequency limits are 17.37 kHz (4.59 kHz). The sizeable difference between the maximum frequency estimates of the two specimens is probably due to the fact that the tips of the laminae in NMV P173220 are damaged, giving an artificially large laminar gap width.

(b) Aetiocetidae

The aetiocetid represented by periotic NMV P229119 (figure 1) probably represents a juvenile individual (see the electronic supplementary material for further details) and is smaller in absolute size compared with the other toothed mysticetes in this study (table 1). The cochlea completes 2.5 turns. This cochlea is not as well preserved as the others, with matrix infilling much of the cochlear canal and destroying most of the more delicate structures. Similar to mammalodontids, the scala tympani is inflated radially along the first quarter turn only, lacking a distinct tympanal recess. The cochlear canal retains its width for the first turn, before tapering in the second turn, becoming narrowest at the apex. The fenestra cochleae is large and opens posteriorly. The canaliculus cochleae for the membranous perilymphatic duct extends dorsally from the cochlear canal. The apical turns are tightly coiled with minor, if any, open space enclosed by the apical turn. The apical-most turn overlaps the section of the cochlear canal below it. The basal ratio is 0.60, and the axial pitch and slope values are 1.31 and 0.09, respectively. The radii ratio of the cochlea is 7.47, a value within the range of living mysticetes. The spiral laminae are poorly preserved so their full extent cannot be estimated; however the secondary spiral lamina extends for at least half a turn, a value similar to the other toothed mysticetes examined. Using the equation of Manoussaki *et al.* [18], the estimated low-frequency limit of NMV P229119 is 35.90 Hz. The maximum frequency limit could not be calculated for the aetiocetid due to internal damage of the cochlea.

4. Discussion

(a) Comparisons

Overall, there are no clear differences between aetiocetid and mammalodontid cochleae. Both groups share the same

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Table 1. Key measurements of cetaceans sampled in this study and their estimated low-frequency limits. CBA, cannot be ascertained; CL, canal length; estd. LFL, estimated low-frequency limit; #T, number of turns; SSL, secondary spiral lamina.

taxon	specimen no.	no. turns	canal length (mm)	radii ratio	% extent of SSL	basal ratio	axial pitch	slope	volume (mm³)	estd. LFL (Hz)
Odontoceti										
Steno bredanensis	NMV C36961	1.5	30.32	3.39	74.18	0.50	3.47	0.11	154.85	378.31
Mysticeti										
Balaenoptera acutorostrata	NMV C4936	2.25	42.78	8.24	44.17	0.53	3.00	0.07	412.34	22.88
Balaenoptera borealis	NMV P166415	2.25	69.56	7.33	32.86	0.47	3.56	0.05	790.72	38.75
Balaenoptera edeni	NMV P171502	2	70.74	7.33	31.15	0.51	4.22	0.06	797.40	38.80
Eubalaena australis	NMV C27879	2.25	52.01	7.22	22.53	0.64	4.28	0.08	748.64	41.42
Megaptera novaeangliae	NMV C28892	2	56.35	7.10	38.40	0.50	4.39	0.08	804.95	44.29
Aetiocetidae indet.	NMV P229119	2.5	15.18	7.47	39.09	0.60	1.31	0.09	CBA	35.90
Mammalodon colliveri	NMV P199986	2.25	33.15	6.77	33.29	0.55	2.57	0.08	145.57	53.81
Mammalodontidae indet.	NMV P173220	2.5	29.26	6.44	42.41	0.58	2.23	0.08	162.13	65.07
Archaeoceti										
Zygorhiza kochii	USNM 214433	2.5	32.83	9.63	41.72	0.67	3.02	0.09	259.14	10.26

