

New Basicrania of Paleocene-Eocene *Ignacius*: Re-Evaluation of the Plesiadapiform-Dermopteran Link

Jonathan I. Bloch^{1*} and Mary T. Silcox²

¹Department of Geological Sciences and Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109-1079

²Department of Anthropology, Pennsylvania State University, University Park, Pennsylvania 16802-3404

KEY WORDS basicranium; Dermoptera; Paromomyidae; Plesiadapiformes; primate origins; Wyoming

ABSTRACT Plesiadapiformes has long been considered to be an archaic group of Primates. Discovery of a paromomyid plesiadapiform skull and independent analysis of referred postcrania have led investigators to conclude that Plesiadapiformes shares a closer relationship to extant flying lemurs (Dermoptera) than to Primates (= Euprimates of Hoffstetter [1977] Bull Mem Soc Anthropol Paris Ser 13 4:327–346). Despite challenges to this interpretation, the plesiadapiform-dermopteran relationship has gained currency in recent years. Here we show that newly discovered crania of *Ignacius graybullianus*, preserving previously undocumented portions of the ear, are more similar to primates than to dermopterans. New specimens confirm that paromomyids lacked the petrosal bulla of primates. However, these new specimens also demonstrate that paromomyids likely

had: 1) a small promontorial branch of the internal carotid artery; 2) a lateral route for the internal carotid nerves crossing the promontorium; and 3) a ring-like ectotympanic with an annular bridge. This pattern is similar to primitive primates and fundamentally different from dermopterans, which have: 1) no internal carotid artery; 2) internal carotid nerves that take a more medial route; and 3) no annular bridge. Recognition of some primate-like traits, documented here by new evidence, indicates that Paromomyidae is likely to be more closely related to other Paleogene Plesiadapiformes and Eocene Primates than to extant Dermoptera. In view of these findings, a link between paromomyids and extant dermopterans (“Eudermoptera”) is not convincingly supported by a single characteristic of the basicranium. Am J Phys Anthropol 116:184–198, 2001. © 2001 Wiley-Liss, Inc.

Plesiadapiformes is a group of Paleocene and Eocene mammals known from North America, Europe, and Asia that includes 11 families (Hooker et al., 1999; Silcox, 2001; Silcox and Gunnell, in press). The bulk of the fossil record for plesiadapiforms consists of teeth and jaws, although well-preserved cranial material is known for four families (Plesiadapidae, Microsyopidae, Paromomyidae, and Carpolestidae; Russell, 1959, 1964; McKenna, 1966; Szalay, 1969, 1972; Szalay et al., 1987; Kay et al., 1990, 1992; Gingerich, 1987; Bloch and Gingerich, 1994; Bloch and Boyer, 2001). Plesiadapiforms have long been considered an archaic radiation of Primates. Evidence cited in favor of a primate-plesiadapiform link has been mostly dental, with particular emphasis on the relatively bunodont, low-crowned, broadly basined molars shared by the two groups (Gingerich, 1975; Rose, 1995). The first discovery of a well-preserved plesiadapiform cranium (MNHN CR-125, *Plesiadapis tricuspidens*; Russell, 1959, 1964) demonstrated that certain features of the ear region might also be shared with primates, including having a petrosal bulla (Russell, 1959; Szalay, 1972; Szalay et al., 1987; but see Russell, 1964; Hershkovitz, 1977). Narrow grooves observed on the promontorium of the petrosal were interpreted as marking the course of promontorial and

stapedial branches of the internal carotid artery (ICA; Russell, 1959, 1964; see Appendix), a condition fundamentally similar in arrangement to primitive primates (Archibald, 1977; MacPhee and Cartmill, 1986). No bony tubes were found surrounding these arterial branches (unlike primates, for which the stapedial and promontorial branches of the ICA are at least partially enclosed in bony arterial tubes). The ectotympanic element was found to be ring-like, and suspended inside the bulla by a series of bony struts, a condition also found in omomyid primates (Gingerich, 1975, 1976; MacPhee and Cartmill, 1986; Beard and MacPhee, 1994). The first paromomyid skull to be described (*Phenacolemur jepseni*; AMNH 48005) was also interpreted to have a petrosal bulla, as well as an ossified tube for a promon-

Grant sponsor: Wenner-Gren Foundation for Anthropological Research; Grant sponsor: Paleobiological Fund; Grant sponsor: Sigma Xi; Grant sponsor: National Science Foundation; Grant numbers: 9815884, EAR-8918023; Grant sponsor: Scott Turner Fund, Department of Geological Sciences, University of Michigan.

*Correspondence to: Jonathan I. Bloch, Museum of Paleontology, University of Michigan, 1109 Geddes Road, Ann Arbor, MI 48109-1079. E-mail: carpo@umich.edu

Received 25 August 2000; accepted 25 June 2001.

torial artery crossing the promontorium of the petrosal (Szalay, 1972).

Observation that the grooves on the promontorium of *Plesiadapis* are very small and irregularly oriented led some investigators (Saban, 1963; Gingerich, 1976; MacPhee et al., 1983) to suggest that they might relate to nerves rather than arterial branches. The small diameter of the posterior carotid foramen (PCF) indicated that this vessel did not provide a significant supply of blood to the brain in *Plesiadapis* (Gingerich, 1975, 1976). MacPhee et al. (1983; see also MacPhee and Cartmill, 1986) showed that some modern rodents have a non-petrosal bulla that can become continuous with the petrosal over the course of ontogeny, leading to an adult morphology that is highly comparable to *Plesiadapis* (see MacPhee and Cartmill, 1986: their Fig. 18). This implies that the true composition of the plesiadapid auditory bulla will remain in question until more adequate developmental evidence becomes available (contra Szalay et al., 1987). Furthermore, the tube thought to have contained the promontorial branch of the ICA in *Phenacolemur* has since been reinterpreted as an imperforate septum (MacPhee et al., 1983; MacPhee and Cartmill, 1986; but see Szalay et al., 1987). MacPhee et al. (1983) suggested that the arterial supply to the brain in paromomyids may have been through an ascending pharyngeal artery (similar to lorises and cheirogaleid lemurs; MacPhee, 1981), based on an apparent middle lacerate foramen in a very damaged specimen of *Ignacius graybullianus* (UM 68006).

In a much better preserved specimen of *Ignacius graybullianus*, USNM 421608, Kay et al. (1990, 1992) noted that the middle lacerate foramen was not present, and argued that its supposed presence in UM 68006 was due to damage. This implied that the supply of blood to the brain was not from an ascending pharyngeal artery. Kay et al. (1990, 1992) did not document any grooves on the promontorium for branches of a patent internal carotid artery, and noted that the PCF was very small. They concluded that *Ignacius* was more similar to dermopterans (a group of extant gliding mammals from Southeast Asia, also known as flying lemurs or colugos) than to primates, in carrying blood to its brain via the vertebral artery.

Kay et al. (1990, 1992) noted the presence of a suture between the auditory bulla and the promontorium, implying that this taxon did not have a petrosal bulla. Based on sutures between the bulla and all the other elements making up the basicranium, they argued that the bulla must have formed from an independently-derived entotympanic bone, an element unknown in Primates but common in other mammalian orders (MacPhee, 1979; see Appendix) and present in all other archontan orders (Chiroptera, Dermoptera, and Scandentia; Wible and Martin, 1993). In addition, they argued that the presence of an entotympanic bone that contacts the basioccipital medially is another derived trait

shared with dermopterans. In all, these authors concluded that at least some plesiadapiforms (plesiadapids and paromomyids) share more derived cranial similarities with dermopterans than with primates, and that the group as a whole should be removed from the order Primates. Evidence from the postcranial skeleton published in the same issue of *Nature* (Beard, 1990; see also Beard, 1993a) reached a similar conclusion.

Although Kay et al. (1990, 1992) considered the ectotympanic in *Ignacius graybullianus* and *Plesiadapis tricuspidens* to be similar in incorporating an elongate, tubular external auditory meatus, they noted a fundamental difference in the absence of a distinct ring-like element separated from the bullar floor by struts in *Ignacius*. Instead, they considered the ectotympanic to incorporate only a crest to support the tympanic membrane, with no subtympenic recess distinguishing the tympanic ring from the bulla, and thus no annular bridge (a sheet of bone between the tympanic ring and the bullar floor, crossing the subtympenic recess; MacPhee and Cartmill, 1986; see also Appendix). Beard and MacPhee (1994) suggested that this ectotympanic morphology could be considered another paromomyid-dermopteran synapomorphy.

Elements of the interpretation by Kay et al. (1990, 1992) have been highly controversial. Considerable informal debate has surrounded the issue of whether the supposed suture separating the auditory bulla from the petrosal may actually be a crack (see also Szalay and Lucas, 1993, 1996). The degree of similarity between paromomyids and dermopterans in features of the bullar floor and in the position of nerves passing through the ear has also been questioned (e.g., Fox, 1993; Wible, 1993; Wible and Martin, 1993). The postcranial evidence has likewise been a source of debate in terms of the identification and association of skeletal elements, and the interpretation of their phylogenetic and functional significance (Krause, 1991; Szalay and Lucas, 1993; Runestad and Ruff, 1995; Stafford and Thorington, 1998; Hamrick et al., 1999). It is beyond the scope of this study to assess the postcranial evidence for a plesiadapiform-dermopteran link (but see Silcox, 2001), although it is worth noting that this source of evidence has come under as least as much attack in the literature as the cranial data. In spite of these controversies, a relationship between dermopterans and paromomyids has gained popular currency and is reflected in the most recent comprehensive classification of mammals (McKenna and Bell, 1997).

