THE CETACEAN EAR: FORM, FREQUENCY, AND EVOLUTION

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INTRODUCTION

Cetaceans evolved from mesonychid condylarths, a cat-like, hooved carnivore, during the mammalian radiation, an explosive period of species development (Barnes et al., 1985; Lipps and Mitchell, 1976). In the Eocene, an amphibious condylarth entered the shallows of the warm, teeming Tethys Sea and stayed. This ancestral condylarth was equipped with a conventional land mammal ear. In the intervening 50 to 60 million years, auditory evolution paralleled that of the rest of the creature and the ancestral terrestrial ear underwent extraordinary modifications. As cetaceans developed into full, obligate aquatic mammals, unable to move, reproduce, or feed on land, their ears changed into highly effective transducers of water-borne sound. In fact, modern cetacean auditory systems are sufficiently specialized that they may no longer be able to encode air-borne signals.

Two extant lines of Cetacea are derived from the Archaeoceti (Fig. 1). One, the Odontoceti, has 65 recognized species (Leatherwood et al., 1976, 1982). They inhabit virtually every aquatic niche, from fresh water to bathypelagic and are morphologically diverse, ranging 1 to 40 m. in length. All are highly efficient predators. The second line, the Mysticeti, has 11 species, all of which are large, pelagic, grazing omnivores (Ridgway, 1972; Gaskin, 1976). Like all animals, cetaceans are faced with a need for locating food, navigating, and finding mates. Once protocetes entered the ocean, these functions had to be accomplished in water, a dark, dense environment in comparison to land. It is not surprising, therefore, that sound is a fundamental sensory and communication channel for cetaceans. All odontocetes tested echolocate; i. e., they "image" their environment by analyzing echoes from a self-generated high frequency signal of up to 200 kHz (Kellogg, 1959; Norris et al., 1961; Kamminga et al., 1989). Mysticetes are not known to echolocate, but many perceive frequencies below 50 Hz (Weston and Black, 1965; Watkins et al., 1987; Edds, 1988; Clark, 1990). Cetaceans, as a whole, therefore have the broadest sound production range of any mammalian order, exploiting both ultra and infrasonic channels.

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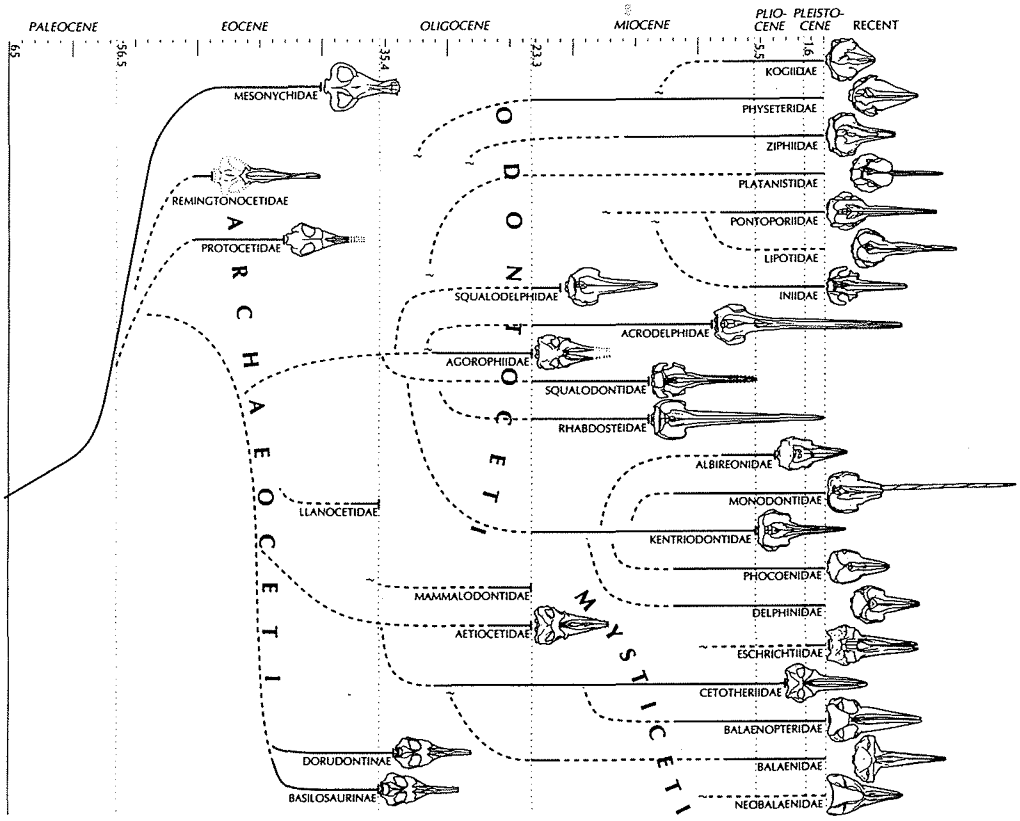


Fig. 1. Cetacean phylogeny. The theoretical development of cetacean families from Mesonychidae to the present. Vertical bars indicate extinctions; dashed lines are probable links; question marks are unestablished links (copyright Folkens and Barnes, 1992).

This paper describes the peripheral auditory system in representative species of extant odontocetes and mysticetes. Inner ear anatomy is explained in terms of functional correlates with species-specific hearing ranges, which, in turn, are correlated with differences in habitat and feeding behavior. By comparing modern and fossil ear anatomy, predictions are made about the hearing capacity and behavior of ancestral Cetacea. These comparisons also are used to trace the progressive shifts from a terrestrial to a fully aquatic mammalian ear.

METHODS

This study builds on previous work on odontocete hearing (Ketten, 1984; Ketten and Wartzok, 1990) and extends the data base to include mysticete and archeocete ears. Middle and inner ears of 11 extant and 5 extinct Cetacea (Table 2) were analyzed using light microscopy and computerized tomography (CT), a form of biomedical imaging in which the interior of objects is displayed in sequential thin slices. Bullae from extant species were CT scanned on a Siemens DR3 in 1 mm sections at a resolution of 160 µm/pixel before processing for histology. Entire bullae were fixed in buffered formalin and decalcified in a modified Schmorl's solution (Ketten, 1984) or fixed in Heidenhein-Sousa and decalcified in EDTA. Decalcification end-points were determined radiographically. Periotics were separated from the tympanic, trimmed, embedded in paraffin or celloidin, sectioned at 20 µm, and stained with hemotoxylin and eosin. Any unstained sections were archived in ethanol. Two-dimensional measurements of basic cochlear parameters were taken from mid-modiolar CT scans and thin sections. Basilar membrane dimensions were determined from three-dimensional reconstructions of thin sections of the cochlear duct. Reconstructions were obtained by digitizing registered sections on a Numonics Model 2200 electrostatic bitpad. The resulting X-Y-Z coordinate files were reconstructed, interpolated, rotated, and displayed by two programs, MacReco and Super 3D, on a Macintosh IIfx.

Data for fossil species were obtained from previously published work (see Table 2). Measurement criteria; e. g., what defines cochlear height, and appellation vary among authors. To obtain a consistent data base, published images were remeasured for this study using the same criteria applied to the extant material. Therefore, the numbers in this paper may differ from values in the original publication and only two-dimensional data are included for extinct species.

