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# The Marine Mammal Ear: Specializations for Aquatic Audition and Echolocation

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## 1. Introduction

"Marine mammal" is a broad categorization for over 150 species that have one feature in common: the ability to function effectively in an aquatic environment. They have no single common aquatic ancestor and are distributed among four orders (see Appendix 1). Each group arose during the Eocene in either the temperate northern Pacific Ocean or in the Tethys Sea, a paleolithic body of water from which the Mediterranean and middle eastern limnetic basins were formed. Otariids (sea lions), odobenids (walrus), and marine fissipeds (sea otters) developed primarily in the Pacific, while the earliest cetacean (whale), sirenian (manatee and dugong), and phocid (true seal) fossils come from regions bordering Tethys Sea remnants (Kellogg 1936; Domning 1982; Barnes, Domning, and Ray 1985). The level of adaptation to the marine environment varies in marine mammals; many are amphibious and only the Cetacea and Sirenia are fully aquatic, unable to move, reproduce, or feed on land. Structural changes in the ears of marine mammals parallel their degree of aquatic adaptation, ranging from minor in amphibious littoral species, such as otters and sea lions, to extreme in the pelagic great whales.

This chapter focuses on the cetacean ear as the most fully adapted auditory system of marine mammals. It first describes peripheral auditory anatomy in the two extant suborders of Cetacea, the Odontoceti (toothed whales, porpoises, and dolphins) and Mysticeti (baleen or whalebone whales), and then compares these structures with what is known of fossil cetacean ears. A functional analysis is given of generalized cetacean ear anatomy emphasizing how unique structures in cetaceans relate to the ability of a mammalian ear to hear in water. Specific anatomical differences among modern odontocete and mysticete ears are discussed in relation to their role in species-specific frequency ranges, which, in turn, are correlated with differences in habitat and feeding behavior. Lastly, a comparison is made of modern and ancestral cetacean cranial features to allow speculations on the auditory capacity and behavior of extinct species. Since Cetacea evolved from terrestrial species and many specimens represent intermediate stages in the transition to water, this comparison also provides an opportunity to trace the progressive refinement of a mammalian auditory system from terrestrial through amphibious to fully aquatic.

### 1.1 Adaptive Radiation of Cetacea

Protocetid fossils center on the northern Tethys Sea. It is likely that cetacean radiations are linked to the tectonic uplift and closure of the Tethys, which generated a warm, productive, shallow sea with abundant food supplies (McKenzie 1970; Davis 1972; Lipps and Mitchell 1976). The exploitation of the Tethys shallows 50 to 60 million years ago by an amphibious, mesonychid condylarth, a cat-like, hooved carnivore, led to the development of the Archaeoceti from which the two extant lines of cetaceans are derived (Fig. 35.1) (Kellogg 1936; Barnes and Mitchell 1978; Fordyce 1980; Gingerich et al. 1983). One line, the Odontoceti, has species in virtually every aquatic habitat, from
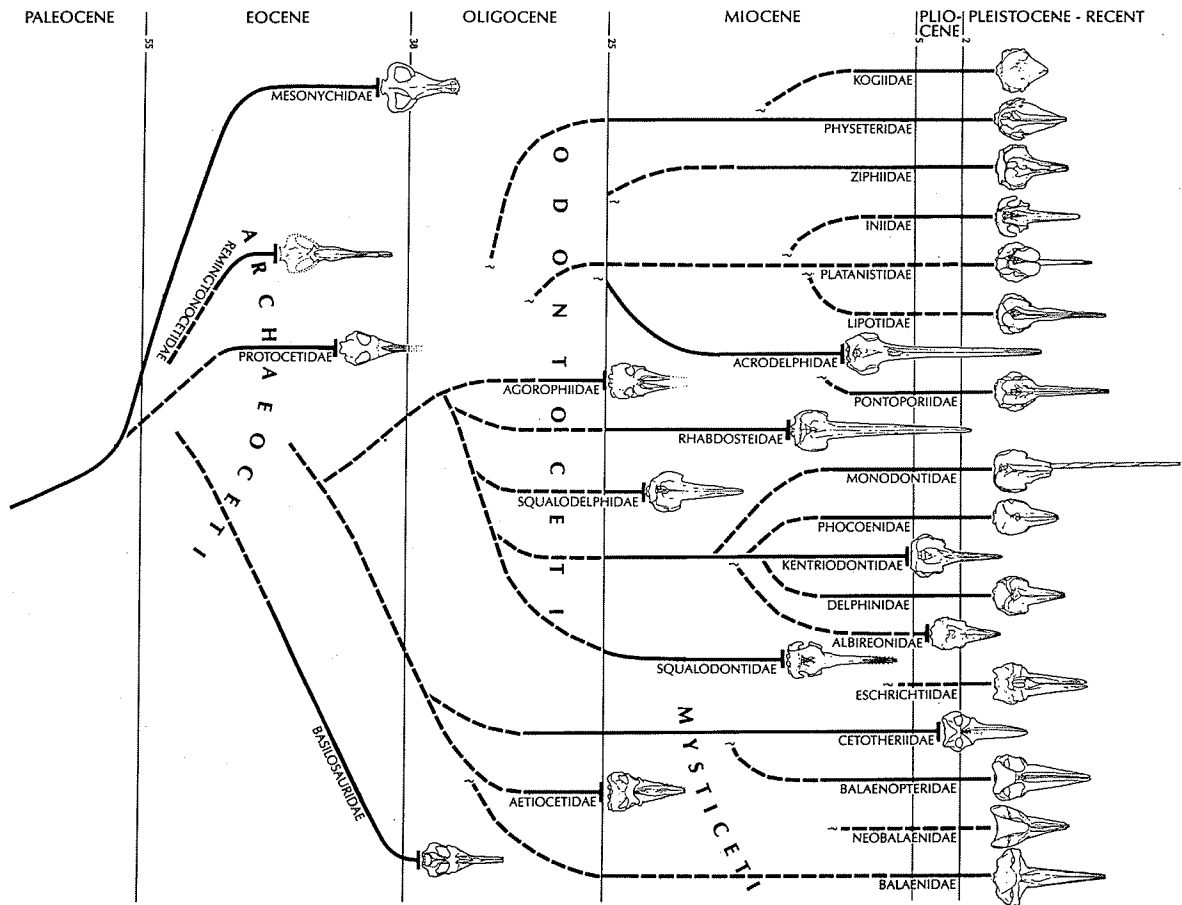
FIGURE 35.1. Cetacean phylogeny. A theoretical phylogenetic tree traces the development of ancestral and modern families of Cetacea. Extinctions are indicated by a cross-bar. Dashed lines indicate estimated links for that family with antecedents. Question marks indicate that links with earlier families cannot be established reliably. This is the case for the freshwater, riverine dolphins which appear abruptly as four distinct lines in the late Miocene and may have evolved in parallel. (Revised version by Barnes and Folkens after Barnes, Domning, and Ray 1985; copyright Pieter A. Folkens.)

estuarine river dolphins to deep-diving, bathypelagic whales. There are over 65 recognized extant odontocete species, of diverse sizes (1 to 30 meters) and shapes, and all are efficient, raptorial carnivores (Leatherwood, Caldwell, and Winn 1976; Leatherwood et al. 1982; Watkins and Wartzok 1985). The second line, the Mysticeti, has 11 species, which are typically large, pelagic planktivores (Ridgway 1972; Gaskin 1976).

Like any mammal, cetaceans are faced with a need for locating food sources, navigating, and finding mates. As Archaeocetes entered the ocean, more of these functions had to be accomplished in water, a dark, dense medium compared to terrestrial environments. The physical demands of water are apparent in virtually every aspect of odontocete and mysticete anatomy. Olfaction and vision in some species are poor compared even to other marine mammals (Dawson 1980; Kastelein, Zweypfenning, and Spekreijse 1990; Kuznetzov 1990; Watkins and Wartzok 1985). It is not surprising, therefore, that sound is believed to be the fundamental sensory and communication channel in Cetacea. All odontocetes tested to date echolocate; i.e., they "image" their environment by analyzing echoes from a self-generated ultrasonic signal of up

to 200 kHz (Kellogg 1959; Norris et al. 1961; Pilleri 1983; Kamminga, Engelsma, and Terry 1989). Mysticetes are not believed to echolocate, but they may use infrasonic frequencies[1] (Weston and Black 1965; Watkins et al. 1987; Edds 1988; Clark 1990; Dahlheim and Ljungblad 1990). Cetaceans, as a group, therefore evolved abilities to exploit both ends of the acoustic spectrum and use the broadest range of acoustic channels of any mammalian order.

## 2. Sound Production Characteristics and Audition

### 2.1 Audiometric Data

In order to accurately interpret auditory structures of any species, it is necessary to have some measure of its sensitivity. For practical and historical reasons, underwater measures of auditory sensitivity are available for very few marine mammals (Watkins and Wartzok 1985; Thomas, Pawloski, and Au 1990; Awbrey 1990). Consequently, most speculations about cetacean hearing are based on inferences from recordings of emitted sounds or on psychophysical data from experiments on very few odontocete species. The available odontocete data are extensively reviewed in McCormick et al. (1980), Popper (1980), Watkins and Watzok (1985), and Awbrey (1990) and are only briefly summarized here. At present, there are no direct audiometric data for mysticetes.

In odontocetes, electrophysiological and behavioral audiograms indicate best sensitivity (the frequency of a pure tone that can be detected at a lower intensity than all others) varies by species from 12 kHz in *Orcinus orca* (killer whale) (Schevill and Watkins, 1966; Hall and Johnson 1971) to over 100 kHz in *Phocoena phocoena* (harbour porpoise) (Voronov and Stosman 1970; Møhl and Andersen 1973). The majority of species measured are delphinids with best sensitivities in the 40 to 80 kHz range (Johnson 1967; Bullock et al. 1968; Bullock and Ridgway 1972; Ridgway

1980; Ridgway et al. 1981; Thomas, Chun, and Au 1988; Popov and Supin 1990a, 1990b). Interspecies comparisons of audiograms are equivocal since techniques vary widely and reports for even the same species vary by as much as two octaves (see Popper 1980). Critical ratio and critical band measurements indicate odontocetes are generally better than most mammals at detecting signals in noise.[2] Critical ratio functions for dolphins parallel those of humans but the absolute dolphin ratios are narrower and the critical bands are not a constant factor of the ratio over a wide range of frequencies (Johnson 1968; Thomas, Pawloski, and Au 1990). Humans have 24 critical bands which are estimated to be ⅓ of an octave or 2.5 times the critical ratio in the frequency range of speech (Pickles 1982). In *Tursiops truncatus* (bottlenosed dolphin), there are 40 critical bands (Johnson 1968) which vary between 10 times the critical ratio at 30 kHz and 8 times the critical ratio at 120 kHz (Moore and Au 1983).

Au (1990) found that echolocation performance as a function of noise in *Tursiops* is 6 to 8 dB lower than that expected from an ideal receiver. Target detection thresholds as small as 5 cm at 5 meters have been reported, implying a minimal angular resolution of ~0.5°, but the most common range is 1° to 4° for both horizontal and vertical resolution (Bullock and Gurevich 1979; Au 1990). Minimal intensity discrimination is 1 dB (equal to human) and temporal discrimination is approximately 8% of signal duration (superior to human). Frequency discrimination in *Tursiops* (0.3 to 1.5% relative discrimination limens) and *Phocoena* (0.1 to 0.2%) is superior to human and rivals that of microchiropteran bats (Grinnell 1963; Simmons 1973; Sukhoruchenko 1973; Thompson and Herman 1975; Long 1980; Pollak 1980). These data, despite limitations in number or consistency of experiments, suggest odontocetes have no single auditory capacity better than that of some other animal, but their

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[1]*Infra* (<20 Hz) and *ultra* (>20 kHz) *sonic* are homocentric classifications for sounds beyond the normal human auditory range of 20 to 20,000 Hz (Sales and Pye 1974; Yeowart 1976).

[2]The critical band is a measure of frequency discrimination based on the ability to detect a signal embedded in noise. At some point, as the bandwidth of masking noise is narrowed, the signal becomes far easier to detect; i.e., the detection threshold drops sharply. Noise bandwidth at that point is the critical band. The critical ratio estimates critical bands based on the signal power/noise power ratio.

combination of abilities is an exceptional package geared to frequency and resolution capabilities consistent with aquatic echolocation.

## 2.2 Cetacean Vocalizations

In contrast to the limited audiometric data, recordings are available of emitted sounds for over 67 species of marine mammals (see Watkins and Wartzok 1985). Although not an optimal measure of sensitivity, spectral and temporal analyses of recorded vocalizations[3] provide indirect estimates of auditory ranges and are currently the most consistent acoustic data base for multispecies comparisons.

There are two functional and three acoustic categories for odontocete signals (Popper 1980):

1. Echolocation signals—broad spectrum clicks with peak energy between 20 and 200 kHz.
2. Communication signals—burst pulse click trains and narrow band, constant frequency (CF) or modulated frequency (FM) whistles ranging from 4 to 12 kHz.

Odontocetes are the only marine mammals known to echolocate (Kellogg 1959; Norris et al. 1961). Individuals can vary pulse repetition rate, interpulse interval, intensity, and spectra of echolocation clicks (Au et al. 1974; Moore 1990), but each species has a characteristic echolocation frequency range (Schevill 1964; Norris 1969; Popper 1980). Based on peak spectra (the frequency of maximum energy) in their typical, broadband echolocation click, odontocete species can be divided into two ultrasonic groups (Ketten 1984): Type I with peak spectra above 100 kHz, and Type II with peak spectra below 80 kHz. These two ultrasonic divisions coincide with differences in habitat and social behavior (Ketten and Wartzok 1990). Type I odontocetes are generally solitary, nonaggregate, inshore or freshwater species whereas Type II species typically form large, offshore groups or pods (Gaskin 1976; Wood and Evans 1980).

Mysticete vocalizations are significantly lower in frequency than those of odontocetes, ranging

[3]There is some question about the validity of the term vocalization for Odontoceti considering their nonlaryngeal sound production mechanisms (see Section 3.2); however, the term is correct for the majority of marine mammals and is used here for simplicity.

from 12 Hz signals in *Balaenoptera musculus* (blue whale) (Cummings and Thompson 1971) to 3 kHz peak spectra calls in *Megaptera novaeangliae* (humpback) (Silber 1986). Most mysticete vocalizations can be categorized as protracted low frequency moans (0.4 to 40 seconds, fundamental frequency <200 Hz); simple (bursts with frequency emphasis <1 kHz) or complex (amplitude and frequency modulated pulses) calls; and "songs," like the now familiar ululations of humpbacks, which have seasonal variations in phrasing and spectra (Thompson, Winn, and Perkins 1979; Watkins 1981; Edds 1982; Payne, Tyack, and Payne 1983; Clark 1990). Infrasonic signals; i.e., below 20 Hz, have been commonly reported in two species of rorquals, *Balaenoptera musculus* (Cummings and Thompson 1971; Edds 1982) and *Balaenoptera physalus* (fin whale) (Watkins 1981; Watkins et al. 1987; Edds 1988). Precise functions for mysticete vocalizations are unclear. Interspecific comparisons of vocalizations are complicated by the diverse categories reported in the literature, and functional analyses currently depend upon field observations of behavior during recordings. Low frequencies have the potential for long distance communication, but this has not been proved.

