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Cover: The image is a 3D reconstruction from CT scans of a left inner ear of an adult male Cuvier's beaked whale (*Ziphius cavirostris*). The image shows the ear from a lateral view with the facial nerve in the foreground. The auditory nerve canal and cochlear canals are just above and behind the facial nerve. Photo courtesy of Darlene R. Ketten.

Library of Congress Cataloging-in-Publication Data
Hearing by whales and dolphins / [edited by] Whitlow Au, Arthur N. Popper, Richard R. Fay.
p. cm.—(Springer handbook of auditory research)
Includes bibliographical references.
ISBN 0-387-94906-2 (hardcover : alk. paper)
1. Dolphins—Physiology. 2. Whales—Physiology. 3. Hearing.
I. Au, Whitlow W.L. II. Popper, Arthur N. III. Fay, Richard R.
IV. Series.
QL737.C432H425 2000
573.8'9195—dc21 99-40947

Printed on acid-free paper.

Production managed by Terry Kornak; manufacturing supervised by Erica Bresler.
Typeset by Best-set Typesetter Ltd., Hong Kong
Printed and bound by Maple-Vail Book Manufacturing Group, York, PA.
Printed in the United States of America.

9 8 7 6 5 4 3 2 1

ISBN 0-387-94906-2 Springer-Verlag New York Berlin Heidelberg SPIN 10558704

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Hearing by Whales and Dolphins

With 152 Illustrations

Springer

2
Cetacean Ears

DARLENE R. KETTEN

1. Introduction

Whales and dolphins are majestic, elusive, charismatic creatures that couple exceptional grace with enormous power. These features may account for much of humanity's enduring fascination with whales, but they are terrible reasons for studying their auditory systems. The principal reason whale ears are worth investigating is . . . Ginger Rogers. Ginger Rogers and Fred Astaire were a famous dance team. Mr. Astaire was renowned for his grace and agility. What people rarely note is that Ms. Rogers not only matched her partner step for step, she did it wearing a cumbersome gown, in high heels, and backwards. Just as Ginger kept pace with Fred but in a different orientation and with added burdens, whales hear as well as land mammals but in a different medium with special acoustic burdens.

This chapter provides an overview of the anatomical foundation of whale hearing. It takes a functional, comparative approach, emphasizing how structures unique to peripheral auditory systems in the two extant suborders of Cetacea, the Odontoceti (toothed whales, porpoises, and dolphins) and Mysticeti (rorquals and baleen whales) relate to the ability of a mammalian ear to hear in water. Commonalities with land mammal ears are discussed in terms of their significance for fundamental hearing mechanisms. Anatomical specializations found across land mammal, odontocete, and mysticete ears are discussed in terms of the role they play in determining species-specific frequency ranges as adaptations to cross-media behaviors and niche substructure.

The primary task of this chapter is to deconstruct whale and dolphin ears to determine which elements are simply mammalian and which are aquatic or devoted to special acoustic tasks. The concept that there is a significant relationship between ear structure and hearing capacity, and that both are related to the animal's niche, is particularly relevant for understanding whale hearing. Analyzing how hearing capacity and auditory structures covary in a range of species can provide important insights into fundamental hearing mechanisms that take place in the auditory periphery

(Fay 1992). If we extend the analyses to ultra- and infrasonic animals, we can learn substantially more about how hearing ranges are determined as well as how to detect and use physical cues that are normally imperceptible to us (e.g., Hinchcliffe and Pye 1968; Webster and Webster 1975). Using ears adapted to different media, we can begin to explore how the auditory system deals with physical features of acoustic cues.

Whales and dolphins fit all three criteria for productive analyses. Even more important, cetacean ears are derived from land mammal auditory systems but may now be more acoustically and physically diverse than any related land mammal group. Whales originally had air-adapted ears. All cetaceans are descended from mesonychid condylarths, catlike, carnivorous, land-based ungulates that became amphibious in the Eocene, probably to exploit food-rich near-shore waters (Thewissen 1998). In the intervening 50 to 60 million years, as these condylarths gradually transformed from hoofed waders into full-fledged, flippered whales, every portion of their anatomy was physically and functionally reshaped to accommodate life in water. Their air-adapted high-frequency mammalian ears had to be coupled to water-borne sound for hearing to remain functional, but ear evolution took place in tandem with other body reconfigurations. Just as the physical demands of operating in water exacted a structural price in the locomotory and thermoregulatory systems of marine mammals, the physics of swimming, diving, and resting on the surface reshaped the head. Modern cetaceans have the most derived cranial structure of any mammal (Thewissen 1998; Cranford, Chapter 3). "Telescoping," a term coined by Miller (1923), refers to the evolutionary revamping of the cetacean face. As the anterior cranial structures pushed up and back, one bone sliding over another, every facet of the auditory periphery was modified: pinnae and external auditory canals were lost, the middle and inner ear capsules fused, and a new ear complex with the bone density of enamel erupted from its intracranial position to settle into a newly formed, cavernous peribullar sinus. Today, all cetaceans are absolute aquatics, unable to move, reproduce, or feed on land, and their ears are so fully adapted to water-borne sound that they may no longer be able to detect or interpret airborne signals. Consequently they have ancestral ear elements in common with land mammals but have added hydro-related specializations that hold clues to media-dependent hearing mechanisms.

Currently, there are 76 extant species of whales, ranging in size from the harbor porpoise (*Phocoena phocoena*, 1 m, 55 kg) to the blue whale (*Balaenoptera musculus*, 40 m, 93,869 kg) (Nowak 1991). Most are members of the suborder Odontoceti (65 species), all of which produce ultrasonic signals and are presumed to echolocate (Nachtigall et al., Chapter 8; Au, Chapter 9). The second suborder, the Mysticeti (rorquals, right, and baleen whales; 11 species) are pelagic omnivores that produce intense infrasonic signals, the function of which remains unknown. Therefore, as a group, they

employ the broadest known acoustic range, spanning low infrasonic (10 Hz) to high ultrasonic (200 kHz) frequencies.

Hearing is arguably the primary sensory and communication channel for cetaceans, and we expect all whale ears are highly evolved. Comparative functional anatomy studies may be the only way to understand the breadth of whale ears because the majority of whale species are not approachable by conventional audiometry. Only about 13% of all species have ever been tested, all those tested are from one suborder, and nearly all are from one family. Given the diversity of habitats, behaviors, and sizes that cetaceans encompass, it would be naive to expect that data from a few species or one division will provide a full picture of cetacean hearing. By analyzing the structure of a broad spectrum of cetacean ears, we can gain insights not only into whale hearing and aquatic adaptations but also into some basic hearing issues. First, similarities between land and aquatic mammal ears are likely to be related to fundamental mammalian ear mechanisms. Second, structures that are common among aquatic species but lacking or significantly different in land mammals are probably key elements for transducing water-borne sound. Third, because of extreme variations among whales in animal size, sound use patterns, and habitats, differences that we see among whale and dolphin ears that have land mammal parallels can teach us something about how auditory anatomy is shaped by physiologic and environmental factors.

Therefore, the most cogent reason for studying whale ears is simply to find out how they to do it, that is, how do they hear—at high speed, under pressure, and underwater.

2. Comparative Acoustics: Sound in Air Versus Water

To understand ears, it is imperative to understand not only how they were evolutionarily tailored by the fundamental needs of the animal but also how the information options were constrained by the acoustic properties of the medium in which each species evolved. To properly assess whale ears and place them in a general mammalian hearing context, it is necessary to understand how the physical properties of water vs. air affect acoustic cues.

Because water is denser than air, sound in water travels faster and with less attenuation than sound in air. Sound speed (c) in moist ambient surface air is approximately 340 m/s. Sound speed in sea water averages 1,530 m/s but will vary with any factor affecting density. The principal physical factors affecting density in sea water are salinity, temperature, and pressure. Because these factors act synergistically, the oceans have highly variable sound profiles that change both seasonally and regionally. This raises the interesting possibility that a whale during a few thousand meter dive could experience theoretically a 10% variation in ambient acoustic velocities, but

for this discussion, we will assume that cetaceans deal with in-water sound speed and wave lengths that are simply 4.5 times greater than in air.

Mammalian ears are generally considered to be intensity detectors (Yost 1994), although the theory that some marine mammals are simple pressure detectors has been proposed. Pressure and intensity are related but are not synonymous. In-air measures of hearing make little distinction between the two, but modeling an ear in water as a pressure versus intensity transducer has far-reaching consequences.

Sound intensity (I) is the acoustic power impinging on a surface perpendicular to the direction of sound propagation; i.e., the sound energy per second per unit area. Intensity is power/unit area (I = P/a). Therefore, intensity can be rewritten as the product of sound pressure (p) and vibration velocity (v): I = pv. For a traveling spherical wave, the velocity component becomes particle velocity (u), which is defined in terms of effective sound pressure (p) and the characteristic impedance of the medium, which is the product of the speed of sound (c) and density of the medium (ρ): u(x,t) = p/ρc.

For an instantaneous sound pressure in an outward traveling plane wave, intensity in terms of pressure, density, and sound speed is: I = pv = p(p/ρc) = $p^2/\rho c$. If we assume average sound speeds and densities for surface air (c = 340 m/s; r = 0.0013 g/cc) and sea water (c = 1,530 m/s; ρ = 1.03 g/cc):

$$I_{air} = p^2/(340\,m/s)(0.0013\,g/cc) = p^2/(0.442\,g\text{-}m/s\text{-}cc)$$

$$I_{water} = p^2/(1{,}530\,m/s)(1.03\,g/cc) = p^2/(1{,}575\,g\text{-}m/s\text{-}cc)$$

To understand the sensory implications of these equations, consider a hypothetical, perfectly amphibious mammal. To hear equally well in water and in air with an intensity-based ear would require the same acoustic power/unit area in water as in air; that is, ($I_{air} = I_{water}$):

$$I_{air} = p^2_{air}/(0.442\,g\text{-}m/s\text{-}cc) = p^2_{water}/(1{,}575\,g\text{-}m/s\text{-}cc) = I_{water}$$

or $\quad p^2_{air}(3{,}565.4) = p^2_{water} \quad$ and $\quad p_{air}(59.7) = p_{water}$

which means this theoretical transmedia ear would require a received sound pressure nearly 60-fold greater in water than in air for an equivalent acoustic percept.

Although the most appropriate measure of intensity is watts/m^2, we capitalize on the fact that intensity is related to the mean square pressure of the sound wave over time and use effective sound pressure level (SPL), which is easier to determine, to describe hearing thresholds. Sound pressure levels are conventionally expressed in decibels (dB), defined as: dB SPL = $10\log(p^2_m/p^2_r) = 20\log(p_m/p_r)$ where p_m is the pressure measured and p_r is an arbitrary reference pressure. Given identical reference pressures, our idealized amphiboid needs a sound level ~35.5 dB greater in water than in air ($10\log 3{,}565.4$), but conventionally, two reference pressures are used. For airborne sound, the conventional reference is 20 µPa rms derived from the minimum level required for a normal human ear to detect 2 kHz (typically our most sensitive frequency), which is a diffuse field pressure of 20 µPa, which has an acoustic power density of approximately 1 picowatt/m^2. Using this pressure as a reference standard, the normal minimum human threshold in air is 0 dB (re 20 µPa rms). For underwater sound, the conventional reference was arbitrarily set at 1 µPa (American National Standards Institute, 1968; see Au 1993).

Therefore, with different reference pressure conventions for air and water, a sound must have a measured pressure 61.5 dB higher in water (re 1 µPa) than in air (re 20 µPa), to have an equivalent intensity.

One approach to the intensity versus pressure issue would be to look for clues in the hearing thresholds of land versus aquatic mammals; that is, are all the thresholds offset by 26 dB or by 61.5 dB? Unfortunately, best thresholds for marine mammals range anywhere from ~25 dB re 1 µPa to more than 60 dB re 1 µPa (Richardson et al. 1995) with the most common odontocete values being about 45 dB re 1 µPa (Nachtigall et al., Chapter 8), which ironically is the most confounding value. Clearly, cetaceans are not going to make it easy for us.

While these equations give a theoretical background for functional ear analyses, they also point out that these numbers are only idealized comparisons. Broad spectrum, cross-species, cross-media, and cross-paradigm studies have far more complex problems than using different referents; in some cases, comparisons may prove to be impossible. Both subtle and gross environmental effects (salinity, temperature, depth, ambient noise, surface reflection, etc.) as well as individual state (motivation, age, pathology) influence results. In most land mammal hearing studies, the test animals are juveniles raised in minimal ambient noise and tested in anechoic conditions. Marine mammal hearing data are commonly obtained underwater with normal ambient noise and the test subject is an adult animal for which there is no auditory history. Cross-media anatomical studies are somewhat less problematic, but the possibility that the results are skewed by small sample size or because of pathological or congenital abnormalities must still be considered.

3. Cetacean Acoustic Divisions

To accurately interpret auditory systems, it is important to have some form of control or external acoustic metric for categorizing ears. Two forms of acoustic data are available for cetaceans: audiometric data, which are available for fewer than 12 odontocete species, and sound recordings, which are available for 67 species of both odontocetes and mysticetes (see Tyack and Clark, Chapter 4; Nachtigall et al., Chapter 8). The consensus of these data is that cetaceans divide grossly into high- and low-frequency sound pro-

ducers that coincide with the two suborders. Odontocetes are fundamentally high-frequency animals-and mysticetes are low-frequency animals.

3.1 *Odontocete Acoustic Categories*

Odontocetes produce multiple signal types including species-stereotypic broadband echolocation clicks with peak energy between 10 and 200 kHz, individually variable burst pulse click trains, and constant frequency (CF) or frequency modulated (FM) whistles ranging from 4 to 16 kHz (Tyack and Clark, Chapter 4). Ultrasonic signals have been recorded from 21 species, although echolocation (or "biosonar") has been demonstrated unequivocally in only 11 species of smaller odontocetes (Au, Chapter 9). All modern odontocetes are assumed, like bats, to be true echolocators, not simply ultrasonic receptors; that is, they "image' their environment by analyzing echoes from a self-generated ultrasonic signal. Captive odontocetes vary pulse repetition rate, interpulse interval, intensity, and click spectra, particularly in response to high ambient noise, but in general, each odontocete species has a characteristic echolocation frequency spectrum (Watkins and Wartzok 1985). Peak spectra of odontocete sonar signals range from approximately 16 kHz in the killer whale (*Orcinus orca*) to over 130 kHz in the harbor porpoise (*P. phocoena*) with typical source levels of 150 to 170 dB although level estimates as high as 230 dB have been reported (Au 1993).

The functional significance of species differences in the spectra of natural echolocation signals has not been directly tested, but there are strong correlations with habitat types and peak spectra (Ketten and Wartzok 1990). Two acoustic categories were established for odontocetes based on the peak frequency at maximum energy of common ultrasonic signals (Ketten 1984): Type I with peak spectra above 100 kHz and Type II with peak spectra below 100 kHz (Tables 2.1 and 2.2). Because frequency and wavelength are inversely related, these types also imply differences in the size of the objects or details detected through echolocation. Type I echolocators tend to be near-shore and riverine species that operate in relatively low-light, acoustically complex waters. For example, the South American boutu (*Inia geoffrensis*) routinely hunts small fish amidst the roots and stems choking silted Amazonian "varzea" lakes and produces signals up to 200 kHz (Norris et al. 1972). A second Type I species, the harbor porpoise (*P. phocoena*), inhabits near-shore waters and shallow seas in colder latitudes and typically uses 110 to 140 kHz signals (Kamminga 1988). Communication signals are rare (or are rarely observed) in most Type I species (Watkins and Wartzok 1985), and, as discussed below, their auditory systems are dominated by ultra-high-frequency adaptations. Type II species are primarily delphinids, which are near- and offshore animals that inhabit low object density environments, generally travel in large pods, are highly social, and employ lower ultrasonic frequencies with longer wavelengths that are consistent with detecting larger objects over greater distances. They also devote substantial acoustic

TABLE 2.1. Cochlear morphometry in cetacean, amphibious, and nonaquatic mammals

Species	Common name	Animal weight (kg)	Audible frequency range (kHz)	Cochlear type	Turns	Basilar membrane length (mm)	Outer lamina (mm)	Basal thickness (μm)	Basal width (μm)	Apical thickness (μm)	Apical width (μm)	Basal ratio (t/w)	Apical ratio (t/w)
Delphinus delphis	Common dolphin	70	–	II	2.25	30.7	†	–	50	–	294	–	–
Grampus griseus	Risso's dolphin	–	2–110	II	2.5	41.0	†	22	40	5	420	0.550	0.0119
Inia geoffrensis	Boutu	130	1–150	I	1.5	38.2	†	–	–	–	–	–	–
Lagenorhynchus albirostris	White-beaked dolphin	–	–	II	2.25	34.8	8.5	22	40	5	360	0.500	0.0139
Lagenorhynchus obliquidens	White-sided dolphin	120	0.3–140	II	2.0	33.8	†	–	35	–	300	–	–
Phocoena phocoena	Harbor porpoise	50	0.5–180	I	1.5	22.5	17.6	25	30	5	290	0.833	0.0172
Phocoenoides dalli	Dall's porpoise	–	–	–	2.0	29.1	†	–	49	404	–	–	
Physeter catodon	Sperm whale	20,000	–	I	1.75	54.3	†	–	50	–	800	0.34	–
Stenella attenuata	Spotted dolphin	100	–	II	2.5	36.9	8.4	25	40	5	400	0.625	0.0125
Tursiops truncatus	Bottlenose dolphin	155	0.2–160	II	2.25	38.9	10.3	25	35	5	380	0.714	0.0132
Balaenoptera acutorostrata	Minke whale	8,000	–	M	2.25	50.6	–	–	100	–	1,500	–	–
Balaenoptera musculus	Blue whale	100,869	–	M	2.25	71.0	–	–	–	–	–	–	–
Balaena mysticetus	Bowhead whale	42,201	–	M	2.25	56.5	–	7	120	2	1,670	0.062	0.0015
Balaenoptera physalus	Fin whale	–	–	M	2.5	64.7	–	5	100	2	2,200	0.050	0.0010
Eubalaena glacialis	Northern right whale	31,837	–	M	2.5	54.1	–	7	125	2	1,500	0.056	0.0017

TABLE 2.1. *Continued*

Species	Common name	Animal weight (kg)	Audible frequency range (kHz)	Cochlear type	Turns	Basilar membrane length (mm)	Outer lamina (mm)	Basal thickness (μm)	Basal width (μm)	Apical thickness (μm)	Apical width (μm)	Basal ratio (t/w)	Apical ratio (t/w)
Megaptera novaeangliae	Humpback whale	30,000	–	M	2.0	60.1	–	7	125	2	1,300	0.056	0.0019
Bos taurus	Cow	500	0.14–22	T	3.5	38.0	–	–	–	–	–	–	–
Cavia porcella	Guinea pig	0.5	0.2–45	T	4.25	18.5	–	7	70	2	245	0.106	0.0082
Chinchilla langer	Chinchilla	0.8	0.09–25	T	3.0	18.5	–	15	248	6	310	0.061	0.0177
Dipodymus marriami	Kangaroo rat	0.05	0.1–25	Sb	3.5	9.8	–	9	100	46	254	0.086	0.1827
Elephas maximus	Elephant	4,000	<0.20–5.7	T	2.25	60.0	–	–	–	–	–	–	–
Felis domesticus	Cat	2.5	0.125–60	T	3.0	25.8	†	12	80	5	420	0.150	0.0119
Homo sapiens	Human	75	0.13–16	T	2.5	33.5	–	–	150	–	504	–	–
Meriones unguiculatis	Gerbil	0.05	0.25–45	T	3.25	12.1	–	10	100	35	250	0.100	0.1400
Mus musculus	Mouse	0.01	5–60	T	2.0	6.8	–	15	40	1	160	0.363	0.0063
Phoca vitulina	Seal	50	0.49–58	A	2.25	–	†	–	–	–	–	–	–
Rattus norvegicus	Rat	0.2	1–59	T	2.2	10.7	–	18	80	2	250	0.300	0.0106
Spalax ehrenbergi	Mole rat	0.08	0.1–10	Sb	3.5	13.7	–	9	120	18	200	0.075	0.0900
Myotis lucifugus	Little brown bat	0.007	12.5–100	Æ	2.25	6.9	†	–	–	–	–	–	–
Pteronotus parnellii	Mustached bat	–	16–100	Æ	2.75	14.3	†	22	50	2	110	0.440	0.0182
Rhinolophus ferrumequinum	Horseshoe bat	0.02	7–90	Æ	3.25	16.1	†	35	80	2	150	0.438	0.0133