Two new specimens of *Ignacius graybullianus* from the latest Paleocene and earliest Eocene of the Clarks Fork Basin, Wyoming, confirm many elements of the description by Kay et al. (1990, 1992) of the cranial morphology of that taxon, including the non-petrosal make-up of the auditory bulla. These new specimens additionally document elements of the ear region less well preserved or obscured in USNM 421608. These features call into question a

TABLE 1. Institutional abbreviations used in the text

Abbreviation	Institution
AMNH	American Museum of Natural History, New York
CM	Carnegie Museum of Natural History, Pittsburgh
CR	Cernay les Reims (for MNHN specimens from that locality)
MNHN	Muséum National d'Historie Naturelle, Paris
MPM	Milwaukee Public Museum, Milwaukee
UM	University of Michigan Museum of Paleontology, Ann Arbor
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM(MA)	Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, DC
USNM	Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC

few of the interpretations by Kay et al. (1990, 1992), and make a tie to Dermoptera much less plausible. Restudy of the *Phenacolemur jepseni* skull (AMNH 48005) shows it to be comparable to *I. graybullianus* in most preserved details of the ear region, suggesting this was the characteristic paromomyid auditory morphology.

The institutions in which the specimens discussed in this paper are stored are listed in Table 1.

MATERIAL AND METHODS

Two new specimens of *Ignacius graybullianus* are described here for the first time. UM 108210 (Fig. 1A) was prepared from a freshwater limestone (University of Michigan locality SC-62, Cf-2, 1380m) by J.I.B. The limestone was dissolved by submersion in dilute buffered formic acid for 2–3 hr at a time. To protect fossils from acid-etching, a thin coating of polyvinyl acetate (PVA) was applied to the surface of all exposed bones. USNM 482353 (Fig. 1B) was similarly prepared from a freshwater limestone (8abc nodule; Beard and Houde, 1989; Beard 1989, 1990, 1993a,b) by P. Houde, using dilute buffered acetic acid for 2 days at a time.

Comparisons were made to previously described fossil specimens of *Ignacius graybullianus* (USNM 421608; UM 65569, 68006), *Phenacolemur jepseni* (AMNH 48005), *Plesiadapis tricuspis* (MNHN CR-125), *Microsyops knightensis* (AMNH 55286), *Cantius abditus* (USNM 494881), *Smilodectes gracilis* (UM 32773 [= MPM 2612]), and *Shoshonius cooperi* (CM 31366, 31367, and 60494). Comparison of AMNH 48005 to better-preserved material of *I. graybullianus* necessitated a reinterpretation of the auditory anatomy of *P. jepseni*, given below. Unpublished specimens of *Plesiadapis cookei* (UM 87990) and *Microsyops* sp. were also examined, thanks to the generosity of P.D. Gingerich and G.F. Gunnell. Modern taxa examined include *Tupaia glis* (USNM[MA] 114553, 154599, 242241), *Ptilocercus lowii* (USNM[MA] 291272, 488061), *Pteropus poliocephalus*

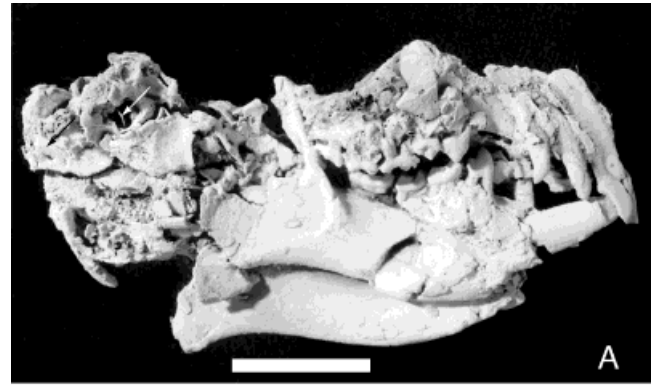


Fig. 1. *Ignacius graybullianus* skulls. **A:** UM 108210, from University of Michigan locality SC-62, in right lateral view. White arrow indicates the cochlea of the right ear, visible through a break in the promontorium; black arrow indicates the inner (dorsal) surface of the left petrosal. **B:** USNM 482353, from locality SC-4, in ventral view. White arrow indicates the right petrosal, which is rotated more than 90°, and is therefore visible in oblique dorsal view. Scale bar, 1 cm.

(USNM[MA] 395262), and *Galeopterus variegatus* and *Cynocephalus volans* (USNM[MA] 83276, 84421, and 307553; UMMZ 117122).

DESCRIPTION OF NEW SPECIMENS AND COMPARISON WITH USNM 421608

A new specimen of late Paleocene *Ignacius graybullianus* (UM 108210), illustrated in Figure 1A, includes upper and lower dentitions, with RI_1-M_3 , I^1-C^1 , P^3-M^3 , and LP_4-M_3 , C^1-M^3 . The specimen includes the maxillae and most of the basicranium including elements of both ears. Mediolateral crushing has brought the two sides of the skull very close together, and displaced some structures, but the roofs of the right and left middle ears are well-preserved and are nearly complete.

A new specimen of early Eocene *Ignacius graybullianus* (USNM 482353), illustrated in Figure 1B, includes right and left upper dentitions (RP^4-M^3 , LM^{1-2}). The specimen is lacking the portion of the

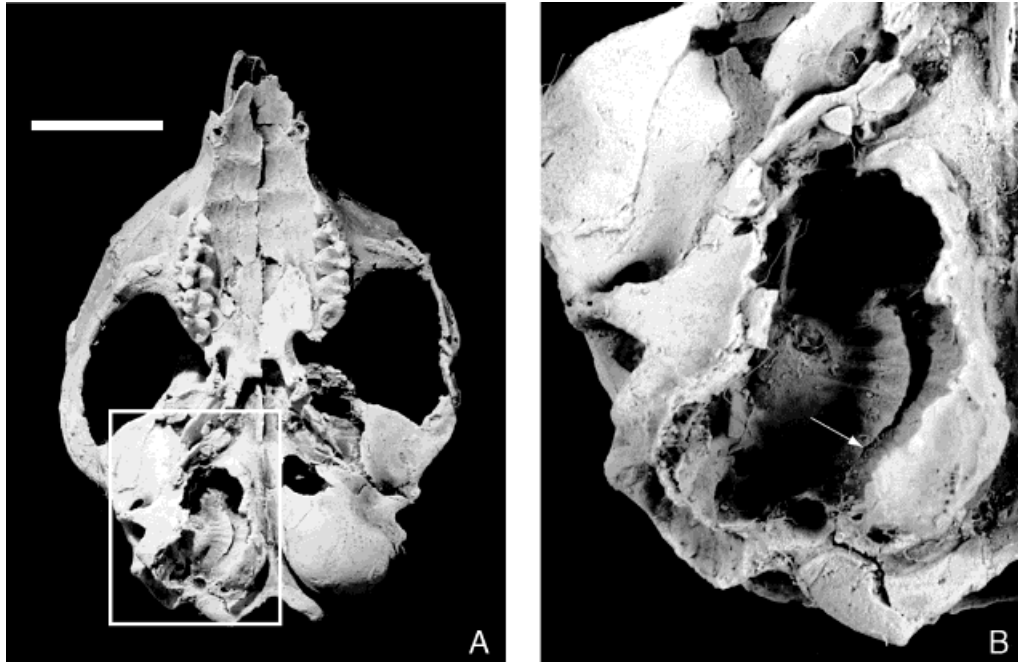


Fig. 2. Previously published (Kay et al., 1990, 1992) specimen of *Ignacius graybullianus* (USNM 421608) that was removed from a freshwater limestone from the early Eocene (Wa-1) of the Clarks Fork Basin, Wyoming. **A:** Whole specimen. **B:** Close-up of detail of right ear region, in ventral view. Note that the edge of the petrosal overlaps the entotympanic at their point of contact (see white arrow). Scale bar in A, 1 cm.

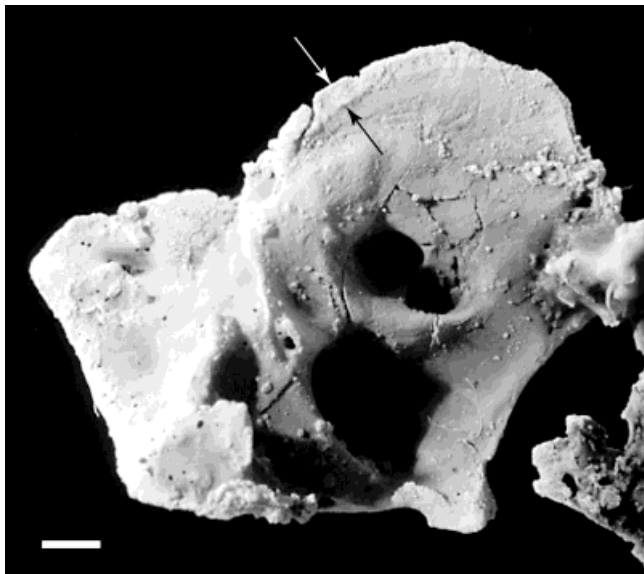


Fig. 3. A petrosal of *Ignacius graybullianus* in dorsal view (USNM 482353). Note the detail of the dorsal surface of the petrosal part of the entotympanic-petrosal suture (between two arrows). As would be expected in an overlapping suture, the dorsal surface thins to a distinctive, continuous border (black arrow), and is faintly grooved. Unlike what would be expected for a break, the outer edge of the bone is smooth where undamaged (white arrow). Scale bar, 1 mm.

snout rostral to P⁴, and the neurocranium was crushed dorsoventrally. On the right-hand side, the roof of the middle ear, including the promontorium, has become largely separated from the rest of the

skull, displaced slightly posteriorly, and rotated 90° in the buccolingual plane (see arrow in Fig. 1B). This petrosal is intact and uncrushed, however, and is still preserved in direct association with the rest of the skull.

In most preserved features, these specimens are similar to the specimen of *Ignacius graybullianus* (USNM 421608) described by Kay et al. (1992). This includes the presence of a distinct, low sagittal crest, a strong postpalatine torus located caudal to M³, broadly splayed zygomatic arches to accommodate enlarged chewing muscles, a pronounced postorbital constriction, and no postorbital bar.