Clearly, there are significant differences in the frequency ranges of sounds produced by odontocetes and mysticetes. These differences imply different perceptual abilities, which presumably have anatomical correlates in the peripheral and central auditory systems. Fortunately for an evolutionary study, much about auditory capacity in a mammal can be inferred from peripheral auditory structures and from associations of the temporal bone with other skull elements, most of which are preserved in fossil material.

## 3. Cetacean Cranial Morphology

All odontocetes and mysticetes have extensive modifications of the cranium, nares, sinuses, petrosal bones, and jaws that are linked to feeding, respiration, and the production and reception of sound while submerged. Whatever the driving force for any single modification, evolution in any one cranial component in cetaceans appears to have strongly influenced the anatomy of other typically unrelated structures. Thus, the structure of
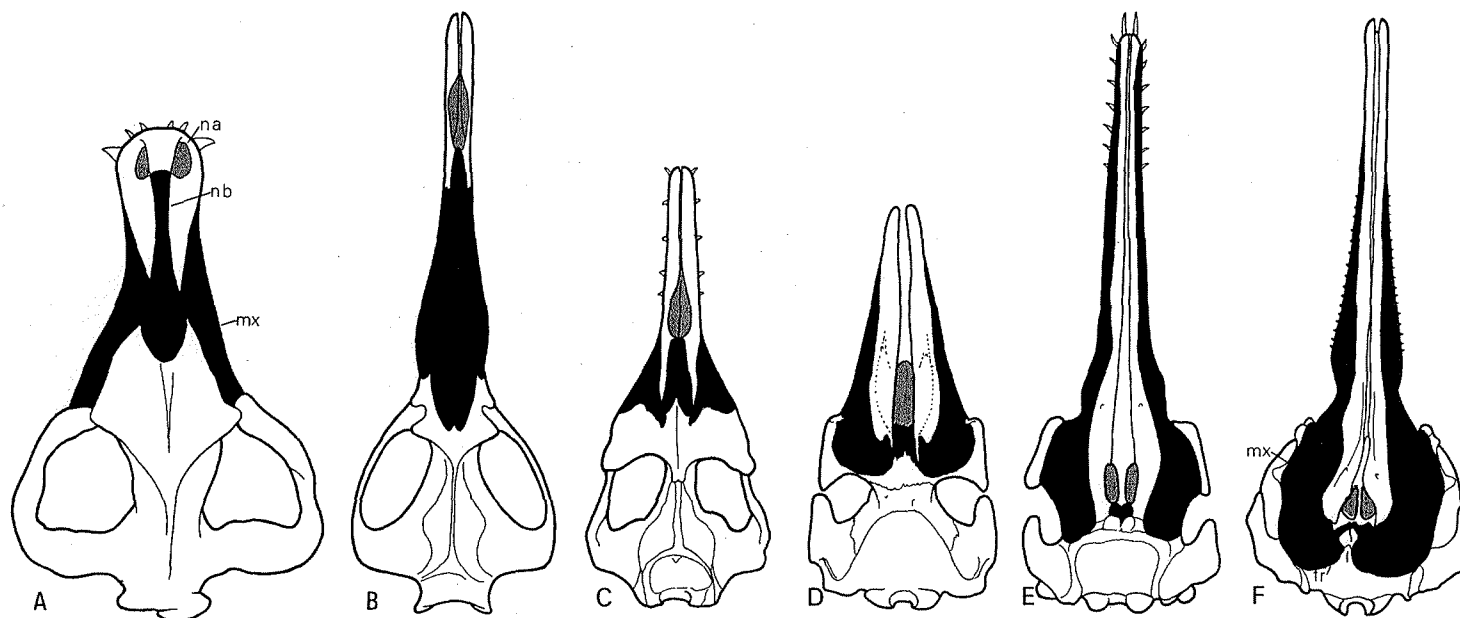
FIGURE 35.2. Telescoping of the cetacean skull. Schematic, dorsal views of skulls of six species illustrate major changes in cranial relationships from Mesonychidae to recent Odontoceti that occur in telescoping. Black areas designate the nasal bones (nb); deep gray, the maxillae (mx); and light gray, the nares (na). The mesonychid condylarth (A–Paleocene) has typical terrestrial cranial relationships. In both *Remingtonocetus harudiensis* (B–early Eocene archaeocete) and *Basilosaurus spp.* (C–early Oligocene archaeocete), the rostrum has narrowed but other relationships are virtually unchanged. The jaw of the primitive odontocetes, *Agorophius pygmaeus* (D–late Oligo-cene) and *Squalodon spp.* (E–Miocene), closely resembles those of modern odontocetes and the nares are well posterior, implying a fully aquatic existence. The anterior cavity in modern odontocete skulls (*Lipotes vexillifer*–F) accommodates the melon, a spheroid, soft tissue mass implicated in the emission of ultrasonic echolocation signals. The melon is cradled by the latero-posterior expansions of the maxillae that cover the frontal bones (fr) (see also Fig. 35.3). The contiguous soft and bony layers of the rostrum act as a shield acoustically separating the melon from the tympano-periotic complex. (Original artwork and copyright, Pieter A. Folkens.)
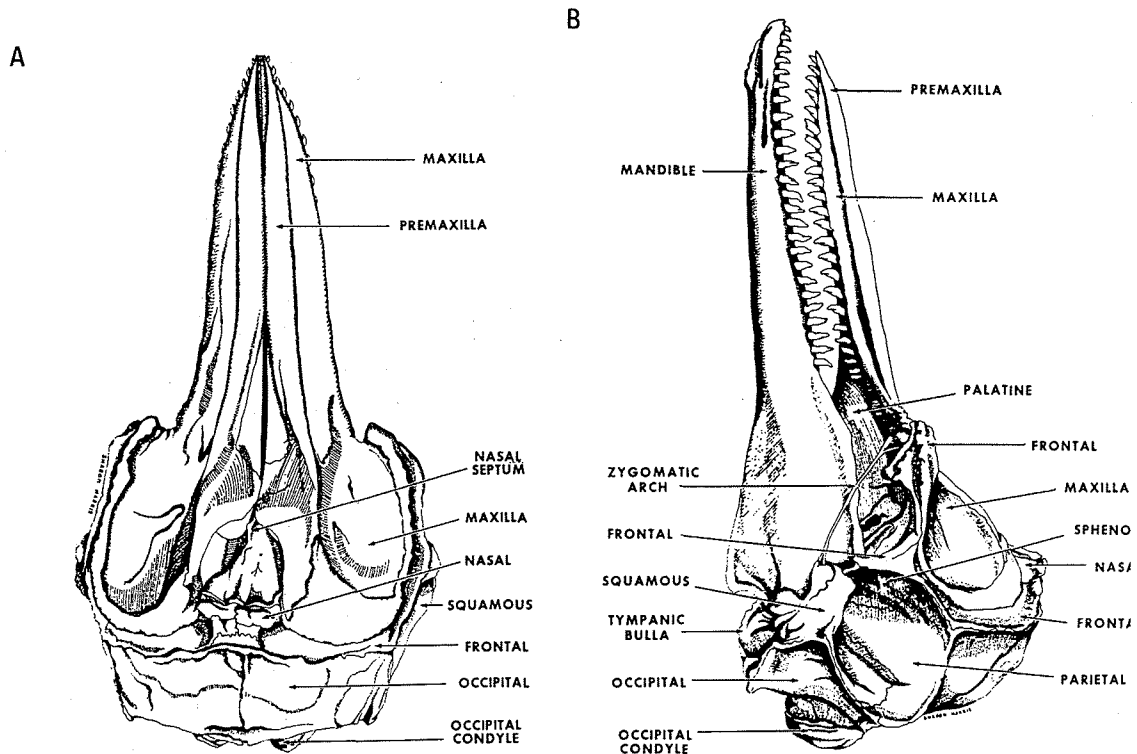
FIGURE 35.3. Modern delphinid skull. The skull of *Tursiops truncatus*, a modern delphinid, shown in (A) dorsal and (B) lateral views. (Reprinted from Ridgway, 1972, courtesy of Charles C. Thomas, Publisher.)

the petrosal bones and inner ear cannot be analyzed in isolation. In odontocetes in particular, it is necessary to examine structures like the jaw and cranial sinuses for atypical acoustic functions, while bearing in mind their conventional roles as well.

## 3.1 Telescoping

Modern cetaceans have the most derived cranial structure of any marine mammal (Barnes and Mitchell 1978; Barnes, Domning, and Ray 1985). Synapomorphic cranial characters common to all Cetacea include dorso-caudal nares, extensive peribullar and pterygoid sinuses, elongated or extensively reconfigured mandibles and maxillae, petrosal bones detached from the skull, and a foreshortened, concave cranial vault (Norris 1980; Barnes, Domning, and Ray 1985; Gingerich, Smith, and Simons 1990; Oelschläger 1990). The majority of these characters are associated with "telescoping," a term coined by Miller (1923) to

describe the evolutionary revamping of the cranial vault (Fig. 35.2) in which the maxillary bones of the upper jaw expanded back to the vertex of the skull and covered the reduced frontal bones. Concomitantly, the rostrum elongated and the cranial vault foreshortened, pulling the nares and narial passages rearward to a superior position behind the eyes. The product, epitomized by the modern delphinid skull (Fig. 35.3), is a frontally compressed, concave cranium with dorsal nares allowing ventilation with only the most dorsal surface of the head above water. While telescoping is clearly related to changes in the respiratory path it also has significant consequences for channeling sound into and out of the cetacean head.

## 3.2 Cranial Paths for Emitted Sounds

The mechanisms for sound production and reception in odontocetes have been intensely investigated and vigorously debated for nearly forty

years (Evans and Prescott 1962; Fraser and Purves 1954, 1960; Norris 1964, 1968; Purves 1967; McCormick et al. 1970; Pilleri 1983; Goodson and Klinowska 1990). Although exclusively laryngeal mechanisms have been suggested (Purves 1967; Pilleri 1983), the preponderance of data supports a nasal sac theory proposed by Norris and Harvey (Norris 1969; Norris et al. 1972; Norris and Harvey 1974). The controversy is relevant for understanding odontocete hearing since echolocators typically have specialized auditory structures for suppressing reception of their outgoing echolocation signal (Pye 1972). Thus, the form and location of sound generators and exit paths may affect construction of the middle and inner ear.

In odontocetes, telescoping forms a frontal concavity occupied by up to five asymmetrically distributed nasal sacs or diverticulae and the melon, a unique, elliptical, multilayered mass of fibrous tissue and fats. The nasal diverticulae act as pressure driven sound generators that produce clicks when the "pneumatic" lock of the ridged nasal flaps (museau de singe) are forced open by sudden expulsions of air from the sacs (Mackay and Liaw 1981; Amundin and Cranford 1990). Each ventral premaxillary sac is believed to act, in conjunction with the melon, as an acoustic lens to focus and beam anteriorly the outgoing ultrasonic signals (Fig. 35.4) (Norris 1964; Amundin and Cranford 1990). This hypothesis is reinforced anatomically by the extensive innervation of the melon by the trigeminal nerve (V), which rivals the auditory nerve (VIII) for largest cranial nerve fiber count in odontocetes (82,000 fibers in P. phocoena) (Jansen and Jansen 1969; Morgane and Jacobs 1972). As an animal ensonifies a target, the melon undulates rapidly. It is likely that the trigeminal, with both sensory and motor roots, controls this motion and may provide the neural mechanism for focusing and monitoring shape of the acoustic lens in echolocation (Ketten unpublished). Anterior reflection of the signal is enhanced by the sandwich of soft and hard tissues of the frontal shield behind the melon (Figs. 35.3, 35.4), which Fleischer (1976) concluded provides a serial impedance mismatch that deflects outgoing pulses generated in the sacs through the melon and away from the tympano-periotic bones. Lastly, the zygomatic arch in odontocetes is exceptionally thin, making it a poor path for bony sound conduction between the rostral and peribullar regions (Fig. 35.3B).
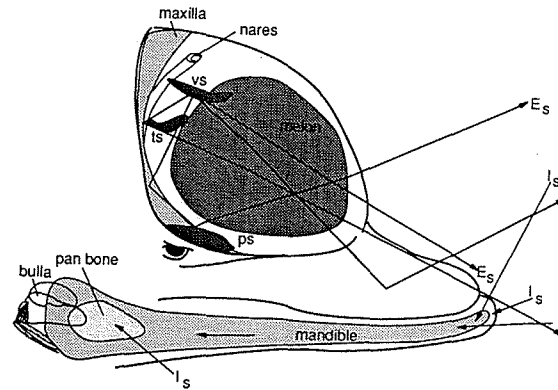


FIGURE 35.4. Sound paths in the Odontocete. Hypothetical sound paths for emission and reception of ultrasonic signals are shown in a schematized dolphin head (revised 1990, after Ketten 1984; copyright DR Ketten). Ultrasonic signals are believed to be generated by the expansion of vestibular (vs) and tubular (ts) nasal sac diverticulae and the subsequent release of air in plosive "gasps." Released air is captured by auxiliary sacs and recycled for subsequent sound production. The signals are reflected off the acoustic shield of the telescoped cranium and the premaxillary sac (ps) and focused by the multilayered fats in the melon into anteriorly directed beams (E$_s$). Incident sound (I$_s$) from a target deflecting that beam enters the jaw area where waxy tissues overlain by the mandibular bone channel the sound to the tympano-periotic complex, rather like fiber optic cables channel or conduct light. Ray diagrams of this type are valid only for ultrasonic signals and are not sufficient to explain directed longer wavelength sounds (Mackay 1987). Best reception characteristics from lateral and low frequency signals are found in the area of the pan bone, but the fatty mandibular channels have the lowest acoustic resistance for sounds from an anterior direction (Bullock et al. 1968; Norris and Harvey 1974; Popov and Supin 1990.)

