

11th European Conference on Underwater Acoustics 2012 (ECUA 2012)
Proceedings of the Institute of Acoustics Volume 34 Pt.3, pp. 572-577. (2012)
Institute of Acoustics (IOA) ISBN: 978-1-62276-192-0; ISSN: 1467-6095

CRITICAL CRANIAL AND COCHLEAR STRUCTURES IN ECHOLOCATORS

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1 INTRODUCTION

Although microchiropteran bats (largely insectivorous predators) and odontocete cetaceans (toothed whales which prey on fish and invertebrates) have different target species and operate in radically different media, both have sophisticated sonar capabilities and evident similarities in their ability to produce, detect and analyze ultrasonic signals.

We expect because of the similarity of tasks and information that odontocetes and microchiropteran bats obtain acoustically from their environments that there are some commonalities in their fundamental biosonar reception and processing mechanisms but also differences related to potentially alternative echolocation strategies and especially to media dependent elements of their auditory system structure and analyses and related behaviours. These include features particularly related to wavelength and speed of sound in each medium with habitat and prey parameters that evolutionarily shaped hearing abilities. These are manifested in differences in the structure and peak spectra of echolocation signals and their representation and in the features that have been shown to be critical for analysis at the peripheral and central levels. In addition, there are niche and task dependent signal elements, such as detection in clutter in bats (1) and the structural variations between Type I and Type II ears associated with upper and lower ultrasonic signal dependence (2,3) that impose critical differences for the extraction of features in air vs water.

The objective of the present study was to understand the similarities and differences of dolphin and bat inner ear topography and morphometrics related to these issues. This paper compares similarities and differences of pinna, middle ear, and cochlear architecture and the implications for ultrasonic encoding and acuity amongst these groups.

2 METHODS

The heads and inner ears of 11 specimens from four species were examined via submillimeter imaging on a conventional clinical computerized tomographic (CT) scanner and with micro CT on an analytical,

fixed head scanner. All scans were performed on post mortem specimens of intact heads and extracted temporal bones. The dolphin and porpoise heads were scanned fresh; i.e., 1 to 24 hours post mortem and were kept chilled at 4 degrees centigrade until scanning. The bat heads and the extracted ears were fixed in formalin and scanned in their solutions. The specimens and the typical echolocation signal parameters they employ are as follows:

Phocoena phocoena (harbour porpoise) peak echolocation frequency approximately 100-110 kHz
n = 5 intact heads adult animal weight 55-78 kg, cochlear length avg 22 mm.

Tursiops truncatus (bottlenosed dolphin); Peak frequency approximately 60-70 kHz
n = 3, 150-650 kg, cochlear length avg 40 mm.

Eptesicus fuscus (big brown bat); Peak range 20 to 110 kHz
n = 2, 14-21 gms, cochlear length avg 9 mm.

Pipistrellus abramus (Japanese pipistrelle); Peak frequency 43 - 52 kHz
n = 1, 4-7 gms, cochlear length avg 7 mm.

For submillimeter scans, heads and ears were examined with a Siemens Volume Zoom at the Woods Hole Oceanographic Institution Computerized Scanning and Imaging Facility (<http://csi.whoi.edu>) using an imaging protocol of 0.5 mm acquisitions. 0.5 mm table speed. KV and effective mAS varied according to the mass of tissue being imaged. Data were acquired with an ultra-high resolution (U90 and U95 head) kernel, 200 FOV for whole heads and 50 FOV for extracted ears. Images were formatted at 0.1 mm slice thickness in the axial plane, and multiplanar reconstructions were produced in the sagittal and coronal planes. Data base magnifications from the raw acquisition data were employed for imaging of the *in situ* ear studies.

For extracted ears, the same parameters were employed and each ear was scanned in a position approximating a prone, anterior first section view for the axial, i.e., short axis, cross-sectional slice images. This orientation gives the best approximation of a mid-modiolar cochlear projection. All images were produced with isotropic 100 micron voxels. Both bone and soft tissue window images were produced for all orientations, and all data and images were archived as both raw acquisition data and formatted image data files. Reconstructions from the Volume Zoom DICOM image data were produced using the programs noted below and also with Siemens proprietary VRT software.

