

STRUCTURE, FUNCTION, AND ADAPTATION OF THE MANATEE EAR

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INTRODUCTION

The West Indian manatee, Trichechus manatus, is common throughout the Caribbean yet little is known about its sensory abilities. Hearing in particular is of interest since large numbers of one subspecies, the Florida manatee (T. manatus latirostris), die annually from collisions with boats in shallow coastal waters and canals. There is no published audiogram for Trichechus manatus and the auditory system has not been fully described. Earlier studies of manatee hearing were based on isolated, dehydrated tympano-periotic bones (Robineau, 1969; Fleischer, 1978). This paper describes all major hard and soft tissues of the peripheral auditory system of T. manatus, presents new information on specialized cranial features that may be important for sound conduction, and provides morphometry-based estimates of the frequency range and sensitivity of West Indian manatee ears.

METHODS

Seven ears from one juvenile and three adult Florida manatees were examined using computerized tomography (CT), conventional dissection, and thin section microscopy. Specimens were obtained as whole heads removed from animals that died during rehabilitation. Two animals had received antibiotic therapy for enteric infections, but none received aminoglycosidic antibiotics which are known to compromise auditory function and distort inner ear anatomy.

Gross structure of the cranium, middle ear space, and inner ear labyrinth were explored first with CT scans of intact, frozen heads. Two major advantages of CT scanning are that it provides registered images for three-dimensional reconstructions and undisturbed, in situ views of cochlear-cranial relationships.

Contiguous, transaxial 1 mm high-resolution CT scans were obtained with a Siemens Somatom DR3 scanner. Scan parameters were equivalent to those used for cetacean material (Ketten and Wart-zok, 1990; Ketten, this volume). X-ray attenuation data were archived on magnetic tape and scan images were copied onto high density X-ray film.

After scanning, the heads were dissected and one tympano-periotic complex from each head was extracted, catalogued, cleaned, weighed, and measured. The periotic and tympanic were separated and the round window was opened for direct formalin perfusion of the cochlea. The periotic was fixed by immersion in Heidenhein-Sousa solution, decalcified in acid-based EDTA, embedded in paraffin, and sectioned at 20 μ m. Hemoglobin and eosin stained serial sections were used to assess basilar membrane dimensions and cochlear duct morphology. The contralateral ear and associated tissues were preserved in buffered formalin and held for future study.

RESULTS

External Ear

Like Cetacea, manatees have no pinnae or superficial auditory structures. The external meatus is a surface dimple, leading to a narrow external auditory canal which is packed with black debris and discarded epithelial cells. It is unclear whether the canals normally transmit sound to the ear.

Tympano-Periotic Complex

Trichechus manatus ears have two distinct components: a large bilobed periotic and a smaller tympanic (Fig. 1, Table 1). X-ray analyses show both are constructed, like cetacean tympano-periotic complexes, of exceptionally dense bone with no multi-chambered, pneumatized areas (Fig. 2). Unlike cetacean tympano-periotics, which are external to the skull, manatee tympano-periotics are attached to the inner wall of the cranium, and occupy a substantial portion of the posterior brain case. There is little difference in the size and weight of adult tympano-periotics, and neonate dimensions vary less than 20% from adult specimens. Thus, like most mammals, manatees appear to have precocial ears; i. e., the auditory system is structurally mature and presumably fully functional at birth. As a consequence, however, the tympano-periotic complex is disproportionately large in young manatees and can constitute 14% of skeletal weight (Domning and de Buffrénil, 1991).

Table 1. Trichechus manatus Tympano-Periotic Morphometrics (Averages for 1 male and 2 female adults)

Structure	A-P Length† (mm)	D-V Depth† (mm)	L-M Width† (mm)	Dry Weight (gms)
Periotic	66.9	95.6	48.6	96.23
Tympanic	51.9	33.6	20.2	23.39
Malleus	27.9	13.6	14.0	3.41
Incus	8.6	15.6	13.2	0.82
Stapes	4.8	6.4	15.3	0.68

†In vivo anterior-posterior, dorsal-ventral, lateral-medial

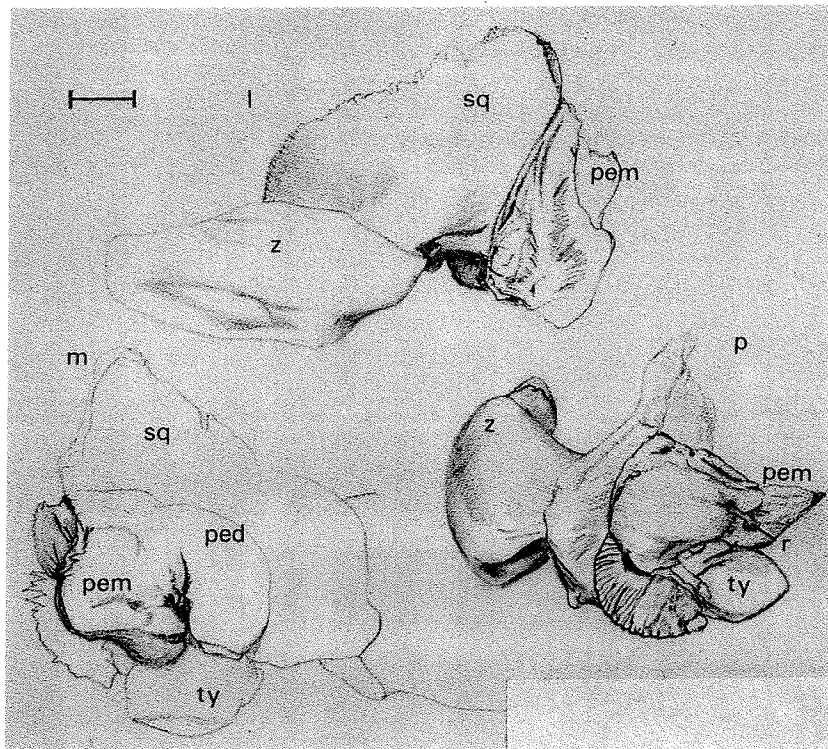


Fig. 1. Manatee left tympano-periotic complex and associated cranial structures drawn in lateral (l), medial (m), posterior views (p). The scale bar represents 25 mm. pars temporalis (dorsal periotic lobe, ped); pars petrosa (medial periotic lobe, pem); round window (r); squamosal (sq); tympanic (ty); zygomatic process (z).