Little is known of the acoustic paths in the mysticete head. Mysticetes do not have a melon and the zygomatic arch is substantial. Both observations are consistent with the assumption that baleen whales do not echolocate. Mysticetes have a larynx but no vocal cords and the cranial sinuses are thought to be involved in phonation (Benham 1901; Hosokawa 1950; Mead 1975; Sukhovskaya and Yablokov 1979; Henry et al. 1983), although no precise mechanism has been demonstrated nor are there comprehensive studies of anatomical correlates of infrasonics in Mysticeti.
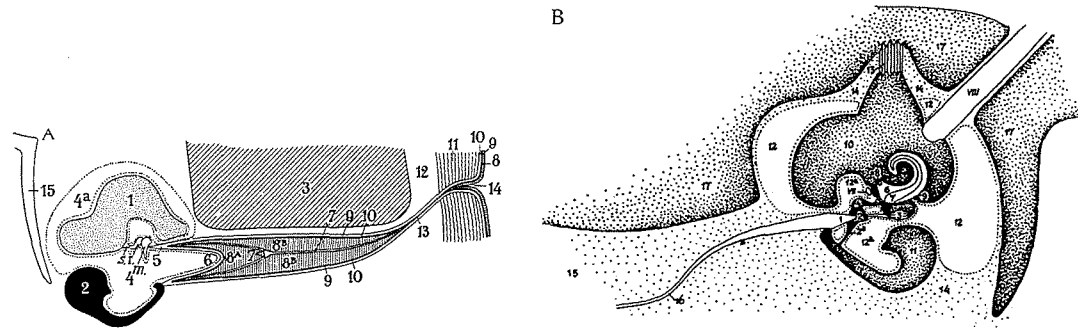
B



FIGURE 35.5. Cross-sections of the peribullar regions. Schematics demonstrate the relationship of the periotic-tympanic complex to surrounding cranial elements and to the external auditory canal in a generalized mysticete (A) and odontocete (B). The original labelling is retained in these illustrations. Figures are not drawn to a common scale. (Adapted from Reysenbach de Haan 1956.) (A) Frontal section of the tympanic region of a whalebone whale (Mysticeti). (1) periotic; (2) tympanic; (3) squamosal; (4) cavum tympani; (4a) peribullar sinus; (5) tympanic conus; (6) protrusion of tympanic membrane or glove finger into the external auditory canal; (7) interfaces of components of the cerumen plug; (8) stratum corneum; (8a, 8b) cerumen plug; (9) statum germina-tivum; (10) corium; (11) blubber; (12) connective tissue; (13) blind end of the external auditory canal; (14) external auditory meatus; (15) occipital; (i) incus; (m) malleus; (s) stapes. (B) Schematic dorsoventral section through the auditory apparatus of the Odontoceti. (1) tympanic conus; (2) malleus; (2a) processus gracilis; (3) tensor tympani; (4) incus; (5) stapes in oval window; (6) scala vestibuli; (7) scala media; (8) vestibule; (9) round window; (10) periotic; (11) tympanic; (12) peribullar sinus; (13) one of five ligamentous bands suspending the periotic in the sinus; (14) peribullar plexus; (15) blubber; (16) external auditory meatus; (17) squamosal and basioccipital; (VII) facial nerve; (VIII) acousto-vestibular nerve.

## 3.3 Cranial Structures for Sound Reception

Whether the external auditory canal is functional in Cetacea is debatable. There are no pinnae, but there is a small external meatus in all species which connects with a relatively narrow auditory canal. In Mysticeti, the canal contains a homogeneous wax and the proximal end flares, covering the "glove finger," a complex, thickened membrane that protrudes laterally from the bulla into the canal and is thought to be derived from the pars flaccida of the tympanic membrane (Figs. 35.5A, 35.7) (Fraser and Purves 1960; Reysenbach de Haan 1956; Lockyer 1974; Van and Utrecht 1981; Ketten in preparation). The glove finger is connected to the tympanic bulla by a fibrous ring, equivalent to the fibrous annulus, but there is no obvious association with any ossicle or with the wax-filled external canal. In odontocetes, the external canal is exceptionally narrow and plugged with cellular debris and dense cerumen (Fig. 35.5B), and the tympanic membrane remains only as a calcified ligament or tympanic conus fused at its distal and ventral margins with the tympanic bulla (Reysenbach de Haan 1956; Ketten 1984).

Reysenbach de Haan (1956) and Dudok van Heel (1962) were among the first researchers to suggest alternative tissue conduction paths in odontocetes, contradicting the theory of Fraser and Purves (1954, 1960) that the external auditory canal, although occluded with debris, is the principal route to the cochlea. Reysenbach de Haan (1956) reasoned that since the transmission characteristics of blubber and sea water are similar, using a canal occluded with variable substances would be less reliable than tissue or bone conduction. Dudok van Heel (1962) concluded the canal was irrelevant since behavioral measures of the minimum audible angle in *Tursiops* were more consistent with an interbullar critical interaural distance than with intermeatal distances.

A probable alternative path for sound conduction in odontocetes is the lower jaw. The jaw structure of all mysticetes is clearly extensively modified for sieving or gulp feeding and has no evident connection to the temporal bone. The jaw of odontocetes appears to be modified to snap prey, but

in actuality, it is a unique composite of fats and bone which serves a second role, to transmit sound to the inner ear. Norris (1968, 1980) observed that the odontocete mandible has two exceptional properties: a concave medial face, which houses a fatty tube that projects from the symphysis back to the temporal bone, and a thin ovoid region, dubbed the "pan bone," near the flared posterior segment of the mandible (Fig. 35.4). The fats in the mandibular channel, like those of the melon, are wax esters with acoustic impedances closer to sea water than any other non-fluid tissues in Cetacea (Varanasi and Malins 1971). Norris (1969) speculated the fat channel acts as an acoustic wave guide and the pan bone, as an acoustic window through which sound is preferentially channeled to the petro-tympanic bullae underlying the jaw. Results of several experiments support this hypothesis. Evoked responses (Bullock et al. 1968) and cochlear potentials (McCormick et al. 1970) in *Stenella* and *Tursiops gilli*, the Pacific bottlenosed dolphin, were significantly greater for sound stimuli above 20 kHz placed on or near the mandible. Measurements with implanted hydrophones in severed *T. truncatus* heads (Norris and Harvey 1974) found best transmission characteristics for sources directed into the pan bone. In recent behavioral studies, Brill et al. (1988) showed encasing the lower jaw in neoprene significantly impaired performance in echolocation tasks. These results argue strongly that the jaw is an acoustic channel, but they do not preclude alternative paths, including the external auditory canal. Both Popov and Supin (1990b) and Bullock et al. (1968) found minimum thresholds for low frequencies were associated with stimuli nearest the external meatus. From the combined results of all these studies, I conclude there may be two parallel systems in odontocetes, one for generation and reception of ultrasonics and one for lower frequency communication signals. No anatomical studies have shown equivalent structural specializations for sound transmission in mysticetes, which underscores the potential for the melon and mandible to be efferent and afferent counterparts of odontocete echolocation.

# 4. The Extant Cetacean Ear

The problems inherent in an aquatic environment for an unmodified terrestrial ear are considerable: increased sound speed, impedance mismatch for an air–fluid refined system, and increased pressures. Adaptations that cope with these problems are apparent throughout the middle and inner ear.

## 4.1 The Tympano-Periotic Complex

The cetacean temporal bone is distinctive and dense, differing from other marine and terrestrial mammalian auditory bullae in appearance, construction, cranial associations, and, in some aspects, function (Fig. 35.6). In all modern Cetacea, the bulla is separated from the skull and comprised of two components, the periotic and tympanic, both of which are constructed from exceptionally dense, compact bone. This tympano-periotic bullar complex is situated in an extensive peribullar cavity formed by expansions of the middle ear spaces (Figs. 35.5, 35.6). In Mysticeti, a bony flange projects posteromedially from the periotic, dividing the cavity and wedging the bulla tightly between the exoccipital and squamosal (Yamada 1953; Reysenbach de Haan 1956; Kasuya 1973). The peribullar cavity is proportionately larger in odontocetes, completely surrounding the bulla, and, except in physeterids, no bony elements connect the bulla to the skull. The tympano-periotic complex is suspended by five or more sets of ligaments in a peribullar plexus of dense "albuminous foam" which fills the cavity (Fraser and Purves 1954; Jansen and Jansen 1969; Ketten and Wartzok 1990). Fraser and Purves (1960) speculated the peribullar spaces were an adaptation in response to the mechanical stress of extreme pressures and were correlated with diving ability. They predicted greater development of air spaces in species from deeper habitats; however, as Oelschläger (1986a) notes, peribullar and pterygoid sinuses are extensively developed in shallow water, riverine species like *Inia geoffrensis*, an ultrahigh-frequency Amazonian dolphin, and less developed in pelagic mysticetes. These observations imply that peribullar sinus development is related to acoustic isolation rather than mechanical stress. In odontocetes, the composite of bullar structure, vascularized plexus, and ligaments could function as an acoustic isolator for echolocation, analogous to the lamellar construction of bat temporal bones (Simmons 1977).

Size and shape of the tympano-periotic complex are species-specific characteristics, but there are
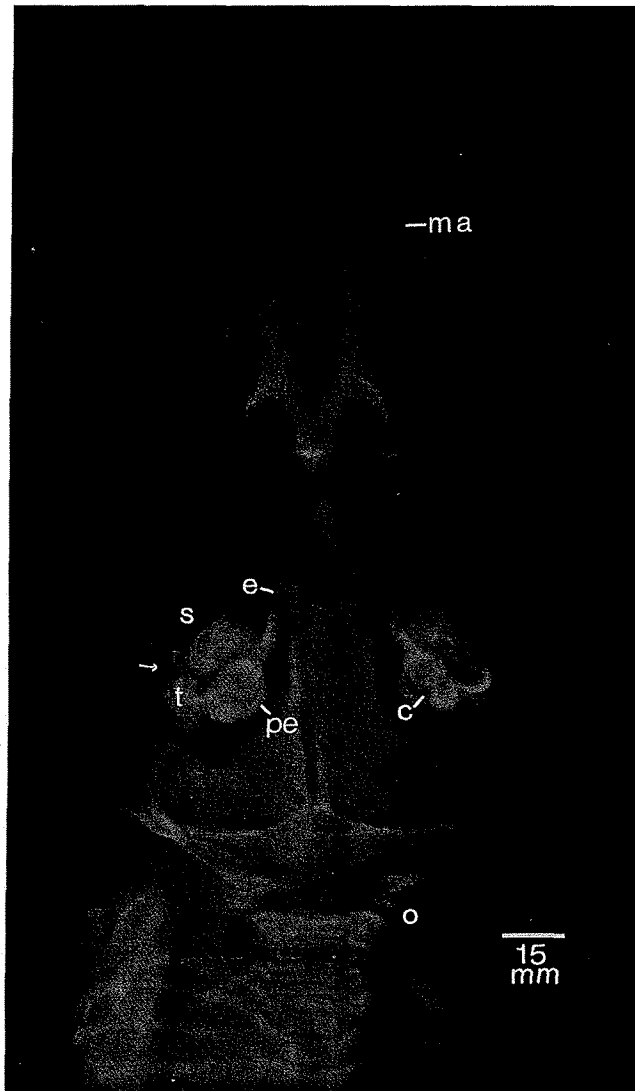
FIGURE 35.6. Radiography of odontocete ears. A single plane X-ray of an odontocete, *Stenella attenuata*, shows the size and density of the bulla in comparison to other skull elements. Radiographs image structures in a grayscale proportional to X-ray attenuation, from white for densest material to black for air. This X-ray image is not enhanced and the whiteness of the bullae in comparison to other skeletal elements is a graphic demonstration of the exceptional mineralization of the odontocete bulla, which has a density (2.7 g/cc) near that of bovine enamel (2.89 g/cc) (Lees, Ahern, and Leonard 1983). The cochlea (C), filled with less dense fluid, is the dark spiral in the periotic (pe), which is medial to the tympanic (t). The eustachian tube (e) is a gray band entering the tympanic anteriorly. Additional structures are the mandible (ma) dotted with dense, white conical teeth; the low density, dark gray region of the foam-filled peribullar sinus completely surrounding each bulla (s); and the occipital condyles (o) anterior to the fused, compressed vertebrae. The frontal ridge is visible only as a white line across the bullae (arrow). In all noncetacean mammals, the tympano-periotic complex is at least partly fused to the brain case.

general characteristics which differentiate mysticete and odontocete bullae at a gross level (Fig. 35.7) (Boenninghaus 1903; Fraser and Purves 1954; Reysenbach de Haan 1956; Kasuya 1973; Fleischer 1976; Norris and Leatherwood 1981; Ketten 1984). Mysticete tympanics are hemispherical and nearly twice the volume of the periotic, which resembles a squat pyramid with the apex pointed medially. In odontocetes, the periotic and tympanic are nearly equal in volume, although the periotic is thicker walled and thus more massive. The tympanic is conical, tapering anteriorly, while the periotic is ovoid with a distinct cochlear promontorium. Species differ in the solidity of the periotic-tympanic suture, the relative volumes of tympanic and periotic, the complexity of surface features, and the degree of attachment to the skull. Surface measurements scale isometrically with animal size, and the mass of the bulla can vary a full magnitude between species (Kasuya 1973; Ketten 1984; Ketten and Wartzok 1990). Differences in size and shape do not correlate directly with frequency ranges but they do relate to differences in the anchoring of the tympano-periotic complex to the skull and thus to its acoustic isolation and reception characteristics.

In vivo, all cetacean bullae are oriented with the periotic dorsal to the tympanic. The periotic is relatively uniform in thickness and encloses the cochlea and vestibular components. The dorsoventral bullar axis is rotated medially 15° to 20° and the long axis angles ventro-medially, which places the cochlear apex ventral to the stapes, orthogonal to conventional terrestrial mammalian formats. This placement, or displacement, of the cochlea may result from the spinal flexion and caudal brain case compression that occurred in Cetacea as they regressed to a fuselloid shape; its utilitarian effect is a shorter, less angular pathway for the acousto-vestibular nerve (VIII), which projects inward from the dorso-medial edge of the periotic (Figs. 35.5, 35.6, 35.7) and enters a dense, bony canal leading to the braincase. The VIIIth nerve is thus "externalized" as it traverses the retroperibullar space (Ketten and Wartzok 1990). The facial nerve (VII) does not parallel the VIIIth, as it does in humans, but remains external to the bulla in many species. The concha or shell of the tympanic encloses the ossicular chain (Fig. 35.7) and is lined with a membranous corpus cavernosum which is a thin fibrous sheet in mysticetes but is substantially thicker and highly vascularized in odontocetes. It has not been determined whether the intratympanic space is air-filled in vivo. In all odontocete bullae examined in situ, a band of fibrous tissue, analogous to the stylo-hyoid ligaments, joins the posterolateral edge of the tympanic bulla to the posterior margin of the mandibular ramus and stylo-basihyal complex (Fig. 35.4), in effect, aligning the bulla with the fatty wave guide of the mandible (Ketten and Wartzok 1990). No such association has been reported in Mysticeti.

