ANATOMY OF MIDDLE-EAR WALLS AND CAVITIES IN NINE SPECIES OF MICROTINE RODENTS

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THOUGH IT MAY have other functions, the middle ear primarily is a transformer which changes air vibrations received from the exterior into fluid vibrations in the inner ear, amplifying the pressure as needed (Békésy, 1960; Webster, 1966). This mechanism, contained in the auditory bulla, typically consists of a three-part lever system connecting two elastic membranes and the muscles, nerves, and nutrients which operate and sustain it.

Among mammals this basic structural plan is augmented and modified in a wide variety of ways, and there may be corresponding adjustments in function. Greatest diversity is seen in the peripheral part of the auditory system (external ear) which is in direct contact with the external environment; moderate diversity obtains for the middle ear and conservatism characterizes the inner ear (Webster, 1966).

That mammals vary greatly in hearing systems is emphasized in many nineteenth-century reports on mammalian anatomy. The studies of Otto (1826), Hyrtl (1845), Winge (1887, edition of 1941), and Tullberg (1899) are cases in point. These and many subsequent contributions, which are summarized by van Kampen (1905) and van der Klaauw (1931), have provided the basis for recent studies of structure and function of various parts of the system, though the work emphasizing the human (Wever and Lawrence, 1954, Békésy, 1960) apparently has not drawn extensively on that of non-human species.

In regard to the middle ear, the ossicular chain and hypertrophied auditory bullae have received a major share of attention and as a result are better known than other middle-ear parts. There is now anatomical

and experimental evidence, for example, that the ossicles and their muscles to some extent control the volume and frequency of input to the inner ear (Wiggers, 1937, Békésy, 1960; Webster, 1966) and that large bullae may reduce damping of the tympanic membrane and enhance sensitivity of hearing in some frequency ranges important to the animal (Webster, 1961, 1962).

Several authors (e.g., van Kampen, 1905; van der Klaauw, 1931; Simkin, 1965) have noted that the walls of the middle-ear system, together with the cavities they form, vary greatly among mammalian species. Information on the Microtinae, in particular, dates back at least to 1826 when Otto noted that the bullar walls in *Lemmus* are made up of fine bony cells, and subsequent studies (listed by van Kampen, 1905; van der Klaauw, 1931; Hooper and Hart, 1962; and Simkin, 1965) have made it clear that within this subfamily there is considerable diversity not only in walls and cavities but also in other parts of the middle-ear system. None of the studies, however, has provided the detailed anatomical information needed as a basis for tests of function of the various kinds of walls and cavities.

The present report compares nine microtine species in regard to anatomy of walls and cavities of the middle ear. They differ in habits and habitat: one *(Clethrionomys gapperi)* is an inhabitant of boreal forests; another *(Lagurus curtatus)* lives on arid sagebrush-studded hills; two *(Lemmus trimucronatus* and *Dicrostonyx torquatus)* are tundra forms; two *(Microtus pennsylvanicus* and *M. ochrogaster)* occur predominantly in temperate grasslands; and three *(Arvicola richardsoni, Neofiber alleni,* and *Synaptomys cooperi)* are closely restricted to wet situations, e.g., bogs, swamps, and streams.

MATERIALS AND METHODS

This study is based on histological sections, stained whole mounts, and dried crania. Numerous crania in the University of Michigan Museum of Zoology provided information on variation in each species and served as guides in dissections of fluid-preserved examples.

The fluid-preserved specimens were treated in various ways. Some were retained in alcohol and dissected without further processing. Lightly stained whole mounts and sections were prepared from thirteen specimens (8 *M. pennsylvanicus* and 5 *C. gapperi*). The head was severed from the body, skinned, placed in 4 per cent potassium hydroxide for 36 hours (several drops of alizarin in the solution for the last 12 hours), and finally moved through graded mixtures of water and glycerin into pure glycerin. The auditory region of the skull

was then sectioned (e.g., Figs. 2 and 3) on a cutting disc located in oral histology laboratories of the School of Dentistry.

Histological sections were made of seven specimens of medium age as follows: *Clethrionomys gapperi,* 109236, Colorado, Gunnison County; *Lemmus trimucronatus,* 112448, Alaska, Point Barrow; *Microtus (Pedomys) ochrogaster,* 109235, Missouri, Boone County; *Microtus (Microtus) pennsylvanicus,* ETH No. 5492, Michigan, Washtenaw County; *Arvicola richardsoni,* 110302, Montana, Carbon County; *Neofiber alleni,* 110456, Florida, Alachua County; *Synaptomys cooperi,* 108544, Michigan, Washtenaw County.

Processing proceeded in the following sequence. The posterior part of the skull bearing the auditory bullae was dissected from the carcass, stripped of overlying tissue, and divided longitudinally. The left segment was retained in alcohol for subsequent use if needed. The right segment was decalcified for approximately 12 hours in "Decal" (Omega Chemical Co., N.Y.), washed in running water for four hours, and dehydrated through increasing concentrations of alcohol to absolute alcohol and ether. The segment was taken through increasing concentrations of celloidin (Parloidion) and then imbedded (Ambrogi, 1960). The celloidin blocks were kept in 70 per cent alcohol until they were serially sliced in the frontal (coronal) plane at 20 microns. The sections were stained with hematoxylin and eosin and mounted in Permount.

Because the specimens were obtained by different collectors and preserved with various degrees of care before being deposited in the Museum, some delicate tissues might have been lost in some specimens prior to fixation. For example, a reticulum of connective tissue was observed in the bullae of the three specimens of *Microtus,* but not in the other species, where it conceivably might have been destroyed by faulty fixation. The fact that the tympanic membrane and some other delicate tissues consistently were preserved in all specimens, however, argues against that possibility.

The three cross-sections shown in Figures 4–6 are approximately as indicated in Figure 1 and as described below.

Level 3: through basisphenoid and bulla posterior to the pterygoid process, and through or near the anterior base of the tentorium cerebelli, thereby cutting off approximately the anterior quadrant (of the longitudinal plane) of the bulla.

Level 2: through the basisphenoid-basioccipital plate near the junction of the two bones, the external auditory meatus near its center, the head of the malleus, and the tympanic membrane.

Level 1: through the posterior half of the basioccipital plate, the
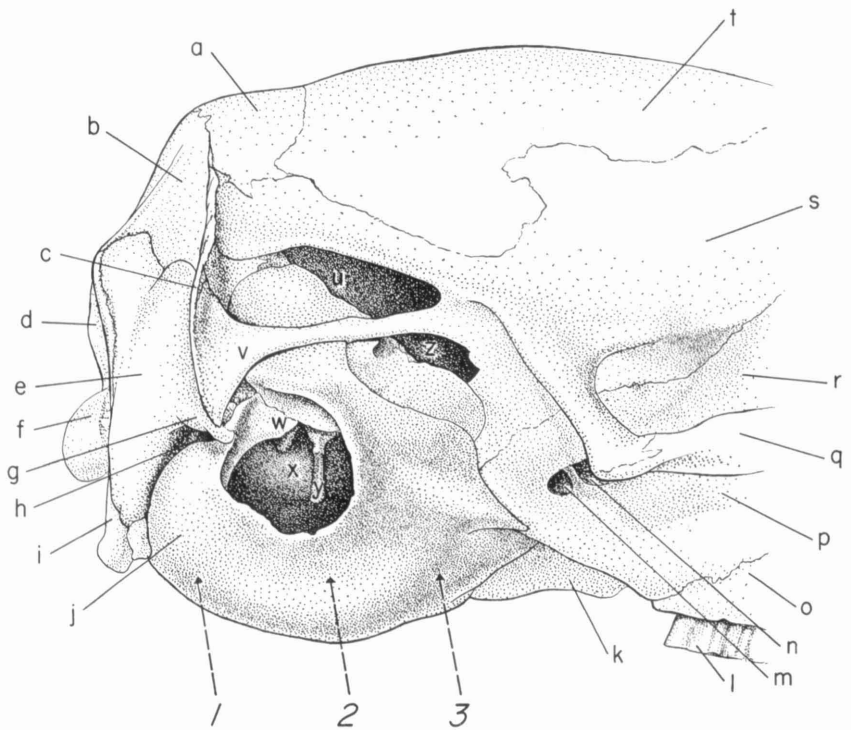
FIG. 1. Right side of skull of *Microtus pennsylvanicus* showing locations of sections in Figs. 4–6 and cranial parts: a, interparietal; b, supraoccipital; c, lambdoidal crest; d, exoccipital; e, mastoid; f, occipital condyle; g, posttympanic process (of mastoid); h, stylomastoid foramen; i, paroccipital process (of exoccipital); j, tympanic; k, internal pterygoid plate (basisphenoid); l, molar tooth (M^3); m, oval foramen; n, alisphenoid canal; o, maxilla; p, external pterygoid plate (of alisphenoid); q, jugal; r, alisphenoid; s, squamosal; t, parietal; u, superior prelambdoidal fenestra (postglenoid foramen, supratympanic fenestra); v, mastoid process (of squamosal); w, ascending arms of tympanic, and dorsomedial wall of recessus meatus externus; x, external auditory meatus; y, manubrium (of malleus); z, inferior prelambdoidal fenestra (premastoid vacuity).

bulla posterior to the external auditory meatus, approximately the center of the exposed face of the mastoid, the parafloccus of the cerebellum, and the semicircular canals.

