

Morphological Adaptations of the Ear in the Rodent Family Heteromyidae¹

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SYNOPSIS. Middle and inner ear structure and auditory sensitivity have been studied in all five genera of the rodent family Heteromyidae. In the most xeric genera (*Dipodomys* and *Microdipodops*) the middle ears are greatly inflated, the tympano-ossicular system very efficient, the organ of Corti extremely modified, and low-frequency sensitivity extremely acute. In the most mesic genera (*Heteromys* and *Liomys*) the middle and inner ears show few modifications and the low-frequency sensitivity is rather poor. *Perognathus* is intermediate in habitat, structure, and low-frequency sensitivity. Experimental data demonstrate that the low-frequency sensitivity in *Dipodomys* is adaptive in predator avoidance.

INTRODUCTION

Comparative studies on adaptation to the environment have usually involved species which are genetically widely divergent; thus they have examined evolutionary strategies that were either parallel or convergent in adapting these divergent species to a common environment. The first such study, however, was done on a genetically similar group of organisms which, under extreme selective pressures, had evolved a variety of morphological adaptations fitting them to diverse habitats. We refer, of course, to Darwin's study on the finches of the Galapagos Archipelago—perhaps the most convincing of Darwin's demonstrations of evolution by natural selection.

For several years we have studied the diversity of peripheral auditory structures (middle and inner ears) found in the rodent family Heteromyidae (Webster, 1961, 1962; Webster and Stack, 1968; Webster and Webster, 1971, 1972, 1975, 1977). The five genera of this family live in vastly different habitats in the southwestern United States, Mexico, and Central America. *Heteromys* is confined to tropical forest areas and *Liomys* is largely confined to tropical grasslands and dense brush in Central America and Mexico; most species of *Perognathus* live in desert grasslands and talus desert slopes of the southwestern

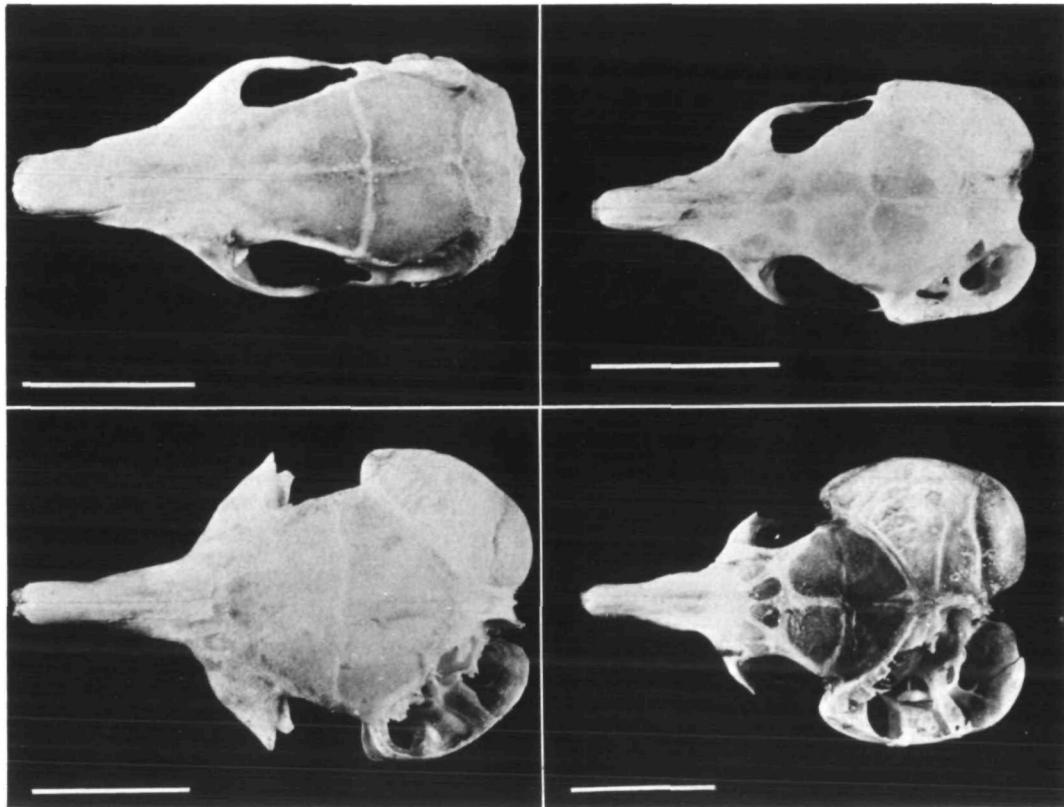
United States, while some are found in extreme deserts and others in chaparral; *Dipodomys* lives mainly in deserts but some species live in chaparral; the two species of *Microdipodops* are confined to high, sagebrush deserts where there is fine, shifting sand. Analysis of the structural and functional diversity of the peripheral auditory system in these five genera, combined with their paleontological history, provides some insights into evolutionary processes.

