

Evolution of the Middle Ear Apparatus in Talpid Moles

Matthew J. Mason*

University of Cambridge, Department of Physiology, Cambridge CB2 3EG, UK

ABSTRACT The middle ear structures of eight species of mole in the family Talpidae (Mammalia: Eulipotyphla) were studied under light and electron microscopy. *Neurotrichus*, *Parascalops*, and *Condylura* have a simple middle ear cavity with a loose ectotympanic bone, ossicles of a “microtype” morphology, and they retain a small tensor tympani muscle. These characteristics are ancestral for talpid moles. *Talpa*, *Scalopus*, *Scapanus*, and *Parascaptor* species, on the other hand, have a looser articulation between malleus and ectotympanic bone and a reduced or absent orbicular apophysis. These species lack a tensor tympani muscle, possess complete bullae, and extensions of the middle ear cavity pneumatize the surrounding basicranial bones. The two middle ear cavities communicate in *Talpa*, *Scapanus*, and *Parascaptor* species. *Parascaptor* has a hypertrophied malleus, a feature shared with *Scaptochirus* but not found in any other talpid genus. Differences in middle ear morphology within members of the Talpidae are correlated with lifestyle. The species with middle ears closer to the ancestral type spend more time above ground, where they will be exposed to high-frequency sound: their middle ears appear suited for transmission of high frequencies. The species with derived middle ear morphologies are more exclusively subterranean. Some of the derived features of their middle ears potentially improve low-frequency hearing, while others may reduce the transmission of bone-conducted noise. By contrast, the unusual middle ear apparatus of *Parascaptor*, which exhibits striking similarities to that of golden moles, probably augments seismic sensitivity by inertial bone conduction. *J. Morphol.* 267:678–695, 2006.

© 2006 Wiley-Liss, Inc.

KEY WORDS: middle ear; fossorial; Talpidae; mole; *Parascaptor*; seismic sensitivity

Airborne sound of a few hundred Hertz has been found to travel best in the subterranean tunnels of the mole-rat *Nannospalax ehrenbergi* (Heth et al., 1986), and many behavioral and electrophysiological studies have shown that the hearing of fossorial rodents is most sensitive within a low-frequency range (Bruns et al., 1988; Müller and Burda, 1989; Heffner and Heffner, 1990, 1992b, 1993; Brückmann and Burda, 1997; Begall et al., 2004). Certain anatomical features of the ear of fossorial rodents have been interpreted as adaptations mediating low-frequency hearing (Burda et al., 1988, 1989, 1992; Lange et al., 2004; Schleich and Busch, 2004). Others, however, have argued that rather than being truly specialized toward low-frequency hearing, the audition of pocket gophers and mole-rats is degen-

erate and merely restricted to a low-frequency range by the loss of high-frequency sensitivity (Heffner and Heffner, 1990, 1992b, 1993). The assumption that the auditory apparatus of these animals is unusually receptive to low-frequency sound is therefore questionable.

One way to establish whether middle ear structures in fossorial mammals are specialized or not is to look for convergent adaptations in unrelated groups. Burda et al. (1992) compared the middle ear structures of a range of fossorial species, including pocket gophers, spalacine, and bathyergid mole-rats, the talpid moles *Talpa* and *Scalopus*, and the golden mole *Amblysomus*, to those of terrestrial mammals. Some striking parallels were identified among the fossorial species, including a relatively larger eardrum lacking a pars flaccida, a larger stapes footplate area, a looser connection between malleus and tympanic bone, and reduced or missing middle ear muscles. In a wider study, Mason (2001) concluded that certain middle ear features such as an enlarged stapes footplate and reduced middle ear muscles are indeed characteristic of subterranean mammals in general.

The importance of appropriate outgroups in such comparative studies cannot be exaggerated. Mice and rats (Muridae) have often been used as “acoustically unspecialized” outgroups for comparison with fossorial rodent species (Burda et al., 1988, 1992; Brückmann and Burda, 1997). However, mice and rats have restricted low-frequency hearing abilities, which is by no means the case in all terrestrial rodents (Heffner et al., 2001). Many of the characteristically “fossorial” features of the middle ear apparatus of the tuco-tuco, *Ctenomys sociabilis*, are also found in this animal’s nonfossorial caviomorph relatives (Mason, 2004b), but not in mice and rats. Using distantly related, high-frequency specialists

Contract grant sponsors: Biotechnology and Biological Sciences Research Council (Ph.D. dissertation funding); Department of Physiology, University of Cambridge.

*Correspondence to: M.J. Mason, University of Cambridge, Department of Physiology, Downing Street, Cambridge CB2 3EG, UK. E-mail: mjm68@hermes.cam.ac.uk

Published online 1 March 2006 in
Wiley InterScience (www.interscience.wiley.com)
DOI: 10.1002/jmor.10430

such as murids as outgroups in this case might therefore yield misleading conclusions about the evolution of the ear apparatus in tuco-tucos, or indeed in other distant relatives, such as bathyergid mole-rats.

Although fossorial rodents have attracted more attention recently, the anatomy of the ear of talpid moles (family Talpidae, order Eulipotyphla) has been of interest for at least 200 years (e.g., Cuvier, 1805). The middle ear morphologies of *Talpa* and *Scalopus* species have been described in detail by several authors (Van Kampen, 1905; Bondy, 1907; Wilkie, 1925, 1929; Gaughran, 1954; Simonetta, 1957; Henson, 1961; Platzer, 1961), but only brief descriptions of middle ear structures in other talpid genera are available (Hyrtl, 1845; Doran, 1878; Van Kampen, 1905; Segall, 1970, 1973, 1976; Burda et al., 1992; Abe, 1995). The most comprehensive comparative study to date was performed by Stroganov (1945), who described the auditory ossicles of 10 genera of moles. Most of these studies are concerned with anatomy or phylogeny rather than with function, and almost nothing has ever been published on the middle ear structures of *Neurotrichus gibbsii* and *Parascalops breweri*, the only members of their respective genera.

The Talpidae is currently considered to contain around 17 extant genera, some of which spend nearly all their lives within burrows, others of which are much more terrestrial in habits. Recent phylogenies suggest that full fossoriality has evolved more than once within the family (Shinohara et al., 2003, 2004; Motokawa, 2004), making the Talpidae ideal for an intrafamily study of ear evolution. Restricting the analysis to one family complements previous, wider-ranging studies, and, by avoiding problems associated with the use of potentially inappropriate outgroups, allows more confidence in the identification of true adaptations to a subterranean environment. In the present study, the ears of talpid moles from seven genera were dissected and studied in detail, and those of a further six genera were also examined. Part of this work stems from a doctoral dissertation (Mason, 1999); some preliminary anatomical findings have been briefly reported (Mason, 2001).

MATERIALS AND METHODS

The following specimens were dissected in this study: European mole, *Talpa europaea* (n = 63, England, UK); eastern mole, *Scalopus aquaticus* (n = 2, Tennessee, US); coast mole, *Scapanus orarius* (n = 1, British Columbia, Canada); Townsend's mole, *S. townsendii* (n = 1, Washington, US); star-nosed mole, *Condylura cristata* (n = 2, Pennsylvania, US); hairy-tailed mole, *Parascalops breweri* (n = 1, Pennsylvania, US); American shrew-mole *Neurotrichus gibbsii* (n = 3, British Columbia, Canada); and white-tailed mole *Parascaptor leucura* (n = 1, Yunnan Province, China). The European mole specimens, originally trapped and killed as pests in several locations in England, were preserved by freezing. The North American specimens had been used in experimental studies conducted in the US and Canada; the corpses were ob-

tained preserved in paraformaldehyde and/or 70% alcohol. The *Parascaptor* specimen was a prepared skull from the Natural History Museum, London (spec. no. 22.10.21.1). The number of individuals of some species dissected was very low, but intraspecific variation among adult middle ear structures is small in comparison to interspecific variation (Nummela, 1995). With the exception of a small number of the *Talpa* specimens, nearly all appeared to be adults.

In addition to these specimens, skulls of talpids belonging to the collection of the Natural History Museum, London, were examined under a light microscope but not dissected: the nature of the ectotympanic in these species, or the loss of surrounding bones, allowed the middle ear regions to be inspected. The skull of a short-faced mole *Scaptochirus moschatus* (spec. no. 1928.1.6.2; Shandong Province, China) was X-rayed. Other species examined included the shrew-moles *Uropsilus andersoni* (n = 3), *U. gracilis* (n = 5), *U. soricipes* (n = 3), *Urotrichus (Dymecodon) pilirostris* (n = 5), and *U. talpoides* (n = 3); the long-tailed mole *Scaptochirus fuscicaudus* (n = 3); the desmans *Desmana moschata* (n = 6); and *Galemys pyrenaicus* (n = 8), and further specimens of *Parascalops breweri* (n = 8); *Condylura cristata* (n = 8); *Neurotrichus gibbsii* (n = 2); *Parascaptor leucura* (n = 11), and *Scaptochirus moschatus* (n = 8). Four sets of histological sections through the middle ear region of *Talpa europaea*, belonging to the University Museum of Zoology, Cambridge, UK, were also examined. The classification used here follows that of Hutterer (1993).

Middle ears were dissected and examined under a binocular light microscope (Wild, Heerbrugg, Switzerland), using magnifications from 6–50 \times . Both ears were dissected in most specimens. Light photomicrographs were taken using a Nikon D1 digital camera attached to the microscope body, and scale diagrams were constructed on 1-mm graph paper using an eyepiece graticule. Most measurements were made from the diagrams; some were made from the digital photographs using Adobe Photoshop CS v.8.0 (San Jose, CA) to calculate lengths and WinSurf v.4.0 (ICOM Informatics, Beverly, MA) to calculate areas. All areas were calculated as flat surfaces. Ossicles were weighed on an automatic electrobalance (Cahn Instruments, Madison, WI, model 29), accurate to 0.3 μ g. Electron microscopy was performed using a Philips XL30 FEG scanning electron microscope. Radiographs were taken with a Nova 30kW machine, using Agfa Mamoray HDR-C Plus mammography film. Images of right ears were laterally inverted so that, for ease of comparison, all illustrations are apparently of left structures.

See Figure 1 for the ossicular anatomical terms used in this study. For simplicity, the rostrally projecting process of the malleus that articulates with the ectotympanic bone is here referred to in all species as the anterior process, although several other names for this structure (or components thereof) are found in the literature (see Henson, 1961). The sides of the malleus and incus facing the plane of the tympanic membrane are here referred to as "external" and those facing into the tympanic cavity as "internal." The anatomical area ratio is defined as pars tensa area divided by stapes footplate area; the anatomical lever ratio is the malleus lever arm ML divided by the incus lever arm IL, where ML and IL are the perpendicular distances from the tip of the manubrium and from the center of the lenticular apophysis, respectively, to the ossicular rotatory axis. The axis is taken to extend between the anterior process of the malleus and the short process of the incus (see Discussion).

RESULTS

Anatomical findings for the seven talpid genera dissected and examined in detail are summarized in Tables 1 and 2, and are described below. The ears of the other genera were not dissected and could not be examined in such detail. However, it was found that the middle ear structures of *Scaptochirus* resemble those of *Parascaptor*, while those of *Uropsilus*, *Uro-*

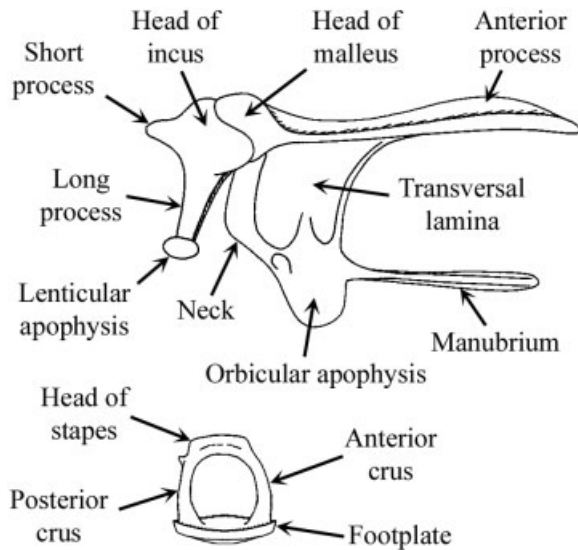


Fig. 1. Idealized left auditory ossicles (malleus, incus, and stapes) of a "microtype" mammal; key anatomical structures are labeled. The head of the stapes articulates with the lenticular apophysis of the incus.

trichus, and *Scaptonyx* are very similar to those of *Neurotrichus*. Desmans (*Desmana* and *Galemys*) appear to lack a pars flaccida and their malleus has a very small orbicular apophysis, but otherwise their ear structures are most similar to those of *Condylura*.

