

CT SCANNING AND COMPUTERIZED RECONSTRUCTIONS OF THE INNER EAR OF MULTITUBERCULATE MAMMALS

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ABSTRACT—The inner-ear structure of four multituberculate petrosals from the Late Cretaceous and Early Paleocene of North America was examined with computerized tomography (CT). Transverse CT scan images of these petrosals were digitized to produce a three-dimensional reconstruction of the acousto-vestibular spaces of multituberculates. Our investigation shows that the acousto-vestibular spaces of multituberculates are characterized by a straight cochlear canal and an extraordinarily enlarged vestibular cavity. Comparison of multituberculate inner-ear structures with those in other major mammalian clades suggests that the cochlea of multituberculates, which is similar to that of *Morganucodon*, is more derived than the cochlea of non-mammalian therapsids but more primitive than the coiled cochlea of therian and monotreme mammals. The extraordinary inflation of the vestibule of multituberculates is a uniquely derived character of most Cretaceous and Tertiary multituberculates, and it may be the synapomorphy of the order Multituberculata. Inflation of the vestibule may be correlated with low frequency hearing.

INTRODUCTION

The petrosal structures underwent fundamental changes in the origin of Mammalia (Romer, 1966; Carroll, 1988). One of the most striking of these changes is the evolution of the coiled cochlea of monotremes and therians. However, with the exception of a few studies (Olson, 1944; Quiroga, 1979; Allin, 1986; Graybeal et al., 1989), the inner ear structures of advanced non-mammalian cynodonts and early mammals have not been extensively documented. Several detailed works on multituberculate petrosals (Kielan-Jaworowska et al., 1986; Hahn, 1988; Miao, 1988; Luo, 1989) have greatly improved our knowledge of the external morphology of multituberculate ear region, but our understanding of the inner ear structures of multituberculates is still rather limited. Previous reports on inner ear structures of multituberculate mammals (Simpson, 1937; Sloan, 1979; Kielan-Jaworowska et al., 1986; Hahn, 1988; Miao, 1988; Luo, 1989) all lacked quantitative measurements of the vestibule and cochlea.

In an attempt to investigate the inner ear structure of the multituberculates from the Late Cretaceous and Early Paleocene of North America, we used computerized tomography (CT) to examine the internal structure of their petrosals. CT examination offers the advantage of providing the internal structural information for a fossil specimen without physical damage. The transaxial images of the internal structure of multituberculate petrosals recorded by CT were used to produce three-dimensional computerized reconstructions of the acousto-vestibular structures of multituberculates. Using available MacIntosh measurement soft-

ware we have measured the dimensions of the vestibule and cochlea from the CT scans of multituberculate fossil petrosals and from histological sections of selected species of extant mammals. These techniques have provided new morphometric information.

The descriptive terminology of the acousto-vestibular spaces varies among authors (e.g., Rowe, 1988; Miao, 1988). The cochlear duct of extant diapsids (reptiles and birds) contains the basilar papilla and the lagenar macula. Cochleae of extant mammals possess the organ of Corti, the homologue of the basilar papilla of other non-mammalian tetrapods (Romer, 1970). Monotremes, however, have a lagena at the apex of the cochlea (Pritchard, 1881), whereas therians have presumably lost this structure. As these anatomical components of the inner ear are not preserved in the endocasts of fossil specimens, we follow the convention of previous anatomical literature (Romer, 1970; Wever, 1978) and use cochlea or cochlear canal, rather than lagena or lagenar canal, for the acousto-vestibular space which contains the membranous auditory sensory structures of reptiles, birds and mammals (Romer, 1970; Wever, 1978; Fay and Popper, 1985). We note, however, that the term "cochlea" may not be perfectly appropriate for the uncoiled membranous auditory structure of some mammals and non-mammalian tetrapods, such as *Morganucodon* and multituberculates (also see Miao, 1988).

Abbreviations—AMNH, American Museum of Natural History; DUCCEC, Duke University Comparative Embryology Collection; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MCZ, Museum of Comparative Zoology, Harvard University; MEEI, Massachusetts Eye and Ear Infir-

TABLE 1. Measurement of the volume of the vestibule and estimation of skull length in selected representatives of major mammalian clades. The volume of the vestibule is measured from the highlighted (black) part of the inner-ear endocasts in Fig. 3. It does not include the volume of semicircular canals. Skull length is measured from rostrum to the occipital condyle along the base of the cranium. The minimum volume of the vestibule in *Lambdopsalis* is estimated from stereophotographs by Miao (1988:figs. 19, 20, 21, and 27).

