MASSIVE MALLEI IN MOLES: MIDDLE EAR ADAPTATIONS SUBSERVING SEISMIC SENSITIVITY

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1 INTRODUCTION

It has been popularly assumed, at least since the time of Pliny the Elder [1], that the hearing of moles and other subterranean mammals is acute, perhaps to compensate for their poor vision. In recent times, behavioural audiograms of subterranean species (most studies have been of rodents) have shown that audition is biased towards unusually low frequencies for such small mammals, typically being restricted to under about 20 kHz at 60 dB SPL [2, 3, 4, 5]. Low frequencies of a few hundred Hertz have been found to travel further than higher frequencies underground [6], so efficient low-frequency hearing has been regarded as adaptively advantageous [7, 8, 9]. Several features of the middle ear apparatus identified in subterranean mammals, such as enlarged ear-drums, enlarged bullar cavities and “freely mobile” ossicles, have accordingly been interpreted as adaptations to improve low-frequency hearing [9, 10, 11]. By contrast, other authors have regarded the hearing of subterranean mammals as “degenerate” or “vestigial”: restricted to low frequencies through loss of high frequency hearing, but not unusually acute at any frequency [2, 3, 4].

In principle at least, air-borne sound is not the only source of input to the ears of subterranean mammals. Several species are believed to communicate or navigate using low-frequency ground-borne (seismic) vibrations [12, 13, 14, 15]. The sensory mechanisms subserving this ability are not always clear: in the case of the mole-rat *Nannospalax ehrenbergi*, whether vibratory sensitivity is primarily conferred by the auditory or somatosensory systems has been a matter of some dispute [12, 16, 17, 18].

The author has examined the middle ear morphology of many species of subterranean mammals, to investigate whether or not the ears are unusually adapted towards the transmission of low-frequency vibrations, conveyed to the animal either as air-borne or as seismic waves. This report focuses on two unrelated families of small, insectivorous, fossorial mammals: the talpid moles (order Eulipotyphla, family Talpidae), familiar animals in North America and Eurasia, and the golden moles (order Afrosoricida, family Chrysochloridae), which occupy a similar ecological niche in sub-Saharan Africa. Some, but not all, genera within both families have long been known to possess greatly hypertrophied mallei [19, 20]. The functional implications of these unusually large ear bones are considered here.

2 MATERIALS AND METHODS

Middle ear morphology was investigated mainly through dissection of specimens under light microscopy; some skulls were examined non-invasively using high-resolution computed tomography (micro-CT). The specimens were either prepared museum skulls, or corpses which had been frozen or chemically preserved. Many of these specimens were from the collections of the University Museum of Zoology, Cambridge, The Natural History Museum, London, or the Transvaal Museum, Pretoria. Full lists of the specimens examined and the exact techniques used are to be found in the original papers from which much of this report is taken [21, 22, 23, 24, 25, 26].

3 MIDDLE EAR MORPHOLOGY

3.1 Middle ear morphology in talpid moles

Talpid moles can be divided into three broad groups, according to their middle ear morphology, these groups probably representing functional rather than taxonomic divisions [21].

“Group 1” talpids include *Neurotrichus*, *Parascalops* and *Condylura*; several other genera, including other shrew-moles and desmans, fall into this category. These animals have a malleus of what has been referred to as the “microtype” morphology [27], characterized by the presence of a large orbicular apophysis and an elongated anterior process (Figure 1a). The anterior process is firmly articulated with the ectotympanic bone, which itself is connected to the basicranium through fibrous tissue only, so there is no complete bony bulla. The tensor tympani muscle is present but very small, and the tympanic membrane has a pars flaccida.

“Group 2” talpids include, among others, those in the genera *Talpa*, *Scapanus* and *Scalopus*. These animals have “freely mobile” ossicles [27], the malleus (Figure 1b) being loosely connected to the ectotympanic by means of an abbreviated anterior process. The orbicular apophysis is very small or absent, but the head of the malleus is enlarged relative to that of “microtype” species. Group 2 talpids have a complete auditory bulla and a stapedial artery enclosed within a complete bony tube; they lack a tensor tympani muscle and the pars flaccida of the tympanic membrane is reduced or absent. *Talpa* and *Scapanus* possess an interbullar connection: some of the basicranial bones, including the basisphenoid, are pneumatized and spongy, the air-spaces within forming a connection between the left and right middle ear cavities.