The periotic is dorsal to the tympanic with substantial dorsal (pars temporalis) and medial (pars mastoideus and pars petrosa) lobes (Fig. 2). The cordate dorsal lobe is solid endosteal bone with no internal subdivisions. The medial lobe is roughly pyramidal with a flattened posterior base and a pointed, medially directed apex that contains the inner ear labyrinth (Fig. 1). In fresh material, the dorsal lobe of the periotic is tightly coupled to the inner surface of the squamosal by a tough fibrous sheet and cartilaginous cap (Figs. 1, 2). In prepared, macerated specimens this attachment is lost, which may account for earlier reports (Fleischer, 1978) that sirenian tympano-periotics are isolated from the skull.

The intracranial position of the periotic and its fusion with the squamosal have important implications for hearing. Anteriorly, the squamosal connects via a bony isthmus to an hypertrophied cranial portion of the zygomatic process (Fig. 1). The periotic is functionally tied to the process by its syndesmotomic joint with the squamosal. In adults, the process measures up to 110 mm anterior to posterior and 50 mm dorsal to ventral (Fig. 1). Microscopy shows it consists of a highly convoluted, cartilagin-

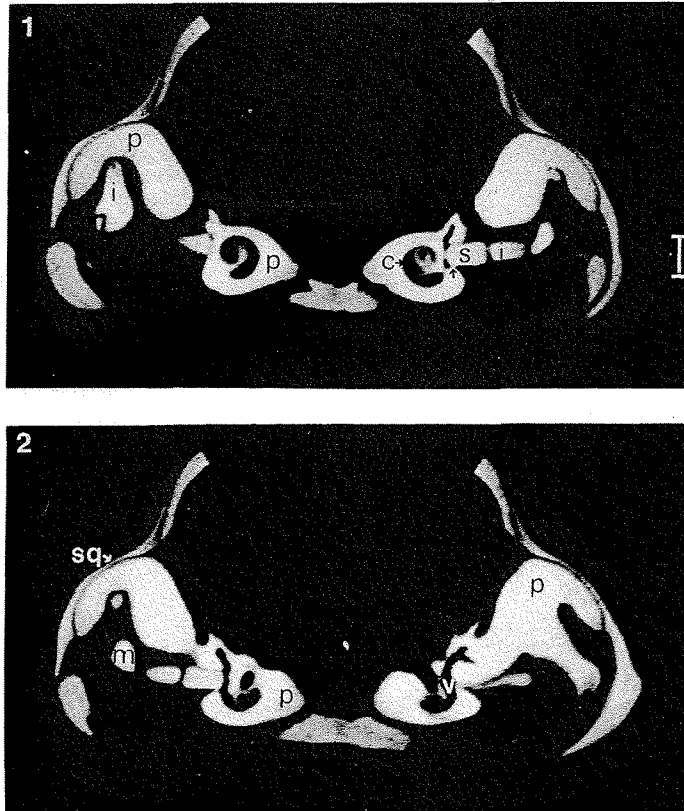


Fig. 2. CT scans of a juvenile *Trichechus manatus* head. 1 mm transaxial scans show the head in cross-section. Tissues are displayed in a gray scale from white (dense bone, >1200 HU) to black (air, -1000 HU). The tympano-periotic ranges 1600 to 2400 Hounsfield Units while the zygomatic process is 900 HU. The scale bar represents 10 mm. Major structures include the ossicular chain (i incus, s stapes, m malleus), squamosal (sq), periotic (p), and inner ear. The dark spirals in scan 1 are fluid-filled apical, middle, and upper basal turns of the cochlea (c). A second arrow points at the flange of the stapedial footplate in the oval window. The intercochlear distance, measured apex to apex, is 56 mm (approximately 70 % of the adult average). Scan 2, 3 mm posterior of 1, shows the lower basal turn, vestibule (v), and portions of the semi-circular canals.

ous labyrinth that resembles trabeculae in spongy bone (fig.3). The lacunae between the cartilage tongues are filled with lipids, which give a distinctive, deep yellow color to the process in dehydrated specimens. The zygomatic process is, therefore, an inflated, oil-filled, bony sponge which has substantial mass but less stiffness than an equivalent structure of compact bone. Considering its construction and relation to the squamosal and periotic, this massive flange may have a significant role in manatee sound reception as a differential low frequency resonator.

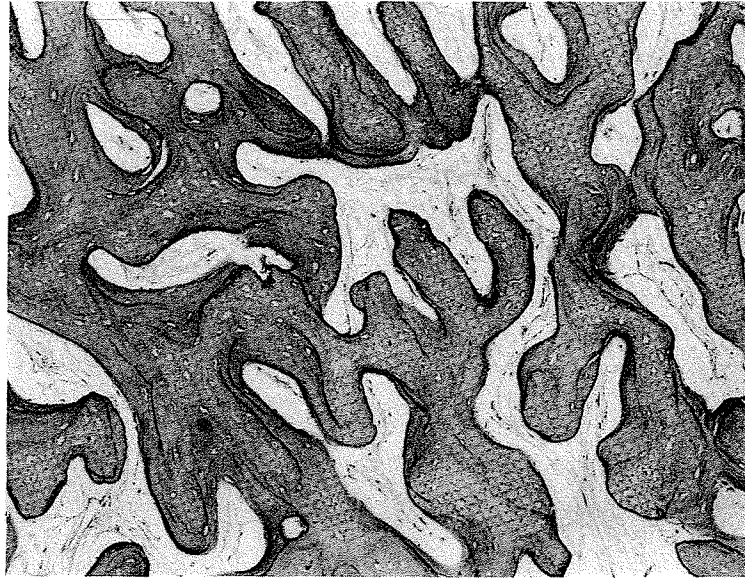


Fig. 3. Zygomatic process. A 20 μm section shows a weakly mineralized labyrinth. The structure is similar to trabecular endochondral bone, which forms the middle layer of mammalian cochlear capsules. The intertrabecular spaces contain moderately cellular fibrous tissue, blood vessels, and lipids.