* Numbers shown are averages of available data for species with multiple reports.
Width = pars arcuata and pectinata; thickness = pars pectinata maximum; † Outer osseous lamina present, length unknown; I = aquatic, peak spectra >100 kHz; II = aquatic, peak spectra < 90 kHz; M = aquatic, peak spectra <2 kHz; Æ = æolian >20 kHz; Sb = fossorial; T = terrestrial; A = amphibious.
Data compiled from Schevill 1964; Wever et al. 1971a, b; Firbas 1972; Pye 1972; Bruns and Schmieszek 1980; Norris and Leatherwood 1981; Ketten 1984, 1992, 1994; Ketten and

TABLE 2.2. Auditory, vestibular, and optic nerve distributions

Species	Common name	Cochlear type	Membrane length (mm)	Auditory ganglion cells	Density (cells/mm cochlea)	Vestibular ganglion cells	Vestibular-auditory ratio	Optic nerve fibers	Optic-auditory ratio	Optic-vestibular ratio
Delphinapterus leucas	Beluga	–	42.0	149,386	3,557	–	–	110,500	0.74	–
Delphinus delphis	Common dolphin	II	34,9	84,175	2,412	4,091	0.05	165,600	1.97	40.48
Inia geoffrensis	Boutu	I	38.2	104,832	2,744	–	–	15,500	0.15	–
Lagenorhynchus obliquidens	White-sided dolphin	II	33.8	70,000	2,071	–	–	77,500	1.11	–
Lipotes vexillifer	Baiji	–	–	82,512	–	3,605	0.04	23,800	0.29	6.60
Neophocoena phocoenoides	Finless porpoise	–	–	68,198	–	3,455	0.05	88,900	1.30	25.73
Phocoena phocoena	Harbor porpoise	I	22.5	70,137	3,117	3,200	–	81,700	1.16	25.53
Physeter catodon	Sperm whale	I	54.3	161,878	2,981	–	–	172,000	1.06	–
Sousa chinensis	Humpbacked dolphin	–	–	70,226	–	3,213	0.05	149,800	2.13	46.62
Stenella attenuata	Spotted dolphin	II	36.9	82,506	2,236	–	–	–	–	–
Tursiops truncatus	Bottlenose dolphin	II	38.9	96,716	2,486	3,489	0.04	162,700	1.68	46.63

TABLE 2.2. *Continued*

Species	Common name	Cochlear type	Membrane length (mm)	Auditory ganglion cells	Density (cells/mm cochlea)	Vestibular ganglion cells	Vestibular-auditory ratio	Optic nerve fibers	Optic-auditory ratio	Optic-vestibular ratio
Balaenoptera physalus	Fin whale	M	64.7	134,098	2,073	–	–	252,000	1.88	–
Megaptera novaeangliae	Humpback whale	M	60.1	156,374	2,602	–	–	347,000	2.22	–
Cavia porcella	Guinea pig	T	18.5	24,011	1,298	8,231	0.34	–	–	–
Felis domesticus	Cat	T	25.8	50,896	1,972	12,376	0.24	193,000	3.73	15.59
Homo sapiens	Human	T	33.5	30,500	910	15,590	0.51	1,159,000	38.00	74.34
Pteronotus parnellii	Mustached bat	Æ	14.3	12,800	895/1,900††	–	–	–	–	–
Rhinolophus ferrumequinum	Horseshoe bat	Æ	16.1	15,953	991/1,750††	–	–	–	–	–

† Average values used when more than one source available for a species.

†† Density near auditory fovea sensu Bruns and Schmiezek (1980).

I = aquatic; peak spectra >100 kHz; II = aquatic; peak spectra <90 kHz; M = aquatic; peak spectra < 2 kHz; Æ = æolian >20 kHz; Sb = fossorial; T = terrestrial; A = amphibious.

Data compiled from Gacek and Rasmussen 1961; Jansen and Jansen 1969; Firbas 1972; Morgane and Jacobs 1972; Bruns and Schmieszek 1980; Dawson 1980; Ketten 1984, 1992; Vater 1998a, b; Nadol 1988; Gao and Zhou 1991, 1992, 1995; Kössl and Vater 1995.

effort to communication signals (Tyack and Clark, Chapter 4; Herzing, Chapter 5).

Audiograms are available currently for seven Type II delphinids, one monodontid (beluga whales, *Delphinapterus leucas*) and two Type I species (Amazonian boutu, *I. geoffrensis*, and the harbor porpoise, *P. phocoena*) (Nachtigall et al., Chapter 8). There are no published audiograms for the largest odontocetes, the sperm whales (Physeteridae) nor for any beaked whale (Ziphiidae), and relatively little is known about their vocalizations; they remain unclassified. Because much of the behavioral and electrophysiologic hearing data on cetaceans is covered in other chapters, only the salient points related to peripheral auditory processing mechanisms and anatomy are mentioned here.

The total hearing range, frequency resolution, localization, and acuity of an ear are dictated primarily by peripheral auditory system anatomy. Current data indicate that odontocetes have a 10 to 12 octave functional hearing range, compared with eight to nine octaves in the majority of mammals. Most have best sensitivities above 30 kHz, with some going as high as 130 kHz (Møhl and Andersen 1973; Supin and Popov 1990). Peak spectra of echolocation types are consistent with the audiometric curves; that is, the signal peaks are near the best frequency of hearing in audiograms from individuals of the same species tested behaviorally. In addition to good ultrasonic hearing, odontocetes have good frequency and angular resolution. Target detection thresholds as small as 5 cm at 5 m have been reported, implying an auditory angular resolution of 0.5° although 1° to 4° for horizontal and vertical resolution are more commonly reported (Au 1993). Minimal intensity discrimination in *Tursiops truncatus* (bottlenose dolphin) is 1 dB, which equals the average human value. Frequency discrimination varies from 0.28 to 1.4% relative discrimination limens (rDL) between 1 and 140 kHz; best values are found between 5 and 60 kHz (Popper 1980). Angular resolution and frequency discrimination in *P. phocoena* (0.5°–1°; 0.1%–0.2% rDL) are similar to values in microchiropteran bats and superior to those for *T. truncatus* and humans (Popper 1980; Kössl and Vater 1995).

An important aspect of any sensory system is the ability to detect signals in noise. Critical bands (CB) and critical ratios (CR) are two measures of the ability to detect masked signals. Fletcher (1940) showed that as the bandwidth of a masking noise narrows, the target suddenly becomes easier to detect. If the ear's frequency resolution is relatively poor, there is a broad skirt of frequencies around the target tone that will initiate a response, and the CB is large. If the membrane is narrowly tuned, the ear responds only to a narrow band of frequencies at each point, and the CB is narrow. Critical bands are thought to depend on stiffness variations in the inner ear. In most mammals, including odontocetes, the critical bandwidths are relatively constant at 0.25 to 0.35 octaves/mm of basilar membrane (Allen and Neeley 1992; Ketten 1992). Critical ratios are a related measure that are calculated

as the threshold level of the target in noise (in dB) minus the masker level (in dB). Critical bands tend to be a constant function of critical ratios throughout an animal's functional hearing range (Fay 1992). Odontocetes are better than most mammals at detecting signals in noise and have more critical bands with smaller critical ratios than other mammals. Odontocete critical bandwidths are not a constant factor of the critical ratio at different frequencies. The classic example is *T. truncatus* with 40 critical bands that vary from ten times the critical ratio at 30 kHz to eight times the critical ratio at 120 kHz (Johnson 1968; see also Nachtigall, Lemonds, and Roitblat, Chapter 8 for review). This ability may be related to having longer basilar membranes than many land mammals (Table 2.1) or better resolution at high frequencies or a combined effect.

3.2 Mysticete Acoustic Categories

Currently, there are no direct measures of hearing for any mysticete. Vocalization data imply mysticetes are predominately low sonic range animals (<5 kHz), and it is likely that several species hear well at infrasonic frequencies. Recent data from deep ocean stationary arrays suggest mysticetes, like odontocetes, have three, distinct sound production groups (Edds-Walton 1997) that parallel three temporal bone morphometric categories among mysticetes, but cross taxonomic lines (Ketten 1992; Ketten personal observation). Habitat and functional relationships for these potential acousto-morphometric groupings are not yet clear. For this discussion, all mysticetes are categorized conservatively as Type M. In general, mysticete vocalizations are significantly lower in frequency than those of odontocetes, with peak spectra between 0.012 and 3 kHz. Most mysticete signals are characterized as low-frequency moans (0.4 to 40 s, fundamental <200 Hz); simple calls (impulsive, peak <1 kHz); complex calls (broadband pulsatile AM or FM signals); and complex "songs" with varied phrasing and spectra. Infrasonic signals between 10 and 20 Hz are well documented in at least two species, the blue whale (*B. musculus*, Edds 1982) and the fin whale, (*Balaenoptera physalus*) (Edds 1988; Watkins et al. 1987). Suggestions that low-frequency mysticete signals are used for oceans basin scale communication or a low-frequency form of echolocation, such as topological imaging, are compelling but have not been definitively demonstrated.

Comparisons of hearing curves and sounds produced by odontocetes indicate that, like most mammals, they have good sensitivity near the frequencies or harmonics of frequencies they emit. It is reasonable to expect this is true for mysticetes as well. Based on the frequency ranges and peak spectra of sounds employed by both odontocetes and mysticetes, ears of cetaceans should fall into distinct morphometric categories that span infra- to high ultrasonic adaptations and are consistent with sound Types I, II, or M. The next question is, then, what structural correlates are there and what can they tell us about cetacean hearing?

4. Fundamental Ear Morphometrics: Generalist Versus Specialist Bauplans

Audible ranges and thresholds vary dramatically from one species to the next. Analyses of how hearing abilities, habitat, and ear anatomy are linked in different species, particularly in animals from diverse habitats, provide insights into how each component in the auditory periphery functions and how different hearing capacities evolved. By observation, we know that many species hear sounds inaudible to humans. Most mammals have some ultrasonic hearing, and some, like African (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) appear to detect infrasonic signals (Payne et al. 1986; O'Connell et al. 1997). Theoretically, "hearing" could extend arbitrarily high, but there are practical limits both in terms of the utility of the information and in the physics of the receptor.

Hearing ranges are related to both animal size and niche. In general, smaller animals have good high-frequency hearing while larger animals tend to have better low-frequency hearing and a lower top frequency. For example, mice have a functional high-frequency limit of approximately 90 kHz; cats, 70 kHz; humans, 20 kHz; cows, 16 kHz; elephants, 12 kHz (Fay 1988). A functional relationship between cochlear length and a species' hearing range has been assumed in several mammalian ear modeling efforts, but this is a shibboleth. Mammalian ear structures, particularly the size of the temporal bone and inner ear canals, scale with body size, but hearing does not (Fig. 2.1) (Ketten 1984). Body mass and cochlear length are strongly correlated because both are products of body scaling processes, but there is no direct, *functional* relationship between cochlear length alone and an animal's hearing range.

A primary assumption of some inner ear models is that all mammalian basilar membranes are constructed of similar components that have a common stiffness gradient (e.g., Greenwood 1990). Think of a mega-membrane composed of graded modules from which each species selected a contiguous set proportional to its body mass. That set dictated its hearing range, which in most mammals covers about nine octaves. The human nine-octave subset lies near the middle of this hypothetical mega-array. Smaller animal ears would be constructed largely of shorter, narrower, stiffer modules towards the high-frequency mega-membrane base and therefore have a higher maximal *and* higher minimal frequency than larger mammals. Large species would have longer membranes but the span would be composed primarily of broad, thin modules from the lower-frequency apical end, where the blue whale, of course has the corner on the last module. For many land mammals, the assumption appears correct, but only because length is an indirect correlate of the real functional feature for basilar membrane resonances, stiffness. For ears that follow this regular modular distribution, termed "generalists" (Echteler et al. 1994), basilar membrane

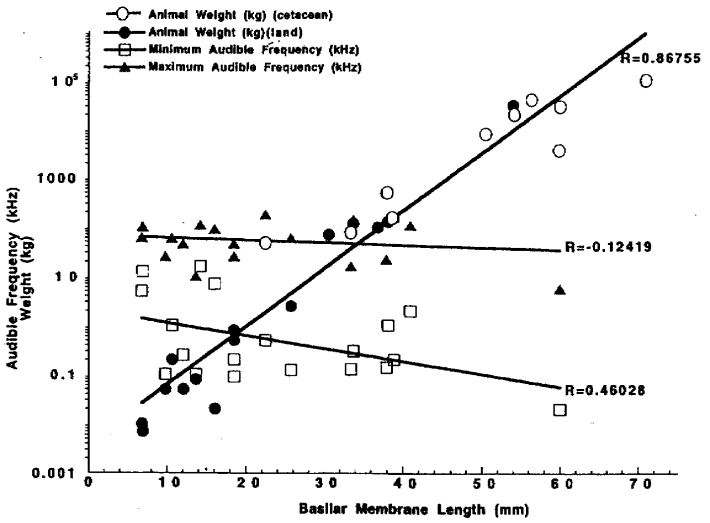


FIGURE 2.1. Cochlear length, mass, and audible frequency correlations. Basilar membrane lengths for mammals ranging in size from microchiropteran bats to blue whales are plotted versus body mass and the upper and lower functional limits of hearing (see also Table 2.1). There is a significant and consistent correlation for body mass and membrane length in both aquatic and land mammals but no significant correlation of length with minimum or maximum audible frequencies. This suggests that cochlear length is a coincident but not a functionally relevant variable for hearing range endpoints. Cochlear length is strongly correlated with animal size and scales similarly for all mammals.

thickness and width covary regularly throughout the ear. In these ears frequency distributions can be derived from one parameter, basilar membrane length, because it is a coincidental correlate to the stiffness at every position along the generalist membrane, that is, the generalist ear is isomorphic.

It is precisely the outliers from the "generalist" size-frequency regression that hold the keys to frequency encoding mechanisms. "Specialist" eared mammals tend to have similar habitats. Regardless of animal or ear size, crepuscular and nocturnal species typically have acute ultrasonic hearing while subterranean species commonly have good infrasonic hearing (Fay 1988). Specialist ears are anisomorphic. They do not have the same thickness-width-length relationship as generalist land mammals and thickness-width relationships frequently vary throughout the cochlea. Effectively the ear is retuned to an atypical range for the body size by altering structures that dictate the resonance and impedance characteristics of the ears, for example, increasing mass in normally thick, stiff "small ear" modules (as in mole rats) or adding stiffening components to increase resonance response characteristics in both small and large inner ears.

4.1 Cetacean Ear Morphometrics: A Zeeöhrplan*?*

How well do marine mammals mesh with the generalist versus specialist land mammal hearing schema outlined above? Considering the problems implicit in an aquatic habitat for an unmodified air-adapted ear, can there be any commonalities? Despite the fact that there are substantial adaptations in all cetacean ears related to coping with increased sound speed, large pressures, and a host of other aquatic demands, whales retained the essentials of air-adapted ears, such as a spiral cochlea and discrete middle ear cavity with a three-part ossicular chain. Consequently, what we see today is a fascinating admixture: highly specialized pressure adaptations, subtle structure-frequency-habitat correlations, leviathan-scale ear structures, and extensive peripheral remodeling, all overlaying a sophisticated but fundamentally mammalian ear.

Most cetaceans are large, massive animals that, by the generalist metric, should have low- to very-low-frequency hearing. The largest whales (Mysticeti; Type M) are acoustically consistent with their extreme size. They produce infrasonic frequencies, and we expect to find they have middle and inner ear adaptations consistent with predominately low-frequency hearing. As such, mysticetes may be simply an extreme of the generalist format. The majority of odontocetes, although smaller than mysticetes, are still very large animals by land mammal standards, and their gross ear dimensions, particularly cochlear length, scale to body size exactly like those of land mammals (Table 2.1, Fig. 2.1). Prior to the first major publication of research on dolphin echolocation (Kellogg 1959), it would have been reasonable to assume from their sonic range signals and size that these large animals had mid- to low-frequency hearing capacities similar to cows. Today, it is clear from their audiograms and sounds that virtually all odontocetes, including the sperm whale, not only hear some range of ultrasonic frequencies despite their size but that ultrasonic analyses dominate their auditory systems. Therefore, Type I and Type II species are acoustically inconsistent with the mid- to low-frequency ear predicted by generalist land mammal ear models, making odontocetes in particular prime candidates for having anisometric ears.

What is the appropriate functional reference for cetacean ears since body mass obviously is not? Water is a dense medium in which light attenuates faster than sound. Consequently, marine mammals are de facto crepuscular species. If we look at cetaceans in terms of hearing fitness for their habitat, good high-frequency hearing is logical and consistent with a similar trend on land where high-frequency hearing is common in nocturnal species, particularly among predators. Mysticetes live under the same low-light conditions, but they are primarily diurnally active, opportunistic feeders. On land, most dusk, dawn, and nocturnal species are small. How do odontocetes manage ultrasonic ears despite their size? Like specialist mammals, they have structural adaptations that override the generalist size-

frequency relationship. While the scaling of gross features of odontocete ears to their body mass is isomorphic with that of land mammals (Fig. 2.1), the scaling of acoustically functional elements, particularly of the inner ear is entirely different. Put another way, cetaceans and land mammals, despite their overt differences in shape, have a similar *bauplan* for gross construction of the ear, but cetaceans evolved a radically different functional acoustic morphometry, effectively a *zeeöhrplan*, that permits underwater ultrasonic hearing in a megascale ear (Ketten 1984, 1992). The next section details the salient features of this alternative aquatic ear.

5. Cetacean Ears

Hearing capacities are the result of the integrated activity of the ear's three fundamental divisions: (1) the outer ear captures sound, (2) the middle ear selectively transfers acoustical power to the inner ear, and (3) the inner ear performs a spectral analysis and transforms the middle ear's mechanical input into neural impulses. In the context of this chapter, the primary question about the outer ear is: How is water-borne sound captured? For the middle ear, the significant issue is: Does an impedance matching function remain? For the inner ear, it is: How do whale ears achieve exceptional frequency representation?

5.1 The Outer Ear

The outer ear is subdivided conventionally into a pinna or ear flap, a funnel-shaped concha, and the ear canal or auditory tube. All three elements are important for the collection and transmission of sound power to the middle and inner ear. External pinnae are important aids also to localization, acting as asymmetric funnels that selectively admit sounds along the pinnal axis (Heffner and Heffner 1992; Rosowski 1994). Clearly these are important functions for a mammalian ear, yet whales and dolphins appear to have abandoned at least two and possibly all three outer ear elements.