“Group 3” talpids are represented by the Asian genera *Parascaptor* and *Scaptochirus*. This group is characterized by the possession of a hypertrophied malleus of unique morphology (Figure 1c): the body is expanded and globular, while the anterior process is a very thin, triangular lamina and the manubrium is unusually delicate. In *Parascaptor*, the malleus mass (around 3 mg) is more than three times that of *Talpa*. The malleus of *Scaptochirus* is considerably larger still: calculations based on a micro-CT reconstruction suggest that it weighs around 20 mg. Other middle ear characteristics of the Group 3 talpids generally resemble those of Group 2 species.

3.2 Middle ear morphology in golden moles

The golden mole family Chrysochloridae is divided into two subfamilies, the Amblysominae and the Chrysochlorinae [28]. Genera in the subfamily Amblysominae (*Amblysomus*, *Neamblysomus* and *Calcochloris*) possess “freely mobile” auditory ossicles (Figure 1d) which are not unusual in size or shape in comparison with those of most terrestrial mammals of similar body mass. Genera within the Chrysochlorinae possess hypertrophied mallei, the size and shape of which vary by genus. The mallei of *Chlorotalpa* and *Carpitalpa* species are enlarged through the expansion of the head, dorsal and rostral to the articulation with the incus, and are 3-4 times the mass of the mallei of *Amblysomus hottentotus*. Other chrysochlorine genera show considerably more pronounced expansion of the malleus head, which is club-shaped in *Chrysochloris* (Figure 1e) and *Cryptochloris*, ovoid or pear-shaped in *Eremitalpa* (Figure 1f) and almost spherical in *Chrysospalax*. The largest malleus in golden moles, that of *Chrysospalax villosus*, may be over 200 times the mass of that of *Amblysomus hottentotus*. In fact, *C. villosus* and *Eremitalpa granti* have the largest mallei relative to body mass found in any mammals [23], and that of *E. granti* is constructed of the densest ossicular bone known in any terrestrial species [26]. The incudes and stapedes are also enlarged in most chrysochlorine golden moles, but these ossicles do not show such extreme hypertrophy. Unusually for mammals, the stapes projects dorsomedially from the lenticular apophysis of the incus, rather than medially, in some of these genera.

Other middle ear characteristics in golden moles are less variable between genera. All golden moles have complete bony bullae and stapedial arteries confined within bony tubes, and they all lack a pars flaccida and the tensor tympani muscle. Contrary to some previous reports, the presence of an interbullar connection has now been confirmed by the author in *Amblysomus*, *Neamblysomus*, *Calcochloris, Chlorotalpa*, *Carpitalpa*, *Chrysochloris* and *Eremitalpa* species, as well as in *Chrysospalax trevelyani*; only in *Chrysospalax villosus* has such a connection been found to be lacking. The interbullar connection takes the form of a relatively wide channel within the basisphenoid in *Chrysochloris* and *Eremitalpa*, but it is much narrower in the other species in which it was found.