MIDDLE EAR DIVERSITY

The qualitative and quantitative morphology of the heteromyid middle ear was studied in 358 middle ears from 27 species drawn from all five genera. The middle ear was dissected, and measurements were made of its volume and of the tympanic membrane and ossicles. An additional 133 ears (27 species; 5 genera) were serially sectioned for microscopic study. (Except for the data on *Heteromys*, we have presented the middle ear portion elsewhere and in more detail [Webster and Webster, 1975].)

Middle ear volume is the most obvious variable (Fig. 1; Table 1). In *Dipodomys* and *Microdipodops*, the two most xeric genera, all three portions of the middle ear are inflated (hypotympanic, antral, epitympanic). The bony walls are paper-thin and the middle ear space is so expanded that no trabeculated air cells remain. In absolute size, the middle ear space is greatest in *Dipodomys*; relative to body size, it is greatest in *Microdipodops*. In *Perognathus* the

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Line = 1 cm

FIG. 1. Dorsal view of the skulls of representative heteromyids with the left middle ear opened. Upper left, *Liomys irroratus*; upper right, *Perognathus formosus*; lower left, *Dipodomys spectabilis*; lower right, *Microdipodops pallidus*.

middle ear volume is larger than it is in most small rodents, but significantly smaller, both absolutely and relative to body size, than those of *Dipodomys* and *Microdipodops*. Each portion of the middle ear has a central open cavity; the periphery is composed of trabeculated bone with air cells whose lumina are continuous with the main cavity. *Liomys* and *Heteromys*, the two most mesic genera, have the smallest middle ears, with small, non-trabeculated hypotympanic and antral spaces and a moderately sized, fully trabeculated antral space.

As in most rodents, the tympanic membrane of heteromyids is approximately circular; its diameter reflects the middle ear volume, being greatest in *Dipodomys* and

Microdipodops, intermediate in *Perognathus*, and least in *Liomys* and *Heteromys*.

In all heteromyids, the ossicular chain is of the parallel type, with the manubrium of the malleus being approximately parallel to the long process of the incus. The ratio of these lever arms (long process of incus to manubrium of malleus) is critical to middle ear efficiency. This ratio is least in *Dipodomys* and *Microdipodops*, intermediate in *Perognathus*, and greatest in *Liomys* and *Heteromys*. The major variable is the length of the manubrium, which in *Dipodomys* is more than twice what it is in the similar-sized genus, *Liomys* (Table 1).

Another critical ratio is that of the area of the stapes footplate to the effective area of the tympanic membrane (that is, $\frac{2}{3}$ of

TABLE 1. Middle ear parameters.