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DESCRIPTION OF WALLS AND CHAMBERS OF THE MIDDLE EAR

Microtus pennsylvanicus

The meadow vole serves as a standard for comparison of the species. A description of its middle-ear walls and cavities follows.

EXTERNAL ASPECTS.—Although as many as ten bones, excluding the three auditory ossicles, may participate in the middle-ear system (van der Klaauw, 1931), only two certainly are involved in *Microtus pennsylvanicus* and the other microtines examined. These are the petromastoid and the "tympanic." The petromastoid or periotic consists of a petrous portion which roofs the main middle-ear chamber and a mastoid segment containing sinuses confluent with the main chamber.

The "tympanic," which forms the bulla proper, may be a composite. Van Kampen (1905), van der Klaauw (1931), and most other authors writing on the subject have indicated that in rodents the bulla is formed entirely by the ectotympanic bone. Howell (1932), however, suggested that in *Dipodomys* and apparently in other Recent heteromyid and geomyid rodents, the bulla consists of both ectotympanic and entotympanic elements. In his view, the annulus (bearing the membrane) and other possible ectotympanic portions are covered by entotympanic and, thus, all the superficial details of the bulla proper are composed of entotympanic elements. He referred to the structure as the "entotympanic bulla," and Webster (1961) continued that usage. In the present paper the issue of number of elements is avoided; the structure is termed the tympanic bone.

The auditory bulla is an inflated, elongate spheroid somewhat flattened ventrolaterally; its transverse diameter is approximately three-fourths its dorsoventral diameter and one-half to three-fifths its longitudinal dimension. Viewed ventrally, its anterior face is somewhat angular; the curvature is interrupted by two styliform processes of which one adjoins the lateral pterygoid ridge and the other abuts on the hamulus of the pterygoid. Its medial face (adjoining the basioc-
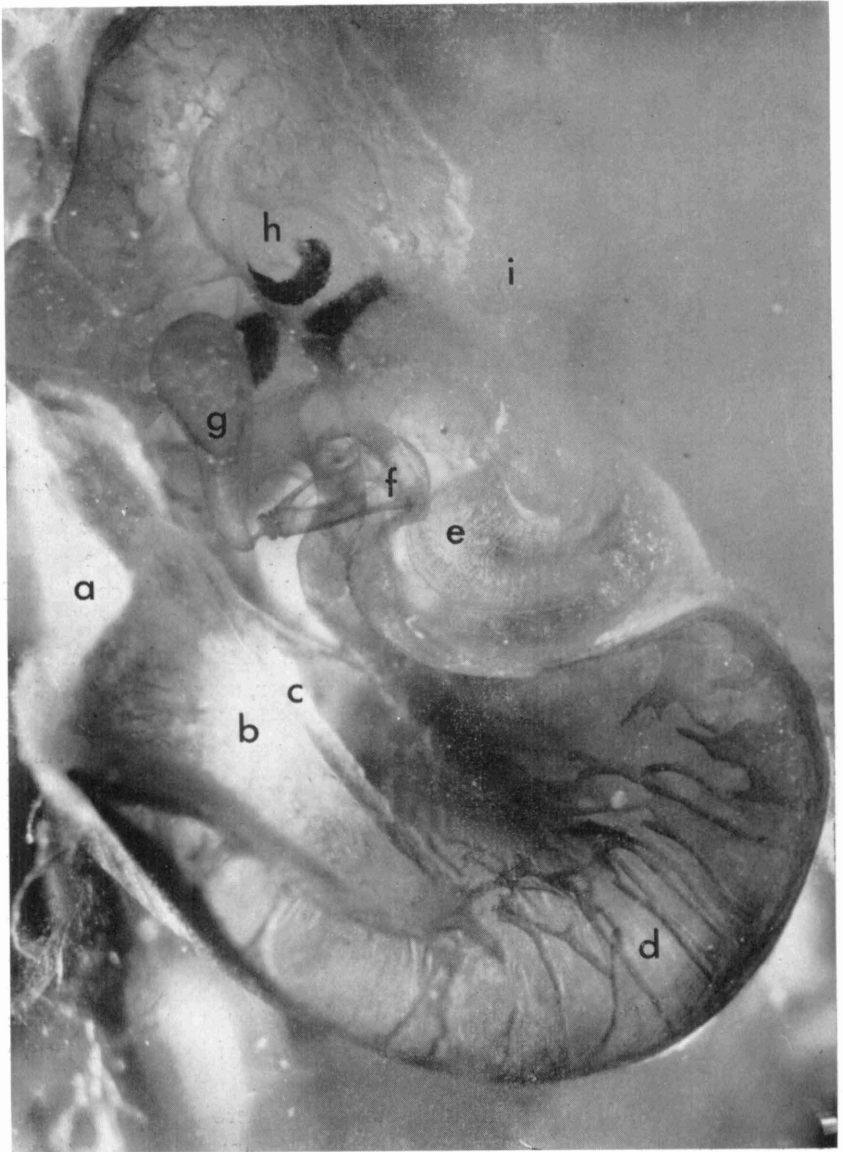
FIG. 2. Transverse section approximately through middle of right auditory bulla of *Microtus pennsylvanicus*. Photograph looking posteriad shows: (a) external auditory meatus, (b) recessus meatus externus, (c) tympanic membrane and annulus, (d) spicule-studded main middle ear cavity, (e) cochlea, (f) stapes, in fossula fenestrae ovalis, the bony tube carrying stapedial artery passing between the two crura of the stapes, (g) incus, its lenticular process abutting against the stapes, situated in epitympanic recess, the passage to mastoid sector visible immediately above, (h) semicircular canals, and (i) brain.

cipital) is evenly contoured except for the slight indentation for the internal carotid artery. Its posterior face, bearing the stapedial foramen, is flattened alongside the jugular (posterior lacerate) foramen in the exoccipital. That posterior face lies anterior to the anterior limits of the foramen magnum and the ventral face lies at or above the occlusal plane of the molar row. The large ear-shaped opening into the bulla (porus acusticus osseus externus) is not tubular; it is formed entirely by the tympanic, though at its large notch below the mastoid process of the squamosal the mastoid (post-tympanic process) impinges on it (Fig. 1). The large opening (its dorsoventral diameter about one-half that of the bulla) is directed principally laterad.

The petromastoid part of the middle-ear system is distinguishable from the tympanic by texture of bone and by sutures. A deep channel for the facial nerve, extending from the stylomastoid foramen diagonally almost to the ventral limit of the mastoid (Fig. 1) demarks the tympanic and mastoid. This channel is an open trough in young animals; it later becomes a tube as a result of overgrowth of mastoid and tympanic tissues, but the juncture of the two bones remains clearly visible. The exposed portion of the mastoid that is cradled dorsally and posteriorly in the exoccipital is slightly inflated and triangular; one apex of the triangle extends almost to the tip of the paroccipital process. The mastoid portion continues without interruption anteriad beneath the mastoid process of the squamosal to the anterior limits of the premastoid vacuity (inferior prelambdoidal fenestrum).

