

Comparative and functional morphology of the middle ear in Zambezian mole-rats (*Coetomys* – *Cryptomys*, Bathyergidae)

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ABSTRACT. Within the family Bathyergidae, the genus *Coetomys* (*Cryptomys*) is the most speciose. However, an unambiguous morphological or morphometrical species diagnosis has not been feasible to date. The middle ear structures involved in sound transmission were examined and measured in six species of Zambezian mole-rats of varying body sizes : *Coetomys amatus*, *C. anelli*, *C. darlingi*, *C. kafuensis*, *C. mehowi* and *C. whytei*. Comparisons revealed many differences in the shape of the middle ear ossicles allowing species differentiation. Bullar volume, eardrum area and cross-sectional area of the bony meatus were positively correlated with body size (as represented by condylo-basal length) whereas the size of middle ear ossicles was rather independent of body size. Middle ears shared typical features with those found in low-frequency hearing mammals. Contrary to the findings in heteromyids and the *Spalax ehrenbergi* species complex, within the genus *Coetomys*, those species occupying more mesic habitats had more efficient tympano-ossicular systems (suggesting more sensitive hearing) than species from drier habitats.

KEY WORDS : middle ear, functional morphology, *Coetomys*, *Cryptomys*, species diagnosis.

INTRODUCTION

Among the five genera of the Bathyergidae (African mole-rats), representatives of the genus *Coetomys* (*Cryptomys*) can be easily recognized, yet to date it is not possible to determine different species within the genus by classical morpho-taxonomic traits like skull, pelage or size. The genus *Coetomys* is the most speciose among the bathyergid genera. At least 16 species distributed from West through Central to South Africa have been described in literature (cf., INGRAM et al., 2004). Most of the species to date have been identified within the Zambezian phytochorion. All the species have been identified on the basis of karyological, allozyme, or DNA analyses.

The existence of cryptic – yet morphologically practically indistinguishable – sibling species parallels the findings in some other subterranean rodents like blind mole-rats (*Spalax*) (NEVO et al., 2001). Nevertheless, various structures and parameters of the ear in the *Spalax ehrenbergi* species complex have proved to be of use for morphological species diagnosis (BURDA et al., 1990) supporting thus also the experience of palaeontologists and taxonomists as reflected by LAVOCAT & PARENT (1985) who noted that the auditory region serves as an excellent guide for following the evolution of the dentition. Moreover, it has been shown that in the blind mole-rat in particular (like in other subterranean mammals in general), middle ear morphology reflects also the species' habitat and way of life (BURDA et al., 1989, 1990, 1992). VON BEKESY (1974) stated that the physical laws served as guidelines for the evolution of the structures and functions of the middle and inner ear. Additionally, morpho-

functional aspects of the middle ear are considered to reflect adaptations to the species' environment (e. g. WEBSTER & WEBSTER, 1975). The study of the ear has a great potential for both comparative taxonomic and functional interpretations.

Taking these facts into account we decided to study the middle ear structures in *Coetomys* species and to test their diagnostic value. Furthermore, since the selected Zambezian species also represent forms occupying different climatic regions, they provide unique opportunity to test general applicability of conclusions derived from the study of the ear in blind mole-rats (see above).

MATERIAL AND METHODS

Middle ears of six species of African mole-rats of varying body sizes (between 60 g in *Coetomys amatus* and 300 g in *C. mehowi*) representing different clades of *Coetomys* were examined. (*Coetomys* represents a newly described genus, INGRAM et al., 2004, which has been previously referred to as *Cryptomys*). They all originate from the Zambezian phytochorion : *Coetomys kafuensis* (adults N = 11, juveniles N = 1) from Itezhi-Tezhi (Zambia), *C. anelli* (adults N = 9, juveniles N = 1) from Lusaka and surroundings (Zambia), *C. amatus* (adults N = 1) from Chibale (Zambia), *C. darlingi* (adults N = 2) from Chimanimani (Zimbabwe), *C. mehowi*, (adults N = 10, juveniles N = 1) from the Copperbelt province (Zambia) and *C. whytei* (adults N = 5, juveniles N = 3) from Karonga (Malawi). All the specimens were preserved in 70%-ethanol for at least 4 weeks.