For the microCT studies, the images were obtained on an X-Tek Micro CT at the Harvard University Center for Nano Systems. For these studies, depending upon the dimensions and mass of the tissue undergoing examination, a Molybdenum or Tungsten anode was used with varying parameters for voltage and exposure times. The X-Tek uses a fixed head with a rotating specimen plate. For these studies, 2000-4000 radial projections were obtained for each study that were then reformatted into transaxial 2D contiguous sections with an isotropic voxel of 11 to 40 microns according to the specimen examined. CT Pro and VG Studio Max software programs on a 64-bit PC were employed to provide the sectional image sets in TIFF formats from the radial projection data.

All image sets were secondarily processed and reconstructed into 3D still and video sequences using Amira 5.4 and Osirix software on 64 bit PC and Mac platforms. Examples of the level of detail that can be obtained with these systems are shown in Figure 1.

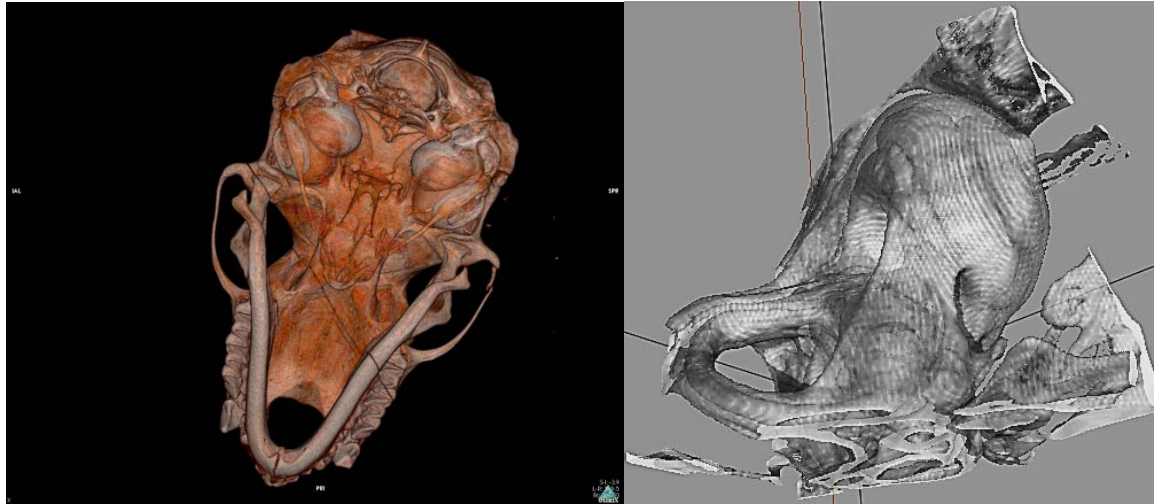


Figure 1. Left: The skull of a pipistrellid bat is shown in ventral view in an OSIRIX reconstruction from a microCT dataset. Only the bony elements are shown, based on auto-segmentation for bony attenuations. The majority of the bone has been set to display with a translucency that reveals the cochlear canals (red) within the bullae. The specimen measures 12 mm in width and 20 mm in length. Right: The cochlear spiral of the right ear is seen in dorsal view showing the 2.25 turns from an aspect along the mid-basal turn. One of the semi-circular canals is shown complete with the bulbous ampulla clearly visualized at its base. The others have been digitally “sliced away” to facilitate the cochlear view. This cochlea is less than 7 mm in total length and less than 2.5 mm in diameter.

3 RESULTS

3.1 Land and Sea Pinnae

As previously reported [4,5], whole head scan images and reconstructions show that odontocetes have characteristic fat lobes aligned with the mandible that are pinna analogues (Fig. 2). The fats in these lobes have distinct chemical make-ups that differ significantly from blubber or other fatty mammalian tissues [6]. They are not altered with emaciation, as is blubber, in either chemical constituents nor in conformation, suggesting that their maintenance of density, volume and shape are important for their functions. The shape and dimensions of these “fatty pinnae” are consistent also with many of the forms seen in bats, and the lobular configurations and distributions along the major axes mirror those of bats and have similar wavelength functional relationships [7,8].

The shape and dimensions of these fats, with respect to wavelength in air vs. water are similar to the range of pinna shapes and gains for peak spectra seen in bats [7,8]. They appear, for the longest lobes, to mimic the typical bi-lobed, elongated canal of bats [8], and to be well suited to provide a 20 dB gain particularly for the lower, midrange communication signals of the odontocetes, just as has been shown for bats [4]. Using the formulae noted by Neuweiler [7] for the estimation of optimal wavelength and wave number and radius of aperture, (ka), the dolphin with an $L = 10$ cm has a value of 0.628 equivalent to a 3 kHz peak in water. Similarly, the porpoise with an $L = 7$ cm calculates to 0.439 or approximately ~ 4.5 kHz.