Taxon (specimen)	Vestibule volume (mm ³)	Cochlear length (mm)	Skull length (mm)	(Skull length reference)
<i>Catopsalis</i> (MCZ 19176)	83.83	6.5	~80	(Kielan-Jaworowska et al., 1986)
<i>Meniscoessus</i> (UCMP 131798)	96.17	5.5	~75	(Archibald, 1982)
<i>Lambdopsalis</i>	>150		~65	(Miao, 1988)
<i>Tachyglossus</i> (DUCEC 8327)	2.84		80	
<i>Ornithorhynchus</i> (DUCEC 8326)	3.06		73	
<i>Didelphis</i>	6.14		106	
<i>Homo sapiens</i> (MH TH1, MEEI)	7.39		131	(Howells, 1973)
<i>Morganucodon</i> (MCZ 20988)	0.93	2.5–3.1	28	(IVPP 8682, IVPP 8684; Graybeal et al., 1989)

mary; UCMP, University of California at Berkeley, Museum of Paleontology. Abbreviations used in figures: ASC, anterior (superior) semicircular canal; br, broken structure; co, cochlear canal (cavity); GSPN, the canal for the greater superficial petrosal nerve (VII); LSC, lateral (horizontal) semicircular canal; OW, oval window; PP, paroccipital process; PR, promontorium; PRS, prootic sinus canal; PSC, posterior semicircular canal; PTC, post-temporal canal; RIC, canal for the ramus inferior of the stapedial artery; RW, round window; SF, subarcuate fossa; T1, T2 & T3, the first, second and third turn of the cochlea; VE, vestibular space (cavity); VII, canal for the facial nerve (VII).

MATERIALS AND METHODS

A sample of 15 isolated multituberculate petrosals from MCZ and UCMP collections were available for this study. They include two *Meniscoessus* petrosals (UCMP 131798 and AMNH 199193), one *Catopsalis* petrosal (MCZ 19176) and three ptilodontoid petrosals (MCZ 19177; MCZ 21345 and UCMP 134822) (for taxonomic description see Clemens, 1964; Archibald, 1982; Luo, 1989). Petrosals identified as *Meniscoessus* are from Lance Creek Locality (Lance Fm. Late Cretaceous) and O'Conner's Site (Hell Creek Fm., Late Cretaceous). Among the multituberculates from these localities, *Meniscoessus* is the only taxon that possesses dentition matching the size of these petrosals (Clemens, 1964; McKenna, pers. comm.). The petrosal of *Catopsalis* from the Bug Creek Anthills locality (Earliest Paleocene: Archibald and Lofgren, 1990) is also tentatively identified by matching the size of the petrosal bone to the size of teeth of multituberculate taxa known from that locality (Kielan-Jaworowska et al., 1986; Luo, 1989). Many of these specimens are broken, exposing the internal structures that cannot be seen on well-preserved, intact specimens.

For comparison we used histological sections of a sub-adult platypus *Ornithorhynchus* (DUCEC 8326), a sub-adult echidna *Tachyglossus* (DUCEC 8327), an adult opossum *Didelphis virginiana* (Electron Microscopy Laboratory, MEEI) and an adult human female

(MH, TH 1, collection of the Cochlear Implant Research Laboratory, MEEI).

We used a Siemens DR3 CT neuroradiological scanner with a 0.3 meter aperture and a resolution of 300 microns. The specimens were scanned in contiguous 1 mm transaxial slices to produce images equivalent to serial transverse sections at 1 mm interval. Our scan parameters included 1,400 projections, 7 second scans, 125 kV, and 0.52 amp-seconds with high-resolution imaging at doubled windows of 2,700/3,500 Hounsfield Units and centers of 600/700 HU. This technique optimized our imaging of the internal structures and enhanced differences between mineralized bone and matrix that may occupy the cavities (Figs. 1, 2). Both absorption data and images were stored on RP06 disks and magnetic tape. All magnifications were data-based. High-resolution 512 matrix images were recorded from a CRT display on Dupont MR 34 Clear Base® film with a Siemens Multispot FA camera. Images at 2–5 fold magnification were digitized with a Kurta IS1 Graphics Tablet®. Three-dimensional reconstructions were produced on a MacIntosh II® computer using the MacReco 3.0® reconstruction package (Otten, 1987). The acousto-vestibular spaces of the multituberculate inner ear were reconstructed from CT scans, and those of other mammals were produced from histological sections.

To correct for allometry in comparing the size of the vestibule and cochlea, we selected the skull length (from the rostrum to the occipital condyles along the base of the cranium) as an approximation of body size for baseline comparisons (Table 1).