To accurately interpret auditory structures, it is necessary to have some consistent measure of sensitivity in control species. For practical and historical reasons, underwater measures of auditory sensitivity are available for very few cetaceans (Thomas et al., 1990; Awbrey, 1990). Extensive reviews of odontocete data are available in McCormick et al. (1980), Popper (1980), and Watkins and Wartzok (1985). At present, there are no direct measures of hearing in mysticetes.

In contrast to audiometric data, recordings of emitted sounds are available for over sixty-seven species of marine mammals (see Watkins and Wartzok, 1985). Emitted, functional sounds, typically called vocalizations, usually have the same peak spectra as the peak sensitivity in the hearing curve of that species (Bruns, 1976; Sales and Pye, 1974; Henson et al., 1990), and spectral analyses of underwater recordings of emitted sounds provide reliable indirect estimates of cetacean hearing (Popper, 1980; Popov and Supin, 1990). Consequently, for a broad based comparative study, emitted sounds are the most consistent acoustic measures available.

The most distinctive odontocete signals are used in echolocation (Table 1). Individuals vary pulse repetition rate, interpulse interval, amplitude, or spectra of echolocation clicks in response to environmental noise (Au, 1990; Moore, 1990), but each species has a characteristic echolocation frequency range (Norris, 1969; Popper, 1980). Based on peak spectra (the frequency of maximum energy in a typical echolocation click), there are two ultrasonic odontocete groups (Ketten, 1984): Type I with peak spectra above 100 kHz and Type II with peak spectra below 80 kHz (Table 1). These ultrasonic divisions coincide with differences in habitat and social behavior. Type I odontocetes typically are solitary, inshore phocoenids and platanistids, whereas Type II species are mostly delphinids that form large, complex social groups or pods (Ketten and Wartzok, 1990).

All mysticete vocalizations are significantly lower in frequency than those of odontocetes (Table 1). Peak spectra range from 12 Hz to 3 kHz (Cummings and Thompson, 1971; Silber, 1986).

Most mysticete vocalizations are categorized as moans (0.4 to 40 seconds, fundamental frequency <200 Hz); simple or complex calls (bursts or AM and FM pulses with frequency emphasis <1 kHz), and "songs", like those of *Megaptera novaeanglia*, with complex variations in phrasing and spectra (Clark, 1990). Infrasonic signals; i. e., below 25 Hz, are well documented in at least two species, *Balaenoptera musculus* (Edds, 1982) and *Balaenoptera physalus* (Watkins, 1981; Watkins et al., 1987; Edds, 1988).

Substantial differences in the sounds produced by odontocetes and mysticetes imply different perceptual abilities and, presumably, significant anatomical differences in their peripheral auditory systems. Since this study is concerned with extreme interspecies acoustic differences, general categorizations of hearing capacity are sufficient. Consequently, all odontocete species have been designated Type I or Type II based on echolocation data. Because very few broadband recordings are available for mysticetes, all have been classed acoustically as Type M.

Table 1. Characteristic Sounds of Representative Cetacean Species (Compiled from Popper, 1980; Norris and Leatherwood, 1981; Watkins and Wartzok, 1985; Clark, 1990.)

Species	Sound	Frequency Range (kHz)	Frequency at Maximum Energy (kHz)
ODONTOCETI			
Type I			
Inia geoffrensis	Click	25-200	95-105
Phocoena phocoena	Pulse	100-160	110-150
Type II			
Delphinus delphis	Whistle	0.2-150	4-9
	Click	0.2-150	30-60
Orcinus orca	Scream	0.25-35	12
Stenella longirostris	Click	1-160	60
	Whistle	1-20	8-12
Tursiops truncatus	Click	0.2-150	60-80
	Whistle	2-20	-
Physeter catodon	Coda	16-30	-
MYSTICETI			
Type M			
Eschrictus robustus	Call	-	1-1.5
Balaenoptera musculus	Moan	0.2-0.20	0.012 - .018
Balaenoptera physalus	Call	0.16-0.75	0.020
Balaena mysticetus	Call	0.1-0.580	0.14 - 0.34†
Eubalaena glacialis	Call	-	<0.200†
Megaptera novaeanglia	Song	0.05-10.0	<4.0

†Recordings below 100 Hz are not available

RESULTS

Tympano-Periotic Complex

Cetacean bullae differ from those of other mammals in appearance, construction, and cranial associations. In modern

Cetacea, the bulla has two distinct components, the periotic and tympanic, both of which are constructed from exceptionally dense compact bone. This "tympano-periotic complex" resides in an ex-