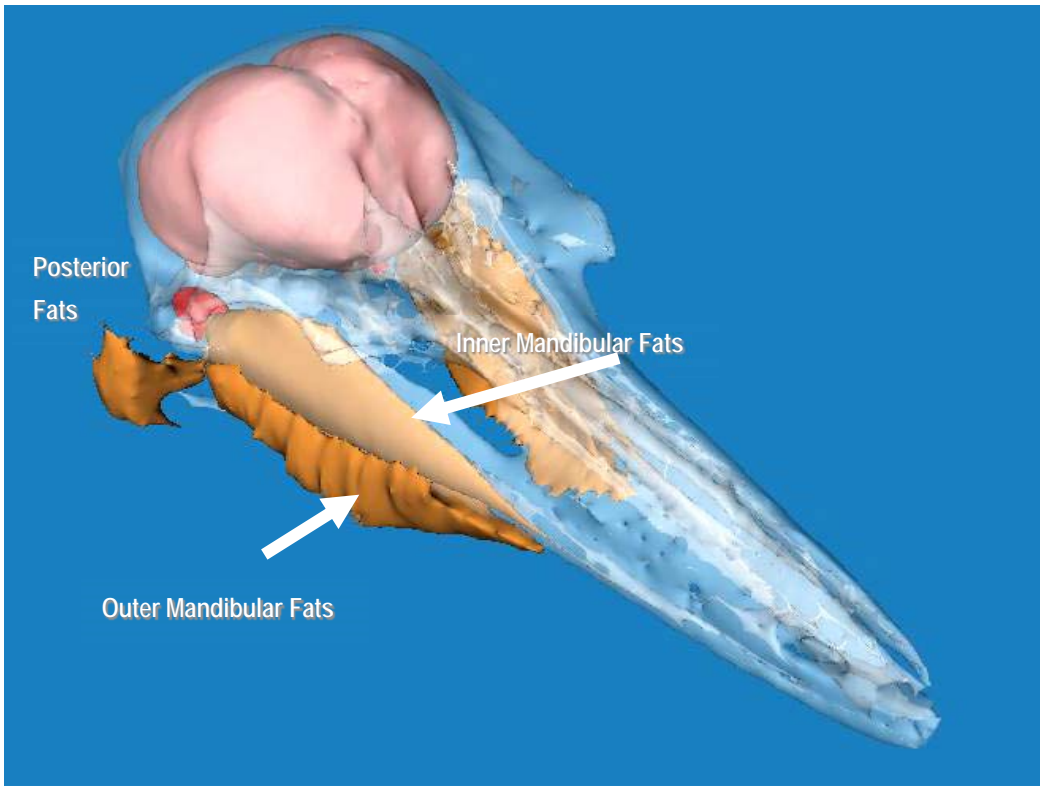


Figure 2. Pinnal analogues formed of fat bodies aligned with the lower jaw. There are three distinct lobes on each side: an external or outer mandibular lobe, an intramandibular lobe and a latero-posterior lobe. All three connect together at their posterior margin and converge forming a direct channel that contacts the tympanic membrane at the lateral edge of the tympano-periotic bone.

3.2 Inner Ear Morphometrics and Cochlear Convergences

Cochlear ear anatomy amongst the bats and cetaceans was fundamentally similar. Data for cochlear measures, including calculations of length and curvature, were obtained following the methods described previously for cochlear morphometric procedures [6,7]. All species examined had substantial outer osseus laminae running 20% at a minimum to over 50% of the basilar membrane length. All had similar basal thickness and width ratios, in some cases verging upon square cross-sections but each differed in the apical regions, implying a narrower octave range in the bat species examined compared to the odontocetes.

There were also unusual fenestral placements for the stapedial input compared to most mammals. Although the two groups varied in exact placement, neither exhibited the relatively simple single curve of the hook that is commonly assumed for mammals and neither had the stapes input located at the base of the single initial basal curve. The data for each of the examined species can be summarized as follows and video and still images demonstrating the cochlear topography in these species can be viewed at <http://csi.who.edu> :

Eptesicus fuscus (Big Brown Bat, Fig. 3)
 Data obtained from Micro CT at 17 micron voxel
 2.25 turns Basilar membrane Length 8.7 mm

Basal width 40 microns Apical width 180 microns
Post-hook Basal turn stapedial input