	<i>Microdipodops</i>	<i>Dipodomys</i>	<i>Perognathus</i>	<i>Liomys</i>	<i>Heteromys</i>
Middle ear volume (cm ³)	0.34	0.68	0.06	0.03	0.03
Incus lever arm (mm)	0.74	0.98	0.73	0.85	0.78
Malleus lever arm (mm)	2.62	3.22	1.71	1.48	1.52
Lever ratio (I/M)	0.28	0.30	0.42	0.57	0.51
Areal ratio [$A_s/2/3(A_d)$]	0.06	0.06	0.05	0.06	0.06
Impedance at tympanic membrane (dynes sec/cm ³)	27	32	48	112	90
Transmission (%)	95	98	99	79	86

its actual area). Although the areas themselves vary greatly among the heteromyid genera, the *ratio* of the two is remarkably constant (Table 1).

These two ratios—of the areas and of the levers—are the most important factors in the ability of the middle ear to transmit sound to the cochlea. The impedance of the mammalian cochlea is about 5,600 dynes sec/cm³; that of the air in the external auditory meatus about 41.5 dynes sec/cm³. The interposed tympano-ossicular system acts as an impedance-matching transformer. Its lever system both increases the pressure and decreases the velocity of the stapes relative to the tympanic membrane; at the same time the force impinging upon the tympanic membrane is resolved upon the much smaller stapes footplate, thus again increasing the pressure but not affecting the velocity. Algebraically, this relationship is represented as follows:

$$\frac{Z_d}{Z_s} = \frac{A_s}{\frac{2}{3}(A_d)} \left[\frac{l_i}{l_m} \right]^2$$

where Z_d = impedance at the tympanic membrane (or "drum");
 Z_s = impedance at the stapes;
 A_s = area of the stapes footplate;
 A_d = area of the tympanic membrane;
 $\frac{2}{3}(A_d)$ = its effective area in moving the ossicles;
 l_i = length of the long process of the incus;
 l_m = length of the manubrium of the malleus.

Thus, the ratio of the impedance at the tympanic membrane to the impedance at

the stapes equals the product of the areal ratio and the squared lever ratio.

If we accept 5,600 dynes sec/cm³ as the impedance of the mammalian cochlea, and measure the middle ear structures which vary from species to species, we can then use this formula to calculate the (apparent) impedance at the tympanic membrane (Z_d) for any specific ear. Such calculations demonstrate that the highest Z_d is found in *Liomys* and the smallest in *Microdipodops* (Table 1), but this does not tell the whole story. A Z_d of 41.5 dynes sec/cm³ would mean that the impedance at the tympanic membrane is perfectly matched to that of the air in the external auditory meatus, and there would be a theoretical 100% transfer of acoustic energy from the external auditory meatus to the cochlea. When Z_d is either greater or less than 41.5 dynes sec/cm³, the theoretical transmission is less than 100%. Among the heteromyid genera, the middle ear mechanism matches these impedances least efficiently in *Liomys*, which has a calculated 79% transfer of energy, and most efficiently in *Perognathus*, which has a calculated 99% transfer (Table 1).

These are the calculated percentages of acoustic energy that theoretically could be transferred, considering only the lever and areal ratio systems; in reality the impedances of the middle ear structures themselves determine how much of this theoretical figure can be attained. Thus, frictional resistance, mass reactance, and stiffness reactance in the middle ear must all be considered. Frictional resistance is negligible in heteromyids because of the delicate suspension of the tympano-ossicular system. Mass reactance is directly

TABLE 2. *Qualitative ear comparisons.*

	<i>Microdipodops</i>	<i>Dipodomys</i>	<i>Perognathus</i>	<i>Liomys</i>	<i>Heteromys</i>
Bullate stapes	yes	yes	no	no	no
Stapedius muscle	yes	yes	no	no	no
Trabeculated bullae	no	no	antral	antral	antral
Extent of annular lig.	full	full	epitympanic hypotympanic tympanic side	both sides	both sides
Stapedial artery	yes	yes	yes	no	no
Epitympanum	large	large	small	small	small
Lever ratio	large	large	small	small	small
Areal ratio	average	average	average	average	average
% transmitted sound	large	large	large	average	average
Antrum	large	large	small	tiny	tiny
Hypotympanum	large	large	small	tiny	tiny
Stapedial crura	rod	rod	arc	arc	arc
Scala tympani	average	average	small	tiny	tiny
Basilar membrane thickness	huge	huge	huge	large	large
Basilar membrane width changes	1st turn	1st turn	little	little	little
Border cells of organ of Corti	huge	huge	huge	average	average