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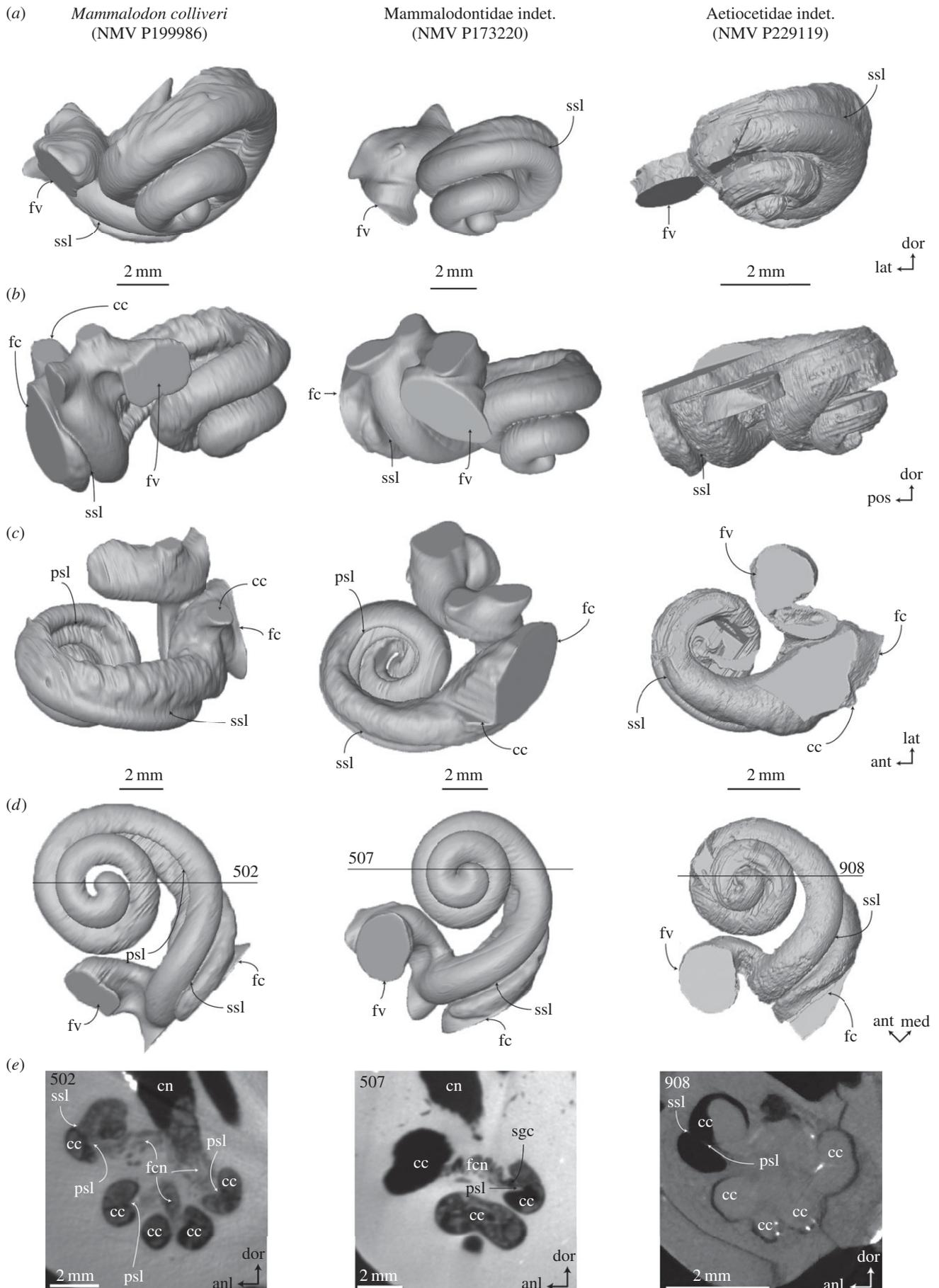

Figure 1. Digital endocasts of cochleae of *Mammalodon colliveri* (NMV P199986), Mammalodontidae indet. (NMV P173220) and Aetiocetidae indet. (NMV P229119) reconstructed from microCT data in (*a*) anterior, (*b*) lateral, (*c*) dorsal and (*d*) vestibular views. Panel (*e*) shows microCT cross-sectional slices through periotics, location of slice indicated by line through cochleae in (*d*). All specimens are shown as right cochlea with NMV P173220 reversed. ant, anterior; cc, cochlear canal; cn, cranial nerve VIII; dor, dorsal; fc, fenestra cochleae; fcn, foramina for cranial nerve VIII; fv, fenestra vestibuli; lat, lateral; med, medial; pos, posterior; psl, primary spiral lamina; ssl, secondary spiral lamina; vc, vestibular curve.

