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The petrosal of *Omomys carteri* and the evolution of the primate basicranium

The first omomyine petrosals, those of *Omomys carteri*, are described. *Omomys* probably had a tympanic bulla and canals for the intratympanic carotid circulation derived from the petrosal bone. The stapedia and promontory canals were complete, large and subequal. The posterior carotid foramen entered the bulla posteromedially. The intratympanic portion of the facial nerve was fully enclosed in bone, the stapedius fossa is extrabullar and the parotic fissure is patent. The mastoid was pneumatized from the epitympanic recess and a supracochlear cavity may have been present. The *Omomys* petrosals exhibit a generic omomyiform morphology, exhibiting no features that can be interpreted as autapomorphies and only one feature shared with adapiforms. The monophyly of Omomyiformes is based on other cranial characters, dental and postcranial characters assessed elsewhere. The similarity of the Shanghuang petrosal to the petrosals of omomyiforms, as well as the ambiguous evidence of its association, suggest that an omomyiform affinity for that petrosal cannot be ruled out.

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Introduction

Two suborders of fossil primates appear in the early Eocene of North America and Europe: the Omomyiformes and Adapiformes (Table 1). These two suborders contain the oldest undisputed representatives of the Primates and constitute the first known radiations of the Order. The radiation of the two groups was roughly equivalent in numbers of taxa [39 genera and 81 species of Omomyiformes *vs.* 31 genera and 74 species of Adapiformes (Covert, 1997; Fleagle, 1999)] but divergent in adaptations. Omomyiforms were mostly small, nocturnal, frugivore–insectivores, while adapiforms were generally larger, diurnal and more inclined to folivory–frugivory (Covert, 1997). There are exceptions to these generalizations, but among adapiforms only *Pronycticebus* has been conclusively shown to be nocturnal and no omomyiforms have been shown to

be diurnal.¹ Postcranial morphology also reveals substantial differences, some of these being present in even the earliest known omomyiform and adapiform postcranial material (Covert, 1997). In contrast, the dentitions of the earliest or most primitive omomyiforms (*Teilhardina belgica* and *Steinius vespertinus*) and adapiforms (*Cantius torresi* and *Donrussellia gallica*) are very similar, so similar in fact that a Late Paleocene divergence of the two groups has been suggested (Rose *et al.*, 1994).

Traditionally, extant strepsirrhines are argued to be descended from an adapiform lineage and haplorhines variously related to one or more omomyiform lineages (e.g., Szalay & Delson, 1979; Martin, 1990; Fleagle, 1999). Some researchers hypothesize that one lineage of omomyiforms gave rise to a clade consisting of *Tarsius* and

¹Here we exclude *Rooneyia* from Omomyiformes following Beard & MacPhee (1994) and Ross *et al.* (1998).

Table 1 Classification of Primates followed here. (Modified from Ross *et al.*, 1998; Fleagle, 1999)*

Order Primates
 Semiorder *incertae sedis*
Rooneyia

Semiorder Strepsirrhini
 Suborder Lemuriformes
 Superfamily Lemuroidea
 Superfamily Lorisioidea
 Suborder Adapiformes
 Family Notharctidae
 Subfamily Notharctinae: **Cantius**, *Copelemur*, **Notharctus**, **Smilodectes**, **Pelycodus**
 Subfamily Cercamoniinae: *Donrussellia*, *Protoadapis*, *Europolemur*, *Periconodon*, *Caenopithecus*, **Pronycticebus**,
Cercamonius, *Anchomomys*, *Heurzeleria*, *Buxella*, *Agerinia*, *Panobius*, **Mahgarita**,
Djebelemur, *Aframonius*, *Omanodon*, *Shizarodon*, *Wadilemur*

Family Adapidae
 Subfamily Adapinae: **Adapis**, *Cryptadapis*, *Microadapis*, **Leptadapis**, *Adapoides*

Semiorder Haplorhini
 Suborder Omomyiformes
 Family Omomyidae:
 Subfamily Anaptomorphinae
 Tribe Anaptomorphini: *Teilhardina*, **Tetonius**, *Pseudotetonius*, *Anaptomorphus*, *Gazinius*, *Aycrossia*,
Strigorhysis, *Tatmanius*, *Absarokiis*
 Tribe Trogolemurini: *Trogolemur*, *Sphacorhysis*, *Anemorhysis*, *Tetonoides*, *Arapahoviis*, *Chlororhysis*
 Tribe Washakiini: *Dyseolemur*, *Loveina*, **Shoshoniis**, *Washakiis*

Subfamily Omomyinae
 Tribe Omomyini: **Omomys**, *Chumashiis*, *Steiniis*
 Tribe Uintaniini: *Uintaniis*, *Jemeziis*
 Tribe Macrotarsiini: *Macrotarsiis*, *Hemiacodon*, *Yaquiis*
 Tribe Ourayini: *Ourayia*, *Wyomomys*, *Ageitodendron*, *Utahia*, *Stockia*, *Chipetaia*, *Asiomomys*
 Tribe *incertae sedis*: *Ekgmowechashala*

Family Microchoeridae
Microchoerus, **Necrolemur**, *Pseudoloris*, *Nannopithec*

Suborder Tarsiiformes
 Family Tarsiidae: **Tarsiis**, *Xanthorhysis*

Suborder Anthropoidea
 Infraorder Platyrrhini
 Infraorder Catarrhini
 Family Propliopithecidae: *Aegyptopithecus*, *Propliopithecus*
 Infraorder Parapithecoida
 Family Parapithecidae: **Apidium**, *Parapithecus*, *Qatrania*, *Simonsiis*, *Serapia*, *Arsinoea*, *Biretia*
 Infraorder *incertae sedis*
 Family Oligopithecidae: **Catopithecus**, *Proteopithecus*, *Oligopithecus*
 Family Eosimiidae: **Eosimias**
 Family Afrotarsiidae: *Afrotarsiis*

*This classification is at the generic level and above and is only exhaustive for Adapiformes, Omomyiformes, and Tarsiiformes. Some basal Anthropoidea are also included. Except for *Tarsiis*, extant genera are not listed. See Fleagle (1999) for a more detailed classification. Generic names in bold indicate taxa to which basicranial data are attributed. See text for discussion of Shanghuang petrosal attributed to **Eosimias**.

Anthropoidea (Cartmill & Kay, 1978; Cartmill *et al.*, 1981; MacPhee & Cartmill, 1986; Kay & Williams, 1994; Ross, 1994, 1996; Kay *et al.*, 1997; Ross *et al.*, 1998). Others have hypothesized that *Tarsiis* and Anthropoidea have their origins among

different groups of omomyiforms, with possible sister taxa to Anthropoidea including *Chumashiis*, *Teilhardina*, *Omomys* and *Ourayia* (Szalay, 1975, 1976; Szalay & Delson, 1979; Hoffstetter, 1980; Kay, 1980; Rosenberger, 1985; Szalay *et al.*, 1987;

Rose *et al.*, 1994) and possible sister taxa to *Tarsius* including microchoerids (Simons, 1972; Rosenberger, 1985; Rosenberger & Dagosto, 1992; Dagosto *et al.*, 1999) or the washakiine omomyiform, *Shoshonius cooperi* (Beard *et al.*, 1991). Recently, Beard & MacPhee have suggested that tarsiers and omomyiforms form a clade (Tarsiiformes) with Anthropoidea as its sister taxon (Beard *et al.*, 1991; Beard & MacPhee, 1994). Consistent with this argument is a small petrosal bone recovered from the same fissure fillings at Shanghuang as the probable basal anthropoid, *Eosimias* (MacPhee *et al.*, 1995). This petrosal lacks features of the middle ear region that have been used to support the tarsier–anthropoid clade (Cartmill & Kay, 1978; MacPhee & Cartmill, 1986; Ross, 1994), suggesting that if it does belong to a basal anthropoid, these tarsier–anthropoid basicranial similarities arose in parallel (MacPhee *et al.*, 1995). However, the assignment of the Shanghuang petrosal to the Eosimiidae has been questioned elsewhere (Ross *et al.*, 1998), an issue further addressed below.