proportional to frequency, while stiffness reactance is inversely proportional to frequency. At one specific frequency, called the resonant frequency, mass and frequency reactances cancel one another, and the middle ear comes as close as possible to its calculated best transmission; above or below this frequency, mass or stiffness, respectively, will decrease efficiency. Therefore, a middle ear with a more massive tympano-ossicular system facilitates low-frequency reception, while one with greater stiffness facilitates high-frequency reception. Small mammals such as mice and bats typically have middle ears with low mass and high stiffness; their best hearing lies well above that of the human ear which has high mass and low stiffness.

In heteromyids—most notably in *Dipodomys* and *Microdipodops*—the middle ear space and the tympanic membrane are both quite large, significantly reducing middle ear stiffness. Even in *Perognathus*, *Liomys*, and *Heteromys* the middle ear space and tympanic membrane are larger than in most rodents, suggesting less stiffness; in addition these three genera have a reduced annular ligament of the stapes and no stapedius muscle, further reducing the stiffness. Furthermore, because all heteromyids are small rodents, they all have

low-mass tympano-ossicular systems. With both mass and stiffness reduced, and an efficient impedance-matching mechanism, one would predict that auditory sensitivity would cover a broad frequency range and be particularly acute for low frequencies. Judging from the morphological characteristics of the middle ear (Table 2), one would expect the greatest sensitivity in *Dipodomys* and *Microdipodops* and the least sensitivity in *Liomys* and *Heteromys*. Other middle ear characteristics listed in Table 2 have little known functional significance but do suggest some taxonomic relationships within the family.

COCHLEAR DIVERSITY

Serial sections in the plane of the modiolus were studied in 133 ears including representatives of all five genera. (Except for *Heteromys*, these data are published in more detail elsewhere [Webster and Webster, 1977].) The cochlear perilymphatic spaces are unremarkable in *Dipodomys* and *Microdipodops*. In *Perognathus*, *Liomys*, and *Heteromys* the apical portion of the scala tympani becomes extremely constricted: between turn 1½ and the apex (turn 3½) the spiral ligament connective tissue extends into what is usually the scala tympani; combined with a very low osseous

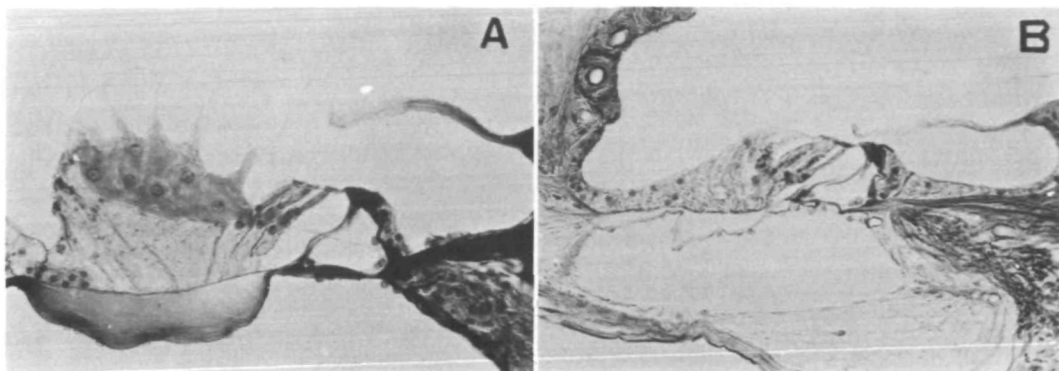


FIG. 2. Radial sections of the organ of Corti of: A, *Dipodomys merriami* with its hypertrophied border cells; and B, *Liomys adserpsus*, with average mammalian border cells. $\times 141$, Mallory stain.

spiral lamina, this reduces the cross-sectional area of the scala tympani to 0.002 mm^2 in *Liomys* and 0.003 mm^2 in *Perognathus* and *Heteromys*. The helicotrema is, of course, comparably smaller than normal in these genera; both helicotrema and scala tympani are of normal size in the other two genera.