INTERNAL ASPECTS.—Porus acusticus leads directly into a large recessus meatus. The dorsomedial wall of this recess is osseous in some species and membranous in others, depending on the extent of closure (amount of "tympanic notch" of authors) of the two ascending arms of the tympanic. In *M. pennsylvanicus* the arms are broadly in contact and the resulting bony wall hides the base of the malleus and the other ossicles from lateral view (Fig. 1). The capacious ventral part of the recess is bounded laterally by the double-layered bullar wall, and medially by the annulus and the tympanic membrane (Fig. 2). The annulus, the inner border of the involuted part of the tympanic, is an incomplete ring; it is complete ventrally, but dorsally its two arms terminate ventral to the tympanic notch (Fig. 3). The keeled inner ring of the annulus (crista tympanica) is bordered laterally by a groove (sulcus tympanicus) in which the tympanic membrane is seated.

The tympanic membrane not only fills the circle circumscribed by the annulus but also covers dorsally adjoining areas (environs of arms
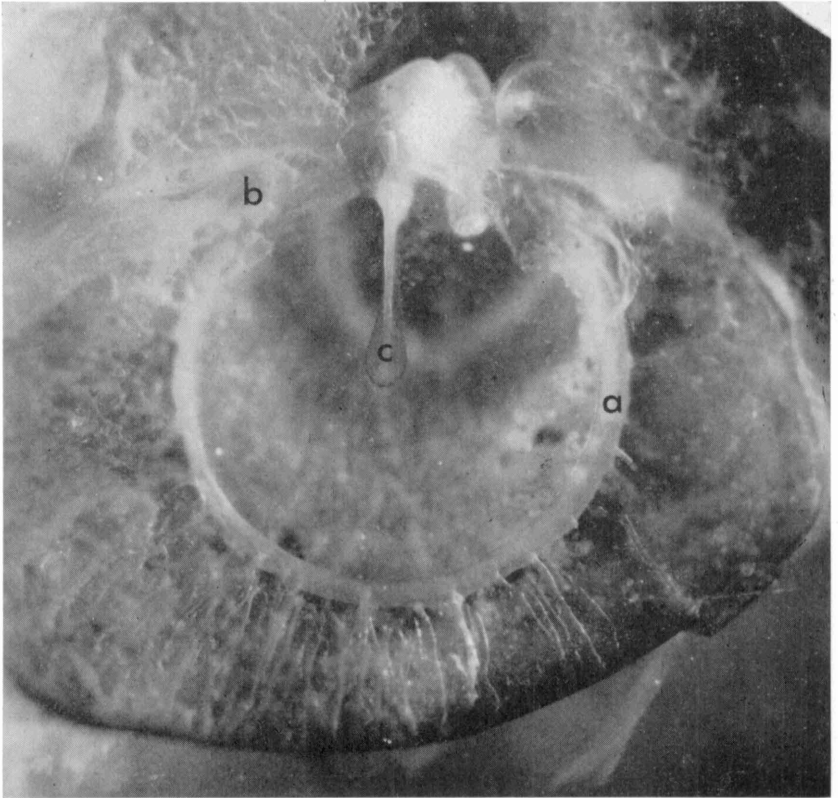
FIG. 3. Sagittal section, on a plane just medial to the tympanic membrane, of right auditory bulla of *Microtus pennsylvanicus*. View looks laterad at (a) annulus and adjoining bony spicules in the tympanic cavity, (b) ascending arms of the tympanic bone, and (c) manubrium of malleus in tympanic membrane, with external auditory meatus in background.

of tympanic), and thus completely separates the external and middle-ear cavities. The pars tensa is shaped like a flat cone, its apex directed mediad. It is seated in the sulcus tympanicus and is attached along the manubrium of the malleus, the spatulate tip of the manubrium determining the apex of the cone (Fig. 3). It consists of three layers: an outer epithelial layer continuous with that of the ectotympanic cavity, an inner layer continuous with the mucosal lining of the middle ear, and a middle area of connective tissue.

Pars flaccida (Shrapnell's membrane) is that part of the tympanic membrane lying dorsal to the lateral process of the malleus and the

flat-topped circle of the annulus (Fig. 1). It rounds out that circle, covering the gap between the lateral process and the two legs of the tympanic and extending onto that bone. It is a small segment of the total membrane; its dorsoventral diameter (lateral process of malleus dorsad to tympanic bone) is less than one-half the length of the membrane face of the manubrium. The two parts of the membrane appear to be closely similar superficially and histologically, but I can not be certain of this in the specimens at hand. Henson (1961:159) notes that, among bats and insectivores, pars flaccida varies considerably. In some forms its limits can not be defined, while in other species it may consist of two or three layers of various thicknesses and be separated from pars tensa by an indistinct band of connective tissue (arcus terminalis).

   Though the middle ear system is a veritable maze of sinuses, recesses, and compartments, these comprise three principal chambers: the main cavity of the bulla, an epitympanic segment, and a mastoid pocket (Fig. 2). The three are broadly interconnected and contain various amounts of bony network and open space. The main cavity, confined to the tympanic, offers the largest amount of open space—a crescent-shaped area skirting the lateral half of the cochlea. The remainder of the cavity is interrupted in various amounts by a network of connective tissue and osseous filaments which line the walls of the cavity. Some of these multishaped slivers of bone brace other osseous structures, the tympanic annulus (Fig. 3) and the conduit for the Eustachian tube, for example. Most of them, typically slimmer than those serving as struts or braces, however, extend directly into the cavity and are imbedded in a reticulum of connective tissue (Figs. 4–6, upper right). The whole mass is like a multipole tent, the roof being the mucosal lining of the middle ear and the poles being the numerous osseous filaments protruding from the mucosa. The roof and underlying strands of connective tissue drape in deep arcs from pole to pole, and thus present a delicate and highly uneven surface to the tympanic cavity. Within this matrix of bone and connective tissue there are many areas which in histologic sections appear as networks of open spaces. What these spaces contain—whether lipid, mucoprotein or other—in living tissues is unknown. To identify the material may well be essential to understanding the function of the cancellous walls of the middle-ear system.

   Dorsal to the main bullar cavity, and continuous with it by way of a channel enclosing the malleus and incus, is an epitympanic cavity (Fig. 2). This space lies below the roof of the middle ear system (tegmen

tympani) in the petrosal. It is essentially a series of confluent sinuses in a mass of spongy bone. This irregularly shaped chamber connects via channels in the bone directly with the mastoid sector.

The mastoid sector also is basically an intricate series of sinuses and passages in a bony network. In a cleaned skull the largest amount of open space which might qualify to be termed a chamber is situated immediately lateral and anterior to the dome (within the middle ear) covering the parafloccus of the cerebellum (Fig. 6, upper right). This chamber interconnects with the main bullar cavity via epitympanic spaces around parts of the ear ossicles and the bony tubes for the seventh nerve and the stapedial artery.

Microtus ochrogaster

The middle-ear system of the prairie vole is similar to that of *M. pennsylvanicus,* but the auditory bullae of *ochrogaster* tend to be slightly more discoidal in shape and less inflated, the mouth of the external auditory meatus slightly smaller, and the tympanic notch in its dorsomedial walls is almost obliterated, the pars flaccida of the tympanic membrane thus slightly smaller than in *pennsylvanicus*. A band of connective tissue at the level of the lateral process of the malleus delineates the two parts of the membrane. The walls and interior of the bullae are as in *pennsylvanicus*.

Arvicola richardsoni

The system in the water vole *(Arvicola)* is much more like that of *Microtus* than of *Clethrionomys, Neofiber,* or other genera sampled. It is similar to that of *M. pennsylvanicus,* though the bullae are more angular and less inflated relative to length of skull. They are among the smallest seen. Their ventral limits lie entirely dorsal to the alveolar plane of the molar row, and the posterior limits are situated well anterior to the foramen magnum. Porus acusticus osseus externus is slightly smaller, directed a bit more dorsad, and is more nearly tubular. The dorsomedial wall of the meatus together with the pars flaccida of the membrane are much as seen in *M. pennsylvanicus,* possibly slightly smaller. The walls and contents of the bullae are essentially as in *M. pennsylvanicus* (Figs. 4–6).

