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Basicranial Anatomy of *Herpetotherium* (Marsupialia: Didelphimorphia) from the Eocene of Wyoming

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ABSTRACT

Cranial anatomy of early Tertiary *Herpetotherium* is described, with an emphasis on the auditory region. The preserved anatomy presents a suite of characters indicating a conservative morphological trend in the ear region. The tympanic cavity floor has a large alisphenoid contribution that resembles the condition seen in *Caluromys*. No other bony structures from the petrosal or surrounding bones contribute to closure of the tym-

panic floor, and it is not known how much was contributed by the ectotympanic. The exit for mandibular nerve (V3) through a rostral incisure of the piriform fenestra is most similar to the condition observed in *Marmosa* and *Monodelphis*. In general, the anatomy of the ear region observed in *Herpetotherium* resembles that observed in extant didelphids; however, changes in spatial morphology appear to distinguish taxonomic groups.

INTRODUCTION

The cranial morphology of three very well-preserved, nearly complete marsupial skulls, referred to the genus *Herpetotherium* (Fox, 1983; Korth, 1994), are described herein. All three fossils were collected by Frick expeditions in Wyoming; two come from the White River Formation in Converse County (AMNHP 127684, 127685) and one comes

from an ash layer in a section 2.5 mi southeast of the Jim Christian Hills (Flat Top Mountain) in Niobrara County (AMNHP 22304). The latter is roughly assigned to what is now considered the late Eocene and the White River Formation is Chadronian, which is also late Eocene (Prothero and Swisher, 1992). Because most of the North

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American marsupial fossils from the Cretaceous and early Tertiary consist of isolated teeth and maxillary, dentary, and rostral fragments, these fossils are especially significant. Their completeness adds significantly to our knowledge, not only of the genus *Herpetotherium*, but also of the evolution of the auditory region in marsupials. The goals of this study are (1) to describe the anatomy of the basicranium of *Herpetotherium*, (2) to compare that anatomy with extant members of the Didelphidae as defined by Marshall et al. (1990) and Kirsch et al. (1997), and (3) to discuss the implications for character evolution of the alisphenoid tympanic process and other features of the auditory region with reference to extinct and extant marsupials.

METHODS AND MATERIALS

Descriptions of three skulls of *Herpetotherium* sp. (AMNHP 127684, represented by a nearly complete cranium and two dentaries; AMNHP 22304, a complete cranium; and AMNHP 127685 represented by a nearly complete cranium and a right dentary) employ the terminology of MacPhee (1981), Novacek (1986), and Wible (1990). All three skulls were utilized to generate the most complete and accurate descriptions. The crania were allocated to the genus *Herpetotherium* on the basis of their dental morphology, which did not present any new features to report. Traits present in the skulls described here that are diagnostic of *Herpetotherium* Cope, 1873 (Korth, 1994) include the following: dominant stylar cusp D on M1-M2, dominant stylar cusp C on M3-M4, and enlarged and procumbent 11 and 12. *Herpetotherium* was established as a North American genus distinct from *Peratherium* by Korth (1994).

The marsupial phylogeny of Marshall et al. (1990) was employed initially to identify appropriate comparative taxa. Marshall et al. (1990) designated caluromyines a subfamily of didelphids, contra Kirsch (1977) who recognized the family Caluromyidae as distinct from Didelphidae. More recent work by Kirsch and Palma (1995) and Kirsch et al. (1997) upheld the assignment of the subfamily Caluromyinae, along with Glironiinae, to the family Caluromyidae (see Patton et al.

[1996] for an alternative interpretation). Thus, taxa from the order Didelphimorphia sensu Kirsch et al. (1997) that were available to the author were used for the comparisons, regardless of the variable subordinal relationships. Two taxa from two different orders of marsupials were arbitrarily selected to permit study of character variation: *Caenolestes* (order Paucituberculata) and *Dasyurus* (order Dasyuromorphia). The following specimens of extant marsupial genera were used to analyze the comparative anatomy: *Caenolestes*, AMNHM 62914, 62902, 64381, 64414, 64389; *Caluromys*, AMNHM 133200, 78101, 96641, 230001, 139783; *Caluromysiops*, AMNHM 208101; *Dasyurus*, AMNHM 154518, 196845; *Didelphis*, AMNHM 128992, 28961, 176700, 172168; *Marmosa*, AMNHM 96698, 184846, 206765, 254508; *Metachirus*, AMNHM 130597, 133110, 267362; *Micoureus*, AMNHM 210397, 267818; *Monodelphis*, AMNHM 261243, 130516, 16125, 130565, 77291; and *Philander*, AMNHM 260033, 96593, 96736, 133064, 67295. Abbreviations: AMNHP American Museum of Natural History, Department of Vertebrate Paleontology; AMNHM American Museum of Natural History, Department of Mammalogy.