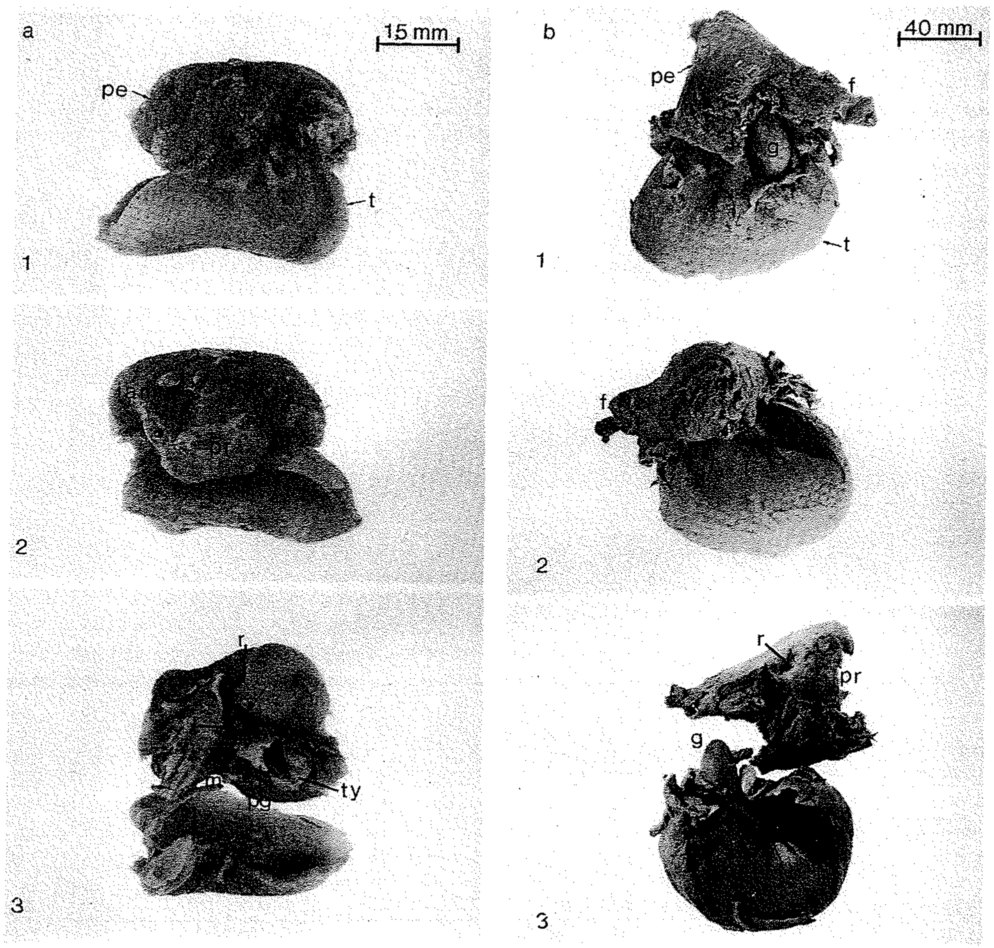


Fig. 2. Cetacean tympano-periotic complex. The left tympano-periotic complex of (a) a Type II odontocete, *Stenella attenuata*, and (b) a mysticete, *Eubalaena glacialis*, in lateral (1) and medial (2) views. In (3), the periotic and tympanic are separated to show the middle ear cavity. *Stenella* has a conical tympanic and an ovoid periotic with a distinct promontorium (pr). The corpus cavernosum has been removed in (a3) to reveal the stiff, fused ossicular chain: (i) incus; (m) malleus; (pg) processus gracilis; (ty) tympanic conus. The arrow points to the stapes crus below the round window (r). The VIIIth nerve is visible in the internal auditory canal (iam). The *E. glacialis* bulla has the characteristic mysticete features of a posterior cranial flange (f); dense hemispheric tympanic (t); triangular periotic (pe); and a thick, membranous glove finger (g). In *Megaptera*, the glove finger is nearly three times the length of that shown here for *E. glacialis*.

tensive peribullar cavity formed from enlarged middle ear sinuses (Oelschläger, 1986). In Mysticeti, a bony flange extends postero-medially from the periotic or tympanic (Fig. 2) and wedges tightly between the exoccipital and squamosal. In some mysticetes; e. g., _B. mysticetus_, the squamosal extends ventrally, forming a tent-like, lateral bony shield around the bulla. The peribullar cavity in odontocetes is proportionately larger than that of mysticetes and is filled with a spongy, membranous peribullar plexus. The tympano-periotic complex is suspended in this tissue by five or more sets of ligaments, and, except in physeterids, no substantial bony elements connect either the tympanic or periotic of odontocetes to the skull. Peribullar sinuses are most extensive in riverine, ultra-high frequency species like _Inia geoffrensis_ and are poorly developed in pelagic mysticetes, which implies that sinus enlargement is related more to acoustic isolation than to mechanical stress (Oelschläger, 1986). In odontocetes, the enlarged cavity and vascularized plexus may help to isolate the ear acoustically, a requisite for echolocation. No acoustic function has been demonstrated for solid bullar-cranial connections in mysticetes; however, the flanges may provide bony sound conduction paths to the ear.

Mysticete and odontocete bullae differ in size and shape and in the relative volumes of the tympanic and periotic (Fig. 2). Bullar dimensions are highly correlated with animal size (Ketten and Wartzok, 1990); therefore, mysticete bullae are two to three times larger than those of most Odontoceti. Mysticete periotics are cuboidal or pyramidal; the tympanic is hemispherical and nearly twice the volume of the periotic. In odontocetes, periotic and tympanic volumes are nearly equal. The periotic is ovoid, massive, and thick-walled. The tympanic is thin-walled and conical, tapering anteriorly. Fine structure of the tympano-periotic and the solidity of the tympano-periotic suture differ among species but their effect on audition is not known (Kasuya, 1973; Ketten, 1984; Ketten and Wartzok, 1990).

External Ear

External auditory canals are present in all Cetacea, but it is debatable whether they are functional. Pinnae are absent and there is a small external meatus which connects with an exceptionally narrow external auditory canal. The canal is plugged with cellular debris and dense cerumen. In Mysticeti, the proximal end of the canal flares, cloaking the "glove finger", a complex, thickened membrane (Fig. 2) derived from the pars flaccida of the tympanic membrane (Reysenbach de Haan, 1956). This tympanic "finger" protrudes laterally from the bulla and is connected to the lateral bullar wall by a fibrous annulus. There is no obvious association with the wax core of the external canal.

In odontocetes, the external canal has no direct connection with the tympanic bulla. Ligaments join the posterolateral edge of the odontocete tympanic to the posterior margin of the mandibular ramus. The lateral wall of the odontocete tympanic has discrete areas of thin bone which align with the pan bone, an ovoid area of less dense bone on the mandible that may function as an acoustic window (Norris, 1969). The tympanic membrane in odontocetes is not membranous. Instead, it is a highly derived, calcified structure, the tympanic conus, which is fused at its distal and ventral margins with the tympanic bulla (Fig. 2). This complex of jaw, fat, and ossified tympanic membrane probably functions together to convey ultrasonic signals to the middle ear, but it is unclear whether this is the only channel for sound reception in odontocetes (Ketten, 1991).

Middle Ear

All cetacean middle ears are adapted to endure extreme pressures. There are no fine-walled, pneumatized areas analogous to the mastoid cavities. The middle ear cavity, defined by the walls of the tympanic, is lined with a thick, vascularized fibrous sheet, the corpus cavernosum. It has not been determined whether the intratympanic space is air-filled *in vivo*, but the elaborate structure and flexibility of mysticete tympanic membranes suggest it is likely. A potential acoustic difficulty for a diving mammal is that changing middle ear volumes would change the resonance characteristics of the middle ear. Neural bundles which penetrate the corpus cavernosum in *B. mysticetus* are speculated to be subdivisions of the trigeminal nerve (personal communication, D. Hillman). If correct, the trigeminal, which is a mixed sensory-motor nerve, may control the size or distension of the corpus cavernosum and therefore provide a mechanism for regulating middle ear volume (Ketten, unpublished). An analogous role in echolocation was proposed previously for the trigeminal; i. e., regulating the shape of the melon to control the "acoustic lens" for outgoing pulses (Ketten, 1991). The cetacean trigeminal and auditory nerves are the largest nerves known in mammals; however, no functional reason for the trigeminal's exceptional size has been demonstrated (Jansen and Jansen, 1969; Morgane and Jacobs, 1972). The dual role proposed here, regulating melon shape and middle ear volume, could account for large fiber densities in both mysticetes and odontocetes.

Other determinants of middle ear resonance characteristics are stiffness and mass of the ossicular chain. Stiffness improves the transmission of high frequencies while increases in mass and volume favor low frequencies (Webster, 1975). Like all other cetacean bone, the ossicles of odontocetes and mysticetes are large and dense. Although massive, ossicles in odontocetes are stiffened by bony struts and ligaments. A bony ridge, the processus gracilis (Fig. 2), fuses the malleus to the wall of the tympanic and the interossicular joints are stiffened with ligaments and a membranous sheath. In some Type I odontocetes, the annular stapedial ligament is calcified, but these data are insufficient to determine whether stapes fixation is an important determinant of Type I vs. Type II ears. Mysticete ossicles are equally massive but have none of the high frequency related specializations of odontocetes. The ossicles are not fused to the bulla and the stapes is fully mobile with a conventional fibrous annular ligament. Further, as noted earlier, the tympanic scales with animal size and is double the volume of the periotic. The mysticete middle ear cavity therefore is substantially larger than that of any odontocete. Thus, the mysticete middle ear consists of a large, open cavity with massive ossicles that are loosely joined; i. e., a characteristically low frequency ear.