The skull length of *Meniscoessus* is extrapolated from a half skull described by Archibald (1982). The skull length of *Catopsalis joyneri* is in the range of 75 mm (pers. comm. from Drs. Clemens and Greenwald) to 80 mm (Kielan-Jaworowska et al., 1986). The skull length of *Lambdopsalis bulla* is about 65 mm (Miao, 1988). The skull length of *Morganucodon* is from the average of three specimens: IVPP 8682, IVPP 8684 and the specimen described by Kermack et al. (1981). The length of the extant mammals was an average

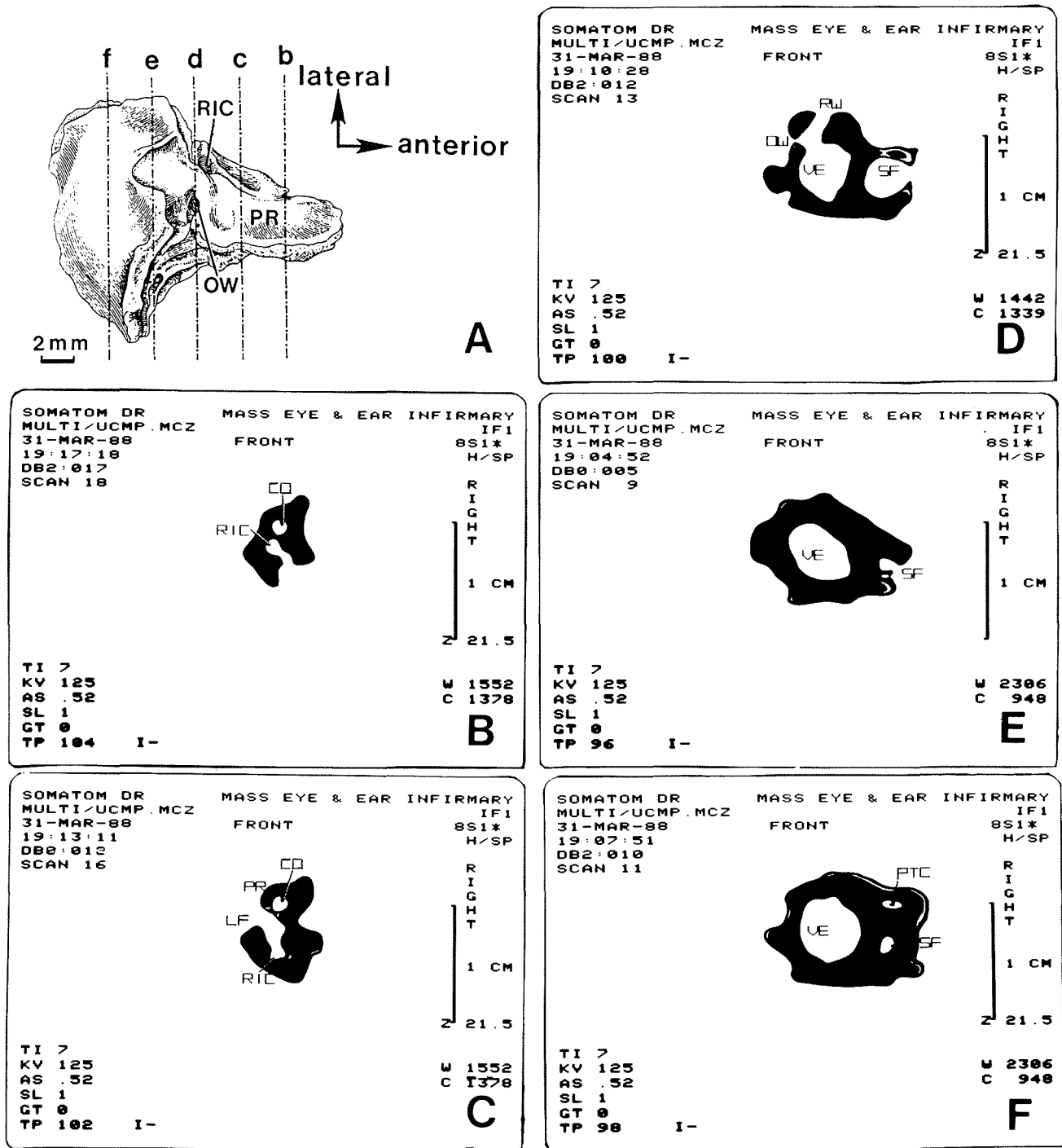


FIGURE 1. CT scans of a right petrosal of *Meniscoessus* (UCMP 131798). A, Ventral view of the petrosal and the approximate position of the illustrated CT scans. B-F, Selected CT scans (cross-sections) in an anteroposterior sequence, showing the internal structure of UCMP 131798. The lateral side of the petrosal facing toward the top of the scans; the dorsal side of specimen toward the right side of the scans. For abbreviations see Introduction.

taken from a number of skull specimens in MCZ: *Tachyglossus*: 10 specimens; *Ornithorhynchus*: 9 specimens; *Didelphis virginiana*: 32 specimens. The skull length of the human female is the mean skull length of European females provided by Howells (1973).