Intracranial periotics mean also that interaural time distances in T. manatus are relatively small. Interaural time distances (IATD, the distance sound travels from one ear to the other divided by the speed of sound) depend upon the sound conduction path in the animal and the medium through which sound travels. In mammals, IATD's have been shown to be directly correlated with the upper frequency limit of species that use phase cues for localizing sounds (Heffner and Masterton, 1990). The narrower the head, the smaller the distance, the higher the frequency an animal must perceive to detect phase differences (Fig. 4). For terrestrial species, the normal sound path is through air, pinna to pinna. Differences in arrival times at the external meatus are important localization cues. The IATD is therefore the intermeatal (IM) distance measured around the head divided by the speed of sound in air. In aquatic animals, sound can travel by straight line tissue conduction, and experiments with delphinids confirm that intercochlear (IC) distances are the most appropriate measure for calculating IATD values in odontocetes (Dudok van Heel, 1962). Even though IC distances are generally one-half to one-third the IM distance, the IC distances of dolphins are acoustically equivalent to a rat or bat IM distance in air because of the increased speed of sound in water. Manatees are large, obligate aquatic animals with a head diameter equal to that of a larger delphinid like Tursiops; manatee IC distances, however, are closer to those of smaller phocoenids (Table 2). Exact sound reception paths are not known in manatees; however, their IATD will fall between a minimum of 58 μsec (calculated from intercochlear distances) and a maximum of 258 μsec (based on the external intermeatal path). If manatees fit the conventional mammalian IATD-frequency regression (Fig. 4), the calculated IATD's imply T. manatus needs an upper fre-

Table 2. Morphometry of Adult Manatee, Bottlenose Dolphin, and Human Cochleae

	<u>Trichechus</u> <u>manatus</u>	<u>Tursiops</u> <u>truncatus</u>	<u>Homo</u> <u>sapiens</u>
Intermeatal Length (mm)	278.00	350.00	164.00
Intercochlear Length (mm)	82.00	128.00	73.00
Cochlear Canal Length (mm)	35.00	40.00	32.00
Canal Diameter (mm)	8.72	9.45	7.50
Basilar Membrane Width Base/Apex (µm)	200/600	30/400	100/600
Membrane Thickness Basal/Apical (µm)	7/5	25/5	10/5
Turns	1.75	2.25	2.50

quency limit of 50 to 90 kHz to use phase cues for sound localization. To date, there is no indication that any species of manatee has acute ultrasonic hearing (Schevill and Watkins, 1965; Bullock et al., 1980; Klishin et al., 1990; Popov and Supin, 1990). A brief behavioral study on a captive T. manatus (Patton and Gerstein, 1992) found a maximal frequency range of 0.15 to 15 kHz. Sound levels were not reported in the study,

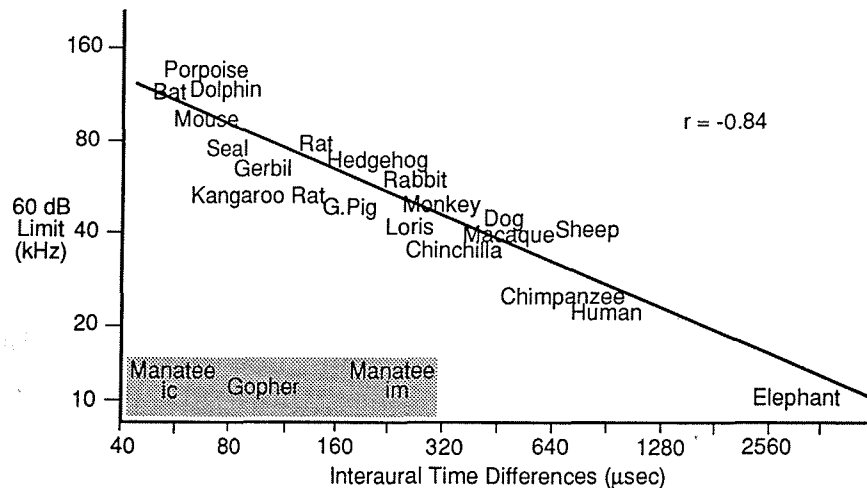


Fig. 4. IATD vs. maximum frequency perceived at 60 dB SPL. Sensitivity data from behavioural audiograms is plotted against the calculated interaural time distances for a wide range of mammals. (Values for non-aquatic species from Heffner and Heffner, 1992). For all species except Cetacea, the IATD is based on the intermeatal distance. Only the point for the pocket gopher and the area (grey) bounded by the theoretical extremes (ic intercochlear; im intermeatal) for the manatee vary significantly from the regression shown.

but the frequency range is similar to that reported for Trichechus inunguis (Klishin et al., 1990; Popov and Supin, 1990), making it likely that T. manatus hears little above 20 kHz and is unable to detect phase differences. Intensity differences from head shadow may provide some directional cues to T. manatus; however, intensity is generally most useful at higher frequencies and it is unclear whether aquatic mammals use intensity differences for localization (Awbrey, 1990).