DESCRIPTION

MID-CRANIAL REGION: Among all of the *Herpetotherium* skulls described here, crushing and fragmentation in the region of the mid-cranium and cranial vault has resulted in the loss of much relational information. In spite of this, nasal and frontal bones appear to have a positional relationship to each other that is found in most marsupials: i.e., with the nasals expanded posteriorly along their contact with the frontals. The frontals extend posteriorly to a position dorsal to the most posterior limit of the orbitotemporal fossa. Parietals continue from the coronal suture posteriorly until they contact the supraoccipital, and form transversely oriented, slightly curved crests. These crests are fragmentary, but it appears they would have eventually met along the sagittal suture.

The jugal articulates anteriorly with the maxilla and lacrimal, curving outward laterally and horizontally from the rostrum. A

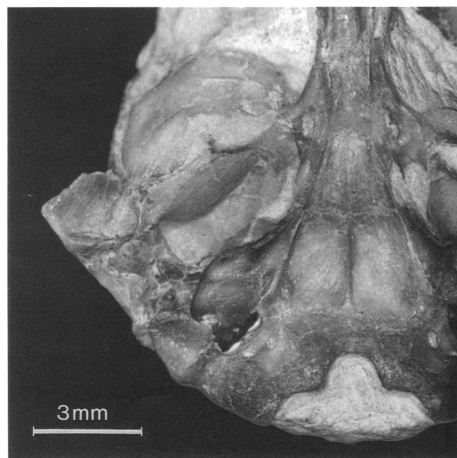
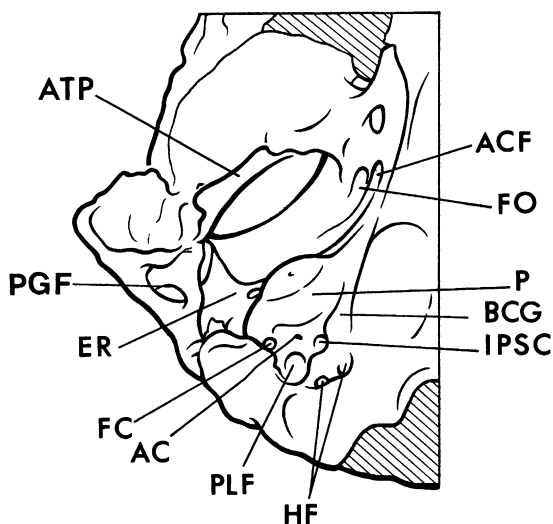


Fig. 1. *Herpetotherium* sp., AMNH 22304. Right auditory region, ventral view. Bulla is not preserved. Abbreviations: AC aqueductus cochleae; ACF anterior carotid foramen; ATP alisphenoid tympanic process has been broken along its rostromedial-caudolateral axis and folded up into the tympanic roof; BCG basicapsular groove; ER epitympanic recess; FC fenestra cochleae; FO foramen ovale; HF hypoglossal foramina; IPSC canal for the inferior petrosal sinus; P promontorium; PGF postglenoid foramen; PLF posterior lacerate foramen.

small postorbital process can be seen on the dorsal aspect of the jugal. The distal portion of the jugal curves gently downward and beneath the zygomatic process of the squamosal, extending posteriorly to form the anterior lip of the glenoid fossa. The glenoid fossa of the squamosal is shallow and slightly convex. It is bounded posteriorly by the postglenoid process and posterodorsally by a large postglenoid foramen, which conveys the postglenoid artery and the sphenoparietal emissary vein in extant marsupials (Wible, 1990: fig. 1).

In the region of the orbits, there are fragments of the lacrimal, orbitosphenoid, palatine, and alisphenoid bones. However, their topological relationships cannot be determined with any certainty. Within the orbito-temporal region, there are several well-preserved features: from anterior to posterior, the sphenopalatine foramen, the posterior edge of the sphenorbital fissure, and the foramen rotundum. (The optic canal is confluent with the sphenorbital fissure in marsupials [Maier, 1987].) The sphenopalatine foramen is in the anteroventral corner of the orbit, presumably in the palatine bone; however, its position is equivocal because of

crushing in this region. It conveys the sphenopalatine artery, vein, and accompanying nerve (Archer, 1976). Posterior to the sphenopalatine foramen, there is a vertically oriented sliver of bone with a well-defined border. This is probably the posterior margin of the sphenorbital fissure. It is not possible to determine which bones border the fissure; however, in extant didelphids, this fissure is at the junction of the alisphenoid and orbitosphenoid (Maier, 1987). The sphenorbital fissure transmits the ophthalmic branch of cranial nerve V and the supraorbital ramus of the ophthalmic branch of the internal carotid artery, in addition to cranial nerves II through IV and VI in marsupials (Archer, 1976). The foramen rotundum, which transmits the maxillary branch of cranial nerve V, is located in the alisphenoid lateral and slightly posterior to the sphenorbital fissure.