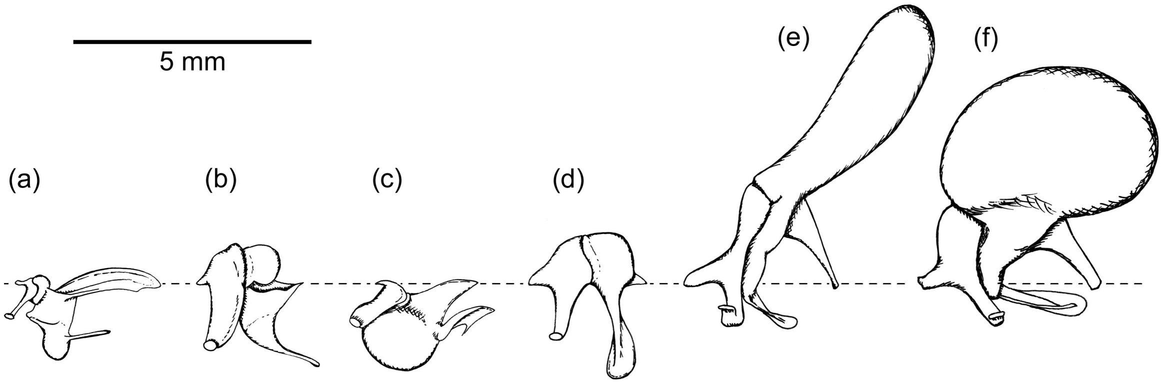

Figure 1. Left auditory ossicles (malleus and incus) in representative talpid moles (a, b, c) and golden moles (d, e, f), internal views. All are drawn to scale and positioned such that the dotted line passes through the tether-points at the short process of the incus (on the left) and the anterior process of the malleus (on the right). Note the distribution of ossicular mass relative to this line. Species depicted, with approximate body masses for comparison: (a) *Neurotrichus gibbsii*, 10 g; (b) *Talpa europaea*, 80 g; (c) *Parascaptor leucura*, 40 g; (d) *Amblysomus hottentotus*, 70 g; (e) *Chrysochloris asiatica*, 50 g; (f) *Eremitalpa granti namibensis*, 20 g.

4 DISCUSSION

4.1 Middle ear evolution and ecology

The “microtype” ossicular morphology of Group 1 talpid moles is also typical of other eulipotyphlan insectivores (shrews, hedgehogs, solenodons), and therefore is almost certainly the primitive condition for the Talpidae [21]. Microtype ossicles are found in bats and many murid rodents too, and are generally regarded as part of a high-stiffness conducting apparatus suitable for the transmission of high frequencies [27]. The moles which retain this ossicular morphology all spend a significant amount of time above-ground, under which circumstances they are presumably exposed to high-frequency air-borne sound.

By contrast, Group 2 talpids are more exclusively subterranean. Although their ossicles do retain some “microtype” features, such as the angle of the manubrium relative to the anterior process and in some genera a vestigial orbicular apophysis, they are loosely connected to the skull and can functionally be regarded as the “freely mobile” type. This low-stiffness ossicular apparatus should be better at transmitting the low frequencies which are propagated well underground. This morphology probably evolved in parallel in the American and Eurasian talpid lineages, in connection with increasingly subterranean habits [21].

Except for their enlarged mallei, the middle ear structures of Group 3 talpid moles resemble those of Group 2 species. Little is known about the ecology of these animals, but one report suggests that *Parascaptor* makes runs in loose ground between the rotten tree-trunks in which its invertebrate prey are found [29].

Among the golden moles, the primitive ossicular type is believed to be “freely mobile”, as found in the amblysomine species [25, 30]. The chrysochlorine genera with the largest mallei all seem to spend part of their time foraging on the surface, and it has been suggested that the enlarged mallei might, paradoxically, augment high-frequency air-borne hearing above-ground [30]. However, as discussed below, ossicular hypertrophy in both golden moles and group 3 talpids is here regarded as an adaptation to improve seismic vibratory sensitivity through inertial bone conduction.

Structure	Group 1 talpids	Group 2 talpids	Group 3 talpids	Amblysomine golden moles	Chrysochlorine golden moles
Bulla	Incomplete	Complete	Complete	Complete	Complete
Interbullar connection	Absent	Present in most	Present	Present	Present in most
Pars flaccida	Present	Small or absent	Small or absent	Absent	Absent
Ossicle type	Microtype	Freely mobile	Hypertrophied	Freely mobile	Hypertrophied
Approx. range of malleus masses, mg	0.3 – 0.7	0.9 – 1.4	3.2 – 20	0.8 – 2.1	3.2 – 220
Tensor tympani	Very small	Absent	Absent	Absent	Absent
Bony tubes around arteries	Incomplete	Complete	Complete	Complete	Complete

Table 1. Summary of middle ear characteristics in talpid and golden moles.