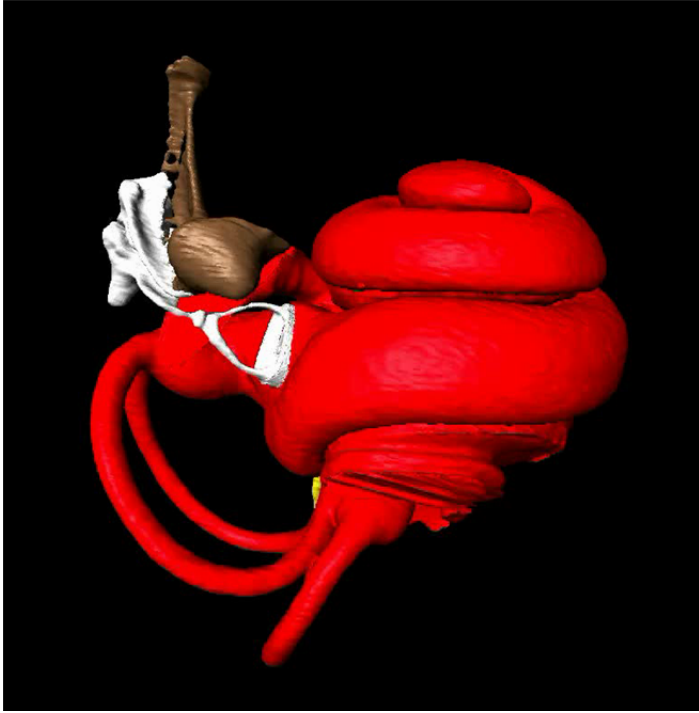


Figure 3. Big Brown Bat inner ear labyrinth with ossicular chain. (Scale bar = 1 mm)

Pipistrellus abramus (Japanese Pipistrelle, Fig. 4)
Data obtained from Micro CT at 11.6 micron voxel
2.25 turns Basilar membrane Length 6.8 mm
Post-hook Basal turn stapedial input
Intracochlear measures not completed

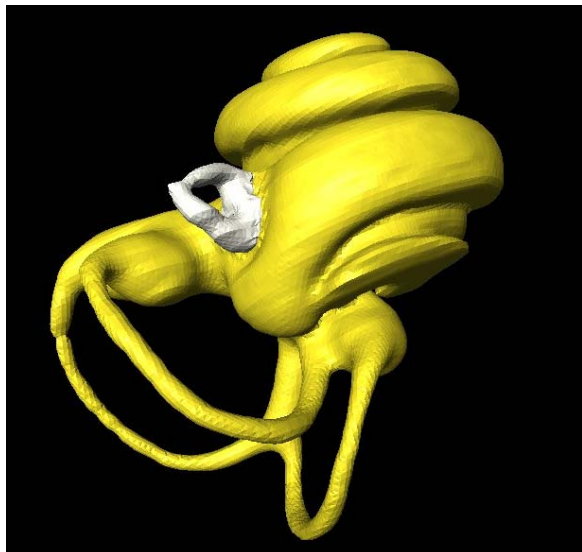


Figure 4. Japanese Pipistrelle inner ear labyrinth with stapes. (Scale bar = 1 mm)

Phocoena phocoena (Harbour Porpoise)

Data obtained from Micro CT at 18 micron voxel
1.5 turns Basilar membrane Length Average 22.5 mm
Basal width 30 microns Apical width 290 microns
Double hook and Vestibule stapedial input