Poor sound localization is unusual in mammals but it is not unprecedented. In extensive behavioral studies, Heffner and Heffner (see 1992 for summary) found two fossorial mammals, Geomys and Sorex, were incapable of localizing sound. Geomys bursarius, the pocket gopher, has an IATD similar to that of Trichechus manatus (Heffner and Heffner, 1990). Points for G. bursarius and T. manatus are plotted in Figure 4. The outlined region shows an area bounded by the high frequency limit of Trichechus inunguis plotted against the IC and IM values of Trichechus manatus. Adult T. inunguis are slightly smaller than T. manatus, and should have an IATD equal to or less than that of T. manatus. Actual IATD values for Trichechus inunguis and Trichechus manatus will fall within this area. The area encompassing all potential points for T. manatus overlaps that of Geomys bursarius and is significantly below the regression determined by Heffner and Masterton (1990) for most mammals, including odontocetes and pinnipeds, strengthening the proposition that the manatee, like the pocket gopher, is poor at sound localization.

Middle Ear

The tympanic bone resembles a thick comma with a bulbous anterior lobe and tapering posterior tail. The tympanic membrane fills the semilunate aperture bordered by the tail and petriotic and forms the lateral wall of the middle ear cavity. Ventrally, the cavity is closed by the soft tissues of the throat (Fig. 2). An ovoid tympanic space or middle ear cavity, which houses the middle ear ossicles, is defined therefore by broad soft-tissue walls inferiorly and laterally and by bony walls superiorly and medially.

The middle ear cavity is large and lined with a thick, vascularized fibrous sheet. This tissue is most abundant in the dorsal, epitympanic region and is readily apparent in CT scans (Fig. 2). In all heads examined, the ventral or hypotympanic region of the cavity, which is sealed by the tympanic membrane, was air-filled. It is not certain the intratympanic space is air-filled in vivo but size of the airspace in these post-mortem specimens and the flexibility and elaborate structure of the tympanic membrane suggest it is likely. The membrane is a laterally convex 18 X 10 mm ellipse with distinct hyaline and dense regions. It is attached to the tympanic bone by a fibrous annulus and is fused along its midline to a deep, keel-shaped manubrium (Fig. 5). Most of the cartilaginous keel is lost in macerated specimens, which may account for lower membrane area estimates in earlier reports (Fleischer, 1978). Despite its deep convexity, the T. manatus tympanic membrane is structurally similar to membranes of terrestrial mammals and has little in common with the tough, fibrous or calcified membranes of Cetacea.

The multilayered, fibrous anterior region ranges from 500 to 650 μm in thickness and extends from the keel to the tympanic rim. The thinner, posterior half is 200 μm thick and flaccid in post-mortem specimens. Calculated as a simple, two dimensional ellipse, membrane surface area averages 150 mm^2 in our samples. Estimates from three-dimensional reconstructions, which take into account the substantial lateral bulge, average 270 mm^2 . The bimorphic construction and complex shape of the tympanic membrane make estimates of active area difficult, but it can be expected to have a complex, frequency dependent response pattern.

The cochlear fenestrae (ovalis and rotunda) are large but conventionally constructed. The oval window (f. ovalis) is 6.7 mm X 4.0 mm and is located on the anterior face of the periotic; the round window (f. rotunda) occupies a hemispherical aperture (3 mm X 7.5 mm) on the ventro-posterior face of the periotic (Figs. 1, 5).

The ossicular chain is massive, nearly straight, and loosely joined (Fig. 5). The stapes and incus lie on a medial-lateral line posterior to the malleus, so that the two major axes of rotation of the ossicles, based on center of mass, form an angle of approximately 140°. The stapes is the most remarkable of the ossicles. It is columnar, resembling the columella of reptiles or the underdeveloped, monocrucial stapes of trisomic humans (Fig. 5). There is no conventional mammalian, stirrup-like crura although there is a small, continuous foramen which houses a stapedial vessel. The stapedial footplate is medially convex with a surface area of 21.5 mm^2 . It bulges into the vestibule and is attached to the oval window by a narrow flange and weak annular ligament. Chorda tympani, a branch of the facial nerve (cranial nerve VII) runs along the stapes and traverses the middle ear cavity. In T. manatus, chorda tympani has a cross-sectional area of 5.88 mm^2 . In humans, chorda tympani conveys taste from the anterior two-thirds of the tongue and carries parasympathetic preganglionic fibers to the submandibular and sublingual salivary glands. The cross-sectional area of chorda tympani in humans averages 10% of the facial nerve (May, 1986; Schuknecht and Gulya, 1986). In manatees, the combined facial nerve bundle has a cross-section of 19.6 mm^2 where it exits the tympanic cavity. The dimensions of chorda tympani in T. manatus imply it represents nearly one-third the fibers of the facial nerve. If chorda tympani serves the same functions in manatees as in humans, its neural investment suggests taste is an extraordinarily important sensory modality in manatees.

The hooklike incus has two narrow pedicles or arms (Fig. 5). One pedicle extends superiorly to a hemispherical depression in the periotic (Fig. 2). A second, medial pedicle ends in a flat, articular plate that abuts the stapes head (Fig. 5). The incus is wedged, therefore, between the periotic and stapes but is not fused to either. Three facets on the anterior surface articulate with the malleus. The incudo-malleal joint is non-weight-bearing and diarthrotic as in humans; i. e., the articulations are not fused and the ossicles are held in apposition by a membranous sheath.