In USNM 421608, a suture is present between the promontorium and auditory bulla, and the petrosal side of this suture forms a fairly sharp, ventrally downturned edge (see Fig. 2B). In this specimen, because the elements of the roof of the middle ear are still essentially intact, it is not possible to see the dorsal surface of this sutural edge. In USNM 482353, the promontorial section of the middle ear has lifted away from the rest of the skull along this border, and so the petrosal portion of the petrosal-entotympanic suture is preserved intact. In UM 108210, both the right and left promontoria have also become separated from the other ear components at this suture. The separation of the roof of the middle ear from the rest of the skull in both specimens makes this surface visible from a dorsal perspective (relative to its original orientation in the skull). In both UM 108210 and USNM 482353, the

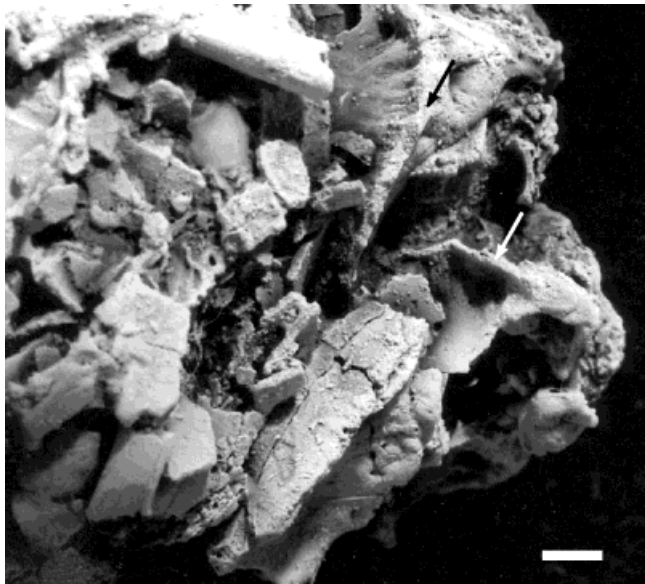


Fig. 4. Caudal portion of the skull of *Ignacius graybullianus* (UM 108210), from left side. Left and right promontoria are preserved (see black and white arrows, respectively), each of which has become separated along the sutural edge from the entotympanic. Note that the shape and general sutural morphology are similar to those preserved in USNM 421608 and 482353. Scale bar, 1 mm.

edge of the petrosal thins medially, forming a discrete change in slope on the dorsal surface, distinguishing the main portion of the bone from the tapering edge that would have overlapped the entotympanic (see Figs. 3, 4). In addition, the dorsal surface is pitted near the sutural edge, for small sutural vessels. Cranial sutures of this type (i.e., overlapping or squamous, such as the squamosal suture in humans) do not necessarily interdigitate, but are characteristically beveled in this manner.

The roof of the middle ear in USNM 421608 is missing rostrally, including the portion lateral to the longitudinal septum (see Figs. 2B, 8). This region is preserved in both the right ear of USNM 482353 and the left ear of UM 108210, and demonstrates a narrow (0.167 mm in diameter) groove just lateral to the longitudinal septum (see Fig. 5). The medial aspects of the promontoria in both USNM 482353 and UM 108210 are marked by fine indentations of the type seen on the promontorium of *Plesiadapis* (see discussion above, and Figs. 6, 7). This groove differs from these less well-defined “creases” in being straighter, more sharply demarcated, and consistently positioned between the two specimens. Comparison to the arterial channels running across the promontorium of several undescribed petrosals belonging to *Microsyops* revealed this groove to be very comparable, although the channel for the promontorial artery is more medially placed in *Microsyops* than was observed in *Ignacius* (see below).

In USNM 421608, the ectotympanic is still articulated with the floor of the auditory bulla on both sides of the skull. This means that the only way to

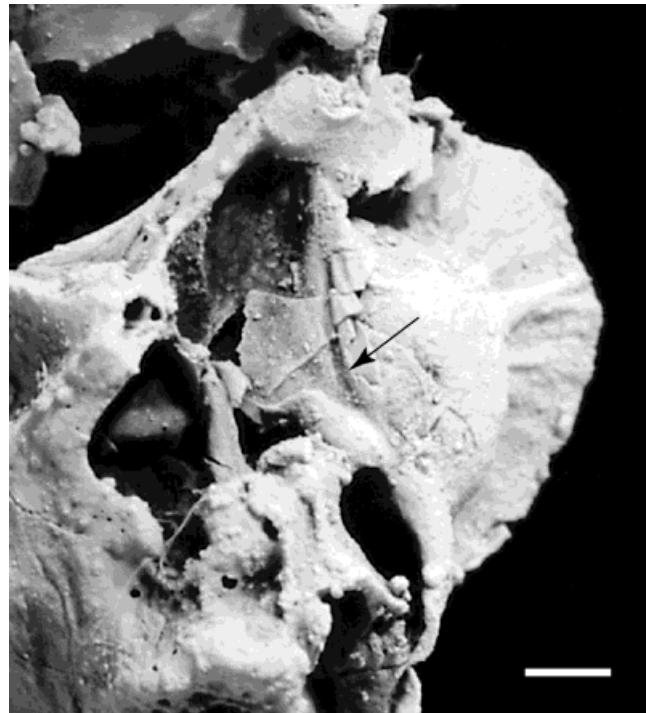


Fig. 5. Ventral view of promontorium of *Ignacius graybullianus* (USNM 482353). Note the distinct groove (arrow) for the promontorial artery and internal carotid nerves present lateral to the longitudinal septum on the promontorium (diameter = 1.67 mm). Scale bar, 1 mm.

observe the inner, dorsal surface of the ectotympanic is through the external auditory meatus, or the opening in the bulla floor that was made to reveal its internal morphology (see Kay et al., 1990, 1992). Viewed from these perspectives, the ectotympanic element seems to support a sharp crest, projecting ventrally into the middle ear. Kay et al. (1992) identified this structure as the crista tympanica (= crest for the tympanic membrane; see Appendix). There is no evidence in USNM 421608 of a distinct ring associated with this crest, which led Kay et al. (1992) to postulate the absence of a subtympanic recess (see Appendix). USNM 482353 preserves a fragment of bone in the epitympanic recess (e.g., the region just above the tympanic membrane that would have contained the articulation between the incus and malleus; MacPhee, 1981; see Appendix) that looks like a remnant of a narrow tympanic ring (Fig. 9). If the morphology of the ectotympanic was originally as Kay et al. (1992) suggested, it would be impossible that a ring-like structure such as that present in USNM 482353 could become separated from the main body of the ectotympanic. The only way to reconcile these apparently conflicting pieces of evidence is to consider the ectotympanic in USNM 421608 to be damaged. The separation of a ring-like element could easily produce the morphology observed in this specimen. The implication is that the supposed crista tympanica in USNM 421608 is actually the remnant of an annular bridge, and that

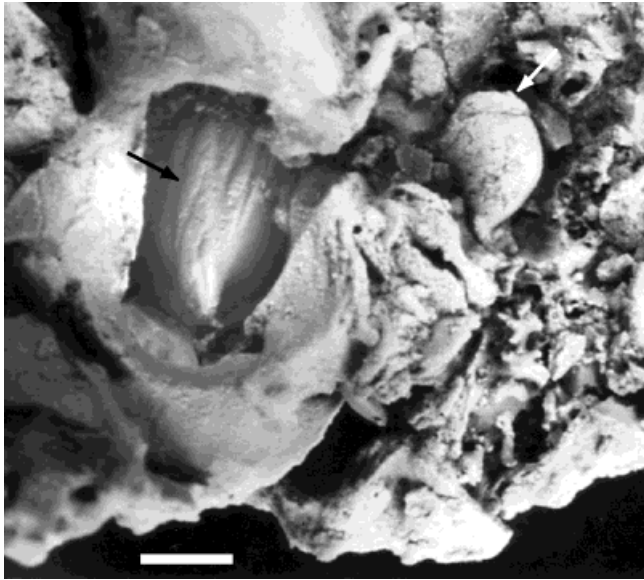


Fig. 6. Photograph of ventral view of promontorium of *Ignacius graybullianus* (UM 108210). Note the distinct groove for the ?promontorial artery and internal carotid nerves present lateral to the longitudinal septum on the promontorium (black arrow). The fainter grooves are less defined, and not consistent between specimens. Similar “creases” are seen in *Plesiadapis* (see Fig. 7), and are considered to be unrelated to the carotid circulation (Gingerich, 1976). White arrow indicates an out-of-place ear ossicle. Scale bar, 1 mm.

the undamaged morphology of the ectotympanic would include a ring-like element supported by a more or less continuous annular bridge.

REINTERPRETATION OF THE EAR REGION OF *PHENACOLEMUR JEPSANI* (AMNH 48005)

When the only known ear region for *Phenacolemur* was initially described in detail (Szalay, 1972), the most relevant material for comparison was the very well-preserved and well-studied cranial material of *Plesiadapis tricuspidens* (Russell, 1959, 1964). In the context of the paromomyid specimens that have become available since 1972, it seems advisable to reconsider the interpretation of the structures preserved in AMNH 48005.

Szalay (1972) argued that the presence of a thin, medial sheet of upturned bone represents the broken edge of a petrosal bulla (Fig. 10). The basis for this is the somewhat similar broken edge of the bulla on the best-known *Plesiadapis tricuspidens* specimen (MNHN CR-125), and his belief that this crest was continuous with a rostral structure that is clearly the broken front edge of the bulla. If this medial crest did, in fact, represent the border of the bulla on AMNH 48005, the tympanic cavity would be very constrained medially compared to either *Ignacius* or *Plesiadapis*. Consideration of the pattern of distortion and breakage that contributed to the current state of AMNH 48005, and comparison with USNM 421608, USNM 482353, and UM 108210, indicates another interpretation. The whole section of the bulla that includes the promontorium



Fig. 7. Right promontorium and ectotympanic of *Plesiadapis cookei* (UM 87990) in ventral view. Note that the ring-like ectotympanic (white arrow) is attached to the floor of the bulla by struts (black arrow). Note fine creases on the promontorium, probably for the tympanic nervous plexus (Gingerich, 1976; MacPhee et al., 1983). Scale bar, 2 mm.

and the crest in question, on the left side of AMNH 48005, was displaced ventrally relative to the rest of the basicranium. The relevant crest is in the same position as the suture between the petrosal and ectotympanic in the *Ignacius* specimens. If the promontorium separated at that suture in the process of being displaced ventrally, then the crest would be the petrosal edge of that sutural contact.

