UNIVERSITY OF SOUTH BOHEMIA, FACULTY OF SCIENCE

Ear morphology in Chinese bamboo rat (*Rhizomys sinensis*): Hearing adaptations to subterranean environment

Master thesis

Bc. Lucie Pleštilová

Supervisor: Doc. RNDr. Radim Šumbera, PhD.
Consultant: Mgr. Ema Hrouzková, PhD.

České Budějovice 2013

Pleštilová, L. (2013): Ear morphology in Chinese bamboo rat (*Rhizomys sinensis*): Hearing adaptations to subterranean environment. Master thesis, in English, 35 p. Faculty of Sciences, University of South Bohemia, České Budějovice, Czech Republic.

Annotation:
I studied outer, middle and inner ear morphology in Chinese bamboo rat (*Rhizomys sinensis*). I compared studied specimen with other subterranean, fossorial and aboveground rodents and assumed degree of its adaptation to subterranean environment.

Declaration:
I hereby declare that I have worked on my master thesis independently and used only the sources listed in the bibliography.

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Financial support: GAČR P506/11/1512

Acknowledgments:

I wish to thank my supervisor Radim Šumbera for enabling this study and for valuable advices and discussions. My particular thanks go to my consultant Ema Hrouzková for specimens and great support in my work. I wish to thank Hynek Burda for my initiation to ear morphology problematic and patience with teaching me. I wish to thank Dr. Matthew Mason for providing his PhD. thesis data and for his advices and goodwill to help me. I also thank to Matěj Lövy and Michaela Syrová for their help.

And last but not the least, I would like to thank my family and friends for their endless support.

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1. INTRODUCTION

1.1 Acoustics in underground burrows

Burrows of subterranean mammals bring many advantages to their inhabitants, such as protection against predators or stabile microclimate (Nevo, 1999). In the result, many mammalian species use these benefits. According to degree of specialization for subterranean activity, amount of time spent there and activity carried in below ground, burrowing mammals could be categorized into three groups: 1. aboveground/non-subterranean species use burrow only as a shelter, they usually do not dig them or alternatively they dig only short and shallow burrows; 2. fossorial species dig and live in extensive burrows, but they usually forage aboveground, not far from the burrow openings and 3. subterranean mammals spending virtually all their lives in sealed extensive underground tunnels, where they search for food, mates and also disperse below ground (Burda et al., 2007, Nevo, 1979, 1999). In literature (see Ebensperger, 1998, Kinlaw, 1999), there are some ambiguities in terminology, because fossorial species are often called "semi-fossorial" and subterranean species are called "fossorial", and sometimes the term "fossorial" is used for all species which are able to dig.

Permanent life in complexes of subterranean burrows brings numerous sensory challenges for their inhabitants. Among the most peculiar and highlighted are difficulties in communication. In the dark burrows, the vocalization is probably the most important channel used for communication (Begall et al., 2007). Nevertheless, airborne sound propagation in subterranean environment is restricted; the sound communication signals are indistinguishable from background noise for distances longer than few meters (Mason and Narins, 2001, Narins et al., 1992). Studies on blind mole rat (*Spalax ehrenbergi*) (Heth et al., 1986) and Zambian mole-rats (*Fukomys mechowii* and *Fukomys kafuensis*) (Lange et al., 2007) showed that low-frequency sounds are transmitted better then high-frequency ones in natural burrows and the acoustic waves of 440 Hz are the least attenuated here (Heth et al., 1986). Importantly, the low-frequency sounds are not only least attenuated, but they are even amplified by so-called stethoscope effect (Lange et al., 2007).

1.2 Hearing in subterranean and fossorial rodents

Hearing ranges of subterranean mammals are tuned for lower frequencies, because these frequencies are best spread in subterranean burrows; the best hearing sensitivity occurs between 0.5 and 1 kHz (Begall and Burda, 2006, Bruns et al., 1988, Heffner and Heffner, 1992, Müller et al., 1992). Moreover, high frequencies are used for localization of the source of the sound, which is useless in underground tunnels (Heffner and Heffner, 1990, 1992). In result, subterranean and to lesser extend also fossorial species have limited capability of high-frequency hearing (Aitkin et al. 1982, Brückmann and Burda, 1997, Heffner and Heffner 1992). In addition, subterranean species have low overall hearing sensitivity to avoid stethoscope effect and congestion by background noise (Burda, 2006). Hearing in fossorial species have to be adapted on both environments, aboveground as well as underground, therefore their hearing cannot be entirely specialized for one of them (Heffner and Heffner, 1992, 1993, Wilkins at al., 1999).

In the beginning of 1990's there was a discussion whether restricted high frequency hearing and low sensitivity of hearing in subterranean mammals is progressive adaptation or regression (c.f. Burda et al., 1992, Heffner and Heffner, 1990). It was suggested that incapability of hearing of certain frequencies in subterranean mammals can be caused by the lack of sensorial stimulation in a similar way like degeneration of vision in mammals living in the darkness or olfactory in cetaceans (Heffner and Heffner, 1990). Further studies on hearing in subterranean mammals and acoustics in burrows (Begall et al., 2004, Heffner and Heffner, 1990, 1992, Heffner et al., 2001, Lange et al., 2007) showed that hearing capabilities are perfectly adapted to acoustic conditions in burrows. In addition, remarkable convergent similarities in ear morphology of different rodent taxa have been described (Burda et al., 1992, Lange, 2004, Mason, 2001). At present, the restricted hearing in subterranean mammals is understood more as convergent adaptation for sensory environment than degeneration (Lange et al., 2007).

1.3 Ear morphology

The ear apparatuses consist of three main sections: external or outer ear, middle ear and inner ear. Outer ear consists of pinna, external meatus and the cuticular and fibrous layer of the tympanic membrane (Frenz et al., 2001). Outer ear serves not only for localization, amplification and transfer of the sound to eardrum (Sinyor & Laszlo, 1973), but also for protection of tympanic membrane and deeper structures of the ear (Johnson et al., 2001).

Middle ear is an apparatus for matching the difference of impedance within transferring vibrations from air outside the ear to fluid inside the inner ear (Møller, 1974, Webster & Webster, 1975). Together with the inner ear it is stored in auditory bulla which is part of temporal bone. Middle ear consists of tympanic membrane (or its mucosal layer), the middle ear cleft and chain of three auditory ossicles with accompanying muscular, neural and connective tissue structures and it is connected with the inner ear by the stapedial footplate which fits into the oval window (Ades and Engström, 1974). It works generally as amplifier; amplification of vibrations is achieved by difference between eardrum and stapedial footplate areas, and difference between length of malear and incudial lever arms (Bekésy, 1960, Møller, 1974).

Inner ear is divided into two parts with distinct functions. First one is the vestibular part which consists of pars superior (vestibular labyrinth) and endolymphatic duct and sac. The second part is pars inferior, or cochlea (Carpenter, 1996).

1.3.1 Middle ear

Middle ear begins with eardrum, or tympanic membrane. It makes barrier between the external bony meatus and the tympanic cavity. It's a thin tight membrane made of three layers which works as a soundwave collector (Lombard & Hetherington, 1993).

As abovementioned, there are three auditory ossicles, malleus (or "hammer"), incus ("anvil") and stapes ("stirrup") in tympanic cavity. Malleus and incus are similar to each other, both bones have bigger round part called head and few processes. Ear muscles or other parts of middle ear are attached to the processes. The last bone of middle ear, stapes, has only small head which is connected with footplate by two crura (fig.1.).

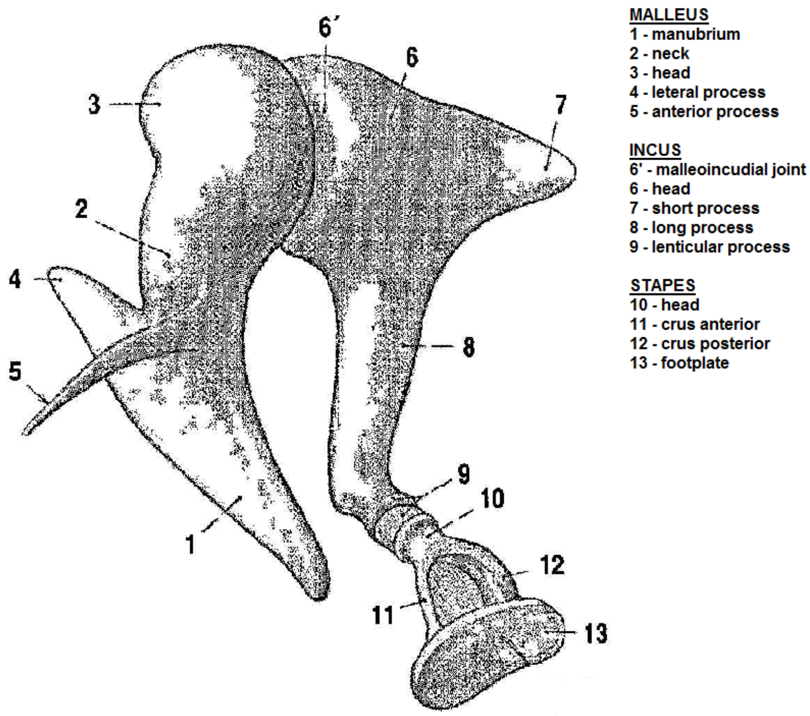

Fig1. Morphology of the middle ear ossicles (Čihák, 2004).

