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The auditory bulla of Dipodomys deserti (Rodentia) and evidence of its adaptive significance

by

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The adaptive modifications of desert rodents, and particularly of the family Heteromyidae, have been of considerable interest to naturalists. These fossorial and saltatorial rodents exhibit morphological and behavioral adaptations which have been prime factors in their successful occupation of certain regions of North and South America. This family includes five living genera; *Perognathus, Microdipodops, Dipodomys, Liomys* and *Heteromys* (SIMPSON, 7). Of these, the three-chambered auditory bulla is known to occur in all but the latter two (WOOD, 8).

The genus *Dipodomys,* exemplified by the kangaroo rats, contains the largest members of the family. Generally considered to be the most highly specialized species is the desert kangaroo rat, *Dipodomys deserti,* a common inhabitant of the sand dune regions in the deserts of the southwestern United States and northwestern Mexico (GRINNELL, 2; SETZER, 6; WOOD, 8).

Although *Dipodomys* has been the subject of numerous studies, most of these have contributed primarily to our knowledge of the taxonomy, ecology and behavior of the group. Relatively few investigators have made studies of the morphological aspects of the genus with any concern to the adaptive significance and selective value of these features. The most thorough investigation of the anatomy of the kangaroo rats is that of HOWELL (5), which is a composite study based largely on *Dipodomys spectabilis.* The present work is based exclusively on *Dipodomys deserti* and extends and confirms Howell's observations; further, it attempts to analyze the adaptive significance of the auditory bullae with regard to the kangaroo rats in general and *Dipodomys deserti* in particular.

OSTEOLOGY

Even among the saltatorial rodents *Dipodomys* presents one of the more significant examples of the extreme development of the auditory bulla. Externally

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this displays itself in a notable widening of the posterior part of the skull, resulting in a distinct triangular shape when viewed dorsally. This feature has been determined by the marked inflation of the mastoid and tympanic elements. The mastoid is a thinwalled structure bordered dorsally and posteriorly by the parietal and supraoccipital respectively, ventrally by the exoccipital and tympanic (which in turn meets anteroventrally with the tympanic of the opposite side), and anteriorly by the squamosal. The external opening of the auditory meatus is located in an approximate medial position in the mastoid. Ventral to the auditory meatus, the stylomastoid foramen is situated in such a position that it terminates the sulcus separating the mastoid and the tympanic elements of the bulla. This sulcus extends from the foramen to the lateral process of the exoccipital. A slight process swells dorsally to the stylomastoid foramen and is apparently part of the mastoid element. The tympanic ring represents the location of attachment of the tympanic membrane and may be viewed, without dissection, as an arc traversing the medioventral part of the tympanic element. In figure 1 the left dorsolateral view shows the margin of the tympanic membrane on the interior surface of the tympanic element.

With the removal of the dorsal and posterior portions of the mastoid bone the internal structure of the mastoid sinuses and the middle ear are easily discernible. The mastoid septum divides the bulla into medial and lateral chambers and extends from the base of the interparietal to the posterior margin of the auditory canal, thereby seeming to bisect the bony labyrinth of the inner ear in a superficial fashion. In one of the five specimens examined this septum was perforated by a large foramen. The mastoid sinuses are separated from the tympanic portion of the bulla by a bony septum extending from the stylomastoid foramen to the posterior root of the jugal.

The lateral mastoid chamber is cavernous and is strengthened by bony buttresses which attach from the lateral, anterior and medial margins of the chamber to the mastoid roof. This chamber communicates with the tympanic cavity by the superior mastoid-tympanic fenestra. Along the margin of this fenestra can be noted the malleus and incus. Medially the anterior portion and ampulla of the superior semicircular canal are conspicuous, as is the anterior part of the lateral semicircular canal just ventral to it (figure 1). The bony labyrinth comprises the major portion of the medial wall.

The margins of the medial mastoid chamber are without the buttresses which are present in the lateral chamber. The sacculus and utriculus are again distinct in an anteromedial position. From the ampulla of the posterior semicircular canal, connected to the lower margin of the utriculus, the major curvature extends ventrally. This curvature connects with the lateral semicircular canal to form the common crus. The ampulla of this lateral canal is situated in a ventral position on the globeshaped sacculus; the canal itself curves anterolaterally through the mastoid septum and into the lateral mastoid chamber (figure 2). Bony struts extend from the posterior margins of the utriculus and sacculus to the inner roots of the interparietal and supraoccipital.