One possible argument against this interpretation is that the edge or crest curves ventrally, as would be expected for an edge of the bulla, but not for a flat portion of the medial tympanic roof. Close inspection of USNM 421608 reveals, however, that the sutural edge on the petrosal is actually upturned in a very similar manner to the supposed bullar edge on AMNH 48005 (see Fig. 2B). The very smooth extremity of this crest in AMNH 48005 also provides support that it represents a separated suture rather than a crack. Close examination indicates that there is a disjunction between this element and the rostral remnant of the auditory bulla that is still in place, implying that the two are not as continuous as Szalay (1972) claimed (Fig. 10B).

There is no groove to the lateral side of the longitudinal septum in AMNH 48005, although this is likely a product of the preparation technique (air abrasion) used in clearing the ear region of matrix. Also, the lateral tympanic roof is clearly damaged, as evidenced by the fact that distorted elements of the facial canal are visible.

Szalay (1972) (see Fig. 10) labeled a canal-like structure at the posterolateral edge of the bulla as a “?cc: ?canal for internal carotid entering the bulla.” This canal is similarly placed to the posterolaterally positioned posterior carotid foramen (PCF) in *Ignacius* (USNM 421608), including being adjacent to a doubled styломastoid foramen in both taxa. The

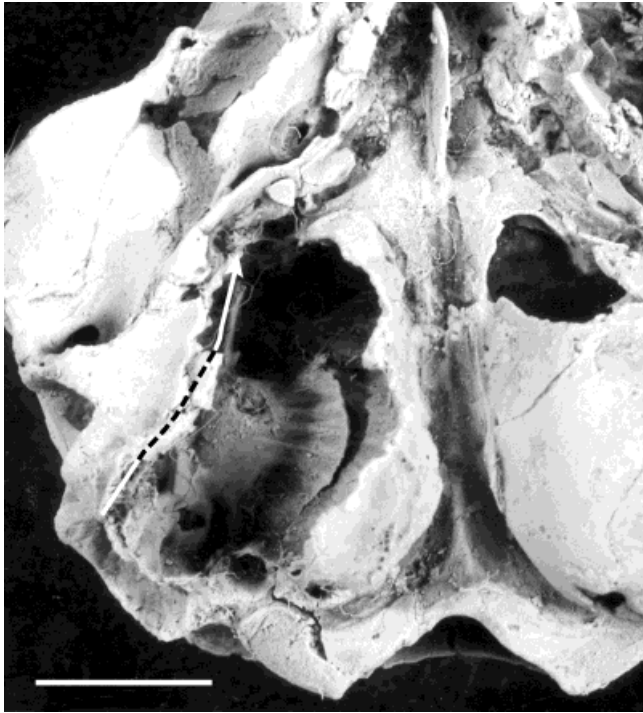


Fig. 8. Basicranium of *Ignacius graybullianus* (USNM 421608) in ventral view. The line (white for unobstructed view, and dashed black for areas covered by bone) indicates the pathway of the internal carotid artery, reconstructed from the position of the posterior carotid foramen in this specimen and the groove lateral to the longitudinal septum in UM 108210 and USNM 482353. This artery passed along the lateral extreme of the promontorium in this taxon. Scale bar, 5 mm.

width of this canal (0.2 mm) is quite similar to that of the PCF in USNM 421608 (~0.17 mm; Kay et al., 1992). The presence of the strong longitudinal septum, just medial to the level of this canal, would constrain the pathway of structures entering via the “?cc” to a course along the lateral extent of the promontorium (i.e., where the groove is located lateral to the longitudinal septum in *Ignacius*).

The ectotympanic element is essentially similar to the description provided by Kay et al. (1992) for *Ignacius*, including a short tubular external auditory meatus and no evidence of a well-demarcated ring. In terms of the latter observation, the very damaged state of this specimen could be influencing this observation (as discussed above for USNM 421608). The other distinctive features of the *Phenacolemur jepseni* ear region are not amenable to reinterpretation by comparison with *Ignacius*. The supposed “hiatus canalis facialis” and “stylo-mastoid foramen definitivum” (see Fig. 10) identified by Szalay (1972: his Fig. 3), for example, are not seen in USNM 482353, USNM 421608, or UM 108210. The most plausible explanation for these structures is that they do represent elements of the facial canal that may have been partially revealed in places and/or distorted.

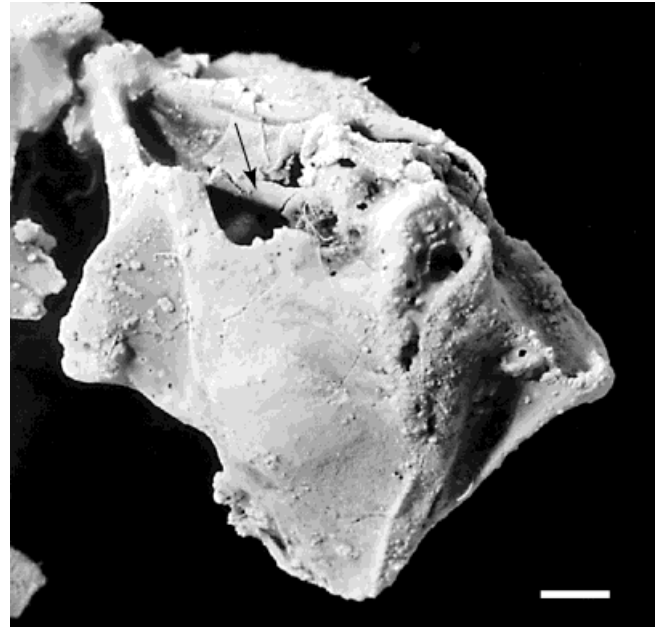


Fig. 9. Ear region of *Ignacius graybullianus* (USNM 482353) in oblique lateral view. Note the curved remnant of the ectotympanic ring (arrow) located in the epitympanic recess. Scale bar, 1 mm.

COMPARATIVE ANATOMY AND INTERPRETATION

Auditory bulla

Both of the new specimens of *Ignacius graybullianus* provide evidence that supports the presence of a suture between the petrosal promontorium and the auditory bulla, indicating that the interpretation by Kay et al. (1990, 1992) of the situation in USNM 421608 was correct. The reinterpretation of the *Phenacolemur jepseni* specimen AMNH 48005 is comparable, implying that this was the characteristic anatomy of the paromomyid tympanic roof. None of these new (or newly interpreted) specimens is informative about which bone actually forms the auditory bulla. Particularly, they are not well enough preserved to indicate whether it was largely formed by the ectotympanic, as in dermopterans (Hunt and Korth, 1980; Wible and Martin, 1993), or composed of some other element such as a large entotympanic, as in scandentians (MacPhee, 1981; Zeller, 1987; Wible and Martin, 1993). Our examination of USNM 421608 indicates that Kay et al. (1990, 1992) were correct in inferring that the bone forming the majority of the bulla is separated by sutures from all the other bones of the basicranium, including the ectotympanic, and therefore must be an entotympanic (see Appendix).

Kay et al. (1990, 1992) claimed that a significant similarity between *Ignacius* and modern dermopterans exists in the contact between the entotympanic and the basioccipital medially. As Wible and Martin (1993) point out, the nature of this contact is very different in these two genera. In modern dermopter-

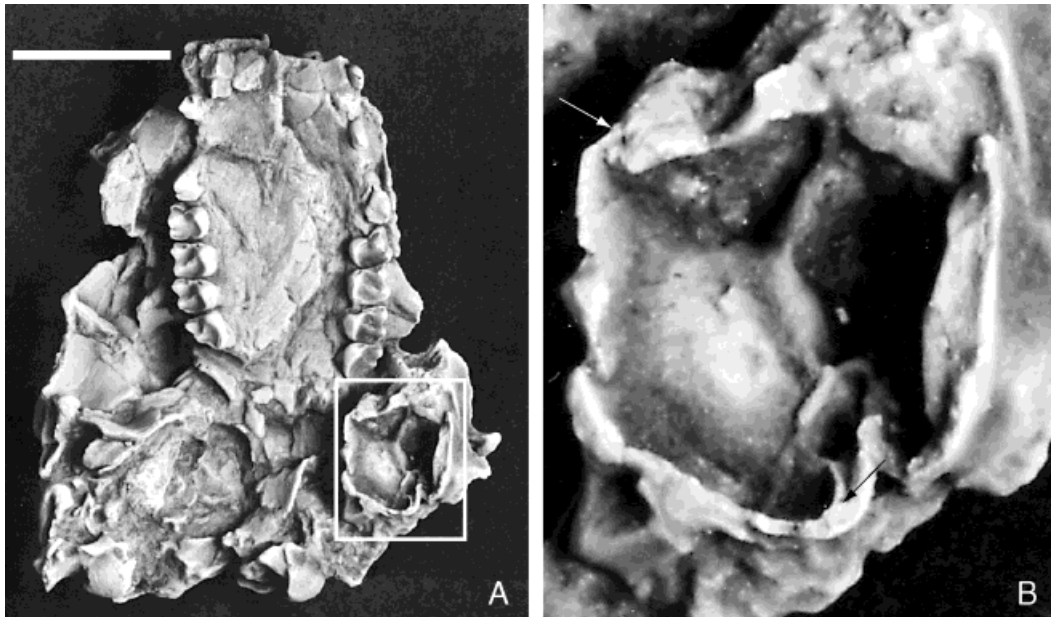


Fig. 10. Skull in ventral view (**A**), and close-up of left auditory region (**B**) of *Phenacolemur jepseni* (AMNH 48005). Black arrow in B indicates a canal-like structure at the posterolateral edge of the bulla (“?cc: ?canal for internal carotid entering the bulla” of Szalay, 1972). White arrow in B indicates separation between the medial crest (interpreted here as the edge of the petrosal part of the entotympanic-petrosal suture) and the rostral edge of the broken auditory bulla. This image contrasts with the representation in Szalay, 1972 (his Fig. 3), which shows these structures as continuous. Scale bar in A, 1 cm.

ans, one (Hunt and Korth, 1980; Wible and Martin, 1993) or two (van der Klaauw, 1922) very small entotympanic elements develop on the medial edge of the predominantly ectotympanic bulla, in close association with the cartilage of the auditory tube (see Appendix). On the other hand, in *Ignacius*, much of the very inflated bulla is entotympanic in origin (Kay et al., 1990, 1992), while the ectotympanic is isolated to the lateral edge and primarily forms the expanded external auditory meatus. A contact between an entotympanic element and the basioccipital is not that uncommon in mammals (Wible and Martin, 1993), occurring in tupaiines (MacPhee, 1981), palaeonodons, some xenarthrans (Patterson et al., 1992), and some carnivorans (Hunt, 1974). The entotympanic bulla of tupaiines is actually more similar to the condition in *Ignacius* than that observed in dermopterans. In *Tupaia*, the entotympanic forms an expanded, bulbous bulla over the middle ear contents. The relationship between the entotympanic and ectotympanic is very different than seen in *Ignacius*, since there is no tubular external auditory meatus in *Tupaia*, but the basic morphology of the entotympanic in these genera appears much more comparable than it is to dermopterans.