OBSERVATIONS

The computerized reconstructions (Fig. 3A, B) are equivalent to the endocasts of the inner-ear spaces contained in the petrosals of these mammals. The com-

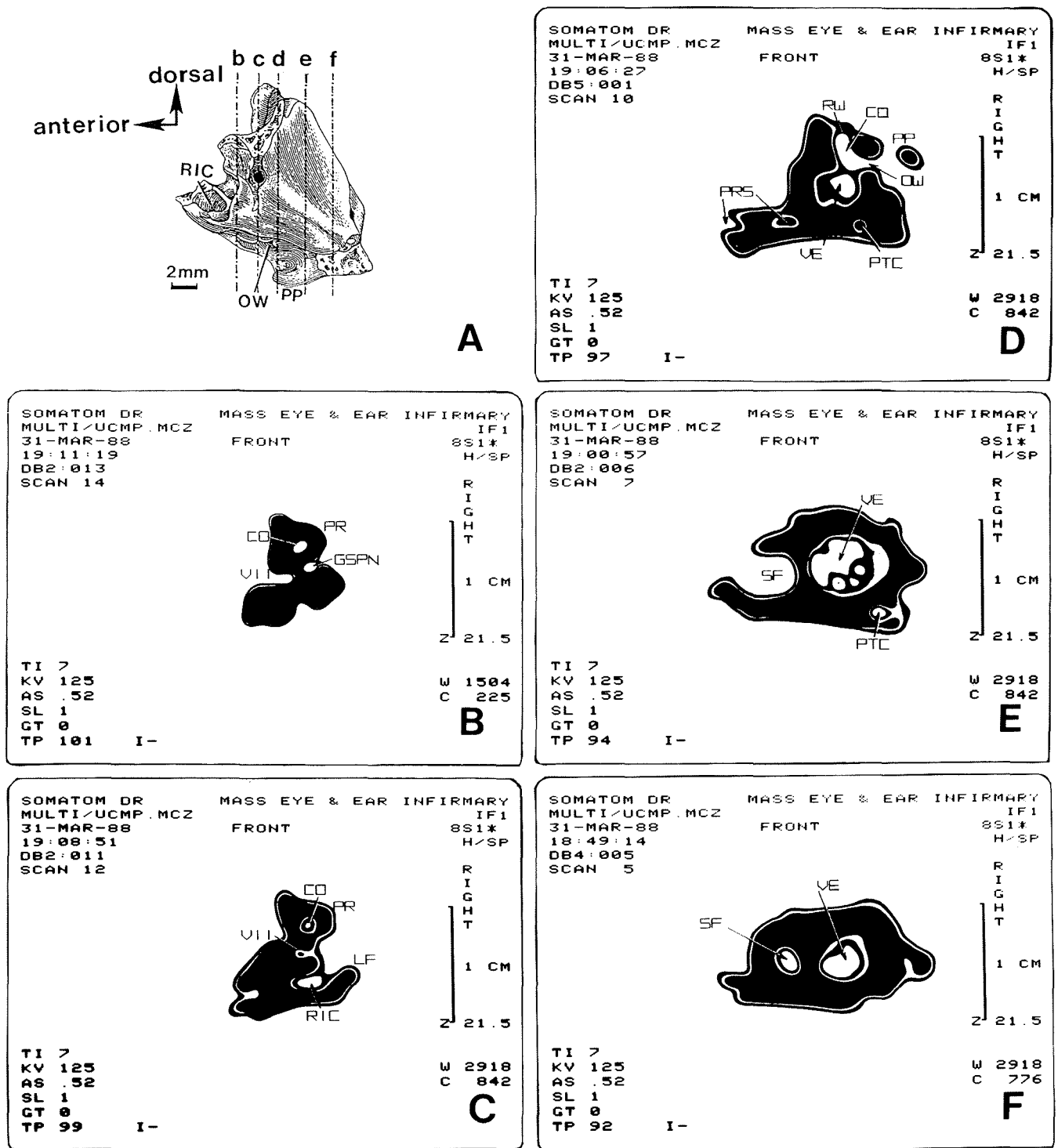


FIGURE 2. CT scans of a left petrosal of *Catopsalis joyneri* (MCZ 19176). A, The lateral view of the petrosal and the approximate position of the illustrated CT scans. B-F, Selected CT scans in an anteroposterior sequence showing internal structures of MCZ 19176. The lateral side of the specimen is toward the bottom of the scans; the ventral side of the specimen toward the right side of the scans. For abbreviations see Introduction.

