

Morpho-functional parameters of the inner ear in *Ctenomys talarum*; Rodentia, Ctenomyidae

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Abstract. We studied the inner ear of *Ctenomys talarum*, a small solitary subterranean rodent distributed in the southern region of Buenos Aires Province (Argentina) using standard staining techniques. The inner ear of this subterranean rodent is characterized by a long basilar membrane, a higher density of cochlear receptors in the apical region of the basilar membrane and a gradual increment of the width of the triad of outer hair cells from the base towards the apex. These anatomical features of the cochlea of *C. talarum* can be interpreted as biomechanical specializations to enhance low-frequency sound reception.

Key words: hearing, cochlea, subterranean rodents

Introduction

Subterranean mammals spend most of their lives in dark and microclimatically stable tunnels, where also foraging, mating and territorial defense take place (N e v o 1979, 1999, R e i c h m a n & S m i t h 1989). This monotonous and simple sensory environment of underground burrows, deprived of most stimuli available aboveground, led to morpho-functional sensory specializations which involve both regression and hypertrophy (B u r d a et al. 1990). Accordingly, sensory ecology of subterranean mammals has attracted considerable attention and the research has experienced a boom within the past fifteen years.

Blind subterranean mammals are expected to rely mostly on audition and olfaction for alertness and communication. Probably the most broadly and deeply studied sensory modality in subterranean mammals has become the acoustic system. It has been shown that vocalization parameters in all subterranean rodents studied to date are shifted towards a low-frequency range (H e t h et al. 1988, P e p p e r et al. 1991, C r e d n e r et al. 1997, F r a n c e s c o l i 1999, V e i t l et al. 2000, S c h l e i c h & B u s c h 2002). This convergence in physical characteristics of vocalizations between phylogenetically unrelated subterranean rodents seems to be the result of adaptation to acoustic communication in the underground tunnel ecotope (B u r d a et al. 1990), where low-frequency sounds (around 100–800 Hz) are transmitted more efficiently than sounds of higher frequencies (H e t h et al. 1986, S i m o n e L a n g e, personal communication). Besides this match with the best transmission frequency in subterranean environments, the spectral characteristics of vocalizations are congruent with hearing being tuned to low frequencies (range of highest sensitivity: 0.5–1 kHz) in all the subterranean species studied (B r u n s et al. 1988, M ü l l e r & B u r d a 1989, H e f f n e r & H e f f n e r 1990, 1992, 1993, K ö s s l et al. 1996, B r ü c k m a n n & B u r d a 1997, B e g a l l et al. 2004). However, the audiological

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studies reveal rather poor hearing sensitivity, leading to claims by some scholars that hearing in subterranean rodents is degenerated (Heffner & Heffner 1992, 1993).

The low-frequency tuning of hearing in subterranean rodents is supposed to be related to the anatomical features recorded in their middle and inner ears. The middle ears of subterranean rodents are characterized by many common traits, like a large eardrum without a pars flaccida, loose or no connection between the malleus and the tympanic bone, rather parallel position of the malleolar manubrium and incudal crus longum, and reduced or missing middle ear muscles. Some of these features are expected to enhance the middle ear's sensitivity to low frequency sounds (cf., Fleischer 1973, Burda et al. 1992, von Mayer et al. 1995, Wilkins et al. 1999, Mason 2001, 2004, Schleich & Busch 2004, Lange & Burda, in press). It should be noted, however, that they are not restricted to subterranean or fossorial rodents, since they were frequently found among non-subterranean caviomorph rodents and might represent plesiomorphic traits (Mason 2004). Low sensitivity of hearing is expected to be partly due to reduced biomechanical performance of the middle ear transmission chain mainly due to enlarged stapes footplate relative to ear eardrum area and enlarged incus relative to the malleus.