basilosaurid-like cochlear morphology and have very similar measurements, with the only source of variation being the absolutely smaller size of the juvenile aetiocetid periotic. The cochleae of the archaeocete and mysticetes examined in this study have numbers of turns ranging from 2 to 2.5. This falls within the range of archaeocete and mysticete cochleae examined in other studies, which have two to three turns (table 1) [3–6,19–22]. The fenestra cochleae is large in all toothed mysticetes examined, similar to that of archaeocetes and extant mysticetes (electronic supplementary material, figure S4). The fenestra cochleae and the bony canaliculus cochleae are enclosed in separate passages, which appear to be the normal condition for all cetaceans except for *Eschrichtius*, which possesses an undivided perilymphatic foramen [3]. In all toothed mysticete specimens examined, there is a high degree of overlap of the basal turn(s) by the apical turns (figure 1). This is again similar to the condition found in archaeocetes and extant mysticetes. The degree of overlap is reflected in the thin walls of bone between the basal and apical turns (figure 1; electronic supplementary material, figure S2; table 1). By contrast, toothed mysticetes and *Eubalaena* have either a closed apex of the cochlea or a small open space, whereas the apex of the cochlea in balaenopteroids is more open (electronic supplementary material, figure S4). None of the toothed mysticete specimens possessed an expanded tympanal recess (figure 1), although Ekdale [4] reported the presence of this feature in an indeterminate toothed mysticete taxon (ChM PV5720). Like the specimens described by Ekdale & Racicot [3], we found that extant balaenopterids possess a tympanal recess and balaenids do not. The expansion of the scala tympani only marginally extends past the basal-most quarter turn in *Zygorhiza* and the toothed mysticete specimen examined by Ekdale [4]. However, as it tapers off very rapidly past this point (unlike the expansions seen in balaenopteroids, *Physeter* and ziphiids), we do not consider this to be a definitive tympanal recess, as explained in the electronic supplementary material.

The basal ratio, axial pitch and slope values for the toothed mysticetes in this study are consistent with those from the archaeocetes and extant mysticetes in this study (table 1). The cochlear volumes of the toothed mysticetes are smaller than those for *Z. kochii* (259.14–341.65 mm^3) and the extant mysticete taxa examined in all studies to date (412.34–974.00 mm^3) [3]. As the sampled toothed mysticetes were probably smaller in body size than both *Z. kochii* and living mysticetes [23,24], smaller cochlear volumes are to be expected. The radii ratio values of the toothed mysticetes examined in this study range from 6.44 to 7.47, similar to living mysticetes (7.10–8.24). The radii ratio value of *Zygorhiza kochii*, however, is higher than any other taxon in this study (9.63). Ekdale & Racicot [3] found a similar value for *Zygorhiza* in their study (10.0). The extent of the secondary spiral lamina in toothed mysticetes is short, like that of extant mysticetes. In the mammalodontids examined in this study, it does not extend more than 43% of the total cochlear length. This is similar to the values obtained for *Z. kochii* (42%) and living mysticetes in this study, except for *Eubalaena australis* (23%).

(b) Hearing across the archaeocete–mysticete transition

A prominent point of debate in the study of cetacean acoustics is the ancestral condition of hearing in Neoceti.