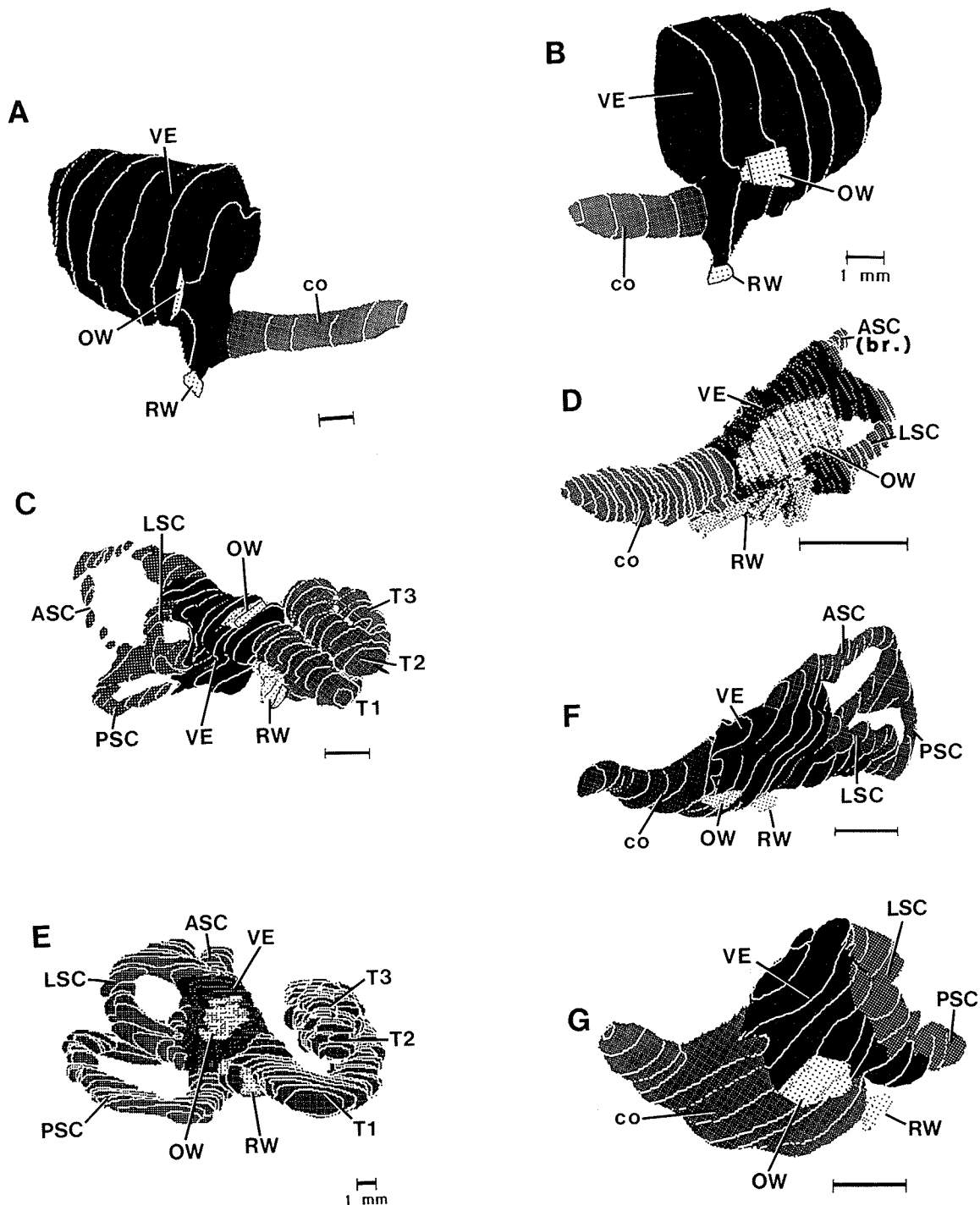


FIGURE 3. Reconstructed endocasts of the inner ear of selected representatives of major mammalian clades (ventrolateral view). The vestibular part of the inner ear is colored in black. **A**, *?Meniscoessus* (Multituberculata, UCMP 131798), reconstructed from CT scans of a right petrosal bone, semicircular canals not illustrated. **B**, *Catopsalis* (Multituberculata, MCZ 19176), reconstructed from CT scans of a left petrosal, semicircular canals not illustrated. **C**, Opposum (*Didelphis virginiana*, Marsupialia, collection of Electron Microscopy Laboratory, Department of Otology & Laryngology, MEEI), reconstructed from serial frontal sections of a right petrosal. **D**, *Morganucodon* (Triconodonta, collection of MCZ), reconstructed from serial cross section of a left petrosal, the anterior semicircular canal is broken and the posterior semicircular canal is missing from the specimen. **E**, Human (*Homo sapiens*, Temporal Bone Bank, Department of Otology & Laryngology, MEEI), reconstructed from serial transaxial sections of the right petrosal of an adult female. **F**, Platypus (*Ornithorhynchus*, Monotremata, sub-adult, DUCEC 8326), reconstructed from cross sections of the left petrosal. **G**, Echidna (*Tachyglossus*, Monotremata, sub-adult, DUCEC 8327), reconstructed from cross sections of the left petrosal. For abbreviations see Introduction.