The medial mastoid chamber is joined to the tympanic cavity by the tympanomastoid fenestra, which is bordered by bony struts supporting the lateral semicircular canal. The stapedial artery is enclosed entirely within an osseous canal and traverses this fenestration within the tympanic chamber (figure 3). Lateral to the fenestration and extending from the proximity of the lateral semicircular canal is the canal of the facial nerve (VII), formed by the overthrust of the mastoid and septal elements. Lateral to the medial terminus of the facial canal is the small fenestration opening to the fossa incudis of the tympanic chamber.

By removing the superficial part of the tympanic element on the ventral surface of the skull the structure of the tympanic chamber is exposed. The malleus and incus are located along the lateral margin of the superior mastoid fenestra. The articulation of these two elements is by an interdigitation of their respective processes. The manubrium of the malleus is attached throughout its length to the tympanic membrane and terminates in a blunt, rounded head. The manubrium extends ventromedially from the lateral surface of the malleus. The tympanic membrane is large (about 5 mm. in diameter) and situated at an angle of about 45 degrees from the vertical, the dorsal portion being the most lateral. It is attached to the margins of the internal auditory meatus and to the tympanic element. As stated earlier, this latter attachment is clearly visible externally as the tympanic ring. The margins of attachment are apparently ossified along the entire perimeter of the membrane. The incus is bifurcated in the posterior portion, forming a short process and a long process; the latter is shaped into a narrow peduncle that curves posteromedially and terminates in an enlarged lenticular process articulating with the head of the stapes. This articulation is simply one of opposing flattened heads. The stapes extends medially. The long crus and short crus are joined by the hemispherical base and thus form an intercrural fenestra enclosing the stapedial canal. The short crus is lodged in the fossa incudis, hence the long crus is the process attached to the fenestra ovalis. The canal for the stapedial artery enters the tympanic chamber on the medial margin and arches toward the fenestra rotunda and the base of the cochlea, passing anteriorly between the crura of the stapes. The cochlear capsule lies fused on the dorsal surface of the tympanic cavity and extends horizontally along the sagittal axis. Transverse constrictions result from the structure of the cochlea in forming at least two completely fused spirals. A central constriction of the elongate capsule is distinct but less conspicuous constrictions can be noted on both the base and apical portions.

DISCUSSION

Probably the most significant considerations in the gross anatomy of the auditory bullae of *Dipodomys deserti* are: 1.) the relatively free suspension of the bony labyrinth within the auditory chambers, 2.) the inflated character of the mastoid and tympanic elements, 3.) the relatively large size of the tympanic membrane accompanied by the elongation of the manubrium and 4.) the interdigitating articulation of the malleus and incus.

HOWELL (5) compares the size of the tympanic membrane in *Dipodomys spectabilis* as being approximately three-fifths as large as this structure in man. This in itself is of importance considering the comparative size of these small rodents. In serving as a lever activating the malleus, the manubrium would increase the sensitivity in direct proportion to its elongation. Further, the interdigitating articulation of the malleus and incus is such that it should greatly enhance the sensitivity of response. Adaptive modifications resulting in the marked inflation of the auditory chambers may well have facilitated the function of these as resonating chambers.

GRINNELL (2) has indicated the inverse correlation between the size of the pinnae and the degree of inflation of the auditory bullae, giving as one example *Dipodomys deserti.* He also states that the selective influences of other factors, such as the amount of digging, modes of predation and type of cover and soil may be significant. The kangaroo rats are most often described as fossorial rodents, but they are, in fact, as much cursorial animals. The adaptations of such habits are generally contrary to one another and although the considerations given by Grinnell may impose some restriction upon auditory perception, it appears that the other enlarged auditory structures of *Dipodomys deserti* may compensate to some degree for this reduction of the external ears. There is inferential evidence presented by the anatomical structure of the bulla to indicate that this species possesses acute auditory perception.

BARTHOLOMEW and CASWELL (1) have concluded that the manner of locomotion in *Dipodomys* places a limitation upon the types of habitat available to the genus. It "... can be expected to occupy successfully only those regions in which smooth-surfaced, sparsely vegetated foraging areas are available". The apparent necessity for *Dipodomys* to restrict itself to the described environment and the high degree of development of the auditory structures may be indicative of the survival value of the auditory sense in certain lines of evolution.

Dipodomys deserti is more restricted in its habitat selection than most other members of the genus. It is known to occupy only areas in which wind-blown sands have accumulated to a degree that permits extensive burrowing (GRINNELL, 3; HALL, 4). Ideally then, the aeolian sand dune areas provide some of the most satisfactory and the largest areas of habitat available to these rodents with the requirement that a minimum amount of plant life be available within foraging distance. In such habitats as these vegetation is sparse and that it, in itself, could provide adequate cover of protection from predators during periods of foraging is unlikely. The success with which *Dipodomys deserti* occupies this habitat reflects the degree of its specialization in the light of the conclusion that throughout the genus there is a tendency for the more highly specialized species to inhabit a more open desert-type of environment (SETZER, 6).