Comparative morphometry

Condylo-basal length (anterior face of the upper incisors to the posterior edge of the occipital condyles) and bullar dimensions (length of the longest axis of the bulla, width and height from the top of the auditory meatus to the bottom of the bulla tympanica) were measured with digital callipers. Middle ear structures were prepared, examined under a stereoscopic binocular and drawn using a drawing tubus at different magnifications. Measurements were taken from drawings considering the respective magnifications (15x – 40x). The following variables were measured : longer and shorter radius (perpendicular to the longest radius) of the eardrum, longer and shorter radius of the cross-section of the bony meatus, length of the mallear lever, length of the incudal lever, longer and shorter radius of the stapedial footplate. Levers were measured perpendicular to the axis of rotation from the axis of rotation to the umbo of the eardrum and to the point of action of the incus. The eardrum, meatus and stapedial footplate area were calculated as ellipses ($\pi \times$ longer radius \times shorter radius), bullar volume was calculated as the product of length \times height \times width. Bullar volume, eardrum area, meatus area, mallear lever, incudal lever and stapedial footplate area were correlated with condylo-basal length (linear regression with ANOVA, SPSS 11.0).

Functional morphology

Movements of the eardrum are transmitted to the mallear-incudal complex and then to the stapes which is attached to the vestibular window of the cochlea. Through the arrangement of this ossicular chain, pressure and force are amplified. This is accomplished by two mechanisms :

the difference in the area of the eardrum and the stapedial footplate leading to the area ratio and the difference in the length of mallear and incudal levers leading to the lever ratio (RELKIN, 1988). The product of both ratios (transformation ratio) expresses the middle ear efficiency in sound transmission and thus middle ear sensitivity (FLEISCHER, 1978).

Climatic data

The mean annual precipitation was calculated from monthly values from about an average of 55 years recorded by the nearest climatological station according to the Global Historical Climatological Network database : <<http://www.ncdc.noaa.gov/ol/climate/research/ghcn/ghcn.html>>.

RESULTS

Comparative morphology

In the studied species, manubrium mallei and crus longum of the incus were rather parallel to each another (Fig. 1). The eardrum was nearly circular, no pars flaccida was apparent. Middle ear ossicles were not fused with the tympanic bone, so the middle ears were of the “freely mobile” type. Malleus and incus were fused whereas the incudo-stapedial joint was rather loose and the malleo-incudal complex separated easily from the stapes. A gonial was missing, the footplate area was quite large and the middle ear (stapedial and tensor tympani) muscles were reduced or missing. The anterior and posterior crura of the stapes were asymmetric, no stapedial artery was found.