The basilar membrane is unusual in heteromyids. In most mammals the basilar membrane is narrowest at the base and becomes progressively wider apically. In *Dipodomys* and *Microdipodops* the basilar membrane width doubles in the first half turn and then increases very little throughout the upper three turns. In *Perognathus*, *Liomys*, and *Heteromys* it increases slightly in the first half turn and then remains almost constant to the apex. There is also an extraordinary thickening of the zona pectinata, caused by an increase in the amount of cottony ground substance between the upper and lower fiber layers. This thickening is very slight in the base, becomes maximal in the second and third turns, and then decreases considerably toward the apex. The thickening is most prominent in *Dipodomys* and *Microdipodops*, and least prominent in *Liomys* and *Heteromys*.

The border cells of Claudius and Hensen are of typical mammalian structure in *Heteromys* and *Liomys*, but are most unusual in *Dipodomys*, *Microdipodops*, and *Perognathus* (Fig. 2). In these three genera, Claudius' cells extend internally to abut against Deiters' cells; Hensen's cells are thus sup-

ported by Claudius' cells. The Hensen's cells are hypertrophied, with long apical processes which rise from the cell bodies and then spread out like flower blossoms to abut against each other, forming a large canopy above the extracellular space they enclose. This extracellular space is continuous with the space of Nuel surrounding the outer hair cells and with the tunnel of Corti. Such unusual border cells have not been described in other mammals. They extend the entire $3\frac{1}{2}$ turns of the cochlea, but are most prominent in the second and third turns.

It is difficult to speculate on the functional significance and adaptive value of such cochlear modifications. Since the modifications are greatest in the apical half of the cochlea, one suspects they are related to low-frequency reception. The rapid attainment of near-maximal basilar membrane width also suggests that most of the cochlear partition might respond to low frequencies. In addition, it raises some basic questions about cochlear mechanics.

In the typical mammalian cochlea the basilar membrane increases in width gradually and constantly from base to apex; this produces a stiffness gradient and therefore a continually changing impedance, and is a necessary condition for the traveling wave motion which is crucial to our understanding of cochlear mechanics. Among heteromyids, however, the change is not constant and continuing; on the contrary, the morphology suggests an actual