## 4.2 The Middle Ear

Cetacean ossicular anatomy is complex and difficult to interpret in the absence of extensive physiological studies of middle ear function (Belkovich and Solntseva 1970; McCormick et al. 1970; Fleischer 1976; Solntseva 1987). Anatomical studies suggest the ossicular chain, like the bullae, has evolved to accommodate dramatic pressure changes. In all species, the ossicles are large and exceptionally dense, and in odontocetes, the structures suggest a compromise between sensitivity and strength. In 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). Equivalent structures made of thin bone in an air-filled middle ear would not withstand the pressure changes in a dolphin dive. In odontocetes the ossicles are more massive than in any terrestrial mammal but a bony ridge, the processus gracilis (Fig. 35.7A), fuses the malleus to the wall of the tympanic bulla and the interossicular joints are stiffened with ligaments and a membranous sheath (Ketten 1984). This rigid set of attachments is sufficient to transmit high frequencies (Sales and Pye 1974; McCormick et al. 1970). In some species, the stapes is fully ankylosed; in others, it is mobile with a conventional annular ligament (Ketten 1984). Mysticete ossicles are equally massive, but they are not fused to the bulla nor are the interossicular joints stiffened with ligaments. Both mysticete and odontocete middle ears contain extensive soft tissue, but this does not preclude air-filled chambers. To date, there are only anecdotal reports (McCormick et al. 1970) and no direct evidence of air in the tympanic cavity.
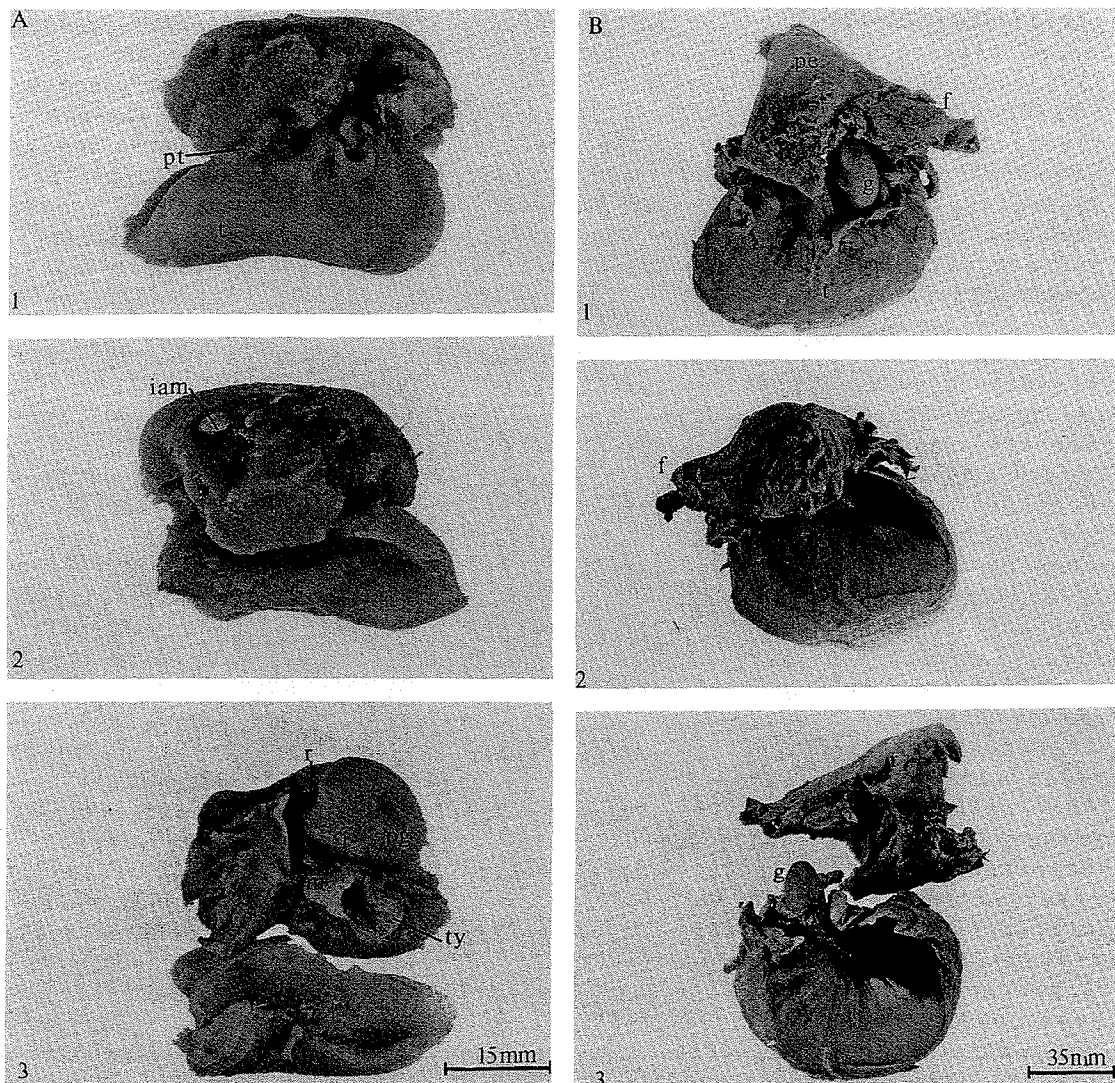
FIGURE 35.7. Cetacean tympano-periotic complex. The left tympano-periotic complex is shown from (A) an odontocete, *Stenella attenuata* (spotted dolphin), and (B) a mysticete, *Eubalaena glacialis* (right whale), as oriented in the cetacean head in (1) lateral and (2) medial views. For (3), the periotic and tympanic were separated in the medial position to show the middle ear space. Characteristic mysticete features include a posterior cranial flange (f); a dense hemispheric tympanic (t); a triangular periotic (pe); and the thick, membranous glove finger (g). The odontocete has a more delicate, conical tympanic and ovoid periotic. The processus tubarius (pt) or accessory ossicle is the outer tympano-periotic connection. The promontorium (Pr) of the periotic houses the cochlea. The corpus cavernosum lining the middle ear in *Stenella* has been removed to reveal the ossicles: (i) incus; (m) malleus; (pg) processus gracilis; (ty) tympanic conus; the stapes crus enters the oval window recess below the round window (r). The size of the VIIIth nerve can be estimated from the diameter of the internal auditory meatus (iam). (Photography by Alison George.)

Based on the principal physiological studies available from delphinids, two possibilities exist for middle ear function: translational bone conduction or conventional ossicular motion. McCormick et al. (1970, 1980) demonstrated in *T. truncatus* and *Lagenorhynchus obliquidens* (pacific white-sided dolphin) that immobilizing the ossicular chain decreased cochlear potentials but disrupting the external canal and tympanic conus had 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 with these findings, suggesting the surgical procedure damaged the precise ossicular mechanism and introduced an artificial conduction pathway. He concluded, from anatomical studies, that the periotic is stable and sound from any path is translated through tympanic vibration to the ossicles which conventionally pulse the oval window. McCormick's theory depends upon tissue conduction and an inertial lag of the cochlear fluids in a vibrating bulla; Fleischer's, on differential resonance of the tympanic and periotic bones. The first theory assumes fixed or fused tympano-periotic joints; the second requires a free moving stapes and flexible tympano-periotic sutures. Neither theory provides a satisfactory or complete general explanation since each is inconsistent with variations in middle ear anatomy in a wide sample of species (Ketten 1984). It should also be considered that the data come from anesthetized vs postmortem specimens. McCormick measured live animals under deep anesthesia after opening the bulla. Fleischer used alcohol-preserved material from previously frozen and thawed *Tursiops* heads in which structural changes, including a loosening of the tympano-periotic sutures, should have occurred. The discrepancies in their conclusions point out a need to consider the complex effects of anesthesia, temperature, and postmortem changes on tissue characteristics (Fitzgerald 1975; Lees, Ahern, and Leonard 1983) as well as the need for replicate and multispecies studies.

To the extent that information can be extrapolated from available anatomical data, the middle ear anatomy of all Cetacea is tailored, in part, to meet environmental pressures and the massiveness and complexity of ossicular structures imply that the middle ear has at least some minimal function.

Mysticetes and odontocetes differ chiefly in the rigidity of the ossicular chain and in the prospect, based on an elaborate tympanic structure, that mysticetes receive auditory stimuli primarily from the ear canal and not from the jaw. If the middle ear space is defined by the volume of the tympanic shell, then the middle ear cavity in Mysticeti is substantially larger than in odontocetes, implying a lower frequency ear (see Webster and Plassman, Chapter 30). In reality, however, these are speculations in search of data and middle ear function remains largely unexplained for any cetacean.

## 4.3 The Inner Ear

### 4.3.1 The Vestibular System

The vestibule is large in Cetacea but the semicircular canals are substantially reduced, tapering to fine threads that do not form complete channels, and it is unclear whether all components of the vestibular system are functional (Ketten and Wartzok 1990). Although size is not a criterion for vestibular canal function, cetaceans are exceptional in having semicircular canals that are significantly smaller than their cochlear canal (Jansen and Jansen 1969; Gray 1951). Innervation is proportionately reduced; i.e., only 10% of the cetacean VIIIth nerve is devoted to vestibular fibers, as compared to 40% in most other mammals (Yamada 1953; Jansen and Jansen 1969; Morgane and Jacobs 1972). In the absence of physiological measurements of odontocete vestibular function, we may speculate that the vestibular system of cetaceans acts precisely as van Bergeijk (1967) suggested; i.e., as a "vehicle-oriented accelerometer." If the semicircular canals are vestigial, these animals may obtain only linear acceleration and gravity cues, but no rotational or three-dimensional accelerational inputs. This may be highly adaptive, permitting rapid rotations in a buoyant medium, exemplified by the flying turns of spinner dolphins, without the side-effects of "space-sickness."

### 4.3.2 The Cochlea

Cetacean cochlea have the prototypic mammalian divisions and relationships. The membranous labyrinth of the scala media (cochlear duct), scala tympani, and scala vestibuli forms an inverted spiral inside the periotic, curving medially and
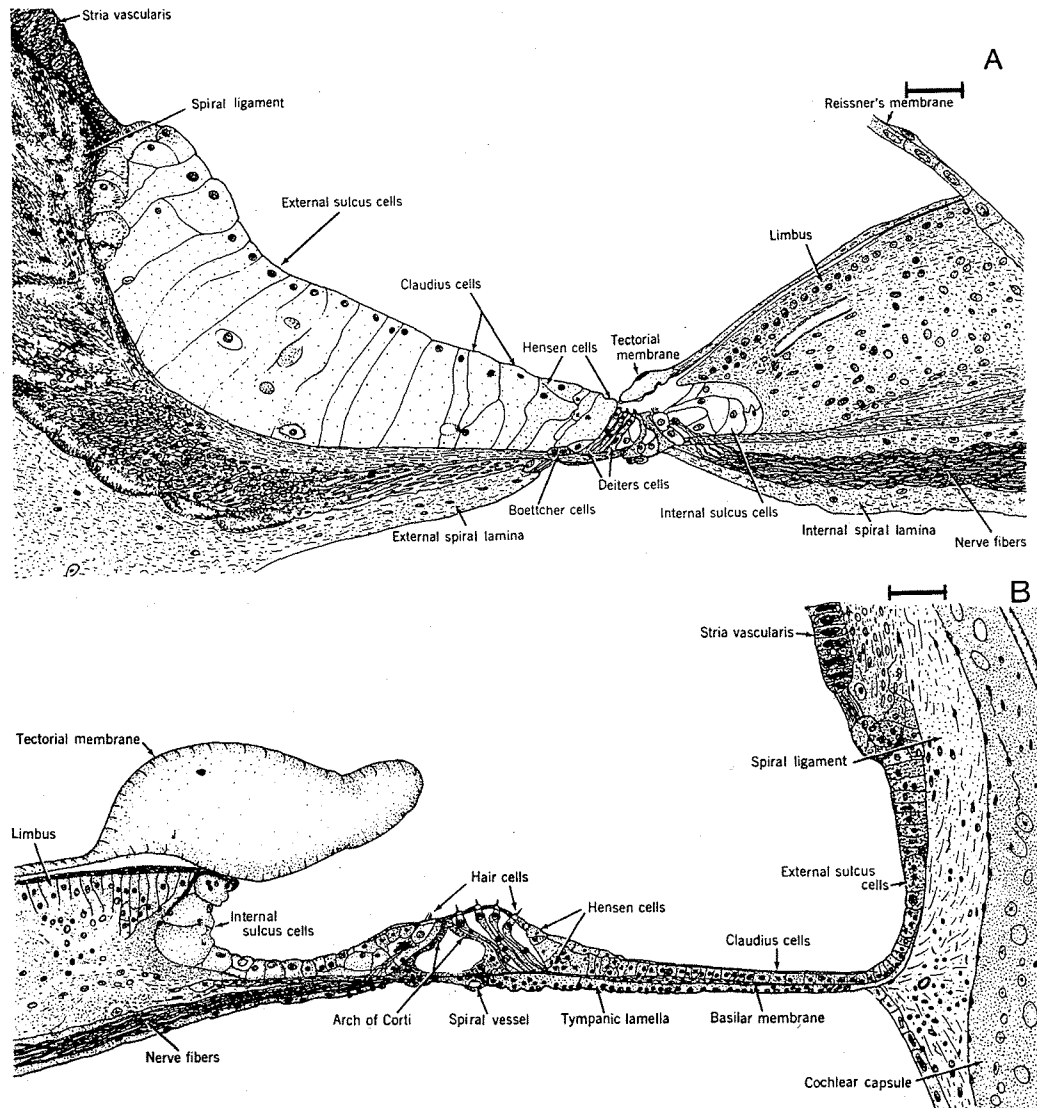
FIGURE 35.8. Cochlear duct cytoarchitecture. Line drawings of two points in the odontocete cochlea (reprinted with permission from Wever et al. 1971a, b) are shown for comparison with light micrographs of 20 μm mid-modiolar sections of the odontocete cochlear duct at equivalent locations (Ketten and Wartzok 1990.) Descriptions in this chapter use conventional neurocentric orientations for the cochlea; i.e., inner or medial are towards the modiolus; outer/lateral refer to the antimodiolar or abneural side. Although in vivo the cochlear apex points ventrally in dolphins, the images are shown in a standard orientation. Tissues in the photomicrographs are from adult animals and represent average odontocete material preserved 5 hours to 4 days postmortem. They show preservation and processing artifacts similar to those of human temporal bones, including disruption and collapse of Reissner's membrane, absent or necrotic organ of Corti, acidophilic staining of the perilymph, and serous protein deposits in scala media (SM). Each scale bar represents 50 μm. (A) The drawing of the lower basal region of *Tursiops truncatus*, a Type II odontocete, illustrates the classic odontocete features of an osseous outer lamina and heavy cellular buttressing. (B) In the apical region, the osseous
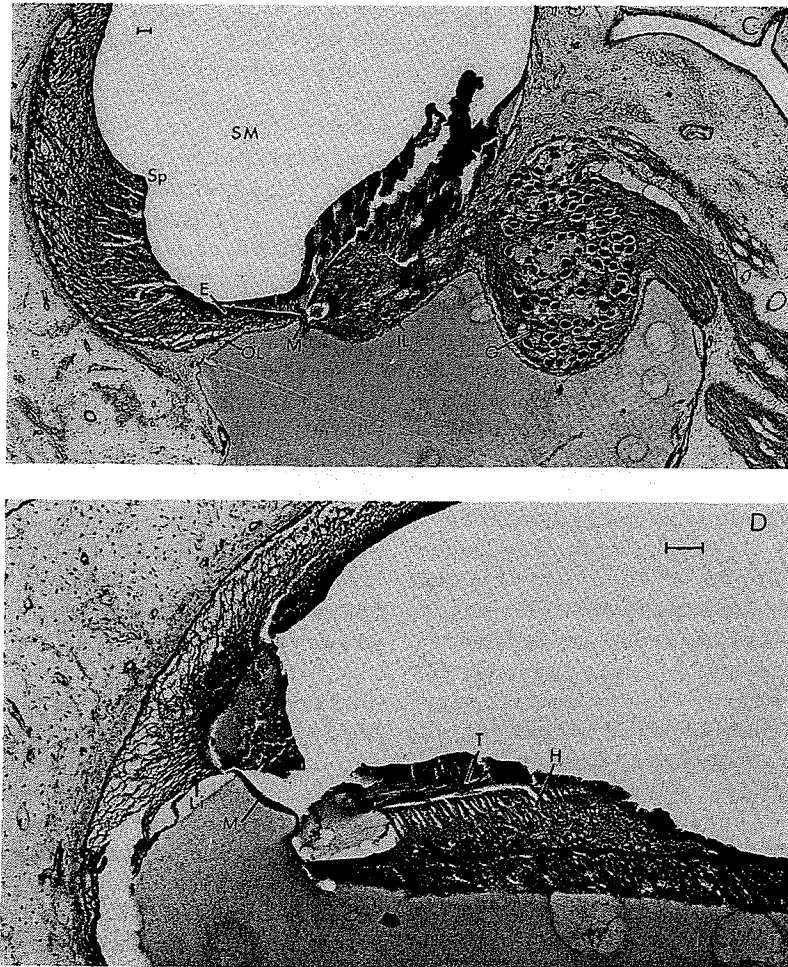
FIGURE 35.8. (*Continued*) outer lamina has disappeared, and the membrane has thinned and broadened. (C) The basilar membrane (M) of *Phocoena phocoena*, a Type I odontocete, in the basal turn (7 mm from the oval window) measures 45 μm × 20 μm and is stretched between inner (IL) and outer (OL) ossified spiral laminae. The outer lamina is 30 to 40 μm thick. The basilar membrane in this species is narrower than that of *Tursiops* throughout the basal turn (see Fig. 35.9). There is heavy staining of the perilymph in scala tympani, but the endolymph of scala media (SM) is not contaminated, indicating the membrane is intact. Blood in scala media is the result of a concussion. A distinctive cellular layer (E) found only in the basal turn in odontocetes lines the lateral basilar membrane recess below the spiral prominence (Sp). Kolmer reportedly dubbed them "ersatzzellen" (Reysenbach de Haan 1956), and although noted by several authors, these cells are unclassified and their function remains unclear. The bulge protruding medially into scala tympani is densely packed with oblate spiral ganglion cells (G) and is characteristic of the spiral ganglia in odontocetes but has not been reported for Mysticeti. (D) In an apical section (4 mm from the helicotrema), the basilar membrane in *Phocoena* is 200 μm wide and 10 μm deep. Only the spiral ligament (Li) supports the lateral edge of the basilar membrane at this point. Huschke's auditory teeth (H) are visible in the spiral limbus immediately below the limbal tectorial membrane (T).