The evidence from the basicranium, particularly the otic region has played an important role in these debates, partly because the otic region preserves fairly well in the fossil record, and partly because the complexity of this region supplies a rich network of potential characteristics for analysis (e.g., MacPhee, 1981; Wible, 1986; MacPhee & Cartmill, 1986). Most importantly, however, many of the generally accepted groupings of extant primates (e.g., Anthropoidea, Platyrrhini, Catarrhini, Lorisioidea) are distinguished from each other by basicranial anatomy (Table 2). This suggests that basicranial evidence might be a useful indicator of higher taxonomic relationships in general, and specifically that the origins of the major groups of extant primates might be traceable to Eocene fossil taxa using basicranial evidence.

These assumptions appeared to have been confirmed in the 1970s by observations that adapiforms and omomyiforms were distinguished from each other by several features of basicranial anatomy, that adapiforms share some features with strepsirrhines, and omomyiforms share some with tarsiers and/or anthropoids (Szalay, 1975, 1976; Szalay & Delson, 1979). This general hypothesis of an adapiform origin of strepsirrhines and an omomyiform origin of haplorhines was not incompatible with the suggestion that tarsiers and anthropoids might be more closely related to one another than either was to any omomyiform (Cartmill & Kay, 1978; Cartmill, 1980; Cartmill *et al.*, 1981; MacPhee & Cartmill, 1986).

Since the mid 1980s, there have been some significant additions to our knowledge of adapiform and omomyiform basicranial anatomy. The adapiform record is augmented by the skulls of the early Eocene notharctine *Cantius abditus* (Rose *et al.*, 1999) and the middle Eocene *Cantius actius* (Gunnell, 1995; Rose *et al.*, 1999). In addition, the basicranium is known for three other genera of notharctines (*Notharctus*, *Smilodectes*, and *Pelycodus*), one cercamoniine (*Mahgarita*) and two adapines (*Adapis* and *Leptadapis*), making it possible to reconstruct the primitive basicranial morphology for adapiforms. The omomyiform basicranium, for a long time represented only by the anaptomorphine *Tetoniuss* and the microchoerid *Necrolemur*, is now also known from the skulls of the washakiine, *Shoshonius cooperi* (Beard *et al.*, 1991; Beard & MacPhee, 1994).

The presentation here of the first evidence on the anatomy of the basicranium in an omomyine, *Omomys carteri*, enables us to present a hypothesis regarding the basicranial morphotypes of Primates and Omomyiformes and evaluate hypotheses regarding the relationships of anthropoids and tarsiers.

Table 2 Distribution of skull characters among extant primates

Characters	<i>Tarsius</i>	Anthroipoidea	Non-cheirogaleid Lemuroidea	Cheirogaleidae	Lorisoidea
Cr 1. Transverse septum	Present	Present	Absent	Absent	Absent
Cr 2. Extent of pneumatization of AAC	Anterior to tympanic cavity	Anterior and medial to tympanic cavity	AAC absent	AAC absent	AAC absent
Cr 3. Mastoid pneumatization from eptympanic recess	Absent	Present	Absent	Absent (except <i>Allocebus</i>)	Present
Cr 4. Perbullar pathway	Present	Present	Absent	Absent	Absent
Cr 5. Anteroposterior position of PCF relative to midpoint of tympanic ring	Anterior	Posterior	Posterior	Posterior	Posterior
Cr 6. Mediolateral position of PCF	Lateral	Medial or midline	Lateral	Lateral	Medial
Cr 7. Ventrodorsal position of PCF	Ventral	Ventral	Dorsal	Dorsal	Dorsal
Cr 8. Position of PCF relative to fenestra cochleae	Anterior	Anterior	Posterior	Posterior	Posterior
Cr 9. Position of the pathway for ICA or ICN relative to the fenestra cochleae	Anterior	Anterior	Runs across ventral lip of fenestra cochleae	Runs across ventral lip of fenestra cochleae	Runs across ventral lip of fenestra cochleae
Cr 10. Position of pathway for ICA or ICN on the promontorium anterior to fenestra cochleae	Contacting cupula only	Ventrolateral	Ventrolateral	Ventrolateral	Ventrolateral
Cr 11. Size of SC and PC	SC absent, PC large	SC absent, PC large	SC large, PC reduced and canal absent	PC and SC absent	PC and SC absent
Cr 12. Morphology of PC on promontorium	Complete canal	Complete canal	Trough	Absent	Absent
Cr 13. Presence or absence of canal for internal carotid artery or nerves	Present	Present	Present	Present	Present
Cr 14. Position of ventral edge of the tympanic bone	Extrabullar	Extrabullar	Intrabullar	Intrabullar except <i>Allocebus</i>	Extrabullar
Cr 15. The shape of the tympanic bone	Laterally expanded	Ribbon-like or tube-like	Ribbon-like	Ribbon-like	Laterally expanded
Cr 16. Morphology of annular bridge	Not analyzable	Not analyzable	Linea semicircularis	Linea semicircularis	Not analyzable
Cr 17. Encroachment of the auditory bulla on the pterygoid fossa	Present	Absent	Absent	Absent	Absent
Cr 18. Contact between lateral pterygoid plate and bulla wall	Laminar	Absent	Laminar	Laminar	Laminar or absent
Cr 19. Extent of contact between the lateral pterygoid plate and the bulla wall	Extensive	Absent	Slight	Slight	Slight

Table 2 Continued

Characters	Tarsius			Anthroipoidea		Non-cheirogaleid Lemuroidea		Cheirogaleidae		Lorisoidea	
	Extensive	Present	Absent	Absent	Present	Absent	Present	Absent	Present/absent, separated by large os planum of ethmoid	Absent	Present/absent
Cr 20. Flange of basioccipital overlapping medial bulla wall	Extensive	Present	Absent	Absent	Present	Absent	Present	Absent	Present/absent, separated by large os planum of ethmoid	Absent	Present/absent
Cr 21. Suprameatal foramen	Present	Patent	Absent	Absent	Absent	Absent	Present	Absent	Present/absent, separated by large os planum of ethmoid	Absent	Present/absent
Cr 22. Parotic fissure	Very large	Postorbital septum	Primarily frontal	Present below CN I	Present below CN I	Present below CN I	Present	Absent	Present/absent, separated by large os planum of ethmoid	Absent	Present/absent
Cr 23. Orbit size	Postorbital septum	Primarily frontal	Present below CN I	Present below CN I	Present below CN I	Present below CN I	Present	Absent	Present/absent, separated by large os planum of ethmoid	Absent	Present/absent
Cr 24. Postorbital closure	Postorbital septum	Primarily frontal	Present below CN I	Present below CN I	Present below CN I	Present below CN I	Present	Absent	Present/absent, separated by large os planum of ethmoid	Absent	Present/absent
Cr 25. Composition of postorbital septum	Postorbital septum	Primarily frontal	Present below CN I	Present below CN I	Present below CN I	Present below CN I	Present	Absent	Present/absent, separated by large os planum of ethmoid	Absent	Present/absent
Cr 26. Zygomatic lacrimal contact	Present below CN I	Present below CN I	Present below CN I	Present below CN I	Present below CN I	Present below CN I	Present	Absent	Present/absent, separated by large os planum of ethmoid	Absent	Present/absent
Cr 27. Pronounced interorbital constriction	Present below CN I	Present below CN I	Present below CN I	Present below CN I	Present below CN I	Present below CN I	Present	Absent	Present/absent, separated by large os planum of ethmoid	Absent	Present/absent
Cr 28. Lacrimal palatine contact	Separated by large os planum of ethmoid	Separated by large os planum of ethmoid	Separated by large os planum of ethmoid	Separated by large os planum of ethmoid	Separated by large os planum of ethmoid	Separated by large os planum of ethmoid	Present	Present	Present/absent, separated by large os planum of ethmoid	Present/absent, separated by large os planum of ethmoid	Present/absent, separated by large os planum of ethmoid
Cr 29. Foramen rotundum	Present	Outside orbit	Fused	Very convergent	Small but distinct	Present	Present	Absent	Present/absent, separated by large os planum of ethmoid	Absent	Present/absent
Cr 30. Position of lacrimal foramen	Present	Outside orbit	Fused	Very convergent	Small but distinct	Present	Present	Absent	Present/absent, separated by large os planum of ethmoid	Absent	Present/absent
Cr 31. Metopic suture in adult	Present	Outside orbit	Fused	Very convergent	Small but distinct	Present	Present	Absent	Present/absent, separated by large os planum of ethmoid	Absent	Present/absent
Cr 32. Orbital convergence relative to relative orbit size	Very convergent	Very convergent	Very convergent	Very convergent	Very convergent	Very convergent	Very convergent	Very convergent	Very convergent	Very convergent	Very convergent
Cr 33. Posterior nasal spine	Small but distinct	Small but distinct	Small but distinct	Small but distinct	Small but distinct	Small but distinct	Small but distinct	Small but distinct	Small but distinct	Small but distinct	Small but distinct
Cr 34. Posterior palatine torus	Present	Medially placed	Present	Present	Present	Present	Present	Present	Present	Present	Present
Cr 35. Pyramidal processes	Medially placed	Medially placed	Medially placed	Medially placed	Medially placed	Medially placed	Medially placed	Medially placed	Medially placed	Medially placed	Medially placed
Cr 36. Medial pterygoid plate	Short	Short	Short	Short	Short	Short	Short	Short	Short	Short	Short
Cr 37. Snout length	Short	Short	Short	Short	Short	Short	Short	Short	Short	Short	Short
Cr 38. Maxillary depth	Deep	Deep	Deep	Deep	Deep	Deep	Deep	Deep	Deep	Deep	Deep
Cr 40. TMJ	AP oriented trough	AP oriented trough	AP oriented trough	AP oriented trough	AP oriented trough	AP oriented trough	AP oriented trough	AP oriented trough	AP oriented trough	AP oriented trough	AP oriented trough
Cr 41. Entoglenoid process	Strong	Strong	Strong	Strong	Strong	Strong	Strong	Strong	Strong	Strong	Strong
Cr 47. Intratympanic portion of facial nerve	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal
Cr 48. Epitympanic crest	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent

