letters to nature

Eocene evolution of whale hearing

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The origin of whales (order Cetacea) is one of the best-documented examples of macroevolutionary change in vertebrates[1–3]. As the earliest whales became obligately marine, all of their organ systems adapted to the new environment. The fossil record indicates that this evolutionary transition took less than 15 million years, and that different organ systems followed different evolutionary trajectories. Here we document the evolutionary changes that took place in the sound transmission mechanism of the outer and middle ear in early whales. Sound transmission mechanisms change early on in whale evolution and pass through a stage (in pakicetids) in which hearing in both air and water is unsophisticated. This intermediate stage is soon abandoned and is replaced (in remingtonocetids and protocetids) by a sound transmission mechanism similar to that in modern toothed whales. The mechanism of these fossil whales lacks sophistication, and still retains some of the key elements that land mammals use to hear airborne sound.

The cetacean sound transmission mechanism has long been known to be near-modern less than 10 million years after the origin of the order Cetacea[4–6]. Fossils documenting transitional ear morphologies were suggestive of pronounced change[7,8], but could not be interpreted in a functional context because of their scarcity and because the function of modern cetacean sound transmission was not understood until recently[9–11].

Our newly discovered cetacean fossils (Fig. 1) allow us to present an integrated interpretation of evolving sound transmission mechanisms as whales took to the water. Our specimens represent four groups of early whales[3]. These include pakicetids (*Ichthyolestes*, *Nalacetus* and *Pakicetus*), the basal cetacean clade known from 50-million-year-old deposits in Pakistan. They also include remingtonocetids (*Andrewsiphius* and *Remingtonocetus*) and protocetids (*Indocetus*), which lived approximately 43–46 million years ago in India, and represent taxa that are successively more closely related to modern cetaceans. Finally, we studied previously described material for basilosauroids[5] (*Basilosaurus* and *Zygorhiza*) from North America, which lived from approximately 35 to 40 million years ago. We did not include ambulocetid whales in this study because no ear ossicles are known for this family.

The ear of the earliest whales, pakicetids, functions in a similar way to that of land mammals when receiving airborne sound (Fig. 2)[8,12,13]. Sounds are transmitted through the air-filled external auditory meatus and cause the tympanic membrane to vibrate[14]. Its vibrations are passed on through a chain of small bones (middle ear ossicles) located in the air-filled middle ear cavity. The last of these ossicles, the stapes, acts as a piston that causes vibrations in the inner ear fluid. Although adequate in air, this mechanism fails underwater where the external auditory meatus fills with water, creating a pressure differential across the tympanic membrane that greatly diminishes its ability to transmit sound. In addition, underwater sound will reach the pakicetid ear by passing through the head tissues. This mode of hearing is called bone conduction[15] and does
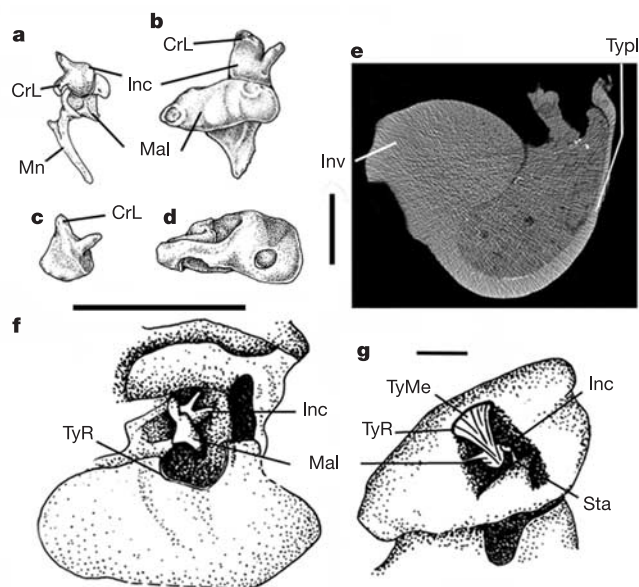