ventrally from the stapes to the helicotrema around a core, the modiolus, containing the auditory branch of the acoustovestibular nerve. Dimensions of the cochlear canal are strongly correlated with animal size, not with frequency. Frequency related variations among species include the number of turns, basilar membrane dimensions, and distributions of membrane support structures (Ketten 1984; Ketten and Wartzok 1990).

Little is known of the comparative structure of the cochlea in mysticetes; i.e., whether there are structural differences related to infrasonic ranges. Present data show few differences from conventional cochlear duct structure in terrestrial mammals (Fraser and Purves 1960; Solntseva 1975; Norris and Leatherwood 1981; Pilleri et al. 1987; Ketten, in preparation). In contrast, odontocete cochlea differ significantly from all other mammalian cochlea. This discussion will outline general characteristics of the cetacean cochlear duct and will discuss in detail two anatomical features of the odontocete inner ear that influence resonance characteristics and frequency perception: basilar membrane construction and osseous spiral laminae configurations. Particularly in the basal turn, these components are exceptional in odontocetes compared to either mysticete or terrestrial ears, and, more important, differences among odontocetes in these two features correlate with the two frequency divisions (Type I and II) of echolocation signals.

A series of papers by Wever et al. (1971a, 1971b, 1971c, 1972) described cellular structure in the cochlear duct for six *T. truncatus* and three *L. obliquidens*. These papers provide the most reliable anatomies of the cochlear duct for these two species available to date and give us a basis for broader discussions of other species from less optimal material. No equivalent data are available for the majority of Cetacea. The cellular descriptions are quite extraordinary compared to other studies (Reysenbach de Haan 1956; Belkovich and Solntseva 1970; Solntseva 1971; Ketten 1984; Ketten and Wartzok 1990) in part because Wever was able to use animals perfused specifically for histology. The papers are a distinctive histologic series which is unlikely to be repeated soon since the animals were obtained in conjunction with electrophysiological studies performed prior to the beginning of current collection restrictions (Ridg-

way and McCormick 1967; Ridgway, McCormick, and Wever 1974; Wever and McCormick, personal communication). They also point out some of the daunting complexities of histology on cetacean temporal bones since only nine bullae out of twenty-five attempted were successfully processed despite the considerable expertise of Dr. Wever's laboratory. Two figures from Wever's papers are included in this chapter (Figs. 35.8A,B) for comparison with micrographs from more conventional odontocete material (Figs. 35.8C,D).

Cellular trends described for *Tursiops truncatus* (Wever et al. 1971a, 1971b, 1971c, 1972) were as follows: a 20-fold reduction in the height of the Claudius cells from base to apex; Boettcher cells distributed throughout the entire length of the cochlear duct with some double rows; substantial cellular buttressing of the basilar membrane in the lower basal turn by Hensen cells; and four rows of outer hair cells in some parts of the apical region. Basilar membrane and tectorial membrane thickness were not discussed, although the basilar membrane was described as a highly differentiated structure with a substantial variation in stiffness. Pilleri (1984) reported deep Azan staining in the basal region of *Monodon monoceros* (narwhal) which he attributed to tonofibrils of the pillar cells. 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 and compact" pillar cells in *Phocoena*. Parallel trends were reported in *Lagenorhynchus* (Wever et al. 1972) although absolute numbers and ratios vary: a 15-fold reduction in the Claudius cells; Boettcher cells in single rows with none basally; and irregular hair cell distributions varying from four rows in one specimen to three or even two rows in another. Hair cell distributions are an important finding of these papers since, as Wever et al. (1972) state, previous workers assumed uniform distributions of three rows. Based on Wever's data, odontocetes appear, like microchiropteran bats (Firbas 1972), to have up to four rows of outer hair cells, but the irregular distributions are puzzling. It should be noted, however, that one or more of the Wever animals received aminoglycosidic antibiotics as part of a regular maintenance regimen (Ridgway, McCormick personal communication). When administered to humans, these can have acute toxic effects

TABLE 35.1. Ganglion cell density

| Species | Type | Total ganglion cells | Membrane length (mm) | Average density (cells/mm) |
|---|---|---|---|---|
| *Phocoena phocoena* | I | 66,933 | 24.31 | 2,753.3 |
| *Lagenorhynchus obliquidens* | II | 70,000 | 34.90 | 2,005.7 |
| *Stenella attenuata* | II | 82,506 | 37.68 | 2,189.6 |
| *Tursiops truncatus* | II | 105,043 | 41.57 | 2,526.9 |
| *Rhinolophus ferrumequinum* | — | 15,953 | 16.10 | 1,000/1,750[a] |
| *Homo sapiens* | — | 30,500 | 31.00 | 983.9 |

[a]whole cochlea/acoustic fovea region.

Species data compiled from Wever et al. 1972; Bruns and Schmieszek 1980; Schuknecht and Gulya 1986; Ketten and Wartzok 1990.

on the inner ear, including partial or complete loss of hair cells (Schuknecht 1974). Similar ototoxic effects in dolphins may account for the irregular hair cell distributions Wever observed.

Neuronal components of mysticete cochlea have not been carefully described, but it is clear that they do not have densities equivalent to those found in odontocetes. The diameter of the auditory nerve, the volume of cells in Rosenthal's canal, and the number of habenular fibers are all disproportionately large in odontocetes (Fig. 35.8), consistent with an hypertrophy of the entire odontocete auditory system (Wever et al. 1971c, 1972; Morgane and Jacobs 1972; Fleischer 1976; Ketten and Wartzok 1990). Ganglion cell to hair cell ratios appear to be proportional to peak frequency in both bats and odontocetes and it is likely that high afferent ratios in odontocetes are directly related to the complexity of information extracted from echolocation signals. Total ganglion cell counts and ganglion cell densities of *Phocoena*, *Tursiops*, *Stenella*, and *Lagenorhynchus* are compared with bat and human data in Table 35.1. Ganglion cell densities in odontocetes are higher than in any other mammal and range from 2000 cells/mm in *Lagenorhynchus* to 2,700 cells/mm in *Phocoena*, (Wever et al. 1971c, 1972; Ketten and Wartzok 1990). Using a mammalian average of 100 inner hair cells/mm (Kiang personal communication) and four rows of outer hair cells/inner hair cell, these data imply a ganglion to hair cell ratio of nearly 6:1 for *Phocoena phocoena*, 5:1 for *Tursiops truncatus*, 4.4:1 for *Stenella attenuata*, and 4:1 for *Lagenorhynchus obliquidens*. The human ratio is 2.4:1; cats, 3:1; and bats average 4:1 (Firbas 1972; Bruns and Schmieszek 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 24:1 for odontocetes, or more than twice the average ratio in bats and three times that of humans (Firbas 1972). Wever et al. (1971c) speculated that additional innervation is required primarily in the basal region to relay greater detail about ultrasonic signals to the CNS in echolocation analyses. Electrophysiological results are consistent with this speculation. CNS recordings in both porpoises and bats imply increased ganglion cells may correspond to multiple response sets that are parallel processed at the central level. Bullock et al. (1968) found three distinct categories of response units in the inferior colliculus of dolphins; i.e., 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 (Schnitzler 1983; Suga 1983). The sum of the data implies extensive monitoring of signal characteristics other than frequency occurs from inputs in the basilar membrane region that encodes ultrasonic echolocation signals.

### 4.3.3 Frequency and Shape

Basilar membrane dimensions are thought to be an important component of the resonance characteristics of the cochlea (von Békésy 1960; Iurato 1962; Zwislocki 1981). In mammalian cochlea, thickness and width vary inversely from base to apex, with highest frequencies encoded in the thicker, narrow, basal region and progressively lower frequencies encoded towards the apex as the

TABLE 35.2. Basilar membrane dimensions

| Acoustic Group and Species | Membrane length (mm) | Outer osseous lamina length (mm) | Basal/apical width (µm) | Basal/apical thickness (µm) | Peak vocalization frequency (kHz) |
|---|---|---|---|---|---|
| Type I | | | | | |
| *Phocoena phocoena* | 25.93 | 17.6 | 30/290 | 25/5 | 120 |
| Type II | | | | | |
| *Grampus griseus* | 40.5 | — | 40/420 | 20/5 | — |
| *Lagenorhynchus albirostris* | 34.9 | 8.5 | 30/360 | 20/5 | 40 |
| *Stenella attenuata* | 36.9 | 8.35 | 40/400 | 20/5 | 60 |
| *Tursiops truncatus* | 40.65 | 10.3 | 30/380 | 25/5 | 60–70 |
| Mysticete | | | | | |
| *Balaena mysticetus* | 61.3 | <10 | 120/1,670 | 7.5/2.5 | <0.20 |
| *Balaenoptera acutorostrata* | — | — | 100/1,500 | — | — |
| *Balaenoptera physalus* | — | — | 100/2,200 | — | .02 |
| *Eubalaena glacialis* | 55.6 | — | 100/1,400 | — | <0.20 |

Species averages compiled from Fleischer 1976; Norris and Leatherwood 1981; Ketten 1984.

membrane broadens and thins. In bats it has been shown that frequency varies inversely with basal turn membrane widths (Hinchcliffe and Pye 1968; Brown and Pye 1975). Wever's data (1971b, 1972) imply a similar relationship for dolphins; i.e., minimum basal width averaged 30 µm for *Tursiops* and 35 µm for *Lagenorhynchus*; apical widths averaged 350 µm. The peak frequency of echolocation signals for these two species are 60 and 40 kHz respectively (Diercks et al. 1971). Recent studies (Ketten 1984; Ketten and Wartzok 1990) found similar membrane widths in most odontocete species (Table 35.2). Thickness decreased 5-fold from 25 µm to 5 µm base to apex, while widths increased 9- to 14-fold. Therefore, the generic odontocete basilar membrane has a nearly square basal cross-section that thins and broadens apically to a 5 µm strip 300 to 400 µm in width (Fig. 35.8). Based upon dimensions alone, odontocete basilar membranes are highly differentiated, anisotropic structures capable of an exceptionally wide frequency response. By contrast, mysticete basilar membranes are consistently thinner and wider; in *Balaena mysticetus* (bowhead whale) the membrane is 7.5 µm thick, 120 µm wide at the base, and 2.5 µm thick, 1,600 µm wide at the apex.