BASICRANIUM: From the basal aspect, the most conspicuous parts of the alisphenoid are the pterygoid processes (not figured) and the tympanic processes (figs. 1, 2, 3). The pterygoid processes are crushed against the basisphenoid, but the tympanic processes are, for the most part, intact. Sutures separating the basisphenoid and alisphenoid have fused

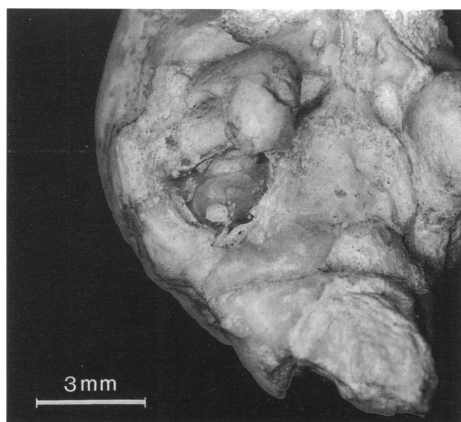
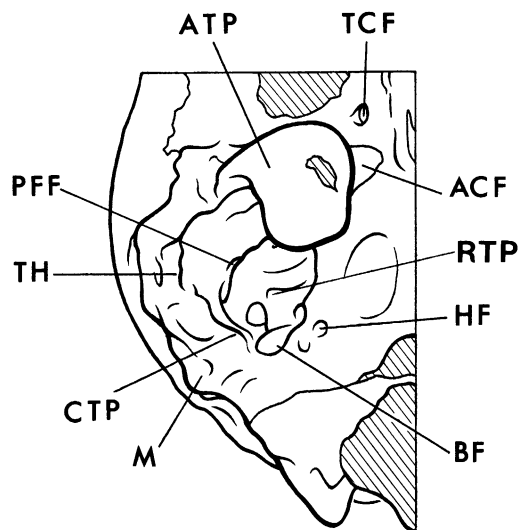


Fig. 2. *Herpetotherium* sp., AMNH 127685. Right auditory region, ventral posterolateral view. Abbreviations: ACF anterior carotid foramen; ATP alisphenoid tympanic process; BF basal fissure containing openings for posterior lacerate foramen and inferior petrosal sinus canal; CTP caudal tympanic process (broken edge); HF hypoglossal foramen; M mastoid region; PFF primary facial foramen; RTP rostral tympanic process of petrosal; TCF transverse canal foramen; TH tympanohyal (broken edge).

forming a "sphenoid complex" that is bounded posteriorly by the auditory bulla and the basioccipital contribution to the occipital. The anterior carotid foramen is located in the posterolateral edge of the basi-sphenoid component of the sphenoid complex, immediately rostral to the sphenoid-basioccipital suture. Based on this position, it is inferred that *Herpetotherium* had an internal carotid artery that ran medial to the auditory bulla, ventral to the basicapsular fissure and entered the braincase directly through the anterior carotid foramen. The exit for the mandibular nerve (= foramen ovale) lies just lateral to the anterior carotid foramen in a common depression anteromedial to the apex of the promontory (fig. 1). The foramen ovale as a distinct feature of the alisphenoid is not present; the exit is demarcated in the anteromedial part of the piriform fenestra and more accurately should be called an incisure. The foramen for the transverse canal (fig. 2) is anterior to the depression containing the foramen ovale and anterior carotid foramen and it appears to be in the ventral part of the alisphenoid; however, because the sutures have fused in this area, its position cannot be determined with cer-

tainty. The basioccipital contribution to the occipital complex is subrectangular and unremarkable. The exoccipital portion of the occipital complex is pierced by two small hypoglossal foramina that are situated anteroventral to each occipital condyle (figs. 1, 2). Condylar foramina, one on each side, are dorsolateral to the condyles. There is no jugular process (= "paroccipital process of exoccipital" sensu Wible, 1990) associated with the exoccipital.

The auditory bulla consists of two elements: the tympanic process of the putative alisphenoid component of the sphenoid and the ectotympanic (figs. 2, 3). A small posterolateral part of the rostral tympanic process of the petrosal may have contacted the posterior crus of the ectotympanic, thus participating in posterior closure of the tympanic floor. The tympanic process of the alisphenoid is the most significant element, accounting for greater than 50% of the bullar floor. It is moderately inflated dorsally, ventrally, and ventromedially. Crushing has displaced the bullae medially in AMNH 127684 and 127685, so the medial extent and subsequent associations most likely do not represent life relationships. Medially, the alisphenoid tym-

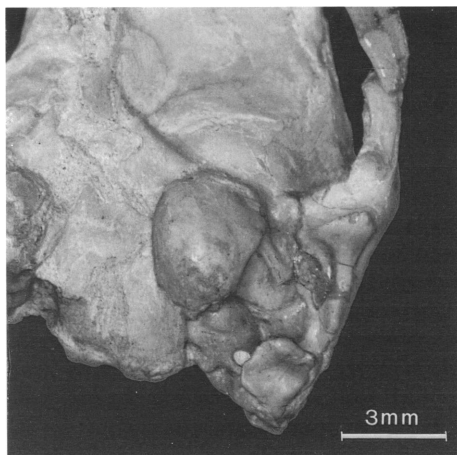
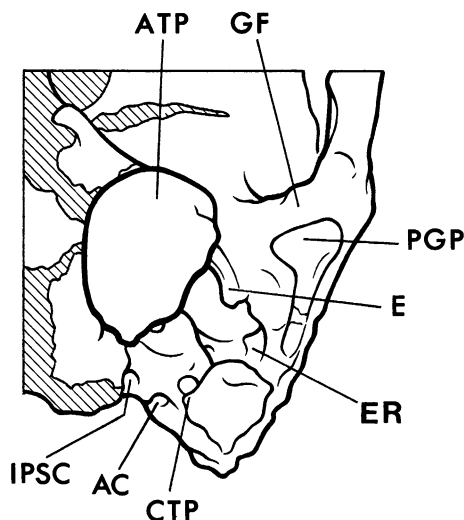