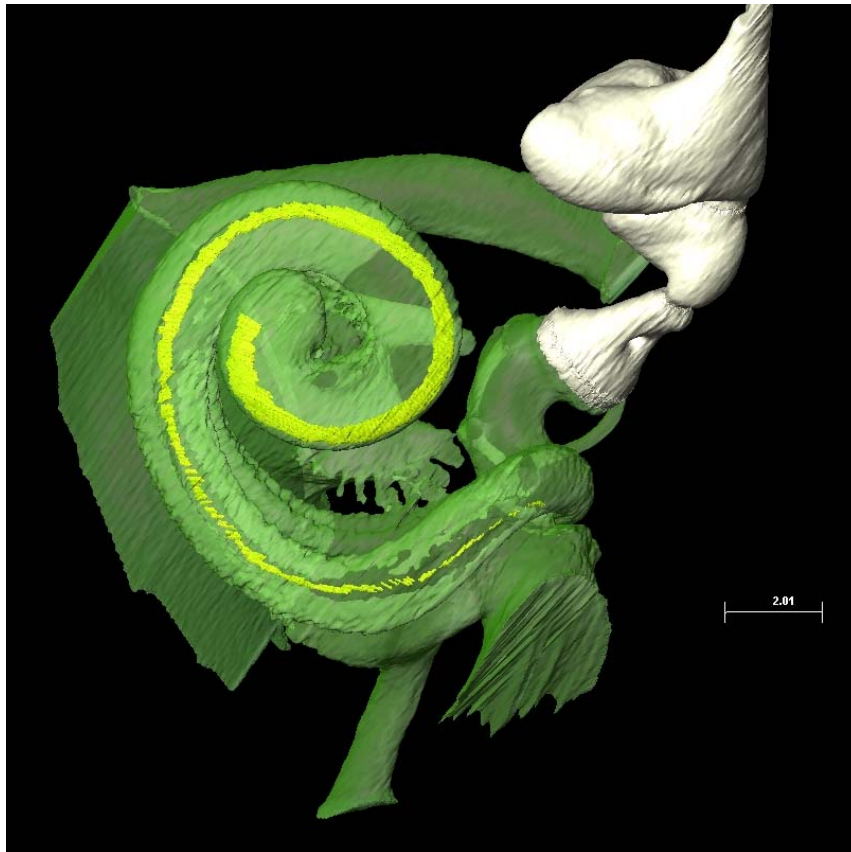


Figure 5. Harbor porpoise inner ear labyrinth with ossicular chain. Labyrinthine fluid compartments (green) are translucent to show the basilar membrane (yellow) (Scale bar = 2 mm)

Tursiops truncatus (Bottlenosed Dolphin)

Data obtained from submillimeter UHRCT at 100 micron voxel
2.25 turns Basilar membrane Length Average 38.9 mm
Basal width 40 microns Apical width 380 microns
Extended hook with Peri-vestibular stapedial input

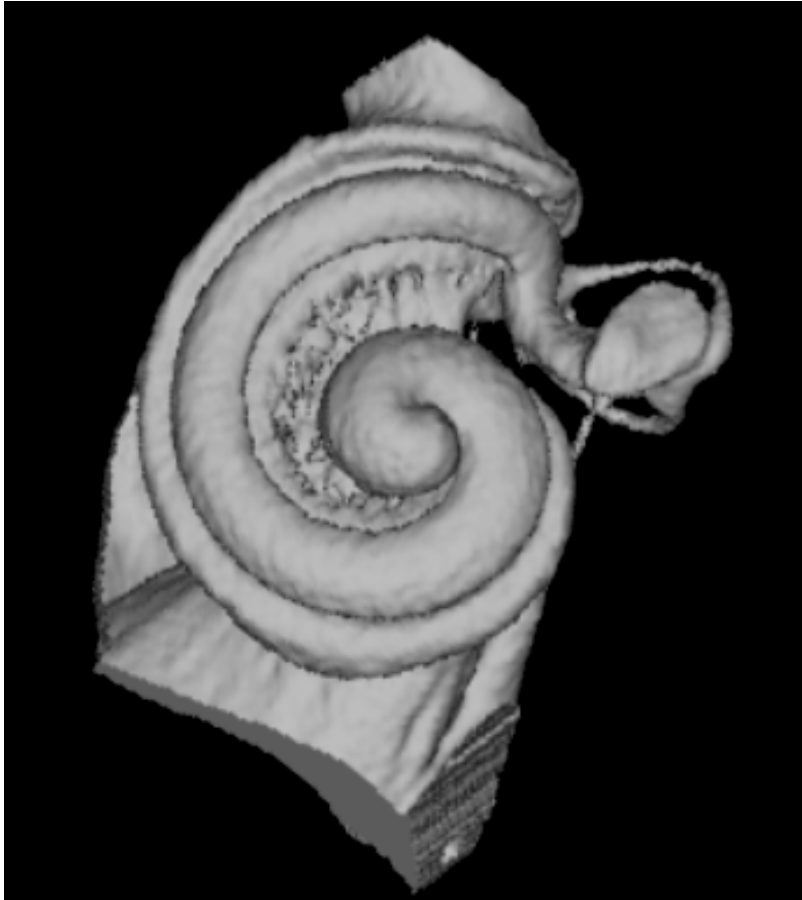


Figure 6. Bottlenosed Dolphin Inner ear labyrinth with characteristic indentation in the scalae outer wall coincident with the outer osseous lamina. The reticulate fiber bundles are visible radiating out from the modiolus to the cordlike band of the collective ganglionic cell bodies that parallels the cochlear scalae. The oval window is shown at the upper left as an ovoid plate. Note the attenuated, narrow, small radii of the semi-circular canals partially visible behind the hook region.