The malleus is a thick ovoid with a ventrolateral manubrial flange (Fig. 5). In fresh material, the manubrium including its cartilaginous keel is 9 mm deep and 17 mm in length with a flattened ridge to which the tympanic membrane attaches. A large

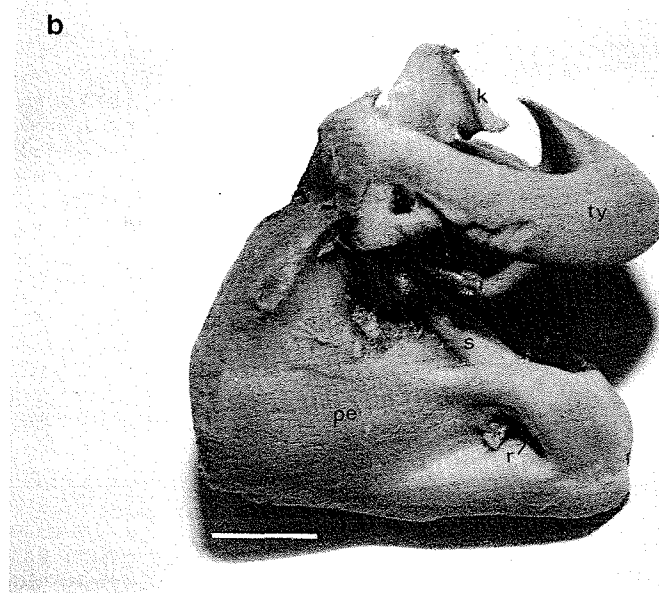
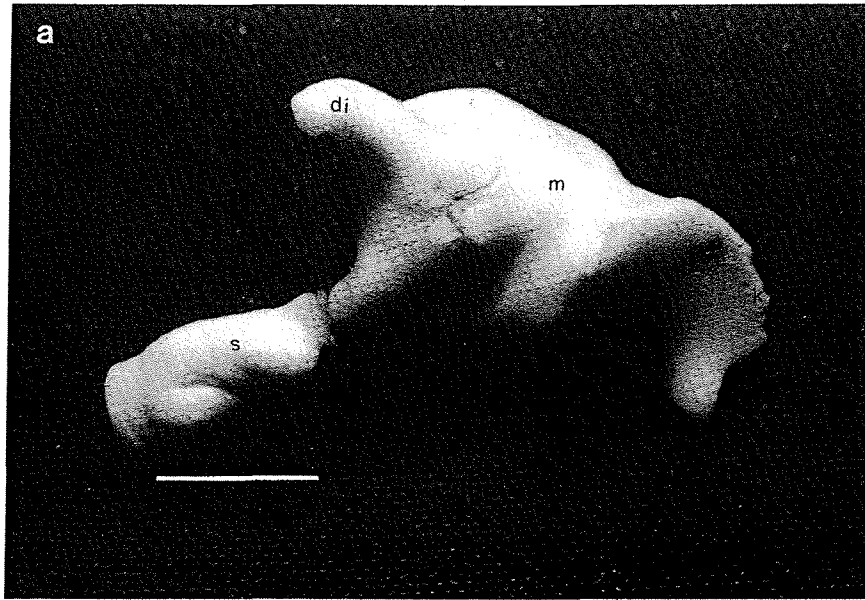


Fig. 5. Ossicular chain and malleal keel. Scale bars represent 10 mm. a) The right ossicular chain has been positioned to duplicate *in vivo* relationships (see Fig. 2). b) The tympanic membrane has been removed to show the malleal keel in a freshly extracted right tympano-periotic. The midline of the tympanic membrane adheres to the flattened ridge of the keel and the rim attaches to the periotic and tympanic. dorsal incudal arm (di); keeled manubrium (k); body of malleus (m); periotic (pe); round window (r); stapes (s); tympanic (ty).

tensor tympani muscle runs from the anterior hypotympanic space to insert on a small lateral malleal pedicle. There is one major pedicle projecting to the epitympanic space. Fleischer (1978) classified the sirenian ossicular chain as a "modified transitional type" based on his observation that the short arm of the incus was fused to the periotic and the malleus to the tympanic, but it is unclear which species he examined. The only fused point in the T. manatus specimens in this study was a weak weld of the anterior surface of the malleus to the tympanic ring, which places the manatee ossicular chain in the freely mobile category.

Inner Ear

The periotic houses the bony and membranous labyrinths of the inner ear which contain the cochlea or auditory organ and the organs of position and acceleration that form the vestibular system.

Vestibular System

Like other obligate aquatic mammals, T. manatus has a vestibular system enclosed within of a large vestibule and poorly developed semicircular canals (Ketten, this volume; Yamada and Yoshizaki, 1959). CT scan resolution is inadequate to determine whether the canals are incomplete or merely exceptionally small. Three-dimensional reconstructions of the entire membranous labyrinth from thin sections are underway to resolve this question.

Cochlea

The cochlea is positioned, as in terrestrial animals, with the central axis parallel to the jaw, the base posterior, and the apex anterior (Fig. 2). This orientation is orthogonal to the cetacean cochlea (Ketten, 1992). Morphometrically, T. manatus cochleae follow the conventional mammalian pattern; i. e., multi-turn equiangular spirals with a length isometric with animal size (Table 2). Cochlear duct structures, however, are poorly developed, particularly at the basal end (Fig. 6). There is no outer osseous spiral lamina. The inner osseous spiral lamina is thin, with a 20 μm thick medial lip and is constructed largely of fibrous tissue intermixed with lightly mineralized bone. The spiral ligament has few fibers, the spiral prominence is small and difficult to differentiate, and the stria vascularis is thin with few cell layers. The spiral limbus is composed of columnar cells with few auditory teeth. The spiral ganglion cells are 20 μm X 10 μm ovoids with 3 - 5 μm diameter nuclei. Spiral ganglion counts were low (<16,000) but this may be the result of postmortem loss. The organ of Corti was not preserved adequately for analysis.

There is little base to apex differentiation in T. manatus basilar membranes (Table 2). At its thickest basal point, the membrane measures 200 μm wide and 7 μm thick. Apically the membrane is 600 μm by 5 μm . Mammalian basilar membranes are tonotopic resonators in which the resonant frequency varies directly with the changing thickness and width of the membrane from base to apex. In general, the greater the variation in thickness and width, the wider the range of frequencies encoded (Hinchcliffe and Pye, 1969; Manley, 1972; West, 1985; Ketten, 1992). The apical basilar membrane of T. manatus is only 3-fold wider and

1.5-fold thinner than the basal end. For comparison, odontocetes, with a functional range of 12 octaves, have 9- to 14-fold base to apex width increases; humans, with a 9-10 octave hearing range, 6-fold increases. Both humans and cetaceans have a 5-fold decrease in thickness. Based on membrane dimensions, manatees have a center frequency similar to humans but a substantially narrower overall range.