The mastoid is clearly distinguishable from the tympanic by the characters indicated for *M. pennsylvanicus*. It is slightly smaller and less inflated relative to size of skull than in that species.
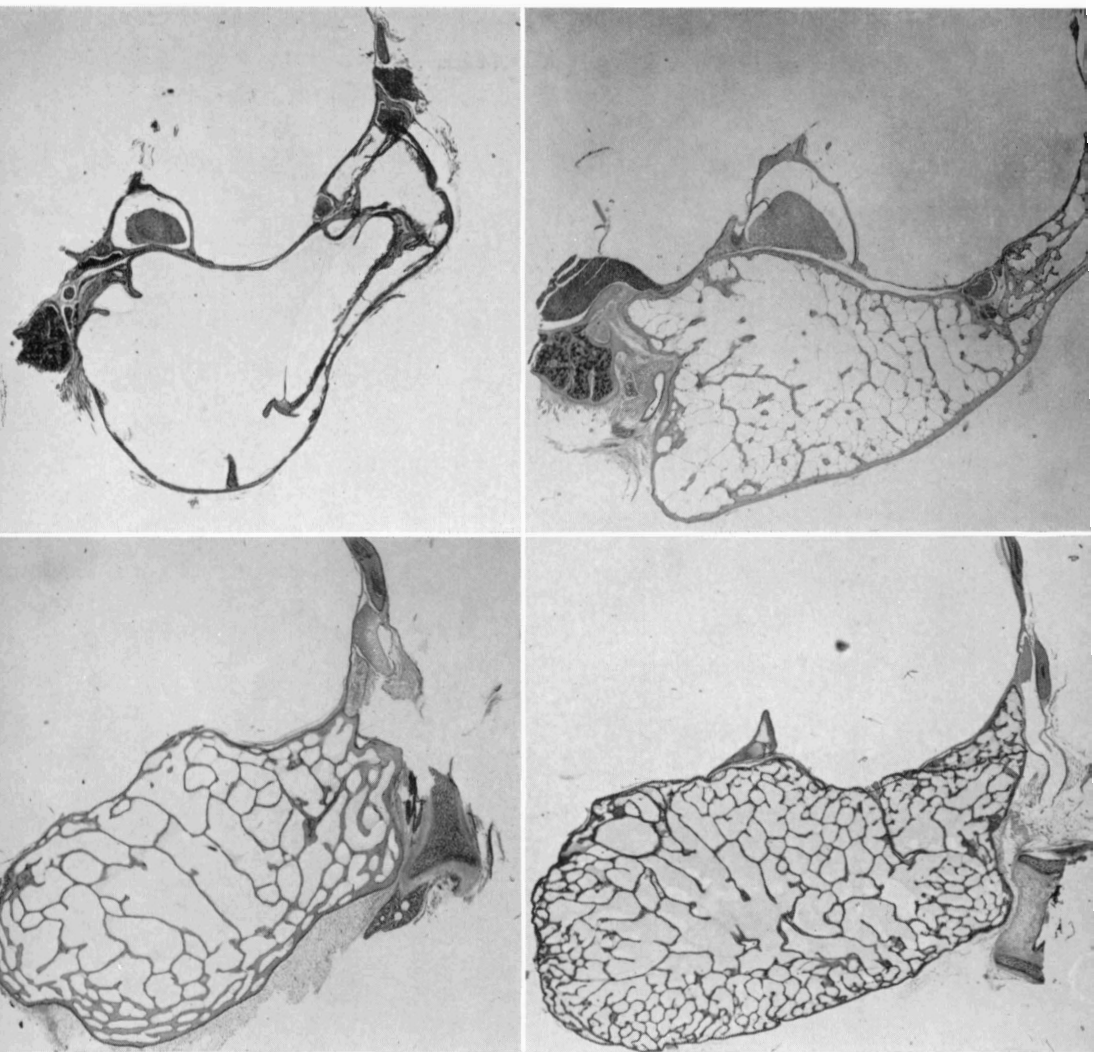
FIG. 4. Histological sections through anterior sector (level 3, Fig. 1) of right bulla of *Clethrionomys gapperi* (upper left), *Arvicola richardsoni* (upper right), *Synaptomys cooperi* (lower left) and *Lemmus trimucronatus* (lower right). Part of basisphenoid at left and of squamosal at upper right. All to same scale.

Clethrionomys gapperi

The redback vole's middle-ear system is simple and uncluttered within by bony networks (Fig. 4). It resembles that of *N. alleni* more than that of any other species here studied and differs from the standard for comparison, *M. pennsylvanicus,* in several features.

Porus acusticus is larger (relative to dorsoventral diameter of bulla) and the dorsal part of recessus meatus is differently constructed. Whereas in *pennsylvanicus* the dorsomedial wall of the recess is mostly osseous, in *gapperi* it is membranous. There is a large osseus gap between the two arms of the tympanic. This tympanic notch is covered by Shrapnell's membrane and thus the incus and base of the malleus are visible laterally. Pars flaccida is thus several times the size of that in *pennsylvanicus;* its dorsoventral diameter (lateral process of malleus dorsad to arm of tympanic) is about equal to the length of attachment of pars tensa to the manubrium (umbo to processus lateralis). Pars flaccida appears more fibrous than pars tensa; the two contrast much more in both structure and size than in *pennsylvanicus.*

Other striking differences from *M. pennsylvanicus* are that the mastoid is smaller, less inflated posteriorly, and contains little or no filamentous bony network. The main bullar cavity is comparatively free of obstruction and the internal walls are smooth with few osseous projections anywhere in the cavity (as in *N. alleni,* Figs. 4–6); the few prominent ones brace the annulus. Finally, the position of the system in the skull is noteworthy. It lies ventrad so that roughly its ventral half is below the occlusal plane of the molar row (bullae mostly or entirely above that plane in *M. pennsylvanicus*). The posterior limits of the bullae lie on a plane with or anterior to the anterior limits of the foramen magnum.

Neofiber alleni

Distinctive features of the middle-ear system of this amphibious vole include: relatively small mastoid and tympanic segments; solid, thick-walled bullae without bony ingrowths, the cavity the least obstructed of all species studied. The species is most like *C. gapperi* in regard to

FIG. 5. Histological sections through medial sector (level 2, Fig. 1) of right bulla of *Neofiber alleni* (upper left), *Arvicola richardsoni* (upper right), *Synaptomys cooperi* (lower left), and *Lemmus trimucronatus* (lower right). Cochlea at left, malleus and tympanic membrane medially, and external meatus at right. All to same scale.

walls and interior of bullae, like *A. richardsoni* in regard to size of tympanic and mastoid segments of the system and direction of mouth of the external auditory meatus. It resembles *M. pennsylvanicus* in position of bullae with respect to plane of molar row (bullae situated dorsal to it) and border of foramen magnum (situated well anterior to it), and in size and shape (but not direction of mouth) of the external auditory meatus.

Porus acusticus is ear-shaped, deeply notched dorsoposteriorly much as in *M. pennsylvanicus,* but directed more dorsad. The dorsomedial wall of recessus meatus is more like that in *M. pennsylvanicus* than in *C. gapperi;* the notch between the tympanic arms is slightly larger than in *M. pennsylvanicus,* and the membrane covering that gap (pars flaccida) also is correspondingly larger (its dorsoventral diameter, however, is less than half the length of the manubrium). The bullar walls are solid, not spongy, and their internal faces are comparatively smooth, without networks of bony processes except in the area of the annulus where about a dozen osseous partitions bind the rim of the annulus to the bullar wall. The main cavity of the bulla is the least obstructed in the several species examined (Figs, 5, 6).

The petromastoid segment of the system is well differentiated from the tympanic segment in both texture and topography. A deep suture marks the junction of the two bones on the lateral face of the skull, and on the posterior face the conspicuous channel for the seventh nerve separates the inflated tympanic segment below and the triangular uninflated mastoid segment dorsally (Fig. 6). All of the mastoid is situated dorsad in the skull; it has no paroccipital process and the lower limits of the bone lie above the ventral rim of porus acusticus osseus externus. The part of the petromastoid exposed anterolaterally is relatively large. Related to the size of that exposure, there is little or no premastoid vacuity and the prelambdoidal fossa occupies approximately one-half the space between the arms of the squamosal. (Fig. 1).