External Ear and Tympanic Membrane

The external auditory meatus opens directly on the side of the head in the mole species dissected, surrounded only by a raised rim of bare skin and hidden under the fur. The size of the opening was largest in *Condylura* and reasonably large in *Parascalops* and *Neurotrichus*, in all of which the opening has an elongated oval shape. The opening is smaller and more rounded in the other genera, and is particularly small in *Scalopus*. The external meatus was patent in all *Talpa* specimens and contained very little cerumen. An ear mite was found in one specimen and soil grains in another, but in general these ears were strikingly clean. In contrast, the external or middle ears were found to be partially filled with a pale exudate in the majority of the American mole specimens examined. The external ear of *Parascaptor* was not examined.

Very unusually, the tympanic membranes of *Scalopus* and *Scapanus* species are teardrop-shaped, pointed end rostral, rather than circular or oval as in most mammals (Fig. 2A,B). The manubrium inserts centrally, approximately along the longest diameter. The membrane is attached to the malleus along the rostral edge of the transversal lamina. A very small pars flaccida appears to be present caudal to the body of the malleus in *Scalopus*.

The tympanic membrane is circular in *Talpa* (Fig. 2C) but for a small, caudolateral extension accommodating the lateral process of the malleus. No pars

TABLE 1. Summary of anatomical findings in seven talpid genera

Characteristic	"Group 1" moles (some above-ground activity)			"Group 2" moles (highly fossorial)			"Group 3" moles (hypertrophied ossicles)
	<i>Neurotrichus</i>	<i>Parascalops</i>	<i>Condylura</i>	<i>Talpa</i>	<i>Scalopus</i>	<i>Scapanus</i>	<i>Parascaptor</i>
Attachment of ectotympanic to skull	Fibrous	Fibrous	Fibrous	Synostosed	Synostosed	Synostosed	Incompletely synostosed
Bony recessus meatus	Very poorly developed	Very poorly developed	Incomplete	Complete	Complete	Complete	Nearly complete
Pars flaccida	Intermediate	Large	Large	Very small or absent	Very small	Very small or absent	Very small or absent
Interbullar connection	Absent	Absent	Absent	Present	Absent	Present	Present
Bony tubes around tympanic arteries	Largely absent	Incomplete only around stapedial artery	Incomplete only around stapedial artery	Complete	Complete	Complete	Complete
Tensor tympani muscle	Present but small	Present but very small	Present but very small	Absent	Absent	Absent	Absent
Ossicle type	Microtype	Microtype	Microtype	Freely mobile	Freely mobile	Freely mobile	Hypertrophied
Malleo-incudal articulation	Saddle-shaped	Saddle-shaped	Intermediate	Flattened	Highly flattened	Highly flattened	Flattened
Area ratio	39.4	28.9	20.4	21.6	12.8	14.7	8.1
Lever ratio	1.66	1.83	1.74	1.33	1.34	1.36	0.71

TABLE 2. Measurements of middle ear structures (mean values) in talpid moles

Species	Condylbasal length, mm	Pars tensa area, mm ²	Stapes footplate area, mm ²	ML, mm	IL, mm	Malleus mass, mg	Incus mass, mg	Stapes mass, mg
<i>Neurotrichus gibbsii</i>	23.0 (n = 3)	3.31 (n = 4)	0.084 (n = 2)	1.13 (n = 2)	0.68 (n = 2)	0.325 (n = 1)	0.071 (n = 2)	0.015 (n = 1)
<i>Parascalops breweri</i>	31.8 (n = 1)	3.82 (n = 2)	0.132 (n = 2)	1.39 (n = 2)	0.76 (n = 2)	0.685 (n = 1)	0.135 (n = 1)	0.026 (n = 2)
<i>Condylura cristata</i>	32.2 (n = 2)	6.19 (n = 2)	0.304 (n = 1)	1.53 (n = 3)	0.88 (n = 3)	0.686 (n = 1)	0.260 (n = 2)	0.055 (n = 2)
<i>Talpa europaea</i>	34.9 (n = 63)	10.55 (n = 109)	0.489 (n = 94)	1.71 (n = 85)	1.29 (n = 91)	0.955 (n = 60)	0.612 (n = 63)	0.084 (n = 88)
<i>Scalopus aquaticus</i>	35.2 (n = 2)	10.29 (n = 3)	0.802 (n = 4)	1.93 (n = 4)	1.44 (n = 4)	1.427 (n = 1)	0.877 (n = 1)	0.137 (n = 4)
<i>Scapanus orarius</i>	32.7 (n = 1)	6.78 (n = 2)	0.507 (n = 2)	1.54 (n = 2)	1.15 (n = 2)	0.876 (n = 1)	0.539 (n = 1)	0.071 (n = 1)
<i>Scapanus townsendii</i>	39.5 (n = 1)	9.60 (n = 1)	0.602 (n = 1)	1.86 (n = 1)	1.34 (n = 1)	1.212 (n = 1)	0.768 (n = 1)	0.085 (n = 1)
<i>Parascaptor leucura</i>	28.1 (n = 1)	6.42 (n = 1)	0.790 (n = 1)	0.60 (n = 1)	0.84 (n = 1)	3.216 (n = 1)	0.291 (n = 1)	0.167 (n = 1)

flaccida was obvious. The tympanic membrane is indented slightly at the central umbo. In *Parascaptor*, the membrane (Fig. 3A) is similar to that of *Talpa* but flatter, and the manubrium does not extend quite to the center.

The pars tensa is oval in shape in *Neurotrichus*, *Parascalops*, and *Condylura* (Fig. 2D–F). As in *Scalopus* and *Scapanus*, the membranes of *Neurotrichus* and *Parascalops* are attached to the rostral margin of the transversal lamina of the malleus, resulting in *Parascalops* in a particularly oblique caudal border. No such connection exists in *Condylura*. There is a relatively large and well-defined pars flaccida in these three species, extending caudolaterally beyond the limits of the separated tympanic crura and covering much of the body of the malleus.

Bullar Structure and Tympanic Cavity

In *Talpa*, *Scalopus*, and *Scapanus*, the ectotympanic is synostosed with the surrounding basicranial bones; in *Parascaptor* the extent of the synostosis is variable in different individuals but is always incomplete rostrally. The tympanic membrane in these species is completely covered by a ventral flange of the ectotympanic that forms the externally visible tympanic bulla, the space between membrane and ventral bullar wall being termed the recessus meatus. The entrance to the recessus is particularly narrow in *Scalopus*, but much wider in *Parascaptor*.

The ectotympanics of *Neurotrichus*, *Parascalops*, and *Condylura* are attached to the basicranium by fibrous tissue; there is no synostosis. In *Condylura* the ectotympanic is overlapped by wings of the basisphenoid medially and alisphenoid rostrally, and it is consequently held in place firmly. In *Parascalops* and *Neurotrichus* the ectotympanic is overlapped by

the basisphenoid alone, only just so in the shrew-mole. The bony recessus meatus is best developed in *Condylura*, but in none of these three species does the recessus wall extend far enough laterally to cover the pars tensa completely.

In the adult *Talpa*, alisphenoid, basisphenoid, and basioccipital bones are indistinguishably fused together. The resulting complex is inflated by extensions of the air-filled tympanic cavity and filled with fine, bony trabeculae that vary in form between individuals, giving it a spongy appearance. The pneumatized region extends rostrally nearly as far as the orbital fissure, and caudally into the occipital condyles (Fig. 4). Communication between the right and left middle ear cavities through the pneumatized basicranium was demonstrated by adding colored water to one middle ear, whereupon it spreads to the contralateral side. The heads of the malleus and incus rest within the dorsolaterally located epitympanic recess. Caudal to the tympanic membrane, the middle ear cavity extends within the petrosal as far as the posterior lacerate foramen. This extension contains the stapes and, more caudally within its own subcavity, the fenestra cochleae (= round window, actually parallelogramic in *Talpa*).

Within the middle ear cavity of *Talpa* all arteries and nerves are contained within bony tubes. The stapedia artery extends within its tube across the deep pelvis ovalis and between the crura of the stapes (Fig. 5B). The bony canal for the facial nerve forms part of the lateral wall of the pelvis ovalis. The small cochlear promontory, surrounded by bony trabeculae, is just caudomedial to the tympanic membrane.

The middle ear cavities of *Scalopus* and *Scapanus* species resemble those of *Talpa*, although the trabeculations are coarser. The pneumatization does not quite reach the occipital condyles in *Scalopus*, and extends even less far caudally in *Scapanus* species,

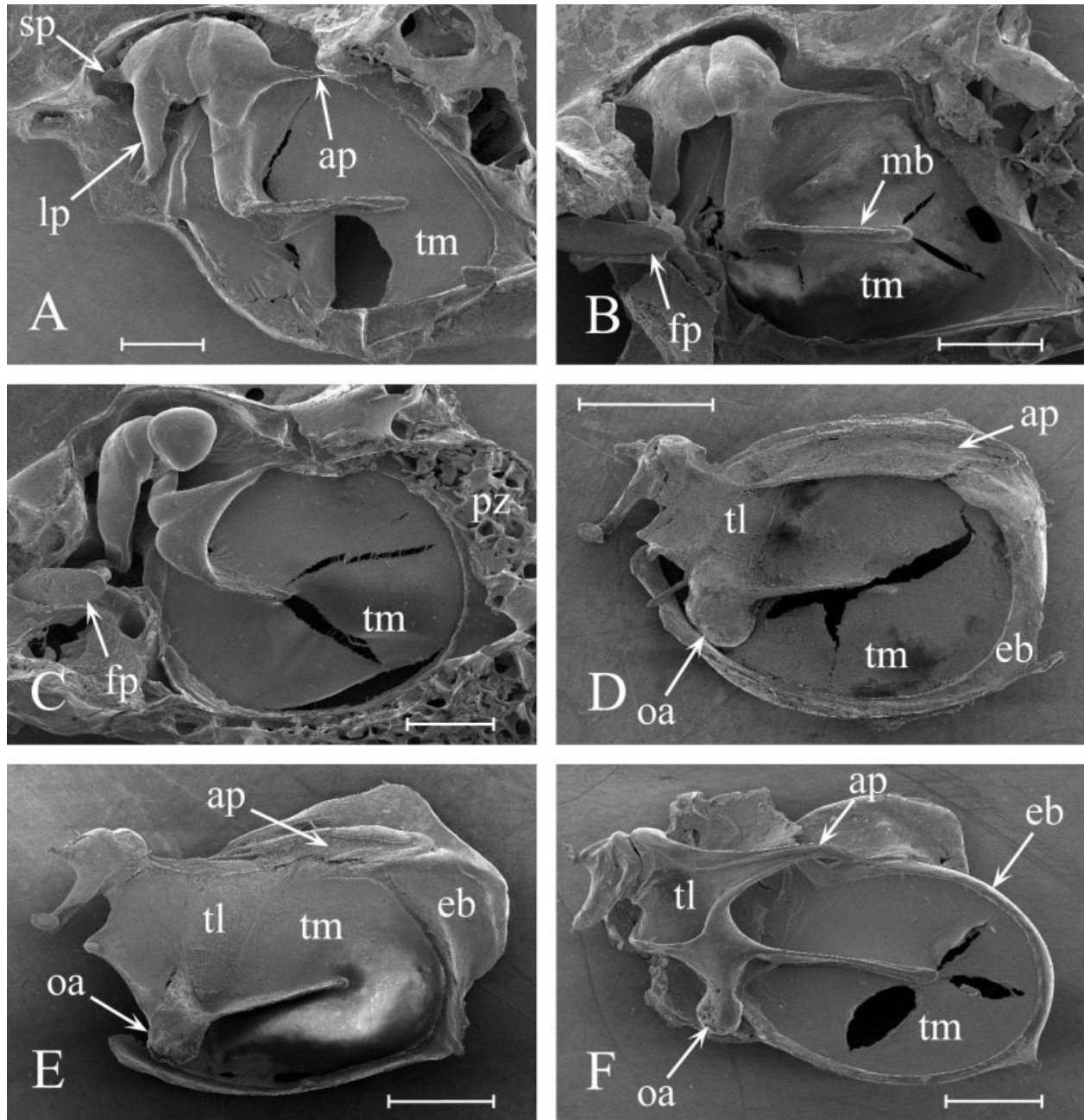


Fig. 2. Left tympanic membranes and ossicles of talpid moles, internal views. SEM. **A:** *Scalopus aquaticus*. **B:** *Scapanus orarius*. **C:** *Talpa europaea*. **D:** *Neurotrichus gibbsii*. **E:** *Parascalops breweri*. **F:** *Condylura cristata*. In **B** and **C**, the stapes footplate on the left projects towards the viewer; the stapes is missing from the other SEMs. Tympanic membranes in all but *Parascalops* ripped during preparation. ap, anterior process of malleus; eb, ectotympanic bone; fp, footplate of stapes; lp, long process of incus; mb, manubrium of malleus; oa, orbicular apophysis of malleus; pz, pneumatized bone; sp, short process of incus; tl, transversal lamina of malleus; tm, tympanic membrane. All scale bars = 1 mm.

in which the basioccipital may not be inflated. In *Scalopus*, dye introduced into one middle ear cavity did not spread beyond the midline, showing that there is no interbullar connection in this species. However, dye placed into the middle ear cavities of both *Scapanus* species did slowly leak into the contralateral ear, apparently through the basisphenoid.