Material examined for scoring of characters listed in Ross (1994). In addition, carotid pathway characters confirmed for Lorisoidea by examining *Nycticebus coucang* (SBAM PNc1) and *Otolemur* sp. (CFR Collection), *Galago senegalensis* (113521), *Galagoides demidoff* (Pg 22, 8117), and cheirogaleids with *Microcebus* sp. (B434).
 Abbreviations: AAC, anterior accessory cavity; CN I, cranial nerve 1, the olfactory nerve; ICA, internal carotid artery; ICN, internal carotid nerve; PA, promontory artery; PC, promontory canal; PCF, posterior carotid foramen; SA, stapedia artery; SC, stapedia canal; TMJ, temporomandibular joint.

Material and provenance

The material, three petrosals, University of Colorado Museum (UCM) 57459, UCM 57460 and UCM 57461, was recovered from the “*Omomys* Quarry” (UCM 93026) discovered in 1993 in Bridger C beds (middle Eocene), Uinta County, Wyoming by a University of Colorado field crew under the direction of Peter Robinson. This quarry has yielded one of the largest and most complete single-species samples of omomyiform material presently known. Roughly 4 m² in area and 10 cm thick, the fossil bearing sediments yielded an unusual assemblage of well preserved fish, birds, bird eggshell, reptiles, and mammals (Murphey *et al.*, 1998). Murphey and colleagues suggest that the fossil accumulation at the *Omomys* Quarry resulted from three separate taphonomic agents/processes: (1) a typical bridger attritional accumulation of both aquatic and terrestrial vertebrates, (2) a large accumulation of anseriform bird bones and eggshell from near a nesting site, and (3) an accumulation of *Omomys* bones from an owl day roost or night feeding station. The locality is named for the surprisingly large number of *Omomys* fossils found there, including associated dental and postcranial material (Murphey *et al.*, 1998). The petrosals are attributed to *Omomys carteri* because this species is both the most frequently occurring omomyiform in this portion of the Bridger Formation and the only primate known from this locality. The extant material examined for scoring of characters in Tables 3–5 is listed in Ross (1994). In addition, a specimen of *Otolemur* sp. belonging to CFR was examined, as were a *Galago senegalensis* (113521), *Galagoides demidoff* (Pg 22, 8117), *Microcebus* sp. (B434), and *Nycticebus coucang* (PNc1) from the Stony Brook Anatomical Sciences Museum (SBAM).

Description

This description invokes character state definitions and character state assignments

published in Ross *et al.* (1998) and summarized in Tables 3–5. The otic capsule consists of the semicircular canals containing the semicircular ducts and their ampullae, the vestibule, housing the saccule and utricle, and the pars cochlearis which lodges the cochlear duct. All three petrosals preserve the pars cochlearis and the vestibule; two petrosals preserve intact semicircular canals. The bony canals which housed various arteries and nerves passing through the otic region are partially preserved on the external surface of the petrosals. In addition, the remnants of bony walls and septa defining the middle ear cavity and its diverticulae are also preserved.

Middle ear cavity. The floor and roof of the tympanic cavity are best preserved in UCM 57460, although damaged (Figure 1). In this specimen, a broken rampart of bone defines the boundary of the tympanic cavity inferomedially and is continuous posteriorly with the small portion of the auditory bulla that remains intact. In UCM 57459 there is a low ridge of bone defining the anterior edge of the tympanic cavity. In all cases these ramparts consist of a single sheet of bone at all points, providing no indication of a pneumatic space within it. The rampart is not shown in Figure 1 because of the angle at which the photo was taken. The surviving bulla fragment is the most posterior portion, forming the posterior wall of the tympanic cavity and the posterior and lateral walls of the sinus tympani. (Sinus tympani is the space lying posterior to fenestra cochleae, see MacPhee, 1981:33). Both the broken ramparts of bone and the surviving bulla portion are seamlessly continuous with the petrosal, providing no evidence to suggest that the bulla was anything but an outgrowth of the petrosal.

Posteriorly, the bulla is separated from the pneumatized mastoid by the stylomastoid foramen, a thin (parotic) fissure, and a small funnel shaped depression lying outside the

Table 3 Distribution of skull characters among *Omomyiformes* and *Tarsius*

Characters	<i>Tarsius</i>	<i>Shoshoniinus</i> (Washakimi)	<i>Omomys</i> <i>carteri</i> (Omomyimi)	<i>Tetomius</i> (Anaptomorphimi)	<i>Necrolemur</i> (Macrotarsimi)	<i>Eosimias?</i> Shanghuang petrosal
Cr 1. Transverse septum	Present	Absent	Absent	Absent	Absent	Absent
Cr 2. Extent of pneumatization of AAC	Anterior to tympanic cavity only	AAC absent	AAC absent	AAC absent	AAC absent	AAC absent
Cr 3. Mastoid pneumatization from epitympanic recess	Absent	Absent	Present	?	Present	Present
Cr 4. Perbullar pathway	Present	Absent	Absent	Absent	Absent	Absent
Cr 5. Anteroposterior position of PCF relative to midpoint of tympanic ring	Anterior	Posterior	Posterior?	Posterior	Posterior	Posterior
Cr 6. Mediolateral position of PCF	Lateral	Lateral	Medial	?	Medial	Medial
Cr 7. Ventrodorsal position of PCF	Ventral	Dorsal	Dorsal	?	Dorsal	Dorsal
Cr 8. Position of PCF relative to fenestra cochleae	Anterior	Posterior	Posterior	?	Posterior	Ventral?
Cr 9. Position of the pathway for ICA or ICN relative to the fenestra cochleae	No shielding, anterior	?	Runs across ventral rim of fenestra cochleae	?	No shielding, slightly anterior	No shielding, slightly anterior
Cr 10. Position of PC on the promontorium anterior to fenestra cochleae	Contacting cupula only	Ventrolateral	Ventrolateral	Ventrolateral	Ventrolateral	Ventrolateral
Cr 11. Size of SC and PC	SC absent	Both SC and PC large and subequal	Both SC and PC large and subequal	Both SC and PC large and subequal	SC slightly smaller than PC	Both SC and PC large and subequal

Table 3 (Continued)

Characters	<i>Tarsius</i>	<i>Shoshonius</i> (Washakiini)	<i>Omomyx</i> <i>carteri</i> (Omomyiini)	<i>Tetonius</i> (Anaptomorphimi)	<i>Necrolemur</i> (Macrotrarsiini)	<i>Eosmias?</i> Shanghuang petrosal
Cr 12. Morphology of PC	Complete canal	Complete canal	Complete canal	Complete canal	Complete canal	Complete canal
Cr 13. Presence or absence of canal for internal carotid artery or nerves	Present	Present	Present	Present	Present	Present
Cr 14. Position of ventral edge of the tympanic bone	Extrabullar	Intrabullar	?	Intrabullar	Intrabullar	?
Cr 15. The shape of the tympanic bone	Laterally expanded	?	?	?	?	?
Cr 16. Morphology of annular bridge	Not analyzable	Complete	?	Complete	Complete	?
Cr 17. Encroachment of the auditory bulla on the pterygoid fossa	Present	Present	?	Present	Present	?
Cr 18. Contact between lateral pterygoid plate and bulla wall	Laminar	Laminar	?	Laminar	Laminar	?
Cr 19. Extent of contact between the lateral pterygoid plate and the bulla wall	Extensive	Extensive	?	Extensive	Extensive	?
Cr 20. Flange of basioccipital overlapping medial bulla wall	Extensive	Extensive	?	?	Extensive	?
Cr 21. Suprameatal foramen	Present	Absent?	?	?	Present	?