Synaptomys cooperi

The middle-ear system of the bog lemming contrasts rather strongly externally and internally with the systems seen in the species described

FIG. 6. Histological sections through posterior sector (level 1, Fig. 1) of right bulla of *Neofiber alleni* (upper left) *Arvicola richardsoni* (upper right), *Synaptomys cooperi* (lower left), and *Lemmus trimucronatus* (lower right). Tympanic bulla in lower segment of each figure below semicircular canals, mastoid sinuses, and parafloccus of cerebellum.
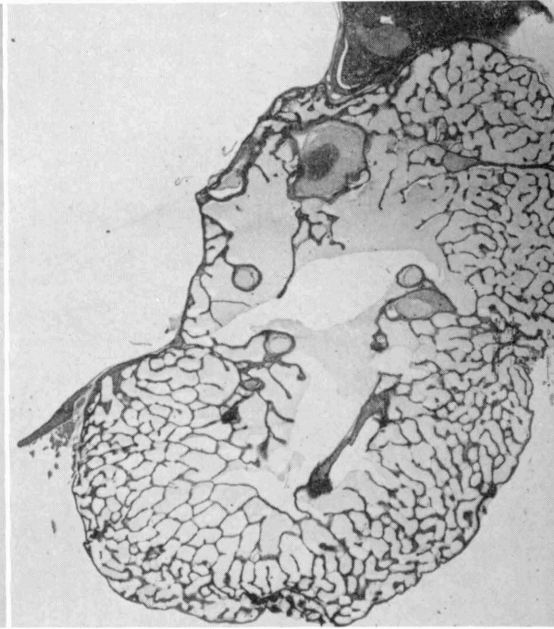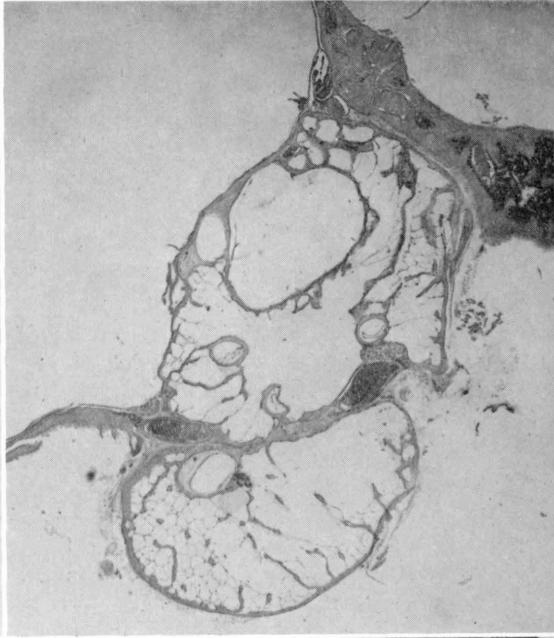
above. Externally, the tympanic and petromastoid appear as one continuous mass of bone without a clearcut distinction between the two, either topographically (e.g., channel for the facial nerve) or in texture of bone. Below the smooth exterior surface, the bone is cancellous, the thick walls a network of osseous tissue (Figs. 4–6).

There are several distinctive features of the auditory bullae. Porus acusticus osseus externus is situated farther anteriad in the bulla than in the other species, and compared with *pennsylvanicus* is smaller, more nearly tubular and circular, and directed primarily dorsad rather than laterad. There is no deep, posterodorsal indentation in the rim as seen in the species discussed above. The dorsomedial wall of recessus meatus is osseous; there is essentially no tympanic notch and no pars flaccida. The flaccid portion is nothing more than a narrow band of tissue at the level of the lateral process of the malleus. The walls of the bullae are essentially the same throughout, consisting of a moderately thick layer of spongy bone; there is not the contrast of walls of external (recessus meatus) and middle-ear portions that is seen in *Neofiber, Microtus, Clethrionomys,* and *Arvicola.* The floor of the main tympanic cavity is compartmentalized by many bony lamelli. These partitions, which are continuous with the thick spongy walls, extend as ribs laterad from the cochlear mass and terminate at the annulus. The annulus is a slight ridge and groove in the spongy system; it contrasts much less with its surroundings than does the annulus in *Clethrionomys, Neofiber, Microtus,* and *Arvicola* (Fig. 5).

The tympanic membrane, seated in the annulus, completely partitions the ectotympanic and tympanic cavities. The membrane appears to be smaller relative to size of bulla than in *M. pennsylvanicus,* and because the manubrium is relatively shorter than in the aforementioned species the amount of membrane attached to the malleus is correspondingly less.

The mastoid segment of the system is small and uninflated. Anterolaterally it does not fill the space between squamosal and tympanic, and as a result there are unusually large prelambdoidal and premastoidal vacuities.

Lemmus trimucronatus

The structure of the walls and cavities in the brown lemming represents an extreme in a series extending from a hollow-shell bulla (e.g., *C. gapperi* and *N. alleni*) to one in which the walls of the tympanic cavity are thick and spongy, and osseous networks take up much of

the space. *Synaptomys cooperi* is near *L. trimucronatus* in that series (Figs. 4–6).

The tympano-mastoid mass of *L. trimucronatus* is externally wedge-shaped both in lateral and ventral aspect, the apex of the wedge directed anteriad. The mass is situated dorsal to the plane of the molar row, as seen in most of the species, but in contrast to the condition in most of them the posterior limits of the mass lie behind the anterior margin of the foramen magnum. The mastoid and tympanic parts are not readily identified externally because the two bones are similar in texture and color, there is no channel for the facial nerve demarcating them, and sutures between them are indistinct.

Meatus acusticus externus contrasts with that seen in other species. Its porus is more nearly tubular, circular, and dorsolaterally directed, and is smaller relative to diameter of bulla than in any other species examined. The short but well-formed tube leads into a capacious smooth-walled recessus meatus which is separated from the exterior by a thick layer of cancellous bone (Fig. 5).

The remainder of the bulla is much as described for *S. cooperi*. The tympanic membrane is mostly or entirely pars tensa. A pars flaccida, if present, is a narrow crescent between the lateral process of the manubrium and the adjoining merged arms of the tympanic. In the floor of the tympanic cavity there is the same type of network of bony partitions radiating anteriorly, posteriorly, and medially from the cochlear mass to the walls of the bulla, and as a result of the presence of these and other osseous networks there is relatively little uncluttered space in the tympanic cavity or elsewhere in the middle ear system (Figs. 4–6).

The amount of mastoid exposed anterolaterally is greater than that seen in *S. cooperi* and about equal to that seen in *M. pennsylvanicus*. Prelambdoidal and premastoidal vacuities are small or absent.

Dicrostonyx torquatus

The following statements regarding anatomy of the middle-ear system of the collared lemming *(D. torquatus)* and sagebrush vole *(Lagurus curtatus)* are based on skulls of conventional study specimens and are unsupported by histologic sections. Though the amount of information on *D. torquatus* and *L. curtatus* therefore is less complete than for the other seven species, nonetheless it is sufficient to indicate major features of the middle-ear system of the two taxa and suggest relationships with other species.

The three "lemmings," *Synaptomys, Lemmus,* and *Dicrostonyx,* clearly do not make a homogeneous group in regard to anatomy of the tympano-mastoid system. While there are important resemblances between *Synaptomys* and *Lemmus, Dicrostonyx* is anatomically more similar to *Arvicola richardsoni* and the species of *Microtus.* As in *Microtus* and *Arvicola* the mastoid and tympanic segments are externally distinct; texture of bone and a prominent channel for the facial nerve indicate their limits posteriorly, and a suture defines them laterally; in size and shape they resemble their counterparts in *Arvicola.* Porus acusticus externus, which is moderately large and deeply notched dorsoposteriorly, and the thin-walled recessus meatus are like those seen in *Arvicola* and *Microtus.* The large annulus which bears a well-defined crest and groove is supported ventrally and laterally by ribs or struts, all of which as usual lie in the tympanic cavity, not in the external recess. The tympanic membrane contains a small pars flaccida, its size approximately that seen in *Arvicola* (the dorsoventral length no more than one-fourth the expanse of membrane on the manubrium).

The bullar walls may be intermediate in character. They resemble those in *Microtus;* they are not thick and spongy as in *Lemmus* or *Synaptomys.* The bony network extending from the walls to the cochlear mass, however, appears to be the type seen in *Synaptomys* and *Lagurus* rather than in *Microtus;* it is more solid and regular than the random mixture of bony spicules and plates in *Microtus.* Histological sections of *D. torquatus* are needed to reveal details.

The mastoid is also like that in *Microtus* and *Arvicola.* It terminates posteroventrally as an attenuate capsule adjoining the paroccipital process. This moderately inflated portion encloses a chamber which connects with the epitympanic and the tympanic cavities. Anterior to the lambdoidal crest the mastoid fills most of the space between the tympanic and squamosal; premastoidal and prelambdoidal vacuities are small or absent.