Contrasting with a plethora of publications on vocalization, hearing, and middle ear parameters, the inner ear has been only sporadically studied in subterranean rodents. The cochlear structure has been examined in detail in three species of subterranean rodents only, *Nannospalax ehrenbergi* (Bruns et al. 1988, Burda et al. 1989), *Fukomys anselli* (designated originally as *Cryptomys hottentotus*, Müller et al. 1992) and *Spalacopus cyanus* (Begall & Burda 2006), while Pye (1977) provided some basic data of the structure of the cochlea and the basilar membrane of *Ctenomys talarum*.

The cochlea of the Eurasian blind mole-rat *N. ehrenbergi* represents a unique organization among mammals and several features of its anatomy may be considered correlates of the low-frequency tuning of hearing (Bruns et al. 1988, Burda et al. 1989, Nevio 1999). The cochlea of the African mole rat *F. anselli* also differs from the generalized plan for the mammalian cochlea, although it presents several features in common with the cochlea of *Nannospalax* (Müller et al. 1992). A marked specialization, called "acoustic fovea", for low-frequency hearing was found in the cochlea of this subterranean rodent (Müller et al. 1992), although an enhanced frequency tuning, which is considered by some authors (e.g. Kössl et al. 1996) to be a feature of acoustic foveas, was absent. The shape and higher number of turns of the cochlea of the South American coruro, *Spalacopus cyanus*, together with a long basilar membrane, are both typical features of the inner ears of subterranean and/or hystricognath rodents. There are three peaks of higher inner hair cell densities along the organ of Corti that are supposed to correlate with tuning of hearing to three different frequency regions reflecting the specific mode of life of these social subterranean rodents with (infrequent) bouts of aboveground activities (Begall & Burda 2006).

In this study we examine the cochlea of another subterranean rodent, the tuco-tuco (*Ctenomys talarum*), adding more information to Pye's preliminary data on *C. talarum*' inner ear, and becoming thus the fourth genus and species of subterranean rodents for which detailed information on the cochlear morphology becomes available. The tuco-tucos (*Ctenomys*, Ctenomyidae) are caviomorph rodents distributed in the southern cone of South America (Reig et al. 1990). *Ctenomys talarum* is a small (120 g and 160 g body mass for females and males, respectively) subterranean rodent that lives solitarily in a system of closed galleries parallel to the soil surface (Busch et al. 1989). *C. talarum* has been subject to several behavioral studies (Vassallo 1992, Zenuto 1999, Zenuto et

al. 2001). Recently, its vocal repertoire was described (S c h l e i c h & B u s c h 2002). Similarly to other species of subterranean rodents studied, *C. talarum* vocalizes at low and medium frequencies (0.2–12 kHz), with the main energy components being within the low frequency range (0.2–0.4 kHz). The middle ear of *C. talarum* displays anatomical modifications that seem to enhance low-frequency sound transmission (S c h l e i c h & B u s c h 2004). Regarding the inner ear, and as explained before, until now only one study presented some preliminary data about the structure of the cochlea of *C. talarum* (P y e 1977).

The main objective of this work was to describe the cochlear anatomy of *C. talarum*, analyzing those structures and parameters suspected to have significant impact on the hearing capabilities. In this way, we complement and extend our knowledge of the auditory system in a species, in which other aspects of the ear and acoustic communication have been already studied. Even more important is the fact that we provide data on the inner ear for a further species of subterranean mammals. Only the availability of comparative data obtained by the study of a broader spectrum of distantly related species living in a similar sensory environment enables us to assess which morphological aspects of sensory organs can be considered convergent adaptations and thus morpho-functional specializations. In the case of the inner ear, a comparative approach can thus also help to enlighten cochlear mechanics, which is still enigmatic in many aspects (A s v o n B é k é s y (1974) put it: "... we may expect that the physical laws served as guidelines for the evolution of the structures and functions of the middle and inner ear."). Due to the observed convergence in vocalization parameters between *C. talarum* and other unrelated animals living in an acoustically similar environment, and to the more efficient transmission of low-frequency sounds in underground burrows, we expect the cochlea of *C. talarum* to show anatomic modifications that keep or enhance hearing abilities at lower frequencies.