Multiple species comparisons (Ketten and Wartzok 1990) demonstrated thickness-to-width ratios were a more significant correlate of frequency than width alone. Comparing bat, odontocete, and mysticete basilar membrane ratios (Fig. 35.9), the odontocete ratios are 2 to 3 times greater than that

of the bat in the most basal, ultrasonic regions, and all three echolocating species have significantly higher basal ratios than the mysticete. The maximum ratio occurs in *Phocoena*, a Type I odontocete. Bats and odontocetes have similar apical ratios, but the mysticete value is significantly lower, which is consistent with a broad, floppy membrane for encoding low frequencies. The basal ratio of the mysticete is equivalent to membrane ratios for the lower apical region of odontocetes. Were all other cochlear duct components equal among these four species, the differences in the basilar membrane dimensions alone could be a significant determinant of the different auditory capacity of each species.

Fleischer (1976) categorized all Cetacea into high (odontocete) vs low (mysticete) frequency users based on basilar membrane width estimates from dehydrated and fossil bullae. Although his absolute values are larger than those in other studies, his curves of basilar membrane base to apex widths have an average slope of 0.3 for odontocetes and 0.8 for mysticetes, consistent with other rates of membrane width changes (Table 35.2) (Wever 1971b, 1972; Norris and Leatherwood 1981; Ketten and Wartzok, 1990). Fleischer also observed that basilar membrane support in the basal turn is stronger in Odontoceti than in Mysticeti and that mysticetes have a greater cochlear height-to-diameter ratio than odontocetes. He concluded perception of high frequencies was "favored" by small ratios and states that common

models of the cochlea oversimplify cochlear relationships, adding that "... the cochlear parameter ... least understood is the mode of coiling."

To date, there is no practical means of estimating frequency ranges for Cetacea based on cochlear dimensions. Basilar membrane lengths in Cetacea, like those of terrestrial mammals, scale isomorphically with body size (Ketten 1984; West 1985). Greenwood (1961, 1962) used membrane lengths as a major variable to predict critical bands and to estimate maximal perceived frequencies for terrestrial species. A major assumption in the equations is that critical bands are equidistant in all mammals (see Fay, Chapter 14). Practically, this means coefficients in the elasticity function are scaled based on human to animal membrane length ratios. Since membrane lengths are proportional to animal size, as the animal gets larger, calculated frequency maxima get lower. For nonspecialized terrestrial mammals, this relationship is correct; i.e., larger animals have lower frequency ranges (Heffner and Heffner 1980; West 1985). Norris and Leatherwood (1981), using Greenwood's equations, estimated a maximal frequency capacity for *Balaena mysticetus* of 12 kHz, similar to the value Greenwood calculated for the elephant, but it is unclear whether these equations apply to aquatic mammals. Odontocetes do not have the same distribution of critical bands as humans (see Section 2.1) which violates Greenwood's primary assumption, and the maximal frequencies the equations predict for any odontocete from the equations; e.g., 15 kHz for *Tursiops truncatus*, are well below any estimations of their auditory capacity based upon sound production and echolocation ability. Similar anomalies need to be considered before using any method to predict hearing in fossil species, particularly for those which may have special or atypical ears.

In terrestrial species, an outer ossified lamina in lieu of a spiral ligament supporting the basilar membrane implies a high frequency ear (Hinchcliffe and Pye 1969; Reysenbach de Haan 1956; Sales and Pye 1974). Inner and outer ossified spiral laminae are present throughout most of the basal turn in all odontocetes (Table 35.2), and the extent and development of these laminae are among the most striking features of the odontocete cochlea (Reysenbach de Haan 1956; Wever et al. 1971a, 1971b, 1971c, 1972; Ketten 1984). Detailed
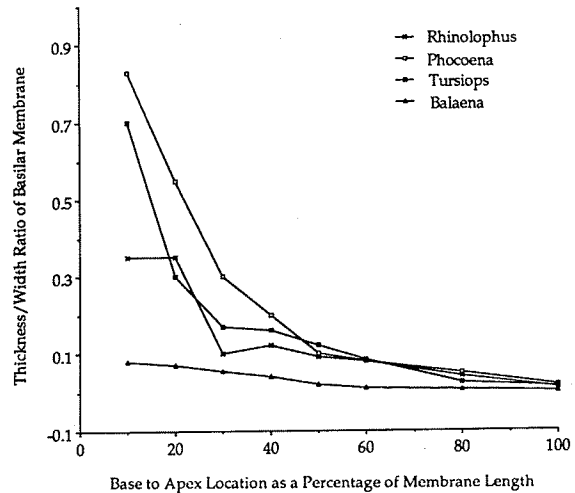


FIGURE 35.9. Basilar membrane ratios. Average thickness to width basilar membrane ratios for the horseshoe bat (*Rhinolophus ferrumequinum*), harbour porpoise (Type I) (*Phocoena phocoena*), bottlenosed dolphin (Type II) (*Tursiops truncatus*), and bowhead whale (Type M) (*Balaena mysticetus*) are plotted as a percentage of cochlear length. (Data from Bruns 1976; Norris and Leatherwood 1981; and Ketten and Wartzok 1990.) High ratios for the bat, porpoise and dolphin reflect a thicker, stiffer membrane which responds to ultrasonic frequencies. Differences in the basal basilar membrane ratios for the three echolocators are consistent with the peak frequency in each species (*Phocoena*, 130 kHz; *Tursiops*, 70 kHz; *Rhinolophus* 40 kHz). Basal ratios in the mysticete cochlea are equivalent to apical ratios for the other three species. The low apical ratio in the bowhead is consistent with a broad, flaccid membrane that encodes extremely low frequencies.

comparisons of the laminae show that they are a major correlate of odontocete ultrasonic ranges (Ketten and Wartzok 1990). The internal osseous spiral laminae, tunneled by the foramina nervosa or nerve fiber tracts, form a bilayered wedge which supports the medial margin (pars arcuata) of the basilar membrane (Fig. 35.8). The thickness of the laminar wedge varies inversely with distance from the stapes. In the lower basal turn, the paired laminae average 50 μm from tympanal to medial lip. In the middle to upper basal turn, the tympanal layer disappears and the medial edge thins to 5 μm, forming a single shelf supporting the spiral limbus. The outer lamina in the lower basal turn in all odontocetes is 30 to 40 μm thick, is heavily

TABLE 35.3. Cochlear Canal Spiral Parameter

| Species | Cochlear type | Turns | Scalae length (mm) | Basal diameter (mm) | Axial height (mm) | Axial pitch[a] (mm) | Basal ratio[b] | Pulse peak frequency (kHz) |
|---|---|---|---|---|---|---|---|---|
| Recent Odontoceti | | | | | | | | |
| *Inia geoffrensis* | I | 1.5 | 38.2 | 8.5 | — | — | — | 200 |
| *Phocoena phocoena* | I | 1.5 | 25.93 | 5.25 | 1.47 | 0.982 | 0.280 | 130 |
| *Grampus griseus* | II | 2.5 | 40.5 | 8.73 | 5.35 | 2.14 | 0.614 | — |
| *Lagenorhynchus albirostris* | II | 2.5 | 34.9 | 8.74 | 5.28 | 2.11 | 0.604 | 40 |
| *Stenella attenuata* | II | 2.5 | 36.9 | 8.61 | 4.36 | 1.75 | 0.507 | 60 |
| *Tursiops truncatus* | II | 2.25 | 40.65 | 9.45 | 5.03 | 2.24 | 0.532 | 60–70 |
| *Physeter catodon* | I,II | 1.75 | 72.21 | 14.3 | 3.12 | 1.78 | 0.218 | — |
| Recent Mysticeti | | | | | | | | |
| *Balaenoptera acutorostrata* | M | 2.2 | — | 17 | 7.5 | 3.41 | 0.441 | — |
| *Eubalaena glacialis* | M | 2.5 | 55.6 | 9.67 | 6.7 | 2.68 | 0.57 | <0.20 |
| Extinct Cetacea | | | | | | | | |
| *Dorudon osiris* | I,II,M | 2.5 | — | 8.2 | 7 | 2.8 | 0.854 | — |
| *Parietobalaena palmeri* | M | 2.3 | — | 13.5 | 6.6 | 2.87 | 0.489 | — |
| *Rhabdosteus spp.* | I,II | 1.5 | — | 9.5 | 3.4 | 2.27 | 0.358 | — |
| *Squalodon spp.* | I,II | 1.6 | — | 10.5 | — | — | — | — |
| *Zygorhiza kochii* | I,II,M | 2.0 | — | 10.5 | 6.75 | 3.38 | 0.643 | — |

[a] $\dfrac{\text{axial height}}{\text{turns}}$     [b] $\dfrac{\text{axial height}}{\text{basal turn diameter}}$

Species averages from Kellogg 1936; Fleischer 1976; Norris and Leatherwood 1981; Ketten and Wartzok 1990.

calcified, and functions as a lateral attachment for the basilar membrane and as a housing for the spiral ligament. Thus, in the extreme basal end, the thick basilar membrane is firmly anchored at both margins to a bony shelf. Differences in the length of outer laminae between Type I and Type II species are consistent with the two acoustic divisions of echolocation signals. In delphinids, all of which are Type II echolocators with typical peak frequency ranges of 40 to 80 kHz, this bony anchor is present for only 25% of the cochlear duct (Table 35.2). In phocoenids, Type I echolocators with peak frequencies above 100 kHz, an outer lamina is present for over 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 than in Type II odontocetes. Type I species use, and presumably hear, higher ultrasonic signals. A longer outer lamina in Type I cochlea increases membrane stiffness, which increases the resonant frequency of that portion of the membrane compared to an equivalent membrane that lacks bony support in Type II cochlea. When combined with the differences observed in membrane ratios, differences in the extent or proportion of outer bony laminae provide a simple but important mecha-

nistic link for species differences in ultrasonic ranges in Odontoceti.

Outer laminae are found in mysticetes as well. Measurements are not available for most Mysticeti, but even qualitative descriptions make it apparent the laminae are not functional equivalents of those in odontocetes (Fleischer 1976; Norris and Leatherwood 1981). The bone is characterized as spongy and meshlike and the outer lamina disappears within the first half turn. These descriptions of mysticete laminae suggest a basilar membrane system opposite that of odontocetes; i.e., a broad thin membrane with insubstantial support. It is likely that the presence of an outer lamina in mysticetes is a residual ancestral condition rather than a derived structure related to mysticete frequency ranges.

Three-dimensional cochlear spiral measurements and reconstructions show striking differences in the construction of the cochlea between odontocetes and mysticetes and between Type I and Type II odontocete species (Ketten 1984; Ketten and Wartzok 1990). Data for eight representative odontocetes are compared with data for two mysticetes and five extinct cetaceans in Table 35.3. There is a strong negative correlation
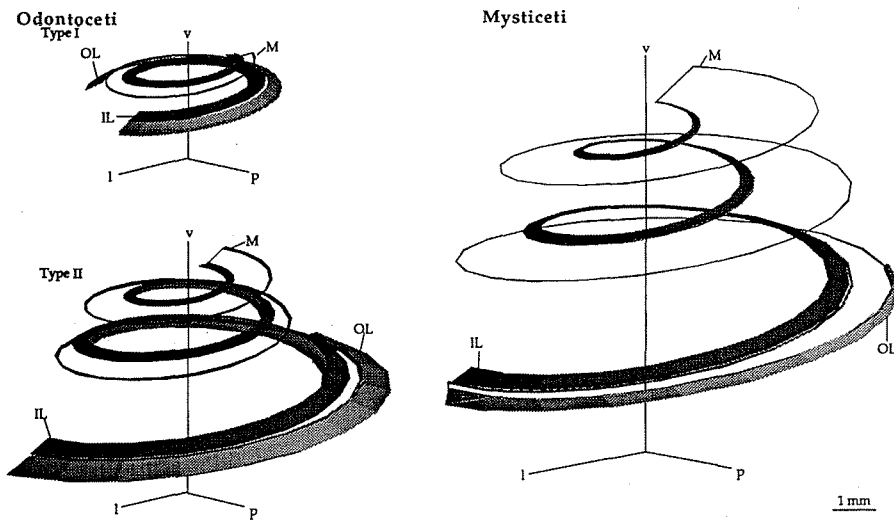
FIGURE 35.10. Basilar membrane and spiral laminae distributions in cetacea. Three-dimensional reconstructions, generated from standardized species data, schematically represent major cochlear duct structural components (IL) inner osseous spiral lamina; (M) lateral edge of basilar membrane attached to the spiral ligament; (OL) outer osseous spiral lamina of Type I and Type II odontocetes and a generalized mysticete. The composites were produced by combining spiral model parameters with cochlear canal data (Tables 35.2, 35.3). Basilar membrane width is equivalent to the distance between the inner osseous lamina and the outer lamina or the spiral ligament, represented here by a thin black line after the outer osseous laminae end. The cochlea are shown inverted from in vivo orientations (l lateral; p posterior; v ventral). Differences in membrane buttressing among the cochlea are clear. The Type I cochlea has proportionately twice as much membrane supported by bony laminae as Type II, and the mysticete laminae is neither strong nor extensive. The basal region of the mysticete 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 resolve lower frequencies than Type I. Differences in laminar support imply Type I cochlea have a higher ultrasonic range.

($-0.968 < r < -0.791$) for characteristic frequency with all spiral variables except scalae length and basal diameter. These two variables are positively correlated with animal length ($0.84 < r < 0.92$). The data indicate three spiral configurations in extant Cetacea differentiated by turns, height, pitch, slope, and basal ratios. Two formats occur exclusively in odontocetes and coincide with Type I and II acoustic divisions. Type I cochlea are shallow, $< 2$ turn spirals, and Type II are steeper with $> 2$ turns. Type I is nearly Archimedian; i.e., it is a constant interturn radius curve, like that formed by a tightly coiled rope. Type II is equiangular, like a nautilus shell, with logarithmically increasing interturn radii. This is also the presumed configuration for most mammalian cochlea. The available mysticete data do not allow a full three-dimensional analysis of spiral shape, but the basic measurements indicate a broad spiral with a steeper pitch than that of odontocetes. The spiral data for modern cetaceans, in combination with basilar membrane and outer osseous laminae data, produce three prototypic cochlear shapes, each of which characterizes a major acoustic division. Schematic three-dimensional reconstructions illustrate the major features of each cochlear format (Fig. 35.10).

If auditory capacity is correlated with habitat and behavior, differences in spiral formats should correlate with specific environments and lifestyles as well. In modern Cetacea, Type I spirals have been found only in inshore phocoenids and riverine dolphins (Table 35.3, App. 1), which are the highest frequency group of aquatic mammals, with echolocation signals that reach 200 kHz (Purves and Pilleri 1983; Ketten 1984; Feng et al. 1990).