Lagurus curtatus

The tympano-mastoid mass of the sagebrush vole *(L. curtatus)* resembles that of *S. cooperi* and to a lesser extent that of *L. trimucronatus,* though the mass is larger relative to skull size than in the other species. Mastoid and tympanic parts are externally similar in texture; a suture clearly marks the boundaries between them. The mass is situated posteriad and ventrad; it extends behind the anterior edge of the foramen magnum and below the occlusal plane of the molar row—the ventral limits approximately as in *M. pennsylvanicus,* not as in *C.*

gapperi. The external walls of both mastoid and tympanic are thick masses of cancellous bone as seen in *S. cooperi.*

Other parts of the middle and external ear systems also are similar to those of *S. cooperi.* Porus acusticus is small, slightly tubular, and directed dorsoposteriad over a broad notch in its rim; the dorsomedial wall of recessus meatus is bony; and pars flaccida is a slim crescent. In the tympanic cavity ribs and struts extend from the cochlear mass to the walls of the bulla. Some of these ribs terminate at the prominent tympanic annulus which contains a well-defined crest and groove.

RELATIONSHIPS AMONG THE SPECIES

STRUCTURE OF THE MIDDLE-EAR SYSTEM.—Variations in the middle-ear system among the nine species may be summarized as follows.

There is no great contrast among the species in relative size and position of the auditory region of the skull, notwithstanding an absolute size range in the order of 1:2 (e.g., cranial length, *Lagurus curtatus; Neofiber alleni*). The same bony elements are involved in all species, and in none is there the hypertrophy seen in many saltatorial rodents (Howell, 1932). The range in relative size of bullae and amount of mastoid inflation is represented by *L. curtatus* and *Lemmus trimucronatus,* near maximum, and *Arvicola richardsoni* and *N. alleni,* near minimum. In most of the species the tympano-mastoid mass is situated entirely anterior to the foramen magnum and dorsal to the alveolar plane of the molar row. In *Lemmus,* however, the mass extends slightly farther posteriorly, in *Lemmus* and *Neofiber* it is restricted farther dorsad, and in *Clethrionomys* it extends well ventral to the aveolar plane. External boundaries between mastoid and tympanic parts of the mass are not as distinct in *Synaptomys* and *Lemmus* as in the other species.

Variations in size and shape of parts of the osseous, external, acoustic chamber are interrelated, and the species may be arranged in a series ranging from a large irregular-shaped porus acusticus externus coupled with a large Shrapnell's membrane to a small tubular porus and essentially no pars flaccida. *C. gapperi* is at one extreme. In it, porus acusticus externus is largest relative to size of bulla (its dorsoventral diameter about one-half that of the bulla); it is ear-shaped, with a deep indentation dorsoposteriorly; and its irregular rim is not drawn together to form a bony tube. The dorsomedial wall of the meatus is mostly membranous, rather than osseous; the dorsoventral diameter

of the membrane (Shrapnell's, or pars flaccida) is about equal to length of membrane face of the manubrium.

At the other extreme are the species of *Lemmus* and *Synaptomys*. In these, porus acusticus is a small (dorsoventral diameter about one-third that of the bulla), evenly oval terminus of a definite though short tube, and the dorsomedial wall of recessus meatus is osseous; pars flaccida is slight or absent. These characteritics are better developed in *Lemmus* than in *Synaptomys*. The other species are variously intermediate; those of *Lagurus, Dicrostonyx,* and *Arvicola* grade toward *Lemmus*, while the species of *Microtus* and *Neofiber* are nearer *Clethrionomys*.

Perhaps the greatest differences observed among the species are in character of walls and in arrangements of bone and connective tissue within the bullae. Three fairly discrete structural arrangements may be recognized. In the simplest one the bulla is a plate of bone and the tympanic cavity is comparatively open. There are few or no osseous processes extending from the walls into the cavity; most of these are struts to the annulus. This arrangement is seen in *Clethrionomys* and *Neofiber*.

In the second arrangement, each bulla contains more osseous material and the amount of open space within it is reduced by many filamentous outgrowths from the walls. These spicules vary in shape, size, and position; some act as braces or struts, but most project freely into the cavity. The spicules lie in a loose reticulum of connective tissue, and the total mass of connective tissue and spicules apparently takes up a major segment of the main tympanic cavity. Contents of the spaces of the reticulum—whether lipid, mucoprotein, or other—are unknown. This arrangement is seen in the two species of *Microtus* and in *Arvicola*.

In the third category the walls of the bullae are thick masses of cancellous bone, and there is little free space within each cavity. The osseous material projecting from the walls is not in the form of spicules; instead it is a battery of partitions and interjoined plates. Some of these form distinct patterns. In the floor of the tympanic cavity, for example, these appear as rather regularly spaced ribs or partitions radiating posteriorly, anteriorly, and medially from the cochlear mass to the walls of the bulla. This structural arrangement is seen in *Lemmus, Synaptomys,* and *Lagurus*.

Where *Dicrostonyx* fits with respect to these three groups is not certain. The plates on the floor of its bullae appear thicker and more regular than the growths in *Microtus* and they somewhat resemble

those seen in *Synaptomys,* but the walls of both the mastoid and tympanic cavities appear to be like those of *Arvicola* and *Microtus* rather than those of *Lemmus* or *Synaptomys*. Histological sections are needed to indicate the fine structures in this genus.

In summary, on the basis of anatomy of the walls and cavities of the middle ear and osseous external ear, the species may be categorized as having an open system, a closed system, or one intermediate in character.

Open system: mastoid and tympanic segments contrasted externally; porus acusticus externus large, ear-shaped, laterally directed, and nontubular; a large pars flaccida present, the bases of the three ossicles laterally visible through it; walls of tympanic and mastoid cavities simple, comprised of plate bone which gives off few processes, the cavities therefore comparatively open. Species: *Neofiber alleni, Clethrionomys gapperi.*

Intermediate system: mastoid and tympanic segments contrasted externally; porus acusticus externus ear-shaped much as indicated above, but slightly smaller; dorsomedial wall of recessus meatus mostly osseous (hiding most of ear ossicles from lateral view); pars flaccida a narrow arc; walls of tympanic and mastoid cavities with numerous, slight, multishaped, osseous outgrowths, most of those of the main tympanic cavity imbedded in a delicate matrix of connective tissue, the total mass constituting a thick lining of the cavity and reducing the cavity's free space. Species: *Microtus pennsylvanicus, M. ochrogaster, Arvicola richardsoni,* and possibly *Dicrostonyx torquatus.*

Closed system: mastoid and tympanic segments not strongly differentiated externally; porus acusticus externus distinctly tubular, small, rather evenly oval, and dorsolaterally directed; dorsal part of recessus meatus enclosed and osseous; essentially no pars flaccida; walls of mastoid and tympanic cavities composed of an outer shell of plate bone; this gives rise mesially to comparatively thick sheets of bone which form a thick-walled cellular network that occupies most of the space in the main tympanic cavity. Contents of the spaces within the osseous network are unknown. Species: *Lagurus curtatus, Synaptomys cooperi,* and *Lemmus trimucronatus.*

CLASSIFICATION OF THE SPECIES.—The three middle-ear types discussed above do not closely accord with current taxonomic classifications. There is perhaps least agreement with the classical arrangement in which the Microtinae are thought to consist of three major groups (Miller, 1896, 1912; and many subsequent authors): (a) *Ellobii* for the

genus *Ellobius;* (b) *Lemmi,* consisting of *Lemmus, Dicrostonyx,* and *Synaptomys;* and (c) *Microti,* comprised of all other species. There is slightly better agreement with Ognev's classification (1948) in which *Clethrionomys, Ondatra* (which also has an open-type middle-ear system), *Phenacomys,* and several other genera removed from *Microti* were placed in a separate "supergenus" *Fibrini.* Some forms with open middle-ear systems were thus segregated, but *Neofiber* still was included in *Microti,* and the group *Lemmi* remained unchanged. Hooper and Hart (1962) suggested (1) that there are good reasons for separating *Neofiber* from *Microtus* and *Arvicola,* and *Dicrostonyx* from *Lemmus* and *Synaptomys,* and (2) that *Clethrionomys* with its thin-walled bullae and other characters represents a generalized condition among microtines. Interspecific relationships as they observed them, thus, would group: *Synaptomys* and *Lemmus* (but perhaps not *Lagurus,* which also has a closed middle-ear system); *Microtus* and *Arvicola* (intermediate middle-ear types); and *Clethrionomys* with some other forms, but probably excluding *Neofiber* (another open middle-ear type). The possibility that the middle ear reflects phylogenetic relationships of the species should be further explored.