Manubrium (or "handle") of malleus adheres to the tympanic membrane. Malleus is the first and the biggest hearing ossicle (Oschman, 1991). The head of malleus fits in the head of incus. Incus is by long process, (or "long arm"), and its lenticular apophysis coupled with head of stapes. Stapes is the last part of middle ear osseous chain and its footplate fits into the oval window of cochlea.

Middle ear includes muscles and ligaments as well. They hold the ossicles in required position (Solntseva, 2007). Malleus and incus are usually fixed to the bullar wall by anterior, superior and posterior ligaments. There are two tendon muscles in the ear, the tensor tympany which is attached to the manubrium of malleus and stapedial tendon which is connected to head or posterior crus of stapes. These muscles (fig. 2.) regulate transition of energy to inner ear and preserve it from overstimulation (Solntseva, 2007).

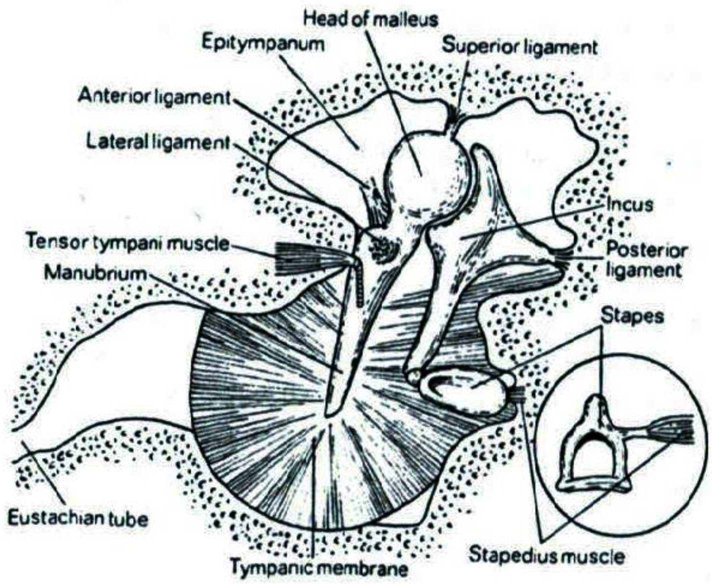

Fig.2. Situation and attachment of hearing ossicles in the middle ear (Møller, 1972).

Based on the shape, position and attachment of hearing ossicles to the bullar wall different middle ear categories were established (fig. 3.). According to Fleischer (1978), there are 6 middle ear types. Out of them there are two types - “microtype” and “freely-mobile” in rodents. The first one is assumed as high frequency adaptation, and it is characterized by malleus with anterior process firmly attached to the tympanic bone. Malleus contains orbicular apophysis, which increases ossicular inertia and moves the ossicular center of mass closer to the manubrium (Fleischer, 1978, Lavender, 2011, Mason, 2013). In contrast, the freely mobile type of ear is considered as adaptation to low frequency hearing, and it is characterized by ligamentous connection to the skull, heavier ossicles, relatively large incus and manubrium roughly perpendicular to axis of rotation (Fleischer, 1978, Mason, 2001, Mason, 2013). Interestingly, Mason (2013) noticed that Ctenohystrica possess some unique features and he suggested specific middle ear category for these rodents. “Ctenohystrica” type of ear exhibits fused malleus and incus, elongated malleus in anerior direction and small or even missing anterior process.

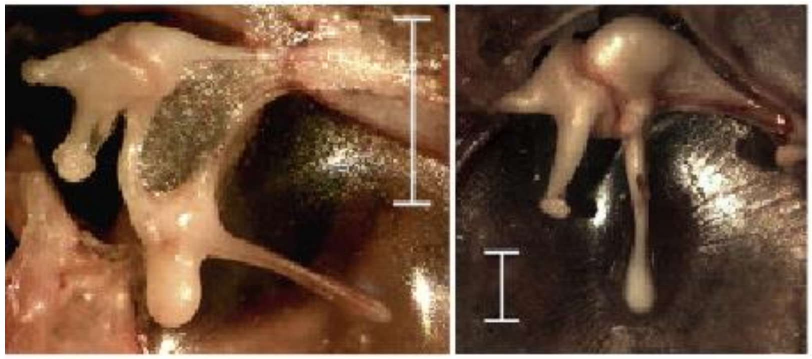

Fig.3. Middle ear types: microtype, illustrated by the mouse *Mus musculus* and freely mobile type, illustrated by the squirrel *Sciurus vulgaris* (Mason, 2013).

Middle ears of hystricomorph rodents studied so far were rather uniform and tuned for lower frequencies (Argyle and Mason, 2008, Heffner and Heffner, 1992, Mason, 2013), whereas middle ear in myomorph rodents varies from low frequency to high frequency specialized species (Burda et al., 1992, Lange et al., 2004, Mason et al., 2010). Nevertheless, there is lack of studies in low frequency or non-specialized murid rodents ears.

1.3.2 Inner ear

The hearing part of inner ear is situated in the otic capsule with two openings, the oval and round windows (Santi and Tsuprun, 2001). Cochlea is fluid filled spiral tube consisting of two layers, the outer bonny layer and the inner membranous layer (Ades and Engström, 1974). The inner part of cochlea is divided into three parts called scalas. The middle one is filled by endolymph, the side parts are filled by perilymph (Ades and Engström, 1974). Scala media, or cochlear duct, is laterally bordered by spiral ligament with stria vascularis, its bottom is formed by basilar membrane and the top by the Reissner's membrane (fig. 4.).

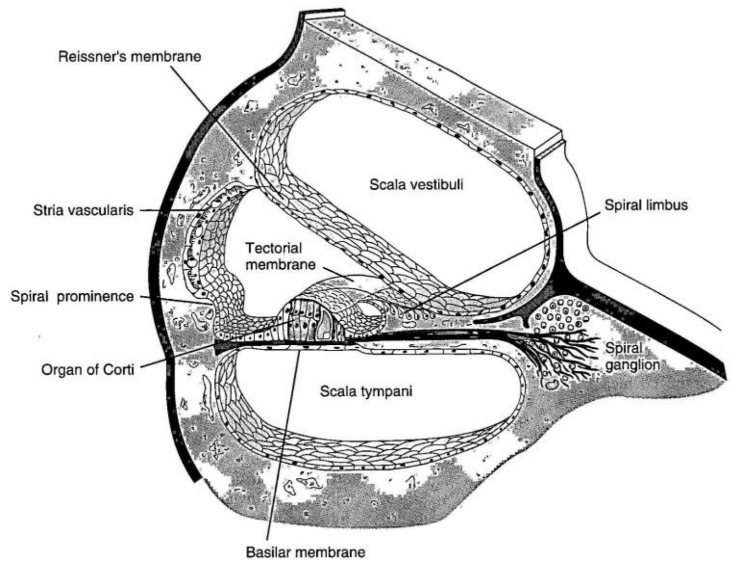

Fig 4. Cross section of one cochlear turn (Hall, 2006).

The basilar membrane is a connective tissue structure which holds organ of Corti, the sensory structure of the ear (Santi and Tsuprun, 2001). The stiffness of the membrane changes across its length, the width is increasing and the thickness decreasing toward the cochlear apex (Békésy, 1960, Eldredge, 1974). This attribute of the basilar membrane is essentially for its tonopicity, what means that the high-frequency waves cause maximal vibrations in the base and low-frequency waves in the apex (Békésy, 1960, Santi and Tsuprun, 2001). The exact position where the particular frequencies are perceived or cochlear map was described in various species (Békésy, 1960, Liberman, 1982, Müller, 1996, 2010, Ou et al., 2000).

The organ of Corti is a spirally directed ridge of tissue where the waves are registered and encoded to impulses for central nervous system (Eldredge, 1974). It contains outer and inner cells with stereocilia, or hair cells separated by tunnel of Corti and their auxiliary cells, and it is covered by acellular tectorial membrane (Santi and Tsuprun, 2001). The inner hair cells form a single row surrounded by supporting cells and they serve as cochlear receptor (Santi and Tsuprun, 2001). The outer hair cells form three rows; the longest one is attached with tectorial membrane by stereocilia (fig.6.). The outer hair cells serve mainly as amplifier; they provide cochlear sensitivity and selectivity (Brown, 2001, Dallos, 1996, Narayan et al., 1998).

1.4 Adaptations of ear in fossorial and subterranean mammals

In mammals with prevalent underground activity there are some modifications in hearing apparatus in comparison with their unspecialized aboveground counterparts. The ear of subterranean species is characterized by low efficiency and it is tuned to lower frequencies. Thus, it is possible to estimate hearing specialization according to morphology and thus the ecology or style of life of particular species.

In subterranean mammals, the pinna is reduced or even missing, which causes worse ability of sound localization (Nevo, 1979, Heffner and Heffner, 1990). Also, narrow auditory meatus filled with cerumen decreases the hearing efficiency (Burda, 1992).

Most adaptations are evident in middle ear morphology and they are also most important for tuning to low frequency sounds (Segall, 1973). The eardrum is rather big, almost round without a distinct pars flacida, the ossicles (especially incus) are heavier and more robust and the stapedial footplate is relatively large (Argyle and Mason, 2008, Burda, 2006, Lange et al., 2004, Lange & Burda, 2005). The ratio between area of eardrum and stapedial footplate and also the ratio between mallear and incudial lever arm are lower in subterranean and fossorial mammals than in aboveground dwellers of similar body size. Lower ratio reduces the efficiency of the middle ear sound transmission.