Table 3 (Continued)

Characters	<i>Tarsius</i>	<i>Shoshonius</i> (Washakini)	<i>Omomyx</i> <i>carteri</i> (Omomyini)	<i>Tetonius</i> (Anaptomorphini)	<i>Necrolemur</i> (Macrotrarsiini)	<i>Eosimias?</i> Shanghuang petrosal
Cr 22. Parotic fissure	Patent	Patent	Patent	Patent	Patent	Closed?
Cr 23. Orbit size	Very large	Very large	Very large*	Large	Large	?
Cr 24. Postorbital closure	Postorbital septum	Postorbital bar	?	Postorbital bar	Postorbital bar	?
Cr 25. Composition of postorbital septum	Frontal bone predominant	Not relevant	?	Not relevant	Not relevant	?
Cr 26. Zygomatic lacrimial contact	Present	Present	?	Present	Present	?
Cr 27. Pronounced interorbital constriction	Present below CN I	Present below CN I	?	Present below CN I	Present below CN I	?
Cr 28. Lacrimial palatine contact	Separated by large os planum of ethmoid	?	?	?	Separated by frontal maxillary contact	?
Cr 29. Foramen rotundum	Present	?	?	?	Absent	?
Cr 30. Position of lacrimial foramen	Outside orbit	Outside orbit	Outside orbit*	Outside orbit	Outside orbit	?
Cr 31. Metopic suture in adult	Fused	?	?	Fused	Fused	?
Cr 32. Orbital convergence relative to relative orbit size	Very convergent	Moderately convergent	?	Moderately convergent	Moderately convergent	?
Cr 33. Posterior nasal spine	Small but distinct	?	?	Small but distinct	Small but distinct	?
Cr 34. Posterior palatine torus	Present	Present	?	Present	Present	?
Cr 35. Pyramidal processes	Medially placed	Medially placed	?	Medially placed	Medially placed	?
Cr 36. Medial pterygoid plate	Short	Short	?	?	Short	?
Cr 37. Snout length	Short	Short	Long*	Short	Long	?

Table 3 (Continued)

Characters	<i>Tarsius</i>	<i>Shoshonius</i> (Washakini)	<i>Onomys</i> <i>carteri</i> (Omomyini)	<i>Tetonius</i> (Anaptomorphini)	<i>Necrolemur</i> (Macrotarsiini)	<i>Eosimias?</i> Shanghuang petrosal
Cr 38. Maxillary depth	Deep	?	?	?	?	?
Cr 40. TMJ	AP trough	AP trough	?	?	AP trough	?
Cr 41. Entoglenoid process	Strong	Strong	?	?	Strong	?
Cr 47. Inratympenic portion of facial nerve	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal
Cr 48. Epitympenic crest	Absent	Present	?	Present	Present	?

Material examined for scoring of characters listed in Ross (1994) except for *Onomys* material listed in Materials and Methods and some data from Alexander & MacPhee (1999).

Abbreviations: AAC, anterior accessory cavity; CN I, cranial nerve 1, the olfactory nerve; ICA, internal carotid artery; ICN, internal carotid nerve; PA, promontory artery; PC, promontory canal; PCF, posterior carotid foramen; SA, stapedia artery; SC, stapedia canal; TMJ, temporomandibular joint.

*Alexander & MacPhee (1999).

Table 4 (Continued)

Characters	<i>Cantius abditus</i>	<i>Adapis parisiensis</i>	<i>Leptadapis magnus</i>	<i>Mahgarita stevensi</i>	<i>Pronycticebus gaudryi</i>	<i>Smilodectes gracilis</i>
Cr 11. Size of SC and PC	SC large, PC reduced	SC large, PC reduced, or PC larger than SC	SC large, PC reduced	PC large, SC absent or very reduced	SC large, PC reduced	Both PC and SC large, PC larger than SC
Cr 12. Morphology of PC	Open trough	Open trough	Open trough	Complete canal	Complete canal	Complete canal
Cr 13. Presence or absence of canal for internal carotid artery or nerves	Present	Present	?	Present	?	Present
Cr 14. Position of ventral edge of the tympanic bone	?	Intrabullar	Intrabullar	Intrabullar	Intrabullar	Intrabullar
Cr 15. The shape of the tympanic bone	?	Ribbon-like, unexpanded	Ribbon-like, unexpanded	Ribbon-like, unexpanded	Ribbon-like, unexpanded	Ribbon-like, unexpanded
Cr 16. Morphology of annular bridge	?	Linea semicircularis	Linea semicircularis	Linea semicircularis	Linea semicircularis	Partial
Cr 17. Encroachment of the auditory bulla on the pterygoid fossa	?	Absent	Absent	Absent	Present	Absent
Cr 18. Contact between lateral pterygoid plate and bulla wall	?	Abutting	?	Laminar	Laminar	?
Cr 19. Extent of contact between the lateral pterygoid plate and the bulla wall	?	Slight	?	Extensive	Slight	?
Cr 20. Flange of basioccipital overlapping medial bulla wall	Absent	Absent	Absent	Absent	Extensive	Absent

Table 4 (Continued)

Characters	<i>Cantius abditus</i>	<i>Adapis parisiensis</i>	<i>Leptadapis magnus</i>	<i>Mahgarita stevensi</i>	<i>Pronycticebus gaudryi</i>	<i>Smilodectes gracilis</i>
Cr 21. Suprameatal foramen	?	Absent	Absent	Absent	Absent	Absent
Cr 22. Parotic fissure	Closed	Closed	Closed	Closed	Closed	Closed
Cr 23. Orbit size	Large?	Small	Small	Small	Small	Small
Cr 24. Postorbital closure	Postorbital bar	Postorbital bar	Postorbital bar	Postorbital bar	Postorbital bar	Postorbital bar
Cr 25. Composition of postorbital septum	Not relevant	Not relevant	Not relevant	Not relevant	Not relevant	Not relevant
Cr 26. Zygomatic lacrimonasal contact	?	Present	?	Absent	Present	Present
Cr 27. Pronounced interorbital constriction	?	Absent	?	?	Absent	Absent
Cr 28. Lacrimonasal contact		Separated by fronto-maxillary contact	?	?	Separated by fronto-maxillary contact	?
Cr 29. Foramen rotundum	?	?	?	?	Present	?
Cr 30. Position of lacrimonasal contact	?	Outside orbit	Outside orbit	Outside orbit	Outside orbit	?
Cr 31. Metopic suture in adult	?	Fused or unfused	?	?	Unfused	?
Cr 32. Orbital convergence relative to relative orbit size	?	Moderately convergent	Moderately convergent	?	Moderately convergent	Moderately convergent
Cr 33. Posterior nasal spine	?	Small but distinct	?	Small but distinct	?	?
Cr 34. Posterior palatine torus	?	Present	?	Present	?	?

Table 4 (Continued)

Characters	<i>Cantius abditus</i>	<i>Adapis parisiensis</i>	<i>Leptadapis magnus</i>	<i>Mahgarita stevensi</i>	<i>Pronycticebus gaudryi</i>	<i>Smilodectes gracilis</i>
Cr 35. Pyramidal processes	?	Laterally placed	Laterally placed	Laterally placed	Laterally placed	Laterally placed
Cr 36. Medial pterygoid plate	?	Absent	Absent	Absent	?	Short
Cr 37. Snout length	?	Short	?	Short	?	?
Cr 38. Maxillary depth	?	Deep	?	Deep	?	?
Cr 40. TMJ	Biconcave and wide	Biconcave and wide	Biconcave and wide	Biconcave and wide	Biconcave and wide	Biconcave and wide
Cr 41. Entoglenoid process	Weak	Weak	Weak	Weak	?	Weak
Cr 47. Inratympanic portion of facial nerve	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal	Enclosed in a bony canal
Cr 48. Epitympanic crest	Present	Present	Present	Present	Present	Present

Material examined for scoring of characters listed in Ross (1994).