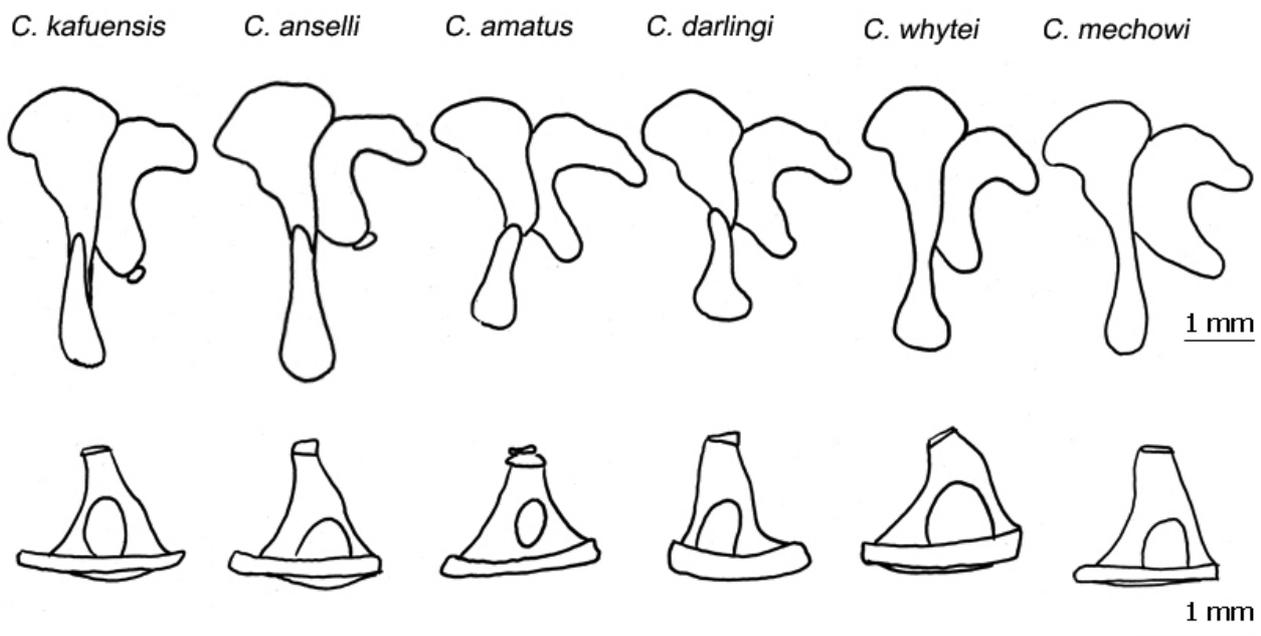


Fig. 1. – Shape of the middle ear ossicles (left - anterior, right – posterior).

The shape of the middle ear ossicles (Fig. 1) was rather similar; nevertheless some species-specific differences were identified. Thus, the head of the malleus was particularly massive in *C. whytei*. The transitional part between manubrium and head of the malleus where the tensor tympani muscle attaches was rather straight in *C. whytei* and *C. amatus*. In the other species, there was a processus which was more (*C. anseli*) or less (*C. kafuensis*) conspicuous. In *C. kafuensis* and *C. darlingi*, crus stapedis posterior was broader than crus stapedis anterior whereas the opposite was true in *C. anseli*, *C. whytei*, *C. amatus* and *C. mechowii*. The attachment of the stapedial muscle was clearly differently located and shaped in the studied

species. Within particular species, no differences were found in shape of middle ear ossicles between adult and juvenile specimens.

Comparative morphometry

The mean values of particular parameters (Table 1) do not include juveniles. Bullar volume, eardrum and meatus area tended to be correlated with condylo-basal length. The stapedial footplate area was absolutely and relatively noticeably small in *C. amatus*, *C. darlingi* and *C. whytei*. Mallear and incudal lever seemed to be independent of body size.

TABLE 1

Measurements (mean values and standard deviations) of middle ear structures. in adult specimens. (LCB = condylo-basal length, Bulla = bullar volume, AM = cross-sectional area of bony meatus, MT = area of membrana tympani, BS = area of basis stapedis, ML = mallear lever, IL = incudal lever)

	N	LCB (mm)	Bulla (mm ³)	AM (mm ²)	MT (mm ²)	BS (mm ²)	ML (mm)	IL (mm)
<i>C. kafuensis</i>	11	27.8 ± 1.8	321 ± 46	1.0 ± 0.2	6.8 ± 1.4	0.59 ± 0.28	2.1 ± 0.1	1.1 ± 0.2
<i>C. anseli</i>	9	33.1 ± 1.9	380 ± 68	0.9 ± 0.3	8.6 ± 1.1	0.53 ± 0.10	2.1 ± 0.3	1.1 ± 0.1
<i>C. amatus</i>	1	32.5	208	0.5	8.9	0.46	1.9	1.0
<i>C. darlingi</i>	2	36.2 ± 3.9	331 ± 11	0.7 ± 0.5	9.7 ± 5.8	0.48 ± 0.3	2.0 ± 0.1	1.0 ± 0.1
<i>C. mechowii</i>	10	45.5 ± 6.4	913 ± 302	1.4 ± 0.3	14.1 ± 2.4	0.62 ± 0.08	2.5 ± 0.2	1.3 ± 0.1
<i>C. whytei</i>	5	36.9 ± 1.8	469 ± 110	0.9 ± 0.1	11.6 ± 1.4	0.50 ± 0.04	2.4 ± 0.1	1.0 ± 0.1