Fig. 3. *Herpetotherium* sp., AMNH 127684. Left auditory region, ventral view. Abbreviations: AC aqueductus cochleae; ATP alisphenoid tympanic process; CTP caudal tympanic process (broken); E ectotympanic (proximal end); ER epitympanic recess; GF glenoid fossa; IPSC inferior petrosal sinus canal; PGP postglenoid process.

panic process approximates a groove that is aligned rostrocaudally. This groove is associated with closure of the basicapsular fissure, which provides a canal for the inferior petrosal sinus that runs immediately dorsal to the groove (fig. 1) (Presley, 1979; Wible, 1983, 1986). The alisphenoid tympanic process contacts the medial petrosal border, although postmortem displacement may be responsible for this contact. The posterior crus and part of the anterior crus of the ectotympanic have been preserved in AMNH 127684 and have been displaced up and under the posterior edge of the alisphenoid tympanic process (fig. 3). It is probable that the ectotympanic would have contributed some portion to the posterolateral wall of the bulla. The anterior crus of the ectotympanic is narrow and columnar, and gradually expands transversely toward the posterior end. It appears that a small sliver of the incudal articular surface of the malleus is preserved along with the anterior crus of the ectotympanic. It cannot be determined whether the ectotympanic was attached to the alisphenoid tympanic process or suspended as a "free ring" as in some Recent marsupials. The posterior tip of the ectotympanic is in contact with the posterolateral portion of the rostral tympanic process of the petrosal, though as previously

mentioned, this contact may be the result of preservation conditions.

Inside the tympanic cavity, the epitympanic recess and the tympanic surface of the petrosal (figs. 1, 3) are visible. The bone in the area of the recess is fragmented, but the epitympanic recess appears to be situated in the extreme lateral edge of the petrosal; the fossa incudis is recognizable at the posterior border of the recess. Medial to the fossa incudis is the crista parotica, which is continuous with the caudal tympanic process posteriorly. The canal for the lateral head vein (= prootic canal), the tympanic aperture of which is at the posterior margin of the epitympanic recess in marsupials, is not identifiable in any of the specimens (Wible and Hopson, 1995). The promontorium is small relative to the bulla and fairly simple in structure; there are two consecutive, anteriorly facing convex ridges on the promontorium (fig. 1). These represent the turns of the cochlear duct. In AMNH 127684, the bone over this duct has not been preserved, so the first two turns of the fossilized duct are visible (fig. 3). There are no features of the promontorium that could be interpreted as vascular grooves or canals; therefore, it is inferred that *Herpetotherium*, like other extinct marsupials, lacks a stapedia artery as do extant marsu-

pials (Wible, 1990; Meng and Fox, 1995a, 1995b). A small bump on the posterior section of the promontorium, ventral to the fenestra cochleae, represents the minimally developed rostral tympanic process of the petrosal. The stapedial ratio (Segall, 1970), as measured on AMNH 22304, is 1.75. Though within the limits as defined by Segall (1970), there may have been some dorsoventral distortion due to crushing, which affects this measurement. The fenestra vestibuli faces laterally and the fenestra cochleae faces posterolaterally. The facial sulcus arcs around the lateral aspect of the promontorium of the petrosal, curving laterally and posteriorly along the roof of the middle ear. The primary facial foramen opens into the sulcus anteromedial to the fenestra vestibuli (fig. 2). The fossa for the stapedius muscle is a shallow, but well-circumscribed depression medial to the posterior continuation of the crista parotica. The tympanohyal and caudal tympanic process of the petrosal are not well-preserved in any of the specimens (fig. 2). Their anatomy cannot be described with any certainty; however, based on AMNH 22304, which preserves the most of both these features, it is possible that one or both of them could have approached the promontorium at or near the rostral tympanic process to form a ledge under the posterolateral segment of the facial sulcus. A stylomastoid notch is not apparent in any of the specimens, presumably because of breakage. An indistinct mastoid prominence can be observed on the ventral aspect of the mastoid region. At the posteromedial apex of the auditory region, at the junction of the basioccipital and petrosal, just opposite the hypoglossal foramina, is a large ventral fissure in the shape of an hourglass (fig. 2). There are two openings that converge at this fissure, one anterior and the other posterior; they are positioned at right angles to each other. The anterior opening is the canal for the inferior petrosal sinus, directed anteroposteriorly. The posterior opening is the posterior lacerate foramen, which is directed dorsoventrally. In living marsupials, the posterior lacerate foramen conducts cranial nerves IX, X, and XI, and, occasionally, a small vein from the transverse sinus (Archer, 1976). The aqueductus cochleae, which carries the perilym-

phatic duct and its vein, also opens into this fissure from the medial aspect of the petrosal.