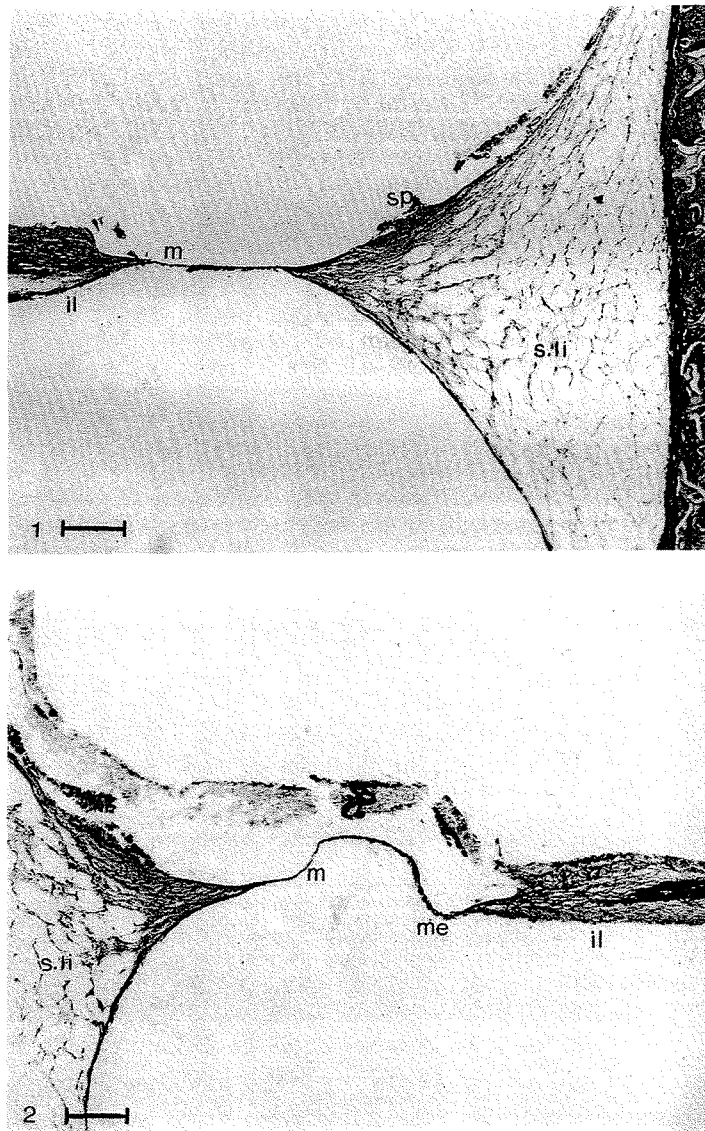


Fig. 6. *Trichechus manatus* cochlear duct. Hemotoxylin and eosin stained 20 μm sections of the 1) basal and 2) apical regions of the cochlear duct of a Florida manatee. Scale bars represent 100 μm . basilar membrane (m); inner ossified spiral lamina (il); mesothelial cells (me); spiral ligament (s.li); spiral prominence (sp).

At the base of the cochlea, the basement membrane is slightly thicker at the lateral edge and a small population of mesothelial cells lines the limbal edge. These cells increase substantially apically and may act to increase the basilar membrane reactive mass at the apex. This would lower the minimal resonant frequency of that cochlear region but is insufficient to push the ear well into the infrasonic range.

CONCLUSIONS

Determining whether *T. manatus* has relatively deficient hearing may be important for understanding human impact on sirenian populations and help explain the substantial hazard boat traffic represents for Florida manatees. Since manatee salvage programs began throughout Florida in 1971, more than 1900 dead manatees have been recovered (Fig. 7). Human activities account, directly or indirectly, for more than half of all deaths over the last fifteen years. Even more important, deaths from collisions doubled in the last decade. In 1991, over 30% of all deaths were associated with watercraft. The danger from collisions may be compounded by the fact that manatees have a low metabolic rate, which is thermally adaptive for a large, tropical mammal, but may be accompanied by slow healing rates (Scholander and Irving, 1941). No direct link has been established between metabolic rate and disease resistance in manatees; however, it is known that manatees become debilitated and die relatively quickly from cold. Manatees that are surrounded by the bacterial soup of Florida's canals may be faced with a compound threat of hypothermia and infection since, coincidentally, winter is also the time when boat traffic is heaviest.

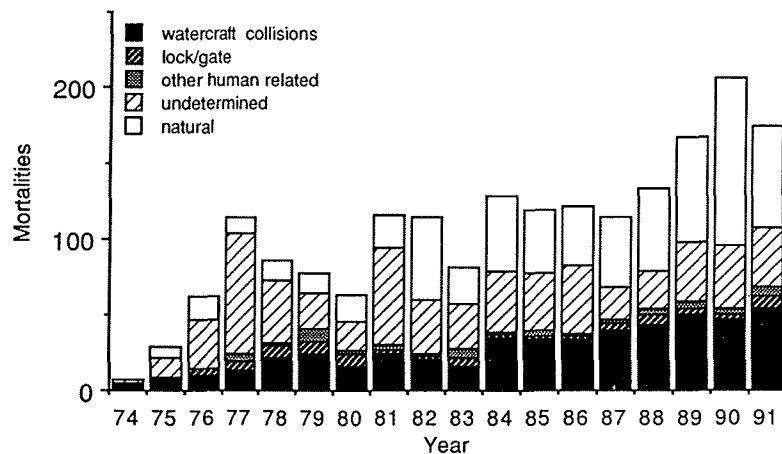


Fig. 7. Manatee mortalities in Florida. (Data excerpted from Ackerman et al., 1992) Mortalities increased exponentially between 1976 and 1991 with the most significant increases in mortalities from collisions and deaths of dependent calves. There was no significant change in deaths related to canal locks or flood control gates. A 1990 peak in natural causes reflects losses during an exceptionally cold winter.