When juvenile specimens were included into the analysis, volume of the tympanic cavity was strongly positively correlated with the condylo-basal length ($R^2 = 0.797$, $p < 0.001$, ANOVA). Eardrum area and cross-sectional area of the bony meatus were less dependent upon the body size ($R^2 = 0.299$, $p < 0.001$, ANOVA and $R^2 = 0.464$, $p < 0.001$, ANOVA) (Fig. 2). The length of mallear and incudal levers ($R^2 = 0.148$, $p = 0.01$ and $R^2 = 0.008$, $p = 0.557$, ANOVA) and the area of the stapedial footplate ($R^2 = 0.205$, $p < 0.005$, ANOVA) were rather independent of the body size (Fig. 3).

Functional morphology

The calculated functional parameters (Table 2) could be related to the mean annual precipitation in the area of occurrence of the particular species: With increasing rainfall the transformation ratio (expressing middle ear sensitivity) increased from 25 in *C. kafuensis* occurring in the driest habitat through *C. anseli* (33), *C. amatus* (37), *C. darlingi* (43), *C. mechowii* (42) to 52 in *C. whytei* living in the most mesic habitat.

TABLE 2

Precipitation in the area of occurrence and morpho-functional parameters (means and standard deviations) of the middle ear in adult *Coetomys* mole-rats of different species. (LCB = condylo-basal length AR = area ratio, LR = lever ratio, TR = transformation ratio (AR x LR))

	N	annual precipitation (mm/year)	LCB (mm)	AR	LR	TR
<i>C. kafuensis</i>	11	787	27.8 ± 1.8	13.1 ± 2.2	1.3 ± 0.3	25.2 ± 6.1
<i>C. anseli</i>	9	822	33.1 ± 1.9	16.4 ± 4.4	2.0 ± 0.4	33.2 ± 10.1
<i>C. amatus</i>	1	1132	32.5	19.3	1.9	36.8
<i>C. darlingi</i>	2	1150	36.2 ± 3.9	20.3 ± 2.7	2.1 ± 0.0	42.7 ± 5.4
<i>C. mechowii</i>	10	1185	45.5 ± 6.4	21.0 ± 4.6	2.0 ± 0.3	42.3 ± 14.4
<i>C. whytei</i>	5	1603	36.9 ± 1.8	23.2 ± 2.0	2.2 ± 0.3	52.2 ± 7.7