Abbreviations: AAC, anterior accessory cavity; CN I, cranial nerve 1, the olfactory nerve; ICA, internal carotid artery; ICN, internal carotid nerve; PA, promontory artery; PC, promontory canal; PCF, posterior carotid foramen; SA, stapedia artery; SC, stapedia canal; TMJ, temporomandibular joint.

Table 5 Distribution of skull characters among some possible primate outgroups

	Scandentia	<i>Plesiadapis tricuspidens</i>	<i>Ignaciuss graybullianus</i>
Cr 1. Transverse septum	Absent	Absent	Absent
Cr 2. Extent of pneumatization of AAC	AAC absent	AAC absent	AAC absent
Cr 3. Pneumatization of mastoid	Absent	?	?
Cr 4. Perbullar pathway	Absent	Absent	Absent
Cr 5. Anteroposterior PCF position relative to midpoint of tympanic ring	Posterior	Posterior	Posterior
Cr 6. Mediolateral position of PCF	Medial	Lateral	Lateral
Cr 7. Ventrodorsal position of PCF	Dorsal	Dorsal	Dorsal
Cr 8. Position of posterior PCF relative to fenestra cochleae	Posterior	Posterior	Posterior
Cr 9. Position of the pathway for ICA or ICN relative to the fenestra cochleae	No shielding	Runs across ventral rim of fenestra cochleae, shielding it ventrally	Runs across ventral rim of fenestra cochleae, shielding it ventrally
Cr 10. Position PA on the promontorium anterior to fenestra cochleae	Ventrolateral	Ventrolateral	Ventrolateral
Cr 11. Size of stapedia and promontory canals	Both canals large and subequal	Both canals absent	Both canals absent
Cr 12. Morphology of promontory pathway, if present	Complete canal	Open groove	No groove
Cr 13. Presence or absence of canal for internal carotid artery or nerves	Canal present	Small canal present	?
Cr 14. Position of ventral edge of the tympanic bone	Intrabullar	Intrabullar	Extrabullar
Cr 15. The shape of the tympanic bone	Ribbon-like, unexpanded	Ribbon-like, unexpanded	Expanded laterally
Cr 16. Morphology of annular bridge	Linea semicircularis	Complete annular bridge	Absent
Cr 17. Encroachment of the auditory bulla on the pterygoid fossa	Absent	Absent	Absent
Cr 18. Contact between lateral pterygoid plate and bulla wall	Absent	?	Absent
Cr 19. Contact between the lateral pterygoid plate and the bulla wall	Absent	?	Absent
Cr 20. Flange of basioccipital overlapping medial bulla wall	Absent	?	Absent
Cr 21. Suprameatal foramen	Present	Absent	Present
Cr 22. Parotic fissure	Patent	Patent	Patent
Cr 23. Orbit size	Small	Small	Small
Cr 24. Postorbital closure	Bar/process	None	None
Cr 26. Zygomatic-lacrimal contact	Present	?	Absent
Cr 27. Pronounced interorbital constriction	Absent	Absent	Absent

Table 5 (Continued)

	Scandentia	<i>Plesiadapis tricuspidens</i>	<i>Ignacius graybullianus</i>
Cr 28. Lacrimal palatine contact	Present	Absent	?
Cr 29. Foramen rotundrum	Absent	Absent	Absent
Cr 30. Position of lacrimal foramen	Outside orbital margin	Outside orbital margin	Inside orbital margin
Cr 31. Metopic suture in adult	Fused	Unfused	Unfused
Cr 32. Orbital convergence relative to relative orbit size	Divergent orbits	?	?
Cr 33. Posterior nasal spine	Absent	Small but distinct	Absent
Cr 34. Posterior palatine torus	Present	Present	Present
Cr 35. Pyramidal processes	Medially placed	Medially placed	Medially placed
Cr 36. Medial pterygoid plate	Long	?	Long
Cr 37. Snout length	Long	Long	Long
Cr 38. Maxillary depth	Shallow	?	?
Cr 40. TMJ	Biconcave and wide	Biconcave and wide	Biconcave and wide
Cr 41. Entoglenoid process	Weak	Strong	Strong
Cr 47. Intra tympanic portion of facial nerve	Canal	No canal	?
Cr 48. Epi tympanic crest	Present	Absent	?

Material examined for scoring of characters listed in Ross (1994).

Abbreviations: AAC, anterior accessory cavity; CN I, cranial nerve 1, the olfactory nerve; ICA, internal carotid artery; ICN, internal carotid nerve; PA, promontory artery; PC, promontory canal; PCF, posterior carotid foramen; SA, stapedial artery; SC, stapedial canal; TMJ, temporomandibular joint.

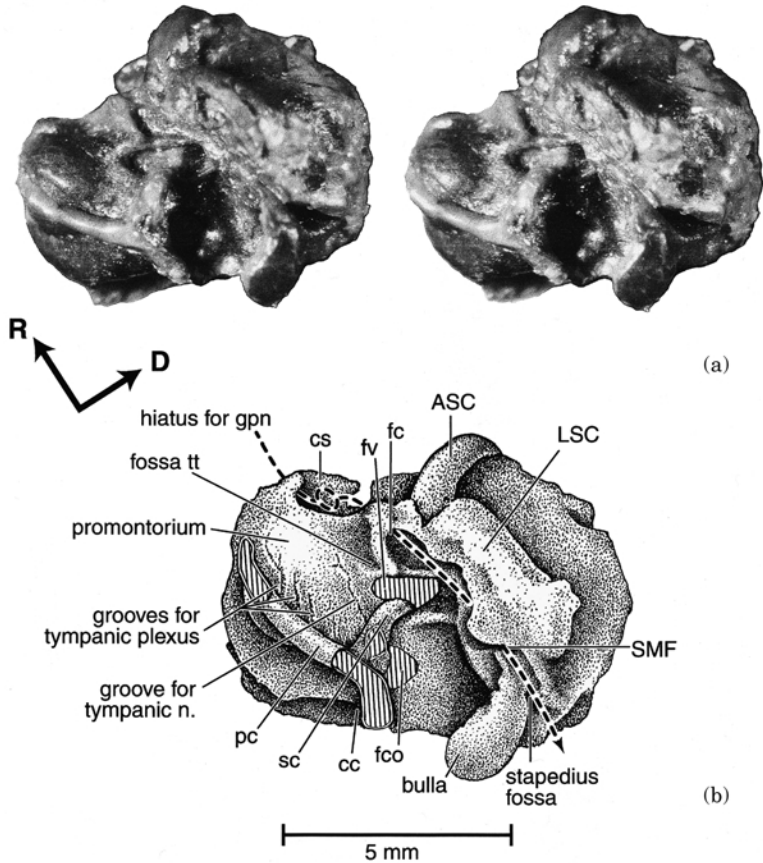


Figure 1. (a) Anterolateral view of left petrosal UCM 57460, stereophoto. (b) Anterolateral view of left petrosal UCM 57460. Hatched lines represent matrix. ASC, anterior semicircular canal; cc, carotid canal; cs, cavum supracochleare; fc, facial canal; fco, fenestra cochleae; fossa tt, fossa for tensor tympani; fv, fenestra vestibuli; hiatus for gpn, hiatus for greater petrosal nerve; LSC, lateral semicircular canal; pc, promontory canal; sc, stapedial canal; SMF, stylomastoid foramen. R and D indicate rostral and dorsal respectively. The dashed circle in cavum supracochleare represents the position of the geniculate ganglion. The dashed lines running rostrally and caudally from the ganglion represent the pathways of the greater superficial petrosal and facial nerves, respectively.