The evolutionary head remodeling process of telescoping mentioned in the introduction is covered thoroughly in other chapters (Cranford, Chapter 3; Aroyan et al., Chapter 10), but some points bear repeating here because of their impact on the peripheral auditory system, particularly on the outer ear. Telescoping had a profound effect on sound reception and ear position. As the rostrum elongated, the cranial vault foreshortened and the nares were pulled rearward to a dorsal position behind the eyes. At the same time, the maxillary bones of the upper jaw were transposed back to the vertex of the skull, overlapping the compressed frontal bones. Telescoping may have been driven essentially by nonauditory influences, such as respiration with only a small portion of the head exposed, but it also produced a multilayer skull that seriously impedes sound transmission through

the head. Telescoping was accompanied also by a dramatic repositioning of the ears (Fig. 2.2). Two classical mammalian auditory features, the pinna and external canal, were effectively decommissioned as the middle and inner ears migrated out from the skull bed. In most odontocetes, the migration is complete; no attachments to the skull other than suspensory ligaments remain (Fig. 2.2A). In mysticetes, the ear forms firm, bony connections to the skull (Fig. 2.2B), but like the ears of odontocetes, the bulk of the ear is well outside the skull. Eventually, these parallel processes of externalization and elimination led to a remarkable design for sound reception.

5.1.1 Sound Reception: External Ear Analogues

External pinnae are absent in Cetacea, although vestigial pinnal rings are found embedded in the subcutaneous fat near the external meatus in some individuals. The meatal opening, generally less than 3 mm in diameter even in the largest mysticetes, is marked externally by a dimple or depression in the skin. Some form of residual external auditory canal is present in all cetaceans; the level of integrity varies by species. In general, odontocete external canals are plugged with cellular debris and dense cerumen, becoming progressively narrower, and ending in a blind caecum that has no observable connection with the tympanic membrane or temporal bones. It is unclear whether any segment of the canal is functional in any odontocete. No true association of the canal with the tympanic membrane or middle ear has been documented in odontocetes.

Reysenbach de Haan (1956) and Dudok van Heel (1962) were among the first to propose that soft tissues of the head served as ear canal analogues for sound conduction to the odontocete ear. Reysenbach de Haan reasoned that since the transmission characteristics of blubber and sea water are similar, using a canal occluded with mixed and variable substances is inefficient compared to a regular soft tissue or bone conduction path. Dudok van Heel concluded the canal was not used for hearing because behavioral measures of minimum audible angle in bottlenose dolphins, *T. truncatus*, were more consistent with intercochlear than intermeatal distances.

At present, the bulk of experimental and anatomical studies indicate specialized fatty tissues in the jaw region are the primary route for conveying sound to odontocete middle and inner ears. The concept of jaw or pan bone hearing was first proposed by Norris (1968) who observed that the posterior area of the odontocete mandible has two exceptional properties: a large cavity that is open medially and houses a fatty cylinder and an ovoid of thin bone called the pan bone with fat overlying it (Figs. 2.2A and 2.3). Norris (1969) described the fat body in the mandibular channel as a "lozenge . . . of pellucid fats," noting that it attached to the surface of the tympanic bone. He also observed that the jaw fats resembled fats in the melon core and were therefore probably acoustically significant (Norris 1968; see also

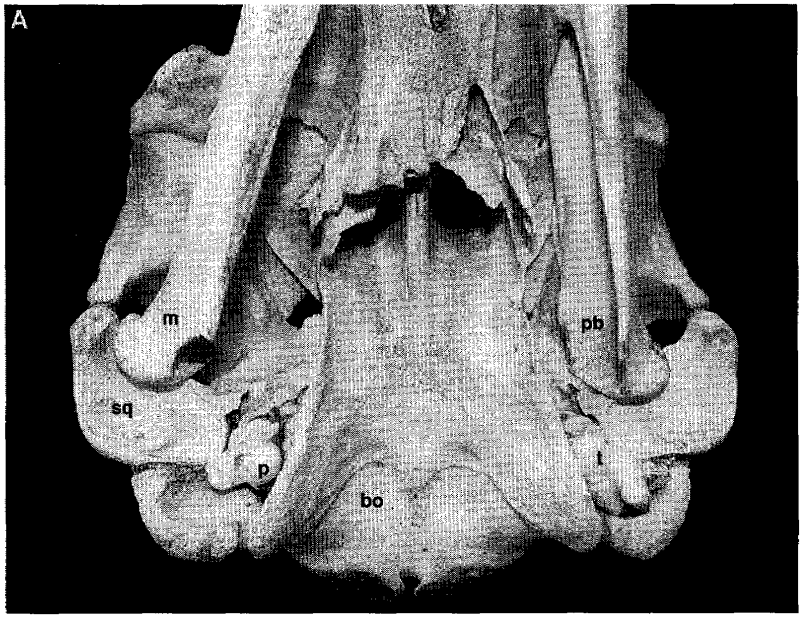


FIGURE 2.2. Cetacean tympano-periotic complex anatomy. Ventral views of (A) adult male bottlenose dolphin (*Tursiops truncatus*) and (B) humpback whale (*Megaptera novaeangliae*) skulls demonstrate the extracranial position of the tympano-periotic complex, size of the peribullar recesses, and differences in shape, size, and skull attachments of odontocete versus mysticete temporal bones. (A) The right tympanic bulla has been removed to show the approximate in vivo position of a dolphin periotic in the peribullar cavity behind the lower jaw. The spherical promontorium on the periotic (p) contains the cochlea. The dimple on the posterior edge of the periotic is the round window. Specialized fats (see Fig. 2.3A) are located in the pan bone (pb) region of the left lower jaw. (B) A drawing of the ventral surface of a humpback whale (*M. novaeangliae*) skull shows the right tympanic and the glove finger (gf) in its in vivo position. The left tympanic has been removed, revealing the periotic and posterior periotic flange (fl) wedged between the occipital and squamosal bones. bo, Basioccipital; eo, exoccipital; m, mandible; oc, occipital condyle; sq, squamosal; t, tympanic bulla. (*T. truncatus* skull collected by W. Schevill; access courtesy of W. Watkins, WHOI. *M. novaeangliae* drawing by I. Milde.)

Cranford, Chapter 3; Aroyan et al. Chapter 10). Norris speculated that the mandibular fats act as a preferential low impedance path to the middle ear and that the pan bone provides an "acoustic window" because of its thinness and position in relation to the fats and the tympanic bone. He also observed that since dolphins rotate their heads while acoustically scanning an object, the outward flare of the jaw in the pan bone area means the fat bodies receive sound from multiple angles during the scan (see Herzing, Chapter 5).

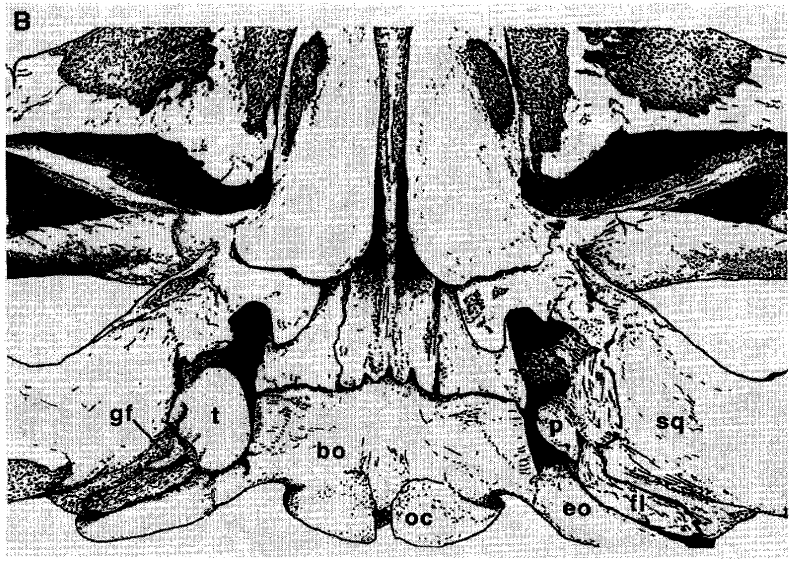


FIGURE 2.2. *Continued*

Several types of data support this hypothesis. Evoked responses (Bullock et al. 1968) and cochlear potentials (McCormick et al. 1970) in two species of dolphins were significantly greater for sound stimuli above 20 kHz placed on or near the mandible. Bullock et al. (1968) also reported substantial changes in the auditory evoked potential (AEP) waveform if a barrier was placed in the sound field between the jaw and sound source and found a masking effect when the surface of the jaw was perturbed. Measurements with implanted hydrophones in severed *T. truncatus* heads (Norris and Harvey 1974) found best transmission characteristics for sources directed into the pan bone. They also reported that the melon consisted of at least two differentiable fatty tissues, a slow velocity core (1,292 m/s) surrounded by a faster velocity shell (1,682 m/s). Varanasi and Malins (1971) reported that the melon and jaw fats are wax esters with acoustic impedances closer to sea water than any other nonfluid tissue. Fitzgerald (1999) recently reported that melon core speeds are highly temperature dependent, ranging from 1,390 m/s at 10°C to 1,280 m/s at 40°C, but his data are essentially consistent with those of the earlier studies. Brill et al. (1988) showed that placing an acoustically opaque neoprene hood over the lower jaw of a captive dolphin trained to do echolocation tasks in a pool dropped the animal's performance to chance levels.

There are, however, conflicting results. As indicated in the preceding paragraph, Bullock et al. (1968) recorded AEPs from midbrain structures that supported the theory of jaw-related reception channels for stimuli above 20 kHz, but they also found for stimuli below 20 kHz that the best

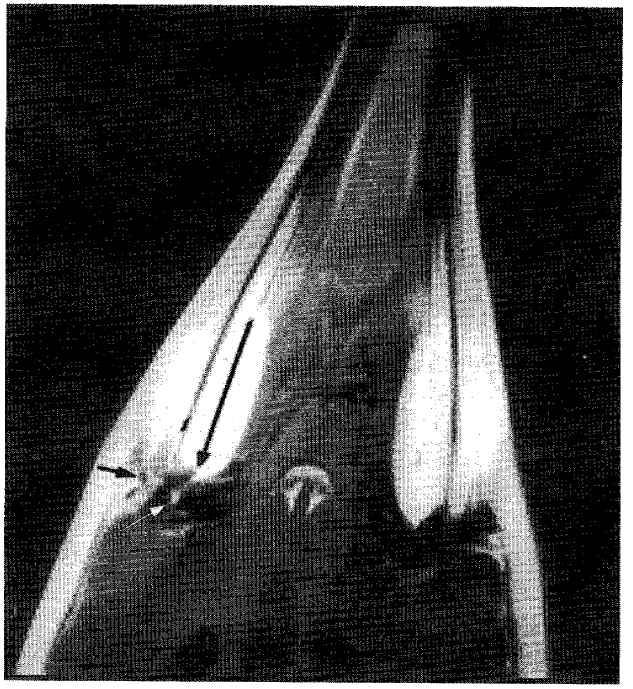
responses were obtained from sources placed on or near the external meatus. Renaud and Popper (1975) similarly found a response split at 20 kHz for sources directed at or behind the jaw in psychophysical localization tests with *T. truncatus*. Popov and Supin (1990) found minimum thresholds were associated with stimuli near the external meatus for multiple lower-frequency stimuli. McCormick et al. (1970) did not do specific frequency versus source location comparisons but commented that they found a strong cochlear microphonic response for 2 kHz airborne sources both placed over the meatus *and* over the jaw.

Data from recent radiologic and anatomical studies of cetacean heads may explain the apparent contradictions among these results. Magnetic resonance images from several species of odontocetes revealed there are multiple lobes of fatty tissues associated with the jaw, including a trumpet-shaped fat body that projects postero-laterally. All have well-defined connections to the tympanic bone and middle ear (Fig. 2.3A) (Ketten 1994). These fat lobes are distinct from all other body fats except for the dense lipid bodies in the melon core. The postero-lateral lobe may explain the discrepancies among the earlier studies since it is positioned slightly below and medial to the external meatus (Fig. 2.3B). It has been suggested that this multilobed structure could function as "segmented" sound conduction channels or have specific tuning properties, for example, the anterior channel may be specialized for capturing ultrasonic echolocation-related signals while the lateral or inferior channels are tuned to lower-frequency communication signals from other pod members (Ketten 1998a).

An alternative to the jaw fat hypothesis proposed by Goodson and Klinowska (1990) is that the teeth of the lower jaw in odontocetes act

FIGURE 2.3. Sound reception paths in the odontocete. (A) A coronal plane T_1 weighted MR image of a common dolphin (*Delphinus delphis*) head at the mid-mandibular level shows three fatty tissue bundles in cross-section that are connected to the middle ear and tympanic bone by narrow necks of tissue: one in the lower jaw (long arrow), one on the external surface of the mandible, and one postero-laterally (small arrows). Only hydrated tissues are imaged in MR images. Fats and fluids are white. Unhydrated tissues (e.g., dense bone) and air spaces are black. Other structures are different shades of gray according to their fluid content. The lateral wall of the lower jaw is a thin black strip in the midst of bright fat bodies in this section. The tympanic cavity and bone are located in the black ovoid space behind the jaw. This image is in the same orientation and position as the skull in Figure 2.2A and is effectively a complementary view of the soft tissues located in that area. (Ketten, in preparation) (B) Norris (1968) suggested fats near the pan bone may have acoustic characteristics close to sea water and therefore act as low impedance sound conduits. This drawing summarizes recent data on the shape and location of specialized fatty tissue bundles that are physically related to odontocete ears. Using biomedical imaging techniques, three discrete lobes of highly differentiated fats have been identified, each oriented in a different axis, which may act as a tripartite sound collecting array in odontocetes (Ketten 1994, 1998a).

as a passive resonator system. They observed that the very regular spacing and conical shape of odontocete lower jaw teeth may allow them to function as independent "end-fire" pressure transducer arrays with the mandibular nerve functioning as progressively shorter delay lines. This cannot, of course, be an exclusive and universal solution for sound reception in odontocetes because it is inconsistent with the excellent echoloca-



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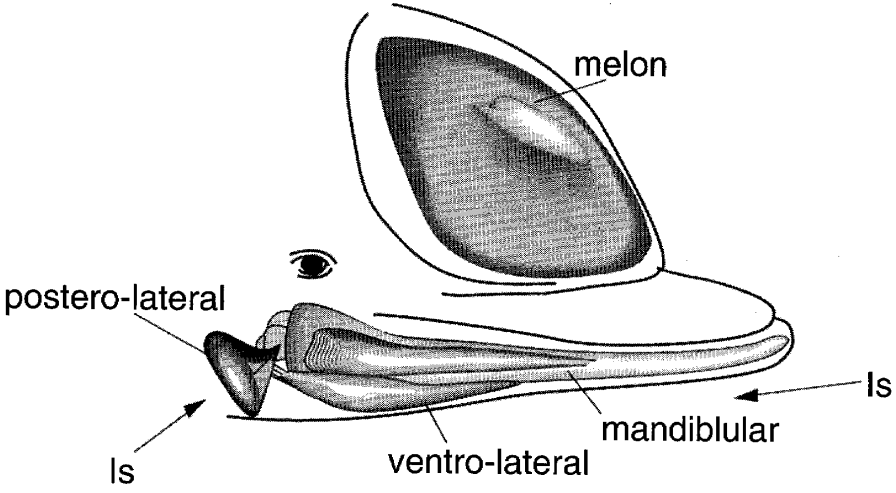


B

tion abilities in essentially toothless species such as the Monodontidae (narwhals and belugas) and Ziphiidae (pelagic beaked whales). It is possible, as they suggest, that this system operates as an adjunct to some other more general system, but the hypothesis is problematic because neural links to auditory centers have not been established.

In mysticetes, no robust theories for sound conduction are currently available. Whether the external canal is functional is unclear. The external canal has a wider bore than in odontocetes and connects directly with the "glove finger," a highly derived, everted tympanic membrane (Fig. 2.4). At its proximal end the external canal flares, forming a cup around the glove finger. Active ceruminous glands in this area secrete a conical wax cap over the tip of the glove finger that accumulates with age (Fraser and Purves 1960). Physically, the glove finger is a long (20 to 50mm), thick-walled (~1mm), and broad (~20mm average diameter) membranous tube with a sealed, blunt outer end, which projects laterally from the middle ear cavity (Figs. 2.2B, 2.4). Exact dimensions and orientation vary by species. In most mysticetes, it lies in a postero-lateral bony channel formed by the squamosal and exoccipital bones (Fig. 2.2B). According to Fraser and Purves (1960), in some species a ligament extends from the manubrium of the malleus into the glove finger lumen, attaching to its inner wall approximately one-third of the way along the membrane's length.

Because of the complex and robust construction of the glove finger and the clear connection with the residual external canal, the consensus of anatomical data is that mysticete external auditory canals are functional, at least as a source and repository for waxy secretions that abut the tympanic membrane. The intimate association of the glove finger and its wax cap with the bony walls and tissues of its squamosal trough strongly suggests sound reception via bone conduction, but to date there is no clear demonstration of any coherent volume of soft tissue or fatty structures that are as clearly connected with mysticete middle ears as the multilobed fat structures found in odontocetes except for the wax plug. Also, an imposing squamosal shield juts outward from the skull, and to varying degrees in each mysticete species, wraps ventrally over each ear bone (Figs. 2.2B, 2.4). Aside from the fact that this shield is between the ear and the world, it has no obvious acoustic element or specialization. However, it is a relatively unique structure, both in terms of shape and association with the whale ear. Like the wax plug, its uniqueness and association make it worth at least preliminary consideration. At this stage, all we know clearly about mysticete sound reception is that the great whales do not have an ear, skull, jaw, and soft tissue suite that is a larger-scale version of the odontocete head; therefore sound reception mechanism differ in the two suborders.

Recent observations on low-frequency sound production and reception in elephants may be relevant to whale hearing. For a little more than a decade there has been an inconsistency in the literature between behavioral observations and the one available elephant audiogram. Field and zoo

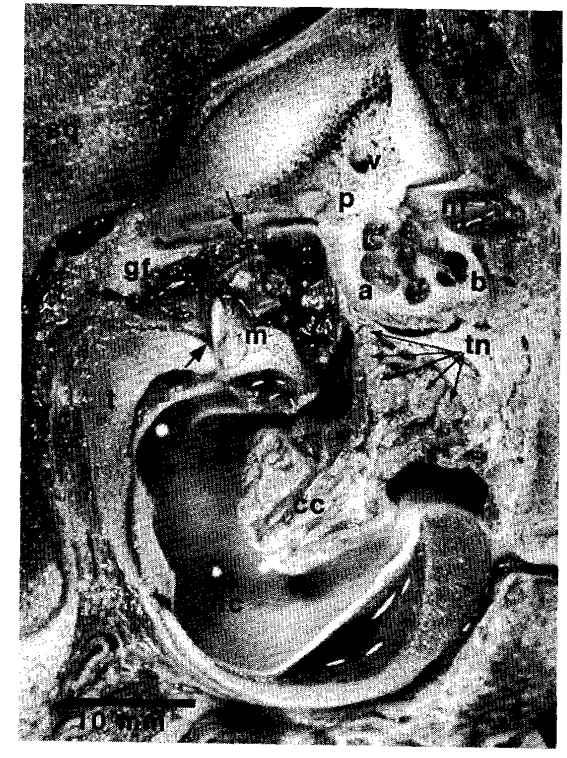


FIGURE 2.4. Middle ear/tympano-periotic complex architecture. A mid-modiolar cross-section is shown of the right tympano-periotic complex *in situ* in a bowhead whale (*Balaena mysticetus*) late-term fetus. The ear is shown in its natural orientation in the whale's head. Characteristic mysticete features include a dense hemispheric tympanic (t); a triangular periotic (p); and a blunt, membranous tympanic membrane (glove finger, gf), which is relatively short in this species. The short arrows indicate the tip and tympanal junctures of the glove finger. Trigeminal nerve (tn) bundles traversing the corpus cavernosum (cc) are indicated by long arrows. The only ossicle visible at this level is the malleus (m). a, Apex; b, basal turn of the cochlea; mc, middle ear cavity; nf, auditory nerve fibers; sq, squamosal; v, vestibule. (Dr. Daniel Hillman of Louisiana State University School of Veterinary Medicine provided access to the specimen and prepared the section.)

studies of both African and Indian elephants show unequivocally that elephants respond to infrasound (Payne et al. 1986; O'Connell et al. 1997), but the published audiogram of an Indian elephant indicates best sensitivity is near 1kHz with fairly steep decline in thresholds for all higher and lower frequencies and no indication of any infrasonic hearing (Heffner and Heffner 1980). O'Connell et al. (1997) showed that elephants produce seismic range vocalizations and use body movements to induce Rayleigh waves, a type of ground surface wave that travels at three-quarters the

speed of sound, attenuating at 1/r rather than $1/r^2$ and therefore has relatively little attenuation within the first kilometer. Elephants clearly respond to infrasonic stimuli within several hundreds of meters of Rayleigh sources. O'Connell et al. (1997) suggest elephants detect the technically subsonic energy via bone and soft tissue conduction. Reuter et al. (1998) commenting on O'Connell et al.'s findings noted that elephants have massive ossicles with extensive soft tissue associations. Elephants also have temporal bone complexes that have both partially and fully ossified skull attachments (Meng et al. 1997). Similar bony attachments to the temporal bullae are common in modern ungulates and are thought to have been a "preadaptive feature" for aquatic hearing that was present in the ungulate condylarts ancestors of whales (Thewissen 1998). Reuter et al. proposed that elephants have a dual reception system of bone/soft tissue conduction for ultra-low signals and pinnal-aerial channels for high-frequency sound reception. Their hypothesis could explain the apparent contradiction in the audiometric and behavioral data. More important, it is an intriguing idea in light of the independently proposed multichannel odontocete sound reception scheme (Fig. 2.3) because Reuter et al. suggest that to accurately determine elephant low-frequency sensitivity, it may be necessary to provide a non-aerial, substrate-coupled source. This is, in effect, what happens in water.