The simple presence of an entotympanic is also unlikely to be a synapomorphy linking dermopterans and paromomyids to the exclusion of other archontans. Entotympanics have arisen convergently many times in the course of mammalian evolution (MacPhee, 1979). All modern non-primate archontans include at least one entotympanic in their bullar make-up. This evidence strongly suggests

that having an entotympanic element in the bulla is a primitive archontan feature. In fact, Wible and Martin (1993) suggested that the presence of an entotympanic with a particular set of developmental relationships is a possible synapomorphy for Archonta, even though it is missing in Primates. The relevant ontogenetic information to assess paromomyids in this context will probably never be available. It is noteworthy, however, that this view suggests that the presence of an entotympanic element is a primitive archontan feature, so that its presence in both paromomyids and dermopterans could be interpreted as a symplesiomorphy rather than a synapomorphy. This would imply that its role in the make-up of the floor of the tympanic cavity in *Ignacius* would merely be a primitive retention not, in and of itself, ruling out a paromomyid-primate relationship. This argument is open to criticism on the grounds that it depends on the monophyly of Archonta, a view that various molecular studies have challenged (e.g., Springer et al., 1997; Pumo et al., 1998; Miyamoto et al., 2000; Madsen et al., 2001; Murphy et al., 2001). These studies do frequently provide some support for Euarchonta, a modified version of Archonta consisting of Primates, Scandentia, and Dermoptera (with Chiroptera being more distantly related; Springer et al., 1997; Madsen et al., 2001; Murphy et al., 2001). If Euarchonta is monophyletic, the same argument still stands with respect to the polarity of the entotympanic (i.e., it might be a feature of the euarchontan morphotype).

Other plesiadapiforms differ from paromomyids in the anatomy of the bulla. Neither *Plesiadapis* nor

Microsyops shows a suture in a position comparable to the petrosal-entotympanic suture in paromomyids. In the former case, this lack has been interpreted as indicating that *Plesiadapis* had a petrosal bulla (Russell, 1959; Szalay, 1972; Szalay et al., 1987), although some authors (MacPhee et al., 1983; MacPhee and Cartmill, 1986; Wible and Covert, 1987) have questioned this view. No microsyopoid is known with a bulla preserved intact, although the existing evidence indicates that if there was a bulla, it was not petrosal in origin (MacPhee et al., 1988). McKenna (1966) argued that the bulla of *Microsyops* (= *Cynodontomys*) was likely to be entotympanic in composition, based on the presence of a rugose surface for the articulation of the bulla on the petrosal in microsyopids. This line of reasoning was based on the presence of a similar roughened surface in lepidictids, which are known to have had an entotympanic bulla. Other authors have indicated that it is possible a bulla made of some other bone articulated with this surface (e.g., the ectotympanic; MacPhee et al., 1988), making the composition of the microsyopid auditory bulla uncertain pending new finds.

Internal carotid artery and nerves

Absence of clear grooves on the promontorium of *Plesiadapis tricuspidens* (see Introduction) and *Ignacius graybullianus* has been used as evidence that the internal carotid artery (ICA) was insignificant in these animals (MacPhee et al., 1983; Kay et al., 1990, 1992; Beard, 1993a). Additional evidence for this viewpoint is provided by the very small size of the posterior carotid foramen (PCF) in both *Plesiadapis tricuspidens* (0.3 mm; Gingerich, 1976) and *Ignacius graybullianus* (~0.17 mm; Kay et al., 1992).

As discussed above, in both USNM 482353 and UM 108210, a groove is clearly visible on the surface of the promontorium (Figs. 5, 6, 8), in an area missing from USNM 421608. There are two possible interpretations as to the contents of this groove. One possibility is that the groove contained only the internal carotid nerves, while the other possibility is that it also housed a small promontory artery.

Three pieces of evidence support the contention that this groove bore a vessel in addition to the internal carotid nerves. First, dermopterans lack any comparable grooves associated with the passage of the internal carotid nerves across the promontorium. Second, there is a marked contrast between this channel and the fine creases marking the more medial aspect of the promontorium in *Ignacius* and *Plesiadapis* (which likely carried elements of the nervous tympanic plexus; see Appendix and above), suggesting that there is a contrast in how heavily nervous structures groove the promontorium relative to vessels. Third, this view is supported by the comparison to *Microsyops* discussed above. Although it is impossible to ever be completely certain what a channel contained in an extinct mammal (e.g., see Conroy and Wible, 1978), these various

lines of evidence are more consistent with this groove carrying a small promontorial artery, rather than simply bearing the internal carotid nerves.

The small caliber of this groove (0.167 mm), almost precisely matching the size of the posterior carotid foramen measured by Kay et al. (1992) in USNM 421608 (~0.17 mm), would imply that the promontorial artery was fairly small. In light of the absence of other foramina in the skull that could provide access for blood to the brain, a substantial contribution from the vertebral arteries is likely. In this way, *Ignacius* is similar to modern dermopterans and unlike primates. On the other hand, the remnant of any branch of the ICA is a contrast to the situation in dermopterans. Coupled with the contrasts in the route taken by the internal carotid nerves detailed below, these data suggest that the reduction of this vessel is not a homologous developmental event in paromomyids and dermopterans.

In both USNM 482353 and UM 108210, the groove that carried the promontorial artery sits just to the lateral side of the longitudinal septum. With the position of the PCF provided by USNM 421608 being at the posterolateral side of the bulla, it is possible to reconstruct the pathway of the promontorial artery as running along the lateral extreme of the promontorium (see Fig. 8), comparable to the pathway seen in some primates (adapids, lemuriforms, and the omomyid *Shoshonius cooperi*; MacPhee and Cartmill, 1986; Beard and MacPhee, 1994; see below). As noted above, a similar lateral entrance and pathway across the promontorium can also be reconstructed for *Phenacolemur jepseni*. The one PCF that has been identified in a specimen of *Plesiadapis* (in the Pellouin skull of *P. tricuspidens*; Gingerich, 1975, 1976) is located lateral to the position of the foramen in most eutherians (including *Cynocephalus*), near the posterior extent of the bulla.

For taxa that lack an ICA, the route that this vessel would have taken can be reconstructed from the position of the internal carotid nerves. In *Cynocephalus*, these nerves enter the middle ear via a posteromedially positioned PCF and pass medially across the promontorium (Wible, 1993). The same pathway can be reconstructed for *Microsyops* (McKenna, 1966; Szalay, 1969; Gunnell, 1989). This more medial route has been suggested as primitive for Mammalia and is also present in Scandentia and Chiroptera (Archibald, 1977; Wible, 1983; MacPhee and Cartmill, 1986; Wible and Novacek, 1988).

The primitive pathway for the ICA in Primates is a matter of some controversy. MacPhee and Cartmill (1986) considered a posteromedial PCF to be a characteristic of the primate morphotype, based on its presence in the omomyids known at that time and the primitive eutherian morphotype, and in spite of the more lateral position observed in adapids and lemuriform primates. Fossils of *Shoshonius cooperi* discovered since then have documented that this omomyid had the more adapid-like, posterolateral PCF (Beard and MacPhee, 1994). The implication of

this finding is that members of the two most primitive primate families, in addition to modern lemuriforms, have a posterolaterally positioned PCF, suggesting that this more lateral route for the ICA through the ear is the primitive morphology for Primates. Reversal to a more common medial position occurred in omomyids more derived than *Shoshonius*. Other features of the ear region in *Shoshonius* (e.g., a nontubular external auditory meatus) also suggest it may be a better model for the primitive omomyid morphology than other members of this family. Wible (1993) indicated that this lateral course is a fairly unusual pathway for the internal carotid artery. He considered this similarity between non-microsypoid plesiadapiforms and some primates to be more significant than the simple reduction in the internal carotid artery, which occurs in many different mammalian groups (including some carnivorans, artiodactyls, rodents, and loriform and cheirogaleid primates; Wible, 1993), and is therefore a feature of less phylogenetic valence. The new evidence given above, combined with the reinterpretation of the primitive primate condition indicated by *Shoshonius*, bolsters the view of Wible (1993). This suggests that a posterolaterally positioned PCF, associated with a promontorial artery that passes along the lateral extreme of the promontorium, is a synapomorphy linking non-microsypoid plesiadapiforms to primitive primates, to the exclusion of Dermoptera.

Ectotympanic

The new evidence available for the morphology of the ectotympanic of *Ignacius* described above indicates that this bone is more similar to that of *Plesiadapis*, with a distinct ring-like element and a subtympanic recess, than to modern dermopterans which lack an annular bridge. It is not possible to determine, based on the current imperfect evidence, whether the annular bridge of *Ignacius graybullianus* was interrupted by a recessus dehiscence (a gap in the annular bridge observed in adapids and lemuriforms, but not omomyids; see Appendix; MacPhee, 1987; Beard and MacPhee, 1994). Other aspects of ectotympanic anatomy (e.g., the tubular external auditory meatus) of paromomyids are more comparable to omomyids and *Plesiadapis*, so it would be predicted that *Ignacius* would lack a recessus dehiscence. New, better-preserved specimens will be required to test this prediction.