Functions of Walls and Cavities of the Middle Ear.—Numerous roles have been proposed for the middle-ear walls and cavities, especially for the auditory bulla. For example, it is generally understood that a principal function of the bulla is to protect the delicate structures having to do with receiving, transmitting, and amplifying sound from the exterior to the inner ear (Békésy, 1960; Webster, 1966). At least one recent author (Tumarkin, 1955, *fide* Simkin, 1965) believes that protection is the sole functional role of the bulla. Another extreme view is that of Keen and Grobbelaar (1941) who suggest that the bulla's main function is itself to conduct sound— that transmission across the air of the cavity and by its walls and partitions is more important than via the ossicles and the fenestra ovalis. They suggest that the bullae evolved to meet demands in sound conduction which the ossicles were not able to satisfy. Most authors, however, suggest that the system serves several functions related to various factors in the animal's environment.

Hypertrophy of bullae has received much attention. Many authors have indicated that enlargement often is associated with desert conditions (Heim de Balsac, 1936; Petter, 1961), and they have suggested specific roles for various parts of the structure. The large cavities may serve as resonators (Howell, 1932) and improve the acuity of hearing

(Heim de Balsac, 1936; Keen and Grobbelaar, 1941; Petter, 1961). The large amount of space afforded by the cavities reduces the damping of the tympanic membrane by increasing the size (thus decreasing the resistance) of the airy cushion behind the membrane (Legouix *et al.,* 1954; Békésy, 1960; Webster, 1962). Parts of the middle-ear system may act as acoustic filters, selecting on the basis of frequency or direction of the sound. For example, in animals which place greater dependence on ground vibrations than airborne sound, the bony partitions in bullae may be principal conductors of this ground-transmitted energy (Howell, 1932; Zavattari, 1938; Simkin, 1965). Possible adaptations for air-transmitted high frequency sounds are: relatively small ossicles (perhaps deep sulci in bones, reducing the mass of the bones); close coupling of malleus and incus, thus allowing little energy loss through friction; and small tympanic membrane (Henson, 1961).

There have been numerous suggested correlations of some middle-ear part with another part of the animal or with a factor in the animal's environment. For example, van der Klaauw (1931) suggested that the bullae tend to be relatively large in small animals, and that there is a relationship between size of bulla and size of external ear. Winge (1941:41), in his discussion of microtines, pointed out that the ears are modified in accordance with the peculiar acoustic conditions of the narrow subterranean tunnels where the animals live. Though he made no attempt to define the controlling factors in the tunnels, he was convinced that there are such factors since "the structure of the ear agrees in certain respects in animals otherwise totally unrelated, such as *Talpa, Mustela,* and *Arvicola.*"

Petter (1961) indicated that in gerbils there is a relationship between size of bullae and population density; bullae tend to be large in races and species characterized by sparse populations. In his view, enlargement of the bulla is one of the most important adaptations which allows these desert animals to communicate despite low populations resulting from aridity of their environment. Species or races of *Meriones* in which the populations are low and individuals well spaced have larger middle-ear cavities than *Meriones* with denser populations. In the laboratory, examples of *M. crassus* (large bullae, sparse populations) yielded stronger microphonic responses in the 500–4000 Hz range (Legouix *et al.,* 1954) than *M. shawi* (smaller bullae, denser populations), suggesting to Petter the ability of individuals of *crassus* to perceive feebler sounds and possibly to communicate with each other over greater distances.

Recent work by Simkin (1965) is noteworthy particularly because

of the many mammalian species which he sampled in his attempt to relate various types of ear cavities to way of life of the animals. From his study of crania of more than seventy species, he recognized five basic types of middle ear cavities and suggested functions for each, as indicated below.

1. Thin-walled, spherical bullae with few or no inner partitions or projections of bone are said to be characteristic of surface dwellers and of species which have "the most sensitive hearing," for some of which there is demonstrated capability for ultrasonic reception or echolocation. Examples are: Microchiroptera, Jaculidae, *Apodemus, Mus, Micromys,* and *Clethrionomys.* Thin walls are considered an adaptation facilitating perception of ultrasonic sounds and of increasing the acuteness of "pedal hearing," *i.e.,* ground-trasmitted signals.

2. Fine-celled spongy bullae are characteristic of mammals living in dense media and of some montane forms. Examples are: *Ellobius, Talpa, Microtus, Lagurus, Lemmus, Myopus,* and *Ochotona.* The "spongy" bone, he suggests, acts as an acoustic filter, screening undesirable "noise" from biologically important frequencies and also serving as a device for determining direction of the sound's source.

3. In the conjunct chamber type, the cavity consists of several interconnected chambers which, it is suggested, may in some way amplify or damp the sound. This type of ear cavity is said to be characteristic of some surface-dwelling forms. Examples: *Citellus* and *Glis.*

4. A large-cell type of bulla characterizes tree-dwellers, for example species of *Sciurus, Eutamias,* and *Pteromys.* The bulla consists of large cells separated by partitions. Simkin suggests that the partitions assist in transmitting sound from the bullar wall to the cochlea, and the combination of cells plus partitions is viewed as a specific adaptation for amplifying sounds received through the ground or through the wood of trees.

5. A complex spherical type, as seen in the Gerbillinae, structurally combines chambers, large cells, and other features indicated above, and the combination allows animals "not only to tune in for the reception of biologically important signals, but also it broadens the spectrum of frequencies amplified."

In regard to microtines, it does not now seem possible to infer functions of middle ear parts from their anatomy because (a) there is not enough detailed ecological and behavioral information on each species to allow for meaningful correlations, and (b) there are too few experimental studies identifying key factors in the environment. Though all microtines produce sounds and the various middle ear arrangements

observed in them may be auditory adaptations, conclusive evidence that they are adaptive is lacking. There is only one experimental study, to my knowledge, of sound production and behavior in microtines. Arvola *et al.* (1962) found that the lemming *(Lemmus lemmus)* produces and responds to a variety of signals. Most of these are in the 500–8000 Hz range, but some voiced elements reach 16,000 Hz. The possibility that the animals also produce and utilize high frequency sounds was not explored. This information on a "closed" middle-ear type when matched by comparable data from an "open" type (e.g., as in *Clethrionomys* or *Neofiber*) should give more precise clues as to how the middle ear arrangements influence hearing.

Ecological significances of the three types are not apparent. The three groups of species represent a peculiar assortment of habitats and habits. The open system is seen in a wide-ranging inhabitant of the floor of boreal forests *(C. gapperi)* and in a wetland, perhaps amphibious, inhabitant of Florida *(N. alleni)*. The redback vole *(C. gapperi)* is less restricted to cover and runways than some other microtines (Bailey, 1936; Hamilton, 1941*b*), and it may be the most generalized in structure and habits of the nine species. *N. alleni* on the other hand somewhat resembles the muskrat *(Ondatra)* in habitat and food (Schwartz, 1953), but it is more of a bog inhabitant than an aquatic animal. Wet "prairies" with sphagnum and peat and muck-bottom ponds may be the preferred habitats: the animals utilize surface runways and subsurface tunnels (Harper, 1927). The two species *(C. gapperi* and *N. alleni)* have different ways of life, and it is not clear how these, as a pair, ecologically contrast with the other seven species.

The closed system occurs in a species associated with bogs *(S. cooperi)*, a member of the sagebrush community of the Great Basin *(L. curtatus)*, and a runway-tending inhabitant of tundra *(L. trimucronatus)*. The xeric, *Artemisia*-studded uplands where the sagebrush vole *(Lagurus)* lives (Hall, 1928; Bailey, 1936; Johnson *et al.,* 1948) certainly contrasts with the low, moist areas supporting *Sphagnum,* grass, and other heavy ground cover where *Synaptomys* is found (Howell, 1927; Hamilton, 1941, *a,b).* Both species construct tunnels in ground and in snow. So does the brown lemming *(Lemmus)* which lives predominantly in soil polygons and other raised areas in wet meadows and tundra and in damp swales in adjoining uplands (Bee and Hall, 1956).