Arguments for possessing both high-frequency [5,9–11] and low-frequency [3,6,25] hearing have been advanced. Most recently, a principal component analysis (PCA) of cochlear measurements by Churchill *et al.* [5] suggested that basilosaurids show greater capabilities for hearing higher frequencies than living mysticetes. Their position in the morphospace is largely driven by: (i) the length of the secondary spiral lamina and (ii) the radius of the spiral ganglion canal. We re-ran their analysis (figure 2), adding the corresponding measurements from the toothed mysticete cochleae in our sample. Like basilosaurids, toothed mysticetes plot in a region of morphospace intermediate to mysticetes and odontocetes (figure 2), potentially showing that they too can hear high frequencies. Nonetheless, there are several lines of evidence suggesting that this is not be the case and that basilosaurids and toothed mysticetes were low-frequency sound specialists. First, archaeocetes (42–45% of cochlear length) and toothed mysticetes (39–42% of cochlear length) have secondary spiral laminae that extend a similar length of the cochlear canal as that of extant mysticetes (22–44% of cochlear length; table 1) [1,19]. Second, high radii ratio values (not calculated by Churchill *et al.* [5]), which strongly correlate to low-frequency hearing [18], are also highly congruent in archaeocetes and mysticetes (table 1). Low-frequency limit estimates for archaeocetes and toothed mysticetes calculated using the equation of Manoussaki *et al.* [18] were also all very low frequencies (less than 54 Hz), contrasting to a considerably higher low-frequency limit of 378.31 Hz for the odontocete *Steno* (table 1). These low-frequency limit estimates cannot yet be verified as no audiograms of mysticetes have been constructed. A simulated mysticete audiogram was generated by Cranford & Krysl [26] which estimated that the lowest frequency detected for a juvenile fin whale was 10 Hz, slightly lower but still consistent with the estimated low-frequency limits of the extant mysticetes examined in this study. The estimated maximum frequencies for the mammalodontids and *Zygorhiza* are also within the limits of modern mysticetes, but are notably much lower than odontocetes, including the xenorophid inner ear described by Park *et al.* [6], which we calculate here to have an estimated maximum frequency limit similar to some modern species (approx. 86 kHz), but not as high as more specialized taxa (electronic supplementary material, figure S5 and table S5). Further indicative of low-frequency hearing are the higher number of turns in archaeocete and toothed mysticete cochleae (more than 2), as well as the large amount of overlap of the basal turn by the apical turn(s). Additionally, preliminary results of a quantitative shape analysis of cetacean cochleae by Ekdale [4] indicate that *Zygorhiza* and an indeterminate species of toothed mysticete (ChM PV5720) plot within the cochlear morphospace of mysticetes. A final point to note is that virtually all studies to date [3–6,9,18–22] on the diversity/evolution of cetacean inner ear anatomy have sampled different taxa/specimens for scanning/analyses under differing protocols. This has resulted in datasets that may not overlap taxonomically or analytically, which hampers comparison of results across multiple studies. It is possible that recent disagreement in the interpretation of cetacean acoustic evolution may reflect this limited degree of comparability in datasets.

Toothed mysticetes could therefore be said to possess the 'Type M' cochlear morphology of Ketten & Wartzok [27] and Ketten [28], although the range of axial pitch values, cochlear
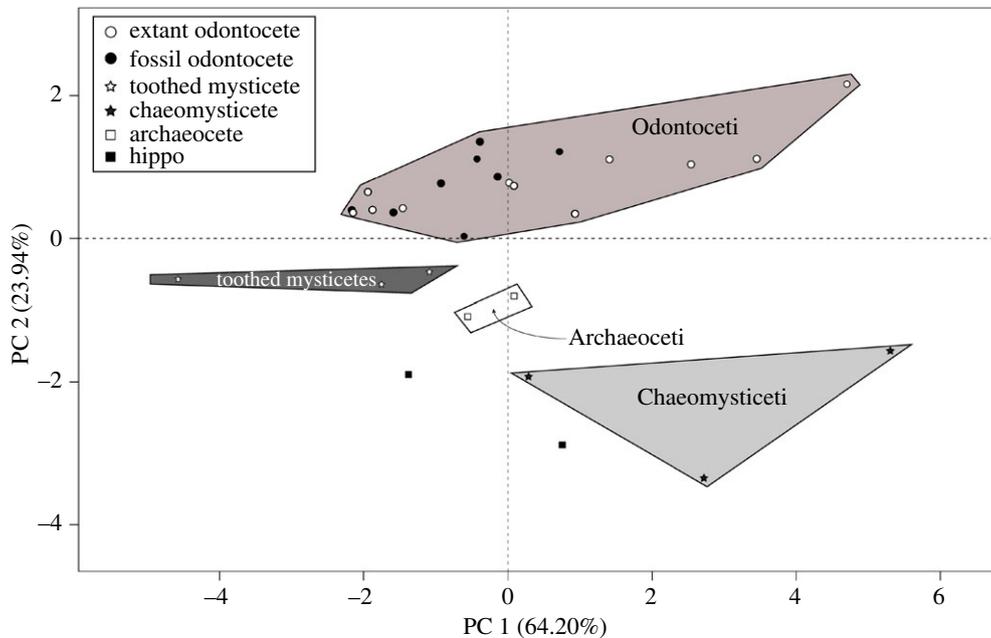
Figure 2. PCA of linear cochlear measurements following the protocols of Churchill *et al*. [5], with the toothed mysticetes from this study added to the analysis. PC 1 mainly represents variation in body size, while PC 2 mainly represents variation in morphological features. See Churchill *et al*. [5] for discussion of principal components and electronic supplementary material, table S4 for PC weightings. (Online version in colour.)