As noted above, the proportion of the bullar floor made up by the ectotympanic is markedly different in modern dermopterans and *Ignacius* (Fox, 1993; Wible and Martin, 1993). Although the tube-like external auditory meatus of *Plesiadapis* has been thought to be ectotympanic in origin (comparable to *Tarsius* and anthropoids), in the absence of any sutures on the bullar floor that would delimit the margins of this bone, the precise dimensions remain unknown (MacPhee and Cartmill, 1986). There is, nonetheless, an overall general similarity between

Plesiadapis and paromomyids in the morphology of the ectotympanic. The form of this bone is unknown for Microsypoidea.

DISCUSSION

The evidence given above provides support for one profound difference between *Ignacius graybullianus* and primates: the former taxon did not have a petrosal bulla. In *Ignacius*, the absence of a significant internal carotid artery, and of arterial tubes, differs from the typical primate situation that is also shared by scandentians. However, comparisons between *Ignacius* and primates for the other features elaborated here temper the significance of these findings. Evidence is provided for a very lateral entry for the internal carotid nerves and artery to the middle ear, and a laterally positioned pathway for the promontorial artery across the roof of the tympanic cavity in paromomyids. This is an unusual course for these structures, differing from the situation in primitive eutherians (Wible, 1993) and most other mammals, but similar to the likely primitive state for Primates. In *Ignacius*, however, the absence of a significant internal carotid artery, and of arterial tubes, differs from the typical primate situation, which is also shared by scandentians. The evidence presented here that *Ignacius graybullianus* may have had an ectotympanic that includes a narrow ring supported by an annular bridge would be similar not only to the situation in *Plesiadapis*, but also to primitive primates.

Other features of the ear region in plesiadapiforms are more derived than would be expected in a primate ancestor. While *Plesiadapis* and some omomyids have a tubular external auditory meatus (EAM), the primitive primate morphotype has been reconstructed as lacking a tubular EAM (MacPhee and Cartmill, 1986). This conclusion is supported by the absence of a tubular EAM in *Shoshonius* (Beard and MacPhee, 1994) as well as in adapids and lemuriforms (MacPhee and Cartmill, 1986). Thus, the phylogenetic implications of these characteristics in paromomyids are seemingly contradictory. While the pathway of the internal carotid nerves and promontorial artery, and the presence of a ring-like ectotympanic element in paromomyids, are similar to the primitive primate morphotype, in other features paromomyids are more derived than might be expected for a Primate ancestor. Variation within Plesiadapiformes further complicates this issue. It is worth noting, however, that many of the crania that are derived for Plesiadapiformes are from taxa that are derived members of their families. For paromomyids, *Ignacius* and *Phenacolemur* are dentally more derived than other known genera (i.e., *Paromomys* and *Elwynella*; Simpson, 1955; Bown and Rose, 1976; Rigby, 1980; Rose and Bown, 1982; Silcox and Gunnell, in press; see also Bloch et al., in press). As such, it is not surprising that these taxa exhibit derived features missing in the ancestral primate morphotype.

Evidence accumulated here indicates some profound differences in details of the auditory morphology between dermopterans and paromomyids, to add to the differences in the precise makeup of the floor of the tympanic bulla already noted by other authors (Wible, 1993; Wible and Martin, 1993). These include the likely presence of a small promontorial artery, differences in the pathway of the internal carotid nerves, and details of the morphology of the ectotympanic. Given these considerations, there remain no unequivocal cranial synapomorphies linking paromomyids and dermopterans to the exclusion of other archontans.

Where, then, do paromomyids belong? Most primate authorities would consider the absence of a petrosal bulla as definitive evidence that they should not be placed in that order. The importance of this character needs to be viewed, however, in a phylogenetic context. The presence of one or more entotympanic elements in all non-primate archontans, which are generally viewed as the most plausible outgroups for primates (i.e., scandentians, dermopterans, and possibly chiropterans; see above), supports the view that the ultimate ancestor of the Primate clade likely included an entotympanic in its bulla, which was subsequently replaced by overgrowth or replacement by the petrosal. The entotympanic bulla could, then, be no more than a retention from an archontan ancestor in *Ignacius graybullianus*, and might actually be expected in the most primitive primates.

It should be noted, however, that in spite of a few derived features shared by paromomyids and primates, the ear regions are phenetically rather dissimilar. Evidence demonstrating that the cranial similarities to modern dermopterans are fairly superficial, given both here and elsewhere, makes that link much less convincing. Variation within Plesiadapiformes, which contrasts with the similarities in dental features in these forms, additionally adds to the lack of a clear resolution. The ultimate conclusion must be that auditory region does not necessarily provide a "touchstone" for the relationships of the Paromomyidae. Dental and postcranial traits will be needed to more fully understand the relationships of paromomyids, and all plesiadapiforms, to other mammalian groups.

CONCLUSIONS

New specimens of the paromomyid *Ignacius graybullianus* and reinterpretation of the skull of *Phenacolemur jepseni* lead to the conclusion that the characteristic-paromomyid cranial anatomy included a nonpetrosal bulla, a laterally positioned route for the internal carotid artery, and an ectotympanic with a tubular external auditory meatus. Evidence known only for *Ignacius graybullianus* supports the presence of a small remnant of a promontorial artery in that taxon, and indicates that the ectotympanic included a ring-like element supported by an annular bridge.

The evidence presented here and elsewhere (Wible, 1993; Wible and Martin, 1993) indicates that purported cranial similarities of dermopterans and paromomyids differ markedly in detail, increasing the probability that they arose through convergence. This includes the reduction of the internal carotid artery, which was less pronounced in paromomyids and involved a vessel running along a different course than in *Cynocephalus* or *Galeopterus*, and the supposed absence of an annular bridge, which was based on imperfectly preserved material. Outgroup comparison indicates that the shared possession of an entotympanic element in the bulla is likely a primitive retention, and the presence of a contact between the basioccipital and entotympanic in tupaiines makes that similarity seem less significant. In all, therefore, there is no compelling cranial evidence to link paromomyids and dermopterans.

The issue of a possible paromomyid-primate relationship is complicated by the derived nature of the paromomyid ear region, relative to the presumed primate primitive morphotype. Nonetheless, the distinctly lateral course of the internal carotid nerves is a possible synapomorphy for a plesiadapoid plesiadapiform-primate clade that would exclude other archontans, including dermopterans, scandentians, and microsypoid plesiadapiforms. This feature needs to be weighed, however, against the similarities in cranial form between scandentians and primates (Wible and Covert, 1987), missing in plesiadapiforms, such as branches of the internal carotid artery that are enclosed in bony tubes. Dental similarities between plesiadapoid and microsypoid plesiadapiforms also argue against this view. Based on this conflicting evidence, it seems that further study of dental and postcranial evidence will be needed to more fully resolve the phylogenetic position of Paromomyidae in relation to Primates and other archontans. Nonetheless, in light of these new findings, the only remaining evidence to support the clade Eudermodoptera is postcranial, and even these characteristics have been seriously questioned (Krause, 1991; Szalay and Lucas, 1993; Runestad and Ruff, 1995; Stafford and Thorington, 1998; Hamrick et al., 1999). Furthermore, newly discovered paromomyid postcrania indicate that primitive paromomyids were probably not gliders (Bloch and Boyer, unpublished observations). While this study is still underway, support for the clade Eudermodoptera is significantly weakened by the new evidence provided here.

ACKNOWLEDGMENTS

P. Houde collected USNM 421608 and 482353, D. Boyer and W. Sanders helped with the preparation of UM 108210, and B. Miljour helped with preparation of the figures. The photograph in Figure 10 was taken by P.D. Gingerich. Earlier versions of the manuscript were improved by comments from D. Boyer, D. Fisher, P. Gingerich, G. Gunnell, K. Rose, W. Sanders, A. Sorin, M. Uhen, and J. Wilson. F.S.

Szalay and two anonymous reviewers also suggested many improvements. P.D. Gingerich, G.F. Gunnell, and K.D. Rose provided useful conversations and guidance on the interpretation of plesiadapiform ear regions. L. Gordon, R. Purdy, R.F. Kay, M.C. McKenna, P.D. Gingerich, K.D. Rose, and G.F. Gunnell provided access to specimens. P.D. Gingerich and G.F. Gunnell are particularly thanked for access to unpublished material, including permission to illustrate the *Plesiadapis cookei* skull. This project was supported by grants from the Wenner-Gren Foundation for Anthropological Research, the Paleobiological Fund, Sigma Xi, and the National Science Foundation (doctoral dissertation improvement grant 9815884) to M.T.S. Field and laboratory research was supported by grants from the National Science Foundation to Philip D. Gingerich (most recently EAR-8918023) and from the Scott Turner Fund, Department of Geological Sciences, University of Michigan, to J.I.B.

APPENDIX: SIMPLIFIED GLOSSARY OF CRANIAL TERMS

Introduction

This glossary is intended to assist in understanding diagrams and descriptions of the nonhuman auditory region at the most basic level. This glossary is not exhaustive, either in the items included, or the taxa sampled, and there are certainly variations in the structures included that are not mentioned here. Various authors (e.g., McDowell, 1958; MacPhee, 1981) have compiled useful summaries of some of the relevant terminology. The glossary in MacPhee (1981) is an excellent resource for experienced researchers, and the reader is referred to this as a more anatomically accurate and precise compilation of terms. References key to compiling this glossary include: Beard and MacPhee, 1994; Hunt and Korth, 1980; McDowell, 1958; MacPhee, 1979, 1981, 1987; MacPhee and Cartmill, 1986; MacPhee et al., 1989; Silcox, 2001; Wible, 1984, 1993; Wible and Martin, 1993 and Williams et al., 1989.