Figure 1 Sound transmission elements in cetaceans and an artiodactyl. **a**, **b**, Left malleus and incus of a pig (**a**) and a bottlenose dolphin (**b**). **c**, Left incus of *Pakicetus* (H-GSP 91035). **d**, Right malleus of *Indocetus* (LUVP 11034). Ossicles are drawn perpendicular to the plane of the lever arms. **e**, Computerised tomography (CT) scan of a section through the left tympanic of *Remingtonocetus* (RUSB 2914). **f**, **g**, Left ear of *Remingtonocetus* (RUSB 2828) in rostro-lateral (**f**) and ventral (**g**) view, with the three ossicles *in situ*, the tympanic ring (TyR) position projected and the tympanic membrane (TyMe) position inferred. Scale bar for **f** and **g** is beside **g**. Abbreviations: CrL, crus longum; Inc, incus; Inv, involucrum; Mal, malleus; Mn, manubrium; Sta, stapes; TyPl, tympanic plate. Scale bars, 10 mm.
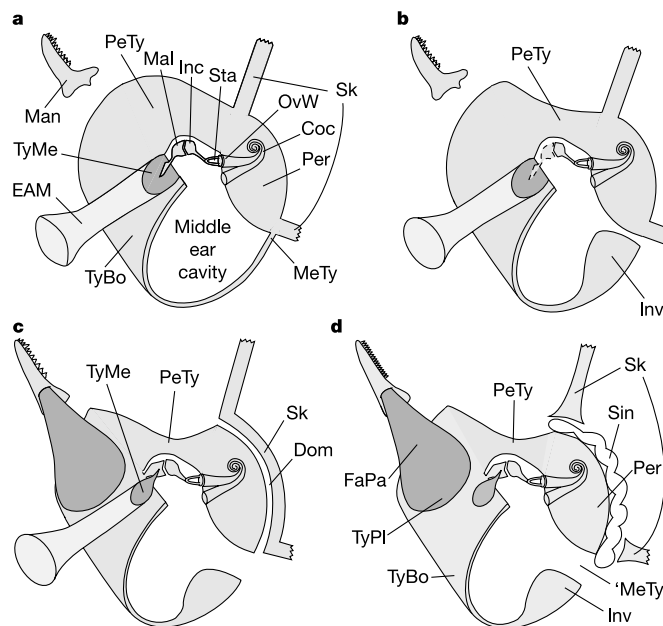

Figure 2 Sound transmission mechanisms in land mammals and whales. Diagram of the ear in a generalized land mammal (**a**), a pakicetid (**b**), a remingtonocetid/protocetid (**c**) and a modern odontocete (**d**). Abbreviations: Coc, cochlea; Dom, dome-shaped depression for periotic; EAM, external auditory meatus; FaPa, fat pad; Inc, incus; Inv, involucrum; Mal, malleus; Man, mandible; MeTy, medial synostosis between periotic and tympanic bone, in cetaceans this synostosis is absent and is homologous to a gap between these bones ('MeTy'); OvW, oval window; Per, periotic bone; PeTy, joint between periotic and tympanic; Sin, air-filled sinuses; Sk, skull; Sta, stapes; TyBo, tympanic bone; TyMe, tympanic membrane; TyPl, tympanic plate.

not allow for directional hearing. In air, bone conduction is nearly absent because the air–body interface reflects most incoming sounds.

Our new fossils show that the tympanic bone of pakicetids, unlike that of land mammals, was not connected rostro-medially to the periotic. This causes the thickened medial side of the tympanic (the pachyostotic involucrum) to form a loosely suspended centre of mass that could vibrate independently of the periotic. This would lead to enhanced transmission of bone-conducted sound when compared with generalized land mammals. An underwater sound transmission mechanism rooted in bone conduction is more sophisticated than that of a land mammal. A similar mechanism is probably used in modern phocid seals[16,17], in which the very heavy ossicles form the independently vibrating mass[16,18] (Fig. 3, seal clusters), as well as in some subterranean mammals[19].

New fossils for remingtonocetid and protocetid whales indicate that their sound transmission mechanism (Fig. 2c) combines aspects of those of pakicetids and modern odontocetes. In modern odontocetes, sound is transmitted to the middle ear by means of a large mandibular fat pad and received by the lateral wall of the tympanic bone (the tympanic plate), not the tympanic membrane[20,21]. Sound passes through the odontocete middle ear by means of two lever-arm systems, and the freely suspended involucrum forms the axis of one of these[10,12].