The anatomical complexity of middle ear structures imply that the ossicular chain has at least some minimal function. Mysticetes and odontocetes differ chiefly in the rigidity of the ossicular chain and in the prospect, based on an elaborate tympanic structure, that mysticetes receive auditory stimuli primarily from the ear canal and not from the jaw. The composite of middle ear characteristics in mysticetes implies a low frequency ear. In contrast, all odontocetes have specializations for perceiving high frequencies, but until additional material is analyzed, it is not possible to determine whether differences exist in middle ear volume or stiffness of the ossicular chain that are related to species-specific ultrasonic ranges.

Inner Ear

The cetacean periotic houses the membranous labyrinth of the inner ear which contains the cochlea or auditory organ and the organs of position and acceleration that form the vestibular system.

Vestibular System

In all Cetacea, the vestibule is large but the semi-circular canals are substantially reduced, tapering to fine threads which do not form complete channels. Incomplete semi-circular canals have been reported previously in odontocetes (Ketten and Wartzok, 1990; Ketten, 1991) and abnormally small canal diameters were noted in earlier descriptions (Boenninghaus, 1903; Gray, 1951). While size is not a criterion for vestibular function, cetaceans are unique in having semicircular canals that are significantly smaller than the cochlear canal (Jansen and Jansen, 1969; Gray, 1951). Innervation is proportionately reduced as well; i. e., only 10% of the cetacean VIIIth nerve is devoted to vestibular fibers, as compared to 40% in most other mammals (Yamada, 1953; Jansen and Jansen, 1969; Morgane and Jacobs, 1972). No equivalent aberrations of the vestibular system have been found in any land mammal, which argues that reduced semi-circular canals are related to a fully aquatic lifestyle. One potential explanation is that fusion of the cervical vertebrae in Cetacea resulted in limited head movements and substantially fewer inputs to the vestibular system, leading to a loss of related receptors. If their semi-circular canals are vestigial, cetaceans receive only linear acceleration and gravity cues but no rotational or three-dimensional accelerational input. This may be highly adaptive for marine species, permitting rapid rotations without the nauseating side-effects so familiar to humans attempting similar manoeuvres.

Cochlea

All cetacean cochlea have the three conventional mammalian divisions: scala media (cochlear duct), scala tympani, and scala vestibuli. Detailed descriptions of odontocete cochlear ducts are available in Wever et al. (1971a, b, c, 1972) and Ketten (1984). This paper discusses in detail three cochlear features which influence resonance characteristics and frequency perception: basilar membrane dimensions, the lengths of the outer bony lamina, and proportions of the cochlear spiral.

The cetacean basilar membrane is a highly differentiated structure with substantial variations in length, thickness, and width (Fig. 3, Table 2). Basilar membrane lengths in Cetacea, like those of terrestrial mammals, scale isomorphically with body size. Greenwood (1961, 1962, 1990) used membrane lengths to estimate frequency ranges for land mammals, but these equations do not predict ranges accurately in marine mammals (Ketten, 1984, 1991). In Cetacea, cochlear length is correlated strongly with

Table 2. Membrane and Cochlear Spiral Measurements

Species	Cochlear Type	Turns	Membrane Length (mm)	Outer Lamina (mm)	Basal/Apical Width (µm)	Basal/Apical Thickness (µm)	Basal Diam. (mm)	Axial Height (mm)	Axial Pitch[1] (mm)	Basal Ratio[2]	Peak Frequency (kHz)
RECENT ODONTOCETI											
Inia geoffrensis	I	1.5	38	-	-	-	8.5	2.3	1.5	0.27	200
Phocoena phocoena	I	1.5	26	17.6	30/290	25/5	5.6	1.4	1.0	0.26	130
Grampus griseus	II	2.5	41	-	40/420	20/5	8.7	5.4	2.1	0.61	-
Lagenorhynchus albirostris	II	2.5	35	8.5	30/360	20/5	8.7	5.3	2.1	0.60	40
Stenella attenuata	II	2.5	37	8.4	40/400	20/5	8.6	4.4	1.8	0.51	60
Tursiops truncatus	II	2.25	41	10.3	30/380	25/5	9.5	5.0	2.2	0.53	70
Physeter catodon	I, II	1.75	54	-	-	-	11.7	3.6	2.0	0.30	-
RECENT MYSTICETI											
Balaenoptera acutorostrata	M	2.25	55	-	100/1500	-	12.8	7.5	3.0	0.59	-
Balaena mysticetus	M	2.25	61.3	<10	120/1670	7.5/2.5	14.3	8.2	3.4	0.57	<0.20
Balaenoptera physalus	M	-	-	-	100/2200	-	-	-	-	-	0.02
Eubalaena glacialis[3]	M	2.5	49.5	<8	125/1400	7/2.5	9.7	6	2.4	0.62	<0.20
Megaptera novaeangliae	M	2.5	54	-	-	-	12.1	7.5	3.0	0.62	<4.00
EXTINCT CETACEA[4]											
Dorudon osiris	I, II, M	2.5	-	-	-	-	8.2	7	2.8	0.85	-
Parietobalaena palmeri	M	2.3	-	-	-	-	13.5	6.6	2.9	0.49	-
Rhabdosteus spp.	I, II	1.5	-	-	-	-	9.5	3.4	2.3	0.36	-
Squalodon spp.	I, II	1.6	-	-	-	-	10.5	-	-	-	-
Zygorhiza kochii	I, II, M	2.0	-	-	-	-	10.5	6.8	3.4	0.64	-

[1] $\frac{\text{axial height}}{\text{turns}}$

[2] $\frac{\text{axial height}}{\text{basal turn diameter}}$

[3] neonate

[4] Compiled from Kellogg (1936); Fleischer (1976).

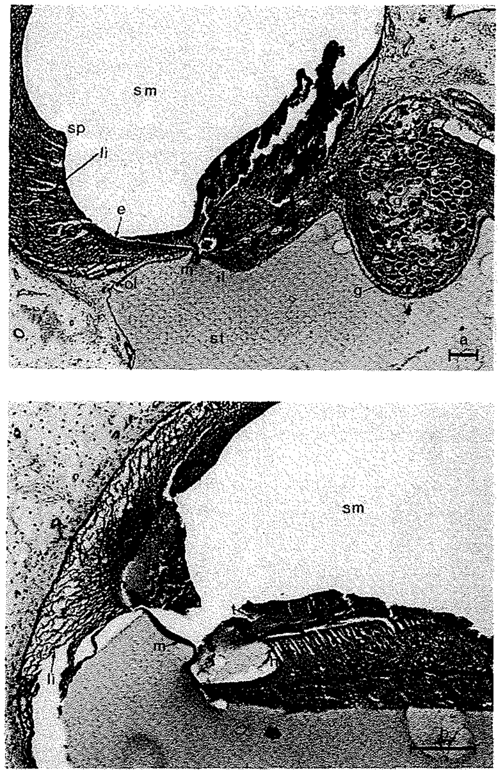
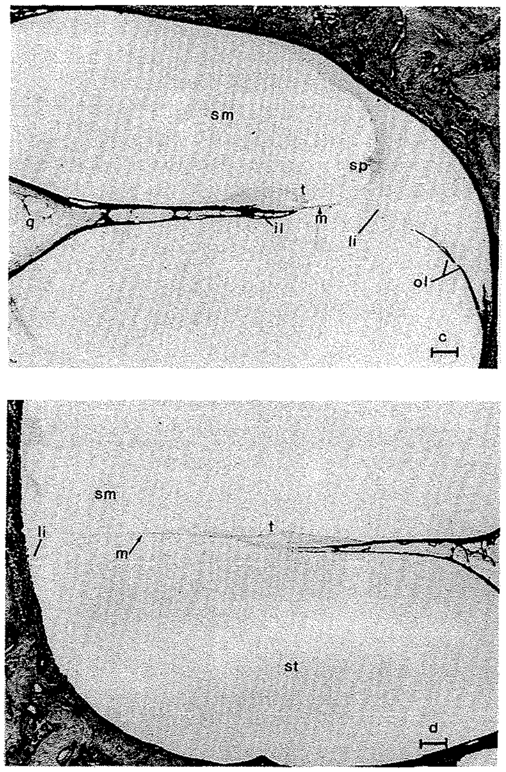