Subterranean and fossorial mammals have “freely mobile type” of middle ear, which means that the ossicles are loosely attached in the tympanic cavity and the middle ear muscles which tunes middle ear to high frequencies are reduced (Burda et al., 1992, Mason 2001, Mason, 2006, Møller, 1974).

The low frequency tuned inner ear exhibits typical features; it is characterized by long basilar membrane with high density of cochlear receptors in apex, and the width of receptor triads is increasing from base to the apex (Lange et al., 2004, Begall and Burda, 2006, Schleich et al., 2006). Another trait considered as low frequency specialization is higher ratio between outer and inner hair cells (Schleich et al., 2006).

Frequencies in basilar membrane are tonotopically mapped from high to low, progressing roughly exponentially from base to apex, i.e. each frequency is represented on appropriate part of basilar membrane (Békésy, 1960). Mammals specialized for hearing of high or low frequencies, such as bats, African mole-rats or blind mole rats, are characterized by acoustic fovea (Kössl and Vater, 1996, Müller et al., 1992, Bruns et al., 1988). Acoustic fovea is the place on basilar membrane wherethe frequencies with biological significance is overrepresented. This fovea is recognizable from constant width of basilar membrane in the area of fovea and from arrangement of hair cells (Bruns, 1988, Müller et al., 1992).

1.5 The biology of *Rhizomys sinensis*

Among fossorial and subterranean mammals, there are still many species in which we do not have any detail knowledge about their biology and hearing apparatuses specifically. Some of them could be very interesting model because of their peculiarity. Among them, the genus *Rhizomys* is worth of studying because of several reasons: this genus contain very large species with almost not known biology, this is muroid species, other genera of this family were studied and showed different degrees of hearing specializations (Bruns et al., 1988, Mason, 2001).

Chinese bamboo rat (*Rhizomys sinensis*; App. 1.) is solitary muroid rodent from family Spalacidae, one of three species of genus *Rhizomys* (Smith et al., 2008). Five subspecies of Chinese bamboo rat are distributed through tropical and subtropical parts of southeastern China and northern Vietnam (Smith et al., 2008).

This species has body length of 230 – 480 mm and tail length of 50 – 200 mm with weight is in the range of about 1 – 4 kg (Nowak, 1991). It is usually found in altitude between 1500 – 2800 m. a.s.l, in evergreen broad-leaved forests in tropical or subtropical climate with annual average temperature 18°C and precipitation over 1100 mm (He, 1984; App. 2.). Diet of *Rhizomys* consists of shoots and roots of bamboo but they could eat also sugar cane or tapioca, which make them agricultural pests (Nevo, 1999).

Chinese bamboo rat lives in underground burrow systems in depth about 20-30 cm and total length more than 30 m (up to 45 m). It is supposed, that their sealed burrow systems are opened only during a short mating period (He, 1984).

1.6 Aims of this thesis

1. To describe morphology of outer, middle and inner ear of Chinese bamboo rat (*Rhizomys sinensis*).
2. To estimate hearing range and efficiency with emphasis on degree of specialization for subterranean life by comparison with data published on ear morphology of different terrestrial, fossorial and subterranean rodent species.

2. MATERIALS AND METHODS

2.1. Ear dimensions

Six specimens of adult Chinese bamboo rat (*Rhizomys sinensis*) originated from Zhangjiajie, Hunan, China, were dissected and examined. The heads were formalin-preserved by injecting 10% solution of formaldehyde to the muscles close to the hearing bullae. Published results contain only right ears from each specimen, for middle ear analysis was used five specimens and in case of inner ear it was only four specimens; due to damaged structures or improper fixation.

Condylobasal length and length of pinna were measured using calipers. The jaw musculature of skinned head was cut through to remove lower jaw. The occipital part of skull was cut to prepare the bulla. Subsequently, the length of meatus was measured, the extracted bulla was cleaned from soft tissues and the length, width and depth of each bulla was measured.

Afterwards, the bulla was dissected and examined using binocular light microscope Nikon SMZ 1500 using magnifications 20-40x.The cross section of bonny meatus was photographed and then the bulla was cut through in the place where bonny meatus entries to the bulla, its lateral wall. After removing part of the bullar wall the eardrum was exposed, captured and carefully removed to not damage the ossicular chain. The ossicles were photographed in situ and in toto and then extracted and weighed by analytical weight A&D GR-202.

The bullar volume was calculated as ellipsoid volume. Cross section of bonny meatus, eardrum, stapedial footplate and levers of ossicles were measured on photos captured by Nikon digital camera DMX 1200 and processed using GIMP 2. The areas of eardrum and stapedial footplate were calculated as area of an ellipse. As lever arms were taken the shortest distances (perpendiculars) between tips of the longest ossicular processes and rotatory axis of malleus and incus (fig. 5.).

The inner ear was dissected after removing the stapes to release both oval and circular window with magnification of 117,5x. The bonny shell on cochlear apex was carefully broken and peeled off to expose scala vestibuli, and the hole was used for coloration of cochlear parts with toluidin blue. After coloration, the membranes and ligaments of inner ear were better distinguishable and were gradually removed.

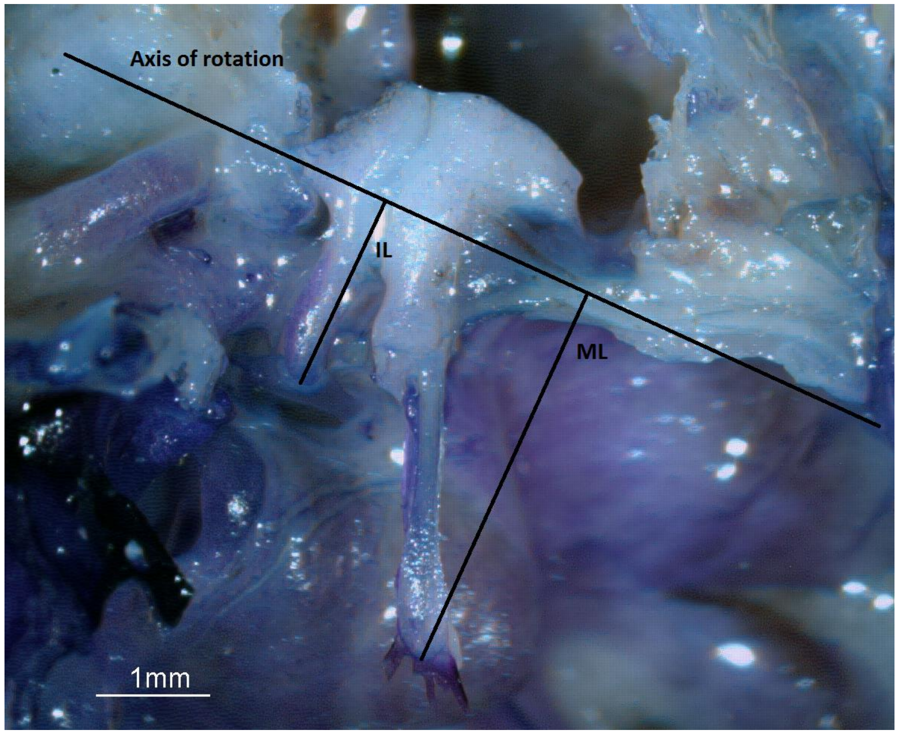

Fig. 5. Incus and malleus of Chinese bamboo rat's right ear with marked axis of rotation and lever arms: IL – incudial lever arm, ML – mallear lever arm.

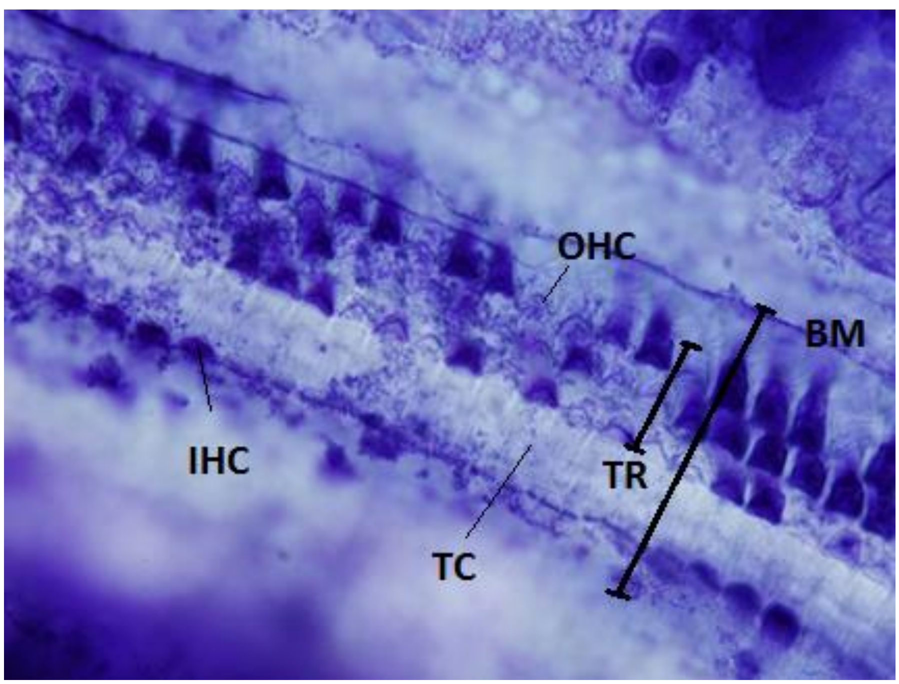

Fig. 6. Organ of corti: IHC – inner hair cells, OHC – outer hair cells, TC – tunnel of Corti, TR – width of triade, BM – width of basilar membrane.