height and cochlear volume values on the other hand are more like that of 'Type II' odontocete cochleae (lower-range ultrasonics; table 1). However, these differences in toothed mysticete cochleae do not indicate that they could hear high frequencies like odontocetes as the features do not affect the stiffness of the basilar membrane, which is critical in determining the frequencies that an animal can detect [29]. They can instead be explained by the smaller body size of toothed mysticetes relative to their living counterparts, with mammalodontids and aetiocetids estimated to have been between 2.94–3.25 m and 2.10–3.50 m total length, respectively [8,30]—smaller than living mysticetes, which range from 5.5 to 33 m [24]. Additionally, it is noteworthy that despite the juvenile age and diminutive size (e.g. estimated bizygomatic width = 192 mm) of the aetiocetid it is still estimated to have detected low-frequency sounds, corroborating the presence of precocial development of the auditory system in early Neoceti [31]. Although toothed mysticetes may not have been capable of detecting infrasonic frequencies (less than 20 Hz) such as has been demonstrated in living species [27], we contend that basilosaurids, mammalodontids and aetiocetids were still specialized for hearing low frequencies (less than 1000 Hz) and were almost certainly incapable of detecting high-frequency sounds approximating the capabilities of odontocetes (more than 30 000 Hz).

(c) Evolution of the extreme biology of baleen whales

The finding that mammalodontid and aetiocetid toothed mysticetes retained the plesiomorphic low-frequency hearing of basilosaurid archaeocetes has significant implications for our understanding of mysticete evolution in a phylogenetic and geochronologic context. First, the specialized high-frequency hearing of odontocetes is confirmed as the derived condition within Neoceti [3], contra Churchill *et al*. [5], Ketten [9], Milinkovitch [10] and Fahlke *et al*. [11] who hypothesized high-frequency hearing in the common ancestor of Neoceti. Second, low-frequency hearing did not evolve in mysticetes as a result of their evolving extremely

large body size. Ketten [1,9,28] speculated that the low-frequency cochlea in mysticetes was a consequence of isometric scaling of cochlear dimensions with the evolution of increasingly larger body size. However, the earliest-diverging toothed mysticetes (Mammalodontidae + Aetiocetidae [32]) were relatively small-bodied animals, up to about 4 m in length [22,33] (but see [33,34]), and already possessed low-frequency-adapted cochleae (figure 3). The estimated maximum body length of the vast majority of mysticetes was less than 7 m until the Middle Miocene [35], and a body length of less than 7 m was likely for primitive Chaeomysticeti [33]. Large-bodied mysticetes (more than 10 m total length) first occur in the Middle Miocene [35] and gigantic mysticetes (more than 15 m total length) first evolved within the last 5 Myr [35,36], all of which is well after the appearance of low-frequency hearing in Mysticeti (figure 3).