Fig. 3. Cetacean cochlear duct. Light micrographs of 20 µm sections of basal and apical regions of scala media (sm). Tissues were preserved 5 hours to 4 days postmortem from stranded animals. Several preservation artifacts are evident, including disruption of Reissner's membrane and necrotic or absent Organ of Corti. Basilar membranes and spiral ganglion cells however were well preserved in all specimens. Scale bars represent 100 µm. (Odontocete material reprinted with permission from Ketten and Wartzok, 1990).

(a) A section in the upper basal turn of Phocoena phocoena (Type I) illustrates the classic odontocete features of an osseous outer lamina and heavy cellular buttressing. The basilar membrane (m) measures 45 µm x 20 µm and is stretched between inner (il) and outer (ol) ossified spiral laminae. The "ersatzzellen" cellular layer (e) is found only in the basal turn in odontocetes below the spiral prominence (sp). The spiral ganglion bulge (g) protruding into scala tympani (st) is characteristic of odontocetes but is not found in Mysticeti.

(b) In the apical region of Phocoena, the osseous outer lamina has disappeared, and the membrane has thinned and broadened. The basilar membrane is 200 µm wide and 10 µm deep. Only the spiral ligament (li) supports the lateral edge of the basilar membrane. Remnants of the Organ of Corti are attached to the tectorial membrane (t) near Huschke's auditory teeth (h).

(c) In E. glacialis, the basal basilar membrane (m) is 7 µm x 125 µm. The spiral prominence (sp) is ev-



ident, but like all other cell layers is reduced substantially compared to those in the odontocete. A narrow outer (ol) ossified spiral lamina is attached to the tympanal edge of the spiral ligament (li) and does not contact the basilar membrane. The light staining of ganglion cells (g) may be a preservation artifact.

(d) In the apical region of *E. glacialis*, the membrane is a fine sheet 2 μm deep and 1200 μm wide. The spiral ligament and inner laminae are less robust than in the basal region.

animal size ($0.8 < r < 0.95$), but there is no significant correlation for length and frequency. Thickness and width, however, are highly correlated with hearing capacity. In all mammalian cochlea, the basilar membrane is a tonotopic resonator. Resonant frequency of the basilar membrane, as in any system, is inversely related to the ratio of its stiffness and mass. If stiffness increases, so does the resonant frequency; i. e., the frequency at a constant intensity which causes the largest displacement of the membrane. Since the basilar membrane has a fairly uniform cellular structure, stiffness and mass are dictated largely by thickness and width. Thickness and width of the membrane vary inversely from base to apex. The membrane is narrow and thick at the base and gradually thins and broadens towards the apex. Highest frequencies are encoded in the stiffer basal end with progressively lower frequencies encoded as it becomes more pliant apically. In land mammals, maximum frequency is inversely related to basal turn membrane width (Pye, 1972; Brown and Pye, 1975;

Manley, 1975; West, 1985). Ketten and Wartzok (1990) showed a similar relationship for odontocetes. In most odontocete species, basilar membrane width is 30 µm at the base and increases to 300 - 500 µm apically. Basal widths of odontocetes are similar to those of bats and one third that of humans (Firbas, 1972; Schuknecht and Gulya, 1986). By contrast, mysticete basilar membranes are consistently wider (Fig. 3; Table 2), varying from 100 µm at the base to 1600 µm at the apex. The basal dimension is similar to that of humans but 3X that of Odontoceti. The apical widths in mysticetes are 3X human, 5X odontocete, and 1.2X the estimates for apical widths in African elephants which are known to perceive infrasonics (Payne et al., 1986; Ketten and Northrup, in preparation). Based on width alone, odontocete and mysticete basilar membranes are highly differentiated structures capable of exceptionally wide but very different ranges of frequency response.

Thickness to width ratios are a more significant correlate of frequency than any single basilar membrane dimension (Ketten, 1991). In odontocetes, thickness decreases from 25 µm to 5 µm base to apex (Table 2). Therefore, a typical cross-section of an odontocete basilar membrane is square at the base and rectangular apically. Mysticete membranes are thin oblongs throughout,

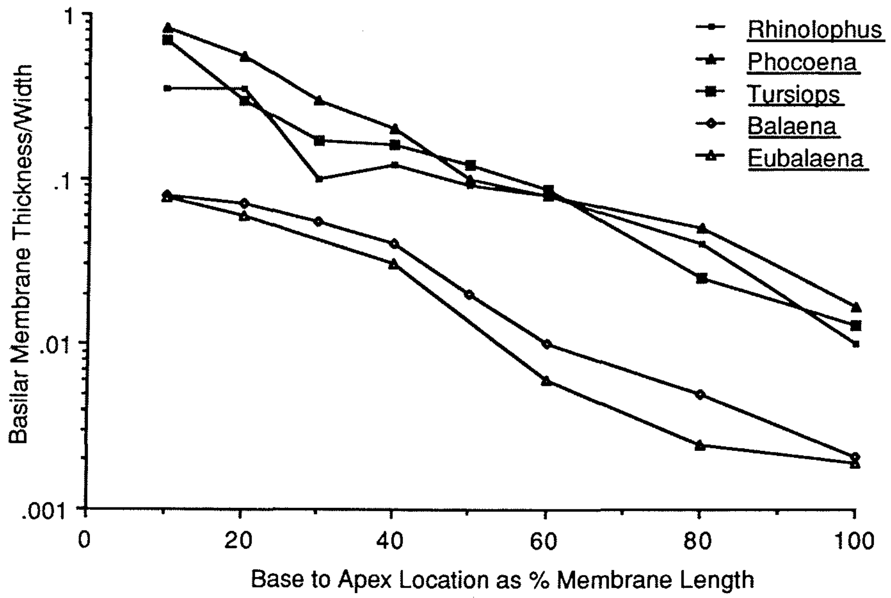


Fig. 4. Basilar membrane ratios. Average thickness:width ratios for the horseshoe bat (Rhinolophus ferrumequinum) (Bruns, 1976), harbour porpoise (Phocoena phocoena), bottlenosed dolphin (Tursiops truncatus), bowhead whale (Balaena mysticetus) and right whale (Eubalaena glacialis) are plotted as a percentage of cochlear length. High values for the bat, porpoise and dolphin reflect a thicker, stiffer membrane that responds to ultrasonic frequencies. The slopes are similar in all four Cetacea, but mysticete values average 10% those of odontocetes.