The arteries of the middle ear are contained within complete bony tubes (Fig. 5A).

The middle ear cavity just behind the tympanic membrane of *Parascaptor* is trabeculated ventrally, but a solid wall is formed rostrally and dorsally by a compact flange of the ectotympanic. The basisphenoid is inflated and trabeculated and there is an

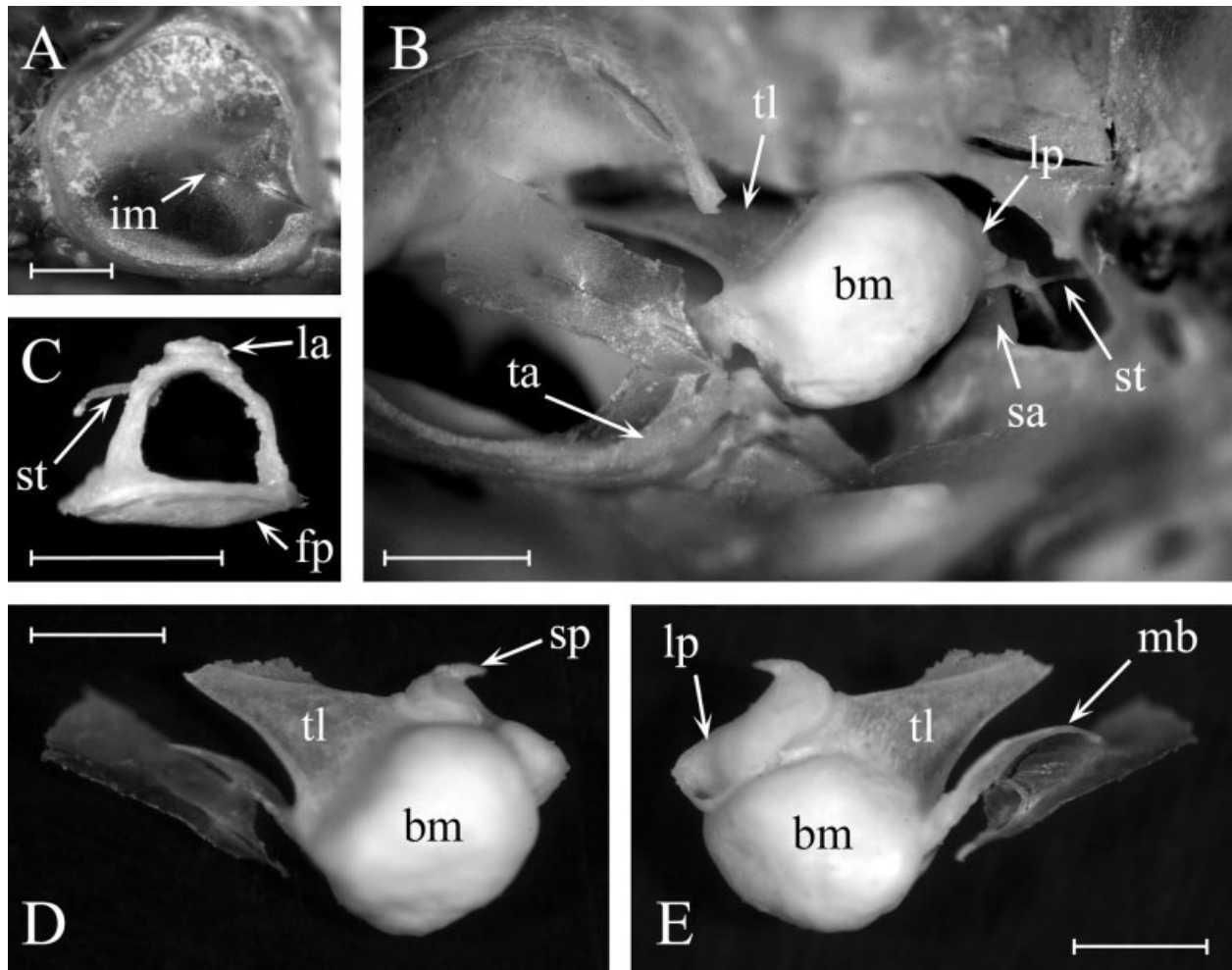


Fig. 3. Photomicrographs of the left middle ear structures of *Parascaptor leucura*. **A:** Tympanic membrane, external view. **B:** Composite photograph of the ossicles in situ, ventrolateral view, much of the tympanic membrane and overlying skull bone having been removed. **C:** Stapes, dorsal view, tendon of stapedius muscle attached. **D:** Malleus and incus, external view. **E:** Malleus and incus, internal view. The lenticular apophysis broke away from the incus but remained attached to the stapes in this specimen; a rectangle of tympanic membrane remains attached to the manubrium in **B,D,E**. bm, body of malleus; fp, footplate of stapes; im, insertion of manubrium into tympanic membrane; la, lenticular apophysis of incus; lp, long process of incus; mb, manubrium of malleus; sa, stapedial artery (in bony tube); sp, short process of incus; st, tendon of stapedius muscle; ta, tympanic annulus formed by ectotympanic bone, the recessus meatus having been removed; tl, transversal lamina. All scale bars 1 = mm.

interbullar connection, but the inflated region does not extend much further rostrally than the tympanic membranes and the basioccipital appears to be solid. The epitympanic recess is greatly expanded, forming a large, smooth-walled cavity caudolateral to the tympanic membrane, which contains the auditory ossicles (Fig. 3B). From this cavity, only the manubrium and anterior process of the malleus project into the tympanic cavity proper. The arteries of the middle ear are again contained within complete bony tubes.

The middle ear cavities of *Neurotrichus*, *Parascalops*, and *Condylura* are much simpler in structure. Some structural septa are present and the arteries of the middle ear form raised ridges, but there are no fine trabeculations. Although they approach each other at the midline, the right and left

cavities remain completely separate. A vertical septum in the medial wall partially divides medial and rostromedial compartments, the latter containing the opening of the Eustachian tube. Lateral to these chambers is the tympanic cavity proper, containing the small promontory, the oval window, and the ossicles, the heads of which are in a shallow epitympanic recess. The fenestra cochleae is found within its own caudal chamber, as in the other moles. In *Condylura* and *Parascalops*, the arteries of the middle ear run in bony tubes that are complete except for a short section of the stapedial artery where it passes through the stapes. In *Neurotrichus*, the arteries are not enclosed in tubes except for the distal part of the promontorial artery. Part of the dorso-medial wall of the middle ear cavity in this species also remains unossified, between promontorial ar-

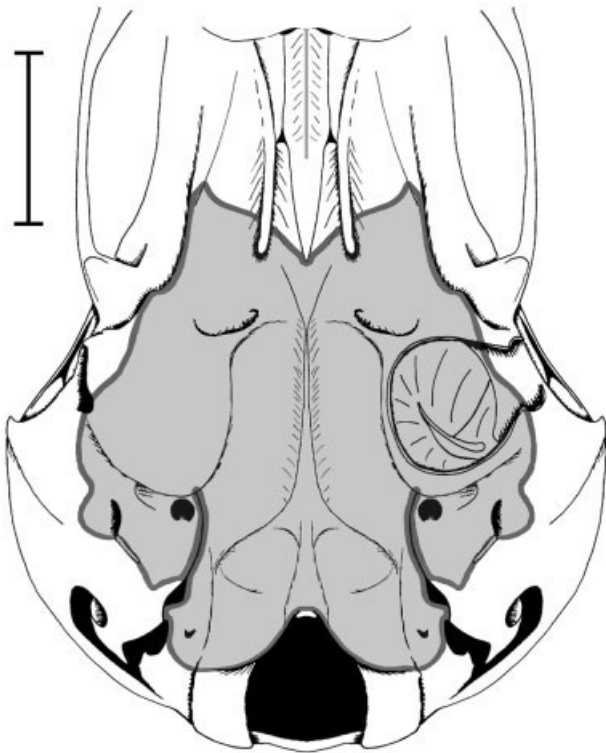


Fig. 4. Basicranium of *Talpa europaea*, ventral view. The left recessus meatus has been opened to reveal the tympanic membrane. The bones surrounding the tympanic cavity in this species are pneumatized by extensions of the cavity, and the left and right sides communicate. The extent of the basicranial pneumatization is indicated by shading. Scale bar = 5 mm.

tery and epitympanic recess. This probably equates to the “pyriform fenestra” described in some other insectivores (McDowell, 1958), although it is much less extensive in *Neurotrichus* than in shrews.

Malleus

In *Talpa*, the almost spherical head of the malleus (Figs. 5B, 6D) is made of compact bone. There is a slight constriction just ventral to the head, beyond which the malleus expands into a flattened, hollow cone, open at the base and extending up to the manubrium. The rostral part of the lateral wall of the cone articulates with the ectotympanic and thus represents the anterior process. The exterior of the body of the malleus is marked with a groove for the chorda tympani nerve.

The manubrium of the malleus is a delicate process projecting rostrally, ventrally, and medially from the rounded apex of the cone. It is shaped like the blade of a scythe, the concave edge of which is flattened along its insertion into the tympanic membrane; it expands only very slightly at the tip. The proximal part of the manubrium, known in the human as the lateral process, is expanded. Owing to the rather horizontal inclination of the tympanic

membrane, the lateral process is actually directed ventrolaterally in moles.

The mallei of *Neurotrichus*, *Parascalops*, and *Condylura* (Fig. 6F–H) are very different in shape, conforming to the “microtype” morphology (Fleischer, 1978). The head of the malleus is very small, the articulation facet on its caudal side more deeply notched than in *Talpa*. Rostrally, the head extends into a long, flattened anterior process that has a wide region of articulation with the lateral crus of the horseshoe-shaped ectotympanic. Much of the mass of the ossicle is concentrated in the orbicular apophysis, a projecting bony hump near the base of the manubrium that is lacking in *Talpa*. Between the apophysis, base of the anterior process, and head is the thin transversal lamina, which is particularly wide in *Parascalops*. The caudal edge of this lamina, the neck of the malleus, bends at an angle, the corner projecting towards the lenticular apophysis of the incus. The tensor tympani muscle inserts almost on this corner-point (*Parascalops*) or just rostral to it (*Neurotrichus*, *Condylura*: Fig. 5D), there being a small muscular process marking the insertion in *Parascalops* and *Neurotrichus*. The neck is folded externally near the head, but internally near the orbicular apophysis. The manubria are thin, and that of *Condylura* is particularly long.

The mallei of *Scalopus* and *Scapanus* species have large, hemispherical heads (Figs. 5A, 6A–C), with flattened articulation facets caudally. From the head projects a columnar neck that turns rostrally to become the manubrium. Between the abbreviated anterior process and the neck extends a relatively small, triangular transversal lamina. The manubria in these species have flattened margins for insertion into the tympanic membrane, wider than in the other species. Near the junction of the manubrium and neck, distally, is a small, thin projection that appears to represent a vestigial orbicular apophysis.