5.1.2 The Tympano-Periotic Complex

In modern Cetacea, the ear bone consists of two connected bullae, properly called the "tympano-periotic complex," that differ from temporal bone complexes of other mammals in form, construction, position, and, possibly, overall function. In all whales, the periotic bulla is dorsal and slightly medial to the tympanic bulla (Fig. 2.2). It houses the inner ear and is partly fused to the tympanic bulla (the "resonant" middle ear bulla) at one or more points on its lateral and posterior faces. The shell-like, hollow tympanic bulla encloses the middle ear space and ossicular chain. Tympanic and periotic dimensions are strongly correlated with animal size ($r = 0.9$) (Ketten and Wartzok 1990). To put the size range of cetacean temporal bones into perspective, a blue whale (*B. musculus*) periotic bulla is approximately the size of a human brain, and with the tympanic bone attached, the complete blue whale ear complex weighs well over a kilogram. The entire tympano-periotic complex of the harbor porpoise (*P. phocoena*) weighs about 16 gm; its periotic bulla would fit reasonably well into the blue whale round window niche.

The tympano-periotic complex resides outside the skull in an extensive peribullar cavity. The extracranial position of the tympano-periotic substantially increases the functional separation of the ears, which is a crucial factor in underwater localization and is discussed in detail later in this section. The peribullar cavity is bounded by the mandible, squamosal, pterygoid, and basi- and exoccipital bones (Figs. 2.2, 2.4). In odontocetes, a specialized spongy, vascularized epithelium, the peribullar plexus, fills the peribullar cavity spaces not occupied by conventional soft tissues normally found in the temporo-mandibular space. Up to five sets of ligaments extend from the periotic bulla to the sinus walls, suspending the temporal bone complex in the center of the cavity. Except in physeterids and some ziphiids there are no distinct connections between the odontocete tympano-periotic complex and the skull. In older animals, bony adhesions (and glue in museum displays) may connect the periotic bulla to the surrounding skull bones, but this is not the usual case. This complex set of straps and foam effectively aligns the tympanic with the mandibular and lateral fatty channels and allows differential motion of both elements of the tympano-periotic complex (Figs. 2.2A, 2.3) (Ketten 1998a).

Fraser and Purves (1960) speculated that the enlarged peribullar spaces were an adaptation for the mechanical stress of high ambient pressures and were correlated with diving ability. Oelschläger (1986) showed, however, that peribullar and pterygoid sinuses were best developed in ultra-high frequency dolphins, like the Amazonian *I. geoffrensis*, but are poorly developed in pelagic mysticetes. He argued that the peribullar plexus and spacious sinuses act primarily to acoustically isolate the ear for echolocation. It is now generally accepted that in odontocetes the mixed tissue plexus and suspensory ligaments in lieu of bony skull attachments are indeed effective acoustical isolators. A threadlike zygomatic arch that borders the peribullar space minimizes sound conduction from the frontal and premaxillary sound-producing regions (Cranford, Chapter 3), completing the picture of a rather sophisticated tissue-based acoustic isolation chamber with the odontocete ear at its core.

In mysticetes the picture is very different. The peribullar space is smaller and is occupied largely by a thick, fibrous peribullar capsule that pads the ventral and posterior surfaces of the tympanic bulla. Long flanges of spongy bone that project medially and posteriorly from the periotic bulla interdigitate with the skull, wedging the periotic tightly against the squamosal and occipital wings (Figs. 2.2B, 2.4). This strongly suggests bony sound conduction to the ear in baleen whales. Mysticete tympanics are typically twice the volume of the periotics. They are hemispherical, resembling a truncated ostrich egg with exceptionally thick (>2 cm) walls of compact bone. Like the tympanics in odontocetes, they are partly fused to the periotic on their lateral and posterior faces. Whether differences in size and shape of the periotic and tympanic and its associated tissues strongly influence hearing abilities of cetaceans has not been directly investigated. The wide range of tympanic sizes, bony attachments, and middle ear volumes suggest, however, that based on the tympanic bulla range alone there are large acoustical differences within even the mysticete ears.

5.1.3 Underwater Ears: Another Place Theory

Sound localization is an important aspect of hearing on which the medium has a profound impact. In land mammals, two binaural cues are important

for localizing sound: differences in arrival time (interaural time) and differences in sound level (interaural intensity). Binaural hearing studies are relatively rare for marine mammals, but the consensus from research on both pinnipeds and odontocetes is that binaural cues are used in underwater localization (Dudok van Heel 1962; Renaud and Popper 1975; Moore et al. 1995). The relatively broad spread between ears in cetaceans because of the extracranial relocation of the tympano-periotic complex may be the crucial adaptation that explains their ability to accurately localize underwater sounds.

In mammals, the high-frequency limit of functional hearing in each species has been shown to correlate with its interaural time distance, IATD, the distance sound travels from one ear to the other divided by the speed of sound (Heffner and Masterton 1990). It is unlikely that the upper functional hearing limit is specifically a factor in localization; it is more likely to simply be a correlate for some other hearing feature underlying localization. Nevertheless, a strong correlation clearly exists between an animal's highest functional frequency and interear spacing that provides a useful framework for discussion. The fundamental assumption of Heffner and Masterton (1990) is that the narrower the head, the smaller the IATD, the higher the frequency an animal must perceive well to detect phase differences at each ear. For example, consider a pure tone (sine wave) arriving at the head. If the sound is directly in front of the head, the sound will arrive at the same time and with the same phase at each ear. As the animal's head turns away from the source, each ear receives a different phase, given that the interear distance is different from an even multiple of the wavelength of the sound. IATD cues therefore involve comparing time of arrival versus phase differences at different frequencies in each ear. Phase cues are useful primarily at frequencies below the functional limit; however, the higher the frequency an animal can hear, the more likely it is to have good sensitivity at the upper end of its frequency range for phase cues.

Clearly, interaural time distances depend upon the sound conduction path in the animal and on the media through which sound travels. For terrestrial species, the normal sound path is through air, around the head, pinna to pinna. The key entry point for localization cues is the external auditory meatus, and the IATD is therefore the intermeatal (IM) distance measured around the head divided by the speed of sound in air. In aquatic animals, sound can travel in a straight line through the head by tissue conduction, given that the head tissues have coherent acoustic impedances similar to sea water.

Experiments with delphinids suggest that intercochlear (IC) or interjaw distances are the most appropriate measure for calculating IATD values in odontocetes. Because of the increased speed of sound in water, the IC distance of an average dolphin is acoustically equivalent to a rat or bat IM distance in air. Supin and Popov (1993) hypothesized that marine mammals without pinnae were incapable of using IATD cues. Recently, however,

Moore et al. (1995) demonstrated that *T. truncatus* has an IATD on the order of 7 μs, which is better than the average human value (10 μs) and well below that of most land mammals tested. If IM distances are used for land mammals and pinnipeds in air and IC distances are used for cetaceans and underwater pinniped data, marine mammal and land mammal data for IATD versus high-frequency limits have essentially the same regression (Fig. 2.5).

Intensity differences can be detected monaurally or binaurally, but binaural cues are most important for localizing high frequencies. In land mammals, intensity discrimination thresholds (IDT) are independent of frequency, decrease with increasing sound levels, and are generally better in larger animals (Fay 1992; Heffner and Heffner 1992). Humans and macaques commonly detect intensity differences of 0.5 to 2 dB throughout their functional hearing range; gerbils and chinchillas, 2.5 to 8 dB. Presumably ITDs in marine mammals depend upon the same reception paths as IATDs. Behavioral and evoked potential data show intensity differences are detectable by odontocetes at levels equal to those of land mammals and that the detection thresholds, like those of land mammals, decline with increasing sound level. Binaural behavioral studies and evoked potential recordings for *T. truncatus* indicate an approximate IDT limit of 1 to 2 dB (Bullock et al. 1968; Moore et al. 1995). In *P. phocoena*, IDTs range 0.5 to 3 dB (Popov et al. 1986). Thresholds in *I. geoffensis* range from 3 to 5 dB (Supin and Popov 1993), but, again, because of small sample size and methodological differences, it is unclear whether these numbers represent true species differences. Fay (1992) points out that the IDT data for land mammals do not fit Weber's law, which would predict a flat curve for IDT.

In summary, the most salient structural features of cetacean temporal bones are that they are extracranial and massive regardless of size, shape, or hearing type. The conclusion is that the fundamental construction of whale and dolphin ears is driven by physical aquatic parameters, particularly high atmospheric pressures, as well as the physical constraints of underwater acoustics. The dimensions of cetacean tympano-periotic bullae, which are stunning in some species, are not acoustically driven but are correlated with animal size like those of land mammals. This does not mean, however, that size, mass, and density of whale tympano-periotic complexes have no acoustic consequences, which brings us to the middle ear.

5.2 *Cetacean Middle Ears*

Cetacean middle ears are complex, and their function is still poorly understood. In all species, the ossicles are well developed, complexly shaped, and massive. Both the middle ear cavity and the ossicles show species- and animal-size-dependent variations. Intense, conflicting opinions abound about whether cetacean middle ears are functional (e.g., Fraser and Purves 1954; McCormick et al. 1970; Fleischer 1978; Ridgway and Carder 1997),

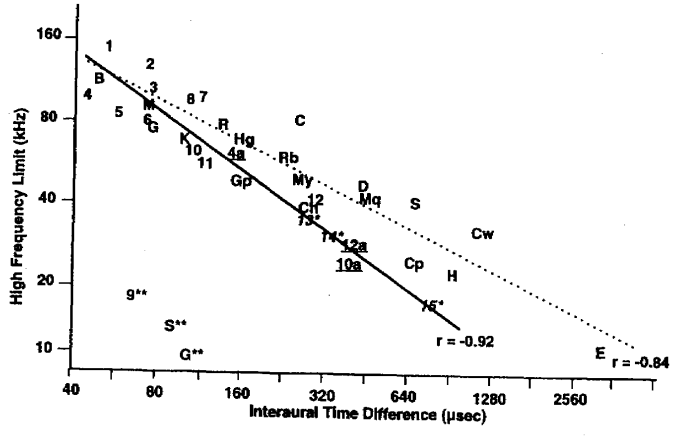


FIGURE 2.5. Interaural time differences versus high-frequency hearing limit. High-frequency functional hearing limits (*sensu* Fay 1992) are plotted against interaural time distances for aquatic and land mammals. For in-air limits, the frequency at 60 dB re 20 μPa was used; for animals in water, the frequency corresponding to 120 dB re 1 μPa. External intermeatal distances were used to calculate interaural time distances (IATD) for land mammals and otarrids tested in air. Intercochlear distances (which are isomorphic with intermandibular distances in odontocetes) were used for cetaceans and underwater pinniped IATD calculations. A separate regression was calculated based on underwater audiometric data alone. Data were compiled from Watkins and Wartzok (1985); Payne, Langbauer, and Thomas (1986); Fay (1988); Heffner and Masterson (1990); Ketten (1992; unpublished data); Heffner and Heffner (1992; personal communication); Richardson et al. (1995). Marine mammals are coded numerically; land mammals, by initial of English name.

Marine mammals: 1. harbour porpoise, *Phocoena phocoena*; 2. bottlenose dolphin, *Tursiops truncatus*; 3. bouto, *Inia geoffrensis*; 4. sea otter, *Enhydra lutris*; 5. Atlantic whitesided dolphin, *Lagenorhynchus acutus*; 6. Risso's dolphin (Grampus), *Grampus griseus*; 7. beluga, *Delphinapterus leucas*; 8. false killer whale, *Pseudorca crassidens*; 9. manatee, *Trichechus manatus*; 10. harbour seal, *Phoca vitulina*; 11. harp seal, *Phoca groenlandicus*; 12. sea lion, *Zalophus californicus*; 13. sperm whale, *Physeter catadon*; 14. humpback whale, *Megaptera novaeangliae*; 15. blue whale, *Balaenoptera musculus*.

Land mammals: C. Cat, *Felis domesticus* Ch. chinchilla, *Chinchilla langer*; Cp. chimpanzee, *Pan paniscus*; Cw. cow, *Bos taurus*; D. dog, *Canis familiaris*; E. elephant, *Elephas maxlmus*; G.** Gopher *Geomys bursarius*; Gp. guinea pig, *Cavia procellus*; Hg. hedgehog, *Paraechinus hypomelas*; B. bat, *Rhinolophus ferrumequinum*; H. human, *Homo sapiens*; K. kangaroo rat, *Dipodomys merriami*; Mq. macaque, *Macacca mulatta*; S** mole rat, *Spalax ehrenbergl*; M. mouse, *Mus musculus*; Rb. rabbit, *Oryctolagus cuniculus*; R. rat, *Rattus norvegicus albino*; S. sheep, *Ovis arles*; My. squirrel monkey, *Saimiri sciureus*.

*Functional hearing limits estimated from cochlear model data (Ketten 1992, 1994, unpublished data).

**Data points not included in regression calculations.—in-air measures for marine species.

and the debate will continue, primarily because so little physiological data are available and the results are equivocal. To provide a framework for assessing this debate, the relevant concepts of middle ear function will first be reviewed.

5.2.1 Middle Ear Functions

Because the basic land mammal ear comprises an air-filled middle ear and a fluid-filled inner ear, there is an air-to-fluid impedance mismatch that must be overcome for efficient transfer of sound energy. Consequently, middle ears are commonly thought of as impedance-matching devices or transformers that counteract the approximately 36 dB loss expected from the impedance differences between air and the fluid-filled inner ear. The impedance transformation is achieved primarily by mechanical advantages derived from the difference in the area of the middle ear membranes (large tympanic versus small oval window) and from the lever ratio of the bony ossicular chain linking the membranes. Acting in concert, these create a pressure gain and concomitant particle velocity reduction at the inner ear. For marine mammals this function may not only be unnecessary but disadvantageous.

Improved power transfer is not necessarily the only function of the middle ear. Recent studies propose a complementary middle ear function, called the peripheral filter-isopower function, in which the middle ear has a tuning role (for comprehensive discussions see Rosowski 1994; Yost 1994). In land mammals, the middle ear is an air-filled cavity with significant differences among species in volume (V), stiffness (K), and mass (M). Middle ears in each species are differentially tuned to a specific middle ear resonance based on the combined chain of middle ear impedances, which, in turn, depend upon the mechanical properties of the middle ear components. For any animal, the sum of impedances is lowest, middle ear admittance is greatest, and energy transmission is most efficient at the middle ear's resonant frequency (f). As might be expected, this frequency also tends to be at or near the frequency with the lowest threshold (best sensitivity) for that species (Fay 1992). Impedance (Z) can be thought of as the sum of resistance and reactance. Because friction is minimal in the middle ear, resistance can be discounted. Reactance (X) is determined by mass and stiffness. Stiffness and mass act inversely in a frequency-dependent system: $f_{resonance} = (1/2\pi)\ (K/M)^{1/2}$. Calculating middle ear impedances is far more complex than simply describing the middle ear elements, but, in general, increasing stiffness in the middle ear system improves the transmission of high frequencies; adding mass to the system favors low frequencies. Consequently, in addition to impedance matching, middle ears may also be evolutionarily tuned by having frequency selective elements with different mass and stiffness in each species. Ultrasonic species have relatively stiff ossicular chains with small, stiff-walled cavities. Low-frequency species, like heteromyid desert rodents, mole rats, and elephants, have large middle ear

cavities with loosely articulated, massive ossicles. Small low-frequency animals often add mass to the system or have disproportionately large, soft-walled middle ear spaces.

5.2. Cetacean Middle Ear Anatomy

Odontocete middle ears appear to be a compromise between enhancing high-frequency sensitivity and strength. In microchiropteran bats, high-frequency sensitivity in the middle ear is achieved by lightening the ossicles and stiffening their attachments (Reysenbach de Haan 1956; Sales and Pye 1974). In odontocetes, the ossicles are more massive than in most land mammals but have multiple stiffening elements as well (McCormick 1970; Ketten 1984, 1992). As noted earlier, there is no conventional, discoid membranous tympanum as is commonly found in land mammals. Instead, the tympanic membrane is a highly derived structure comprised of a strip of hyaline membrane backed by the tympanic conus, a compressed, fibrous, partly calcified funnel that attaches to the body of the malleus with a strap-like ligament. A bony ridge, the processus gracilis, connects the malleus to the outer wall of the tympanic bulla. This is the one ossicle that is clearly normally fixed in all cetaceans. The other two major interossicular joints are stiffened with ligaments and a membranous sheath but are flexible. The incus is freely mobile. The stapes is mobile with a moderately thick but conventional annular ligament. A substantial stapedial ligament attaches to the head of the stapes; the crus is generally closed.

The consensus of the anatomical data is that odontocete middle ear anatomy is fundamentally consistent with a middle ear system tuned to high frequencies. There are no obviously degenerated or aberrant structures that suggest the middle ear cavity or ossicular chain is vestigial or dysfunctional in any cetacean species documented to date. Sporadic reports in the cetacean literature that indicate odontocete ossicles are either wholly or partially fused are occasionally cited as evidence that odontocete middle ears are dysfunctional, but there are good reasons to be cautious about these conclusions. Whale research is plagued by small sample sizes and lack of comprehensive, controlled subject histories, and the possibility that the ear under study is abnormal must always be considered. In humans, ossicular ankylosis occurs in ~5% of the population (Schuknecht 1993). It has recently been shown that dolphins are subject to presbycusic (age-related) hearing loss and several forms of irrecoverable ear disease (Brill et al. 1997; Ketten et al. 1997; Ridgway and Carder 1997). If odontocetes have incidences similar to humans of other hearing related pathologies, we can expect that 1 in 20 adult animals may have a compromised middle ear.

Mysticete middle ears contrast sharply with the high-frequency odontocete model. Mysticete ossicles are larger and more massive with none of the high-frequency-related specializations common among odontocetes.

The interossicular joints are not fused nor are they apparently stiffened by auxiliary ligaments. While there are no clear patterns of ossicular ligaments in mysticetes, this does not preclude them. Ossicular ligaments and muscles have been reported but the descriptions are inconsistent (e.g., Hyrtl 1845; Boenninghaus 1903; Fraser and Purves 1960). Long post-mortem times and poor preservation are common in baleen material and the inconsistencies could be the result of post-mortem change rather than normal variations or species differences. The ossicles, with the exception of a stalked malleus, are not fused to the bulla. There is no indication of stapedial fusion or calcification of the annular ligament. As noted earlier, the tympanic bulla scales with animal size and is double the volume of the periotic bulla. 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.