Materials and Methods

Adults of both sexes (4 males and 4 females) of the tuco-tuco, *Ctenomys talarum* (Rodentia: Ctenomyidae), were captured in Mar de Cobo (37° 45' S, 57° 56' W, Buenos Aires Province, Argentina) with live traps and transported to the laboratory where they were killed by deep final narcosis and decapitated. The heads were immersed in 10% solution of formaldehyde for at least three weeks. Then the cochleae (from 8 right and 5 left ears) were processed under the stereoscopic microscope (Olympus Type SZH10 Research Stereo, with drawing tube, max. 70x magnification) using ophthalmologic scalpels and fine watchmaker's tweezers to standard surface specimens of the cochlear partition. The cochleae were opened at their cupula (apex), and the cochlear duct was stained with toluidine blue and Ehrlich's hematoxylin. The Reissner's and tectorial membranes were removed using tweezers and fine water stream, and the cochlear partition (basilar membrane with the organ of Corti) was separated from its anchoring at the lateral cochlear wall and at the modiolus, and mounted in glycerol for light microscopic examination.

The organs of Corti were analyzed under a light microscope (Olympus Type AH-3) with a magnification of at least 400x. Measurements were taken and cells were counted from surface specimens in each visual field along the whole cochlear partition by means of image analysis software (AnalySIS, SIS). The length of the basilar membrane corresponds here to the length of the Corti organ along and above the middle of the roof of the Corti tunnel. The

density of hair cells was determined indirectly from the length of a segment occupied by ten cells in a particular row in each visual field. Outer and inner hair cells were counted and the width of the triad of outer hair cells (width of the strip occupied by cuticular plates of three parallel rows of outer hair cells) and the width of the roof of the Corti tunnel (projected upon the cuticular plates of inner pillar cells) were measured. Each cochlear partition was divided into 10 segments of equal length (= 10% of the total length). All measurements taken within each segment of all examined ears were then pooled together, and mean values and standard deviations (given here as \pm) were calculated.

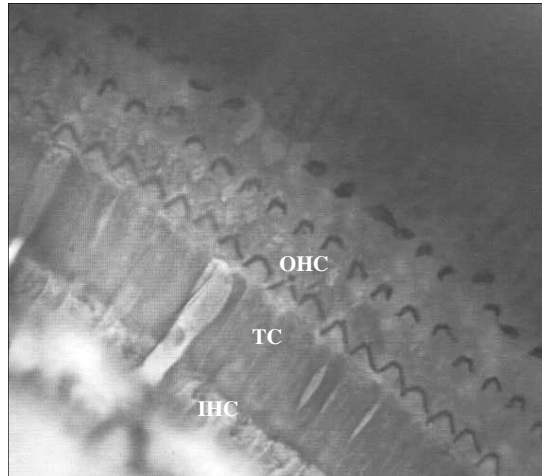


Fig. 1. Photomicrograph showing the reticular lamina of the organ of Corti of *Ctenomys talarum* from the middle region of the basilar membrane. OHC = triad of outer hair cells, IHC = inner hair cells, TC = tunnel of Corti.