An obvious and recurring question is why don't manatees avoid boats. Peak sound spectra of smaller power boats generally falls below 5 kHz (personal communication, N. Brown, Outboard Motor Corporation, 1991), well within the estimated hearing range of manatees. Nevertheless, many animals carry scars from repeated collisions. Setting aside cognitive issues, the essential question is what level and frequency of sound are required for a manatee to perceive an oncoming boat in time to avoid impact? The answer revolves around two aspects of manatee hearing addressed in this paper: sensitivity and localization.

The principal findings of this study are that Florida manatees have several superficial characteristics that are typical of aquatic mammal ears; however, their inner ear structures imply they lack sensitivity and directionality compared to most mammals. Like Cetacea, manatees have a tympano-periotic complex constructed of dense, compact bone and they possess a specialized, lipid filled structure analogous to the fibro-fatty filling of the mandibular canal of odontocetes. There, the resemblance to the acute, wide-frequency ear of cetaceans ends. First, manatee periotics are intracranial, closely spaced, and attached to bone. The middle ear is large, soft-walled, and has loosely articulated, massive ossicles. Finally, the inner ear structures are poorly developed with little longitudinal variation. All these features are consistent with a low-frequency, non-acute ear.

The highly derived zygomatic process raises important questions about novel sound conduction mechanisms in manatees. This structure is more inflated in Trichechus than in other sirenians and more so in T. manatus and T. senegalensis than in T. inunguis (Domning and Hayek, 1986). There is no obvious non-acoustic function consistent with the extraordinary hypertrophy of the zygomatic process, but there are several acoustic possibilities. The zygomatic-squamosal-periotic relationship is reminiscent of the mandible-tympano-periotic association of Odontoceti. In odontocetes, the fatty tissues filling the mandible are sufficiently close to the density of sea water to be a low impedance channel to the ear (Norris, 1964; Varanasi and Malins, 1971). It is unclear without further analyses whether the oil-filled manatee labyrinth acts like the fat in odontocetes as a preferential sound channel, although, contra Norris (1964), the mandibular canal in the manatee probably does not serve the same function. It is probable, however, that the inflated zygomatic process has unique resonance characteristics compared to the rest of the skull, and it may function as a low frequency channel. This speculation is consistent with observations during evoked potential measurements in the Amazonian manatee, Trichechus inunguis, that the best sensitivities are obtained from stimuli overlying the zygomatic region (Bullock et al., 1980; Klishin et al., 1990).

In terrestrial ears, the middle ear acts as a transformer which counteracts a 30 dB loss from the impedance mismatch between air and the fluid filled cochlea. Middle ears are also "tuned" in that each species has a characteristic middle ear resonance based on the mechanical properties of its middle ear components. This is generally the frequency of best sensitivity for that species. Impedance is least; i. e., middle ear admittances are greatest and energy transmission is most efficient, for sounds near the middle ear resonant frequency.

Mathematically, impedance (Z) is the sum of resistance (R) and reactance (X):

$$Z = \sqrt{R^2 + X^2}$$

Friction is minimal in the middle ear and thus resistance can be discounted. Reactance is determined by mass and stiffness; therefore, species-specific peak sensitivity is determined chiefly by the stiffness and volume of the cavity and stiffness and mass of the ossicular chain. Stiffness (K) and mass (M) act inversely in a frequency (f) dependent system; i. e.:

$$X = (X_M - X_K) \text{ where } f \propto \sqrt{K/M}$$

Increasing stiffness in the system improves the transmission of high frequencies while large ossicular mass and voluminous middle ear cavities favor low frequencies (Webster and Webster, 1975). In ultrasonic species like microchiropteran bats and odontocetes, the ossicles have auxiliary bony struts and fused articulations (Pye, 1972; Sales and Pye, 1974; Ketten and Wart-zok, 1990); low frequency species like heteromyid desert rodents have large middle ears (Webster, 1962; Hinchcliffe and Pye, 1969; Fleischer, 1978). The middle ear system of T. manatus is large and mass dominated, implying it is tuned to low frequencies, but the extreme density of the ossicles adds stiffness. Consequently, transmission of low frequencies will be less efficient and the sharpness of tuning will be decreased. Thus, T. manatus has a characteristically low frequency ear but can be expected to have relatively poor sensitivity.

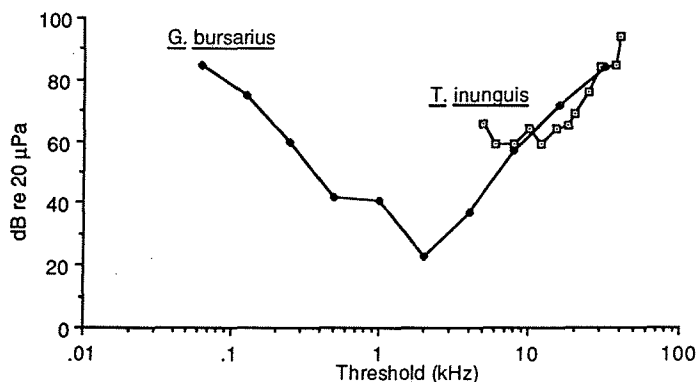


Fig. 8. Audiograms of the pocket gopher and Amazonian manatee. A behavioral audiogram from G. bursarius (Heffner and Heffner, 1990) is plotted with evoked response data for T. inunguis (Popov and Supin, 1990). Behavioural and evoked potentials are not equivalent measures of hearing; however, Dallos et al. (1978) found there is a consistent and predictable relationship between the two families of curves in many mammals. In general, behavioral thresholds are 15-20 dB better than AP thresholds in the most sensitive regions. Two minima, as shown for the manatee, are typical of AP data. These points generally straddle the single minimum obtained with behavioral techniques. Based on these findings, T. inunguis should have a peak sensitivity near 8 kHz at a level of 40 dB.