After elimination of apical part of cochlear skeleton above first cochlear turn the Reissner's membrane, spiral ligament and tectorial membrane were removed. Thus the basilar membrane with organ of Corti was exposed for coloration by Ehrlich's hematoxylin and later removed. After extraction, the basilar membrane with the organ of Corti was placed into a drop of glycerin on a microscope slide.

Whole cochlea was prepared by same method and examined with microscope Lambda DN45 using magnification 400x. Total length of basilar membrane, its width and the width of "triade" (three rows of outer hair cells) in each 10% of basilar membrane length was measured (fig.6). The place taken by ten hair cells of inner and each outer row was measured and its density per 1mm was calculated.

2.2. Statistics

Results of morphological measurements are presented as mean ± SD. Middle ear dimensions in *Rhizomys sinensis* were compared with available data on other rodents sorted according to style of life (subterranean species spending practically all their life including feeding underground, fossorial species living largely in underground and feeding aboveground and terrestrial species with dominance of aboveground activity Burda et al., 2007, Nevo, 1979, 1999).

The relationship between ratio of eardrum and stapedial footplate was analysed using linnear regression (body mass was logaritmically transformed). The ratio of mallear and incudial lever and logarithmically transformed ossicular mass were analyzed the same way. For comparison each pair of ecological groups the residuals from the data points representing aboveground species were calculated and then compared using Wilcoxon matched pair test (Statistica 9, StatSoft).

The classification into the ecological categories were done by Discriminant Function Analysis (DFA in Statistica 9, StatSoft), the loadings of the variables were ratio of eardrum and stapedial footplate areas, ratio of mallear and incudial levers, and ossicles mass divided by body mass size. Classification success of each category is shown by percentile rate; whereas Wilk's lambda, expressing the probability distribution, was used to verify the success rate. After processing the ecological groups and the middle ear parameters by the DFA method *Rhizomys sinensis* was classified into one of those ecological groups.

The width of basilar membrane and "triade", density of inner and outer hair cells and ratio between both densities are presented in form of scatter plots to better description of the basilar membrane slope. These values were compared with inner ear dimensions for available studies.

3. RESULTS

3.1. Middle ear parametres

Middle ear parameters of each specimen are showed in tab. 1. Mean length of pina iIn *Rhizomys sinensis* is 16.5 mm (± 1.46). The bony meatus comes to tympanic bulla under low angle. There is a stiff protective inner layer in the bonny meatus which ends by thick part on the top of eardrum. Cerumen was present in three individuals. Mean bullar volume was 636.5 mm^3 (± 69.59).

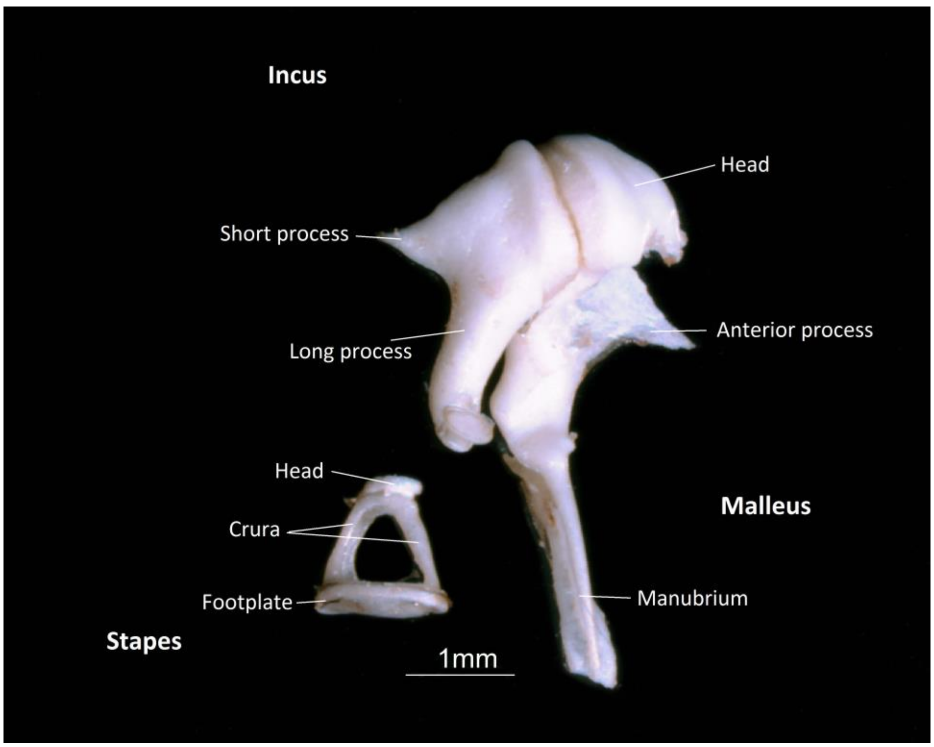

Fig. 7. Middle ear ossicles of Chinese bamboo rat (*Rhizomys sinensis*).

The tympanic membrane was nearly round, flat and without evident pars flaccida. Middle ear ossicles (fig. 7.) are massive and loosely attached to the bullar wall by ligaments, the middle ear is thus of freely mobile type. The manubrium is rigid; it has triangular shape and is connected with eardrum by flat and relatively large surface. Malleus is attached at its anterior process and at the back of the beginning of manubrium. Malleus is firmly attached (in some cases its separation was very difficult) with incus.

Incus was attached to the bullar wall by ligamentst. End of long process is curved into lenticular process, thus the stapes was perpendicular to other part of ossicular chain. The stapes was attached by remarkable lenticular apophysis.

Stapes has triangular shape with slightly asymmetric position of the head, and the stapedial muscle is attached to the shorter and ticker posterior crus. The stapedial artery doesn't pass through. The footplate is of slightly asymmetrical oval shape.

The mean value of lever ratio in *R. sinensis* was 2.13 (± 0.11); the area ratio was 18.79 (± 0.82).

	CB [mm]	P [mm]	BV [mm^3]	MCS [mm^2]	M [mm]	ED [mm^2]	SF [mm^2]	ML [mm]	IL [mm]	MM [mg]	IM [mg]	SM [mg]
R1	79.9	19.2	638.3	4.9	19.1	18.45	0.93	3.54	1.75	3.5	2.4	0.5
R2	65.6	16.3	701.0	4.9	18.9	17.10	0.92	3.53	1.62	4.1	2.7	0.3
R3	64.2	15.9	706.8	4.5	18.9	16.96	0.90	3.69	1.61	4.0	2.7	0.4
R4	64.3	15.2	502.7	4.6	19.6	17.11	0.87	3.71	1.65	3.6	2.8	0.3
R5	69.4	15.9	667.2	4.2	17.0	16.33	0.96	3.84	2.02	3.1	2.6	0.3
Mean	70.2	16.2	636.5	4.6	18.7	17.19	0.92	3.66	1.73	3.7	2.6	0.4

Tab.1. Middle ear parameters measured in five *Rhizomys sinensis* specimens R1 – R5, in the last line is the average of values: CB – condylobasal length, P – pina length, BV – bullar volume, MCS – area of cross section of bonny meatus, M – length of meatus, ED – area of eardrum, SF – area of stapedial footplate, ML - mallear lever, IL – incudial lever, MM – mallear mass, IM – incudial mass, SM – stapedial mass.

3.2. Inner ear dimensions

Cochlea in *R. sinensis* has three and quarter turns. Length of basilar membrane was 18.9 mm in average (± 0.76) and the width increased from base to apex; in 10% it was 60.5 µm in average (± 2.69) and in 80% 85.3 µm in average (± 2.05); the mean width of basilar membrane was 74.1 mm (± 8.76) (fig. 8). The width of three rows of outer hair cells, or "triade", increased from 23.75 µm (± 1.48) in 10% to 34.0 µm (± 0.82) in 80%; the mean was 29.3 mm (± 4.12) (fig. 9). Width of basilar membrane as well as width of three rows of outer hair cells showed similar trend, they were increasing linearly from the base to apex and there was lower slope in 60% of length from basis. This change in slope in basilar membrane and "triade" width is likely to signify the part of better hearing, but it is not distinctive enough to be an acoustic fovea.

Distance from basis	10%	20%	30%	40%	50%	60%	70%	80%	90%
BM width (µm)	60.50 (±2.69)	62.75 (±4.38)	70.00 (±2.24)	74.75 (±2.59)	77.50 (±0.87)	80.75 (±2.17)	83.00 (±2.55)	85.33 (±2.05)	81.33 (±1.25)
Triade width (µm)	23.75 (±1.48)	25.00 (±2.12)	26.50 (±2.50)	29.25 (±3.77)	31.00 (±2.45)	31.75 (±2.17)	33.00 (±1.22)	34.00 (±0.82)	31.33 (±2.62)
IHC density /mm	102.31 (±5.26)	102.35 (±5.53)	105.09 (±3.19)	109.80 (±4.73)	114.04 (±2.97)	120.97 (±3.84)	118.56 (±5.04)	122.89 (±7.34)	128.79 (±2.08)
OHC density /mm	325.11 (±14.86)	321.56 (±2.04)	328.53 (±10.34)	331.97 (±10.17)	333.90 (±2.94)	350.67 (±7.76)	348.58 (±5.54)	366.64 (±13.37)	387.24 (±9.49)

Tab.2. Mean and SD of inner ear parameters measured along basilar membrane: BM – basilar membrane, Triade – three rows of outer hair cells, IHC – inner hair cells, OHC – outer hair cells.