varying in thickness between 7 μm at the base to 2 μm at the apex. Comparisons of bat, odontocete, and mysticete basilar membrane ratios (Fig. 4) reveal that echolocators have significantly higher basal ratios than mysticetes and that odontocete ratios are higher than for the bat in the most basal regions where ultrasonics are encoded. Differences in basal ratios are consistent with species differences in peak ultrasonic frequency. Phocoena, a Type I odontocete, has the maximum basal ratio of 0.9 and a peak frequency of 130 kHz. Tursiops, a Type II odontocete, has a ratio of 0.7 and a peak signal of 70 kHz, and Rhinolophus, a bat, a 0.3 ratio and a 40 kHz echolocation signal. All three have apical ratios near 0.01. Mysticete ratios range 0.1 to 0.001 base to apex; i. e., the mysticete basal ratios are equivalent to mid-apical ratios in the three echolocators and decrease steadily to a value one-tenth that of odontocetes at the apex. The exceptionally low apical ratio in Mysticeti is consistent with a broad, flaccid membrane that may encode infrasonics.

A striking feature of odontocete basilar membranes is that they are supported by extensive outer bony laminae. In terrestrial mammals, ossified outer spiral laminae are found in very high frequency ears (Reysenbach de Haan, 1956; Sales and Pye, 1974). Thick outer bony laminae are present throughout the basal turn in all odontocetes (Table 2), and the proportional extent of outer laminae are a principal correlate of odontocete ultrasonic frequency ranges (Ketten and Wartzok, 1990). The outer lamina in the lower basal turn in all odontocetes is heavily calcified and is 30 to 40 μm thick, matching the depth of the basilar membrane (Fig. 3). Thus, in the basal, high frequency region of the cochlea, odontocete basilar membranes resemble thick girders, stiffened by attachments at both margins to a rigid bony shelf. Length of outer laminae differ in Type I and Type II odontocetes. In Type I echolocators with peak frequencies above 100 kHz an outer lamina is present for 60% of the cochlear duct (Table 2; Fig. 5). Type II echolocators with typical peak frequencies of 40 to 80 kHz have a bony anchor for 25 to 30% of the duct. The Type I basilar membrane therefore is coupled tightly to a stiff ledge for twice as much of its length as a Type II membrane. In regions where Type I and Type II membranes have similar thickness:width ratios, longer outer laminae in Type I cochlea would increase membrane stiffness and resonant frequency in comparison to a Type II membrane without bony support. Like membrane ratios, differences in the extent or proportion of outer bony laminae are an important mechanistic key to species differences in ultrasonic ranges.

Both inner and outer laminae are present in mysticetes but they are morphologically and functionally very different from those of odontocetes. The inner laminae are infiltrated with multiple, large lumina, producing a spongy and fragile, reticulated appearance (Fig. 3). Mysticete outer laminae are narrow spicules located on the tympanal edge of the spiral ligament. They do not attach to the basilar membrane and they disappear within the first half turn. Unlike the spiral laminae of odontocetes, mysticete outer laminae have no direct role in basilar membrane support. The broad, thin membrane attaches only to the flexible spiral ligament. It is likely that the spike-like outer lamina in mysticetes is a remnant of an ancestral condition rather than a functional acoustic structure and that basilar membrane ratios and cellular mass are the principal factors deter

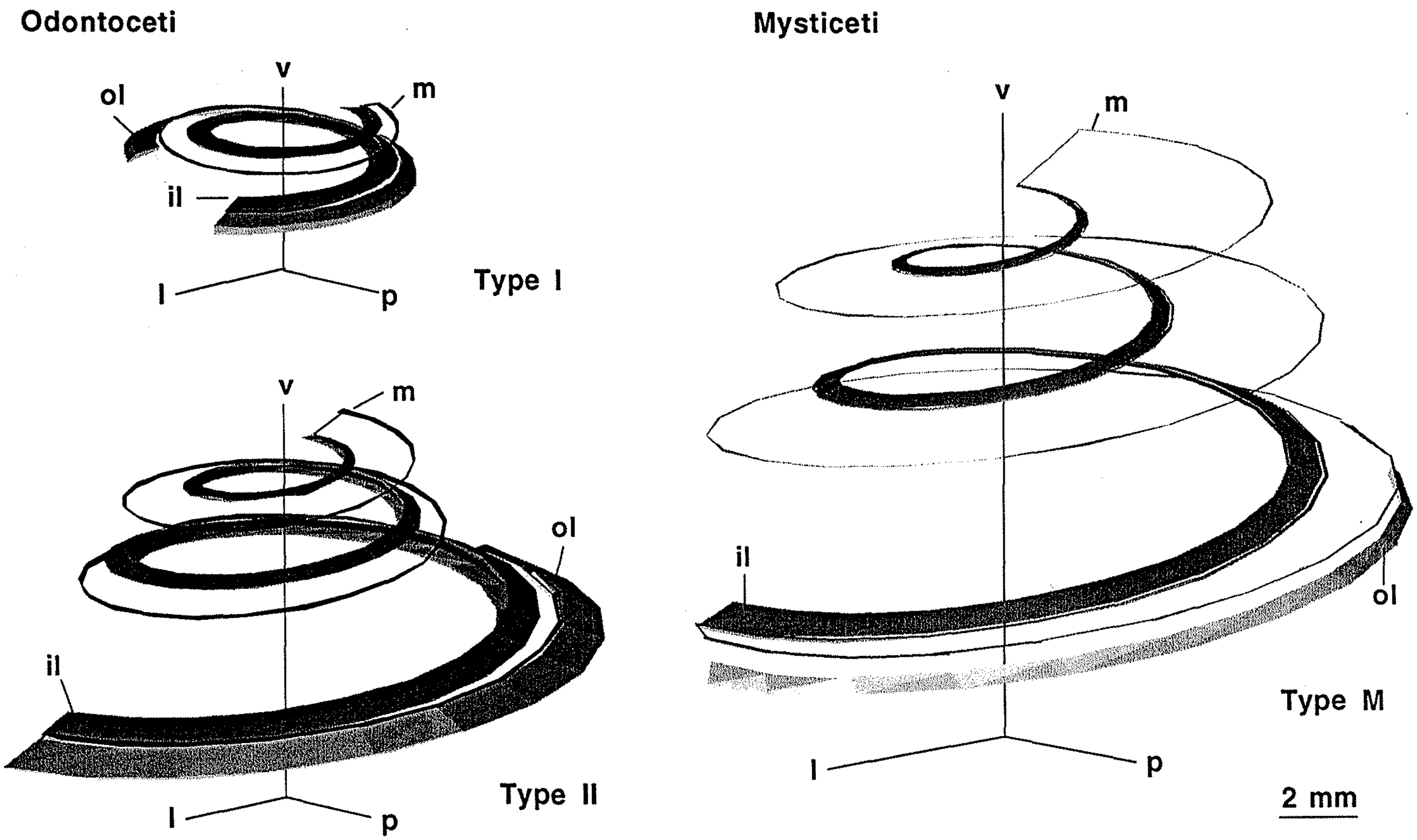


Fig. 5. Basilar membrane and spiral laminae distributions in Cetacea. Three-dimensional schematics summarize major cochlear duct components in Type I, Type II, and Type M inner ears. The cochlea are shown inverted from <u>in vivo</u> orientations. (il) inner osseous spiral lamina; (m) basilar membrane; (ol) outer osseous spiral lamina; (l) lateral; (p) posterior; (v) ventral.

mining mysticete frequency ranges. To date, few mysticete species have been analyzed for very low frequency sensitivity, but the inner and middle ear anatomy argues strongly that most perceive infrasonic sounds.