The malleus of *Parascaptor* (Figs. 3D,E, 6E) consists of an almost spherical mass of apparently solid bone. The small articulation facet for the incus projects slightly from its dorsomedial surface; caudal to this is a shallow concavity for the long process of the incus. A very thin, triangular lamina projects rostrally from the spherical body, articulating with the ectotympanic at its tip. Ventral to this lamina is the manubrium (Fig. 3E), shaped like a cleaver with a narrow “handle” and a laminar “blade.” The “blade” inserts into the tympanic membrane along what would be its sharp edge. The manubrium is extremely delicate, the blade part so thin that it is translucent and appears membranous. Its inserting margin is only about half the radius of the tympanic membrane in length and does not extend quite to the center of the membrane: a connective tissue strand extends caudally from the lateral process of the manubrium to the notch in the membrane’s perimeter. The manubrium is not only unusually flimsy, but its orientation relative to the incus and stapes differs

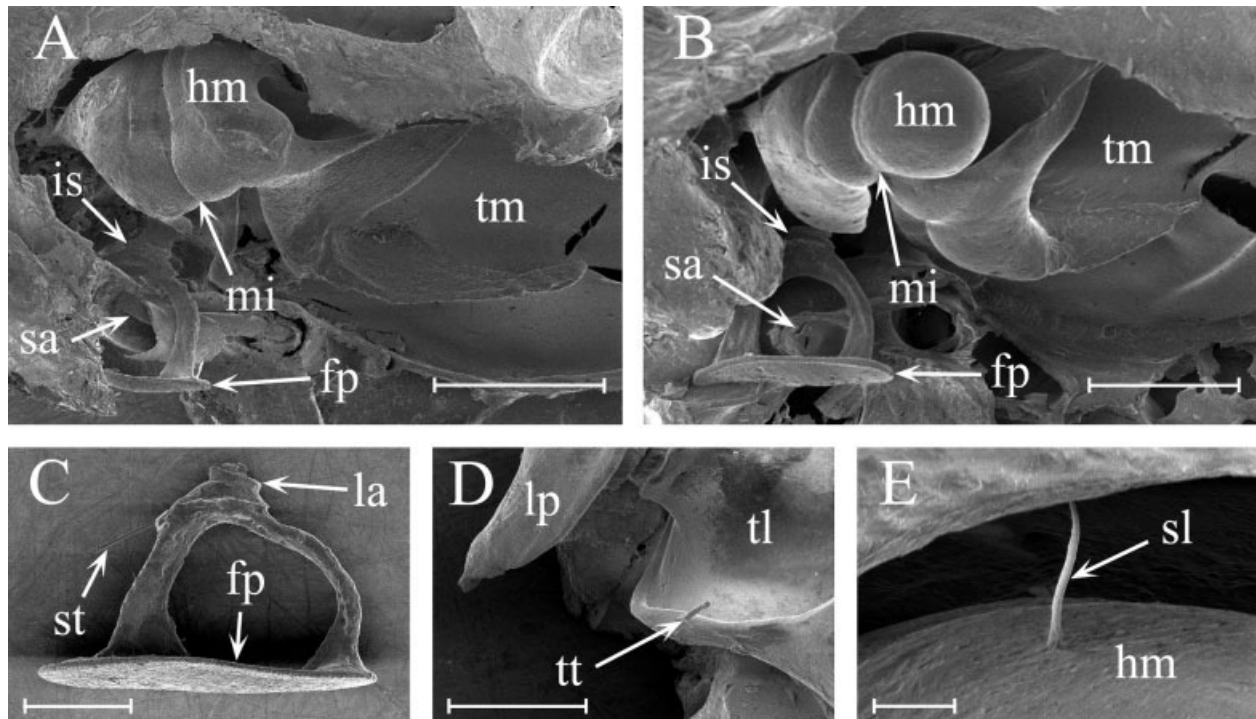


Fig. 5. Left middle ear structures of talpid moles. SEM. **A:** Ossicular chain of *Scapanus orarius*, dorsal and slightly lateral view. Scale bar = 1 mm. **B:** Ossicular chain of *Talpa europaea*, dorsal and slightly lateral view. Scale bar = 1 mm. **C:** Stapes of *Scalopus aquaticus*, dorsal view. Scale bar = 500 μ m. **D:** Close-up of part of the incus (lenticular apophysis missing) and malleus of *Condylura cristata*, showing insertion of the tensor tympani tendon, internal view. Scale bar = 500 μ m. **E:** Superior ligament of the malleus of *Talpa europaea*, dorsal and slightly lateral view. Scale bar = 50 μ m. fp, footplate of stapes; hm, head of malleus; is, incudo-stapedial articulation; la, lenticular apophysis of incus; lp, long process of incus; mi, malleo-incudal articulation; sa, stapedial artery (in bony tube); sl, superior ligament of malleus; st, stapedius tendon; tl, transversal lamina of malleus; tm, tympanic membrane; tt, tensor tympani tendon.

from that of the other moles examined (Fig. 6). At its base is a small swelling that may represent an orbicular apophysis.

Incus

The relatively large incus of *Talpa* (Fig. 6D) has a smaller head than that of the malleus, the flattened articulating facet situated rostrally. The short process is small and conical. The long process is hollowed out by a deep groove (the sulcus incudis), open rostrally, such that the process, although broad, is constructed only from a thin shell of bone. The head of the incus is partly excavated by an extension of this sulcus. At the tip of the long process is a narrow pedicle supporting the flattened, oval lenticular apophysis. The pedicle is made of very thin bone, and in moles in general it was found to be flexible and very easily broken.

The incudes of *Scalopus* and *Scapanus* species (Fig. 6A–C) have large heads and thin, tapering long processes. Those of *Neurotrichus*, *Parascalops*, and *Condylura* (Fig. 6F–H) are much smaller relative to the size of the mallei. The long process is excavated

in all of these species, although this is barely noticeable in *Neurotrichus*.

The incus of *Parascaptor* (Figs. 3D,E, 6E) has a robust, rectangular long process that is closely apposed to the malleus along its rostral edge. The long process is markedly constricted at its base, and although not hollow like that of *Talpa*, it is excavated just proximal to the pedicle. The short process is very small and tapering. The orientation of the incus within the epitympanic recess is unusual: the impression given is that this ossicle has been rotated by the expansion of the malleus, squeezing the long process against the malleus body and leaving the short process dorsal in position.

Stapes

The stapes is the smallest ossicle. In all species examined, it possesses a wide intercrural foramen, through which passes the stapedial artery, and a flat head, which forms a bridge above the convergence of the crura. In *Scalopus*, *Scapanus*, and *Talpa* (Figs. 5C, 6A–D) the crura are almost laminar, the thickening of the external edge being most pronounced in *Talpa*. The posterior crus is straighter than the an-

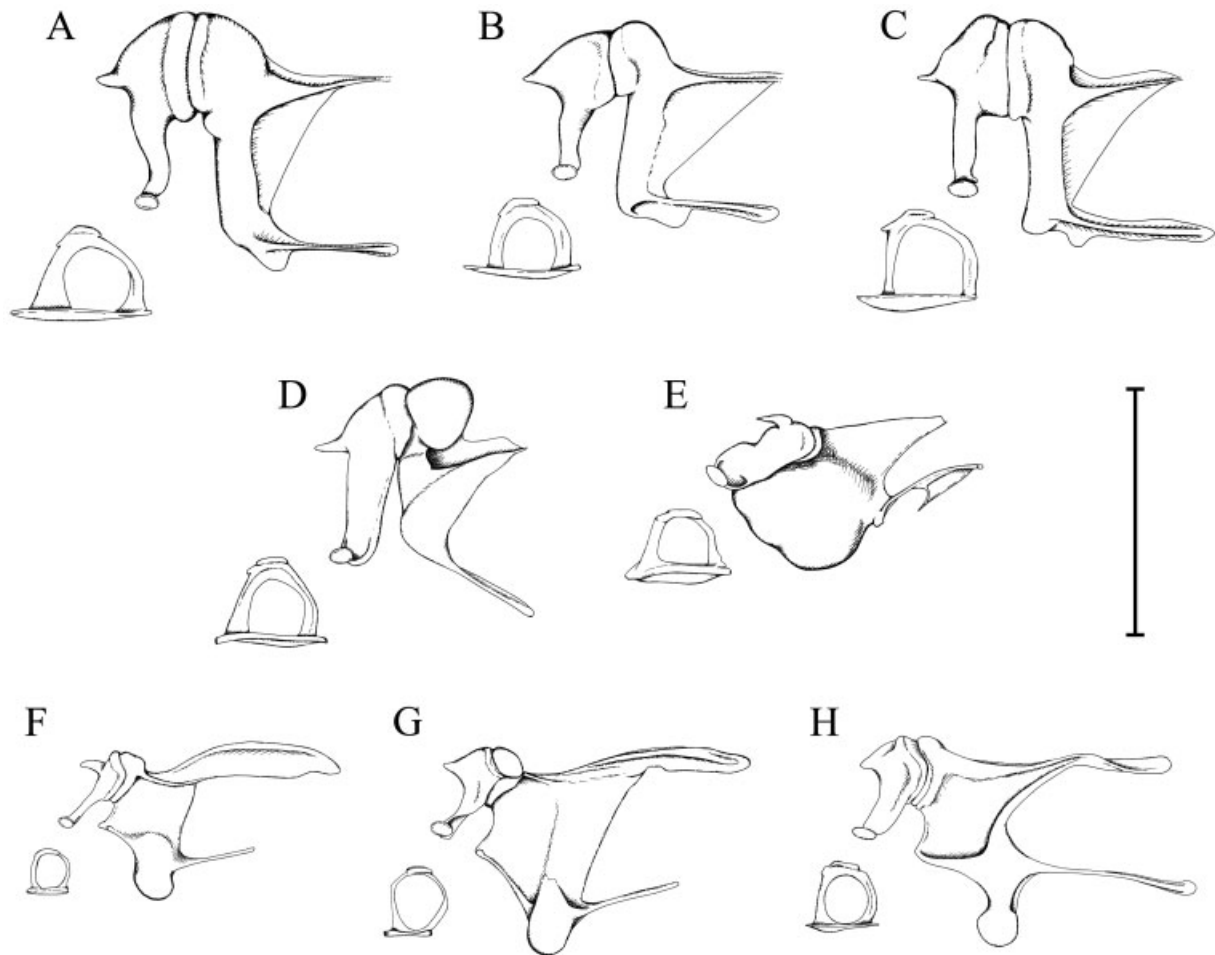


Fig. 6. Left auditory ossicles (malleus, incus, and stapes) of eight talpid species, internal views, drawn to scale. **A:** *Scalopus aquaticus*. **B:** *Scapanus orarius*. **C:** *Scapanus townsendii*. **D:** *Talpa europaea*. **E:** *Parascaptor leucura*. **F:** *Neurotrichus gibbsii*. **G:** *Parascalops breweri*. **H:** *Condylura cristata*. Scale bar = 3 mm. Note in particular the relative sizes of the malleus and incus and the relative lengths of the anterior processes.

terior and bears a small muscular process near the head. The footplates in these species are broad, and in *Scalopus* particularly flat, whereas in *Scapanus townsendii* the slight convexity of the footplate is most pronounced towards its posterior pole. The stapes of *Parascaptor* (Figs. 3C, 6E) is similar but more robustly built. The footplate, oriented within the vertical plane, is more convex in this species and the crura are not laminar; indeed, the base of the posterior crus is slightly concave internally.

The stapes of *Neurotrichus* and *Parascalops* (Fig. 6F,G) are much more delicately built than those of the species previously mentioned. The narrow crura are widely bowed outwards to accommodate the stapedia artery and the footplates are small and flat. These ossicles resemble the stapes of shrews or hedgehogs (Henson, 1961; Burda, 1979).

The stapes of *Condylura* (Fig. 6H) is somewhat intermediate between the first and second types described. The convexity of the footplate is greatest near the posterior pole.

Articulations, Ligaments, and Muscles of the Middle Ear

In no species are the ossicles synostosed. The malleo-incudal articulation (Fig. 5A,B) is unusually loose in *Talpa*, the articulating facets being flattened and the synovial cavity between appearing capacious. The incudo-stapedial articulation (Fig. 5A,B), between lenticular apophysis and the head of the stapes, was found to be firm in all species.

The very tip of the anterior process is synostosed to the ectotympanic in *Talpa*, *Scalopus*, *Scapanus* species and *Parascaptor*, this articulation being supported more proximally with a loose web of connective tissue. Despite the synostosis, this articulation is very flexible, presumably because the anterior process is so narrow and thin at the tip. The distal part of the much longer anterior process of *Condylura* is synostosed to the ectotympanic over a larger area. In *Parascalops* and *Neurotrichus* the articulation between anterior process and ectotympanic is

even more extensive: it appears mainly fibrous but is very firm. The superior ligament of the malleus, extending between the head of this ossicle and the epitympanic recess, was observed in some specimens of *Talpa* (Fig. 5E) and may have been present in the other species too: this is an extremely fine strand of tissue that is unlikely to limit the movements of the ossicle.