COMPARATIVE MORPHOLOGY

As discussed in the Introduction, most descriptions of marsupial fossils from North America concern teeth-bearing fragments. However, research on the cranial anatomy of extinct marsupials has been accumulating. Matthew (1916) assigned a fragment of temporal bone to the stagodontid genus *Eodelphis* from the Oldman Formation of Alberta. Gazin (1935) described a partial skeleton of *Herpetotherium* that had been preserved on a slab of shale, mostly as impressions. The skull and right mandible were present, but crushed flat. Clemens (1966: figs. 55, 56, pp. 75 and 76) described a squamosal fragment and a petrosal-squamosal fragment referred to the genus *Didelphodon*, a stagodontid marsupial from the Late Cretaceous. Archibald (1979) identified a marsupial petrosal from the Hell Creek Formation as possibly belonging to *Pedimys* or *Alphadon*. Wible (1990) presented a comprehensive study on fossil marsupial ear anatomy, describing isolated petrosals from the Late Cretaceous. Meng and Fox (1995a, 1995b) also describe the anatomy of the Late Cretaceous marsupial petrosals from Montana and Alberta, respectively. Wible's (1990) descriptions serve as the anatomical atlas for this analysis of *Herpetotherium*.

Herpetotherium was considered to be a member of the subfamily Herpetotheriinae by Marshall et al. (1990). Kirsch et al. (1997) elevated the herpetotheriines to family level within Didelphimorphia but designated them incertae sedis. To make discussion of character evolution of the ear region appropriate, comparative anatomical analysis focused on didelphimorphs of the family Didelphidae and subfamily Caluromyiinae. *Herpetotherium* specimens AMNH 127684, 127685, and 22304 were compared to the living genera *Didelphis*, *Metachirus*, *Monodelphis*, *Micoureus*, *Marmosa*, *Philander* (subfamily Didelphinae), and *Caluromys* and *Caluromysiops* (subfamily Caluromyiinae). (*Caenolestes*, a caenolestid and *Dasyurus*, a dasyurid, were also used for outgroup comparison.)

The anatomy of the bullar floor of the mar-

supials studied herein is associated with several variables: number of contributory elements, inflation of contributory elements, and relative closure of the bullar floor, all of which have been discussed by other authors (e.g., Archer, 1976; Reig et al., 1987; Maier, 1989). The minimal condition of two bullar floor elements, uninflated or expanded and ventrally open, can be observed in *Philander* and *Metachirus*. In these taxa, the alisphenoid tympanic process and the rostral tympanic process of the petrosal define the anterior and posterior limits of the bullar floor, respectively. The ectotympanic in both taxa is narrow, contacts the rostral tympanic process, and contributes little to the lateral wall of the bullar floor. *Didelphis* differs only in having a relatively more inflated alisphenoid tympanic process and an ectotympanic that does not contact the rostral tympanic process of the petrosal. *Monodelphis*, *Micoureus*, and *Marmosa* all expand the posterior crus of the ectotympanic toward the midline of the bullar floor and thereby effectively raise the number of bullar floor elements to three. The bullar floor is open ventromedially, as is true to some degree in all these taxa. Of these three, only *Marmosa* shows any significant inflation of the alisphenoid tympanic process. Among the didelphid taxa included in this study, *Caluromys* and *Caluromysiops* exhibit the greatest extent of bullar floor closure; in both, the inflated alisphenoid tympanic process contributes 50% or greater to the bullar floor. The alisphenoid tympanic process and the rostral tympanic process meet (or nearly meet) over the promontorium, leaving only a small ventromedial slit in the bullar floor. Unlike *Marmosa*, *Monodelphis*, and *Micoureus*, *Caluromys* and *Caluromysiops* have only two bullar floor elements, the ectotympanic being aphaneric. In addition, the latter taxa are easily distinguished from the other taxa bearing two floor elements (*Philander*, *Metachirus*, and *Didelphis*), which do not elaborate either of the contributory elements. The alisphenoid tympanic process in *Herpetotherium* resembles that of the caluromyine opossums: it is greatly inflated and makes up approximately 50% of the bullar floor.

Most of the anatomical characters from the tympanic aspect of the petrosal showed little

variation among taxa. One of the features that displays observable variation is the rostral tympanic process of the petrosal. Unlike any of the didelphids in this study, *Herpetotherium* possesses a rudimentary rostral tympanic process that does not appear to play a role in forming the bullar floor. In didelphids, the rostral tympanic process attains its greatest development at its most posterolateral extent. There, it is tabular and projects laterally. *Metachirus* and *Didelphis* are the least developed of the didelphids with respect to this trait, but both attain a condition of greater development than does *Herpetotherium*. The rostral tympanic process of the petrosal in caluromyines is greatly expanded rostrally and rostrolaterally to form a kind of petrosal plate. This condition was also observed in *Dasyurus*. *Caenolestes* demonstrates a condition similar to that obtained in *Herpetotherium*, but with slightly greater lateral development.