Whereas pakicetids retain the land mammal morphology of the mandible, remingtonocetids and protocetids have a large mandibular foramen that indicates that the mandibular fat pad was present, and that the tympanic plate was functional during underwater hearing. The contact between periotic and tympanic bones in remingtonocetids and protocetids is more reduced than in pakicetids, and the involucrum is not attached to the periotic. The tympanic membrane (as evidenced by the morphology of the malleus and tympanic ring) is not the flat structure of generalized mammals, but has an elongated conical shape intermediate between land mammals and modern cetaceans. The size and shape of the ossicles, and the relation between ossicular mass and tympanic plate area (the underwater sound input area, Fig. 3) in these Eocene whales is similar to that in modern whales. Presence of the large mandibular foramen, suspension of the involucrum, and size and shape of the ossicles indicate that the modern whale underwater sound transmission mechanism was realized.

Airborne sound reached the ear of remingtonocetids and protocetids through the external auditory meatus, a structure that is not patent in modern odontocetes. The remingtonocetid and protocetid malleus and incus are heavy and resemble those of modern cetaceans. The heavy ossicles imply that the frequency range for airborne sound was shifted to lower frequencies[17]. The malleus lacks a functional manubrium and is synostosed to the tympanic bone. These features indicate that reception of high-frequency airborne sound using the generalized mammalian system was present but poor.

In addition to the presence of the external auditory meatus, the remingtonocetid and protocetid ear differs from that of modern toothed whales in that it lacks air-filled sinuses that isolate the ear acoustically. The dorsal side of the ear (periotic) is dome-shaped (Fig. 2c) and fits in a dome-shaped depression in the skull (squamosal). These bones are not synostosed, but were probably connected by ligaments. These ligaments provide some, but very incomplete, acoustic insulation from bone-conducted sound. Hence, directional hearing was poor underwater. Transmission of airborne sound in remingtonocetids and protocetids was severely compromised by modifications of the ear for underwater hearing.

Basilosauroids follow protocetids chronologically, and are higher than protocetids on the cladogram[22] (Fig. 4). The outer, middle and inner ear of basilosauroids is well-known[4,13,23–25] and is functionally modern. A major functional innovation with respect to remingtonocetids and protocetids is that basilosauroid ears are acoustically isolated by the insertion of air-filled sinuses between the ear and the skull[13,23]. Unlike modern cetaceans, basilosauroids have a large external auditory meatus that may have been patent. However, these whales were obligately marine[22] and airborne sound was probably unimportant for them.

The history of Eocene cetaceans, as documented by our new fossils, shows that different organ systems followed a variety of evolutionary trajectories to reach modern morphologies and proportions. The dentition[3] and the osmoregulatory system[26] show
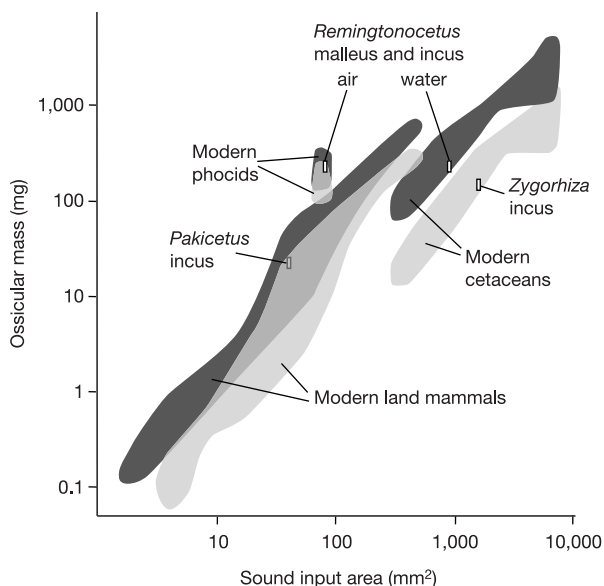

Figure 3 Bivariate plot of ossicular mass versus sound input area. Outline envelopes are for a representative sample of land mammals, phocid seals and modern cetaceans (see Methods and Supplementary Information). Ossicular mass is the combined mass of the malleus and the incus (dark grey) and the individual mass of the incus (light grey).
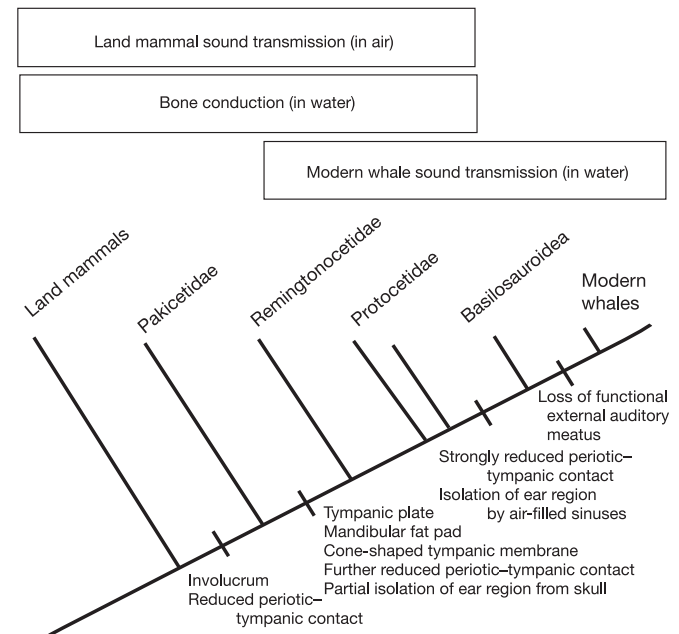