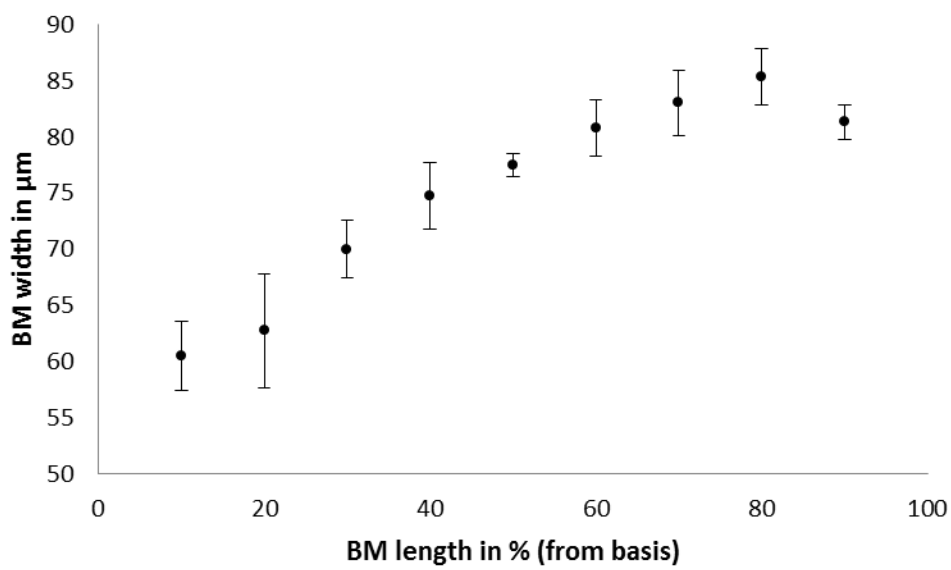

Fig.8. Course of width of basilar membrane (mean, SD) from basis to apex.

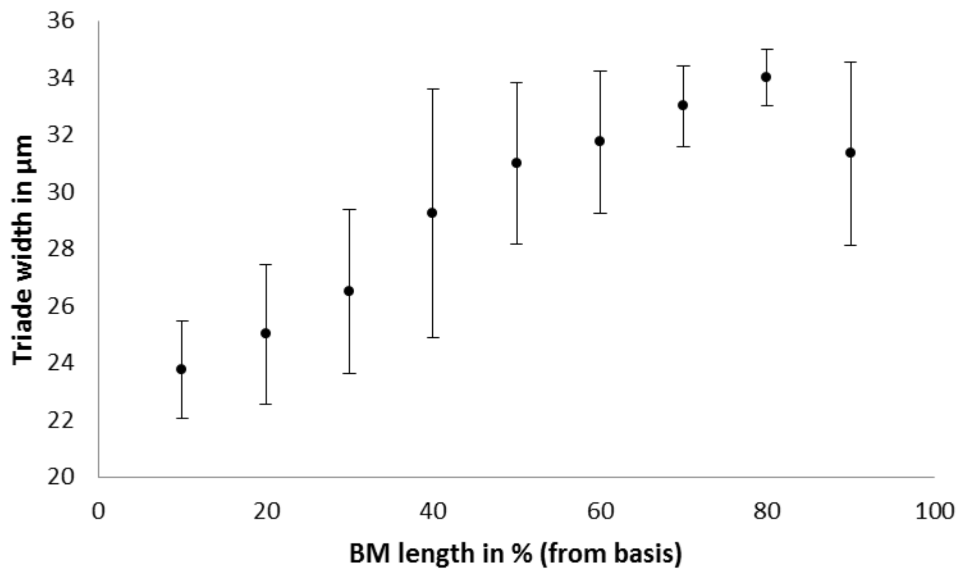

Fig. 9. Course of width of three rows of outer hair cells (mean, SD) from basis to apex.

Cochlear receptors were arranged in geometrically regular pattern. Their density increased from base to apex; average density was 113.9 cells (± 7.31) per mm in inner hair cells, and 343.8 (± 21.87) in outer. The ratio between outer and inner hair cells slightly decreases from basis to apex; there is depression around 60% (fig. 12.).

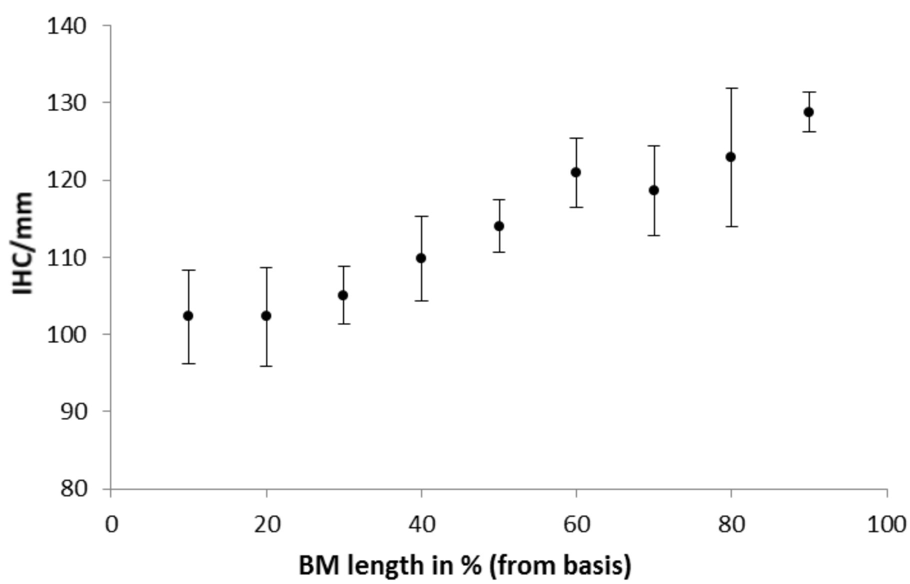

Fig. 10. Course of density of inner hair cells (IHC) (mean, SD) along the basilar membrane (BM).

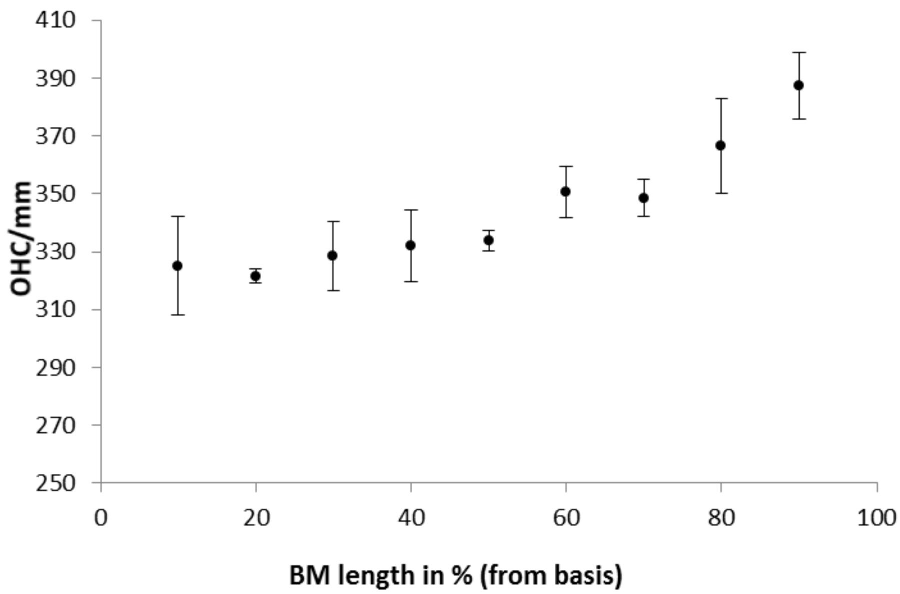

Fig.11. Course of density of outer hair cells (OHC) (mean, SD) along the basilar membrane.

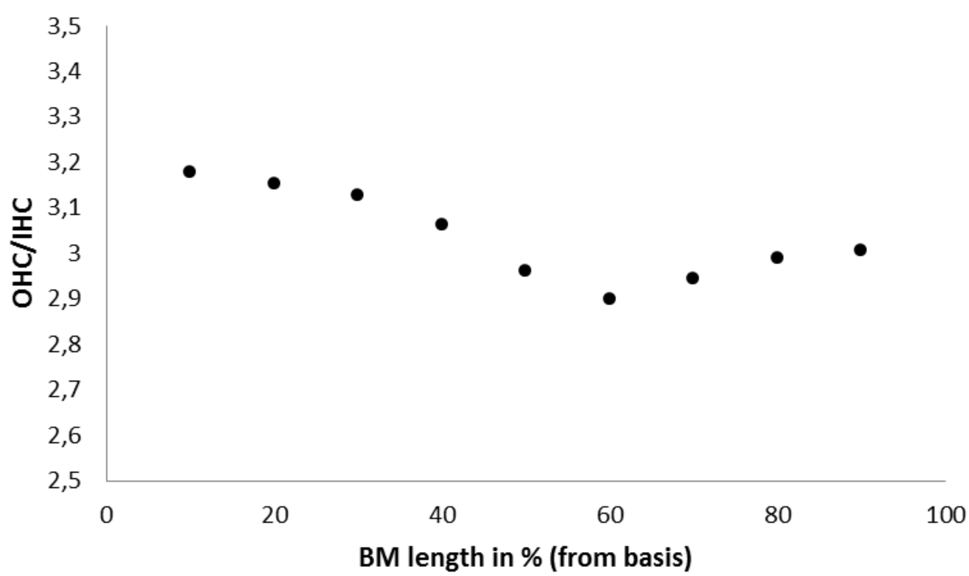

Fig. 12. Course of ratio of mean outer hair cells and inner hair (OHC/IHC) cells along the basilar membrane.