In *Talpa* the short process of the incus is attached to the wall of the tympanic cavity mainly by means of a tough lateral ligament, with some looser fibers dorsally at the tip. There are separate medial and lateral ligamentar bands in *Scalopus* and *Scapanus* species. In *Parascaptor* there is a short caudomedial ligament and an unusually long rostralateral ligament that connects the short process to a small papilla on the dorsal wall of the epitympanic recess. In *Parascalops* there is a short, wide terminal ligament and also a long lateral band: this seemed to be the case in *Neurotrichus* too. The nature of the attachment in *Condylura* was not determined.

The annular ligament of the stapes, which connects the footplate to the rim of the oval window, was rather loose in all moles, and the footplates were consequently easily extracted.

A relatively small stapedius muscle was found in all eight species that were dissected. In *Talpa* the long, thin muscle belly originates on the ventral basicranium, on the connective tissue that closes the mastoid canaliculus externally. It travels rostromedially through its own tunnel in the petrosal to emerge from the posterior wall of the pelvis ovalis as a thin tendon, which inserts on the posterior crus of the stapes. The course is similar in other species, although the tendon is shorter and stouter in *Neurotrichus*, *Parascalops*, and *Condylura*. There was no trace of an element of Paaw within the stapedius tendon of any species. The tensor tympani muscle is missing in *Talpa*, *Scalopus*, *Scapanus* species and *Parascaptor*. This muscle is present in *Neurotrichus*, *Parascalops*, and *Condylura*, but it is very weakly developed. Its body is located just rostral to the oval window, between stapedia and promontorial arteries: it takes an oblique course caudolaterally to insert on the malleus by means of a thin tendon (Fig. 5D). *Neurotrichus* has relatively the largest tensor tympani muscle of the moles examined.

DISCUSSION

The anatomical findings of this study largely agree with previous accounts listed in the Introduction, but there are some discrepancies, including the following. The description of the malleus of *Scalopus* in the classic work of Doran (1878) mentions a muscular process and tensor tympani, and so may not in fact refer to this species; his assertion that the short process of the incus in *Talpa* is "almost obsolete" is misleading, given that this process is the insertion point of the strongest ligament in the ossicular chain

in this species. Hyrtl (1845) denied the presence of an interbullar connection in *Talpa*, and Van der Klaauw (1931) asserts erroneously that the cavity of the inflated alisphenoid does not communicate with the tympanic cavity. The middle ear apparatus said to be that of *Talpa europaea* illustrated in Segall's work (1970, 1973) is instead probably a *Euroscaptor* species, whereas the basicranium illustrated by MacPhee et al. (1988) and labeled as the golden mole *Chlorotalpa* is actually a talpid mole, probably *Talpa*. The suspicions (Gaughran, 1954; Henson, 1961) that Wilkie (1929) had mistaken the chorda tympani for part of the anterior ligament of the malleus in *Talpa* are here confirmed. Pye's (1972) observation that the stapedius muscle appears to be absent in this species presumably refers in fact to the tensor tympani. Although Whidden (2000) was unable to find a tensor tympani muscle in any of the 12 species of moles that he studied, this muscle is present in at least three of those species (*Condylura cristata*, *Parascalops breweri*, and *Neurotrichus gibbsii*).

The fact that the *Talpa* specimens dissected all had clean and healthy external and middle ears, whereas many of the American specimens showed signs of infection, probably reflects the fact that the *Talpa* specimens were wild-caught, whereas the others had been maintained alive in laboratories for a period of time.

The middle ear structures of talpid moles are surprisingly varied (Fig. 6; Table 1), but they fall into three broad groups. "Group 1" includes *Neurotrichus*, *Parascalops*, and *Condylura*. These moles possess ectotympanic bones that are not fused to the rest of the skull, relatively simple middle ear cavities, and tensor tympani muscles. The malleus conforms to Fleischer's "microtype" morphology, found also in shrews, mice, and bats (Fleischer, 1978). Microtype ossicles are associated with high-frequency hearing, and are characterized by the possession of a large orbicular apophysis, the functional significance of which is unclear. Desmans, the shrew-moles *Uropsilus* and *Urotrichus*, and the long-tailed mole *Scaptonyx* also fall into Group 1, although the condition of the tensor tympani is not known in most of these species and the orbicular apophysis is small in desmans. Given that the ear morphologies of other eulipotyphlan insectivores, both shrews, and larger species such as hedgehogs and *Solenodon*, are similar (Henson, 1961; Segall, 1970; Burda, 1979), it is clear that the Group 1 middle ear morphology is ancestral for the Talpidae.

Moles in Group 1 have been classified as "ambulatory" (*Uropsilus*), "semi-fossorial" (*Neurotrichus*, *Urotrichus*, *Scaptonyx*), "semi-aquatic" (desmans), or "semi-aquatic/fossorial" (*Condylura*) (Whidden, 2000; Shinohara et al., 2003, 2004). Only *Parascalops*, often placed as the sister-group to *Scalopus* and *Scapanus* (Yates and Moore, 1990; Grenyer and Purvis, 2003; Shinohara et al., 2003, 2004), is con-

sidered “highly fossorial.” However, *Parascalops* is known to forage on the surface at dawn and dusk (Hamilton, 1939; Graves, 2002), so all Group 1 species apparently undertake more above-ground activity than the Group 2 moles described below.

“Group 2” includes *Talpa*, *Scalopus*, and *Scapanus* species, all considered “highly fossorial” (Shinohara et al., 2003). In *Scalopus* and *Scapanus*, the orientation of the manubrium of the malleus parallel to the anterior process, the presence of a transversal lamina, and what appears to be a vestigial orbicular apophysis (although Henson, 1961, interpreted this projection as a lateral process) are all indicative of a microtype ossicular ancestry. However, the enlarged heads of the malleus and incus, the loose articulation of an abbreviated anterior process with the ectotympanic, and the relatively large incus in all Group 2 moles are “freely mobile” characteristics, found also in many other placental mammals including humans (Fleischer, 1978). The incudal long process is excavated by a sulcus in most talpids, but only in *Talpa* among the species examined are large parts of the malleus and incus hollow. *Euroscaptor* and *Mogera* species, also “highly fossorial,” have similar ossicular morphologies to *Talpa* (Stroganov, 1945). Eight other derived features of the middle ear in this group are discussed below.

The gestalt of the ossicles suggests a close relationship between the American *Scalopus* and *Scapanus* species, and between the Eurasian *Talpa*, *Mogera*, and *Euroscaptor* species, in accordance with recent talpid phylogenies (Yates and Moore, 1990; Whidden, 2000; Grenyer and Purvis, 2003; Shinohara et al., 2003, 2004; Motokawa, 2004). Although Whidden (2000) proposed that full fossoriality evolved only once within the Talpidae, more recent phylogenies, both morphological and molecular, suggest parallel evolution, once within the Eurasian lineage and at least once within the North American lineage (Shinohara et al., 2003, 2004; Motokawa, 2004). Given that the ossicular morphologies of the Eurasian and American Group 2 species differ, parallel evolution from a microtype ancestral state certainly seems possible.

Parascaptor has some Group 2 characteristics (see Table 1), but its highly unusual, hypertrophied ossicles demand its placement in a separate group, “Group 3,” which will receive special attention below. *Scaptochirus* is a second member of Group 3.

Derived features shared by Group 2 moles, which may have evolved convergently in North American and Eurasian lineages in association with increased levels of fossoriality, include: 1) the ectotympanic fused to the basicranium; 2) an extensive recessus meatus; 3) a very small or absent pars flaccida; 4) extensive pneumatization of the bones bordering the tympanic cavity, resulting in an interbullar connection in some species; 5) tympanic arteries contained within complete bony tubes; 6) loss of the tensor tympani muscle; 7) “freely mobile” ossicles with 8) a

flattened malleo-incudal articulation, and 9) low anatomical area and lever ratios (see Table 1). Some of these characteristics, e.g., 1, 2, and 3, may well not be independent of each other; the same goes for 7, 8, and 9. Bearing this in mind, the possible functional consequences of these nine features will be examined separately.

Characteristics of Group 2 Moles

Characteristic 1. Possession of “complete” bony bullae is a common feature among mammals in general (Novacek, 1977). It may permit a more vertical orientation of the tympanic membrane, potentially allowing a larger membrane and a more capacious middle ear cavity. If the acoustical stiffness of the cavity and membrane is limiting, expansion will reduce the overall stiffness of the middle ear, improving low-frequency sound transmission. Accordingly, certain gerbils and kangaroo-rats, small mammals known to have sensitive low-frequency hearing, have relatively enormous auditory bullae (Lay, 1972; Webster and Webster, 1975). In moles, however, the tympanic membrane remains quite horizontal in position and the bulla is flattened, rather than forming a hemispherical salience on the basicranium, as is typical in mammals. Moles therefore lack markedly enlarged tympanic membranes and middle ear cavities on the scale of those seen in gerbils and kangaroo-rats, even when basicranial pneumatization is taken into account (Mason, 2001).

Webster (1966) suggested that the fusion of the ectotympanic to the basicranium in moles might improve the transmission of bone-conducted vibrations from the rest of the skull to the ear. Conversely, it is here proposed that a “free” ectotympanic would, due to its inertia, inevitably be able to vibrate relative to the skull within a certain frequency range, passing these vibrations via the ossicular chain to the inner ear. If so, fusion of the ectotympanic might actually reduce the overall bone conduction response within this range, reducing the impact of low-frequency bone-conducted noise on hearing. These competing hypotheses remain to be tested.

Characteristic 2. The ventrolateral part of the auditory bulla in many mammals represents a bony recessus meatus. Segall (1976) proposed that an expanded recessus meatus in fossorial species might function as a Helmholtz resonator to improve low-frequency hearing, but this has apparently not been tested experimentally. It is not clear that the recessus meatus of moles is any more expanded than in other mammals.

Characteristic 3. Many species, both fossorial and otherwise, lack any significant pars flaccida (Kohllöffel, 1984; Burda et al., 1992). The pars flaccida has not been found to have a significant role in middle ear pressure buffering, at least in rats and gerbils (Hellström and Stenfors, 1983; Dirckx et al.,

1998). However, acoustical shunting through the pars flaccida at low frequencies reduces the sound pressure difference across the pars tensa, resulting in a transmission loss at these frequencies (Kohllöffel, 1984; Rosowski and Lee, 2002). Kohllöffel noted the presence of a large pars flaccida in species lacking low-frequency sensitivity, including hedgehogs. It is therefore possible that the loss of the pars flaccida in Group 2 moles might reflect an increased emphasis on low-frequency hearing.

Characteristic 4. Pneumatization of surrounding bones by expansion of the middle ear cavity is relatively common in mammals, perhaps allowing an appropriate air volume in a skull that could not accommodate a sufficiently voluminous bulla (Fleischer, 1978). Trabeculation may also dampen acoustic resonance (Fleischer, 1978). The presence of a connection between right and left middle ear cavities, presumably a secondary result of the very extensive basicranial pneumatization in Group 2 talpids, is much more unusual. It was first recorded in *Talpa* by Pye and Hinchcliffe (1968), and was here identified in *Parascaptor* and *Scapanus* species too. Certain golden moles (family Chrysochloridae) are the only other mammals known to have an interbullar connection (von Mayer et al., 1995; Mason, 2003b, 2004a).

Small mammals are expected to require high-frequency sound for accurate localization: fossorial rodents with hearing restricted to low frequencies have poor localization abilities (Heffner and Heffner, 1992a). Of course, accurate sound localization may not be important for many fossorial species living in essentially one-dimensional burrow systems (Heffner and Heffner, 1990). However, the interbullar connection in some moles potentially allows sound localization by an alternative mechanism. It has been shown that there is good acoustic transmission through the head of *Talpa europaea* at frequencies up to around 6 kHz (Coles et al., 1982). Sound therefore has access to both sides of the tympanic membrane, with phase differences depending on the direction of the source. Coles et al. (1982) propose that the ear acts as a pressure-difference receiver, as in some nonmammalian vertebrates: such a system could allow localization of sound even at low frequencies. Kudo et al. (1990) relate the well-developed medial superior olive in the brainstem of *Mogera* to the localization possibilities afforded by this pressure-difference detection system.