Third, low-frequency hearing in mysticetes did not evolve as a result of the ecomorphological shift to bulk filter feeding and/or the appearance of baleen. It has been implied that mysticetes were initially sensitive to high frequencies [9], but as they evolved bulk filter feeding, baleen and migration to high-latitude feeding grounds there was reduced selection pressure for maintaining high-frequency hearing [9,28]. Irrespective of whether *Aetiocetus weltoni* possessed an incipient form of baleen, as has been suggested by Deméré *et al*. [15], the presence of low-frequency cochleae in mammalodontids, aetiocetids and basilosaurids suggests that the common ancestor of mammalodontids and aetiocetids also had low-frequency hearing. Crucially, this stem mysticete would have probably lacked baleen, which would refute this hypothesis [37]. Finally, the low-frequency-adapted cochleae of toothed archaic mysticetes, coupled with their lack of nasofacial osteological correlates of soft tissues that generate or modify outgoing signals (as supported by character optimization [7]), suggest the earliest mysticetes were not capable of echolocation [13].

The signature innovations of mysticetes (baleen) and odontocetes (echolocation) were acquired at different stages in their evolutionary history: anatomical specializations for
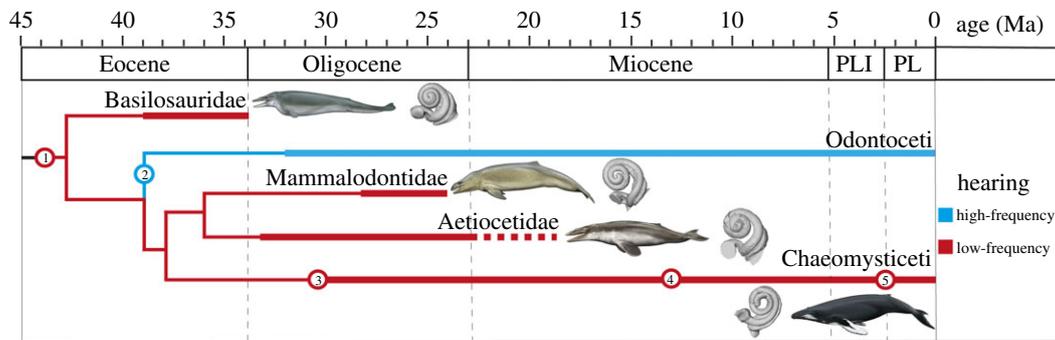
Figure 3. Evolution of mysticete hearing based on the phylogeny of Marx & Fordyce [32] in relation to other key mysticete features, illustrating how low-frequency hearing evolved prior to the evolution of filter feeding and large body size in mysticetes. Cochlea renderings are of *Zygorhiza kochii* (USNM 214433), *Steno bredanensis* (NMV C36961), *Mammalodon colliveri* (NMV P199986), Aetiocetidae indet. (NMV P229119) and *Megaptera novaeangliae* (NMV C28892). Thickened bars indicate stratigraphic ranges of cetacean clades, following [32]. 1, evolution of low-frequency hearing in Cetacea; 2, evolution of high-frequency hearing in Odontoceti; 3, appearance of obligate filter feeding using baleen; 4, acquisition of large body size (more than 10 m); 5, acquisition of giant body size (more than 15 m). Dates for events in mysticete body size evolution from [34,35]. PL, Pleistocene; PLI, Pliocene. Illustrations by Carl Buell, used with permission.

bulk filter feeding were not present in the earliest stem mysticetes [8,13,14], contrasting with the presence of echolocation in basal odontocete lineages [5–7]. Nevertheless, our findings show that the characteristic low-frequency mysticete cochlear morphology was present in the earliest members of the group, having been retained from their archaeocete ancestors.

Data accessibility. All additional data are in the electronic supplementary material.

Authors' contributions. T.P. and A.R.E. constructed three-dimensional models of the periotic and cochleae. E.M.G.F. photographed NMV P229119. S.J.G. established the horizon and age of NMV P173220. A.R.E and E.M.G.F. guided the data analysis. T.P. analysed the data. T.P. and E.M.G.F. wrote the manuscript with input by A.R.E. All authors approved the final draft of the manuscript.

Competing interests. We have no competing interests.

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