Exactly how "massive" are whale ear bones? Lees et al. (1996) measured weight, density, and sonic velocities of relatively fresh fin whale and human ossicles and periotics (Table 2.3). Ossicular weights from a mixture of formalin preserved and dehydrated ears were reported also by Norris and Leatherwood (1981). Lees et al. found that although fin whale tympanic, periotic, malleus, and incus bones had weights 50 to 250 times adult human equivalents, the densities were only 10% greater than in humans (Table 2.3). The density of the porpoise periotic was 2.7 gm/cc or 10% greater than a fin whale periotic and 20% greater than the human temporal bone. Lees et al. calculated that the specific acoustic impedance of the porpoise periotic (14.09 megarayles) is nearly twice that of a human femur and 20% greater than that of an average fin whale periotic (11.7 megarayles). They concluded that three inter-related parameters, high density, high sonic velocity, and high specific acoustic impedance, increase acoustical contrast of the periotic with the other bones, and, like Reuter et al. (1998) for the elephant, concluded also that the large mass of mysticete ossicles suggests a low ossicular chain resonance.

5.2.3 Cetacean Middle Ear Dysfunction: The Debate

Reysenbach de Haan's remark (1956) that "all possible efforts have been made (unsuccessfully) to eliminate the middle ear mechanism . . . as a sound transmission system" is still a fair summary of the state of the whale middle ear debate. The fundamental issue is that in air, the external and middle ear act more efficiently than other channels to deliver acoustic power to the oval window, which induces cochlear motion and differential movement of the round window (for detailed discussions see Rosowski 1994; Yost 1994). If tissues in contact with the ear and both cochlear windows are all equally efficient, then no differential motion of the cochlear windows occurs and the inner ear membranes are not displaced. Many soft tissues have impedances close to sea water. The questions that are

TABLE 2.3. Ossicular weights

Species	Common name	Malleus (mgs)	Incus (mgs)	Stapes (mgs)	Total ossicular mass (mgs)	References
Delphinus delphis	Common dolphin	81	20	5	106	Norris and Leatherwood 1981
Grampus griseus	Risso's dolphin	208	50	18	276	Norris and Leatherwood 1981
Orcinus orca	Killer whale	773	-	50	-	Norris and Leatherwood 1981
Phocoena phocoena	Harbor porpoise	65	16	9	90	Norris and Leatherwood 1981
Phocoenoides dalli	Dall's porpoise	72	18	10	100	Norris and Leatherwood 1981
Tursiops truncatus	Bottlenose dolphin	135	33	9	177	Norris and Leatherwood 1981
Balaena mysticetus	Bowhead whale	1,183	529	169	1,881	Norris and Leatherwood 1981
Balaenoptera physalus	Fin whale	3,180	1,360	590	5,130	Lees et al. 1996
Elephas maximas	Indian elephant	-	-	-	650	Reuter, Nummela, and Hemilä 1998
Equus	Horse	-	-	-	50	Reuter, Nummela, and Hemilä 1998
Homo sapiens	Human	23	27	3	53	Schuknecht 1993

important for cetacean middle ears are: (1) Is there an acoustically superior channel? (2) If so, to what does it connect?

There are currently two competing theories. Both are problematic. One is that bulk motion of the head sets the inner ear in motion. This implies stimuli are delivered simultaneously to each ear, but this means sound localization verges on impossible. The second theory is that body tissues (predominately bone) conduct sound directly to the ear producing differential movement but at very small amplitude of the cochlear windows. Support for one theory comes from experiments by McCormick et al. (1970, 1980) with anesthetized *T. truncatus* and *Lagenorhynchus obliquidens* (Pacific white-sided dolphin), in which immobilizing the ossicular chain decreased cochlear potentials by 18 dB, but disrupting the external canal, tympanic conus, and malleus had little (4 dB) or no effect. They concluded sound entering from the mandible by bone conduction produces a "relative motion" between the stapes and the cochlear capsule. Fleischer (1978) disagreed. He suggested the surgical procedure damaged the normal ossicular mechanism. From anatomical studies of preserved material he had concluded that sound from any tissue path is translated through tympanic vibrations to the ossicles which then pulse the oval window. McCormick et al.'s theory depends upon tissue conduction and an inertial lag of the cochlear fluids in a vibrating bulla and assumes fixed or fused tympano-periotic joints. Fleischer's theory depends upon differential resonance of the tympanic and periotic bones, a freely mobile stapes, and flexible tympano-periotic sutures. In fact, neither theory is consistent with the range of known middle ear variations among cetacean species.

Middle ear air volumes are another topic of debate. The tympanic space defined by the bullar cavity is relatively large in all cetaceans but bony walled bullar volume may not be the relevant middle ear space for a whale. To understand functional middle ear space, soft tissue influences must be considered.

The middle ear cavity in both odontocetes and mysticetes is lined with a thick, vascularized mucosa, the corpus cavernosum (Fig. 2.4). This is a distensible tissue, capable of filling the tympanic chamber, but it does not necessarily preclude air in the middle ear cavity. Computerized tomographic images of live animals show that animals in air at sea level have substantial and equal volumes of air in the middle ear cavities although the corpus cavernosum is not totally relaxed (Ketten 1998b). What we do not know is whether there is normally air in the middle ear of any submerged or diving marine mammal.

Changing middle ear volumes are generally undesirable auditorially. For diving mammals there are two options: (1) the volumes are somehow maintained, or (2) the volumes are somehow irrelevant. A recent experiment with *D. leucas* (the beluga whale) (Ridgway and Carder 1997) found that although the whale's whistle spectra changed with depth, the hearing thresholds did not. Their conclusion was that "sound is conducted through

whale head tissues . . . without the usual ear drum/ossicular chain amplification of the aerial middle ear." However, these data could equally be interpreted to mean that there is a middle ear mechanism in *D. leucas* that maintains middle ear impedance characteristics independent of depth.

The corpus cavernosum is a prime candidate for regulating the middle ear space. It is not only distensible, it also contains large bundles of trigeminal nerve fibers (Fig. 2.4). It is not known whether these fibers actually innervate the cavernous tissue or are simply transiting it, but it has been suggested (Ketten 1992) that the trigeminal, which is a somato-sensory nerve with up to 500,000 fibers in cetaceans versus 140,000 in humans (Morgane and Jacobs 1972) is in the right position to subserve a middle ear regulatory function.

One other anatomical observation may be relevant to this issue. Beaked whales (Ziphiidae) are perhaps the deepest diving mammals. Ears from three ziphiid species were recently examined for adaptations related to their diving abilities or, more precisely, to their ability to avoid barotrauma (Ketten 1998b). Among the specialized structures unique to these ears is a newly described function for a bony strut associated with the anterior edge of the tympanic bulla. This sigmoid bone attaches to the Eustachian tube at its entrance to the tympanic bulla and prevents the tube from collapsing. The question is, of course, why a species, if it does not have air in the middle ear, would have a mechanism for maintaining Eustachian tube patency? It could be argued that air is required and therefore maintained in the middle ear to allow differential motion of the cochlear windows but that the space per se is acoustically moot. Coordinated oppositional motion of the windows does not actually require an air cavity if the corpus cavernosum is compressible, leaving still a need to explain an air pocket that is sufficiently large that it requires equilibration. Finally, a less cogent but anatomically correct argument is that the middle ear structures in whales are sufficiently complex, organized, and conservative across species that it runs contrary to basic functional principles to dismiss them as simply auditory bric-a-brac.

To the extent that information extrapolated from available anatomical data are reliable, the middle ear anatomy of all Cetacea appears to be tailored to sustain large ambient pressures. The massiveness and complexity of cetacean ossicles suggest that the middle ear has at least some minimal conventional impedance matching or energy transfer 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 laterally from the ear canal or via bone conduction to the membrane and not from specialized bundles of soft tissues. If the middle ear space is defined by the volume of the tympanic shell, then mysticete middle ears are substantially more voluminous than those of odontocetes, or in fact than of any other extant animal. Functions for odontocete middle ear cavities and ossicular chains are simply unclear.

In fact, at this moment, middle ear functions are unresolved for all cetaceans. Curiously, middle ears are more obtainable than many other whale ear structures. They simply have not been well explored, and, in the absence of new data, the debate goes on.

5.3 The Inner Ear

The cetacean inner ear is subdivided into the auditory and vestibular systems.

5.3.1 The Vestibular System

The vestibular system is not generally considered part of the auditory system, although it has been implicated in low-frequency hearing (Yeowart 1976) and there are some special features of cetacean vestibular systems that are worth noting briefly. Size is not a criterion for a functional vestibular system, but cetaceans have semicircular canals that are "disproportionately minute" compared to cochlear canal diameters and volumes (Boenninghaus 1903; Gray 1951). This reduction is most extreme in odontocetes but it is true also for mysticetes. Semicircular canals in some individuals are compressed, the ampullae are nearly acellular, and the vestibular fiber counts are commensurately small (Ketten 1992; Gao and Zhou 1995). Both the average cell count for Scarpa's ganglia (<4,100) and the proportion of eighth nerve fibers that are vestibular (<5%) are exceptionally low compared to an average of 30% in most mammals (Table 2.2).

No other mammal, including pinnipeds, is known to have similar vestibular reductions, which argues that attenuated semicircular canals are related to an obligate aquatic lifestyle. One possibility is that the fusion of the cervical vertebrae that occured in whales limited head movement, reducing inputs to the vestibular system and decreasing its utility, which led to an evolutionary diminution. The modern cetacean vestibular system may act therefore purely as van Bergeijk (1967) suggested, that is, as a "vehicle-oriented accelerometer," obtaining only linear acceleration and gravity cues but no rotational or three-dimensional acceleration inputs. Studies of labyrinthectomized cats and congenitally alabyrinthine humans found that the absence of functional semicircular canals eliminates motion sickness (Graybiel 1964). An attenuated vestibular system may therefore be highly adaptive for cetaceans, permitting high-flying spins without "space-sickness" side-effects.

Two cetacean groups have been found to have noticeably larger vestibular systems. Bowhead whales (*Balaena mysticetus*) and Northern right whales (*Eubalaena glacialis*) have large semicircular canals and very similar bullar shapes (Fig. 2.4) (Yamada and Yoshizaki 1959). While the vestibular system in these whales is still much smaller than in most land mammals, it is approximately double the size of vestibular systems in other mysticetes.

No behavior in bowhead and Northern right whales has been reported that appears to relate to greater vestibular effort than in any other mysticete. Nevertheless, the similarity of bullar shape as well as inner ear structures in these two species suggests that whale ears may have suites of explicitly functional (as opposed to morphometric) characters that are worth analyzing for systematic affinities. The second group that had well-developed vestibular elements was the Ziphiidae. The ziphiids noted earlier had exceptionally large, bulbous vestibules, and distinct, moderately sized semicircular canals (Ketten 1998b). Unfortunately, so little is known about the behavior of most ziphiid species that these observations only raise more questions than they answer at this time.

5.3.2 The Cochlea

Slepecky (1996) provides a comprehensive overview of mammalian cochlear structure and the functional role of specific elements. Because different names are occasionally employed for common mammalian ear structures in the animal versus human literature, some basic concepts and terms will be reviewed briefly. Only notable differences between cetacean ears and a prototypical mammalian cochlea will be discussed in depth.

The cetacean cochlea has the same fundamental organization as other mammalian inner ears. It is a fluid-filled, gnomic spiral with a decreasing radius and uniform rise divided by membranes into three chambers or scalae (Figs. 2.4, 2.6): scala media (cochlear duct), scala tympani, and scala vestibuli. The scalae appear to be three parallel tubes but are actually two. An outer U-shaped tube formed by scala tympani and scala vestibuli surrounds the cochlear duct, which is an epithelial walled space that houses the organ of Corti. The cochlear duct, or scala media, is bounded by the basilar and vestibular (Reissner's) membranes. The coiled scalae lie inside the periotic like a spiral staircase. The core of the stair is the modiolus, a bony tunnel housing the fibers of the auditory branch of the eighth nerve. The tread of the staircase is the basilar membrane, a graded resonator that responds as a series of bandpass filters. The organ of Corti, a complex set of cells that transduces mechanical stimuli into neural responses, is spread atop the basilar membrane. The diameter of the spiral is greatest at the base (basal turn) and narrows gradually towards the apex (apical turn). Turn number varies from 1.5 to 4.5, depending upon the species (Figs. 2.4, 2.7).

The orientation of the cochlear canal in the periotic is probably not an acoustically significant feature in any mammal, but because it is unusual in cetaceans and its significance has not been analyzed, it is mentioned here. The emigration of the tympano-periotic complex carried with it, literally, the cochlear spiral. In land mammals, including humans, the cochlear or modiolar axis is oriented anteriorly; that is, the base of the cochlea is posterior and slightly superior to the apex. The main axis of the spiral is oriented parallel to the ground. In most mammals this puts the base of the