bination of reconstructions with measurements of the multituberculate inner ear provides a more accurate estimation of the volume, shape and the relative proportions of the cochlea and vestibule of multituberculate mammals than has been available in previous studies (Kielan-Jaworowska et al., 1986; Miao, 1988; Luo, 1989).

The cochlea of multituberculates is rod-like and straight (Fig. 3). This confirms the observation of Miao (1988) on *Lambdopsalis bulla*, but differs from the suggestion of Sloan (1979) that *Ectypodus*, a neoplagiulacoid multituberculate, has a "hooked cochlea." The length of the cochlear cavity is about 6.5 mm in *Catopsalis* and 5.5 mm in *Meniscoessus*. The cochlear length of multituberculates relative to skull length is about the same as in *Morganucodon* (Table 1). As has been extensively documented, the cochlea of extant diapsid reptiles is short and straight (Oelrich, 1956; Wever, 1978; Bellair and Kamal, 1981). This primitive condition is also present in non-mammalian therapsids (Olson, 1944; Allin, 1986). The cochleae of multituberculates and *Morganucodon* (Graybeal et al., 1989) (Fig. 3) are longer, thus more derived than those of non-mammalian therapsid outgroups. They are, however, much more primitive than the cochleae of monotremes and extant therian mammals, which have at least one-half turn. The promontorium of multituberculate petrosals, although much larger than those of non-mammalian therapsids, is less pronounced than that of the platypus (*Ornithorhynchus*), and much less than those of therians (Fig. 1A). The small size of the promontorium in multituberculates is associated with the lack of coiling of the cochlea.

The vestibule of the petrosal of taeniolabidoid multituberculates is extremely large, suggesting that the membranous labyrinth of the vestibule, including the saccule and utricle, was tremendously inflated. We measured the volume of the vestibule of two multituberculate genera and the selected representatives of several major mammalian clades. We also estimated the volume of *Lambdopsalis* (Miao, 1988) (Table 1). Our morphometric data show that the absolute volume of the multituberculate vestibule is two orders of magnitude larger than that of *Morganucodon* (Morganucodontidae, Triconodonta), thirty-fold that of the platypus (*Ornithorhynchus*) and the echidna (*Tachyglossus*, Monotremata), and more than ten-fold that of the opossum (*Didelphis virginiana*, Marsupialia) and man (*Homo sapiens*, Eutheria). If the length of the skull base is taken as an approximation of skull size, the volume of the vestibule of three taeniolabidoid multituberculates is still much larger than would be expected from the regression equation derived from other representative mammalian species (Fig. 4).

The inflation of the vestibule is correlated with the disproportionately large size of the mastoid region of the petrosal of taeniolabidoid multituberculates from the Late Cretaceous and the Earliest Paleocene of North America (Luo, 1989). Figures from an earlier report (Kielan-Jaworowska et al., 1986) on the Cretaceous

taeniolabidoid and eucosmodontid multituberculate petrosals from Mongolia show substantial enlargement of the vestibule in comparison to other mammals. Ptilodontoid petrosals from the Earliest Paleocene of North America have also developed moderate inflation, but to a lesser degree than those of taeniolabidoids (Luo, 1989). Among later multituberculates, an extreme example of vestibule inflation is found in *Lambdopsalis bulla*, a taeniolabidoid from the late Paleocene of China (Miao, 1988); the size of vestibular cavity in *Ptilodus* (Simpson, 1937) is not known.

Two multituberculate petrosals from the Jurassic have been described (Prothero, 1983; Hahn, 1988). The internal structures are not adequately exposed to show the size of the vestibule, but one specimen's mastoid and paroccipital region (Prothero, 1983) is rather large, thus may have an enlarged vestibule. The consistent presence of vestibular inflation in known multituberculates from the Cretaceous and Tertiary strongly suggests that it is a characteristic of their shared common ancestry. Whether the inflation of the vestibule is a synapomorphy of the entire Multituberculata (sensu Clemens and Kielan-Jaworowska, 1979) depends on future verification from better Jurassic fossil materials.