Multivariate analyses of cochlear spiral measurements of extant species (Table 2) show that 91% of the variance amongst species is attributable to the ratio of body size to spiral geometry and that frequency groups are predicted reliably at 0.1% confidence level by basilar membrane ratios, turns, pitch, and basal ratios. Peak frequency is strongly negatively correlated ($-0.97< r <-0.8$) with all spiral variables except scalae length and basal diameter. These variables are positively correlated with animal length. When the spiral data are combined with basilar membrane and spiral laminae dimensions, they produce three cochlear formats that are consistent with the acoustic divisions. Differences in membrane dimensions and membrane buttressing are obvious distinctions among these formats. Type I cochlea have proportionately twice as much membrane supported by bony laminae as Type II. Mysticete laminae are neither strong nor extensive. The basal region of the mysticete membrane is three times as wide and one-third as thick as that of odontocetes; at the apex it is four times the width and half the thickness of odontocete membranes. The Type II membrane is broader than the Type I at the apex, suggesting Type II species may resolve lower frequencies than Type I. Differences in basal ratios and laminar support imply Type I cochlea have a higher maximum frequency but poorer resolution of lower frequencies. Type M cochlea are large and have less stiff membranes which are tuned to substantially lower frequencies than those of Type I or Type II cochlea. Three-dimensional reconstructions illustrate the major features of each cochlear type (Fig. 5). Type I and II spirals occur exclusively in Odontoceti. Type I are shallow equiradial spirals (< 2 turns, pitch <1.5); Type II are steep equiangular spirals (> 2 turns, pitch 2 to 2.5). The mysticete data imply broad, equiangular, multi-turn spirals with a significantly steeper pitch (>3). Like the acoustic category, this format is designated Type M. It should be noted, however, that although the available mysticete data are consistent, they were obtained from few individuals and the results are tentative.

Extinct Cetacean Ears

It is difficult to judge the level of aquatic adaptation of the most ancient archaeocetes, the Protocetidae (Fig. 1), since little is known of their post-cranial skeleton and cranial remnants show few changes that would indicate an aquatic lifestyle. Teeth and sinus patterns suggest they were high frequency predators (Gingerich and Russell, 1981; Gingerich et al., 1983). They have a thin zygomatic arch, a large concave mandible, and a well-defined periotic, but this is considered a "pre-adaptive" feature from Mesonychidae since separate periotics also are found in ungulates (Barnes and Mitchell, 1978; Barnes et al., 1985; Oelschläger, 1986, 1990). The tympanic in protocetids has four articulations with the squamosal and basioccipital (Gingerich and Russell, 1981), and Gingerich et al. (1983) concluded that protocetids were basically amphibious, freshwater carnivores and were not fully aquatic.

Late Eocenic Basilosauridae exhibit a mixture of primitive and derived characters and are the hypothetical stem point for the separation of mysticete and odontocete lineages (Fig. 1).

Some basilosaurids retain intermediate hindlimbs that are completely formed but too insubstantial for terrestrial locomotion (Gingerich et al., 1990). All have one or more bullar modifications similar to modern Cetacea. Their most primitive auditory characteristics are anterior and posterior bullar flanges that wedge between the squamosal and occipital, but smaller dorudontine basilosaurids (see D. osiris, Z. kochii Table 2, Figs. 1, 6) also have enlarged sinuses, massive ossicles, and a periotic decoupled from the mastoid (Kellogg, 1936; Oelschläger, 1986). Like mysticetes, they have an inflated, bulbous tympanic but, like odontocetes, the periotic is distinctly ovoid and strongly resembles those of modern Physeteridae. Cochlear measurements also are combinations of Type I, II, and M parameters. Dorudon and Zygorhiza (Table 2) have steep, two turn spirals with mixed axial pitch and basal ratios. Dorudontines, at least in terms of inner ear structure, appear to have a functional aquatic ear, but

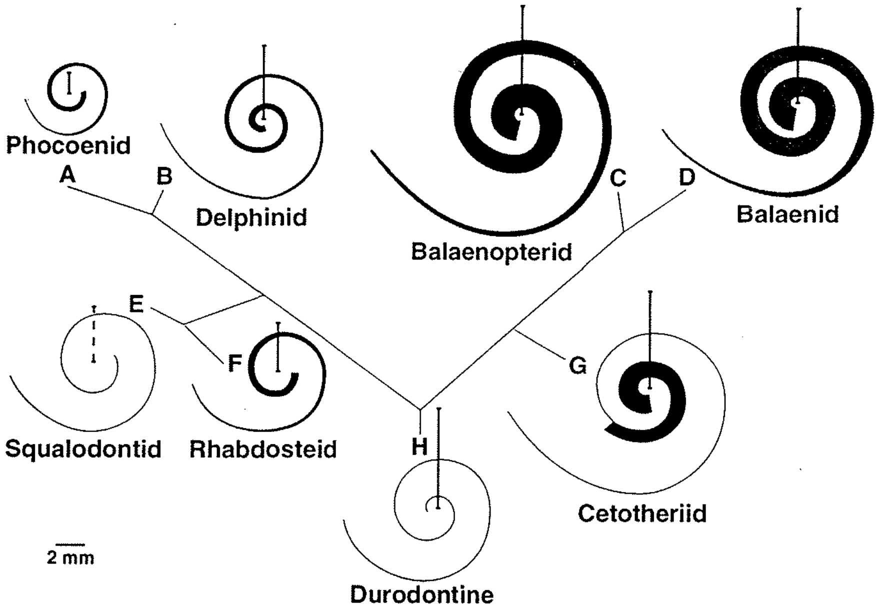


Fig. 6. Two-dimensional basilar membrane reconstructions. Reconstructions based on spiral data (Table 2) and interlaminar distances (Fleischer, 1976) illustrate the two dimensional profile of the basilar membrane in four extinct and four extant species. Basilar membrane widths are represented by filled areas; vertical bars represent axial height. Only the midline of the spiral is shown for extinct species for which laminar data are not available. Based on these schematics, cetaceans can be divided into 5 evolutionary stages: mixed high and low frequency ancestral (H Zygorhiza kochii); high frequency stem odontocete (E Squalodon; F Rhabdosteus); Type II echolocator (B Tursiops truncatus); high ultrasonic Type I echolocator (A Phocoena phocoena); and low frequency stem or modern mysticete (C Balaenoptera acutorostrata; D Eubalaena glacialis; G Parietobalaena). (revised Ketten, 1992, after Ketten, 1991.)

it is neither distinctively odontocete nor mysticete in format. They are the probable ancestors of squalodonts which led to modern odontocetes, but they have several acoustic features in common with later Mysticeti.