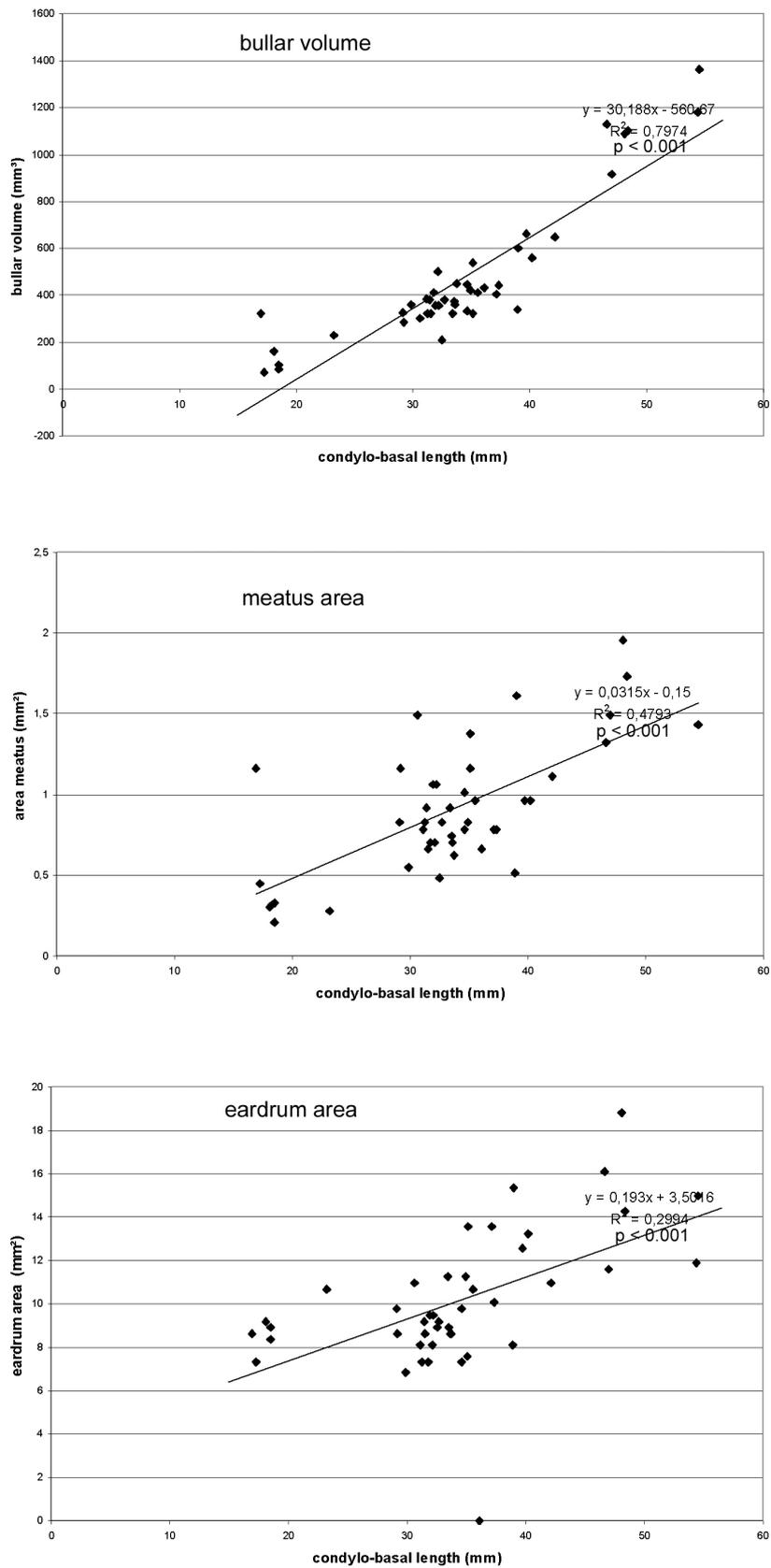


Fig. 2. – Linear regression of condylo-basal length and size of middle ear structures : bullar volume, meatus and eardrum area.