The significance of the auditory structure in *Dipodomys* with respect to its saltatorial abilities requires further study and experimentation beyond that attempted within the immediate scope of this work. A comparative study of the auditory structure of other heteromyids, especially *Perognathus,* should provide a better understanding of adaptations within the family.

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SUMMARY

The osseous structure of the auditory bullae of the desert kangaroo rat, *Dipodomys deserti,* has been studied. The most significant modifications of this structure are the relatively free suspension of the bony labyrinth, the inflated character of the mastoid and tympanic bones, the enlarged tympanic membrane and elongated manubrium and an intrincate articulation of the malleus and incus.

Evidence based upon habitat selection and the degree of specialization of this species would seem to indicate that these features have accompanied other adaptations as an important supplement. It seems likely that auditory perception has been an adaptation of selective value in the evolution of *Dipodomys deserti.*

RESUMEN

Se estudia la estructura ósea de la bula auditiva de la rata saltadora del desierto, *Dipodomys deserti.* Las modificaciones más importantes de esta estructura son la suspensión relativamente libre del laberinto óseo, la inflación marcada de los huesos mastoide y timpánico, la membrana timpánica agrandada con alargamiento proporcional del manubrio, y la articulación interdigitada del martillo y el yunque.

La selección de habitat y el grado de especialización de esta especie parecen indicar que aquellos caracteres han acompañado a otras adaptaciones como suplemento importante. Parece probable que la percepción auditiva muy aguda ha sido una adaptación de valor selectivo en la evolución de *Dipodomys deserti.*

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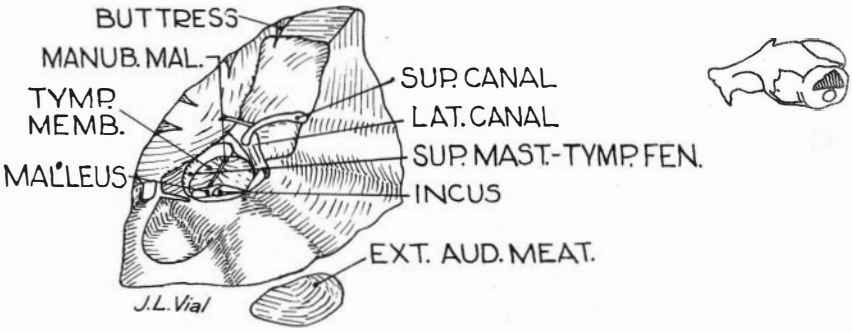
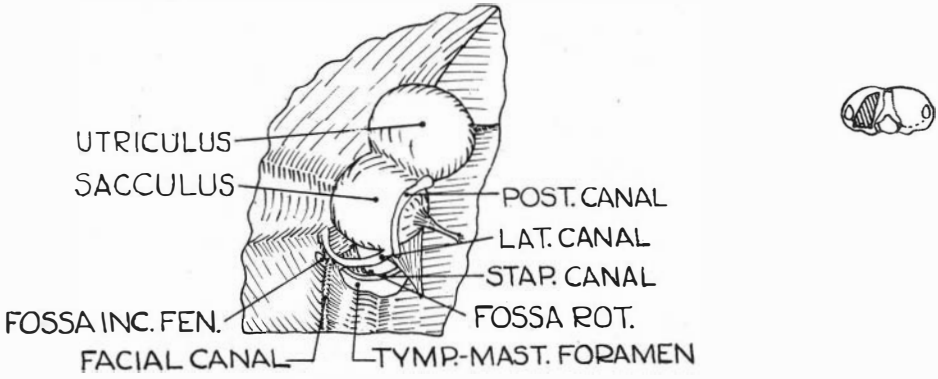


Figure 1.



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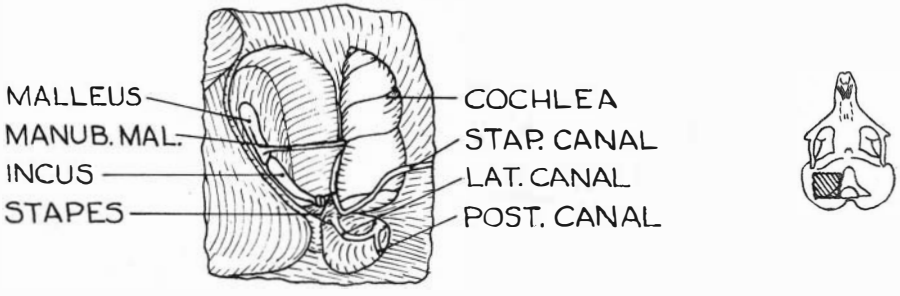

Figure 3.