bulla. Breakage of the bulla has destroyed the intrabullar orifice of the parotic fissure, but judging from the orientation of the extrabullar fossa, it must have lain posterolateral to the fenestra vestibuli. The fissure leads into the funnel-shaped extrabullar fossa which lies inferior and medial to the stylomastoid foramen. Because the lateral wall of the facial canal is broken away in this specimen, the parotic fissure can be seen to lie inferior to the facial canal separated from it by the apposition of the bulla to the floor

of the facial canal. On this basis the extrabullar depression is reconstructed as the stapedius fossa and the fissure as the conduit for the tendon of m. stapedius (Cr. 22). Although similar detail cannot be reconstructed for other taxa, an extrabullar stapedius fossa is found in a similar position in *Necrolemur*, *Shoshonius*, and *Tarsius* among primates, as well as in tree shrews, most Insectivora and possibly plesiadapiforms (MacPhee, 1981; Beard & MacPhee, 1994; Ross, 1994). Together, the

stylomastoid foramen and the stapedius fossa/parotic fissure make a "figure-eight" outline, similar to that seen in scandentians, *Ignacius*, *Plesiadapis*, *Necrolemur*, *Microchoerus*, *Tarsius*, and *Shoshonius* (Kay *et al.*, 1992; Beard & MacPhee, 1994; Ross, 1994). The position of the stapedius fossa in the Shanghuang petrosal might be a small depression posterior to the lower part of the facial canal, and outside the tympanic cavity and inside the mastoid cavity, or it might have been intratympanic leaving no obvious fossa.

There is no evidence of a transverse septum arising from the lateral surface of the cochlear housing or the small portion of the bony canal for the promontory artery (see below). In anthropoids the transverse septum arises from the entire length of the promontory and internal carotid canals except for the area of the apical aditus immediately anterior to the promontorium. In anthropoids, the portion of the promontory canal that corresponds with the portion preserved in *Omomys* exhibits a ventrally directed flange corresponding to the transverse septum. The absence of such a flange suggests that an anterior accessory cavity did not form inside the bulla wall (Cr. 1) and the internal carotid artery did not run inside the bulla wall (Cr. 4). Fossil Anthropoidea, such as *Apidium* and *Aegyptopithecus*, exhibit broken remnants of such a septum even when the petrosals are fairly battered (e.g., DU 2568, MacPhee & Cartmill, 1986; Ross, 1994) suggesting that there would be some remnant if an intrabullar transverse septum had been present.

A small fragment of the tympanic is preserved adhering to a septum projecting laterally from the lateral semicircular canal of UCM 57461, but it allows nothing to be said regarding the morphology or position of the tympanic ring.

Arteries. The most important (and largest) intrabullar arteries in primates are the inter-

nal carotid artery, the proximal stapedia artery and the promontory artery. The internal carotid artery (ICA) runs from the posterior carotid foramen to the promontorium, along the anteroinferior edge of a septum, the posterior septum. A posterior septum is present in lemuriforms, omomyiforms, adapiforms, anthropoids and cheirogaleids running to the medial bulla wall ventral to the fenestra cochleae (Ross, 1994). It may carry an ICA or the carotid plexus (post-synaptic sympathetics). This septum is preserved in UCM 57460. Shortly after reaching the promontorium the internal carotid gives off a dorsolaterally directed branch, the proximal stapedia artery, before continuing rostrally across the ventrolateral surface of the promontorium as the promontory artery. In primates, the proximal stapedia artery runs dorsally, through the obturator foramen in the stapes before piercing the roof of the tympanic cavity and passing into the braincase. Normally the term "proximal stapedia artery" terminates with division of the artery into the ramus superior and ramus inferior. As most primates lack a large ramus inferior (Cartmill & MacPhee, 1980), the term stapedia artery can be applied within primates to refer to the proximal stapedia artery and its only branch, the ramus superior.

The canals for the internal carotid, promontory and stapedia arteries are best preserved in UCM 57460. The internal carotid canal is open along its entire preserved length, but this is probably an artefact of postmortem breakage because the broken rims of the canal are preserved irregularly along its edges. Immediately after branching off the carotid canal, the stapedia canal is damaged, although remnants of the canal roof itself are preserved adjacent to the carotid canal and the fenestra vestibuli. The promontory canal is preserved up to the apex of the promontorium, but its roof is broken off rostrally. On the rostral surface of the cochlea only a bony ridge is preserved

running dorsally to terminate near the hiatus for the greater petrosal nerve (Figure 1). Thus, it cannot be determined whether the carotid canal was complete, but the stapedia and promontory canals were complete at least where they remain undamaged (Cr. 12).

The position of the posterior carotid foramen in the bulla cannot be established with great precision, although with sufficient accuracy to say it would certainly have lain posterior to the fenestra cochleae (Cr. 8), in the medial aspect of the bulla surface (Cr. 6), and adjacent to the basioccipital (i.e., dorsal) (Cr. 7). It was probably slightly more posteriorly positioned than that of the Shanghuang petrosal assigned to *Eosimias* (MacPhee *et al.*, 1995). The carotid canal does not shield the fenestra cochlea ventrally (Cr. 9, Cr. 13). The promontory canal courses across the ventrolateral surface of the promontorium and across the cupula of the cochlea (Cr. 10), beyond which point it is not preserved. The stapedia canal ascends towards the fenestra vestibuli, ending at its lower edge. The stapedia and promontory canals are subequal in size and both are large (Cr. 11).

Nerves. The superior aspect of UCM 57460 bears a low ridge along the superior aspect of pars cochlearis; this ridge defines the broken edge of the roof of cavum supracochleare, which in life houses the geniculate ganglion of the facial nerve (Figure 1, dashed circle). The primary facial foramen, which carries the facial nerve from the internal acoustic meatus to the cavum supracochleare is also preserved. A small hiatus Fallopii opens rostrally for the greater petrosal nerve and the secondary facial foramen pierces tegmen tympani superior to the fenestra vestibuli. The canal for the facial nerve runs posteriorly and inferiorly in an almost straight line to the stylomastoid foramen. In UCM 57460 its lateral wall is broken away, but in UCM 57461 the entire tympanic portion of

the facial nerve was enclosed in a canal. The lateral wall of the stylomastoid foramen is broken away in UCM 57460, but medially it is continuous with the stapedius fossa via a narrow gap. In UCM 57460 the groove for the tympanic nerve is preserved crossing the lower part of sinus tympani and part of the promontorium (Figure 1). In addition, several faint grooves indicate places where sympathetic contributions to the tympanic plexus left the promontory canal and extended out onto the promontorium (Figure 1).

Pneumatization. UCM 57460 and UCM 57461 preserve some details of pneumatization. In UCM 57461 the base of the broken exocranial wall is preserved lying posterolateral to the posterior limb of the lateral semicircular canal. Three bony septa run from the semicircular canal to this broken wall. This is interpreted here as indicating some degree of mastoid pneumatization. In UCM 57460 the broken remnant of the exocranial wall of this mastoid cavity is preserved immediately posterior and superior to the stapedius fossa. In this specimen, the lateral surface of the lateral semicircular canal is also roughened along the most lateral moiety. MacPhee *et al.* (1995) observe that in living animals a smooth lateral surface of the lateral semicircular canal indicates that mastoid pneumatization has displaced the exocranial wall away from the lateral semicircular canal. The reverse of this is not true, however: i.e., it is possible to have a roughened lateral portion of the lateral semicircular canal and some mastoid pneumatization. For example, in specimens of *Otolemur crassicaudatus* and *Galagoides demidoff* dissected for this study, one or more bony septae run across the pneumatic mastoid space from the lateral semicircular canal to the exocranial wall. Were these to be broken, a roughened lateral semicircular canal would be present in the context of extensive mastoid pneumatization.

In UCM 57641 the lateral and posterior walls of the subarcuate fossa are exposed by breakage into the mastoid pneumatic spaces. The subarcuate fossa, which houses the paraflocculus of the cerebellum in life, was quite extensive, but did not reach the exocranial surface of the mastoid. Evidently, the mastoid was more pneumatized than in *Microcebus* (in which the subarcuate fossa meets the exocranial skull wall), but less so than in *Galago* or *Otolemur* in which the subarcuate fossa and the lateral semicircular canal are separated from the exocranial wall by a pneumatic space.