4.2 Convergent evolution of the middle ear in talpid and golden moles

Middle ear characteristics in talpid and golden moles are summarized in Table 1, above. Like Group 2 talpids, all golden moles possess complete auditory bullae and stapedial arteries enclosed within complete bony tubes, while they lack both tensor tympani muscles and a pars flaccida of the tympanic membrane. The primitive ossicular structure in golden moles is “freely mobile”, as in Group 2 talpids. Many of these characteristics are shared with other fossorial mammals [7], suggesting the convergent evolution of a low-stiffness middle ear suitable for transmission of low-frequency air-borne sound underground. However, most “freely mobile” terrestrial mammals have very similar middle ear morphologies: the ossicles, tympanic membranes and cavity volumes of Group 2 talpids and amblysomine golden moles (and also most fossorial rodents) are not conspicuously enlarged compared to terrestrial species [23] and do not, therefore, imply unusual sensitivity to low-frequency sound. There are, however, three strikingly unusual features of the middle ears in certain talpid and chrysochlorid species which do demand special attention.

Firstly, there is a connection within the basicranium between the right and left middle ear cavities in many Group 2 and Group 3 talpids, and also in most species of golden moles. These are apparently the only mammals in which such an interbullar connection is present. It has been suggested that the connection in *Talpa* might allow a form of pressure-difference sound localization at low frequencies [31]. The interbullar connection in talpids and chrysochlorids might therefore represent a convergently-derived adaptation associated with a restriction in hearing range to low frequencies, such a restriction apparently being typical of fossorial mammals [2, 3, 4, 5, 32].

Secondly, the tensor tympani muscle has been completely lost in all golden moles examined to date, as well as in all Group 2 and Group 3 talpids. Other fossorial mammals typically show reduced or missing middle ear muscles, although in fossorial rodents it always appears to be the stapedius which shows the greater reduction [7, 9, 33]. The loss of the tensor tympani has been documented in some unrelated terrestrial mammals, including tree-shrews and pangolins [27, 34, 35]: its loss does not seem to be consistently correlated with any particular feature of audition and is here regarded as enigmatic.

Thirdly, ossicular hypertrophy is found in all chrysochlorine golden mole genera, as well as in Group 3 talpid moles. In the golden moles, the head of the malleus is expanded dorsal to its articulation with the incus. The more limited expansion of the body of the malleus in Group 3 talpids is ventral to the incudal articulation, perhaps reflecting the “microtype” talpid ancestry, since the bulk of the ossicular mass in “microtype” ossicles is also located ventral to this articulation. Ossicular hypertrophy has never been reported in any other extant fossorial mammal, but it has been documented in the fossorial Oligocene palaeanodonts *Epoicotherium* and *Xenocranium* [36].

4.3 Ossicular inertial bone conduction in moles

If skull vibration results in the ossicular chain vibrating with a different amplitude or phase, the movement of the stapes relative to the oval window would represent an effective input to the cochlea. Bárány [37] devised a simple mathematical model of this mechanism, referred to as inertial bone conduction, which is represented below as Equation 1 and illustrated in Figure 2.

$$\xi = \frac{M \cdot \omega \cdot x \cdot d \cdot l^{-1}}{\sqrt{R^2 + \left[\omega \cdot \left(m_f + J \cdot l^{-2}\right) - \left(C \cdot \omega\right)^{-1}\right]^2}} \qquad (1)$$

Equation 1 can be used to predict the displacement amplitude of the stapes footplate within the oval window, ξ, for an effective displacement amplitude of the skull, x, where ω is the radian frequency of excitation, M is combined ossicular mass, d is the distance between the rotatory axis and the centre of mass of the ossicular chain, l is the distance between stapes and axis, R is the resistance and C the compliance affecting the ossicular chain, J is the rotatory inertia of the ossicles, and m_f is the inner ear fluid mass. The rotatory axis was taken to extend between the tether-points at the anterior process of the malleus and short process of the incus, as is often assumed for mammalian ossicles in general [27, 37].