Specialist ears are present in both groups, suggesting that like some CF-CM bats, one or more odontocete species have cochleae with specialized basilar membrane “foveal” regions. Like the hipposiderid bats [10], the harbour porpoise possesses a basilar membrane variant very similar to that of the horseshoe bat with thickened, nearly constant depth areas that possess both longitudinal and transverse or radial fibers that act as stiffening agents and relatively dense neural inputs. These areas, dubbed “foveal” regions, are singularly devoted to the peak spectra of their echolocation signals (100-110 kHz for the porpoise; 80-86 kHz for the bat) in these species and thus represent a stretching of the frequency map that occurs in the basal portion of the cochlea. It is notable also that these are species with more complex and displaced stapedial inputs.

4 Conclusions

Cochlear specializations are similar in both groups and are primarily linked to peak spectra of the echolocation signals, with, in some species, similarly configured, expanded frequency representation. One speculation is that the stapedial placements and uniform, robust basilar membrane structure may

enhance tuning in adjacent ear segments by generating standing wave phenomena. In the Vespertilionid bats, the stapedial locus may result in a bi-directional flow. In the phocoenids, the double hook may serve to attenuate low frequency penetration and thus reduce LF sensitivity while stretching the HF map. The delphinid odontocetes more closely but imperfectly resemble the terrestrial generalist ear, with a Peri-vestibular Input and diminished double hook. In all species examined, the cochlear canal curvatures are consistent with the highest frequency terrestrial species [10].

ACKNOWLEDGEMENTS

This work was supported through grants to D.R. Ketten by CNO/N45-US Navy Environmental Division and the Office of Naval Research

REFERENCES

1. Stamper, S. A., Simmons, J. A., DeLong, C. M., and Bragg, R. (2008). Detection of targets co-localized in clutter by echolocating big brown bats (*Eptesicus fuscus*). *J. Acoust. Soc. Am*, 124, 667-673.(2008)
4. Ketten, D.R. and D. Wartzok Three-dimensional reconstructions of the dolphin ear. In: *Sensory Abilities of Cetaceans: Field and Laboratory Evidence*, J. Thomas and R. Kastelein (eds.), Plenum Press, Proc. NATO ASI Ser. A, Life Sci., vol. 196 pp. 81-105 (1990)
4. Wartzok, D. and D.R. Ketten *Marine Mammal Sensory Systems*. In: *Biology of Marine Mammals*. J. Reynolds and S. Rommel (eds.), Smithsonian Institution Press, pp. 117-175. (1999)
4. Ketten, D.R. *Structure and Function in Whale Ears*, *Bioacoustics*, vol. 8, no. 1, pp. 103-136. (1997)
5. Ketten, D.R. *Cetacean Ears*. In: *Hearing by Whales and Dolphins*. W. Au, R. Fay, and A. Popper (eds.), SHAR Series for Auditory Research, Springer-Verlag, pp. 43-108.(2000)
6. Koopman, H.N., S.M. Budge, D.R. Ketten, and S.J. Iverson. The topographical distribution of lipids inside the mandibular fat bodies of odontocetes: Remarkable complexity and consistency. *IEEE Journal of Oceanic Engineering*, vol. 31(1), pp. 95-106. (2000)
7. Neuweiler, G. *Biology of Bats*, Oxford University Press, 320 pp. (2000)
8. Ma, J. and R. Müller A method for characterizing the biodiversity in bat pinnae as a basis for engineering analysis *Bioinspir. Biomim.* 6 026008 [doi:10.1088/1748-3182/6/2/026008](https://doi.org/10.1088/1748-3182/6/2/026008) (2011)
9. Ketten, D.R., Skinner, M., Wang, G., Vannier, M., Gates, and Neely, G. *In vivo Measures of Cochlear Length and Insertion Depths of Nucleus® Cochlear Implant Electrode Arrays*. *Annals of Otology and Laryngology*, vol. 107, no. 11, pp. 1-16 (1998)
10. Manoussaki, D., Chadwick, R.S, Ketten, D.R., Arruda, J., Dimitriadis, D., O'Malley, J.T. The Influence of Cochlear Shape on Low-Frequency Hearing. *Proc. Natl. Acad. Sci*, Vol. 105(6): 6162-6166. (2008)
11. Bruns V and Schmieszek E Cochlear innervation in the greater horseshoe bat: Demonstration of an acoustic fovea. *Hearing Res* 3:27-43. (1980)