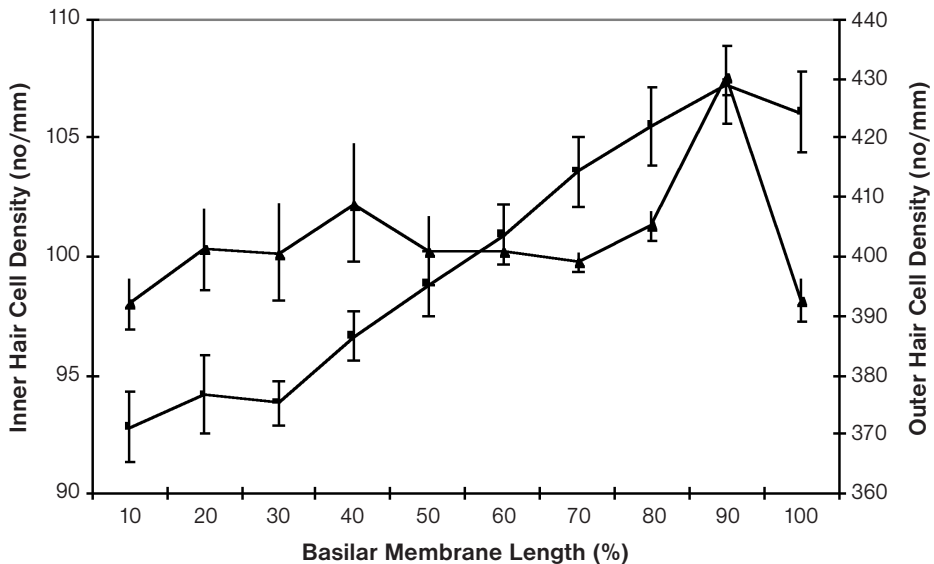


Fig. 2. Distribution of mean (\pm SEM) inner (triangles) and outer (squares) hair cell densities along the basilar membrane of *Ctenomys talarum*.

Results

The cochlea was cylindrical and coiled into 3.25 turns. Whereas the cochlear wall was thin, the bony wall of the modiolus was thick, though the modiolus itself was rather fragile and broke easily during preparation. The basilar membrane was firmly attached to a prominent primary spiral lamina. The length of the basilar membrane amounted to $10.58 (\pm 1.22)$ mm. The mean density of outer hair cells (OHC) was $400 (\pm 22)$ cells per mm of the length of the organ of Corti, whereas the density of inner hair cells (IHC) was $101 (\pm 3)$ cells per mm (Fig. 1). However, there were differences in the densities of outer and inner hair cells along the basilar membrane (Fig. 2). Outer hair cell densities tended to increase towards the apex, reaching

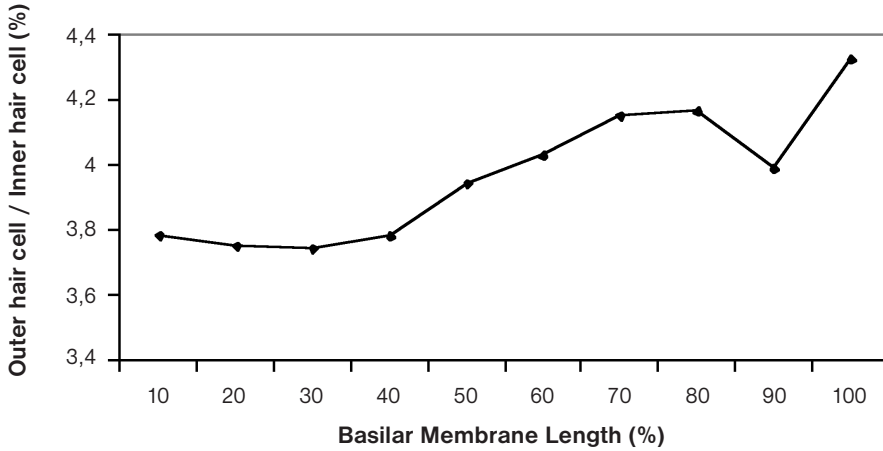


Fig. 3. Outer and inner hair cells ratio along the basilar membrane of *Ctenomys talarum*.