TABLE 35.4. Bullar-cranial associations

| Group | Cochlear type | Nonsynostotic joints with the skull | Synostotic joints with the skull | Pedicles (connections) |
|---|---|---|---|---|
| Protocetidae | — | X | X | 4 (t–b) |
| Dorudontinae | I,II,M | X | (in some species) | 1.5 (p–t) |
| Squalodontidae | I,II | X | — | 2 (p–t) |
| Delphinidae | II | (in some species) | — | 2 (p–t) |
| Phocoenidae | I | — | — | 2 (p–t) |
| Platanistoidae | I | (in one species) | — | 2 (p–t) |
| Physeteridae | I,M | (in some species) | — | 2 (p–t) |
| Mysticeti | M | X | X (p–b) | 1 (p–t) |

(t), tympanic; (b), basioccipital region; (p), periotic.
Data compiled from Kellogg 1936; Kasuya 1973; Gingerich et al. 1983; Ketten 1984.

These species live in turbid waters where ultrahigh frequency, short wavelength signals would be advantageous for distinguishing fine detail. Type II formats are common to delphinids which are off-shore and pelagic species with lower frequency echolocation signals. The mysticete format is known only in low-frequency pelagic planktivores. Both groups of echolocators are active predators; the mysticetes are opportunistic feeders. With these characteristics in mind, it is possible to speculate on the functional implications of the cochlear structure of extinct species.

# 5. The Extinct Cetacean Ear

Fossil evidence indicates that the ability to utilize high frequencies may have originated early in cetacean history, but we are not able to link specific auditory structures with entry into the water. Osteological remnants of the earliest Eocene cetaceans, the protocetid Archaeoceti (Fig. 35.1, App. 1), show relatively few changes from the typical terrestrial mammalian skull (Fig. 35.2), although small accessory air sinuses and a separate periotic are already present. These may reflect "preadaptive" features in Mesonychidae since they are also found in ungulates and are not found in other non-cetacean mammals (Barnes and Mitchell 1978; Barnes et al. 1985; Oelschläger 1986a, 1986b, 1990). Karyotypic and seral studies (Boyden and Gemeroy 1950; Ishihara et al. 1958; Lowenstein 1987) indicate close relationships for Cetacea with ungulates, particularly suids, lending credibility to preadaptation theories. In the most ancient Archaeocetes, *Pakicetus inachus, Pappocetus lugardi,*

and *Protocetus atavus* (Protocetidae), little is known of the postcranial skeleton, making it difficult to judge their level of adaptation to water, but teeth and sinus patterns suggest they were predatory echolocators (Fordyce 1980; Gingerich and Russell 1981; Gingerich et al. 1983). The protocetids have the cetacean cranial characters of a thin zygomatic arch, a large concave mandible, and a well-defined periotic, although long anterior and posterior processes wedge the periotic between the squamosal and mastoid bones, making separation of the tympanic and periotic bones from the skull incomplete (Gingerich and Russell 1981; Gingerich et al. 1983; Oelschläger 1986a, 1986b). The tympanic in *Pakicetus* has four nonsynostotic articulations with the surrounding skull elements (Table 35.4) (Gingerich and Russell 1981). Gingerich et al. (1983) suggest that the malleus was fused to the tympanic bulla, as in modern odontocetes, and that this permitted *Pakicetus* to hear while submerged; however, they also noted that the air sacs were small and that the tensor tympani fossa was exceptionally large, implying a functional tympanic membrane which is difficult to link theoretically with a fused malleus. They concluded that protocetids, which are common in fluvial sediments, were probably amphibious, freshwater carnivores that were not fully adapted to water.

Basilosauridae exhibit a mixture of plesiomorphic (primitive) and apomorphic (derived) characters which makes them a reasonable, although unestablished stem point for the separation of mysticete and odontocete lineages (Fig. 35.1). They are found only in marine sediments and are pivotal in the development of modern Cetacea (Fig. 35.2C) (Fordyce 1980; Gingerich et al. 1983). One
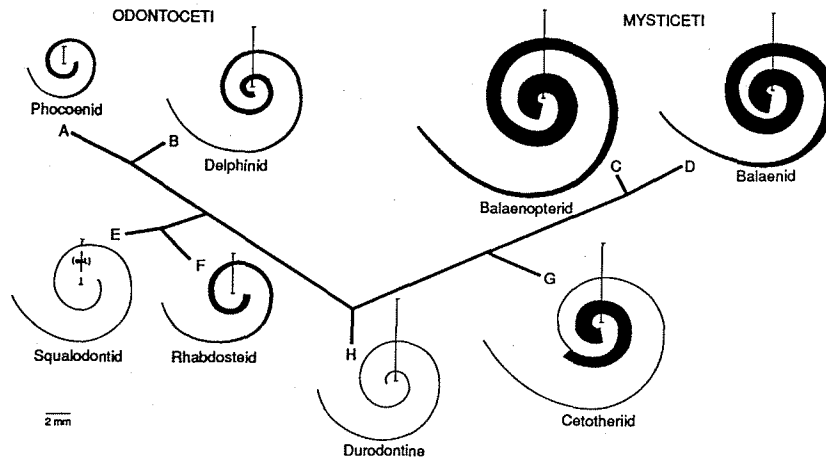
FIGURE 35.11. Two-Dimensional basilar membrane reconstructions. Two-dimensional reconstructions illustrate differences in the shape and dimensions of the cochlear spiral and basilar membrane in four extinct and four modern species. (Data compiled from Kellogg 1936; Fleischer 1976; Norris and Leatherwood 1981; Ketten and Wartzok 1990.) Basilar membrane widths are represented by filled areas. The vertical bar extending from the origin of each spiral represents the axial height. In some species, complete data are not available, and only the path of the cochlear canal is shown (see Table 35.3). In Cetacea, frequency ranges are inversely correlated with basilar membrane width, axial height, and number of turns. Based on these criteria, the spirals shown can be divided into 5 broad categories: mixed high and low frequency ancestral (H *Zygorhiza kochii*; 2 turns; tall); high frequency stem odontocete (E *Squalodon*; F *Rhabdosteus*; ≤ 2 turns, narrow membrane, average height); low ultrasonic Type II odontocete (B *Tursiops truncatus*; > 2 turns, narrow membrane, average height); high ultrasonic Type I odontocete (A *Phocoena phocoena*; < 2 turns, narrow membranes, low basal ratios); and low frequency stem or modern mysticete (C *Balaenoptera acutorostrata*; D *Eubalaena glacialis*; G *Parietobalaena*; >2 turns, wide membranes, tall). Differences may exist among fossil and recent mysticetes for infrasonic perception which are not reflected in these data.

basilosaurine, *Basilosaurus isis*, an Archaeocete originally misclassified and infamously misnamed as a reptile (Kellogg 1936), has recently been shown to be an important intermediate form with hindlimbs that are completely formed but too insubstantial for terrestrial locomotion (Gingerich, Smith, and Simons 1990). All basilosaurids show some cranial modification consistent with a modern cetacean cranial format. Smaller dorudontine basilosaurids (e.g., *Dorudon osiris*, *Dorudon intermedius*, *Zygorhiza* spp.) have the most extensive changes, including elongated maxillae, inflated bullae, large mandibular channels, higher occipital shields, posterior migration of the nares, enlarged sinuses, massive ossicles, and a periotic decoupled from the mastoid (Kellogg 1936; Barnes and Mitchell 1978; Oelschläger 1986a, 1990). Their most primitive characteristic is that the periotic-tympanic complex remains affixed to the

braincase with anterior and posterior flanges wedged between the squamosal and occipital (Table 35.4). A review of Kellogg's descriptions (1936) in the context of modern spiral data shows the dorudontines have a bullar structure and cochlear spirals that are composites of Type I, Type II, and mysticete parameters (Table 35.3, Fig. 35.11). Like mysticetes, they have an inflated, bulbous tympanic which is closed anteriorly but, like odontocetes, they have inner and outer pedicles and prominent posterior tympanic processes (Table 35.4). The dorudontine periotic is distinctly ovoid and strongly resembles those of modern physeterids. *Zygorhiza* has two turns but a steep spiral with an axial pitch and basal ratio that mix characteristic modern mysticete and odontocete values. A few basilosaurid species like *Kekenodon* are sufficiently modern, with full inner and outer bullar pedicles, medial and lateral prominences, and

extensive air sacs, that their status as late Archaeocetes has been questioned (Kellogg 1936; Kasuya 1973; Barnes, Domning, and Ray 1985). Despite the absence of full telescoping in the anterior cranial bones in some specimens, dorudontines, at least in terms of acoustic structures, are the probable ancestral link to squalodonts which superseded the Archaeocetes and are the link to modern cetaceans.

Within 10 million years after the extinction of *Zygorhiza*, Agorophiidae (Fig. 35.2D), an Oligocene squalodontoid family, displays most overt odontocete skull traits (Barnes, Domning and Ray 1985): (1) telescoping of the skull; (2) nares at the vertex of the skull; (3) hollow mandible; and (4) tympano-periotic isolation in an extensive cranial sinus. In modern Cetacea, these features are associated with significant soft tissue developments which are principally related to underwater echolocation; e.g., the presence of a melon or spermaceti organ that channels sounds outward, the lining of the mandibular concavity with fat that acts as an acoustic wave guide, and filling of the peribullar sinus with vascularized foam that acts as an acoustic insulator (Reysenbach de Haan 1956; Fraser and Purves 1960; Norris 1968; McCormick 1972; McCormick et al. 1975; Ketten 1984). The presence and extent of related osteological changes (telescoping, concave mandible, separate bullae, and enlarged peribullar spaces) in agorophiids are sufficient for them to be considered intermediate to the squalodonts from which modern odontocetes are derived (Kellogg 1936; Barnes, Domning, and Ray 1985; Oelschläger 1986a; Pilleri, Gihr, and Kraus 1986).

Spiral parameters in later Squalodontoidae; e.g., *Rhabdosteus* and *Squalodon* (Fig. 35.2E), have characteristics of both phocoenid (Type I) and delphinid (Type II) cochlea (Table 35.3, Fig. 35.11). Squalodontid bullae, similarly, show mixed, overt characteristics of modern platanistid, physeterid, and ziphiid forms (Kellogg 1936). In most respects, therefore, these earliest odontocetes are considered to already have the functional acoustic properties of modern odontocetes; it is likely they were carnivorous echolocators. From this point forward, cetacean development follows family lines which are still fully represented today (Fig. 35.1). Kasuya (1973), in a comprehensive analysis of dried odontocete bullae, devised a series of phyletic subdivisions based on surface morphom-

etry and patterns of tympano-periotic fusion. He concluded the physeterids and platanistids follow a primitive pattern while the delphinids have the most recent structure and the phocoenids fall between primitive and recent forms. Phocoenids and delphinids both appear to be descended from kentriodonts and have developed similar skull asymmetries associated with complex dorsal air sinuses. It is unclear whether river dolphins arose from a common ancestor or, alternatively that they developed as four separate, parallel lineages. The mysticetes are generally considered modern but they have some osteological features in common with more primitive species; e.g., there is only one inner pedicle, the periotic retains long anterior and posterior processes which wedge firmly against the skull, and all species except some Balaenidae have a distinctive hemispheric bullae (Table 35.4) (Kellogg 1936; Kasuya 1973). This construction, which is consistent with a low frequency, nonecholocating ear, is not evident prior to *Parietobalaena* (Fig. 35.11) in the middle Miocene.

A controversy arises in the literature at this point concerning both terminology and function of the bony bullar structures (Yamada 1953; Reysenbach de Haan 1956; Kasuya 1973; Oelschläger 1986a, 1986b, 1990). All authors agree that a major structural development tied to a fully aquatic existence for Cetacea was the disassociation of the tympanic and periotic bones from the skull. To produce modern odontocete ears from Archaeoceti, it was necessary to isolate the periotic by replacing anterior and posterior skull processes with bony, synostotic tympano-periotic connections. During this transition, the tympanic lost its associations with the squamosal and pterygoid and formed pedicular or pillar-like attachments to the periotic; i.e., the nonsynostotic articulations of the bullar flanges with the squamosal, exoccipital, and basioccipital found in Protocetidae are gradually replaced with two synostotic tympano-periotic pedicles (the posterior petrotympanic process and the processus tubarius) in modern odontocetes (Fig. 35.7A) (Oelschläger 1986a, 1986b; Pilleri, Gihr, and Kraus 1987). Modern mysticete bullae characteristically have one lateral pedicle and a distinct mastoid flange (Fig. 35.7B), which connects either or both bullar components to the skull and may function in transmitting low frequencies (Yamada 1953; Reysenbach de Haan 1956; Kasuya

1973); i.e., to produce a mysticete ear, it was necessary to retain and fuse one posterior process to the skull, forming only one auxiliary pedicle (Table 35.4). Authors disagree about the role of the mastoid in this progression, particularly since its actual location and whether it fuses with the tympanic and periotic are not clear in present Cetacea (Kasuya 1973, Oelschläger 1986b). Recent work by Oelschläger 1986b, 1990) provides evidence that the mastoid does not form a fused structure with either the periotic or tympanic, as traditionally suggested, but is retained in its relative position to the squamosal and exoccipital, resulting in a reduction of the periotic processes and rotation of the tympano-periotic complex to the present position.

The presence of a cranial process is coincident with a lower frequency ear, while its absence may be an indicator of echolocation abilities. Consequently, the form and number of attachments of the periotic with the tympanic and with the skull are important diagnostic characteristics distinguishing mysticetes from odontocetes, and thus can be used to classify intermediate forms (Kasuya 1973). Different stages in this tympano-periotic metamorphosis are found in dorudonts, squalodonts, and kentriodonts. Shared characters of Mysticeti and Odontoceti; e.g., horizontal flukes, median dorsal fins, extensions of the middle ear sinus, vertebral ankylosis, and cranial distortions, imply a fairly early common ancestor, probably a dorudontine Archaeocete. Odontocetes antedate mysticetes, therefore, the earliest cetacean was probably a high, but not ultrahigh, frequency user, and the low frequency characteristics of mysticete ears are a relatively recent development.

# 6. Cetacean Auditory Adaptations

## 6.1 Comparative Speculations

Piecing together the fossil, cochlear, and acoustic data, we expect the terrestrial ancestor of Cetacea to be a small, high-frequency carnivorous mammal, possibly with some ultrasonic capacity, that exploited the niche vacated by the icthyosaurs. On entering the water, it faced substantial competition and predation from resilient, ancient, well-adapted species like sharks. Perhaps the likeliest animal to succeed would have been a nocturnal

carnivore, a predator preadapted to a dark environment. It would be interesting, therefore, to examine mesonychid fossil assemblages for evidence of ultrasonic cochlear adaptations. It must be noted, however, that even if evidence of a high frequency mesonychid were found, it is fairly certain the early Archaeocetes were not *aquatic* echolocators, since they have no melon. Echolocation is a two-way function. For an ancestral cetacean to qualify as an effective echolocator, there must be a coordinated means of generating a highly directional signal and receiving its altered echo. Modern odontocetes are true echolocators, not simply ultrasonic receptors, and it is important to determine at what point the ultrasonic source (nasal diverticuli; rostral concavity) and receiver (isolated tympano-periotic and narrow basilar membrane) coexist in Cetacea.