Figure 4 Generalized phylogeny for the cetaceans in this paper, with the characters relevant to hearing indicated at the nodes where they appeared. Boxes indicate the different sound transmission mechanisms used by these whales. The generalized mammalian sound transmission system was present in the cetacean sister group, here indicated as 'land mammals'.

intermediates. The organ of balance attained its modern proportions quickly and seemingly without transitional forms[27], and the locomotor system underwent a protracted and complex sequence of changes, representing a variety of functional patterns[3,28]. The changes of the ear were complex because the physical properties of sound in air are very different from those in water. As a result, cetaceans totally reorganized sound transmission through the outer and middle ear (Fig. 4), while keeping the cochlea in the inner ear relatively unchanged.

This macroevolutionary change in the ear of cetaceans was nearly completed in four to seven million years. The functional end members of this evolutionary sequence—generalized mammalian hearing and modern whale hearing[12]—are widely distributed in modern forms; they can be seen as evolutionarily stable configurations[29]. We propose that in these evolutionary end members all parts of the ear are optimized for collaboration with each other and are kept stable by internal selection[29]. As the ancestors of cetaceans took to the water, the environmental tolerances of this system were exceeded and natural selection for the transmission of waterborne sound played its part. In pakicetids this resulted in a functional trade-off for the existing transmission mechanism, in which anatomical elements used for generalized sound transmission are now also important in bone-conducted hearing. The result is a sound transmission mechanism that works in air and in water, but performs poorly in both when compared with either land mammals or modern whales. A new evolutionarily stable configuration was not reached until new anatomical elements assumed a function in hearing in remingtonocetids and protocetids, and some old elements were eliminated as sound transmitters. The mandible is one of the most important elements added to the cetacean hearing mechanism and could be considered a keystone character[29] that catalysed the major transformation of the cetacean ear. ☐

Methods

In Fig. 3, sound input areas are those parts of the middle ear that are the sound receiver. For modern land mammals and phocid seals the sound input area is the tympanic membrane area, whereas for modern cetaceans it is the tympanic plate area. The tympanic membrane and tympanic plate are functionally analogous, but they are not evolutionarily homologous. For *Pakicetus* (H-GSP 91035), the tympanic membrane is the sound receiver; its area was plotted on the *x* axis. *Remingtonocetus* (RUSB 2914) used the tympanic membrane for receiving airborne sound, but the tympanic plate for receiving waterborne sound; hence, it was plotted twice in this figure. *Indocetus* is not shown because no incus is known for this taxon. The point for *Zygorhiza* was made on the basis of LSUMG V160A. The areas of the tympanic membrane and tympanic plate were determined using a method described elsewhere[16,30]. Fossil taxa are plotted as ranges on the *y* axis because their density can only be estimated. The lower and upper range for the ossicular mass presented were calculated by multiplying the measured volumes by the minimum and maximum ossicular densities; that is, those for land mammals ($2.0\,g\,cm^{-3}$) and modern cetaceans ($2.7\,g\,cm^{-3}$), respectively[30]. For data sources see Supplementary Information.

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Pinyon jays use transitive inference to predict social dominance

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Living in large, stable social groups is often considered to favour the evolution of enhanced cognitive abilities, such as recognizing group members, tracking their social status and inferring relationships among them[1–4]. An individual's place in the social order can be learned through direct interactions with others, but conflicts can be time-consuming and even injurious. Because the number of possible pairwise interactions increases rapidly with group size, members of large social groups will benefit if they can make judgments about relationships on the basis of indirect evidence[5]. Transitive reasoning should therefore be particularly important for social individuals, allowing assessment of relationships from observations of interactions among others. Although