Annular bridge: “. . .the annular bridge has come to mean any sheet of bone that bridges the gap between the ectotympanic’s crista tympani and the internal aspect of the bullar wall.” Beard and MacPhee (1994, p. 66).

Auditory bulla: the balloon-like bony structure that forms the floor (ventral side) of the tympanic (middle ear) cavity in many mammals. The bones that make up the bulla are highly variable within mammals and may include the petrosal, ectotympanic, entotympanic, basisphenoid, or alisphenoid. The bulla may also be partly or fully membranous (i.e., non-ossified).

Auditory tube (= Eustachian tube): connection between the middle ear (tympanic) cavity and the pharynx, supported by an elongate cartilaginous element (the tubal cartilage; MacPhee, 1981).

Crista tympanica (= crista tympani): the ridge on the ectotympanic to which the tympanic membrane (eardrum) largely attaches (MacPhee et al., 1989). This is a constant feature of the ear region, independent of the precise form of the ectotympanic. As such, this is the bony delimiter between the external and middle ear cavities.

Ectotympanic (= tympanic, Hunt and Korth, 1980): a bone that is an invariable part of the ear region, since it bears the crista tympanica and supports the tympanic membrane (eardrum). The ectotympanic bone may or may not form part of the bulla itself. In some cases (e.g., lemuriform primates), it is a ring-like structure that is located inside another bone (the petrosal) that forms the auditory bulla, while in others (e.g., modern dermopterans) it is expanded to form the majority of the floor of the bulla.

Entotympanic: independently developing elements that contribute to the floor (and occasionally the roof) of the tympanic cavity in a diverse assortment of mammals. The name has been applied to any element that forms without a relationship to one of the other bones of the posterior basicranium (i.e., directly within the fibrous membrane of the tympanic cavity; van der Klaauw, 1931; MacPhee, 1979), and as such, bones given this name are not necessarily strictly homologous with one another (MacPhee, 1979). These elements frequently occur in caudal and rostral pairs (van der Klaauw, 1922). Again, all caudal entotympanics are probably not homologous, and all rostral entotympanics are unlikely to be homologous (Wible and Martin, 1993).

Epitympanic recess: the region dorsal to the tympanic ring that contains the articulation between the incus and malleus (MacPhee, 1981).

Internal carotid nerve(s): postganglionic sympathetic fibers passing from the superior cervical ganglion of the sympathetic chain into the skull to supply sympathetic, autonomic innervation to cranial structures. In most mammals, the internal carotid nerve(s) accompanies the internal carotid artery, forming a plexus around this vessel in humans (Williams et al., 1989). When the internal carotid artery is absent, the internal carotid nerve(s) can be used to reconstruct the pathway of this vessel before its loss (Wible, 1993). While the internal carotid artery may be functionally replaced by other vessels (e.g., the ascending pharyngeal or vertebral arteries), the internal carotid nerve(s) is always present (MacPhee and Cartmill, 1986).

Petrosal: component of the posterior basicranium that houses the inner ear structures, formed by ossification of the otic capsule (McDowell, 1958). In euprimates, the petrosal is expanded outward to form the auditory bulla (or homologous structures) enclosing the contents of the middle ear (homologous to the petrosal portion of the temporal bone in humans; McDowell, 1958). The petrosal origin of the auditory bulla is reflected in the continuity of the bone from the promontorium (see below) and audi-

tory bulla (although such a continuity can also form as a result of remodeling of sutures in animals with a bulla that is non-petrosal in developmental origin; see MacPhee et al., 1983; MacPhee and Cartmill, 1986).

Posterior carotid foramen (= PCF): opening in the auditory bulla through which the internal carotid nerves and artery (when present) enter the middle ear cavity in animals that retain a transpromontorial (through the middle ear cavity, across the promontorium; see MacPhee and Cartmill, 1986) route for the internal carotid artery. In taxa that have a perbullar course for the internal carotid artery (e.g., extant haplorhines; MacPhee and Cartmill, 1986), the posterior carotid foramen leads into a canal that bypasses the tympanic (middle ear) cavity proper to travel through the wall of the bulla (e.g., the carotid canal of humans). The PCF is not equivalent to the posterior lacerate (= jugular) foramen, which is associated with the passage of the internal jugular vein, cranial nerves IX, X and the cranial root of cranial nerve XI.

Promontorium (= promontory): the ventral structure, bulging into the middle ear cavity that is formed by the bony covering of the cochlea. It is formed invariably from the petrosal, and pierced by the fenestra rotunda (= fenestra cochleae, round window, cochlear window) and fenestra vestibuli (=fenestra ovalis, oval window). This structure is the primary landmark in the roof of the middle ear, and may be grooved by branches of the internal carotid artery, the internal carotid nerve, and/or elements of the tympanic nervous plexus (see below).

Promontory artery: branch of the internal carotid artery that contributes to the cerebral arterial circle, supplying the brain. In animals that have a transpromontorial pathway of the internal carotid artery and both a stapedia and promontory artery, the latter branches off after the entrance of the internal carotid artery to the middle ear (through the posterior carotid foramen), passing across the surface of the promontorium to an opening to the neurocranium (the anterior carotid foramen; MacPhee, 1981). The distal "internal carotid artery" of humans is roughly the equivalent of the promontory artery as used here, since humans (and other anthropoids) lack a stapedia artery. In humans this structure does not pass through the middle ear, however, but takes a modified version of the perbullar pathway seen in all extant haplorhines (MacPhee and Cartmill, 1986).

Recessus dehiscence: a gap in the annular bridge present in extant lemurs, separating the tympanic ring from the floor of the bulla (MacPhee, 1987). The presence of a recessus dehiscence demonstrates that the annular bridge is petrosal in origin, since there is a space between the bridge and the body of the ectotympanic itself. In the absence of a recessus dehiscence, the bone that forms the annular bridge

cannot be deduced without developmental evidence (MacPhee, 1987).

Subtympanic recess: a recess between the tympanic ring and the floor of the bulla. This may take the form of a gap, may be spanned by a membrane, may be partly spanned by a sheet of bone from the bulla that is separated from the tympanic ring by a gap (the recessus dehiscence; see above), or may be completely spanned by an annular bridge (e.g., *Plesiadapis*; see above). If the ectotympanic forms part of the bullar floor and the tympanic ring is fused with the bulla, the subtympanic recess will be absent (e.g., modern dermopterans; Kay et al., 1992).

Stapedial artery: branch of the internal carotid artery that passes through the stapes. The stapedial artery primitively divides into various rami: the ramus inferior that supplies the upper and lower jaws, the ramus superior that supplies the dura and orbital region, and the ramus posterior that feeds the mastoid area (MacPhee, 1981; MacPhee and Cartmill, 1986; Wible, 1984). All anthropoids (including humans) lack a stapedial artery, so this area of distribution is taken over by other vessels (e.g., branches of the external carotid artery; see Bugge, 1974, his Fig. 2 for a summary of variations among mammals in the sources of supply to the stapedial's area of distribution).

Tympanic nervous plexus (= tympanic nerve, nerve of Jacobson): branches of cranial nerve IX (glossopharyngeal) that extend over the promontorium, supplying the mucosa of the tympanic cavity and auditory tube (Williams et al., 1989).

LITERATURE CITED

- Archibald JD. 1977. Ectotympanic bone and internal carotid circulation of eutherians in reference to anthropoid origins. *J Hum Evol* 6:609-622.
- Beard KC. 1989. Postcranial anatomy, locomotor adaptations, and paleoecology of Early Cenozoic Plesiadapidae, Paromomyidae, and Micromomyidae (Eutheria, Dermoptera). Baltimore: Johns Hopkins University School of Medicine. Ph.D. dissertation.
- Beard KC. 1990. Gliding behavior and palaeoecology of the alleged primate family Paromomyidae (Mammalia, Dermoptera). *Nature* 345:340-341.
- Beard KC. 1993a. Phylogenetic systematics of the Primatomorpha, with special reference to Dermoptera. In: Szalay FS, Novacek MJ, McKenna MC, editors. *Mammal phylogeny: placentals*. New York: Springer-Verlag. p 129-150.
- Beard KC. 1993b. Origin and evolution of gliding in Early Cenozoic Dermoptera (Mammalia, Primatomorpha). In: MacPhee RDE, editor. *Primates and their relatives in phylogenetic perspective*. New York: Plenum Press p. 63-90.
- Beard KC, Houde P. 1989. An unusual assemblage of diminutive plesiadapiforms (Mammalia, ?Primates) from the early Eocene of the Clark's Fork Basin, Wyoming. *J Vert Paleontol* 9:388-399.
- Beard KC, MacPhee RDE. 1994. Cranial anatomy of *Shoshonius* and the antiquity of Anthropoidea. In: Fleagle JG, Kay RF, editors. *Anthropoid origins*. New York: Plenum Press. p 55-97.
- Bloch JI, Boyer DM. 2001. Taphonomy of small mammals in freshwater limestones from the Paleocene of the Clarks Fork Basin. *Pap Paleontol Univ Mich* 33:185-198.