There is some evidence that the mastoid pneumatization in *Omomys* arose in the epitympanic recess (Cr. 3). In UCM 57641 a smooth, curved wall of bone superior to the fenestra vestibuli is probably the medial wall of the epitympanic recess. This wall is in smooth continuity with both the superior surface of pars cochlearis and the pneumatized area of the mastoid. This suggests that the mastoid pneumatization arose in the epitympanic recess and was continuous with a supracochlear cavity (*sensu* MacPhee, 1981)² of unknown dimensions.

Inferior aspect of the petrosal. The cochlear canaliculus is preserved in UCM 57460 and UCM 57461. It lies in the roof of a small notch lying anteromedial to the point where the posterior septum carrying the carotid canal meets the medial bulla wall. This notch would have lain in the lateral portion of the jugular fossa. In humans a similar pyramid-shaped notch in this position houses the inferior ganglion of CN IX and receives the cochlear canaliculus at its apex (Williams & Warwick, 1980:329). A similarly shaped and positioned notch sur-

rounding the inferior orifice of the cochlear canaliculus has been noted previously in the Fayum petrosals attributable to *Apidium* and *Aegyptopithecus* (Ross, 1994).

Discussion

Omomys and the primate morphotype

The otic characters preserved in the *Omomys* specimens reported here are summarized in Table 3 along with character states for skull characters amongst other omomyiforms. The ear region of *Omomys* shares several features with all omomyiforms and adapiforms, implying that these were present in the last common ancestor of these two taxa: lack of a perbullar pathway of the promontory artery; lack of an anterior accessory cavity; posterior carotid foramen positioned posterior to the fenestra cochleae; a complete canal for the intratympanic portion of the facial nerve; and probably (although not demonstrably) a bulla derived from outgrowths of the petrosal.

Absence of a perbullar pathway for the promontory artery, absence of an anterior accessory cavity and a posteriorly positioned posterior carotid foramen are present in all the outgroup taxa listed in Table 5, as well as in most eutherians, and are not synapomorphies of Primates. The remaining two features may be primate synapomorphies depending on the outgroup relationships of Primates. The facial nerve is demonstrably not within a bony canal in plesiadapids, paromomyids or microsypids (Wible & Covert, 1987), although it is enclosed by an outgrowth of the petrosal in treeshrews, as in extant and (probably) fossil primates. The composition of the bulla in possible primate outgroups is variable, with scandentians having a bulla derived from a single entotympanic element, *Ignacius* probably having an entotympanic bulla (Kay *et al.*, 1992), and *Plesiadapis* resembling adapiforms and omomyiforms in having a bulla smoothly continuous with the petrosal. The bullae of

²This supracochlear cavity of MacPhee is not the cavum supracochleare *sensu stricto*, which houses the geniculate ganglion of the facial nerve. MacPhee's supracochlear cavity (a) lies above cavum supracochleare, separated from it by a sheet of bone, and (b) arises by pneumatization from the epitympanic recess.

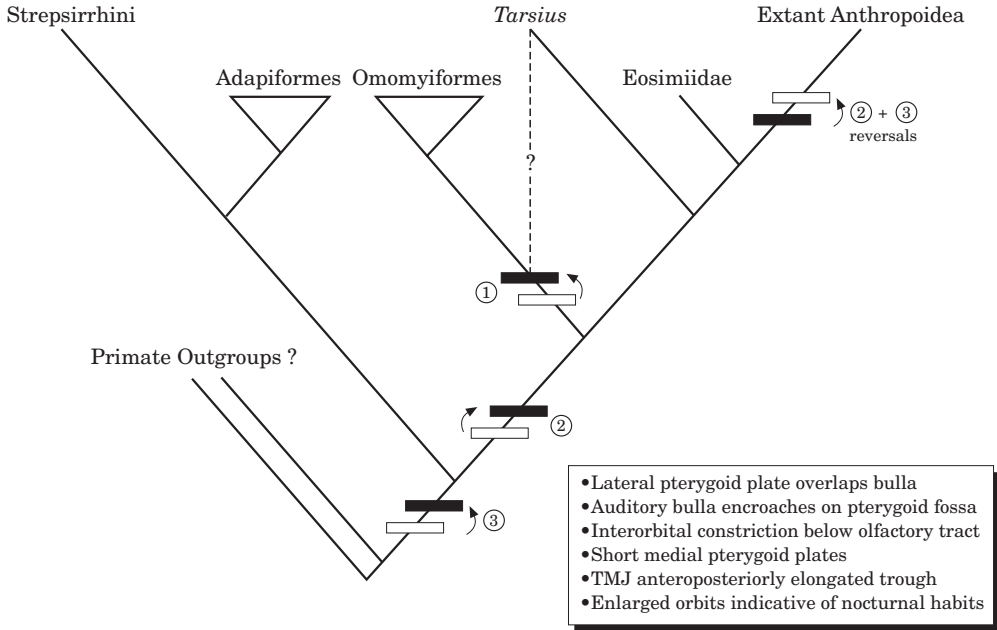


Figure 2. Phylogenetic tree of Primates illustrating three possible ways in which tarsier-omomyiform similarities may have arisen. A closed rectangle represents the origin of the character states listed in the box. An open rectangle represents other states of these characters. Option 1: similarities are synapomorphies of a *Tarsius*+*Omomyiformes* clade, with *Tarsius* possibly nested within omomyiforms. Option 2: similarities arose in stem lineage of Haplorhini [here defined as ((*Tarsius*+*Anthropoidea*) *Omomyiformes*)]. Tarsiers are more closely related to anthropoids and these features were lost in the anthropoid stem lineage. Option 3: similar to option 2, except tarsier-omomyiform similarities are primitive for Primates and subsequently lost in Strepsirrhini and Anthropoidea. Just considering the data presented here, Option 1 seems most parsimonious. However, this pattern of character evolution assumes omomyiform monophyly. If omomyiforms are paraphyletic (with anthropoids nesting within them) then Options 2 & 3 are equally parsimonious to Option 1. Option 2 is the most parsimonious in context of all dental, postcranial and cranial data (Ross *et al.*, 1998).

adapiforms and omomyiforms—including *Omomys*—are assumed to be petrosal in origin because these taxa are demonstrably related to living primates, but this reasoning cannot be applied to *Plesiadapis*. Thus, a petrosal bulla may well be a synapomorphy of Primates as traditionally stated, or it may characterize a more inclusive clade of Primates and *Plesiadapis* plus its relatives.

Several features found in other omomyiform skulls, but not preserved in this *Omomys* material, are also found among all adapiforms for which the anatomy is known (Table 4). These add to the conglomerate of character states likely to have characterized the last common ancestor of adapiforms and

omomyiforms: moderately convergent orbits surrounded laterally by a postorbital bar; a lacrimal foramen positioned outside the orbit (Alexander & MacPhee, 1999); a posterior nasal spine which is small but distinct; an epitympanic crest on the tympanic roof; and a fenestra cochleae shielded ventrally by a carotid canal running across its ventral margin.

Omomys and the omomyiform morphotype

The petrosals of *Omomys carteri* are unique among omomyiforms in possessing a ventrally shielded fenestra cochleae, probably a primitive feature shared with adapiforms, *Plesiadapis* and *Ignacius*. Other features

O. carteri does not share with all omomyiforms are mastoid pneumatization (present in *Necrolemur*, absent in *Shoshonius*), the medial position of the posterior carotid foramen (medial in *Necrolemur*, lateral in *Shoshonius*), and the large subequal dimensions of the promontory and stapedial canals (in *Necrolemur* the stapedial canal is slightly smaller than the promontory). It is not clear whether *Shoshonius* and *Necrolemur* are derived among omomyiforms in these respects. Regardless, with the exception of these features, *Omomys* can be said to have a generic, if slightly primitive, omomyiform ear region.

The ear region of *Omomys* shares several features with all other omomyiforms that are not found in most adapiforms: there is a complete canal for the promontory artery; the parotic fissure is patent and the stapedius fossa lies outside the bulla. These features would have characterized the last common ancestor of Omomyiformes, but all are found among inferred primate outgroups (Table 5) making it difficult to determine whether they are synapomorphies or symplesiomorphies without knowing the relationships among primates and their possible outgroups.