The tympanohyal and the caudal tympanic process of the petrosal also showed variable relationship to each other and to the stylomastoid notch/foramen. In *Didelphis*, *Marmosa*, and *Philander*, the tympanohyal and the caudal tympanic process of the petrosal are both small. They are situated lateral and medial, respectively, to the stylomastoid notch, which gives egress for the facial nerve (Wible, 1990). The morphology is similar in *Micoureus*, where the stylomastoid notch is bordered on each side by the caudal tympanic process and tympanohyal. In some taxa, such as *Metachirus*, *Dasyurus*, and the caluromyines, the squamosal has a platelike process that overlays the lateral wall of the facial canal near the tympanohyal. The most extreme condition was observed in the caluromyines, where the caudal tympanic process of the petrosal and the posttympanic process of the squamosal converge to close the posterior space near the fenestra cochleae. This has the effect of creating a stylomastoid "foramen" in *Caluromys* and *Caluromysiops*. It is of interest to note the conditions in the outgroup taxa: in *Caenolestes*, the tympanohyal and caudal tympanic processes are strongly developed ventrally, creating a deep stylomastoid notch. The most elaborate condition was observed in *Dasyurus*: the tympanohyal and caudal tympanic

process of the petrosal meet laterally, posterolaterally, and ventrally to form a stylomastoid canal that opens in the usual posterolateral corner of the auditory region. The extent to which the tympanohyal and caudal tympanic process are developed in *Herpetotherium* is not known, but judging from the anatomy of the broken surfaces, it is not likely that these features were extensive.

With the exception of *Philander*, the jugular process contributes a rostral process that varies in degree of participation of posterior wall closure in extant didelphids (Note: Archer [1976] discussed a feature called the tympanic wing of the paroccipital process, which is undoubtedly the same as the rostral process of the jugular process. Archer's terminology is not used here for two reasons. First, the feature in question on the jugular process does not always contribute to tympanic anatomy. Second, the so-called paroccipital process of the petrosal in cynodonts and early mammals on the ventral surface of the petrosal [Rougier et al., 1992] is nonhomologous with the "paroccipital process of exoccipital." Therefore, the term jugular process [World Assoc. of Vet. Anat., N.A.V., 1994] is preferred to avoid confusion.) The jugular process in *Didelphis* sends a rostral process toward the petrosal without meeting it, constraining the space ventral to the fenestra cochleae. In *Monodelphis*, the rostral process is incipient, but noticeably present and similar in morphology to that of *Didelphis*. The rostral process of the jugular process is developed ventrally, medially, and laterally to contact the caudal tympanic process of the petrosal and the processus recessus in *Micoureus* and *Metachirus*, thereby limiting the posterior extent of the tympanic cavity. In *Caenolestes*, the jugular process curves anteroventrally to meet the caudal tympanic process of the petrosal and close the postero-medial aspect of the tympanic cavity; thus, there is no obvious rostral process. *Dasyurus* presents extensive development of the jugular process, which sends out a massive, fan-shaped wing covering the caudal tympanic process and contacting the rostral tympanic process. As stated above, *Herpetotherium* has no jugular process.

The relative positions of the anterior carotid foramen and the foramen ovale were

observed to be variable. In all taxa, the anterior carotid foramen was situated in the rostral end of a groove in the posterolateral corner of the basisphenoid, but the groove length varied. In *Didelphis*, *Philander*, and *Herpetotherium*, for example, the anterior carotid foramen was closer to the basisphenoid-basioccipital juncture than in *Caluromysops*. Nevertheless, the anterior carotid foramen was constrained anatomically as a feature of the putative basisphenoid portion of the sphenoid complex. The positional anatomy of the foramen ovale, on the other hand, was more variable. A rostral incisure in the piriform fenestra serves as the exit for the mandibular branch of the trigeminal nerve (V_3) in *Marmosa*, *Monodelphis*, and *Micoureus*. An intermediate condition is observed in some specimens of *Didelphis*, most specimens of caluromyines, and *Metachirus*. In these taxa, the foramen ovale is mostly contained in the alisphenoid; however, the foramen is partitioned posteriorly from the piriform fenestra by small struts from the alisphenoid that are incomplete, thus leaving the foramen largely continuous with the fenestra. Finally, there is the condition observed in *Philander*, *Caluromysops*, and most specimens of *Didelphis* where the foramen ovale is definitively in the alisphenoid, separated from the piriform fenestra, and displays a complex anatomy of primary and secondary foramina (for a detailed analysis of this anatomy, see Gaudin et al., 1996). The condition in *Herpetotherium* is the same as observed in *Marmosa*, *Monodelphis*, and *Micoureus*, where an incisure in the piriform fenestra is the marker for the exit of V_3 . The outgroups proved to have variable anatomy of the foramen ovale—with *Dasyurus* approximating the condition obtained in *Herpetotherium*, *Marmosa*, *Monodelphis*, and *Caluromys*; and *Caenolestes* showing complete bony separation of the foramen ovale from the piriform fenestra.