3.3. Comparison with other rodent species

I analyzed relationship between area ratio, lever ratio and malleus and incus masses and body mass in rodents with different style of life (tab. 3.). Both ratios and ossicle mass were compared with body mass and the regression lines with equations given in figs. 13. - 15. were calculated for aboveground species. Area ratio in subterranean species was significantly different from aboveground ($p = 0.015$); in fossorial species the area ratio was similar to that in aboveground species ($p = 0.208$) (fig.13.). Lever ratio of subterranean species was significantly different from aboveground ($p = 0.003$); between fossorial and aboveground species was no significant different ($p = 0.263$) (fig. 14.). There was no significant different in ossicle mass between each pair of group of species ($p = 0.086, 0.779$) (fig. 15.).

DFA statistic method classified particular species from different ecological groups by square ratio, lever ratio and ossicles mass (relative to body mass). Area ratio and lever ratio were significant parameters ($p=0,009$, $p=0,039$ respectively). Influence of ossicle mass was not significant.

The most consistent groups were subterranean rodents with 92% and terrestrial rodents with 64% of success rate. Fossorial group wasn’t separated (25%). *Rhizomys sinensis* fitted into subterranean group. Wilks' lambda was 0.42.

Species	**ecology**	**LR**	**AR**	**OM/BM**
Blind mole rat (*Spalax ehrenbergi*)[1]	S	2,16	19,84	0,009
East African mole rat (*Tachyoryctes splendens*)[1]	S	2,09	20,60	0,011
Chinese zokor (*Eospalax fontanierii*)[1]	S	2,09	17,56	0,018
Whyte’s mole-rat (*Fukomys whytei*)[4]	S	2,40	23,20	0,018
Giant mole-rat (*Fukomys mechowii*)[4]	S	2,08	21,64	0,012
Damaraland mole-rat (*Fukomys damarensis*)[4]	S	1,85	17,31	0,014
Ansell’s mole-rat (*Fukomys anselli*)[4]	S	2,20	16,15	0,030
Highveld mole-rat (*Cryptomys pretoriae*)[4]	S	2,00	17,07	0,013
Naked mole-rat (*Heterocephalus glaber*)[5]	S	1,90	23,91	0,013
Northern mole-vole (*Ellobius talpinus*)[2]	S	1,60	17,00	0,027
Plains pocket gopher (*Geomys bursarius*)[2,3]	S	2,16	17,09	0,011
Botta's pocket gopher (*Thomomys bottae*)[5]	S	1,78	19,96	0,019
Field vole (*Microtus agrestis*)[5]	F	2,26	23,69	0,052
Common vole (*Microtus arvalis*)[6]	F	2,13	18,00	0,028
Bank vole (*Myodes glareolus*)[5]	F	2,84	23,44	0,028
Talas tuco-tuco (*Ctenomys talarum*)[7]	F	2,47	20,76	0,022
Social tuco-tuco (*Ctenomys sociabilis*)[7]	F	2,49	26,35	0,008
Water vole (*Arvicola terrestris*)[6]	F	2,00	22,50	0,005
Mongolian gerbil (*Meriones unguiculatus*)[8,9]	F	3,32	23,02	0,012
Roborovski hamster (*Phodopus roborovskii*)[5]	F	2,05	18,69	0,008
Merriam's kangaroo rat (*Dipodomys merriami*)[10]	T	3,41	24,98	0,063
Pale gerbil (*Gerbillus perpallidus*)[5]	T	2,99	23,63	0,038
Common rat (*Rattus norvegicus*)[2]	T	2,42	21,99	0,004
Guinea pig (*Cavia porcellus*)[5]	T	2,51	34,11	0,013
House mouse (*Mus musculus*)[2]	T	2,42	24,17	0,010
Common rabbit (*Oryctolagus cuniculus*)[5]	T	3,08	19,63	0,003
Central American agouti (*Dasyprocta punctata*)[5]	T	2,41	29,70	0,003
Long-tailed chinchilla (*Chinchilla lanigera*)[5]	T	3,66	32,37	0,028
Eastern gray squirrel (*Sciurus carolinensis*)[5]	T	2,18	34,27	0,011
Wood mouse (*Apodemus sylvaticus*)[5]	T	2,61	25,25	0,040
Yellow-necked mouse (*Apodemus flavicolis*)[5]	T	2,28	22,82	0,023

Tab.3: List of values obtained from existing publications. Ecology: S - subterranean, F – fossorial, T – terrestrial, LR –ratio of mallear and incudial levers, AR –ratio of eardrum and stapedial footplate areas, OM – mass of malleus and incus, BM – body mass.

References: 1 – Mason et al., 2010, 2 – Burda et al., 1992, 3 – Wilkins et al., 1999, 4 – Lange et al., 2005, 5 – Mason, 1999, 6. Lange et al., 2004, 7 - Mason, 2004, 8 – Hemilä, 1995, 9 – Nummela, 1995, 10 – Webster and Webster, 1975.

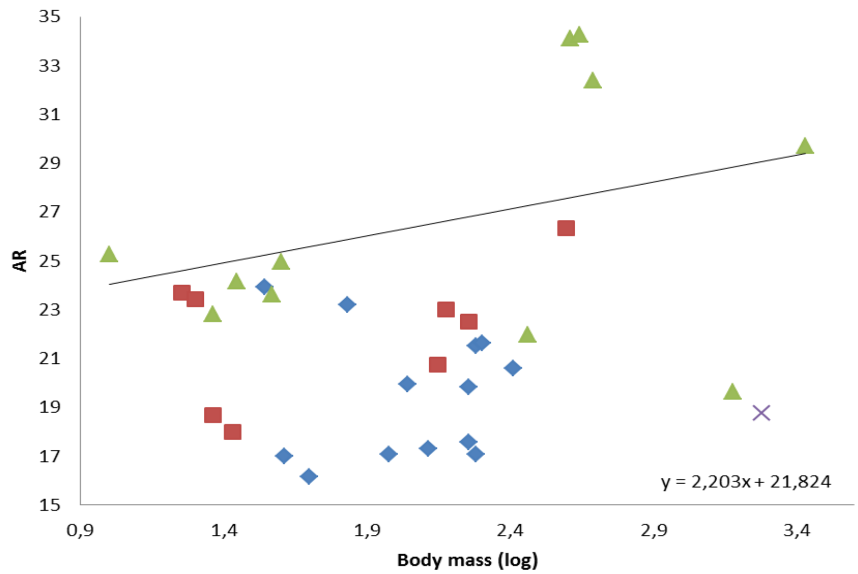

Fig. 13. Relationship between area ratio and body mass of various rodent species with different level of subterranean life. Triangles – aboveground species, squares – fossorial species, diamonds – subterranean species, cross – *Rhizomys sinensis*; the regression line was calculated for abovegroung species.

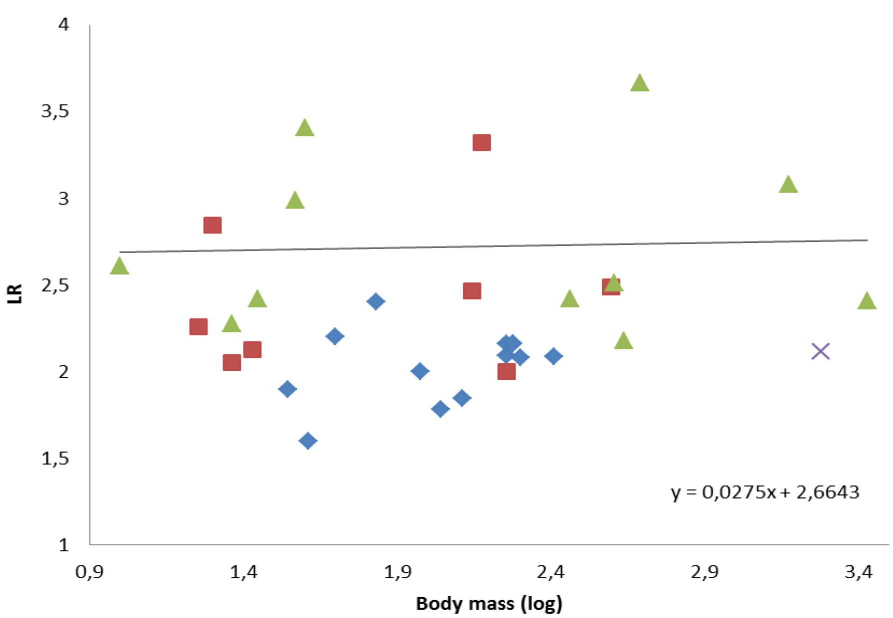

Fig. 14. Relationship between lever ratio and body mass of various rodent species with different level of subterranean life. Triangles – aboveground species, squares – fossorial species, diamonds – subterranean species, cross – *Rhizomys sinensis*; the regression line was calculated for abovegroung species.