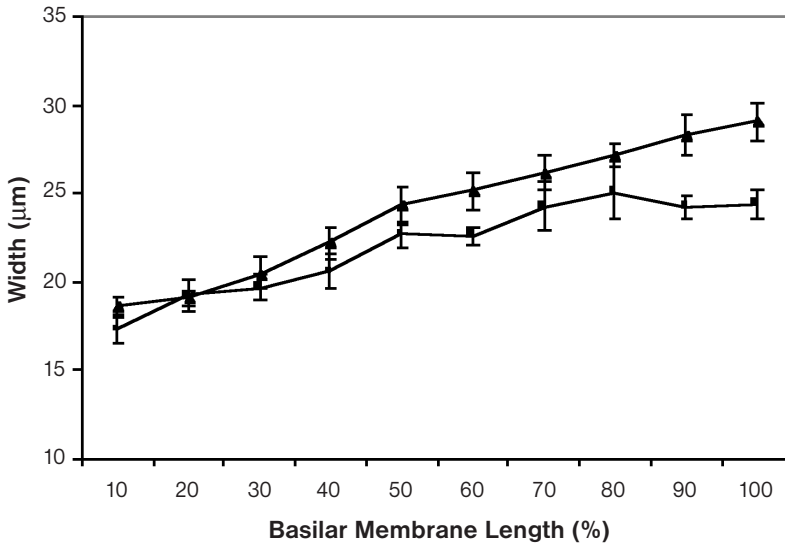


Fig. 4. Mean width (\pm SEM) of the triad of outer hair cells (triangles) and the Tunnel of Corti (squares) along the basilar membrane of *Ctenomys talarum*.

a peak of 429 OHC/mm at the end of the basilar membrane (at about 90% of the length of the BM). The densities of IHC remained nearly constant along the basilar membrane, with the exception of a high-density peak near the apex. The organ of Corti contained on average 4,629 OHC and 1,066 IHC. The ratio between outer and inner hair cells amounted to $3.9 (\pm 0.2) : 1$ and tended to decrease towards the apex (Fig. 3). The radial width of the triad of OHC and the width of the tunnel of Corti also increased from $18.59 (\pm 3.77) \mu\text{m}$ and $17.27 (\pm 2.17) \mu\text{m}$ at the base to $29.09 (\pm 1.6) \mu\text{m}$ and $24.39 (\pm 1.87) \mu\text{m}$ at the apex, respectively (Fig. 4).

Discussion

The mammalian cochlea performs analysis of the frequency spectrum of auditory signals by processing different frequencies at different locations along the cochlear duct. Low-frequency sounds are analyzed at the apex while high-frequency sounds are processed at the base of the cochlea. This frequency-analysis distribution in the cochlea (known as tonotopy principle, cf. Georg von Békésy, Nobel Prize 1961) is supposed to be related to mechanical properties of cochlear structures such as the basilar membrane, the tectorial membrane and inner and outer hair cells (e.g. Jahn & Santos-Sacchi 1988). These structures have been observed to vary among species that occupy wide ranges of habitats (i.e. hearing generalists) and species adapted to a particular type of acoustic environment (i.e. hearing specialists) (Brunns et al. 1988, Burda et al. 1988a,b, Müller 1991, Müller et al. 1992).

The length of the basilar membrane (10.6 mm) of *Ctenomys talarum* (body mass 140 g) was comparable to that found in the fossorial European water vole, *Arvicola terrestris* (10.5 mm, 130 g; Lange et al. 2004) and in the subterranean rodent *Spalacopus cyanus* (11.6 mm, 90 g, Begall & Burda 2006). Related to body mass, it was longer than in the guinea pig (18–19 mm, 500g; West 1985) and the chinchilla (18.5 mm, 600g; West 1985), two non-subterranean caviomorph rodents, and than in the Norway rat, *Rattus norvegicus* (10.7 mm, 325 g; Burda et al. 1988a), a hearing generalist, yet slightly shorter than in a truly subterranean rodent, the Eurasian blind mole-rat, *Nannospalax ehrenbergi* (12.6 mm, 135 g; Burda et al. 1989). A longer basilar membrane is supposed to be related to an extension of the frequency range and expansion of biologically relevant frequencies and, as a consequence, with an improvement of frequency and intensity discrimination (Burda et al. 1988a), especially in the low-frequency region, since basilar membrane length is negatively correlated with the low-frequency limits of hearing (West 1985). Also, the basilar membrane length is negatively correlated with the high-frequency limit, i.e. shorter basilar membranes occur in mammals that are more sensitive to high frequencies (West 1985, Rosowski 1992).