As a final note, it is of interest to mention that among the didelphimorphs included in this study, *Caluromys* does not have a transverse canal in the basisphenoid in the usual sense of that term (Archer, 1976). The absence of a transverse canal has been reported for *Pucadelphys andinus* as well (Marshall and Muizon, 1995). A structure present in

Caenolestes has been called by the same name, but there is now some doubt as to whether it is, in fact, homologous across marsupial taxa (Sanchez-Villagra, in prep.).

DISCUSSION AND CONCLUSIONS

The recovery of new structural data concerning the basicranial anatomy of *Herpetotherium* brings up several questions concerning character evolution among late Cretaceous/early Tertiary marsupials. The most controversial of these is the anatomy of the bulla. The morphology of the piriform fenestra/foramen ovale and the observable variation of the caudal tympanic process, tympanohyal, and rostral process of the jugular process also merit discussion.

Bullar floor composition in *Herpetotherium* is most like the condition obtained in the caluromyine didelphids, *Caluromysiops*, and *Caluromys*. The alisphenoid complement of the bulla in all three taxa is quite inflated and makes up at least 50% of the bullar floor. Unlike *Herpetotherium*, the caluromyines elaborate the rostral tympanic process of the petrosal to wall off the posterior aspect of the tympanic cavity. However, it is certain that the rostral tympanic process of the petrosal did not contribute to the closure of the posterior part of the bulla in *Herpetotherium* because of its small size. The contribution of the ectotympanic to the bullar floor in *Herpetotherium* cannot be assessed; therefore, it is not possible to designate the bullar floor as "bipartite" or "tripartite" as discussed by Reig et al. (1987). Given their definition of "bipartite" bullae as consisting of alisphenoid anteriorly, rostral tympanic process posteriorly, and a thin, noncontributory ectotympanic, the morphology observed in *Herpetotherium*, with its very small rostral tympanic process, would represent a departure from this arrangement. However, if the ectotympanic did contribute to the lateral aspect of the bullar floor, then the bulla in *Herpetotherium* would be "bipartite," but from different constituents. A minimal reconstruction hypothesis would leave the entire posterior part of the bullar floor in *Herpetotherium* open, with little or no contribution from either the ectotympanic or the rostral tympanic process of the petrosal. Obviously, the

resolution of this requires a phylogenetic analysis, but it is conceivable that bullar evolution in North American didelphids proceeded by the successive acquisition or elaboration of bony elements in the auditory region beginning with the alisphenoid tympanic process.

Recent papers by Muizon (1991, 1994), Muizon et al. (1997), Marshall and Muizon (1995), Trofimov and Szalay (1994), and Szalay and Trofimov (1996) presented important information about bullar composition in Paleocene and Cretaceous marsupials that is pertinent to future phylogenetic studies. The two Paleocene marsupials described by Muizon are from South America. One is a didelphid, *Pucadelphys* (Muizon, 1991; Marshall and Muizon, 1995) and the other a borhyaenoid, *Mayulestes* (Muizon, 1994), both from the early Paleocene of Bolivia. Muizon (1991: 589–590 and fig. 6, p. 589) reported the absence of an alisphenoid tympanic process in *Pucadelphys*; in fact, no evidence of a bulla of any kind; the same was true for *Mayulestes* (Muizon, 1994). Muizon (1994) argued that the primitive condition of the tympanic cavity floor for marsupials is the lack of any contribution by bones surrounding the auditory region. This contrasts with the consensus opinion (e.g., Marshall, 1979; Clemens, 1979; Reig et al., 1987; Marshall et al., 1990) that the presence of an alisphenoid tympanic process is diagnostic for Marsupialia (this process is present in all living marsupials except vombatids [Springer and Woodburne, 1989] and is absent in Cretaceous eutherians and the prototribosphenidan *Vincelestes* [Kielan-Jaworowska, 1981 and Rougier et al., 1992, respectively]).

Based on the cladogram included in Muizon (1994), derived borhyaenoid marsupials acquired tympanic processes from adjacent bones, but not the same as those in didelphids; thus, tympanic floor contributions arise at least twice in marsupials from completely different precursor bones. Muizon's (1994) interpretation is based on a second-order inference concerning the putative relationship between borhyaenids and deltatheroidans suggested by Marshall and Kielan-Jaworowska (1992). In the latter paper, deltatheroidans were determined to be the sister taxa to the borhyaenoids + didelphoids

based on the presence of an alisphenoid tympanic process (Kielan-Jaworowska and Nessov, 1990) and other dental and skeletal characters (some of which are of uncertain polarity, e.g., jugal participation in the glenoid fossa), making the alisphenoid complement of the bulla a primitive trait given the Cretaceous age of deltatheriodans. Muizon (1994), however, argued, on the basis of a cladogram that included only borhyaenids and *Pucadelphys*, that the alisphenoid tympanic process is not primitive for marsupials. More recently, Muizon et al. (1997) have furthered this hypothesis, arguing that their interpretation is supported by the condition in the stagodontids *Eodelphis* and *Didelphodon* (Matthew, 1916; Clemens, 1966, respectively). Neither of these taxa are represented by material from the pertinent region of the alisphenoid. There is a very slim fragment of the alisphenoid preserved at its sutural boundary with the squamosal in *Didelphodon*, and Clemens (1966: 80) remarked that it was possible that the alisphenoid contributed a bullar process.