Characteristic 5. The enclosure of middle ear arteries within bony tubes occurs in several groups of mammals. It has been argued that this would reduce low-frequency arterial noise within the middle ear (Packer, 1987), an adaptation that would improve low-frequency hearing. Tests have not been performed on live animals.

Characteristic 6. The reduction or loss of middle ear muscles is common among fossorial mammals,

and is also seen in some terrestrial species, including monotremes, tree shrews, pangolins, and some heteromyids (Webster and Webster, 1975, 1984; Fleischer, 1978; Zeller, 1986). In fossorial rodents, if a middle ear muscle is lost it is always the stapedius, whereas in other fossorial mammals it is always the tensor tympani (Burda et al., 1992; Mason, 2003b, 2004b).

Contraction of the middle ear muscles increases the stiffness of certain middle ear structures, such as the annular ligament of the stapes (Pang and Peake, 1986), reducing transmission at low frequencies. By reducing the masking effects of low-frequency noise, middle ear muscle contraction can, in principle, be used to “tune in” to higher frequencies (Møller, 1974; Murata et al., 1986). The reduction or loss of the tensor tympani in moles might therefore reflect a reduction in the ecological importance of high-frequency hearing, this reduction being most extreme in the Group 2 moles. However, tree shrews also lack a tensor tympani and yet retain good high-frequency hearing (Heffner et al., 1969), implying that there may be other reasons for the loss of this muscle. Among the heteromyids, it is the species with the smallest bullae and tympanic membranes that lack a stapedius muscle, rather than those with extreme low-frequency adaptations (Webster and Webster, 1984).

Characteristic 7. “Freely mobile” ossicles have a low-stiffness articulation between malleus and ectotympanic, potentially improving the transmission of low-frequency sound. Accordingly, the hearing of freely mobile rodent species such as guinea pigs and kangaroo rats is more acute at low frequencies than that of microtype species such as mice and rats (Heffner and Heffner, 1993; Heffner et al., 2001).

The high-frequency hearing of subterranean gophers and mole-rats is unusually limited, not exceeding 20 kHz at 60 dB SPL (Heffner and Heffner, 1990, 1992b, 1993; Brückmann and Burda, 1997). Although the audition of talpid moles has not been investigated as thoroughly, Aitkin et al. (1982) found behavioral and electrophysiological responses to frequencies between 0.2 and 15 kHz in *Talpa europaea*, while Konstantinov et al. (1987) found electrophysiological responses up to 16 kHz in this species, and from 0.1 to 22 kHz in *Mogera robusta*. These results suggest that audition in Group 2 moles is also restricted to frequencies largely within the sonic range. Models of middle ear function, however, predict that hearing in fossorial rodents and talpids should extend to high ultrasonic frequencies (Hemilä et al., 1995; Mason, 2001). Although heavier than the microtype ossicles of Group 1 moles (Table 2), the freely mobile ossicles of Group 2 species are simply not large enough to restrict high-frequency hearing significantly. Either other parts of the auditory system limit high-frequency hearing in these species, or high-frequency transmission through the middle ear is not, as is commonly as-

sumed, limited by mass reactance (Overstreet and Ruggero, 2001). The functional significance of the location of the center of mass in the auditory ossicles is discussed below.

Characteristic 8. Flattened malleo-incudal articulation surfaces have been identified in many fossorial mammals (Segall, 1973; Burda et al., 1992). A flattened articulation is likely to be looser than one that is saddle-shaped, and increased flexibility between ossicles results in losses in sound transmission (Nakajima et al., 2005). This feature cannot, therefore, be interpreted as an adaptation to improve auditory acuity. Alternatively, flexibility in the ossicular chain might reduce excessive stapes displacement and consequent inner ear damage in response to static pressure changes across the eardrum (Cancura, 1980; Hüttenbrink, 1988), as might be experienced by a mole diving into and running through narrow tunnels. The malleo-incudal articulation is synostosed in some fossorial rodents (Burda et al., 1992; Mason, 2004b), so there is no universal trend among subterranean mammals in this respect.

Characteristic 9. Fossorial mammals generally have lower anatomical area and lever ratios than nonfossorial species (Burda et al., 1992; Mason, 2001). The mean area ratio for 102 nonfossorial mammals is 28.27 (Mason, 2001): all Group 2 talpids have area ratios below this value (Table 1). Anatomical lever ratios in all talpids are below the nonfossorial mean of 2.24 (Mason, 2001), and are also lowest in Group 2 species (Table 1). Area and lever ratios are believed to contribute to the impedance-matching function of the middle ear (Relkin, 1988). Although anatomically measured ratios often differ from functional values measured in vivo (Khanna and Tonndorf, 1972; Decraemer and Khanna, 1994), low ratios are generally expected to result in poorer impedance matching, and thus less efficient transmission of sound through to the inner ear. However, rather than being caused by degenerative reduction of the pars tensa or malleus, the lower area and lever ratios in Group 2 moles are actually the result of an enlarged stapes footplate and an enlarged incus, respectively (Mason, 2001). The selective advantage associated with these characteristics, if any, is unknown.

In their comparative study, Burda et al. (1992) identified features 3, 6, 7, 8, and 9 as being characteristic of the ear of fossorial mammals in general. Their conclusions are fully supported by the identification in the present study of the same characteristics as derived features of the ear in the highly fossorial Group 2 talpids. They therefore appear to represent convergent adaptations to a subterranean environment, but it is interesting to note that the adaptive values of three of them (6, 8, 9) are unclear. Although experimental confirmation is sorely lacking, six of the nine derived features of Group 2 talpids (1, 2, 3, 4, 5, 7) potentially improve low-

frequency hearing. This would be adaptively advantageous to a fossorial mammal, exposed primarily to low frequencies that travel better underground. However, most of these six characteristics are relatively common among mammals, and there is little evidence to suggest that talpid low-frequency hearing would be superior to that of terrestrial species with freely mobile middle ears. A similar conclusion holds for fossorial rodents: although low-frequency auditory sensitivity in these animals is superior to that of "microtype" species such as rats, it is similar to (or worse than) that of other "freely mobile" rodents (Heffner and Heffner, 1993).

Group 1 talpids spend more time above ground than Group 2 species, whereupon they will be exposed to high-frequency auditory cues. Although the apparent reduction of the tensor tympani muscle is a typically "fossorial" characteristic, Group 1 moles have otherwise retained an ancestral ear morphology similar to that of shrews, apparently suitable for high-frequency hearing. *Neurotrichus* seems to respond behaviorally to frequencies between 8 and 30 kHz (Dalquest and Orcutt, 1942), supporting the prediction that the hearing range of Group 1 talpids extends to higher frequencies than that of Group 2 species. Hearing is known to extend to higher frequencies in burrowing rodents that spend time above ground than in more exclusively subterranean species (Heffner et al., 1994, 2001; Begall et al., 2004).

Ossicular Mass Distribution and Bone Conduction in Moles

Experimental work in cats and humans has shown that the motion of the ossicles in response to airborne sound is much more complicated than a simple rotation about a fixed axis (Decraemer et al., 1991, 1994; Decraemer and Khanna, 1994). As a first approximation, however, it is assumed in the following discussion that the ossicles are constrained to rotate about such an axis, extending between the anterior process of the malleus and the short process of the incus (Dahmann, 1929; Wever and Lawrence, 1954). This approximation is likely to be reasonable at low frequencies.

The center of mass in a microtype malleus lies near the orbicular apophysis, on the stapelial side of the rotatory axis (Fleischer, 1978). By contrast, freely mobile mallei lack an orbicular apophysis, while the heads of both malleus and incus, on the opposite side of the rotatory axis, are much expanded: the center of mass of freely mobile ossicles therefore lies much closer to the axis (Bárány, 1938; Fleischer, 1978). The consequent reduction in ossicular inertia is not what would be expected for a "low-frequency" ear, and it demands explanation.

Low-frequency seismic vibrations transmitted through the soil may be communicated to the skull of a fossorial mammal by direct or indirect contact;

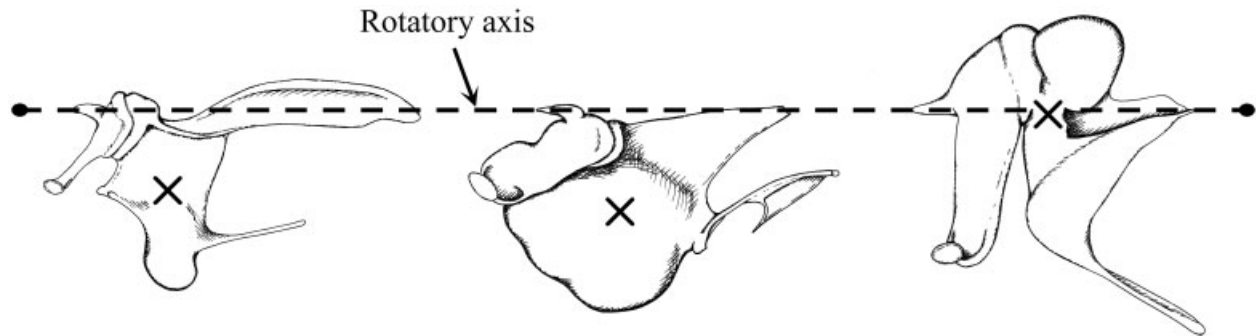


Fig. 7. Left auditory ossicles (malleus and incus) of talpid moles, drawn to scale. The dotted line represents the anatomically defined rotatory axis of the ossicles; the crosses represent the estimated positions of the centers of mass. The ossicles of *Neurotrichus* (left) are taken to be representative of the ancestral, "microtype" structure. In *Parascaptor* (center) the center of mass is in a similar position relative to the axis but the malleus is hypertrophied; the center of mass in the "freely mobile" ossicles of *Talpa* (right) is much closer to the rotatory axis.

chewing, digging, and vocalizing represent further sources of skull vibrations. Skull vibrations may, in turn, be transmitted to the inner ear by any of several routes collectively referred to as "bone conduction" (Tonndorf, 1972). Semi-fossorial Group 1 talpids might not be greatly troubled by bone-conducted noise, especially if their auditory systems are tuned to high frequencies. However, bone conduction will be more significant for a highly fossorial mole, especially if the articulation between anterior process and ectotympanic is loosened and the ossicular mass is increased. In this case, bringing the center of mass of the ossicles closer to their rotatory axis will reduce transmission of bone-conducted vibrations to the inner ear by the ossicular inertial route (Bárány, 1938). As mentioned above, fusion of the ectotympanic to the basicranium in moles might reduce a different but comparable form of inertial bone conduction.

Although bone conduction in most mammals is usually regarded as a source of unwanted, low-frequency noise that interferes with normal hearing, ground-borne vibrations potentially represent a useful source of sensory information for a fossorial mammal, and several species exploit this communication medium (see Mason and Narins, 2001). Although the mass distribution within the "freely mobile" ossicular chains of Group 2 moles apparently serves to minimize inertial bone conduction, there are other modes of bone conduction by which vibrations could be transmitted to the inner ear. Vibratory sensitivity can also be conferred by the somatosensory system: *Nannospalax* mole-rats have recently been shown to be able to use their paws to detect seismic signals (Kimchi et al., 2005). The cortical representations of both paws and snout are remarkably developed in talpid moles (Catania, 2000), so it would be surprising if talpids did not use their somatosensory systems to detect ground vibrations.

Middle Ear Apparatus of Group 3 Moles

Certain golden moles (family Chrysochloridae) have greatly hypertrophied mallei in which the center of mass is displaced far from the rotatory axis, two key adaptations believed to increase seismic sensitivity through inertial bone conduction (Lombard and Hetherington, 1993; Mason, 2003a,b, 2004a). Although the ossicular hypertrophy is much less extreme than in some golden mole genera, the malleus of *Parascaptor leucura* shows similar adaptations. The center of mass of the ossicular chain is located near the middle of the malleus in this species, well displaced from the rotatory axis (Fig. 7). The *Parascaptor* ossicles resemble the microtype ossicles of Group 1 moles in this respect, but they are considerably heavier (Table 2) and are only loosely attached to the skull. In golden moles, the center of mass lies on the opposite side of the rotatory axis; this difference in location is presumably the result of ancestry.