The densities of outer and inner hair cells per mm in *C. talarum* (399 ± 21 ; 100 ± 2 respectively) were within the range described for mammals (378 ± 20 ; 103 ± 10 , respectively; Burda et al. 1988a), although the mean number of outer hair cells were at the top of the mammalian average. Contrary to the distribution of cochlear receptors in several species of mammals studied, outer and inner hair cells presented high density peaks at the apical region of the basilar membrane, in a trend similar to the situation observed in the subterranean rodent *N. ehrenbergi* (Burda et al. 1989). This higher density of receptors in the apical region of the basilar membrane is usually related to a better hearing sensitivity at lower frequencies, since it is this location of the cochlear duct where low-frequency sounds are analyzed (Burda et al. 1988a, 1989).

The mean ratio between outer and inner hair cells in *C. talarum* appeared similar to the ratio found in *N. ehrenbergi* (Burd a et al. 1989), but it was higher than in other caviomorph rodents studied thus far – *Cavia porcellus* (3.59 OHC : 1 IHC) and *Spalacopus cyanus* (3.63 OHC : 1 IHC) (Burd a 1984, B e g a l l & B u r d a 2006). Usually, lower values of this ratio are found in mammalian species that possess high-frequency sensitivity. Therefore, the high mean ratio between outer and inner hair cells observed in *C. talarum* could be considered as another cochlear trait that indicates a general tuning of hearing to low frequencies.

Similarly to the majority of the mammalian species studied, the width of the triad of outer hair cells (which correlates with the width of the reticular lamina and reflects the basilar membrane width) increased gradually from the base towards the apex. Values of this parameter were also equivalent to the ones found in *N. ehrenbergi* (Burd a et al. 1989). Higher values of the width of the triad of outer hair cells may also indicate a general tuning of hearing to low frequencies (Burd a et al. 1989). Though the width of the triad of outer hair cells increased gradually towards the apex, a previous study on the cochlea of this subterranean rodent showed that the width of the basilar membrane decreased from the base to the middle part of the cochlea, and then increased towards the apex (Pye 1977). Although in mammals both parameters are usually correlated, this seems not to be the case in *Ctenomys talarum*. However, we cannot explain this apparent contradiction between our and Pye's results.

The gradual changes in values of several parameters (width of OHC triad, OHC and IHC densities, OHC/IHC ratio) along the organ of Corti indicate that in *C. talarum* there is no "acoustic fovea" comparable to that reported for the African mole-rat, *Fukomys anselli* (Müller et al. 1992). This would implicate that hearing in *Ctenomys* is less specialized than in *Fukomys*, a situation reflecting also the fact that *Ctenomys* is presumably less strictly bound to underground ecotope than *Fukomys*. In this aspect *Ctenomys* resembles *Spalacopus* (Sabine B e g a l l, personal communication), although the number of distinct peaks of inner hair cells differ between these two species, being only one in *C. talarum* compared to three peaks in *Spalacopus* (B e g a l l & B u r d a 2006). This may indicate that aboveground hearing, although important, is less differentiated in *Ctenomys* and serves alertness rather than vocal communication; a situation reflecting solitary habitats of *C. talarum* compared to sociality and highly differentiated vocalization in *Spalacopus* (cf. Veitl et al. 2000). From this point of view, the study of the ear of social species of *Ctenomys* may prove to be of interest.

In conclusion, the inner ear of *C. talarum* exhibits anatomical features that can be interpreted as biomechanical specializations to enhance low-frequency sound reception. These modifications, also found in some species of distantly related fossorial and subterranean rodents, coincide with the dominant low-frequency vocalizations of this rodent and with the best transmission frequency in subterranean environments, providing evidence for the existence of adaptive sensory convergence.

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