Trofimov and Szalay (1994) and Szalay and Trofimov (1996) described and named *Asiatherium*, from the Late Cretaceous of Mongolia and placed it in a new order, the Asiadelphia, which they speculated was a lineage of marsupials distinct from deltatheroidans and North American marsupials. They reported that *Asiatherium* possesses an alisphenoid tympanic process, in addition to contributions by the rostral and caudal tympanic processes of the petrosal. This would ostensibly support the idea that an alisphenoid tympanic process is primitive for Marsupialia, given the purported basal position of asiadelphians and deltatheroidans. With this in mind, it would be more parsimonious to assume the loss of the alisphenoid tympanic process in *Pucadelphys* and basal borhyaenids, than it would be to infer that it was independently acquired in asiadelphians, deltatheroidans, and living marsupials. Moreover, the condition of the alisphenoid is not known in certain relevant extinct taxa, such as stagodontids (the putative sister group to didelphids according to Marshall and Kielan-Jaworowska [1992]) and the Late Cretaceous/Early Paleocene didelphids *Peradectes* and *Albertotherium*. Finally, it is conceivable

that *Pucadelphys* might be a very primitive borhyaenoid based on the secondary loss of the alisphenoid contribution to the bulla. Until a phylogenetic analysis of all relevant taxa is conducted, this issue will remain unresolved.

The relationship between the piriform fenestra and the foramen ovale is variable across Mammalia and particularly complex within Marsupialia (Gaudin et al., 1996). Nevertheless, Gaudin et al. (1996) were able to partition the observable variation of the true foramen ovale among extinct and extant marsupials into three character states: (1) wholly within the alisphenoid, (2) between the alisphenoid and petrosal, and (3) between the alisphenoid and the squamosal. The third condition is the least common taxonomically. Gaudin et al. (1996) were unable to determine the primitive state for the foramen ovale with their data set and accordingly scored Marsupialia as a polymorphic taxon.

The morphology of the piriform fenestra/foramen ovale obtained for *Herpetotherium*, and also observed for *Marmosa*, *Monodelphis*, and *Caluromys*, is described by character state 2 above. The condition of the foramen ovale in the early Paleocene didelphoid *Pucadelphys* was reported by Muizon (1991) to be between the alisphenoid and squamosal, but this interpretation was changed in Marshall and Muizon (1995) to be between the alisphenoid and petrosal. The condition in the early Paleocene borhyaenoid *Mayulestes* is the same as that of *Herpetotherium*. This would imply that the primitive condition for marsupials is between the alisphenoid and petrosal, making the condition in *Herpetotherium* a retention. Wroe (1997) arrived at a similar conclusion for the primitive condition of the foramen ovale in marsupials in an analysis of dasyurid marsupial synapomorphies.

Finally, the morphological variations observed in the rostral process of the jugular process, as well as those of the tympanohyal and caudal tympanic process of the petrosal, suggest that there may be some systematic significance to be gleaned with respect to stylomastoid foramen morphology and closure of the posterior bullar floor. For example, the outline of a morphocline for the rostral process of the jugular process can be seen, rang-

ing from *Herpetotherium*, where there is no jugular process, to *Philander*, where there is a jugular process but no rostral process, to *Caluromys*, where the rostral process of the jugular process contributes to the closure of the posterior tympanic cavity. The stylomastoid notch/foramen presents similar transformations related to the variable development and relationship of the tympanohyal and the caudal tympanic process of the petrosal. The egress for the facial nerve varies in morphology from a simple, relatively shallow notch, as observed in *Didelphis*, to a circumscribed foramen in caluromyines.

It is obvious that the recovery of anatomical information about *Herpetotherium* and the subsequent comparative survey has engendered the need for a reevaluation of basicranial characters among didelphids. The documented variation in many important anatomical traits makes simple evolutionary transformation assessments impossible. The reassessment of basicranial anatomy would contribute to a more robust hypothesis of marsupial evolution across several taxonom-

ic boundaries. This would be pertinent to work being done by many researchers (e.g., Marshall et al., 1990; Muizon, 1991, 1994; Szalay, 1994; Trofimov and Szalay, 1994; Luckett, 1994; Gaudin et al., 1996; Wroe, 1997; Kirsch et al., 1997, Springer et al., 1997) that has been directed toward better understanding of the higher-level relationships among the Marsupialia.

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