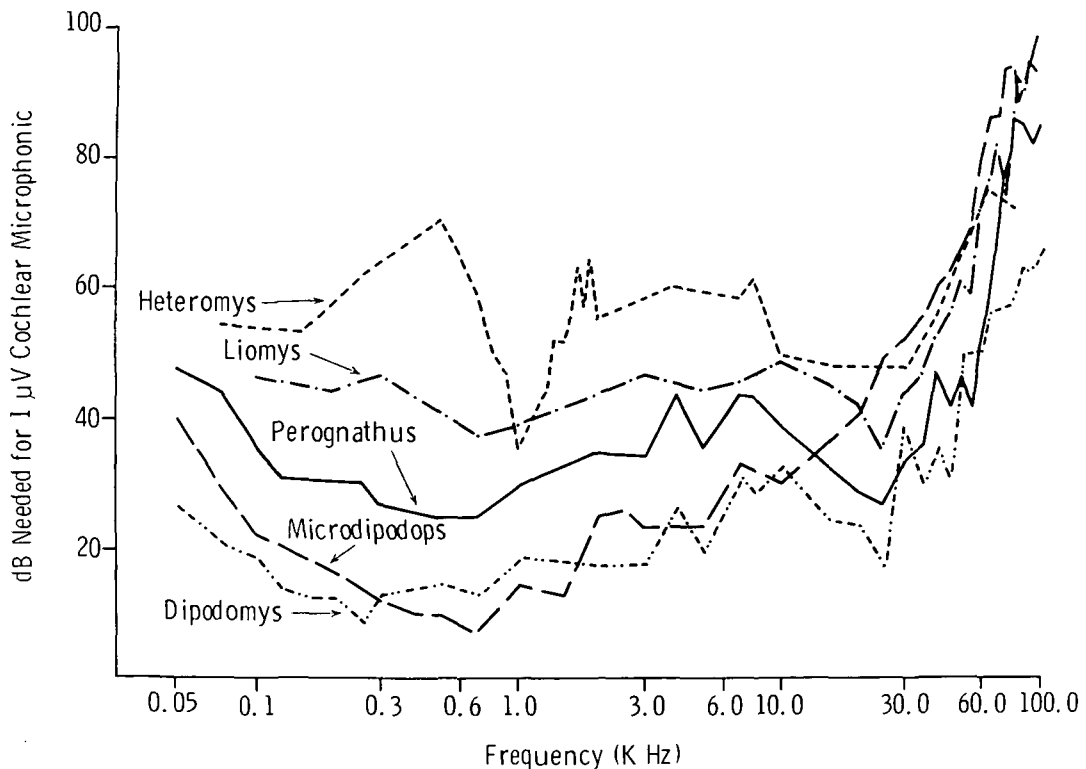


FIG. 3. Mean auditory sensitivity of each genus of Heteromyidae as measured by cochlear microphonics.

impedance discontinuity. This suggests strongly that a standing wave, rather than a traveling wave, occurs in the heteromyid cochlea. The same could be true in certain other mammals, such as bats. Such a phenomenon should facilitate very sensitive hearing, but blur frequency discrimination.

AUDITORY SENSITIVITY

The sensitivity of heteromyid hearing was measured using the cochlear microphonic (CM) as an index. The CM is an AC bioelectrical potential of the organ of Corti, whose voltage is proportional to the intensity of the stimulating sound and whose frequency mimics it. In our experiments we determined what sound pressure was necessary to cause a 1- μ V CM in the frequency range from 50 Hz to 100 kHz, for 93 ears from all five heteromyid genera (Webster and Strother, 1972). Many of the experiments were done in collaboration with Dr. William Strother of

Princeton University; some of the animals were tested by Dr. Ernest Peterson of Miami University.

The data are summarized in Figure 3. It should be noted that although all the genera have a broad area of sensitivity up to 30 kHz, there are distinct differences. *Dipodomys* and *Microdipodops* have the most sensitive CM, particularly at low frequencies. Less than 20 dB SPL is required to produce the 1- μ V CM in *Dipodomys* (at 75–3,000 Hz), and in *Microdipodops* (at 200–2,000 Hz). These two genera are about 20 dB more sensitive at low frequencies than *Perognathus*, and about 40 dB more sensitive than *Liomys* and *Heteromys*. The extremely sensitive peak at 1,000 Hz in *Heteromys* is difficult to explain as a middle ear phenomenon; it could be produced in the inner ear as a result of standing wave phenomena.

Both physiological and behavioral studies on *Dipodomys* demonstrate that experimentally reducing middle ear volume re-

duces auditory sensitivity by 15–25 dB for frequencies below 4,000 Hz (Webster, 1961; Webster and Webster, 1972). Thus the enlarged middle ear cavities, which decrease middle ear stiffness, facilitate low-frequency transmission by the tympano-ossicular system.

ADAPTIVE VALUE OF LOW-FREQUENCY HEARING

We asked what might be the adaptive value of the heteromyids' unusual low-frequency sensitivity. It is obviously not to facilitate intraspecific communication, since vocalizations are very rare among heteromyids and, when they do occur, lie outside their range of greatest auditory acuity. The next most obvious adaptation for survival would be for predator avoidance. We therefore examined the interaction of Merriam's kangaroo rat, *D. merriami*, and two common rodent predators, rattlesnakes and owls. Both these animals are nocturnal, like heteromyids, and both have specific adaptations for hunting in total darkness.