It remains unclear from our CT scans of the petrosal and previous studies (Kielan-Jaworowska et al., 1986; Miao, 1988; Luo 1989) whether the vestibular inflation of multituberculates relates to the enlargement of the saccule, the utricle, or both.

DISCUSSION

The discovery of *Steropodon* (Archer et al., 1985), an Early Cretaceous monotreme with molar cusps in reversed triangular arrangement, has led to the hypothesis that monotremes are the sister group of therians with tribosphenic or nearly tribosphenic molars, which includes aegialodontids, pappotheres, deltatheriids, marsupials and eutherians (Archer et al., 1985; Kielan-Jaworowska et al., 1987). A major corollary of this hypothesis would be that monotremes and extant therians are more closely related to each other than either group is to multituberculates. A contrary hypothesis was advocated by Rowe (1986, 1988) who hypothesized that multituberculates are the sister group of extant therians, to the exclusion of monotremes and *Morganucodon*.

These competing hypotheses on the relationships of major mammalian clades predict different character distributions for straight versus coiled cochlea amongst mammalian clades. According to Rowe's hypothesis (1988 and pers. comm.), the coiled cochleae in monotremes and extant therians were independently derived and the straight cochlea of multituberculates is the primitive character retained from the common ancestry of monotremes, multituberculates, and therians. According to the hypothesis that monotremes are the sister group of advanced therians (Archer et al., 1985; Kielan-Jaworowska et al., 1987), the coiled cochlea of

monotremes and extant therians would be derived from their shared common ancestry, without any convergence or reversal of the coiling of the cochlea.

The cochleae of *Ornithorhynchus* and *Tachyglossus* are coiled through 270 and 180 degrees, respectively. *Ornithorhynchus* has a lagena at the apex of the cochlea, but no apical lagena is present in extant therians (Pritchard, 1881). Unlike the coiled cochleae of therian mammals, in which the membranous labyrinth is supported in a spiral bony lamina ("bony labyrinth"), the coiled membranous labyrinth in monotremes is not supported by the cartilaginous spiral septum or the osseous spiral laminae in the cochlear cavity (Alexander, 1904; Zeller, 1989). Because the bony cochlear cavity does not coil in correspondence to the coiled membranous labyrinth in monotremes as the cochlear canal does in therians, the endocasts of the monotreme cochlear cavities do not show significant coiling (Fig. 3F, G). Differences in the cochlear configuration between monotremes and therians suggest that they are derived through quite different developmental paths and therefore may not be homologous (Zeller, 1989 and pers. comm.). The coiling or curvature greater than 180 degrees in both monotremes and therians is perhaps the only aspect of the cochlear morphology that can be interpreted as evidence for the hypothesis of monotreme-therian sister group relationship. The hypothesis of multituberculate-therian sister group relationship (Rowe, 1988) is not supported by the distribution of straight vs. coiled cochleae among major mammalian clades. But the hypothesis of monotreme-therian sister groups is also shadowed by the problem of structural differences between monotreme and therian cochleae. With these uncertainties in mind, we tentatively interpret the coiling of the cochleae as a corroboration of monotreme-therian sister group relationships; yet we stress that a single character does not make a phylogeny and that the cochlear character is by no means the final arbiter of relationships of major mammalian groups.

The vestibules of diapsid reptiles and non-mammalian therapsids are comparatively small (Olson, 1944; Quiroga, 1979; Bellair and Kamal, 1981; Allin, 1986). Evidently, the great inflation of the vestibule in multituberculates is a uniquely derived condition which is not present in the non-mammalian therapsid outgroups, nor in any other mammalian groups. Distribution of this character suggests that it is a synapomorphy for Cretaceous and Tertiary multituberculates, and maybe for all Multituberculata (sensu Clemens and Kielan-Jaworowska, 1979). It is a useful diagnostic cranial character in addition to the highly specialized dentition.

In interpreting the functions of the extremely inflated vestibule of *Lambdopsalis bulla*, Miao (1988) suggests that this multituberculate was adapted to low frequency hearing, based on the similarity of the enlarged vestibule of this species to those of some extant vertebrates. Several case studies on the hearing function of vertebrates indicate that the enlarged vestibules may