- Bloch JI, Gingerich PD. 1994. New species of *Carpolestes* (Mammalia, Proprimates) from Clarkforkian late Paleocene limestones of the Clark's Fork Basin, Wyoming: teeth, skulls, and femur. *J Vert Paleontol* 14:17–18.
- Bloch JI, Boyer DM, Gingerich PD, Gunnell GF. In press. New primitive paromyid from the Clarkforkian of Wyoming and dental eruption in Plesiadapiformes. *J Vert Paleontol*.
- Bown TM, Rose KD. 1976. New early Tertiary primates and a reappraisal of some Plesiadapiformes. *Folia Primatol* (Basel) 26:109–138.
- Bugge AJ. 1974. The cephalic arterial system in insectivores, primates, rodents and lagomorphs, with special reference to the systematic classification. *Acta Anat* (Basel) [Suppl] 87:1–160.
- Conroy GC, Wible JR. 1978. Middle ear morphology of *Lemur variegatus*: some implications for primate paleontology. *Folia Primatol* (Basel) 29:81–85.
- Fox RC. 1993. The primitive dental formula of the Carpolestidae (Plesiadapiformes, Mammalia) and its phylogenetic implications. *J Vert Paleontol* 13:516–524.
- Gingerich PD. 1975. Systematic position of *Plesiadapis*. *Nature* 253:111–113.
- Gingerich PD. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *Pap Paleontol Univ Mich* 15:1–116.
- Gingerich PD. 1987. Early Eocene bats (Mammalia, Chiroptera) and other vertebrates in freshwater limestones of the Willwood Formation, Clarks Fork Basin, Wyoming. *Contrib Mus Paleontol Univ Mich* 27:275–320.
- Gunnell GF. 1989. Evolutionary history of Microsypoidea (Mammalia, ?Primates) and the relationship between Plesiadapiformes and Primates. *Pap Paleontol Univ Mich* 27:1–157.
- Hamrick MW, Rosenman BA, Brush, JA. 1999. Phalangeal morphology of the Paromyidae (?Primates, Plesiadapiformes): the evidence for gliding behavior reconsidered. *Am J Phys Anthropol* 109:397–413.
- Hershkovitz P. 1977. Living New World monkeys (Platyrrhini) with an introduction to primates, volume 1. Chicago: University of Chicago Press.
- Hoffstetter R. 1977. Phylogénie des Primates: confrontation des résultats obtenus par les diverse voies d'approches de problème. *Bull Mem Soc Anthropol Paris Ser* 13 4:327–346.
- Hooker JJ, Russell DE, Phélizon A. 1999. A new family of Plesiadapiformes (Mammalia) from the old world lower Paleogene. *Palaeontology* 42:377–407.
- Hunt RM Jr. 1974. The auditory bulla in Carnivora: an anatomical basis for reappraisal of carnivore evolution. *J Morphol* 143:21–76.
- Hunt RM Jr, Korth WK. 1980. The auditory region of Dermoptera: morphology and function relative to other living mammals. *J Morphol* 164:167–211.
- Kay RF, Thorington RW Jr, Houde P. 1990. Eocene plesiadapiform shows affinities with flying lemurs not primates. *Nature* 345:342–344.
- Kay RF, Thewissen JGM, Yoder AD. 1992. Cranial anatomy of *Ignacius graybullianus* and the affinities of the Plesiadapiformes. *Am J Phys Anthropol* 89:477–498.
- Krause DW. 1991. Were paromyids gliders? Maybe, maybe not. *J Hum Evol* 21:177–188.
- MacPhee RDE. 1979. Entotympanics, ontogeny and primates. *Folia Primatol* (Basel) 31:23–47.
- MacPhee RDE. 1981. Auditory regions of primates and eutherian insectivores: contributions to primatology no. 18. Zurich: Karger.
- MacPhee RDE. 1987. Basicranial morphology and ontogeny of the extinct giant lemur *Megaladapis*. *Am J Phys Anthropol* 74:333–355.
- MacPhee RDE, Cartmill M. 1986. Basicranial structures and primate systematics. In: Swisher DR, Erwin J, editors. *Comparative primate biology, volume 1: systematics, evolution, and anatomy*. New York: Alan R. Liss. p 219–275.
- MacPhee RDE, Cartmill M, Gingerich PD. 1983. New Paleogene primate basicrania and the definition of the order Primates. *Nature* 301:509–511.
- MacPhee RDE, Novacek MN, Storch G. 1988. Basicranial morphology of early Tertiary erinaceomorphs and the origin of Primates. *Am Mus Nov* 2921:1–42.
- MacPhee RDE, Cartmill M, Rose KD. 1989. Craniodental morphology and relationships of the supposed Eocene dermopteran *Plagiomena* (Mammalia). *J Vert Paleontol* 9:329–349.
- Madsen O, Scally M, Douady CJ, Kao DJ, DeBry RW, Adkins R, Amrine HM, Stanhope MJ, de Jong WW, Springer MS. 2001. Parallel adaptive radiations in two major clades of placental mammals. *Nature* 409:610–614.
- McDowell SB Jr. 1958. The greater Antillean insectivores. *Bull Am Mus Nat Hist* 115:117–214.
- McKenna MC. 1966. Paleontology and the origin of Primates. *Folia Primatol* (Basel) 4:1–25.
- McKenna MC, Bell SK. 1997. Classification of mammals above the species level. New York: Columbia University Press.
- Miyamoto MM, Porter CA, Goodman M. 2000. *c-Myc* gene sequences and the phylogeny of bats and other eutherian mammals. *Syst Biol* 49:501–514.
- Murphy WJ, Eizirik E, Johnson WE, Zhang YP, Ryder OA, O'Brien SJ. 2001. Molecular phylogenetics and the origins of placental mammals. *Nature* 409:614–618.
- Patterson B, Segall W, Turnbull WD, Gaudin TJ. 1992. The ear region in xenarthrans (= Edentata, Mammalia). Part II. Pilosa (sloths and anteaters), palaeonodons and a miscellany. *Fieldiana Geol* 24:1–79.
- Pumo DE, Finamore PS, Franek WR, Phillips CJ, Tarzami S, Balzarano D. 1998. Complete mitochondrial genome of a neotropical fruit bat, *Artibeus jamaicensis* and a new hypothesis of the relationships of bats to other eutherian mammals. *J Mol Evol* 47:709–717.
- Rigby JK Jr. 1980. Swain Quarry of the Fort Union Formation, middle Paleocene (Torrejonian), Carbon County, Wyoming: geologic setting and mammalian fauna. *Evol Monogr* 3:1–179.
- Rose KD. 1995. The earliest primates. *Evol Anthropol* 3:159–173.
- Rose KD, Bown TM. 1982. New plesiadapiform primates from the Eocene of Wyoming and Montana. *J Vert Paleontol* 2:63–69.
- Runestad JA, Ruff CB. 1995. Structural adaptations for gliding in mammals with implications for locomotor behavior in paromyids. *Am J Phys Anthropol* 98:101–119.
- Russell DE. 1959. Le crâne de *Plesiadapis*. *Bull Soc Geol Fr* 4:312–314.
- Russell DE. 1964. Les mammifères Paléocène d'Europe. *Mem Mus Nat Hist Nat Ser C* 13:1–324.
- Saban R. 1963. Contribution à l'étude de l'os temporal des primates. *Mem Mus Nat Hist Nat Ser A* 29:1–324.
- Silcox MT. 2001. A phylogenetic analysis of Plesiadapiformes and their relationship to Euprimates and other Archontans. Baltimore: Johns Hopkins University School of Medicine. Ph.D. dissertation.
- Silcox MT, Gunnell GF. In press. Plesiadapiformes. In: Janis CM, Gunnell GF, Uhen MD, editors. *Evolution of Tertiary mammals of North America, volume 2: marine mammals and smaller terrestrial mammals*. Cambridge: Cambridge University Press.
- Simpson GG. 1955. The Phenacolemuridae, new family of early Primates. *Bull Am Mus Nat Hist* 105:415–441.
- Springer MS, Burk A, Kavanagh JR, Waddell VG, Stanhope MJ. 1997. The interphotoreceptor retinoid binding protein gene in therian mammals: implications for higher level relationships and evidence for loss of function in the marsupial mole. *Proc Natl Acad Sci USA* 94:13754–13759.
- Stafford B, Thorington RW Jr. 1998. Carpal development and morphology in archontan mammals. *J Morphol* 235:135–155.
- Szalay FS. 1969. Mixodectidae, Microsypidae, and the insectivore-primate transition. *Bull Am Mus Nat Hist* 140:195–330.
- Szalay FS. 1972. Cranial morphology of the early Tertiary *Phenacolemur* and its bearing on primate phylogeny. *Am J Phys Anthropol* 36:59–76.
- Szalay FS, Lucas SG. 1993. Cranioskeletal morphology of Archontans, and diagnoses of Chiroptera, Volitantia, and Archonta. In: MacPhee RDE, editor. *Primates and their relatives in phylogenetic perspective*. New York: Plenum Press. p 187–226.

- Szalay FS, Lucas SG. 1996. The postcranial morphology of Paleocene *Chriacus* and *Mixodectes* and the phylogenetic relationships of archontan mammals. *Bull New Mex Mus Nat Hist* 7:1–47.
- Szalay FS, Rosenberger AL, Dagosto M. 1987. Diagnosis and differentiation of the order Primates. *Yrbk Phys Anthropol* 30:75–105.
- van der Klaauw CJ. 1922. Über die Entwicklung des Entotympanicums. *Tijdschr Ned Dierkd Ver* 18:135–174.
- van der Klaauw CJ. 1931. On the auditory bulla in some fossil mammals, with a general introduction to this region of the skull. *Bull Am Mus Nat Hist* 62:1–352.
- Wible JR. 1983. The internal carotid artery in early eutherians. *Palaeontol Polon* 28:281–293.
- Wible JR. 1984. The ontogeny and phylogeny of the mammalian cranial arterial pattern. Durham, NC: Duke University. Ph.D. dissertation.
- Wible JR. 1993. Cranial circulation and relationships of the colugo *Cynocephalus* (Dermoptera, Mammalia). *Am Mus Nov* 3072:1–27.
- Wible JR, Covert HH. 1987. Primates: cladistic diagnosis and relationships. *J Hum Evol* 16:1–22.
- Wible JR, Martin JR. 1993. Ontogeny of the tympanic floor and roof in archontans. In: MacPhee RDE, editor. *Primates and their relatives in phylogenetic perspective*. New York: Plenum Press. p 111–146.
- Wible JR, Novacek MJ. 1988. Cranial evidence for the monophyletic origin of bats. *Am Mus Nov* 2911:1–19.
- Williams PL, Warwick R, Dyson M, Bannister LH, editors. 1989. *Gray's anatomy*. London: Churchill Livingstone.
- Zeller U. 1987. Morphogenesis of the mammalian skull with special reference to *Tupaia*. In: Kuhn H-J, Zeller U, editors. *Morphogenesis of the mammalian skull*. Hamburg: Verlag Paul Parey. p 17–50.