In studies using recently captured kangaroo rats in outdoor desert enclosures, we learned that even in nearly total darkness kangaroo rats could avoid the predatory attempts of both owls and rattlesnakes by leaping away a fraction of a second before potential capture. On the other hand, kangaroo rats with experimentally reduced middle ear volume were unable to avoid these predatory strikes (Webster, 1962). Sonograms demonstrated frequencies within the kangaroo rat's best-hearing range immediately before the predator's strike, apparently caused by the snake pushing against the substrate, or by the braking maneuver of owls as they slow down their dive to strike.

In further experiments with rattlesnakes and kangaroo rats, we found that totally blind kangaroo rats could avoid predatory strikes, as could kangaroo rats with reduced middle ear volume, provided there was sufficient light (*e.g.*, moonlight); kangaroo rats that had undergone both experimental blinding and middle ear volume reduction could not avoid rattlesnakes. In a final experiment (Webster and Web-

ster, 1971), recently captured kangaroo rats were code-marked and then underwent (1) surgery to reduce middle ear volume, or (2) surgery in which the bullae were opened but left normal and weights were inserted under the skin above the skull, or (3) no surgery; after recovery all were released at their capture site. For the following month the area was systematically retrapped every fourth night as a census of the three groups. Two-thirds of both the normal and the mock-operated animals were routinely found in the live traps and released. However, after the second week, only two of the nine animals with reduced middle ears were ever found in the traps. It was during the dark phase of the moon that these animals with reduced auditory sensitivity disappeared from the census. Thus the greater low-frequency auditory sensitivity resulting from enlarged middle ears is necessary for detecting predatory strikes when there is insufficient light in the environment.

HABITAT, STRUCTURE, AND EVOLUTIONARY DIVERSIFICATION

Our data, summarized above, demonstrate that the most conservative ears and the least sensitive hearing are found in *Liomys* and *Heteromys*, most of which inhabit tropical forests and grasslands; the most extremely modified ears and the best hearing are in *Dipodomys* and *Microdipodops*, most of which inhabit deserts. *Perognathus* is intermediate in structure, hearing, and habitat. The correlation of habitat diversity with ear structure and hearing is more understandable when the family's fossil record is considered (Reeder, 1957). The earliest known heteromyids, which resembled the present-day *Heteromys* and *Liomys*, lived along streams in the subtropical climate of what is now Colorado and surrounding states. Diversification was coincident with the gradual rising and drying of western North America: at least 14 genera became extinct, while others either migrated or became adapted to the changing environment. The *Heteromys-Liomys* lineage moved south along with the tropical to subtropical habitats to which they were adapted. The lineage leading to *Di-*

podomys and *Microdipodops* stayed where they were but became greatly modified, along with their environment; thus they evolved greatly inflated middle ears and other characteristics (such as a super-efficient kidney) to enable them to survive in a desert habitat. The *Perognathus* lineage became adapted to semiarid regions, where most species of this genus still live. The correlation of genus with habitat is not complete because of late evolutionary radiations within genera. For instance, some *Perognathus* species today are found only in very dense chapparal (e.g., *P. californicus*), and others only in extreme deserts (e.g., *P. penicillatus*).

The selective pressure for these auditory modifications such as we see in heteromyids is no doubt especially strong for nocturnal species in a desert environment, where discontinuous vegetation allows little natural cover and reduced food availability requires that considerable time be given to foraging. In fact, similar modifications are found in several old world desert rodents (e.g., gerbils, jerboas, and the spring haas) and the African elephant shrews. There is also a fossil record of South American marsupials with greatly inflated middle ears. All these are small, desert-dwelling mammals. On the other hand, there are rodents with similar environmental problems which lack these auditory specializations, such as deer mice, pack rats, ground squirrels, and grasshopper mice. Auditory specialization is not the only way for such mammals to avoid over-predation. It is, however, an evolutionary strategy developed independently and successfully in several groups of small desert

mammals. Among the heteromyids, each genus gives some clues as to this evolutionary process.

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