Bárány concluded that the ossicular chain of most mammals would be little excited by vibrations of the skull, primarily because the ossicular centre of mass falls very close to the rotatory axis, minimizing d. In humans and many other mammals, skull vibrations come mainly from chewing and vocalization, and largely represent unwanted noise. However, if the skull of a fossorial animal were coupled to a vibrating substrate, inertial bone conduction would, in principle, allow seismic vibration detection. It has been suggested that the enlarged ossicles of golden moles are adapted for this purpose [38].

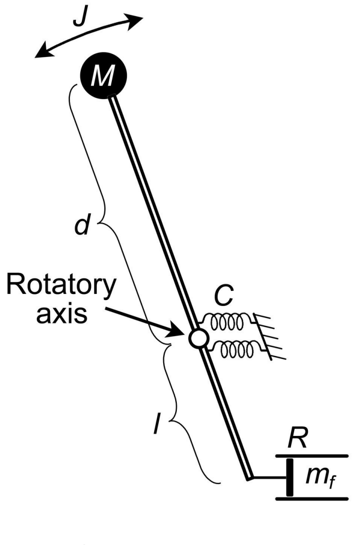

Figure 2. Mechanical analogue of the middle ear ossicles, according to Bárány’s model. The model seeks to establish the displacement amplitude of the stapes within the oval window (represented as the piston within the dashpot) for a given skull displacement amplitude (a translatory vibration applied at the rotatory axis). See text for details.

Ossicular hypertrophy in moles, increasing both M and J in Equation 1, will increase the peak bone-conduction response and bias it towards lower frequencies. Equally importantly, the ossicular centre of mass is moved further from the rotatory axis, increasing d as well as J, an effect augmented by the elongation of the anterior process of the malleus. Using a modified version of Bárány's model, the hypertrophied mallei of *Chrysochloris*, *Eremitalpa* and *Chrysospalax* species were predicted to improve low-frequency inertial bone conduction considerably, increasing the ratio ξ/x by 30-60 dB compared to *Amblysomus*, at frequencies under 500 Hz [24]. Recent laser vibrometric studies of the ossicles of *Chrysochloris* [39, 40] support the conclusion that the enlarged ossicles promote transmission of bone-conducted skull vibrations, although they have revealed that the vibratory modes are more complicated than that considered by the Bárány model.

Field data obtained in the Namib Desert suggest that *Eremitalpa* uses its hypertrophied ossicles to detect the low-frequency (around 300 Hz) vibrations generated by the grassy tussocks in which it finds its prey, these vibrations being transmitted through the sand [15, 41]. The mole is believed to pick up these vibrations either as it "sand-swims" just below the surface, or through periodically dipping its head into the sand if it is walking on the surface. Loose sand conducts *P*-waves and Rayleigh waves at one tenth of the velocities measured in other substrates, in principle facilitating localization if this were based on time-of-arrival differences between spatially-separated receptors [42]. Surface waves such as Rayleigh waves are also expected to travel further than compressional waves within the substrate itself [42]: this might explain why the evolution of ossicular hypertrophy within both talpid and golden moles seems, ironically, to be linked with foraging on or near the surface.

Low-frequency air-borne hearing, even if not unusually acute in subterranean mammals, might predispose the ear towards the detection of the low-frequency substrate vibrations to which these animals will inevitably be exposed, leading in some genera to specialization through ossicular hypertrophy. The use of the auditory rather than the somatosensory system for vibration detection probably relates to the improved localization possibilities afforded by a system pre-adapted to obtaining cues via binaural comparison. Even if the skull of these animals vibrates as a unit, excluding time-of-arrival cues, binaural cues useful for localization might still be available if the horizontal component of particle velocity in surface Rayleigh waves excites the left and right ossicular chains to different extents [41]. Ossicular hypertrophy has not been documented in any fossorial rodent: this might reflect their herbivorous diets (vibratory cues being less useful in foraging), or perhaps it is because the high-amplitude skull vibrations associated with gnawing would prove damaging to an ear that was specialized in this way.

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