Cochlear data may also be used to speculate on the development of the Mysticeti. Their appearance occurs within a reasonable geologic time scale of the breakup of Gondwanaland (Fordyce 1977). This dispersal of the continents resulted in the opening of new oceanic regions in the southern oceans and the creation of the circumpolar Antarctic currents. While these changes produced terrifically productive waters which are still major repositories of marine biomass today, they also brought about substantial reductions in surface temperatures in the higher latitudes. Cetacea inhabiting those regions would be faced with an abundance of food and less pressure to compete, but also with an even greater risk of hypothermia than was faced in warmer, northern waters. In colder southern waters, increased size offers a substantial metabolic advantage. Since surface area increases more slowly than volume as a structure expands, increasing size may help retain body heat; i.e., a larger whale is a warmer whale. We also know that odontocete cochlea scale isometrically with animal size. It is likely that mysticete cochlea scale in a similar if not identical way. If basilar membranes broadened and lengthened without thickening as cetaceans increased in size, a lower frequency encoding cochlea would result as a consequence of the greater mass in mysticetes. With less pressure to echolocate as a foraging strategy in more productive waters, a decrease in the audibility of higher frequencies may not have been a significant disadvantage. We might hypothesize that colder, richer feeding grounds provided

the appropriate pressure for development of larger, low frequency baleen whales. If correct, there should be a predictable temporal and latitudinal distribution of fossils with odontocetes dominating earlier northern faunas and larger mysticetes increasingly common in more recent southern fossil records. One difficulty in obtaining such data may be that it resides literally at the ocean bottom, since the majority of baleen deaths may deposit carcasses offshore in major pelagic regions that have not shifted significantly despite climatic changes.

Lastly, little is known of the primitive amphibious mammalian ear. Origins of two orders, the extinct Desmostylidae ("sea horses") and Sirenia ("sea cows," manatees, and dugongs), are poorly understood in comparison to Cetacea. Little acoustic or anatomical data are available for the manatee and dugong, although compared to Cetacea, Sirenia are more accessible, and they offer substantial promise of useful data related to low-frequency aquatic adaptations. Both Desmostylia and Sirenia show clear anatomical affinities with two other low frequency mammals, elephants and hippopotami (Barnes, Domning, and Ray 1985; Domning 1982). Recent studies show exceptional low-frequency capability in the elephant (Heffner and Heffner 1980; Payne, Langbauer, and Thomas 1986); but the hippopotamus is virtually unknown acoustically. It is reputed to produce audible clicks underwater and to swim by flicking its rear legs in tandem rather than trotting in the shallows (K. Norris personal communication). Since its adaptation to water is less complete than that of most marine mammals, studies on hippopotamus may provide intriguing insights into the behavioral adaptations of early, amphibious species.

## 6.2 Future Directions and Open Questions

A great many functional aspects of the cetacean ear are not fully understood. There is no satisfactory model of hearing in Cetacea, yet it is clear they have a substantially different cochlear and middle ear construction from terrestrial mammals. A pressing problem related to developing such a model is that cetacean cochlear anatomy differs significantly among families and variations are not fully described. The second difficulty is that the anatomy that has been well described is perplex-

ing. Facetiously, the odontocete ear could be described as a jaw with windows overlying a rock with strings attached. Although purposely trivial, this description conveys the difficulty of interpreting the elegant and subtle relationships of these complex structures without more extensive studies both in basic anatomy and audiometry, particularly for the mysticetes. Specific answers are needed for: (1) What are the transmission paths for sound to the ear in Mysticeti? (2) Do the sinuses play a significant role in directional hearing in all Cetacea or is their function primarily in echolocation? (3) Does the extreme density of the bulla resist extreme pressure or is it a necessary component for signal detection? (4) Are the ossicles functional and how do they receive sound? A more global question is whether there are, at least in the odontocetes, perhaps two parallel systems for processing sound: one for echolocation and one for lower frequencies. Is the odontocete cochlea a shared property, with two anatomical inputs from two acoustic channels? It is a proposition that fits well with the conflicting evidence for two potential sites of sound production and of many potential paths for sound reception, particularly in light of the two types of sounds odontocetes produce. To my knowledge, this is a novel alternative that has yet to be researched.

One of the most difficult tasks in producing this chapter was to determine a means of characterizing the auditory capability of marine mammals. Aside from the diversity of species, and range of adaptations that implies, comparatively little data exist that match the fairly rigorous and conventionally accepted means of classifying hearing in a mammal. As Watkins and Wartzok (1985) pointed out, information and research in marine mammals ranges ". . .from intensive to eclectic." Much of the available data are difficult to synthesize into a coherent analysis since techniques vary widely and sample sizes are often small. This is not a reflection of poor science in the field. Indeed many experiments verge on the ingenious and heroic considering the environmental, practical, and legal complications implicit in marine mammal research. It is apparent, however, that attention to two areas of experimental design are needed. First, it is imperative that the data base be expanded. Even within a relatively homogeneous group like Odontoceti, one species cannot be used to reliably characterize

the entire suborder. Cochlear variations coupled with species differences in echolocation pulse intervals and frequency imply that more than one echolocation model exists, and no ultrasonic model is likely to explain infrasonic mechanisms in mysticetes. Secondly, if experiments are not carried out on live animals under their normal environmental conditions, they must be carefully interpreted with full assessments of the response changes an abnormal, nonaquatic environment may induce. Similar caveats hold for any work with postmortem tissue. These are not trivial analyses to make, but they are sorely needed and an expansion of our knowledge of these animals is imperative for any realistic understanding of their adaptations and abilities.

## 7. Summary

By the late Miocene, four major cranial trends associated with the environmental pressures of an aquatic habitat and audition were established in both the Odontoceti and Mysticeti: (1) telescoping of the skull; (2) dorso-caudal nares; (3) enlarged peribullar sinuses; and (4) a tympano-periotic bullar complex partly or wholly disassociated from the skull. Environmental influences are equally evident in the gross anatomy of the cetacean auditory system. There are no pinnae and no major pneumatized areas analogous to the mastoid cavities. Cetacean periotics, tympanics, and ossicles are all similarly constructed of massive, porcelaneous bone. The odontocete tympano-periotic complex is completely detached and acoustically isolated from the skull; mysticetes retain a medioposterior skull connection. In Odontoceti, telescoping produced a frontal concavity that accommodates the melon and nasal sacs which function in production of ultrasonic echolocation signals. The position, construction, and ligamentous associations of odontocete bulla support the "pan bone" theory of jaw conduction in which ultrasonic echoes are received by a fatty acoustic wave guide in the mandible. The path of sound reception in mysticetes is unknown, but they retain a highly derived tympanic membrane analogue and the external auditory canal may be functional.

Modern cetaceans divide into three acoustic groups: mysticetes (potentially infrasonic); Type I odontocetes (upper range ultrasonics); and Type II odontocetes (lower range ultrasonics), which parallel habitat and behavioral divisions. The acoustic divisions coincide with three cochlear formats that differ principally in the construction and support of the basilar membrane. The odontocete cochlea is clearly adapted for ultrasonic perception, with an exceptionally narrow basilar membrane, high spiral ganglion cell densities, and extensive bony outer spiral lamina. Basilar membrane cross-sectional dimensions interact with its composition and support to determine resonance characteristics. Membrane thickness-to-width ratios are higher for the basal turn of odontocetes than for any other mammal investigated to date. Mysticete basilar membranes are exceptionally wide and thin, implying that they are specialized for encoding extremely low frequencies, but there is insufficient data to determine whether low frequency specializations are present in mysticete cochlear ducts.

Major indicators for assessing the auditory capacity and level of aquatic adaptation of extinct species include the presence or absence of skull attachments, the number of tympano-periotic pedicles, and cochlear spiral morphometry. Protocetid cranial structure implies the earliest Archaeocetes were amphibious predators. Later dorudontine Archaeoceti were fully aquatic and had the cetacean characters of enlarged air sinuses and reduced attachments of the auditory bulla to the skull. Squalodonts from the late Oligocene have a nearly fully telescoped skull, a well-isolated tympano-periotic complex, and a cochlear spiral with both Type I and Type II characteristics, implying they were at least protoaquatic echolocators. Oligocene paleobalaenids clearly fit low frequency cochlear formats. It is likely that, auditorially, Cetacea are derived from a high-frequency form of mesonychid, but there is little evidence for echolocation in the Archaeoceti. It is suggested that scaling of cochlear structures may place mechanical limitations on the resonance characteristics of the basilar membrane and that size of the great whales limits their auditory capacity to lower frequencies.

Barbara Burgess, Diane DeLeo Jones, Gregory Early, Joseph Geraci, James Gilpatrick, Richard Lammertson, Daniel Odell, William Perrin, James Mead, and Charles Potter. Radiographic studies were provided by Frank Starr, III. James Anderson, Arthur Rosenbaum, and Alan Walker provided knowledge about structure and opportunities for research. Douglas Whittington gave encouraging support and helpful criticisms at each stage. Extensive and insightful reviews of the manuscript were provided by Peggy Edds, Nelson Kiang, James Mead, Douglas Wartzok, and Alexander Werth, who also gave invaluable advice on paleontological literature and nomenclature. Reconstructions were produced with the cooperation of the Cochlear Implant Research Laboratory and the Eaton-Peabody Laboratory for Auditory Physiology. Lastly, I am particularly grateful to the organizers of this symposium, Arthur Popper, Douglas Webster, and Richard Fay, for providing the impetus and opportunity for many stimulating discussion with participants.

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# Appendix I—Marine Mammal Divisions

This listing is provided as a general reference, since many species and groups mentioned in the text may be unfamiliar to most readers. Common names are listed for representative recent species; extinct divisions are designated by †. Geologic periods indicate the point in the fossil record at which the taxa were first clearly represented. Although conventional scientific names are used and ordered in an apparent hierarchy, the subdivisions are only relative and no attempt is made at formal classification rankings. Classification of marine mammals is undergoing continual revision, and as recently as 1989 a new family of Archaeoceti was proposed as were major changes in the distribution of families in the suborders Mysticeti and Odontoceti. For an accurate classification, the reader is referred to Barnes, Domning, and Ray (1985) and Mitchell (1989).

Throughout this chapter, the conventional terms dolphin, whale, and porpoise are used sparingly since they represent largely false distinctions. Whale actually relates to size and is correctly applied to both odontocetes and mysticetes. The term dolphin is used often to designate smaller beaked delphinids, and porpoise, nonbeaked phocoenids, but the distinctions are blurred and all of these animals porpoise. Consequently, the terms odontocete (toothed whales/dolphin/porpoise), mysticete (baleen/whalebone whales), and cetacean (all whales), although somewhat formal, are preferred.

**Cetacea**—Whales, dolphins, and porpoises
  **Archaeoceti**†—Early Eocene
    Protocetidae—Eocene (*Pakicetus*)
    Remingtonocetidae—early Eocene
    Basilosauridae—late Eocene
      Basilosaurinae (*Basilosaurus = Zeuglodon*)
      Dorudontinae (*Dorudon, Zygorhiza*)
      Kekenodontinae
  **Odontoceti**—Early Oligocene
    Squalodontoidea—shark-toothed stem odontocetes
      Agorophiidae†—late Oligocene
      Squalodontidae†—Miocene (*Squalodon*)
      Rhabdosteidae†—Miocene (*Rhabdosteus*)
      Squalodelphidae†—late Oligocene (*Squalodelphis*)

Delphinoidea—dolphins and small toothed whales
  Kentriodontidae†—early Miocene (*Kentriodon*)
  Albireonidae†—late Miocene
  Monodontidae—white whales

| | |
|---|---|
| *Monodon monoceros* | Narwhal |

  Phocoenidae—porpoises

| | |
|---|---|
| *Phocoena phocoena* | Harbour porpoise |

  Delphinidae—dolphins, coastal toothed whales, orcans

| | |
|---|---|
| *Delphinus delphis* | Common dolphin |
| *Feresa attenuata* | Pygmy killer whale |
| *Globicephala macrorhynchus* | Short-finned pilot whale |
| *Grampus griseus* | Risso's dolphin |
| *Lagenorhynchus albirostris* | White-beaked dolphin |
| *Stenella attenuata* | Spotted dolphin |
| *Stenella coeruleoalba* | Striped dolphin |
| *Stenella longirostris* | Long-beaked spinner |
| *Tursiops truncatus* | Bottlenosed dolphin |

Platanistoidea—river dolphins
  Acrodelphidae†—Miocene
  Iniidae

| | |
|---|---|
| *Inia geoffrensis* | Amazonian boutu |

  Lipotidae—beiji
  Platanistidae—Asian river dolphins
  Pontoporiidae—franciscana
Ziphioidea
  Ziphiidae—beaked whales
Physeteroidea
  Kogiidae—pygmy sperm whale
  Physeteridae—sperm whale, cachalot

| | |
|---|---|
| *Physeter catodon* | sperm whale |

**Mysticeti**—Miocene
  Aetiocetidae†—late Oligocene (*Aetiocetus*)
  Cetotheriidae†—Pliocene (*Paleocetus*)
  Balaenidae—right whales

| | |
|---|---|
| *Eubalaena glacialis* | Northern right whale |
| *Eubalaena australis* | Southern right whale |
| *Balaena mysticetus* | Bowhead |

  Neobalaenidae

| | |
|---|---|
| *Caperea marginata* | Pygmy right whale |

  Eschrichtiidae

| | |
|---|---|
| *Eschrichtius robustus* | Grey |

  Balaenopteridae—rorquals

| | |
|---|---|
| *Balaenoptera acutorostrata* | Minke |
| *Balaenoptera borealis* | Sei |
| *Balaenoptera edeni* | Bryde's |
| *Balaenoptera musculus* | Blue |
| *Balaenoptera physalus* | Fin |
| *Megaptera novaeangliae* | Humpback |

**Desmostylia**† — Miocene — sea horses
    Desmostylidae
    Paleoparadoxidae

**Carnivora**
  **Fissipedia** — Pleistocene — sea otters and sea minks†
    Mustelidae
  **Pinnipedia** — Oligocene — seals, sea lions, walrus
    Phocidae — true seals
    Otarioidea

    Otariidae
      Enaliarctinae†
      Otariinae — sea lions
    Odobenidae — walruses
**Sirenia** — Eocene — sea cows
  Prorastomidae†
  Protosirenidae†
  Trichechidae — manatees
  Dugongidae — dugongs, Steller's sea cow