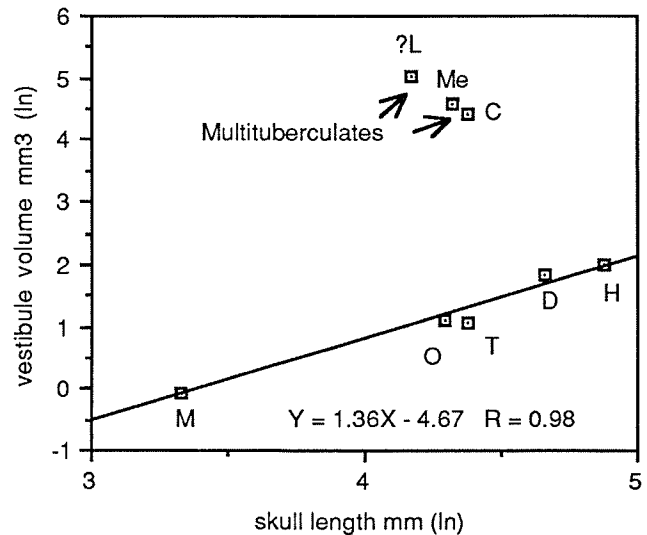


FIGURE 4. Variation in the volume of the vestibule in mm^3 (Ln) relative to skull length in mm (Ln) among the selected representatives of major mammalian clades. For estimation of the skull length, see Table 1. C, *?Catopsalis* (Multituberculata). D, *Didelphis virginiana* (Marsupialia). M, *Morganucodon* (Triconodonta). Me, *?Meniscoessus* (Multituberculata). O, *Ornithorhynchus* (Monotremata). T, *Tachyglossus* (Monotremata). H, *Homo sapiens* (Eutheria). ?L, The probable position of *Lambdopsalis bulla* (Multituberculata).

be an adaptation for low frequency hearing. Frogs have very large vestibules (Patterson, 1960) and are capable of communicating with seismic-range low frequencies (Lewis et al., 1985). Lewis and Narins (1985) and Wever (1985) have demonstrated that burrowing caecilian amphibians with enlarged vestibules are sensitive to low frequency substrate vibration. Bramble (1982) noted that *Gopherus polyphemus*, a burrowing turtle from the Tertiary, developed a very large vestibule and massive otolith. He hypothesized that such an ear would be similarly sensitive to low frequency substrate vibration. Physiological studies (Rosowski et al., 1988) have shown that modern lizards, which develop a larger vestibule than those of other extant reptiles, can receive both low frequency air-borne sound and substrate vibration.

Krause and Jenkins (1983; see also Jenkins and Krause, 1983) suggested that multituberculates were primitively aboreal animals. In contrast, Miao (1988; see also Miao and Lillegraven, 1986, and Kielan-Jaworowska and Qi, 1990) argued that *Lambdopsalis bulla* was a burrowing animal on the basis of some postcranial skeletal features. Kielan-Jaworowska (1989) noted that the postcranial skeletons of a Late Cretaceous multituberculate were adapted for fossorial living. Miao went further to suggest that the large vestibule of *L. bulla* was a part of the burrowing adaptation of this animal. Whether multituberculates were primitively adapted to burrowing or climbing should be tested by more postcranial characters of more taxa. We

believe that the functional studies of enlarged vestibules in extant vertebrates provide unambiguous support for low frequency hearing in multituberculates.

CONCLUSIONS

1) The straight cochlea of multituberculates is approximately the same proportion of skull length as in *Morganucodon*. This condition is primitive by comparison to the coiled cochleae of monotremes and therians.

2) The character distribution of straight versus coiled cochleae favors the hypothesis of monotreme-extant therian sister group relationship over the hypothesis of multituberculate-therian sister group relationship.

3) The unique presence of an enlarged vestibular space in multituberculate petrosals of known Cretaceous and Tertiary multituberculate groups indicates that this is a diagnostic character derived from their shared common ancestry, possibly a synapomorphy of Multituberculata. The enlargement of the vestibular space in multituberculates is probably indicative of adaptation for low frequency hearing.

ACKNOWLEDGMENTS

We thank Drs. William A. Clemens, Alfred W. Crompton, J. Howard Hutchison, J. David Archibald, Malcolm C. McKenna and Mr. Charles Schaff for making available specimens used in this study. Dr. A. Weber allowed access to the CT facility at Massachusetts Eye and Ear Infirmary. Drs. R. D. E. MacPhee and R. S. Kimura provided histological sections of monotremes and marsupials. Dr. Miao Desui has allowed study of his unpublished specimens. We also thank A. Graybeal and A. W. Crompton for allowing us to use their serial sections of *Morganucodon* petrosals and D. F. Kong for his assistance in computer programming. Drs. W. A. Clemens, A. W. Crompton, J. A. Hopson, Nelson Y. S. Kiang, J. Rosowski, E. F. Allin, J. D. Archibald, N. S. Greenwald, D. Bramble, T. Rowe and D. Miao have made valuable suggestions on earlier versions of this paper. The research was supported by NSF grant 81-19127 AO2, BSR 85-13253 to Professor William A. Clemens, and NSF grant BRS 88-138898 to Professor A. W. Crompton.

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Received 30 April 1990; accepted 27 August 1990.