As in golden moles, these features of the *Parascaptor* ear are expected to augment inertial bone conduction at low frequencies. However, an improved bone conduction response may come at the cost of reduced hearing sensitivity in air. The flimsy manubrium of *Parascaptor* is angled toward the rotatory axis, yielding an anatomical lever ratio less than one: this feature is shared with the golden mole *Chrysospalax villosus* (Mason, 2004a) but is not known in any other mammal. Coupled with a very low area ratio, also a feature of certain golden moles (Mason, 2001), the impedance-matching of the *Parascaptor* middle ear is expected to be very inefficient, and the relatively heavy ossicles may restrict high-frequency hearing (but note earlier caveats regarding predictions of this nature).

Almost nothing is known of the ecology of *Parascaptor leucura*. Cranbrook (1962) noted that the runs, made in loose substrate, "go from rotten tree trunk to rotten tree trunk, running down the length

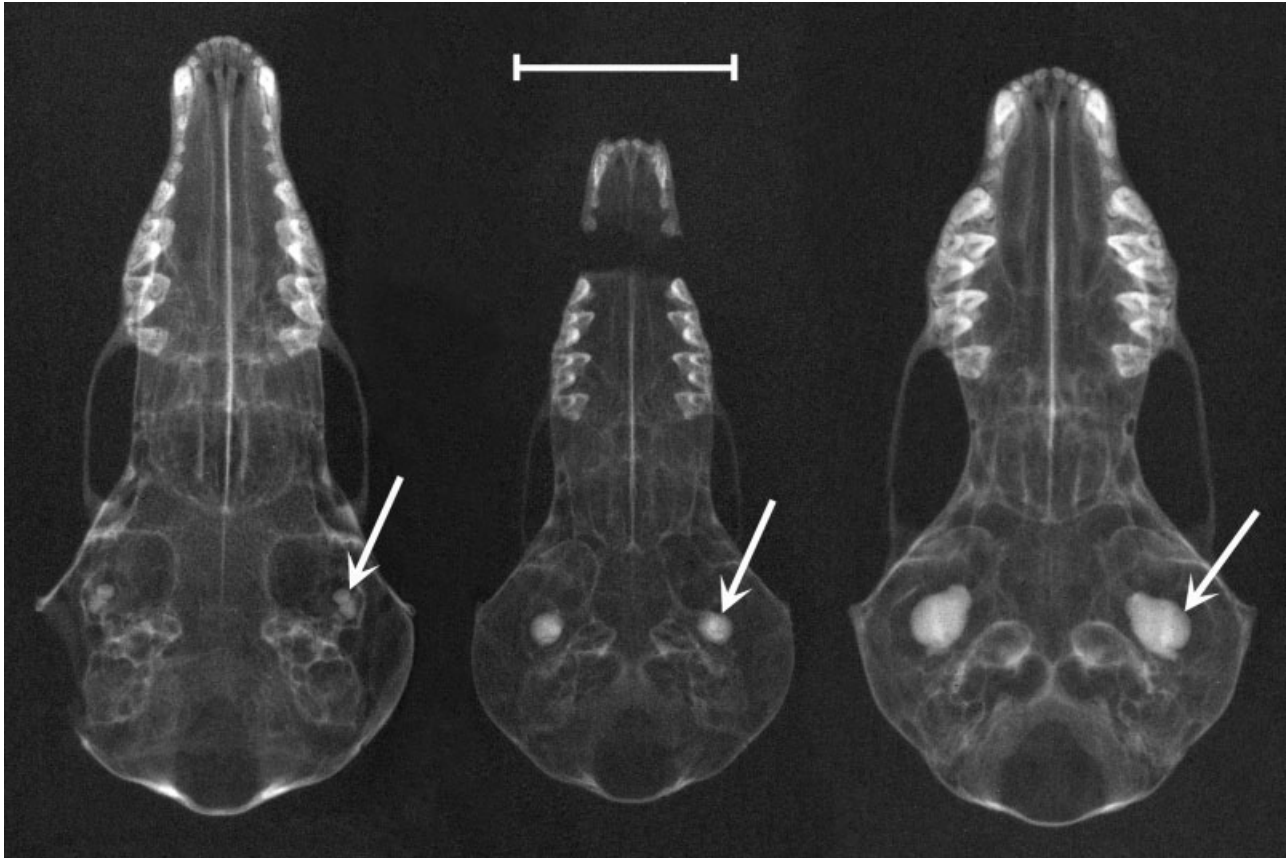


Fig. 8. Radiographs of the skulls of *Talpa europaea* (left), *Parascaptor leucura* (middle), and *Scaptochirus moschatus* (right). The auditory ossicles are indicated with arrows. The rostral snout was broken off from the rest of the skull in the *Parascaptor* specimen and part of the calvarium on the left side of the *Talpa* skull was missing. Scale bar = 10 mm.

of the trunk and out the other end, then making with an uncanny sense of direction for the end of the next tree trunk." Direct paths taken in the loose sand between adjacent grassy tussocks were used as evidence that the golden mole *Eremitalpa* detects the seismic cues generated by the tussocks (Narins et al., 1997). It is here proposed that *Parascaptor* uses its enlarged ear ossicles for an analogous form of sensory-guided foraging.

Although classified as a species of *Talpa* in the past, *Parascaptor leucura*, known from Burma, Assam, Yunnan, and neighboring regions, is now considered to be the only member of its genus (Hutterer, 1993). The only other talpid known to have enlarged ossicles is the short-faced mole, *Scaptochirus moschatus* (Fig. 8), a species from northeastern China that is also the only member of its genus. The ear ossicles of *Scaptochirus* were illustrated by Stroganov (1945), who referred to this species as "*Parascaptor grandidens*": they appear to be very similar to those of *P. leucura*, but are considerably larger and the malleus has an expanded orbicular apophysis. The auditory region of the skull is similar too, except that the pneumatized region in *Scaptochirus* extends further rostrally into the alisphenoid (this

study). The generic separation of *Scaptochirus* and *Parascaptor* is based on cranial, dental, and pelvic structure (Grulich, 1982). Recent phylogenies place both within the Talpini clade, together with *Talpa*, *Mogera*, and *Euroscaptor*, but not as sister-groups (Grenyer and Purvis, 2003; Motokawa, 2004). The relationships between these moles demand further attention, but the similarity of their ear apparatus warrants their placement in a separate group from the other species examined, referred to here as "Group 3."

CONCLUSION

Middle ear morphologies vary considerably in talpid moles, but can be divided into three groups. The ancestral, microtype morphology is found in moles that spend at least some time on the surface: these species ("Group 1") are likely to be able to hear into the ultrasonic range. More exclusively subterranean moles ("Group 2") have a suite of middle ear characteristics that may have evolved convergently in the American and Eurasian talpid lineages. Several of these characteristics can be interpreted as low-frequency adaptations, although physiological ex-

periments are needed to confirm this. Ossicular hypertrophy in both *Parascaptor* and *Scaptochirus* ("Group 3") is probably associated with augmented seismic sensitivity through inertial bone conduction.

ACKNOWLEDGMENTS

I thank Adrian Friday and the staff of the University Museum of Zoology, Cambridge, UK, for their help and support throughout this project. Paula Jenkins kindly allowed the use of material from the Natural History Museum, London, while Kevin Campbell and Ken Catania provided North American specimens. Dave Ellington of DRE Pest Control (Swavesey, Cambridgeshire, UK), Julian Robb and Andrew Newton of NRA Central Contracts (Ely, Cambridgeshire, UK), and John and Graham Burton provided most of the *Talpa* specimens, with others provided by D. Aldridge, J. Flowerdew, M. Page, N. Smith, N. Toogood, G. Tuck, E. Tufton, and M. Wells. The SEMs were taken by Tony Burgess in the Department of Anatomy, University of Cambridge, and the radiographs by Gilly Thorp and Julie Sales in the Department of Veterinary Medicine. Peter Tuck and Lutz Lauterbach provided translations of the German literature.

LITERATURE CITED

- Abe H. 1995. Revision of the Asian moles of the genus *Mogera*. *J Mamm Soc Jpn* 20:51–68.
- Aitkin LM, Horseman BG, Bush BMH. 1982. Some aspects of the auditory pathway and audition in the European mole, *Talpa europaea*. *Brain Behav Evol* 21:49–59.
- Bárány E. 1938. A contribution to the physiology of bone conduction. *Acta Otolaryngol Suppl* (Stockh) 26:1–233.
- Begall S, Burda H, Schneider B. 2004. Hearing in coruros (*Spalacopus cyanus*): special audiogram features of a subterranean rodent. *J Comp Physiol [A]* 190:963–969.
- Bondy G. 1907. Beiträge zur Vergleichenden Anatomie des Gehörorgans der Säuger. (Tympanicum, Membrana Shrapnelli und Chordaverlauf). *Anat Hefte* 35:293–408.
- Brückmann G, Burda H. 1997. Hearing in blind subterranean Zambian mole-rats (*Cryptomys* sp.): collective behavioural audiogram in a highly social rodent. *J Comp Physiol [A]* 181:83–88.
- Bruns V, Müller M, Hofer W, Heth G, Nevo E. 1988. Inner ear structure and electrophysiological audiograms of the subterranean mole rat, *Spalax ehrenbergi*. *Hear Res* 33:1–10.
- Burda H. 1979. Morphology of the middle and inner ear in some species of shrews (Insectivora, Soricidae). *Acta Sc Nat Brno* 13:1–46.
- Burda H, Müller M, Bruns V. 1988. The auditory system in subterranean mammals. In: Elsner N, Barth FG, editors. *Sense organs. Interfaces between environment and behaviour*. Stuttgart: G. Thieme.
- Burda H, Bruns V, Nevo E. 1989. Middle ear and cochlear receptors in the subterranean mole-rat, *Spalax ehrenbergi*. *Hear Res* 39:225–230.
- Burda H, Bruns V, Hickman GC. 1992. The ear in subterranean Insectivora and Rodentia in comparison with ground-dwelling representatives. 1. Sound conducting system of the middle ear. *J Morphol* 214:49–61.
- Cancura W. 1980. On the statics of malleus and incus and on the function of the malleus-incus joint. *Acta Otolaryngol* (Stockh) 89:342–344.
- Catania KC. 2000. Cortical organisation in Insectivora: the parallel evolution of the sensory periphery and the brain. *Brain Behav Evol* 55:311–321.
- Coles RB, Gower DM, Boyd PJ, Lewis DB. 1982. Acoustic transmission through the head of the common mole, *Talpa europaea*. *J Exp Biol* 101:337–341.
- Cranbrook Earl of. 1962. Notes on the habits and vertical distribution of some insectivores from the Burma-Tibetan frontier. *Proc Linn Soc Lond* 173:121–127.
- Cuvier GLCFD. 1805. *Leçons d'anatomie comparée*. Paris: Baudouin.
- Dahmann H. 1929. Zur Physiologie des Hörens; experimentelle Untersuchungen über die Mechanik der Gehörknöchelchenkette, sowie über deren Verhalten auf Ton und Luftdruck. *Z Hals-Nasen-Ohrenheilkunde* 24:462–497.
- Dalquest WW, Orcutt DR. 1942. The biology of the least shrew-mole, *Neurotrichus gibbsii minor*. *Am Midl Nat* 27:387–401.
- Decraemer WF, Khanna SM. 1994. Modelling the malleus vibration as a rigid body motion with one rotational and one translational degree of freedom. *Hear Res* 72:1–18.
- Decraemer WF, Khanna SM, Funnell WRJ. 1991. Malleus vibration mode changes with frequency. *Hear Res* 54:305–318.
- Decraemer WF, Khanna SM, Funnell WRJ. 1994. A method for determining three-dimensional vibration in the ear. *Hear Res* 77:19–37.
- Dirckx JJJ, Decraemer WF, von Unge M, Larsson C. 1998. Volume displacement of the gerbil eardrum pars flaccida as a function of middle ear pressure. *Hear Res* 118:35–46.
- Doran AHG. 1878. Morphology of the mammalian *ossicula auditus*. *Trans Linn Soc Lond*, 2nd ser 1:371–497.
- Fleischer G. 1978. Evolutionary principles of the mammalian middle ear. *Adv Anat Embryol Cell Biol* 55:1–70.
- Gaughran GRL. 1954. A comparative study of the osteology and myology of the cranial and cervical regions of the shrew *Blarina* and the mole *Scalopus*. *Misc Pub Mus Zool Univ Mich* 80:1–82.
- Graves GR. 2002. Crepuscular surface foraging of the hairy-tailed mole (*Parascalops breweri*). *J N C Acad Sci* 118:206–209.
- Grenyer R, Purvis A. 2003. A composite species-level phylogeny of the 'Insectivora' (Mammalia: Order Lipotyphla Haeckel, 1866). *J Zool* 260:245–257.
- Grulich I. 1982. Zur Kenntnis der Gattungen *Scaptochirus* und *Parascaptor* (Talpini, Mammalia). *Folia Zool* 31:1–20.
- Hamilton WJ. 1939. Activity of Brewer's mole (*Parascalops breweri*). *J Mammal* 20:307–310.
- Heffner RS, Heffner HE. 1990. Vestigial hearing in a fossorial mammal, the pocket gopher (*Geomys bursarius*). *Hear Res* 46:239–252.
- Heffner RS, Heffner HE. 1992a. Evolution of sound localization in mammals. In: Webster DB, Fay RR, Popper AN, editors. *The evolutionary biology of hearing*. New York: Springer. p 691–715.
- Heffner RS, Heffner HE. 1992b. Hearing and localization in blind mole rats (*Spalax ehrenbergi*). *Hear Res* 62:206–216.
- Heffner RS, Heffner HE. 1993. Degenerate hearing and sound localization in naked mole rats (*Heterocephalus glaber*), with an overview of central auditory structures. *J Comp Neurol* 331:418–433.
- Heffner HE, Ravizza RJ, Masterton B. 1969. Hearing in primitive mammals. III. Tree shrew (*Tupaia glis*). *J Aud Res* 9:12–18.
- Heffner RS, Heffner HE, Contos C, Kearns D. 1994. Hearing in prairie dogs: transition between surface and subterranean rodents. *Hear Res* 73:185–189.
- Heffner RS, Koay G, Heffner HE. 2001. Audiograms of five species of rodents: implications for the evolution of hearing and the perception of pitch. *Hear Res* 157:138–152.
- Hellström S, Stenfors L-E. 1983. The pressure equilibrating function of pars flaccida in middle ear mechanics. *Acta Physiol Scand* 118:337–341.
- Hemilä S, Nummela S, Reuter T. 1995. What middle ear parameters tell about impedance matching and high frequency hearing. *Hear Res* 85:31–44.