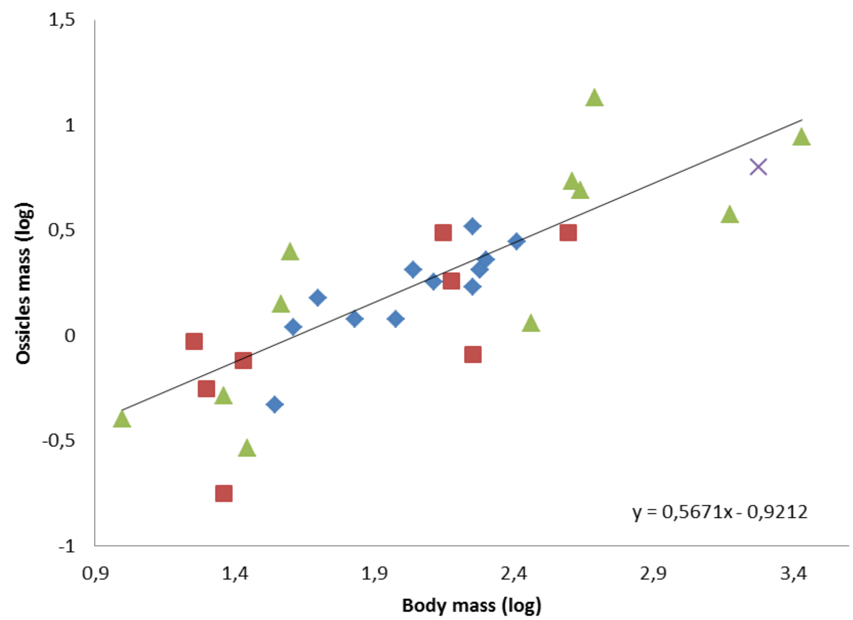

Fig. 15. Reationship between Malleus and incus mass and body mass of various rodent species with different level of subterranean life. Triangles – aboveground species, squares – fossorial species, diamonds – subterranean species, cross – *Rhizomys sinensis*; the regression line was calculated for abovegroung species.

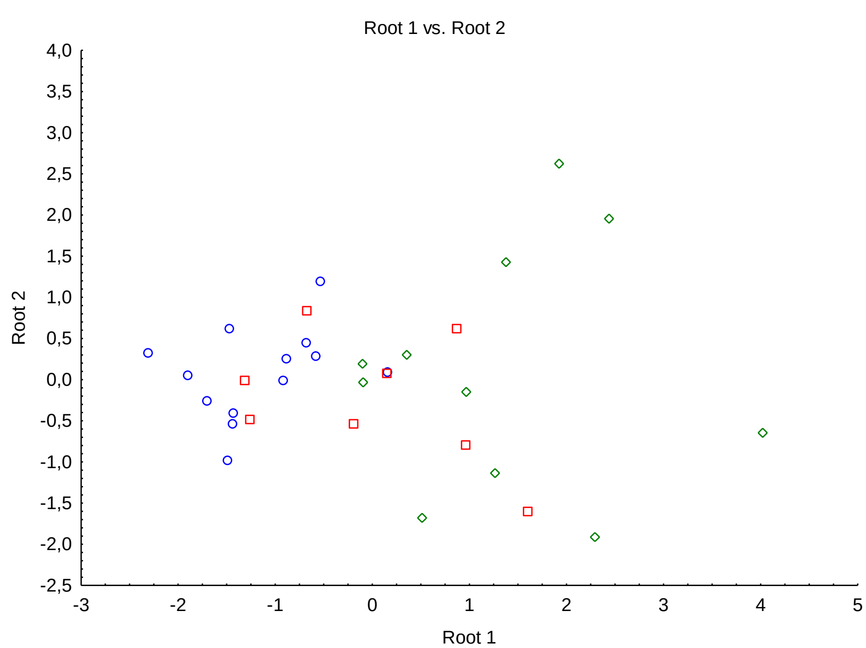

Fig.16. Distribution of rodent species with different style of life using DFA method. Circles – subterranean rodents, squares – fossorial rodents, diamonds – aboveground rodents.

4. DISCUSSION

Ecology and style of life of the many mammalian species is mirrored in ear morphology (Burda et al., 1992, Mason, 2001). In these cases, we should be able to estimate some aspects of species ecology based on its ear morphology. This approach is useful especially in species difficult to study, because they live in inaccessible places or countries, or they are very rare or even extinct (Coleman et al., 2010, Gleich et al., 2005). In my study, I analyzed ear morphology of species very little known for science and I tried to reconstruct the ecology with the special focus on degree of its fossoriality. I also tried to find the typical ear morphology characters of the fossorial species by the comparison of results published so far.

4.1. Hearing specialization

The first question in my study is how to define the unspecialized ear. Rodents often considered as generalists like mice and rats are frequently used for the comparison with low frequency specialists (e.g. Burda et al., 1992, Lange, 2004). However, it was already highlighted that they should be regarded more as high-frequency specialists (Heffner et al., 2001, Mason, 2001, Vater et al., 2010). In addition, the microtype middle ear in myomorphs (in contrast with freely mobile type) doesn't occur in all families; hence it can be neither ancestral, nor unspecialized type (Argyle and Mason, 2008).

On the other hand the "freely-mobile" type of ear common in low frequency specialists (Burda et al., 1992) is not necessarily unique for them, because it was found also in some aboveground species as chinchilla or squirrel (Mason, 2001, 2013, Puria and Steele, 2010). Hence the question, how unspecialized rodent middle ear looks like or does even exist unspecialized ear, is still unanswered and opened.

Another problem in studies on comparative morphology of the ear is the lack of studies on phylogenetically closely related species. Some features considered as ecological specialization might be results of close phylogenetic origin (Argyle and Mason, 2008). Recently, "Ctenohystrica type" of middle ear was suggested as unique for auditory apparatus in hystricomorphs (Mason, 2013). This ear type has certain similarities with the subterranean mammal's middle ear, such as enlarged mallei head, relatively large incus and reduction of middle ear muscles. Those similarities can be caused simply by the fact that most of the described middle ears in subterranean mammals are from suborder hystricomorpha and also that other studied species of hystricomorph rodents such as the guinea pig or chinchilla hear rather low-frequencies so they could be regarded as low-frequency specialist (Bruns et al., 1988, Burda 1984, Burda et al., 1988, Müller, 2010).

4.2. Outer and middle ear

In spite that pina is often reduced or even missing in subterranean mammals (Nevo, 1979). In Chinese bamboo rat, its length is more than 1.5 cm; it indicates fossorial or even aboveground way of life, which is supported also by non-specialized eyes and relatively long tail. In some specimens was found large amount of cerumen, which is in subterranean mammals considered as a way to decrease the ear efficiency (Burda et al., 1992). In some rodents expanded bulla works as a Helmholtz resonator and increases the sound pressure in low frequencies (Plassmann and Kadel, 1991). Therefore, large bullar volume indicates good low-frequency hearing (Argyle and Mason, 2008). The bullar volume related to body mass was in Chinese bamboo rat lower than in subterranean mole-rats (Burda et al., 1992). Nevertheless, there are also subterranean species specialized on low frequency hearing with normal size of bullae such as *Spalax ehrenbergi* or *Heterocephalus glaber* (Bruns, 1988, Heffner and Heffner, 1992, 1993, Schleich and Vassallo, 2003).

Subterranean species generally possess relatively larger tympanic membrane without pars flaccida, or Shrapnell's membrane, which increase hearing sensitivity to low frequencies (Burda et al., 1992, Fleischer, 1978, Mason, 2006, Schleich and Busch, 2004). There was no apparent pars flaccida in Chinese bamboo rat, but the tympanic membrane wasn't enlarged compared to unspecialized species (Hemilä et al., 1995). Manubrium of malleus generally divides eardrum in anterior and posterior section. In species with separate hearing ossicles the posterior section is larger than the anterior one, while in species with synostosed malleus and incus both parts are roughly equally large (Puria and Steele, 2010). In Chinese bamboo rat, both eardrum sections are approximately of the same size, though the ossicles are not synostosed. Separation of malleus and incus during the dissection was particularly difficult in some specimens. It is thus possible that ossicles are moving during the rotation around the axis as if are synostosed. The synostosed malleus and incus is typical feature of hystricomorphs which are considered as low frequency specialists (Argyle and Mason, 2008, Mason 2013).

The middle ear in Chinese bamboo rat is clearly of freely mobile type, due to absence of orbicular apophysis in malleus and also because of its large head (Fleischer, 1978). Some other traits coupled with this type of middle ear were found; the ossicles loosely attached to the bulla due to reduction of middle ear muscles and relatively large incus compared to malleus (Fleischer, 1978, Mason, 2013).

In *Spalax*, *Eospalax* and *Tachyoryctes* which are species closely related to bamboo rats, special type of perception seismic signals by ear, so called jaw listening, was observed (Mason, 2010, Rado et al., 1989). One way how seismic signals are transmitted into ear is the articulation between incus and periotic bone through so called bonny cup (Mason, 2010). We found structure similar to the bony cup in Chinese bamboo rat, but the short arm of incus wasn't firmly anchored in this structure. The incus was connected with the bonny cup only by ligaments. Therefore, the seismic signals probably cannot be transmitted into the ear this way.