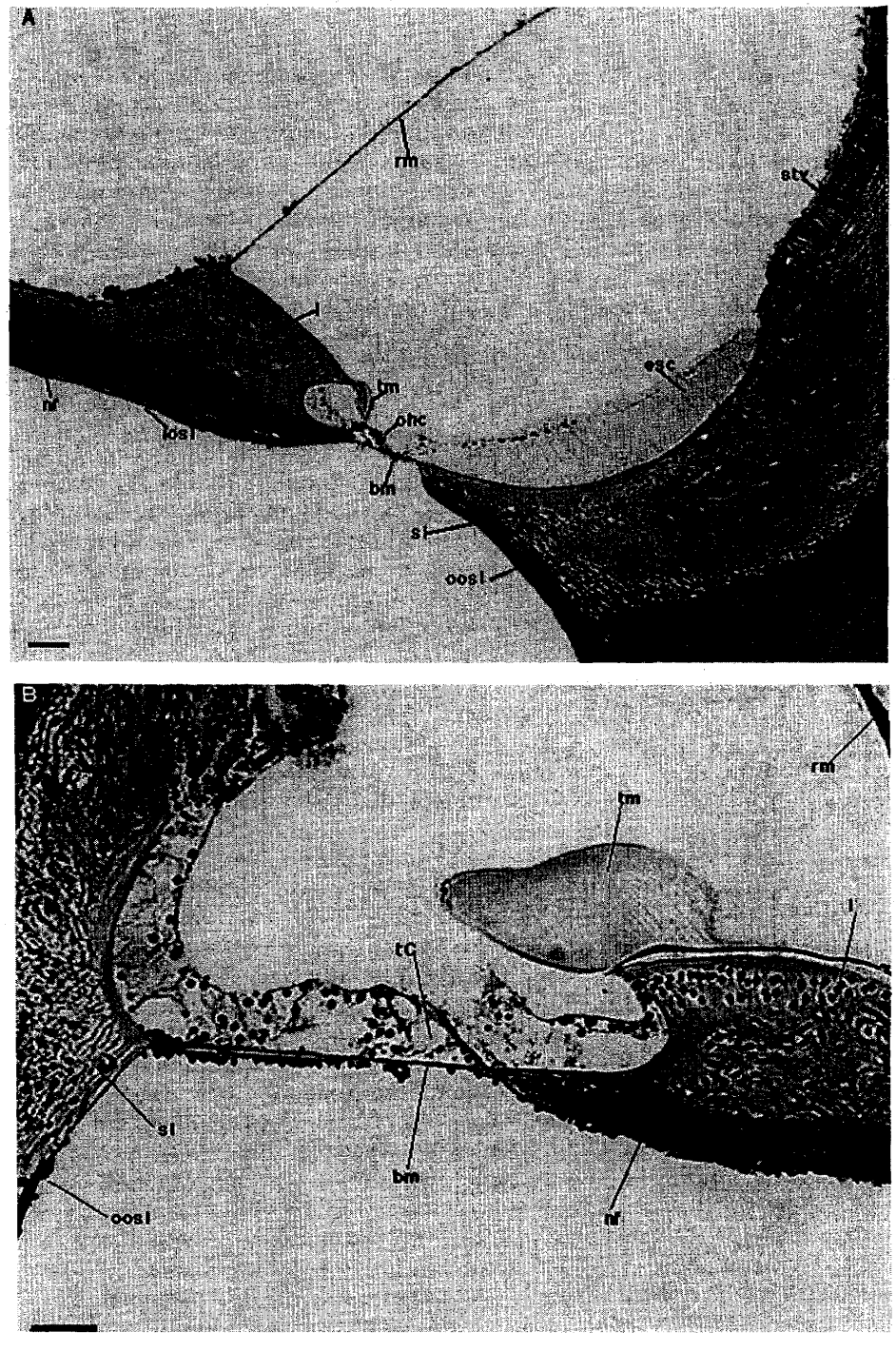


FIGURE 2.6A,B

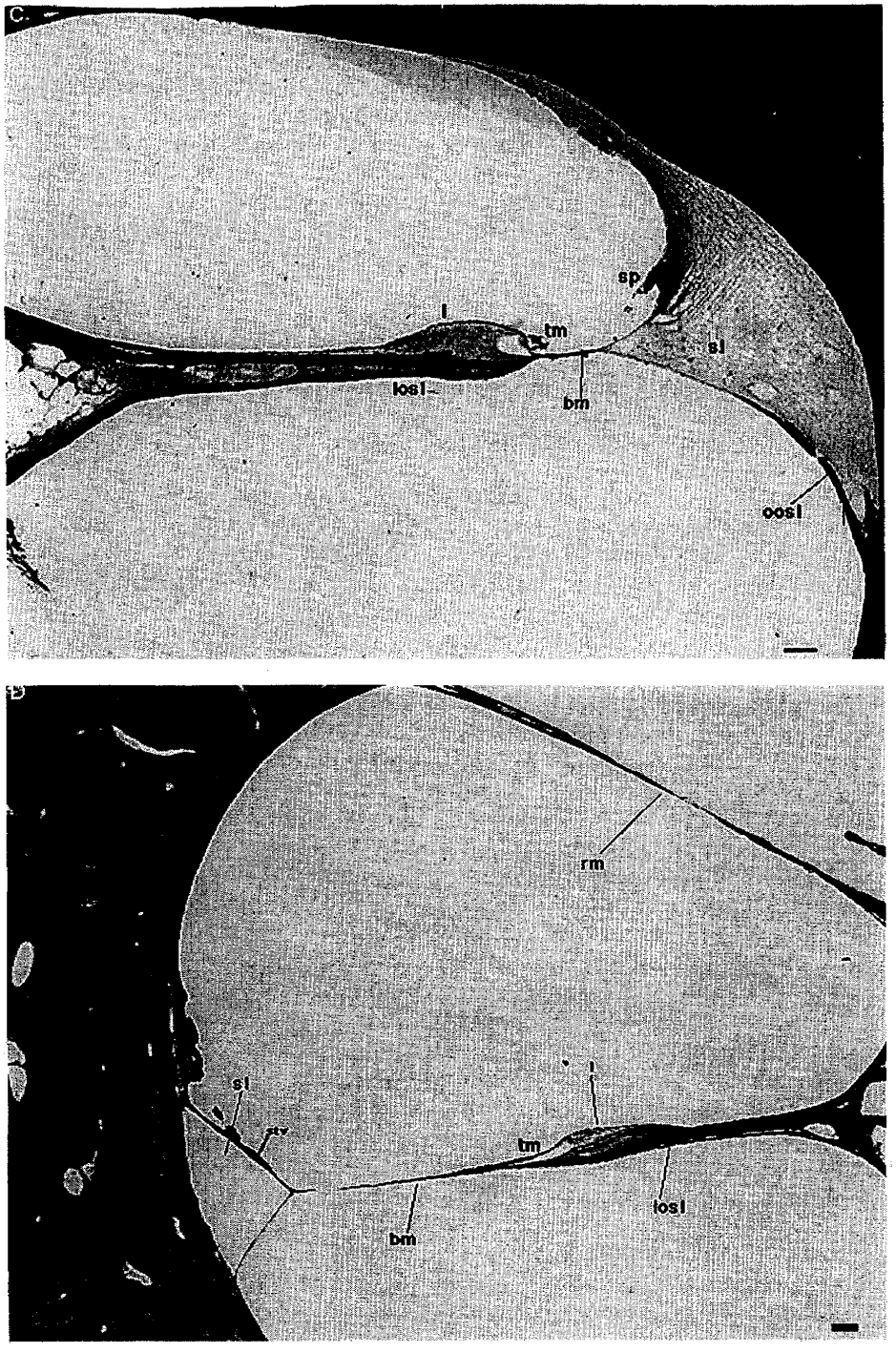
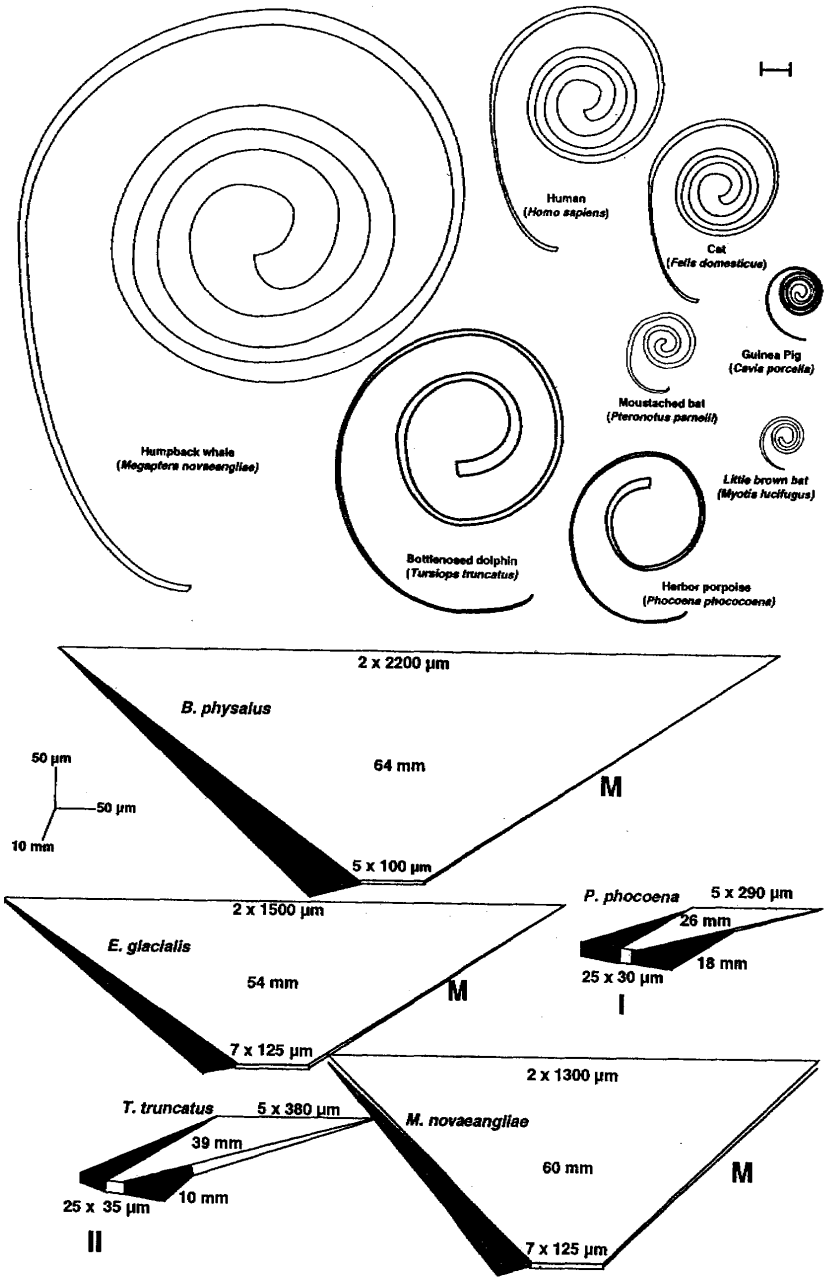


FIGURE 2.6C,D

cochlea towards the back of the head and the apex oriented in the same direction as the nose. In a dog, cat, or seal, a modiolar plane is consequently a coronal section. In humans, because of the reorientation of the head atop the spinal column, the modiolar plane is transaxial but in terms of the cochlea's relation to the planes of the head and normal direction of motion, the inner ear has the same orientation as in other mammals. In cetaceans, the modiolar axis runs orthogonal to the common mammal orientation. That is, in a resting whale on the surface, the cochlear apex points down. Cetacean cochlear spirals run dorso-ventral/base-apex with the round window posterior and medial to the oval window (Fig. 2.4). In this chapter, to ease comparisons of cetacean ears with ears of other animals, cochlear anatomy and reconstructions are shown in the conventional display posi-

FIGURE 2.6. Cochlear duct cytoarchitecture. Micrographs of 25 μm celloidin sections illustrate similar basal and apical turn positions in Type I, Type II, and Type M cochleae. The images are shown in a conventional orientation, although in vivo, the cochlear apex points ventrally in cetaceans (see also Fig. 2.4). Tissues were collected 5 to 48 h post-mortem and have preservation and processing artifacts similar to human temporal bones, including disrupted Reissner's membrane, necrotic organ of Corti, and ganglion cell loss. Scale bar = 100 μm. (A) The basilar membrane (bm) (60 μm × 20 μm) of *Phocoena phocoena*, a Type I odontocete, in the mid-basal turn is stretched between inner (iosl) and outer (oosl) ossified spiral laminae. The outer lamina is 40 μm thick. A distinctive dark cellular layer known only from the basal turn of odontocetes lines the lateral basilar membrane recess. Although noted by several authors, these cells are unclassified and their function remains unclear. The dense collagenous basketwork of the spiral ligament, darkly stained hypercellular stria vascularis, and tight packing of nerve fibers are classic odontocete basal turn structures common to both types. The strong development of support cells shown in this section is characteristic of Type I odontocete ears. (B) In an apical section, the basilar membrane of an Atlantic white-sided dolphin (*Lagenorhynchus acutus*, Type II odontocete) is thin and broad compared to the basal anatomy. Only the spiral ligament (sl) directly supports the lateral edge of the basilar membrane. Note the inverse development of the tectorial membrane in comparison to the basilar membrane. (C) In an adult Northern right whale (*Eubalaena glacialis*), a mysticete, the basilar membrane (m) is 5 μ × 125 μ in the lower basal turn. The level of cellular development of the spiral ligament is similar to that of the odontocete apical region in (B). The inner osseous laminae are also noticeably thin with a large central lumen. Lack of supporting cells and nerve fibers is probably the result of post-mortem necrosis and does not represent a normal density. (D) A mid-apical section of *Eubalaena glacialis* shows a characteristically lissome mysticete basilar membrane that is ~1,200 μm by 3 μm. The spiral ligament is intact but is sufficiently acellular that it is difficult to detect in this micrograph. The tympanal plate of the inner osseous lamina is negligible as a support element. bm, Basilar membrane; esc, external sulcus cells; l, spiral limbus; nf, auditory nerve fibers; ohc, *outer hair cells*; rm, Reissrers membrane; sl, spiral ligament; sp, spiral prominence; stv, stria vascularis; tC, tunnel of Corti; tm, tectorial membrane.



tion with the apex up, but to be accurate, this is backwards to a whale ear's normal position in the real, aquatic world.

The contents of the cochlear duct are bathed in endolymph that travels between the cochlear duct and the endolymphatic sac via the endolymphatic duct, which runs inside a bony canal, the vestibular aqueduct. Scala tympani and scala vestibuli are filled with perilymph, which is transported via the perilymphatic duct (periotic duct). In land mammals, the periotic duct connects scala tympani to the subarachnoid space. The bony passage that houses the perilymphatic duct is the cochlear aqueduct.

There are significant variations in the structure of the cochlea and its related ducts and canals among cetaceans. Virtually all cochlear duct structures are hypertrophied in odontocetes. Mysticete ears appear to be less well endowed, but some of the reported low level of cellular development may be post-mortem artifact. Both odontocetes and mysticetes have exceptionally high ganglion cell counts and extreme basilar membrane constructions.

Comprehensive reports on cochlear duct anatomy in two species of dolphin (*T. truncatus* and *L. obliquidens*) are available in Wever et al. (1971a,b,c; 1972). More recent studies reported on cochlear structures in phocoenids, monodontids, and 10 additional delphinid species (Ketten 1984; Ketten and Wartzok 1990; Solntseva 1990). Although perfusion is not an option for cetacean tissues, improvements in stranding network communications have drastically reduced post-mortem collection time, and many specimens can now be obtained with equal or better preservation than the average human temporal bone. The consensus of available data is that all cellular elements of the organ of Corti in odontocetes are larger, more densely packed, and have stronger size gradients than in other mammals. There is a 15-to 20-fold reduction in the height of the Claudius cells from base to apex (Fig. 2.6). Boettcher cells are distributed throughout the entire length of the cochlear duct with double rows in some species. Hensen cells reinforce the basilar membrane in the lower basal turn. Although Wever et al. (1971a) reported four rows of outer hair cells in some parts of the apical region of *T. truncatus*, all other authors report no more than three rows. The discrepancy may be due to individual variability or to oblique sectioning artifacts. Pilleri, Kraus, and Yihr (1987) reported

FIGURE 2.7. Two-dimensional representations of mammalian basilar membranes. (A) Basilar membranes from high- and low-frequency mammals drawn to a common scale in orthogonal projection illustrate differences in width, length, and turns. Scale bar = 1 mm. (B) Type I, Type II and a range of Type M basilar membrane systems are drawn using a dual scale to show differences in the thinkness and width (µm scale) versus membrane length and extent of outer laminar support (mm scale).

deep Azan staining in the basal region of *Monodon monoceros* (narwhal) that they attributed to tonofibrils of the pillar cells, which would act as membrane stiffeners. This is consistent with Wever et al.'s observation that the pillar cells are exceptionally thick in the lower basal turn and Reysenbach de Haan's (1956) earlier description of "short . . . compact" pillar cells in *P. phocoena*.

An important functional feature of all odontocete ears is an exceptionally dense stria vascularis and a spiral ligament with a tightly woven collagen infrastructure (Fig. 2.6A). Stria vascularis, or specifically its marginal cell layer, is considered to be the source of high potassium ion concentrations in the endolymph that control endocochlear potentials (see Wangemann and Schacht 1996). Recent transmission electron microscope images show that odontocetes have up to five layers of marginal cells in the basal stria vascularis (Burgess and Ketten, in preparation). The spiral ligament has the conventional five divisions of cellular types, but again, like other cochlear duct elements, cells are heavily packed. In particular, the collagen fiber density is two- to fivefold that of most mammals with only moderate decreases in the cell packing density in the most apical regions. The ligament's marginal region, which contains fibroblasts that anchor and add tension to the basilar membrane, has dense cellular packing throughout the cochlea.

The significance, if any, of the size of each cochlear canal is not yet known for any mammal, but there are such dramatic differences between land and cetacean ears in some canals that they are worth noting. In cetaceans, there are large changes in the cross-sectional area of scala tympani and of scala vestibuli from base to apex. Scala tympani in all cetaceans has a large area at the basal end of the cochlea that tapers to an apical area that is approximately half that of the base. The large basal scala tympani area is coincident with the entrance of the cochlear aqueduct, which is also exceptionally wide in all cetaceans (up to 5 mm versus 0.2 mm in humans) (Ketten 1998a,b; Schuknecht 1993). Scala vestibuli tapers as well, but more slowly and, interestingly, can have a smaller cross-section in mysticetes than in odontocetes.

Further, because the periotic is disjunct from the skull, the cochlear aqueduct ends at the medial edge of the periotic in the peribullar plexus, not the subarachnoid space. This does not preclude the perilymphatic duct traversing the retro-bullar space to the skull, but it has not been shown specifically to do so. Whether it does or not has implications about the origin, flow, and contents of the perilymph. Although it was originally assumed that some filter mechanism was in place in the perilymphatic duct, it is now clear that in most mammals there is a free communication with the subarachnoid space through which a variety of cells pass (Schuknecht 1993). In fact, in cases of subarachnoid hemorrhage, large deposits of blood in scala tympani enter the ear by the cochlear aqueduct and/or the internal auditory canal. The fact that cetaceans with concussive injuries have the same phenomenon of blood deposits in scala tympani (Ketten 1995) begs the question of where both major cochlear ducts connect in whales and whether they serve equivalent functions in land and aquatic animals.

Disproportionately large cochlear aqueducts have also been noted in constant frequency/frequency modulated (CF/FM) bats (Kössl and Vater 1995). Kössl and Vater suggest that large cochlear aqueducts may prevent damage from intracochlear reverberant oscillations, but if that were the function, why is the cochlear aqueduct significantly larger in all cetaceans? Do cetaceans have greater amplitude oscillations because of greater acoustic pressures? Is this another pointer to low-frequency sonar in baleen whales? It is tempting to draw functional conclusions, but current data are essentially anecdotal. Comprehensive morphometric analyses of the cochlear duct and other canal structures in cetaceans, particularly in mysticetes, may help determine whether similarities between cetaceans and microchiropteran bats are functionally important. If similarities were found among some Type M species, the data would serve also as a valuable guide to which species are worth investigating behaviorally for "mega" sonar. Even more important, this is a clear case where deciphering the anomalous canal structures could lead to a solution for the general case.

The hallmark of mysticete cochlear ducts is bigger structures with fewer cells. Mysticete cochleae (Figs. 2.4, 2.6C,D), with a few exceptions, have cellular trends that are clearly and consistently the opposite of those in odontocetes, even taking into account cellular losses because of poor preservation. Inner ear material from odontocetes with similar postmortem times retain clear evidence of hypercellularity and, even with advanced decay, do not resemble the ears of mysticetes. There is insufficient data to make definitive comments on the cellular distributions in any mysticete organ of Corti. The stria and supporting cells are unremarkable in comparison to the average human cochlea, and the spiral ligament has poor cellular development in comparison to many land mammal cochleae. The same scalar trends are found in mysticetes as in odontocetes. Scala tympani is inflated in the basal turn and there is an exceptionally large cochlear aqueduct. As noted in the previous section, the decrease in scala vestibuli is more pronounced in mysticetes than in odontocetes. Unfortunately, no complete cochlear studies are available for elephants, hippopotami, or other exceptionally large land mammals, which are the species most appropriate for comparing with mysticete whales. Such comparisons are crucial for answering definitively whether mysticetes are on a continuum with larger land mammal ears or if they represent a leap to exceptional dimensions. Clearly there is a distinct hole in the auditory database for larger mammalian ears that hampers our ability to understand and interpret the breadth of cochlear adaptations for low-frequency hearing.

5.3.3 Basilar Membrane Shape and Support

The foundation of frequency analysis in the cochlea is the basilar membrane. The spiral shape of the auditory organ in mammals is generally con-

sidered a significant evolutionary development that accommodates a longer basilar membrane in a confined space. The longer membrane allows more frequencies to be encoded, and consequently, mammals generally have expanded upper frequency ranges and better high-frequency sensitivity compared to other vertebrates.

Basilar membrane dimensions are thought to be an important component of the resonance characteristics of the cochlea (von Békésy 1960). In mammalian cochleae, thickness and width vary inversely from base to apex. The construction of the basilar membrane mechanically tunes the ear to a specific set of frequencies. The highest frequency each animal hears is encoded at the base of the cochlear spiral, where the membrane is narrow, thick, and relatively stiff. Moving towards the apex of the spiral, as the membrane becomes broader and more compliant, progressively lower frequencies are encoded (Table 2.1; Figs. 2.6, 2.7, 2.8). Interspecific differences in hearing ranges are dictated largely by differences in stiffness and mass that are the result of differences in basilar membrane thickness and width along the cochlear spiral. For an animal to "hear" a sound, its basilar membrane must have a point along the membrane that resonates at the sound's constituent frequencies. Therefore, mammalian basilar membranes are essentially banks of tonotopically arranged resonators, arrayed high to low from base to apex, rather like a guitar with densely packed strings covering multiple octaves.

For any input signal within the hearing range of the animal, the entire basilar membrane will respond to some degree. At any one moment, each region of the membrane will have a different amount of deflection and a different phase related to the input signal. Over time, changes in amplitude and phase at each point give the impression of a traveling response wave along the cochlea, but because membrane segments with resonance characteristics closest to frequencies in the signal have greater displacements

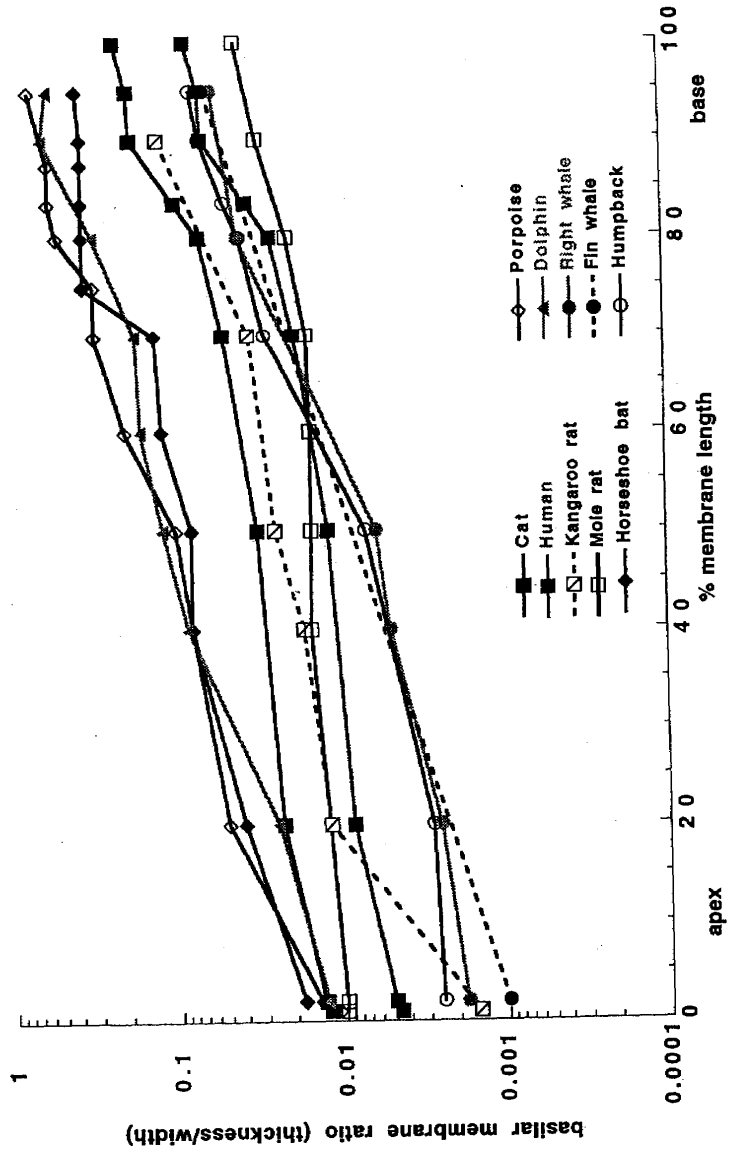


FIGURE 2.8. Basilar membrane ratios. Average thickness/width basilar membrane ratios are plotted as a percentage of cochlear length for five land mammals and five cetaceans. High ratios reflect a thicker, stiffer membrane capable of responding to ultrasonic frequencies. Differences in the basal basilar membrane ratios among the echolocators are consitent with the peak frequency differnces among species. Plateaus followed by steep declines in the porpoise and bat curves reflect foveal regions. Basal ratios in the low-frequency cochleae are similar to the mid-cochlear ratios of higher frequency animals. The fin whale has a basal ratio similar to two other mysticetes but a steeper slope and a significantly lower apical ratio. Species included in the plot are: harbour porpoise, *Phocoena phocoena*; bottlenose dolphin, *Tursiops truncatus*; Northern right whale, *Eubalaena glacialis*; humpback whale, *Megaptera novaeangliae*; fin whale, *Balaenoptera physalus*; horseshoe bat, *Rhinolophus ferrumequinum*; human, *Homo sapiens*; kangaroo rat, *Dipodomys merriami*; mole rat, *Spalax ehrenbergi*; cat, *Felis domesticus*.

than other segments of the membrane, a characteristic profile or envelope develops for the signal.