The cochlea is consistent with the conclusion of a low frequency, non-acute ear. None of the specializations or hypertrophy of cochlear duct structures in cetacean ears is evident. Some features in T. manatus inner ears, like the small difference in basal and apical dimensions of the basilar membrane, suggest a narrow frequency range. Further, the low level development of stria vascularis, spiral ligament, and osseous spiral laminae in the manatee are inconsistent with the extreme cellular development commonly found in cochlear ducts of acute, high frequency animals.

Cochlea and middle ear anatomy imply that T. manatus has a narrow frequency range with a peak sensitivity near or slightly above 5 kHz but with a relatively poor sensitivity overall. This prediction is near the peak frequency range (2 to 5 kHz) of T. manatus vocalizations but below that reported for Trichechus inunguis (Schevill, 1965; Bullock, et al., 1980). Poor sensitivity is consistent with the relative flatness of Trichechus inunguis audiograms (Fig. 8) and with levels reported for Geomys bursarius, the pocket gopher, which Heffner and Heffner (1990) considered vestigial. Popov and Supin (1990), monitoring auditory brain stem responses, determined that Trichechus inunguis had exceptionally high thresholds of 25-30 dB re 1 mPa, a steep high frequency roll-off, and a stimulus rate slower than 100/sec. Heffner and Heffner (1990) found Geomys could not localize either isolated 100 msec noise bursts or trains of 100 msec bursts. Based on anatomy, T. manatus will perform similarly.

Given the extraordinary auditory abilities of most marine mammals, is the conclusion that sirenians have remarkably poor hearing tenable? Specifically, are their behavior and evolutionary history consistent with the development of such an ear? The terrestrial condylarth ancestor of Sirenia is likely to have had a reasonably acute ear, and there is no indication that land dwelling ungulate descendants of this group are auditorially deficient. Did environmental pressures that influenced the evolution of Sirenia differ in some important way from those of their terrestrial counterparts and from other marine mammals that may relate to the apparent differences in hearing?

Sirenians first appear in the fossil record with the early Eocene genus Prorastomus, which is structurally close to the common ancestor of the entire order. Their closest affinities are with proboscideans and tethytheres, and, like Cetacea, they arose from unknown ungulate stock in the broad sense (Thewissen and Domning, in press). Based on their advanced grade of bone density, prorastomids were already adapted to at least a partially aquatic lifestyle by the early to middle Eocene (Savage, et al., in preparation). A radiation in the later Eocene led to modern dugongids and trichechids (Barnes et al., 1985). The pan-Tethyan marine angiosperms or seagrasses (Hydrocharitaceae and Potamogetonaceae), which remain important components of modern sirenian diets, were present in the Eocene (Eva, 1980), and probably provided the substrate for early establishment of the sirenian morphotype (Domning et al., 1982). With the exception of Stellar's sea cow (Hydrodalmis), sirenians have remained tropical animals dependent on sea grasses and other aquatic angiosperms from the Eocene onward (Domning, 1977, 1981).

The tympano-periotic complexes of extinct Sirenia are remarkably similar to that of modern T. manatus. All have a columnar stapes, large middle ear space, and a malleal shape consistent with a heavy keel. Keeling is an important feature of fully aquatic auditory systems. Large, everted (laterally convex) tympanic membranes are common in obligate aquatic mammals but are relatively rare in non-aquatic species. In Cetacea, everted tympanic membranes take the form of either a dense, fibrous "glove finger", as found in mysticetes, or a highly derived, calcified tympanic conus, as in odontocetes. The middle ears of fossil Sirenia are therefore consistent with fully aquatic animals. More important, the structural commonalities between fossil and modern manatee ears imply that few functional changes have occurred in the sirenian auditory periphery since the Eocene.

West Indian manatees are docile, slow grazers that live in fresh or estuarine environments. The Florida manatee averages 400 kg in weight and 3 meters in length but can exceed 4 meters (Odell et al., 1981; Ridgway, 1972). They lumber through the water at an average speed of 3 km/hr and seldom attain speeds over 20 km/hr even when alarmed (Reynolds, 1981). For most mammals, sounds related to predators, mates, and food sources are important selection pressures. T. manatus evolved in a radically different acoustic world from most mammals. If humans are discounted, Florida manatees have virtually no natural predators, and it is unlikely they use sound to detect food. T. manatus evolved in an acoustically complex shallow water environment with high background noise. If subtle acoustic cues carried little or no survival advantage, whatever level of sensitivity that existed in early ancestors may have been lost. Consequently, manatees may represent a unique exception to the convention that audition is the most significant and developed of marine mammal senses.

How then does the manatee sense its world? The dimensions of chorda tympani hint that gustation or tactition may be important, and a highly developed chemosensory apparatus would be a useful adaptation for an aquatic herbivore. Exceptional tactile abilities are now well documented for pinnipeds (Denhardt, 1990; Kastelein, 1991). If fiber distributions in this study are any indication, similar investigations with sirenians would be worthwhile.

Concerning future acoustic research, these anatomical results are far from definitive. Behavioral experiments that test these conclusions and determine range and sensitivity in all species of Sirenia are clearly warranted. Dugongs in particular are of interest because they are a marine species and inhabit a relatively hazardous environment compared to freshwater trichechids. Dugong ears may be consequently more sensitive than those of manatees.

In summary, T. manatus has an essentially aquatic but non-acute ear. The preliminary anatomical findings suggest this is a low frequency ear with a relatively narrow range, poor sensitivity, and poor localization ability. Evolutionarily, trichechids developed in a relatively stable environment with few predators. As a result, the devastating effect of present human activities on West Indian manatee populations may be the result of the manatee being unable, literally, to perceive the threat.

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