Stapedial footplate in subterranean species is enlarged to decrease the ratio between areas of eardrum and stapedial footplate (Burda, pers. com., Mason, 2001, Mason, 2006). In Chinese bamboo rat, the tympanic membrane is of normal size, but the area ratio is low (fig. 13.). It is reduced by surface of stapedial footplate which is higher than in aboveground species. The stapedial muscle was present, but apparently weak, which is typical for freely mobile type of middle ear (Fleischer, 1978).

Middle ear of Chinese bamboo-rat seems to be specialized for underground acoustic conditions. Freely mobile type of ossicles attachment is considered as low frequency specialist's trait (Begall and Burda, 2006, Burda et al., 1992, Mason, 2006, Mason, 2013). On the other hand it's also typical for mammals with medium or larger bullae (Fleischer, 1978, Lavender, 2011), as Chinese bamboo rat. In comparison with other rodent species the ratio of mallear and incudial levers and ratio of eardrum and stapedial footplate were low (fig. 13., 14.); this trait determines poor sound wave transmission and thus low sensitivity of middle ear (Burda et al., 1992, Mason, 2001) which is considered as protection against overstimulation in underground environment (Burda et al., 1992, Wilkins et al., 1999). The DFA analysis confirmed these assumptions by classification Chinese bamboo rat as subterranean species. Therefore, we are not able to determine if the Chinese bamboo rat is subterranean or fossorial based solely on the middle ear morphology.

4.3. Inner ear

The number of cochlear coils is species specific and also family specific in some cases (Burda et al, 1988). It wasn't find any direct relation between numbers of coils and hearing range so far, but it is probably influenced by hearing ecology to a certain extent (Fleischer 1978). In subterranean species the cochlea has more than three turns (Begall and Burda, 2006, Burda et al., 1988, Müller et al., 1992); besides subterranean species the high number of cochlear coils is typical for hystricognaths (Schleich et al., 2006, West, 1975). In Chinese bamboo rat, the cochlea has three and a quarter turns, which is relatively high for non-hystricognath rodent species (Begall et al., 2007, Vater and Kössl, 2011), which possibly suggests the subterranean way of life.

Basilar membrane length is negatively correlated with the high and low frequency hearing limit (Rosowski, 1992, West, 1985). It means that the hearing range of species which possess shorter basilar membrane is shifted toward high frequencies (Echteler et al., 1994) and conversely, increases in basilar membrane length are correlated with a downward shift in audible frequencies (Vater and Kössl, 2011).

West (1985) studied relationship between number of cochlear turns, width of basilar membrane and hearing limits in ground dwelling mammals. He excluded any hearing specialist, low or high frequency, because the correlation between these values is very weak in the specialized species (Echteler et al., 1994). The hearing range calculated in Chinese bamboo rat according West (1985) is ten octaves. As far as we cannot clearly say the extent of Chinese bamboo rat hearing specialization, the estimated hearing range could be lower. Hearing range of specialists is lower than expected by length of basilar membrane due to overrepresentation of some frequencies, so called acoustic fovea (Bruns et al., 1988, Müller et al., 1992).

According to Békésy (1960) basilar membrane is tonotopically arranged and its width and thickness are the parameters which correspond with basoapical distribution of frequencies along its length. We used the width of three rows of outer hair cells, or "triade" rather than basilar membrane width for comparison of Chinese bamboo rat with other species, because measurement of basilar membrane width is inaccurate and dependent on measuring method (Burda, pers. com.). Nevertheless, the basoapical trend is very similar when measured on basilar membrane width or triade width. The width was lower in the base and increased toward the apex, as in other studied species (Burda et al., 1988, Burda and Brains, 1988, Schleich et al., 2006). The slope of basilar membrane and the triade width varied along its length. In basal half and in the part from 70% to apex the slope was relatively steep; meanwhile in part around 50 - 60% from basis the width was almost constant (fig. 8.,9.). This change in slope of basilar membrane and the triade width wasn’t as obvious as in *Spalax ehrenbergi* or *Cryptomys hottentotus*, which possess acoustic fovea (Bruns et al., 1988, Burda et al., 1989, Müller et al., 1992, Lange, 2005) (fig. 17.), but it corresponds with better resolution capabilities in lower frequencies (Burda et al., 1989, Burda, pers.com., Echteler et al., 1994).

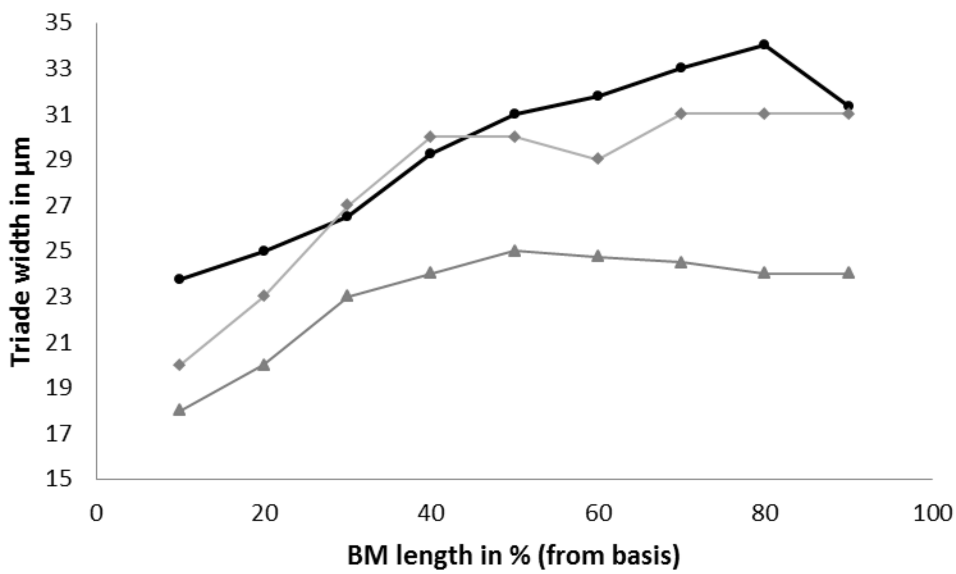

Fig. 17. Comparision of the slope in width of three outer hair cell rows. Black circles – *Rhizomys sinensis*, grey diamonds – *Cryptomys hottentottus*, grey triangles. *Spalax ehrenbergi*. In *C. hottentotus* and *S. ehrenbergi* acoustic fovea can be seen between 50 and 80% of BM width.

The density of cochlear hair cells of both types increased toward the apex, phenomenon which is correlated with the best sensitivity of hearing restricted to lower frequencies (Burda et al., 1989, Schleich, 2006). The density of both types of hair cells was slightly higher in 60% of basilar membrane length (fig. 10. – 12.). Moreover, the ratio of outer and inner hair cells in this cochlear part was lower than expected; the increase in density of inner hair cells (cochlear receptors) was higher than in density of outer hair cells (cochlear amplifiers). The high number of receptors per millimeter signifies place of best hearing (Burda et al., 1988, Burda et al., 1989); high density of receptors in 60% of basilar membrane length correspond to lower frequencies.

4.4. Degree of subterranean specialization in Chinese bamboo rat

Outer ear of the Chinese bamboo rat carry features typical for aboveground or fossorial species (the pinna is relatively large) whereas, the middle ear indicates more ambiguous situation. There are few parameters with uncertain meaning (small bullar volume, or absence of bonny cup). On the other hand all the other parameters suggest that this species can be considered as a subterranean specialist (freely mobile type of ear, absence of pars flaccida, low ratio between the areas of eardrum and stapedial footplate, low ratio between mallear and incudial lever). Low-frequency specializations prevail in inner ear of Chinese bamboo rat (the high number of cochlear coils, the length and slope of basilar membrane or increasing density of hair cells towards the cochlear apex). However, the acoustic fovea is not present, which suggest only imperfect specialization.

The only article about ecology of the Chinese bamboo rat is from He (1984). He wrote that length of subterranean system of the Chines bamboo rat 30 meters in average. For comparison the system lengths in subterranean solitary rodents like silvery mole-rat (*Heliophobius argenteocinereus*) or blind mole rat (*Spalax ehrenbergi*) are twice as long (Šumbera et al., 2003, Lövy, pers. com.). The burrow system length in Chinese bamboo rat is of comparable length as in solitairy fossorial rodents as pocket gophers (*Geomys bursarius*) or tuco-tuco (*Ctenomys talarum*) (Wilkins and Roberts, 2007, Schleich and Antenucci, 2009).

Our findings suggest that we are able to distinguish between aboveground and subterranean species of rodents based solely on their ear morphology, but we are not able to differentiate the fossorial rodents reliably. The fossorial species share features of both subterranean and aboveground group and they could be distinguished only indirectly. It is very useful if we could use although information about species ecology and overall morphology besides ear morphology.

5. CONCLUSIONS

I examined morphology of outer, middle and inner ear in Chinese bamboo rat (*Rhizomys sinensis*). Many features typical for subterranean specialists were presented there, such as freely mobile type of the middle ear, low ratio of malear and incudial levers, low ratio of eardrum and stapedial footplate area, low slope of basilar membrane and higher hair cells density in the apical part of cochlea. On the other hand, this species lack other features typical for subterranean species, as reduced pinna or acoustic fovea. Based on my conclusions, overall body morphology and ecological data published so far, is possible to consider the Chinese bamboo rat as fossorial species.

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7. APPENDICES

App. 1. Chinese bamboo rat (*Rhizomys sinensis*).

App. 2. Biotope typical for Chineese bamboo rat occurring.