Based on length alone, cetacean basilar membranes are highly differentiated, anisotropic structures capable of exceptionally wide frequency responses. However, it is well established that multiple basilar membrane paramenters are functional correlates of hearing characteristics (von Békésy 1960; Manley 1972; Ketten 1984; West 1985). Peak spectra and hearing ranges have been shown to correlate (with varying degrees of robustness) with length, width, thickness, etc., but the key to interpreting these relationships is to determine to what extent and how any one parameter relates to function. Thickness and width both have distinct gradients in mammalian basilar membranes. The combination of the two appear to give the highest correlation with hearing characteristics (Ketten 1984). Cetaceans, as a group, have the most extreme range of basilar membrane developments of any known mammal and are therefore excellent subjects for basilar membrane functional analyses.

Humans have an unspecialized, mid-range, generalist ear; average basilar membrane length is 33.5 mm with an approximately fivefold increase in width (125 to 500 μm) and three-fold decrease in thickness (7 to 2 μm) base to apex (Schuknecht 1993; Ketten et al. 1998). In the typical odontocete, width increases 10-fold (35 to 350 μm) while thickness decreases fivefold from 25 to 5 μm base to apex. Mysticete basilar membranes display as much or more base to apex variation (100 to 2,200 μm wide, 10 to 2.5 μm thick) but are consistently thinner at each point than their odontocete counterparts. In comparison to human membranes, we obviously expect odontocetes to have significantly higher and mystictes, significantly lower, functional hearing.

Thickness to width (T/W) ratios are consistent with the maximal high and low frequencies each cetacean species hears and with differences in their peak spectra (Ketten and Wartzok 1990) (Table 2.1; Figs. 2.7B, 2.8). For example, *P. phocoena*, a Type I odontocete, has a basal T/W ratio of 0.83 and a peak frequency of 120 to 130 kHz. *T. truncatus*, a Type II odontocete, has a T/W ratio of 0.71 and a peak signal of ~80 kHz; *Rhinolophus*, a CF/FM bat, a 0.44 T/W ratio and a 40 kHz echolocation signal with significant harmonics near 80 kHz. All three echolocators have terminal apical ratios of 0.01 to 0.02. Mysticete (Type M) T/W apical ratios are commonly 0.001, that is, mysticete membrane ratios start at the basal end at a point equivalent to middle or low apical ratios in the ultrasonic species and decrease steadily to a value a full magnitude lower at the apex than odontocetes. *B. mysticetus* has a basal ratio of 0.062 and produces calls with peak spectra of ~150 Hz. The high T/W ratio areas in bats and dolphins are accompanied by other cochlear duct stiffening elements, creating a high-frequency resonating complex that is entirely independent of membrane length. The mysticete basal ratio is only slightly lower than that of human membranes, implying some mysticetes and humans have similar functional high-frequency limits, but the exceptionally low apical ratios of mysticetes are consistent with broad, flaccid membranes that encode infrasonics well below human lower functional limits of hearing.

Obviously these are very gross approximations. They are presented primarily to illustrate how structure underlies, and implies, exceptional hearing abilities in whales, but they also underscore how functional features may interact and how a single metric can mislead. Odontocetes, on average, have basilar membranes two to five times as long as those of microchiropteran bats, yet they evolved similar hearing capacities. For odontocetes and bats, basilar membrane stiffness distributions are the overarching feature related to the membrane response. Length in both cases is irrelevant.

The most extreme example of this is found among CF/FM Rhinolophid and Pteronotid bats. These bats have basilar membranes with remarkable tuning characteristics. A disproportionate amount (4 to 5 mm) of the total available membrane (14 to 16 mm) encodes a frequency difference of less than 10 kHz. As much as 30% of the basilar membrane, starting from the basal end, has a relatively constant thickness and width. This segment terminates in a cliff where the membrane thickness drops from 30 to 5 μm within 1 mm. The region of rapid change and low neural density is commonly called the acoustic fovea (Bruns and Schmieszik 1980).

There is preliminary evidence for an acoustic foveal region in *P. phocoena*, a Type I odontocete (Ketten 1998a) but it is unclear whether the membrane shapes serve the same acoustic purpose as in bats. *P. phocoena* has a membrane segment that has excessive thickness, stable contours, and bidirectional fibers, all of which have been mentioned as features of CF/FM bat foveal areas (Kössl and Vater 1995; Ketten 1998a). One function proposed for the basilar membrane foveal region is that it provides a reflection zone that engenders standing waves (see Kössl and Vater 1995 for review). In bats, the frequencies represented in this nearly constant cross-sectional area correspond to CF_2, the second harmonic of their echolocation signal. The specialized regions of the basilar membrane optimize detection and analysis of Doppler-shifted echoes by providing a mechanism to enhance the CF_2 signal in comparison to an overlapping call and to detect subtle features in the echo related to prey wing beat patterns (Grinnell 1995). One difficulty in extrapolating this function to an odontocete is that there is no evidence that dolphins or porpoises use Doppler, particularly since the faster sound speed in water implies dolphins can obtain multiple echoes in a short time, negating the advantage that Doppler affords bats in air of being able to resolve prey velocity from one echo (Au 1993).

Aside from inherent stiffness, the next most significant cochlear feature related to basilar membrane resonance is the structure and extent of basilar membrane support. Bony spiral paired laminae are a striking and archetypal feature of high-frequency cochlea. As with other cochlear structures, odontocetes take them to extremes. There are inner and outer bony laminae in all odontocete cochlea (Figs. 2.6, 2.7B, 2.9). The internal laminae form a wedge that runs the full length of the basilar membrane. The thickness of

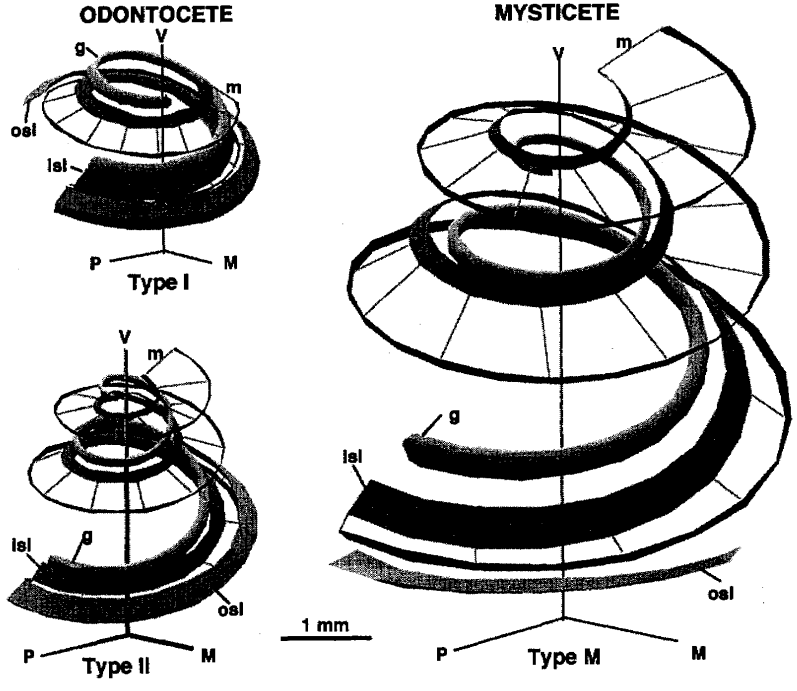


FIGURE 2.9. Basilar membrane and spiral laminae distributions in Cetacea. Three-dimensional composites from cochlear morphometry (Table 2.1) summarize basilar membrane and support element differences among Type I, Type II, and Type M cetaceans. The schematics are drawn to the same scale for the species illustrated. Because of the extreme dimensions of cetacean inner ears, basilar membrane thickness cannot be accurately visualized at this scale. The Type I cochlea has proportionately twice as much membrane supported by bony laminae as the Type II. The outer lamina in Type M ears does not contact the membrane. The basal region of the Type M membrane is three times as wide and one-third as thick as that of the odontocetes; at the apex it is four times the width and half the thickness of the odontocete membranes. The Type II membrane is broader than the Type I at the apex, suggesting Type II species may have somewhat better lower frequency sensitivity than Type I species. More extensive laminar support in the Type I cochlea is consistent with a higher upper limit of functional hearing. g, spiral ganglia; isl, inner osseous spiral lamina; m, mandible; M, medial; osl, outer osseous spiral lamina; P, posterior; V, ventral.

the inner laminae varies approximately 10-fold, base-to-apex, from bilayered shelves that are 50 μm in the lower basal turn to 5 μm apically. The outer lamina in the basal turn in all odontocetes is 30 to 40 μm thick, heavily calcified, and functions as both a support for the spiral ligament and as a buttress for the basilar membrane.

The actual length of the outer lamina in odontocetes is a species-specific characteristic, but when expressed as a percentage of membrane or cochlear duct length, the laminae divide into two distinct groups that coincide with ear and echolocation signal types (Fig. 2.9). In Type II delphinids (peak frequency 40 to 80 kHz), the outer bony lamina is present for less than 30% of the cochlear duct (Table 2.1). In Type I phocoenids (peak frequencies >100 kHz), the outer lamina is present for more than 60% of the cochlear duct. The basilar membrane therefore has substantial buttressing at both edges over twice as much of its length, proportionally, in Type I versus Type II odontocetes. Type I species use, and presumably hear, higher ultrasonic signals. A longer outer lamina in Type I cochleae presumably increases membrane stiffness, which increases the resonant frequency of that portion of the membrane compared to an equivalently shaped membrane in a Type II animal without bony outer membrane support. When combined with the differences observed in membrane ratios, differences in the percentage of membrane buttressed by outer bony laminae provide a simple but important mechanistic link for species-specific ultrasonic ranges in Odontoceti.

Fleischer (1976a) suggests that because dolphin basal inner osseous laminae are constructed of compact bony fibers interwoven to form a dense meshwork, dolphin inner laminae have virtually the same rigidity as solid bone but with less mass. He concluded, based on changes in the solidity and cross-sectional area of the inner laminar plates in the typical *T. truncatus* inner ear, that the stability gradient of the inner osseous lamina changes one hundred-fold from base to apex in dolphins. The outer osseous spiral lamina, by comparison, is largely solid compact bone at the basal end with noticeable fibrous inclusions only as it begins to disappear apically. Fleischer therefore estimated a magnitude greater; i.e., a thousand-fold base-apex stiffness gradient, for dolphin outer laminae. If these observations and gradient estimates are even vaguely correct, they suggest that differences amongst species in both the mass and stiffness of the outer versus inner suspension of the basilar membrane are highly significant elements affecting membrane motion that are generally overlooked in basilar membrane models (see de Boer 1996).

In low-frequency mammals, the inner laminae are poorly developed and outer laminae are reduced or absent. Mysticetes are no exception to this pattern. The cross-sectional separation of the tympanal and vestibular plates is large in mysticetes (300 μm, 60 μm at the apex), but the struts are so thin that the two lightweight laminar plates appear to be disjunct in many places (Fig. 2.6C,D) (Norris and Leatherwood 1981). Towards the apex the struts disappear, leaving only parallel, uncoupled laminae or, in some cases, a single plate for support in the upper apical turn. The outer lamina is absent or reduced to a disjointed thread. It is assumed to be dysfunctional and is probably vestigial in mysticetes.

One other point on laminar construction should be made. In part because of their rarity and post-mortem condition, whale ears, like fossil material,

occasionally have only bony structures available for analysis. In many studies of both fossil and extant species, interlaminar widths have been construed as synonymous with basilar membrane widths. Careful examination of membrane attachment points (see Fig. 2.6) shows that interlaminar distances do not equal basilar membrane widths. In the apical turn in odontocetes, using laminae to cochlear wall distances as an indicator of basilar membrane position overestimates membrane width by approximately 26%; in mysticetes at the basal end, interlaminar distances overestimate membrane widths by approximately 110%. While the construction of the laminae are certainly an important feature of basilar membrane support and the absence/presence of robust outer laminae alone may be a useful diagnostic of generic high- versus low-frequency hearing, the separation of inner and outer laminae per se, particularly relatively friable laminae, is not a valid alternative measure of membrane dimensions from which frequency characteristics can be accurately calculated.

5.3.4 Neural Morphometry

Auditory fiber and ganglion cell counts are remarkable in all cetaceans, particularly considering, as noted earlier, that many counts are based on residual neural populations from stranded animals (Table 2.2). Before describing neural distributions and morphometry, one curious feature about cetacean eighth nerves is worth noting. While the acousto-vestibular nerve is clearly important to cetaceans, it is also remarkably vulnerable. The extracranial position of the periotic, whether it came about for hydrodynamic or acoustic reasons, requires the eighth nerve to cross the retro-bullar space without the protection of bony canals before entering the brain case. In some species, this means the nerve is exposed along a path of 3 cm or more. This "externalization" of the auditory nerve may be unique in cetaceans. In odontocetes, the nerve has a dense fibrous sheath covering its exposed segments as well as thick, fibrous gaskets at its entry to the periotic, but, curiously, not at its entry point in the basi-cranium (Ketten 1992).

Whale auditory fiber diameters range from 2 to 40 μm, with a mean of 12 μm in odontocetes and 5 μm in mysticetes, compared to a land mammal range of 1 to 15 μm and an average of 3 μm (Morgane and Jacobs 1972; Ketten 1984, 1992; Nadol 1988; Gao and Zhou 1992, 1995). Ridgway et al. (1981) suggested that these diameters are consistent with shorter latencies in dolphin auditory brain stem responses (ABRs). Spiral ganglion cell bodies are also larger in cetaceans than in other mammals. The largest spiral ganglion cells, with axial lengths 50 μm by 31 μm, are found in the sperm whale (*Physeter catodon*) (Ketten, unpublished data). One of the smallest cetaceans, *P. phocoena*, has spiral ganglion cells that average 35 μm by 25 μm. In delphinids, most auditory ganglion cells are 40 μm by 25 μm. There is no clear correlation of auditory nerve fibers and ganglion cells with Type I or Type II ears. Instead, the numbers hint at a correlation with body size, but this has not been explicitly demonstrated in any mammal.

Auditory ganglion cell totals for cetaceans are more than double the human average. More important, both odontocete and mysticete auditory innervation denstities are significantly greater than those of other mammals. Auditory ganglion cell totals range from 68,000 in *P. phocoena* to over 160,000 in *B. physalus*. Auditory ganglion cell densities in Type I odontocetes average 2,900 cells/mm of basilar membrane; 2,500 cells/mm for Type II odontocetes; and 2,300 cells/mm for mysticetes (Table 2.2). Given 100 inner hair cells/mm and three rows of outer hair cells/inner hair cell in whales, these data imply a ganglion to hair cell ratio of approximately 7.3:1 for Type I species, 6.5:1 for Type II, and 5.7:1 for Type M. The human ratio is 2.4:1; for cats it is 3.7:1; and for bats, 4:1 (Firbas 1972; Bruns and Schmiezek 1980). Since 90% to 95% of all afferent spiral ganglion cells innervate inner hair cells, the average ganglion cell to inner hair cell ratio is 27:1 for cetaceans, or more than twice the average ratio in bats and three times that of humans.

Wever et al. (1971c) speculated that additional innervation is required in the odontocete ear to relay greater detail about ultrasonic signals to the central nervous system in echolocation analyses. Electrophysiological results are consistent with this speculation. Bullock et al. (1968) found three distinct categories of response units in the inferior colliculus of dolphins: those that were signal duration specific, those that responded to changes in signal rise time, and those that were specialized to short latencies with no frequency specificity. This division of signal properties among populations of neurons is consistent with, although not identical to, observations in bats of multiple categories of facilitation and analysis neurons (Suga 1983; see also Ridgway, Chapter 6). Clearly, it is reasonable to assume that high ganglion cell ratios in odontocetes are related to the complexity of information extracted from echolocation signals, but this does not explain equally dense auditory innervation patterns in mysticetes. Similar odontocete and mysticete ganglion cell densities suggest that baleen whales have equally complex auditory processing, which raises a new and intriguing question: What do baleen whales extract acoustically from low to infrasonic signals?

Comparisons of the ratios of auditory, vestibular, and optic counts in cetaceans and land mammals underscore the importance of hearing in whales (Table 2.2). As indicated earlier, vestibular counts in all cetaceans are exceptionally low. Whale vestibular to auditory ratios are approximately one-tenth those of land mammals. Optic to auditory ratios in Type II odontocetes and mysticetes are one-half to one-third those of land mammals, while ratios in Type I odontocetes (0.2 to 0.3) are nearly a magnitude lower. The most extreme contrast in optic-auditory ratios is the 200-fold difference between the vision top-heavy human value of 38.0 versus the 0.15 ratio for *I. geoffrensis*, a riverine Type I odontocete that has the lowest visual acuity of any aquatic mammal (Mass and Supin 1989). Optic to vestibular ratios for all cetaceans (25 to 45), except *I. geoffrensis* (6.6), are midway between those of cats (15.6) and humans (74.3), suggesting that on

average, similar reductions occurred in both optic and vestibular systems in whales.

6. Gedanken Experiments

6.1 Functional Predictions from Anatomy

Greenwood's equations (1961, 1990) are the most commonly used methods for estimating the frequency distribution map (range and location of frequencies along the basilar membrane) in different species. They are based on the distribution of critical bands in the human and on von Békésy's (1960) elasticity-position-frequency measurements for six mammals and one bird. Greenwood's equation for resonant frequency at point (x) of the basilar membrane is: $F = A\ (10^{ax} - k)$. The empirical values for the related constants for humans are $A = 165.4$, $k = 0.88$, $a = 0.06$. For all species, $ax = 2.1$ for 100% length. Using these values, it is possible to estimate the distribution of frequency along the cochlea. To estimate basilar membrane-frequency (BMF) maps for other mammalian species, A is calculated as:

$$A_{animal} = (A_{human})(\text{human length}/\text{animal length})^2$$

Greenwood's formulae have one free parameter (length) and one assumption: all membranes are isomorphic with the human. Therefore, the subject membrane is represented in the calculation as a proportion of average human length. As discussed earlier, length is an indirect representation for stiffness in generalist ears; Greenwood's calculated curves have the same form as von Békésy's membrane-elasticity curves. Fay's extrapolation (1992) of Greenwood's work shows that the BMF distribution equation can be used to derive estimates of critical bands (CB), critical masking ratio (CRB), and frequency discrimination thresholds (FDT) that are comparable to psychophysical values for species with generalized ears. They have recently been shown, with limitations, to be applicable also at an individual level (Ketten et al. 1998).

However, none of these estimators are robust for specialized ears, particularly not for aquatic echolocators. Some specialized ears are in a sense cryptomorphic in that their key features are difficult to extract from their predominately generalist structure. Type II odontocetes fall into this category. Based on conventional measures, Type II odontocetes have few structural deviations from a general terrestrial mammal ear. Nonetheless, these are specialized ears that violate Greenwood's primary assumption: stiffness and mass do not covary with length with the same function as land mammal ears. For example, standard land mammal length-derived hearing models (e.g., Greenwood 1961, 1990) predict an upper limit of hearing of approximately 15 kHz for the bottlenosed dolphins, *T. truncatus*, based on basilar membrane length of 39 mm (Table 2.1). *T. truncatus* actually has a functional high-frequency hearing limit near 160 kHz (Nachtigall et al., Chapter 8). Just as CF/FM bats have basal turn membrane anomalies and mole rats add apical mass, all dolphins have anomalously narrow, thick membranes for their length, and they add auxiliary stiffeners to the mix (Ketten 1984, 1992).