The "intermediate" category includes two species which are closely restricted to networks of runways in open grassland *(M. pennsylvanicus* and *M. ochrogaster),* a semi-aquatic species of western mountains *(A.*

richardsoni), and perhaps a tundra inhabitant *(D. torquatus).* The meadow vole *(M. pennsylvanicus)* and prairie vole *(M. ochrogaster)* apparently have fairly similar requirements, but the meadow vole prefers lower moister areas while the prairie vole lives principally in drier situations, at least where the two species are sympatric (De Coursey, 1957). The water vole *(A. richardsoni)* lives in burrows on banks of streams and in other wet areas and depends in part on water for escape and protection (Bailey, 1936). Aspects of its habits and habitat recall those of *Neofiber* and *Synaptomys.* The collared lemming *(Dicrostonyx)* occupies a variety of situations, but probably prefers upland areas, and, at least where sympatric with *Lemmus,* may make more extensive burrows, use surface runs less, and occur in more exposed situations than the brown lemming (Bee and Hall, 1956).

These attempts by various authors to correlate middle-ear anatomy with environment provide food for thought and hypotheses for testing, but they have been inadequate even to frame tentative answers—perhaps because of the complexity and interactions of the hearing-influencing elements in the environment and the complexity of auditory physiology. What are needed are experimental treatments, together with detailed ecological and behavioral information commensurate with that now available on anatomy.

LITERATURE CITED

AMBROGI, L. 1960. Manual of histologic and special staining techniques. New York: McGraw-Hill.

ARVOLA, ALPO, M. ILMÉN, AND T. KOPONEN. 1962. On the aggressive behaviour of the Norwegian lemming (Lemmus lemmus), with special reference to the sounds produced. Arch. Soc. Zool. Bot. Fenn. Ven., 17:80–101, 11 figs.

BAILEY, VERNON. 1936. The mammals and life zones of Oregon. N. Amer. Fauna, 55:1–416, 102 figs.

BEE, JAMES W., AND E. R. HALL. 1956. Mammals of northern Alaska on the Arctic slope. Misc. Publ. Univ. Kan. Mus. Nat. Hist., 8:1–309, 4 pls., 127 figs.

BÉKÉSY, GEORG VON. 1960. Experiments in hearing. (Translated and edited by E. G. Wever.) New York: McGraw Hill, 745 pp.

DE COURSEY, G. E., JR. 1957. Identification, ecology and reproduction of *Microtus* in Ohio. Jour. Mamm., 38:44–52, 11 figs.

HALL, E. R. 1928. Notes on the life history of the sage-brush meadow mouse *(Lagurus).* Jour. Mamm., 9:201–04.

HAMILTON, WILLIAM J., JR. 1941*a*. On the occurrence of Synaptomys cooperi in forested regions. Jour. Mamm., 22:195.

———— 1941 *b*. The food of small forest mammals in eastern United States. *Ibid.,* 22:250–63.

HARPER, FRANCIS. 1927. The mammals of the Okefinokee Swamp region of Georgia. Proc. Boston Soc. Nat. Hist., 38:191–396, 4 pls.

HEIM DE BALZAC, HENRI. 1936. Biogéographie des Mammifères et des Oiseaux de l'Afrique du Nord. Bull. Biol. France et Belgique, Paris. Suppl. 21:1–446, 7 pls., 16 figs.

HENSON, O'DELL W., JR. 1961. Some morphological and functional aspects of certain structures of the middle ear in bats and insectivores. Univ. Kans. Sci. Bull., 42:151–256, 37 figs.

HOOPER, EMMET T., AND B. S. HART. 1962. A synopsis of Recent North American microtine rodents. Misc. Publ. Mus. Zool. Univ. Mich., 120:1–68, 11 figs.

HOWELL, A. B. 1927. Revision of the American lemming mice (genus *Synaptomys*). N. Amer. Fauna, 50:1–38, 2 pls., 11 figs.

———— 1932. The saltatorial rodent Dipodomys: the functional and comparative anatomy of its muscular and osseus systems. Proc. Amer. Acad. Arts & Sci., 67:377–536, 28 figs.

HYRTL, JOSEPH. 1845. Vergleichend-anatomische Untersuchungen über das innere Gehörorgan des Menschen und der Säugethiere. Prag: F. Erlich. Pp. viii + 139, 9 pls.

JOHNSON, MURRAY L., C. W. CLANTON, AND J. GIRARD. 1948. The sagebrush vole in Washington State. Murrelet, 29:44–47.

KAMPEN, P. N. VAN. 1905. Die Tympanalgegend des Säugetierschädels. Morph. Jahrb., 34:321–722, 96 figs.

KEEN, J. A., AND C. S. GROBBELAAR. 1941. The comparative anatomy of the tympanic bulla and auditory ossicles, with a note suggesting their function. Trans. Roy. Soc. South Africa, 28:307–329, 78 figs.

KLAAUW, C. J. VAN DER. 1931. The auditory bulla in some fossil mammals, with a general introduction to this region of the skull. Bull. Amer. Mus. Nat. Hist. 62:1–352, 18 figs.

LEGOUIX, J. P., F. PETTER, AND A. WISNER. 1954. Etude de l'audition chez les mammifères a bulles tympaniques hypertrophiées. Mammalia, 18:262–271, 5 figs.

MILLER, GERRIT S., JR. 1896. The genera and subgenera of voles and lemmings. N. Amer. Fauna, 12:1–84, 3 pls., 40 figs.

———— 1912. Catalogue of the mammals of western Europe. London: British Museum. Pp. xv + 1019, 213 figs.

OGNEV, S. I. 1948. Mammals of the U.S.S.R. and adjacent countries. The mammals of eastern Europe and northern Asia. Vol. VI. Moscow: Acad. Sci. U.S.S.R. Pp. 1–559, 11 pls., 260 figs.

OTTO, A. W. 1826. De animalium quorundam, per hiemem dormientium vasis cephalicis et aure interna. Nova acta phys.-med. Acad. Caes. Leop. Carol. Nat. Cur., 13, pt. 1:23–86, 1 pl.

PETTER, F. 1961. Repartition geographique et ecologie des rongeurs desertiques (du Sahara occidental à l'Iran oriental). Mammalia, 25, No. special:1–222, 93 figs.

SCHWARTZ, ALBERT. 1953. A systematic study of the water rat *(Neofiber alleni)*. Occ. Pap. Mus. Zool. Univ. Mich., 547:1–27, 3 pls.

SIMKIN, G. N. 1965. Types of ear cavities of mammals in relation to distinctive features of their mode of life. Zool. Zhur., 44:1538–1545, 2 figs.

TULLBERG, TYCHO. 1899. Über das System der Nagethiere, eine Phylogenetische Studie. Kongl. Vetensk. Soc. i Upsala (Nova Acta Reg. Soc. Sci. Upsaliensis), ser 3, 18, Sec. Med. Hist. Nat., Pp. v + 514, 57 pls

WEBSTER, DOUGLAS B. 1961. The ear apparatus in the kangaroo rat, *Dipodomys*. Amer. Jour. Anat., 108:123–138, 5 pls., 3 figs.

————— 1962. A function of the enlarged middle-ear cavities of the kangaroo rat, *Dipodomys*. Physiol. Zool., 35:248–255, 2 figs.

————— 1966. Ear structure and function in modern mammals. Amer. Zool., 6:451–466, 9 figs.

WEVER, E. G., AND M. LAWRENCE. 1954. Physiological Acoustics. Princeton Univ. Press, 454 pp.

WIGGERS, H. C. 1937. The functions of the intra-aural muscles. Amer. Jour. Physiol., 120:771–780, 5 figs.

WINGE, HERLUF. 1941. The interrelationships of the mammalian genera. Vol. II. Rodentia, Carnivora, Primates. Translated from Danish by E. Deichmann and G. M. Allen. Kobenhavn: C. A. Reitzels, 376 pp.

WISNER, A., J. P. LEGOUIX, AND F. PETTER. 1954. Etude histologique de l'oreille d'un rongeur a bulles tympaniques hypertrophiées: *Meriones crassus*. Mammalia, 18:371–374, 2 figs.

ZAVATTARI, E. 1938. Essai d'une interprétation physiologique de l'hypertrophie des bulles tympaniques des Mammifères sahariens. Mammalia, 2:173–176.