Within 10 million years of dorudontine extinction, Oligocene Squalodontoidae had acquired skull traits consistent with underwater echolocation including a hollow mandible and complete tympano-periotic isolation (Barnes et al., 1985). Miocene squalodontoids; e. g., Rhabdosteus and Squalodon (Table 2, Fig. 6), have distinctly odontocete cochlea with mixed Type I and Type II spiral parameters. Their bullae, similarly, show mixed characteristics of modern platanistid, physeterid, and ziphiid forms (Kellogg, 1936). In other words, the earliest recognized Odontoceti already have the functional acoustic anatomy of modern odontocetes and were probably carnivorous echolocators. From this point, odontocetes developed along family lines which are still fully represented (Fig. 1). Ironically, no cochlear canal data are available yet for recent ancestors of modern Cetacea, and it is not known at what point Type I and Type II spirals differentiated.

Although mysticetes have some primitive osteological features; e. g., long anterior and posterior cranial flanges and hemispheric bullae, they appear comparatively recently in the fossil record and generally are considered modern (Fig. 1, Barnes et al., 1985). A distinctively Type M cochlear format, consistent with a low frequency, non-echolocating ear, is not apparent until Parietobalaena in the early Miocene (Table 2; Fig. 6). The absence of a distinctively mysticete structure in the early fossil record and the number of shared characters in Mysticeti and Odontoceti; e. g., extensive middle ear sinuses and separate tympanics and periotics, make it unlikely that mysticetes arose earlier in the fossil record and developed in parallel with odontocetes. A more probable theory is that all Cetacea developed from late Eocene Archaeoceti. The common ancestor would have been a high frequency animal from which low frequency cetacean ears subsequently evolved.

CONCLUSIONS

Aquatic influences are most evident in the gross anatomy of cetacean auditory systems. There are no pinnae and no pneumatized areas analogous to land mammal mastoids. All cetacean periotics, tympanics, and ossicles are constructed similarly of massive, porcelaneous bone. The odontocete tympano-periotic complex is detached completely and isolated acoustically from the skull. The location and isolation of odontocete bullae support the "pan bone" theory of transmission of ultrasonic signals to the middle ear via a fatty acoustic wave guide in the mandible. The path of sound reception in mysticetes is unknown, but they have bony skull connections and a highly derived tympanic membrane which connects to the external auditory canal.

Modern Cetacea have three inner ear formats which coincide with major acoustic groups: low to infrasonic Type M mysticetes; upper range ultrasonic Type I odontocetes; and lower range ultrasonic Type II odontocetes. Type I and Type II cochlea clearly are adapted for ultrasonic perception, with exceptionally stiff basilar membranes. Basilar membrane thickness to width ratios are higher for the basal turn of odontocetes than for any other mammal. Mysticete (Type M) cochlea have exceptionally wide and thin basilar membranes, implying they are specialized for encoding infrasonics.

These cochlear formats and frequency ranges also coincide with specific habitats and feeding behaviors. In modern Cetacea, Type I spirals have been found only in the highest frequency group of known mammals, inshore phocoenids and riverine platanistid dolphins (Purves and Pilleri, 1983; Ketten, 1984; Feng et al., 1990). These species live in turbid waters and use ultra-high frequency, short wavelength signals that can convey fine detail of nearby objects. Type II formats are common in offshore and pelagic delphinids. Their slightly broader, less rigid membranes suggest a better low frequency resolution than Type I as well as lower frequency echolocation signals. This is consistent with highly social species that use 1-10 kHz signals to communicate and lower frequency, longer wavelength ultrasonic signals to detect predators and prey over moderate to long distances. Type M formats are known only in large, pelagic opportunistic feeders. A specific advantage for low to infrasonic frequencies has not yet been demonstrated although several possibilities exist. First, mysticete ears may simply be tuned to their own sounds, which are constrained mechanically by a large larynx or resonating cavity to low frequencies. Second, it has been suggested, but not demonstrated, that extremely low frequencies could be used to communicate over long distances (Watkins and Wartzok, 1985). Finally, infrasonics could be used in off-shore navigation and long-range migrations to detect major topographic details (C. Clark, personal communication). Any or all of these hypotheses are possible, but to answer such questions a better understanding of the sensitivity and vocalizations of many more mysticete species is required.

General auditory characteristics of extinct Cetacea can be estimated by combining cochlear morphometry with the characteristics of tympano-periotic-skull connections. Structures in protocetids imply the earliest Cetacea were amphibious predators. Later Archaeoceti were fully aquatic with enlarged air sinuses and few skull attachments. Oligocene squalodonts had an isolated tympano-periotic complex and cochlear spirals with mixed Type I and Type II characteristics and were at least proto-aquatic echolocators. Paleobalaenids have a low frequency Type M cochlear format and were probably pelagic omnivores. The chronology of auditory structures in extinct species imply all Cetacea are derived from high not low frequency Mesonychidae, but there is little evidence for early echolocation.

Based on cochlear formats, the proposed terrestrial ancestor of Cetacea was a small, high frequency carnivorous mammal that exploited an aquatic niche. Aquatic echolocators developed soon after, followed by low to infrasonic balaenid ears. Are these speculations logically consistent with other evidence from the fossil record? On entering the water, the ancestral mesonychid faced substantial competition from ancient, well-adapted predators like the shark. It is reasonable that a nocturnal predator would be more successful initially than a large herbivore in this environment. To be an echolocator, an animal must both generate a directional signal and perceive its echo. In the absence of any evidence for a melon analogue in early Archaeoceti, it is unlikely they were effective *aquatic* echolocators. Modern odontocetes are true echolocators, not simple ultrasonic receptors, and it has not yet been determined when an ultrasonic source and receiver coexisted in Cetacea.

Mysticetes appear geologically near the time new oceans opened in southern latitudes (Fordyce, 1977, 1980). Even today these high latitude waters are terrifically productive, but they also are substantially colder than the original warm, shallow Tethys Sea. Ancient cetaceans invading polar regions from low latitude temperate seas would find an abundance of food and less competition but a greater risk of hypothermia. Since surface area increases more slowly than volume, bigger mammals can have a substantial metabolic advantage in cold water; i.e, a large whale is a warmer whale. It is likely that increased animal size coincided with success at surviving in cold seas. Cochlea scale isometrically with animal size. If basilar membranes broadened and lengthened without thickening as a consequence of increasing animal size, a lower frequency cochlea would necessarily result. With less pressure to echolocate in more productive waters, decreased sensitivity to higher frequencies in a large cochlea would not be a major disadvantage. Therefore, as larger Mysticeti evolved, scaling of cochlear structures may have mechanically constrained the resonance characteristics of the inner ear to progressively lower frequencies. If so, colder, richer feeding grounds provided the selective pressure for large baleen whales, and low frequency ears were a coincident and relatively recent sensory development in Cetacea.

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