With sufficient parameters, an accurate estimate can be calculated for frequency distributions for any animal. The first step is to determine the rules for how ear structures scale from one animal to the next and how structural parameters correlate with frequency. Multivariate analyses of the published data on whale cochlear morphometrics data show frequency ranges and peak spectra are reliably predicted (0.1% confidence level) by a composite of basilar membrane thickness/width ratios, laminae/length ratios, and turn number (Table 2.1) (Ketten 1984). This composite boils down to a morphometric description of how stiffness varies with spiral position (Fig. 2.9). Type I odontocetes have a basal ratio of greater than 0.8, outer laminar support for greater than 60% of cochlear length, and peak frequency of greater than 100 kHz. They also have low rise spirals of less than 2 turns. Type II odontocetes have a basal ratio of less than 0.75, less than 30% outer bony support, and a peak signal of less than 90 kHz. Type II cochleae are steep spirals of greater than 2 turns. Type M spirals can be viewed two ways. They are consistent proportionately with Type II formats but have lost high-frequency features. Alternatively they are simply very large generalists. They do not, of course, have outer bony support elements or other stiffeners. Commensurate with their body type, mysticete basilar membranes are exceptionally long. In terms of generalist fits, they are also exceptionally broad and thin, implying very low stiffness and low to infrasonic hearing abilities. At this point, primarily because of a lack of adequate cochlear duct data, there are no data that show Type M ears to be anything except an extended generalist.

These composite cochlear schematics, stripped to three parameters, are the cetacean analog of Greenwood's human-derived formula for land mammals. This accomplishes the first step in representing specialized ears: establishing the minimal and/or optimal set of parameters needed for comparing species.

It also provides the basis for the second step: formulating a media-blind estimator of frequency ranges. Historically, researchers have progressively added more parameters into the equation, but only rarely has there been an attempt at retrospective analyses that selectively remove noncrucial elements (see Fay 1992). For mammalian ears, hearing range estimates for both generalist and specialized ears are radically improved, up to a point, if more than one parameter is used. That point is the watershed that differentiates predominantly individual versus species-level adaptations (Ketten 1984). In mammalian ears, based on comparisons of model versus audiometric data for species with both available, two functionally related parameters, thickness and width, are sufficient (Ketten and Wartzok 1990). Further additions will improve the tails of the hearing range estimates, but the ratio of thick-

ness to width provides a surprisingly close approximation of the static stiffness gradient for a mammalian cochlea (von Békésy 1960; Ketten 1984).

For most species, therefore, the BMF equation devolves to, not surprisingly, a simple expression that reflects the exponential gradient of most cochleae: $f = A\ e^{(ax)}$, where A is a stiffness coefficient derived from the thickness:width ratio, a is the species size factor dictated by the basilar membrane interturn radii, and x is the intracochlear position (Ketten 1994; Ketten et al. 1998 for detailed discussions). This equation, for obvious reasons, has the same form as Greenwood's analyses; the fundamental difference is that it is cochleocentric rather than homocentric and, therefore, does not presume a generalist format and constant gradient.

On the other hand, this equation does presume a regular spiral and membrane substructure. While the equation is sensitive to membrane gradients, at this stage it does not accomodate multiple gradients. For specialized species like CF bats and, possibly, Type I odontocetes with dichotomous membrane profiles, more than one expression is required. Even more important, as the curves for the kangaroo and mole rat in Figure 2.8 demonstrate, a t/w ratio-based equation addresses one aspect (stiffness) of a fundamental mechanism (membrane resonance) and can differentiate between generalist and specialist ears for which a stiffness irregularities *internal* to the basilar membrane are the principal variable, but it is blind to auxilliary structural effects. Mass-loading is just one alternative side to laminar buttressing coin. Certainly, there are more sophisticated and computationally complex models (see de Boer 1996 for review) that attempt to address these issues, but few are based in the anatomy and even fewer are aimed at understanding species-specific variations. For a comprehensive morphometric model, a third step is now required—and like most interesting mathematical issues raised in book chapters, the solution is left, of course, to the student.

There has been comparatively little work done on inner ear correlates of low-frequency hearing, but at least one interesting correlate with canal configurations has been reported. Dallos (1970) found radically different magnitude and phase responses in two high-frequency species (cat and chinchilla) and two low-frequency species (guinea pig and kangaroo rat) that have similar middle ear transfer functions. The differences were consistent with differences in the acoustic input impedances of the cochlea, helicotrema dimensions, and cochlear spiral turns. Low-frequency sensitivity was *inversely* related to both helicotrema area and cochlear turns. The guinea pig and kangaroo rat had areas approximately one-tenth those of the cat and chinchilla. They also had scala vestibuli that decreased rapidly in area towards the apex and cochleae with greater than 4 turns. Cat and chinchilla by contrast had slower rates of decrease in scala vestibuli and cochleae with less than 3 turns. The rate of change in sensitivity functions at low frequencies were twice as large (–12 dB) in animals with large helicotrema (cat and chinchilla) as in the animals with small helicotrema (–6 dB). Dallos suggested that these features are consistent with and, in the case of helicotrema size, are a major influence on the acoustic filter characteristics at the apex. While there are no comparable data for cetaceans at this time, it is intriguing that the 1.5-turn cochlea of a small Type I odontocete, *P. phocoera*, has a scala vestibuli area approximately equal to that of a 2.5-turn cochlea of *Megaptera novaeargliae* (the humpback whale) at an equivalent position. This general description is consistent with Dallos's assessment and with the projected differences in the low-frequency abilities of a Type I (poor low-frequency sensitivity) versus Type M (good low-frequency sensitivity) ear. This also suggests that the fundamental mechanics for low-frequency hearing are similar in cetaceans and land mammals.

6.2 *Cross-Boundary Comparisons*

Cochlear formats and frequency ranges in cetaceans coincide with habitats and feeding behaviors. Type I formats are found in inshore phocoenids and riverine platanistids. These species live in turbid waters and use ultrahigh-frequency, short wavelength signals consistent with analyzing fine details of nearby objects. Type II formats are common in offshore and pelagic delphinids. Their slightly broader, less rigid membranes suggest better mid-to low sonic range hearing than Type I ears as well as lower frequency ultrasonic ranges. These hearing characteristics are consistent with highly social species that use 1 to 10 kHz communication signals and lower frequency, longer wavelength ultrasonic signals that can resolve predators and prey at greater distances than the Type I signals.

Are these format differences uniquely aquatic? Structurally, yes; functionally, perhaps not. If sound use is correlated with habitat, and in turn with function, structural adaptations found in one medium should be found in parallel in animals that use similar sounds and at some level similar behavior in a different medium. Put simply, ears should parallel habitat and signal types. Echolocators offer the chance to make multispecies cross-media comparisons.

Superficially, bat and dolphin echolocation signals and processing appear to have little in common. Dolphin echolocation signals are generally shorter, broader band waveforms with higher peak spectra (~50 µs, 40 to 150 kHz) than most bat signals (several milliseconds, 16 to 80 kHz). Bats and dolphins are comparable at discriminating shape and size, but dolphins are superior at detecting target range and composition and may be better at detection in noise (Au, Chapter 9). However, if we put performance data together with anatomy, habitat, and hunting characteristics, there are several intriguing parallels.

Basic echolocation frequency differences between the groups are consistent with wavelength differences in the two media and with prey sizes; that is, the frequencies used by dolphins are only two- to threefold higher than those of most bats, not 4.5-fold, but moth wing profiles are, acoustically, proportionately smaller than most fish profiles. Source energy flux density (efd)

of a *T. truncatus* signal (Type II dolphin; –21 dB re 1 j/m^2) is greater than in other dolphins and substantially different from that of the Type I, *P. phocoena* signal (–74 dB re 1 j/m^2) (Au 1993). Among bats, *Eptesicus fuscus*, the big brown bat, is a *T. truncatus* parallel with an efd (–66.4 dB re 1 j/m^2) only slightly larger than that of the Type I dolphin but substantially larger than that of other bats. *T. truncatus* is primarily an open water forager; *E. fuscus* (FM bat) is an open field forager. Both use comparatively high-energy, lower range ultrasonic signals tolerant to Doppler shift in an open environment. By comparison, both *P. phocoena* and its parallel, *Rhinolophus ferrumequinum* (the horseshoe bat, CF/FM), have low-energy, high-frequency, narrow band signals. Both also have good discrimination and deal primarily with imaging small objects in "cluttered" habitats that acoustically are filled with time-smeared echoes from twigs, leaves, etc. and their submerged, shallow water counterparts. Structurally, *P. phocoena* and *R. ferrumequinum* both have highly specialized basilar membrane structures with foveal regions and high ganglion cell densities. This is consistent with the conclusion that habitat and task-dependent signal characteristics are tied to species-specific inner ear filter and response characteristics.

These comparisons are tenuous and are brought forth here primarily to engender discussion. The similarities in relative signal parameters and common cochlear formats between bats and dolphins raises interesting questions about how overtly different habitats may have had common selection pressures that led to parallel echolocation strategies. They also suggest that cross-species hunts for task-related auditory adaptations in different habitats could be a useful tool for understanding fundamental auditory mechanisms.

The structural commonalities between CF/FM bat cochleae and Type I odontocetes suggest that parallel processing strategies may have evolved across media, despite the differences in scale and signal characteristics. The CF/FM bat auditory system is thought to be geared in large part to process Doppler phenomena; there is no evidence for odontocetes that Doppler shift analyses are employed, and because of the broadband nature of the majority of dolphin sonar clicks, there is good reason to think that they, like the signals of FM bats, are Doppler tolerant (i.e., Doppler insensitive) (Au, Chapter 9). However, it is also worth noting that the majority of data on odontocete signals that propel us to this conclusion comes from Type II animals. Au (1993) makes the comment that *P. phocoena* and, indeed, several related phocoenid species produce narrow band, low-intensity, ultra-high signals (peak spectra >120 kHz) that are markedly different from those of delphinids. Those observations do not mean that Type I animals are signal and processing aquatic clones of CF/FM bats. However, if the signal data are reviewed in the context of ganglion cell densities an intriguingly consistent picture begins to form. All relevant data are preliminary, but ganglion cell spikes to over 10,000/mm (Ketten 1998a) located in the mid basal turn segment of the *P. phocoena* ear are coincident with the projected 120 to 130 kHz region of the *P. phocoena* estimated basilar membrane frequency distribution map (Ketten 1994; Ketten et al. 1997).

At the moment, we cannot affirm or deny any these proposed bat-dolphin commonalities. Recent anatomical studies in bats are heavily weighted towards CF acoustic foveal mechanisms. In the last 10 years, more than 70% of papers on bat periphery dealt with neural and basilar membrane specializations of *Pteronotus parnelli* (the mustache bat) and *R. ferrumequinum*. In these bats, normal basilar membrane tapering is disrupted by one or more constant cross-section segments where spatial and neural representation of a narrow frequency band is grossly expanded (Kössl and Vater 1995). The consensus is that this adaptation provides exceptionally narrow tuning and enhancement of CF and CF2 in noise, consistent with the ability of these bats to handle clutter. Ironically, there are fewer broad interspecies comparative studies of bat inner ears than of whale ears and almost no studies that address functional cochlear structure in less specialized FM bat species. If the necessary data are obtained for both groups, comprehensive cross-species/cross-media/cross-ear comparisons focusing on task-dependent adaptations could provide not only a better understanding of echolocation but also a new way to think about hearing from a task in habitat perspective.

6.3 Deep Ears

Type M inner ear formats are known only in large, pelagic whales. A specific use for infrasonic frequencies by whales has not yet been demonstrated, although several possibilities exist. Low frequencies could be used to communicate over long distances and even to echolocate seabed and coastal topographic details as aids for offshore navigation and long-range migrations. Whatever the present function, ultra-low-frequency hearing in mysticetes may simply have evolved as an outgrowth of mechanical constraints imposed by larger ear size.

The ears of mysticetes are less derived than those of odontocetes because their bullar and inner ear proportions are consistent with their mass. Put simply, these ears are huge. All middle and inner ear structures scale to body size, which suggests that ear configurations dominated by low-frequency characteristics is a morphometric by-product of being large and was not fundamentally driven by a special advantage from infrasonic detection. If so, their hearing capacities are a secondary effect of rather than in defiance of their body size, as is speculated to be the case in odontocetes. However, even if the theory is correct that a bigger ear came after rather than before the baleen body and that infrasonic hearing abilities were a de facto result, that does not preclude a subsequent sophisticated exploitation of the mysticete ear's low-frequency capacity.

Because of the extreme divergence in the ears and in their associated skull features between extant mysticetes and odontocetes, even fragmen-

tary evidence about squamosal development, bullar proportions, or skull attachments and level of fixation in a fossil could be surprisingly revealing about its hearing. Much of the work on fossil whales and their hearing capacity has focused on the middle and inner ear anatomy, but in some of the most interesting forms, the bullae are lacking or damaged. In these cases, looking at the remainders of the ear suite could produce useful insights into the hearing of archaeocetes and, therefore, help determine which came first, the clicking or the tympanic egg.

Mysticetes appear geologically near the time new oceans opened in southern latitudes (Thewissen 1998). Even today, these high-latitude waters are terrifically productive, but they are also colder than the temperate seas in which whales first evolved. Surface area increases more slowly than volume, therefore bigger mammals have a substantial thermal advantage in cold water; large whales are warmer. Inner ear membranes scale with animal size. It is likely that increased body size coincided with successful adaptation to cold seas and, in turn, with large ears. As ears grew, basilar membranes would, given no counter pressure to retain high-frequency hearing, simply expand to scale. A lower frequency cochlea would be the product of this nonspecialized expansion. At the same time the tympanic bulla grew. Therefore, as larger whales evolved, ear scaling may have forced inner ear and middle resonance characteristics to progressively lower frequencies, ultimately reaching the practical and profound limits of the blue whale.

7. Summary

An underlying assumption of this chapter is that systematic comparisons of land and cetacean peripheral auditory systems can provide insights into how whales hear in water. The available data reveal a complex, highly derived peripheral auditory architecture with specializations for extended hearing ranges, as well as reception and localization of water-borne sound.

Aquatic influences are most evident at the gross anatomical level. There are no pinnae. All cetacean periotics, tympanics, and ossicles are constructed of dense, compact bone. The odontocete tympano-periotic complex is isolated acoustically from the skull, which is adaptive for aquatic echolocation. The position and isolation of odontocete bullae support the jaw theory of ultrasonic signal reception via fatty acoustic wave guides in and around the mandible. Sound reception mechanisms in mysticetes are unknown, but bony skull connections and a highly derived tympanic membrane (glove finger) suggest combined bone and soft tissue mechanisms. The extracranial location of the ear in all whales is advantageous for underwater sound localization.

Cetacean middle ears divide grossly into low- versus high-frequency composites that follow the suborders. Inner ear anatomy varies more by species. Cochlear lengths correlate with animal size, ranging 20 to 70 mm. Cochlear

turns range 1.5 to 2.5 and are independent of animal size. Odontocete cochlear duct structures are hypercellular. Stria vascularis and spiral ligament in particular are densely packed with duplicate cell populations, which suggest relatively rapid metabolic processes that are consistent with the importance of hearing to cetaceans and with moderately high background noise in ocean environments. Auxiliary outer osseous laminae support 20% to 60% of the basilar membrane length in odontocetes, adding stiffness.

In mysticetes, the spiral ligament is less well developed and outer osseous laminae are absent or reduced. The cochlear duct cytoarchitecture of mysticetes is unremarkable. Mysticete basilar membranes scale consistently with land mammal generalist ears.

Spiral ganglion cell densities are significantly greater in whales than in land mammals, averaging 2,000 to 4,000 cells/mm. Greatest densities are found in the highest frequency odontocetes, but all whales have densities and fiber diameters that are significantly greater than those of land mammals. Vestibular elements are disproportionately small in all whales, possibly reflecting reduced azimuthal cues as a result of cervical fusion and limited head motion.

Modern Cetacea have three inner ear structural formats that coincide with 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 cochleae are adapted for ultrasonic ranges with exceptionally stiff basilar membranes and extensive bony membrane buttressing. Basilar membrane thickness to width ratios are higher for the basal turn of Type I odontocetes than for any other mammal. Mysticete (Type M) cochlea have exceptionally wide, thin basilar membranes and no stiffening agents, implying they are adapted to low to infrasonic frequencies.

The debate on middle ear function desperately needs to be invigorated with measures from more than one species, particularly if a general solution is to be obtained for odontocetes and mysticetes. Middle ear anatomies are sufficiently different between odontocetes and mysticetes, particularly with respect to couplings to other head tissues that it seems unlikely that a common mechanism is at work. Therefore, new data must come from both groups.

Data on mysticete ears continue to be relatively scarce, but what is available suggests they are adapted for sonic to infrasonic frequencies, which is consistent with mysticete vocalization data.

Psychophysical research on odontocetes ranks among the best available in the world, but at the moment, cetaceans do not afford the same controlled research opportunities, particularly direct physiologic measures, that are possible in other species. In that sense, cetacean auditory research is not physiologically competitive. However, as techniques improve and become more accessible for high-speed, high-resolution, noninvasive measurements of neural activity, such as functional magnetic resonance imaging (fMRI) and evoked potentials, it will be possible to dramatically broaden our cetacean physiologic database. Comparative anatomy has a role in these

studies. When anatomical information precedes the acquisition of psychophysical data, it can act as a guide for optimizing stimuli and recording sites. When it follows in vivo studies, it provides the necessary structural data for understanding the underlying mechanisms of a physiologic response.

Acknowledgments. One last note is in order. It is impossible to explore virtually any aspect of cetacean biology, particularly dolphin acoustics, without crossing and re-crossing the firm and continuing footprint of Ken Norris. It is appropriate and regrettably timely that this book is dedicated, in part to Ken's memory. Many of the contributors to this volume knew Ken far better than I, and I suspect that has made their writing all the more difficult, for writing any one of these chapters is a constant remainder of his loss. It is also a reminder of an important Norris lesson. Ken, I suspect, never lost much time. When he had an idea, he pursued it with vigor and intelligence. The volume and quality of his work are not only scientifically astonishing, they are a testimony to the richness of his imagination and the rollicking good time he must have had putting it all together. Early in my graduate career, I invented a verb: The wise marine mammalogist always checks, before spouting his/her most recent brilliant idea in public, to determine whether it has been "Norrised." Odds are if it was a good idea, Ken had been there already. He may not have solved that particular problem, but you could be reasonably sure he had given it some thought. I am grateful that his writings will perpetually teach this lesson along with all the others: pursue your interests with passion, generosity, and an open mind. As for being Norrised—in fact, the lesson is to take heart. If you and Ken have similar ideas, you must be on the right track.

I am honored to be included among the authors of this volume and the SHAR series. For that, as well as their consideration and patience, I am extremely grateful to the editors, Whitlow Au, Richard Fay, and, above all, Arthur Popper, for his continual encouragement, generous intellect, and invaluable professional guidance.

Funding from the Mellon Foundation, the Seaver Institute, and the Office of Naval Research supported preparation of the manuscript and related research by this author. Douglas Whittington and Scott Cramer provided helpful proofreadings of the text. Diane Jones, Barbara Burgess, Richard Cortese, and Jennifer O'Malley assisted with specimen preparation and microphotography. Cheryl Condon, Eileen Hadley, and Gina McDermott, R.T., assisted with radiologic images contributing to the chapter.

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