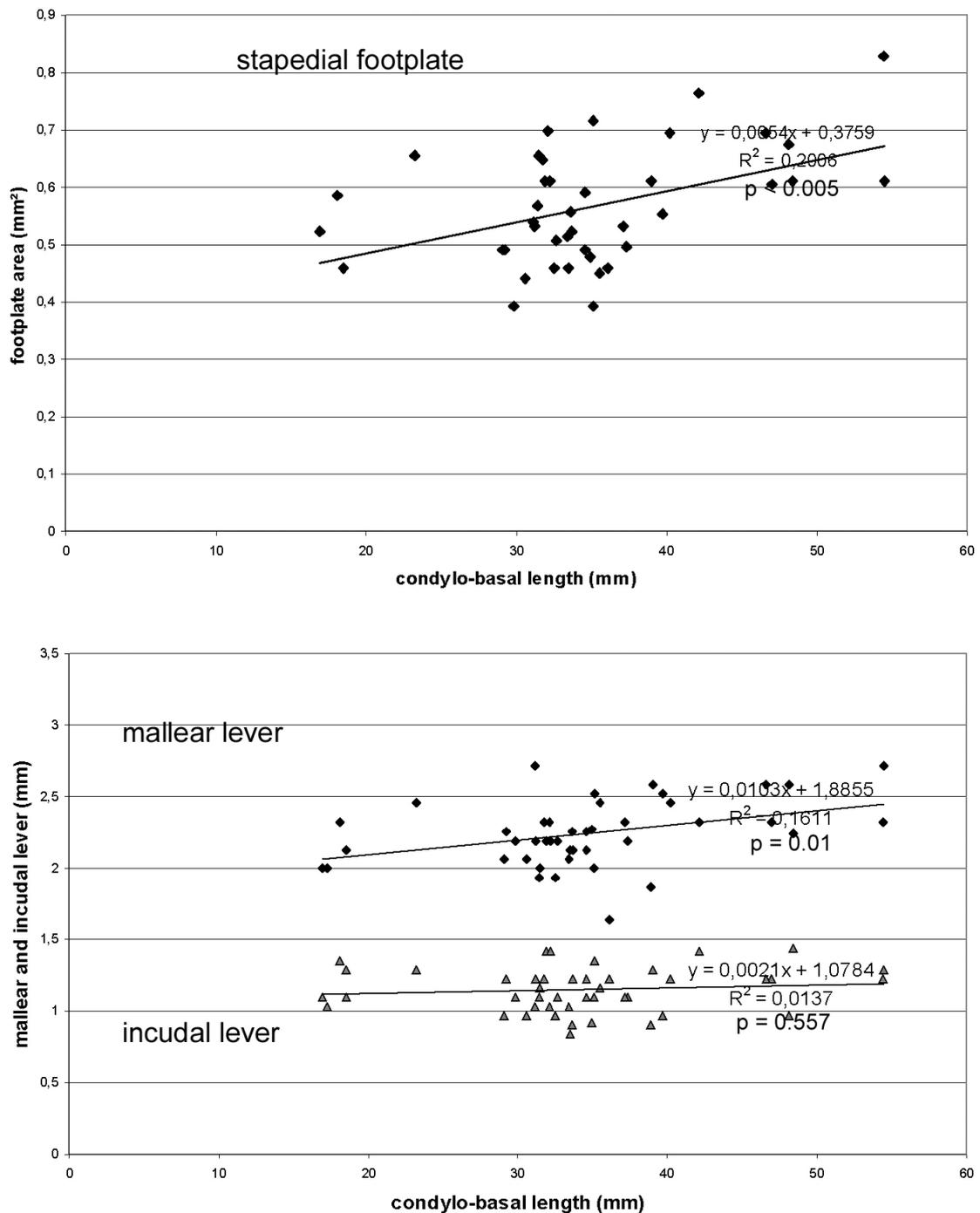


Fig. 3. – Linear regression of condylo-basal length and size of the middle ear ossicles : stapedial footplate area, malleal and incudal lever.

DISCUSSION

Comparative morphology

Morphology of the middle ear ossicles can be applied to enable species diagnosis. Although the sample sizes in *C. amatus* and *C. darlingi* are very small, there is good reason to assume that morphology described on the basis of just one or few individuals is representative of a species. Middle ear morphology is known to be a reliable

species-specific trait with minimum individual variability (BURDA, 1979). Actually, in some cases it is not necessary to consider middle ear morphology if the species can be easily distinguished on the basis of the geographic origin and/or the general body size.

Since the morphology and morphometry of the middle ear ossicles (which derive from the endocranium) is almost adult-like at birth, even juvenile specimens can be reliably determined.

Freely mobile middle ears are considered as a typical trait characterizing low-frequency hearing mammals. The studied species shared with low-frequency hearing forms also other traits like fused ossicles, lacking gonial, large stapedial footplate and reduced middle ear muscles (cf., BURDA et al., 1992). These traits are considered as adaptations to optimize low-frequency hearing (MASON, 2001; FLEISCHER, 1978, 1973) in underground burrows where low frequencies of around 500 Hz are best transmitted (HETH et al., 1986) whereas lower and higher frequencies are absorbed more rapidly.

Functional morphology

In the studied species, the effectiveness of the middle ear in sound transmission increased with increasing humidity of their particular habitats. This relationship is surprising because in *Spalax ehrenbergi* (BURDA et al., 1990) and several heteromyids (WEBSTER & WEBSTER, 1980), the opposite correlation was found and interpreted as adaptation to the environment. Sound transmission is influenced by several factors from which relative humidity is one (BASS et al., 1995): with increasing humidity attenuation first increases and after a turning point it decreases again. *Spalax* and heteromyids are adapted to the attenuation which increases with increasing aridity in their habitat. At least for heteromyids, acoustic communication over long distances and predator avoidance is of great importance (WEBSTER & WEBSTER, 1980, 1992).

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