- Henson OW. 1961. Some morphological and functional aspects of certain structures of the middle ear in bats and insectivores. *Univ Kansas Sci Bull* 42:151–255.
- Heth G, Frankenberg E, Nevo E. 1986. Adaptive optimal sound for vocal communication in tunnels of a subterranean mammal (*Spalax ehrenbergi*). *Experientia* 42:1287–1289.
- Hüttenbrink KB. 1988. The mechanics of the middle-ear at static air pressures: the role of the ossicular joints, the function of the middle-ear muscles and the behaviour of stapedial prostheses. *Acta Otolaryngol Suppl* (Stockh) 451:1–35.
- Hutterer R. 1993. Order Insectivora. In: Wilson DE, Reeder DM, editors. *Mammal species of the world: a taxonomic and geographic reference*. Washington, DC: Smithsonian Institution Press. p 69–130.
- Hyrtil J. 1845. *Vergleichend-anatomische Untersuchungen über das innere Gehörorgan des Menschen und der Säugethiere*. Prague: Verlag von Friedrich Ehrlich.
- Khanna SM, Tonndorf J. 1972. Tympanic membrane vibrations in cats studied by time-averaged holography. *J Acoust Soc Am* 51:1904–1920.
- Kimchi T, Reshef M, Terkel J. 2005. Evidence for the use of reflected self-generated seismic waves for spatial orientation in a blind subterranean mammal. *J Exp Biol* 208:647–659.
- Kohllöffel LUE. 1984. Notes on the comparative mechanics of hearing. III. On Shrapnell's membrane. *Hear Res* 13:83–88.
- Konstantinov AN, Movchan VN, Shibkov AA. 1987. Functional properties of the auditory system and acoustic signalling in insectivores. *J Evol Biochem Physiol* 23:321–328.
- Kudo M, Nakamura Y, Tokuno H, Kitao Y. 1990. Auditory brainstem in the mole (*Mogera*): nuclear configurations and the projections to the inferior colliculus. *J Comp Neurol* 298:400–412.
- Lange S, Stalleicken J, Burda H. 2004. Functional morphology of the ear in fossorial rodents, *Microtus arvalis* and *Arvicola terrestris*. *J Morphol* 262:770–779.
- Lay DM. 1972. The anatomy, physiology, functional significance and evolution of specialised hearing organs of gerbilline rodents. *J Morphol* 138:41–120.
- Lombard RE, Hetherington TE. 1993. Structural basis of hearing and sound transmission. In: Hanken JH BK, editor. *The skull*. Chicago: University of Chicago Press. p 241–302.
- MacPhee RDE, Novacek MJ, Storch G. 1988. Basicranial morphology of early Tertiary erinaceomorphs and the origin of primates. *Am Mus Novitates* 2921:1–42.
- Mason MJ. 1999. The functional anatomy of the middle ear of mammals, with an emphasis on fossorial forms. PhD thesis. Cambridge, UK: University of Cambridge.
- Mason MJ. 2001. Middle ear structures in fossorial mammals: a comparison with non-fossorial species. *J Zool* 255:467–486.
- Mason MJ. 2003a. Bone conduction and seismic sensitivity in golden moles (Chrysochloridae). *J Zool* 260:405–413.
- Mason MJ. 2003b. Morphology of the middle ear of golden moles (Chrysochloridae). *J Zool* 260:391–403.
- Mason MJ. 2004a. Functional morphology of the middle ear in *Chlorotalpa* golden moles (Mammalia, Chrysochloridae): predictions from three models. *J Morphol* 261:162–174.
- Mason MJ. 2004b. The middle ear apparatus of the tuco-tuco *Ctenomys sociabilis* (Rodentia, Ctenomyidae). *J Mammal* 85: 797–805.
- Mason MJ, Narins PM. 2001. Seismic signal use by fossorial mammals. *Am Zool* 41:1171–1184.
- McDowell SB. 1958. The Greater Antillean insectivores. *Bull Am Mus Nat Hist* 115:113–214.
- Møller AR. 1974. The acoustic middle ear muscle reflex. In: Keidel WD, Neff WD, editors. *Handbook of sensory physiology*, vol. V/1. Auditory system. Berlin: Springer. p 519–548.
- Motokawa M. 2004. Phylogenetic relationships within the family Talpidae (Mammalia: Insectivora). *J Zool* 263:147–157.
- Müller M, Burda H. 1989. Restricted hearing range in a subterranean rodent, *Cryptomys hottentotus*. *Naturwissenschaften* 76:134–135.
- Murata K, Ito S, Horikawa J, Minami S. 1986. The acoustic middle ear muscle reflex in albino rats. *Hear Res* 23:169–183.
- Nakajima HH, Ravicz ME, Merchant SN, Peake WT, Rosowski JJ. 2005. Experimental ossicular fixations and the middle ear's response to sound: evidence for a flexible ossicular chain. *Hear Res* 204:60–77.
- Narins PM, Lewis ER, Jarvis JUM, O'Riain J. 1997. The use of seismic signals by fossorial southern African mammals: a neuroethological gold mine. *Brain Res Bull* 44:641–646.
- Novacek MJ. 1977. Aspects of the problem of variation, origin and evolution of the eutherian auditory bulla. *Mammal Rev* 7:131–149.
- Nummela S. 1995. Scaling of the mammalian middle ear. *Hear Res* 85:18–30.
- Overstreet EH, Ruggero MA. 2001. Development of wide-band middle ear transmission in the Mongolian gerbil. *J Acoust Soc Am* 111:261–270.
- Packer DJ. 1987. The influence of carotid arterial sounds on hearing sensitivity in mammals. *J Zool* 211:547–560.
- Pang XD, Peake WT. 1986. How do contractions of the stapedius muscle alter the acoustic properties of the ear? In: Allen JB, Hall JL, Hubbard A, Neely ST, Tubis A, editors. *Peripheral auditory mechanisms*. New York: Springer. p 36–43.
- Platzer W. 1961. Die Ossicula auditus von *Talpa europea*. *Anat Anz* 109:130–136.
- Pye A. 1972. Variations in the structure of the ear in the different mammalian species. *Sound* 6:14–18.
- Pye A, Hinchcliffe R. 1968. Structural variations in the mammalian middle ear. *Med Biol Illus* 18:122–127.
- Relkin EM. 1988. Introduction to the analysis of middle-ear function. In: Jahn AF, Santos-Sacchi J, editors. *Physiology of the ear*. New York: Raven Press. p 103–123.
- Rosowski JJ, Lee C-Y. 2002. The effect of immobilizing the gerbil's pars flaccida on the middle-ear's response to static pressure. *Hear Res* 174:183–195.
- Schleich CE, Busch C. 2004. Functional morphology of the middle ear of *Ctenomys talarum* (Rodentia: Octodontidae). *J Mammal* 85:290–295.
- Segall W. 1970. Morphological parallelisms of bulla and auditory ossicles in some insectivores and marsupials. *Fieldiana Zool* 51:169–205.
- Segall W. 1973. Characteristics of the ear, especially the middle ear, in fossorial mammals, compared to those in the Manidae. *Acta Anat (Basel)* 86:96–110.
- Segall W. 1976. Further observations on the ear in fossorial mammals with special consideration of *Chlamyphorus truncatus* (Harlan). *Acta Anat (Basel)* 94:431–444.
- Shinohara A, Campbell KL, Suzuki H. 2003. Molecular phylogenetic relationships of moles, shrew moles, and desmans from the New and Old Worlds. *Mol Phylogenet Evol* 27:247–258.
- Shinohara A, Suzuki H, Tsuchiya K, Zhang YP, Luo J, Jiang XL, Wang YX, Campbell KL. 2004. Evolution and biogeography of talpid moles from continental East Asia and the Japanese islands inferred from mitochondrial and nuclear gene sequences. *Zool Sci* 21:1177–1185.
- Simonetta A. 1957. Anatomia e significato morfologico e sistematico dell'orecchio medio e delle strutture ad esso connesse in alcuni insettivori (*Suncus*, *Talpa*, *Chrysochloris*). *Arch Ital Anat Embriol* 62:55–94.
- Stroganov SU. 1945. Morphological characters of the auditory ossicles of Recent Talpidae. *J Mammal* 26:412–420.
- Tonndorf J. 1972. Bone conduction. In: Tobias JV, editor. *Foundations of modern auditory theory*. London: Academic Press. p 197–237.
- Van der Klaauw CJ. 1931. The auditory bulla in some fossil mammals, with a general introduction to this region of the skull. *Bull Am Mus Nat Hist* 62:1–352.
- Van Kampen PN. 1905. Die Tympanalgegend des Säugetierschädels. *Gegenbaurs Morphol Jahrb* 34:321–722.
- von Mayer A, O'Brien G, Sarmiento EE. 1995. Functional and systematic implications of the ear in golden moles (Chrysochloridae). *J Zool* 236:417–430.
- Webster DB. 1966. Ear structure and function in modern mammals. *Am Zool* 6:451–466.

- Webster DB, Webster M. 1975. Auditory systems of Heteromyidae: functional morphology and evolution of the middle ear. *J Morphol* 146:343–376.
- Webster DB, Webster M. 1984. The specialized auditory system of kangaroo rats. In: Neff WD, editor. Contributions to sensory physiology, vol. 8. Orlando, FL: Academic Press. p 161–196.
- Wever EG, Lawrence M. 1954. Physiological acoustics. Princeton, NJ: Princeton University Press.
- Whidden HP. 2000. Comparative myology of moles and the phylogeny of the Talpidae (Mammalia, Lipotyphla). *Am Mus Novitates* 3294:1–53.
- Wilkie HC. 1925. The auditory apparatus of the common mole, *Talpa europæa*. *Proc Zool Soc Lond* 1925:1281–1292.
- Wilkie HC. 1929. The attachments of the auditory ossicles of the common mole (*Talpa europæa*). *Proc Zool Soc Lond* 1929:61–65.
- Yates TL, Moore DW. 1990. Speciation and evolution in the family Talpidae (Mammalia: Insectivora). In: Nevo E, Reig OA, editors. Evolution of subterranean mammals at the organismal and molecular levels. New York: Wiley-Liss. p 1–22.
- Zeller UA. 1986. Ontogeny and cranial morphology of the tympanic region of the Tupaiidae, with special reference to *Ptilocercus*. *Folia Primatol (Basel)* 47:61–80.