The general similarities among all omomyiform ear regions reflect a general uniformity in overall skull anatomy in this group. Several features not preserved in the *Omomys* material described here are found in all omomyiforms that are sufficiently well known: a complete annular bridge extends from the tympanic ring to the bulla wall; the auditory bulla encroaches on the pterygoid fossa; a basioccipital flange overlaps onto the medial bulla wall; there is an extensive, laminar contact between the lateral pterygoid plate and the lateral bulla wall; there is a pronounced interorbital constriction below the olfactory tract; the metopic suture is fused in adults; the pyramidal processes are medially placed; the medial pterygoid plate is short; and the TMJ is an antero-

posteriorly elongated trough with a strong entoglenoid process. In addition, all omomyiforms in which the orbits are well enough preserved—including *Omomys carteri* (Alexander & MacPhee, 1999)—have orbits at least large enough to indicate nocturnal habits. Among the primate outgroups, *Plesiadapis* also manifests a complete annular bridge, scandentians have a fused metopic suture as adults, all three outgroups assessed here have medially placed pyramidal processes, and both *Plesiadapis tricuspidens* and *Ignacius graybullianus* have a strong entoglenoid process in the TMJ. This leaves seven features as definitive omomyiform synapomorphies: a basioccipital flange overlapping the bulla wall; the auditory bulla encroaching on the pterygoid fossa; an extensive, laminar contact between the lateral pterygoid plate and the lateral bulla wall; pronounced interorbital constriction below the olfactory tract; short medial pterygoid plates; a TMJ that is an antero-posteriorly elongated trough; and enlarged orbits indicative of nocturnal habits.

Omomyiforms and tarsier relationships

As summarized in the Introduction, and elsewhere (Ross, 1994; Ross *et al.*, 1998), omomyiform origins for *Tarsius* have often been suggested. The strongest argument is that presented by Beard and colleagues. Beard *et al.* (1991) suggested that *Tarsius* might be more closely related to *Shoshonius* than to any other omomyiform (see also Beard & MacPhee, 1994). Placement of *Tarsius* somewhere in the omomyiform clade is advocated by Beard & MacPhee (1994) on the basis of narrow and peaked choanae, presence of a patent parotic fissure, a basioccipital flange on the bulla, and the lateral pterygoid plate overlapping the lateral aspect of the bulla.

The first of these characters, choanal shape, is argued elsewhere to be related to orbital hypertrophy and hence not an independent character for phylogeny

reconstruction (Ross, 1994; Ross *et al.*, 1998). Beard & MacPhee (1994:81) question these claims because *Necrolemur* has relatively smaller orbits than either *Tarsius* or *Shoshonius* and yet still exhibits peaked choanae. The second feature, a patent parotic fissure, is universally present among omomyiforms and widespread among possible primate relatives, suggesting that it is probably primitive for primates and not indicative of tarsier-omomyiform relationships (Ross, 1994).

However, the basioccipital flange, the lateral pterygoid plate overlapping the bulla and several other features flagged as omomyiform synapomorphies in the previous section are indeed found in *Tarsius*: the auditory bulla encroaching on the pterygoid fossa; pronounced interorbital constriction below the olfactory tract; short medial pterygoid plates; a TMJ that is an antero-posteriorly elongated trough; and enlarged orbits indicative of nocturnal habits. Being absent in adapiforms and putative primate outgroups, these features are possibly synapomorphies of a tarsier-omomyiform clade.

An alternative interpretation of these features is that they are synapomorphies of an [Omomyiformes + (Anthropoidea + *Tarsius*)] clade, with the loss of these features characterizing Anthropoidea. In the context of a large dataset including postcranial and dental characters, this interpretation is more parsimonious than that advanced by Beard and his colleagues, but only marginally so (Ross *et al.*, 1998). It is, therefore, not possible at present to say with certainty whether tarsiers are more closely related to omomyiforms or to anthropoids.

The hypothesis of an omomyiform origin for tarsiers is strengthened if *Tarsius* can be shown to nest deep *within* omomyiforms, being more closely related to one particular clade of omomyiforms than others. This requires one group of omomyiforms to share similarities with *Tarsius* not seen in other

omomyiformes. Among omomyiforms, only *Shoshonius* possesses features of the ear region shared with *Tarsius* to the exclusion of other omomyiforms: lack of mastoid pneumatization and a laterally positioned posterior carotid foramen. Neither of these is particularly compelling evidence for a *Tarsius*-washakiine clade as lack of mastoid pneumatization also characterizes Scandentia, lemurids, and *Pronycticebus*, and a laterally positioned posterior carotid foramen is found in *Plesiadaptis*, cheirogaleids, lemurids and adapiforms.

Perhaps the best cranial evidence for a *Tarsius*-*Shoshonius* clade is the relatively enlarged orbits and, if it is indeed homologous (Ross, 1994), the suprameatal foramen (Beard & MacPhee, 1994). However, Alexander & MacPhee (1999) report that *Omomys carteri* has larger orbits than *Shoshonius*, suggesting that extreme orbital hypertrophy might characterize a more inclusive clade than just washakiins, or might have evolved more than once among omomyiforms. One of us has raised questions elsewhere regarding the homology of the "suprimeatal foramina" of *Tarsius* and *Shoshonius* (Ross, 1994:507). The foramina are differently positioned and of different sizes in the two taxa and, moreover, a suprimeatal foramen of some sort is also found among possible outgroup taxa (Scandentia, *Ignacius*) and in *Necrolemur*. This feature is regarded by us as being of dubious homology and polarity (see also Beard & MacPhee, 1994).

The petrosals of *Omomys* described here, like those of other omomyiforms, fail to provide convincing synapomorphies for an omomyiform-tarsier clade to the exclusion of other primates. Morphological and functional analysis of the postcranial evidence suggests omomyiforms are not more similar to tarsiers than they are to other extant primates (Covert & Murphey, 1994; Covert, 1995, 1997; Anemone & Covert, n.d.), although phylogeny reconstruction on the

basis of only postcranial (Ross *et al.*, 1998), or mixed postcranial and cranial data (Dagosto *et al.*, 1999), does provide support for a tarsier–omomyiform clade.

The Shanghuang petrosal and anthropoid origins

The unusual cranial features shared by tarsiers and anthropoids—the postorbital septum, perbullar pathway for the internal carotid artery and an anterior accessory cavity in the ear region—continue to provide the most compelling argument for anthropoid and tarsier relationships. Citing Simons & Rasmussen (1989), Beard & MacPhee (1994) argue that the tarsier postorbital septum cannot be homologous with that of anthropoids because of morphological differences between them. Simons & Rasmussen (1989) argue that because the tarsier postorbital septum consists primarily of frontal bone and that of anthropoids consists primarily of zygomatic, the contact between the zygomatic and alisphenoid must have evolved independently. This point has been addressed elsewhere (Cartmill, 1980; Ross, 1994). Suffice it to say here that the different proportions of legs and arms in a frog and a human have never been invoked to argue that they evolved their limbs independently. Similarly, to exclude the zygomatic–alisphenoid contact from a dataset on the grounds of differing proportions of the bones in the septum (Beard & MacPhee, 1994) is arbitrary. Recent analyses of postcranial and cranial data together suggest that Beard agrees (Dagosto *et al.*, 1999).

The only way to definitively determine whether the tarsier–anthropoid similarities are homologous is the fossil record. Thus, the recent recovery of a petrosal lacking these features from the Middle Eocene fissure fillings at Shanghuang in China is of great interest, because these fissures also contain remains of possible early anthropoids. The Shanghuang petrosal lacks an

anterior accessory cavity and a perbullar pathway for the internal carotid artery, so if two conditions are met, this petrosal would support hypotheses that the tarsier–anthropoid otic similarities evolved in parallel, weakening the tarsier–anthropoid hypothesis. The two conditions are (1) that eosimiids are early anthropoids and, (2) the petrosal is that of an eosimiid.

(1) The evidence linking eosimiids to anthropoids is compelling. Beard *et al.* (1994, 1996) presented several features of the eosimiid dentition linking the two known species to Anthropoidea and phylogenetic analyses of an extensive morphological data set place eosimiids as the sister taxon to all extant and fossil anthropoids (Kay *et al.*, 1997; Ross *et al.*, 1998). There are doubts among some workers as to the anthropoid affinities of eosimiids, but no-one has presented an alternative hypothesis based on the data at hand.

(2) The evidence relating the petrosal to an eosimiid is less compelling. The petrosal comes from Fissure D, one of five fissures at Shanghuang yielding fossil primate material. Fissure D is apparently older than the other fissures at Shanghuang (MacPhee *et al.*, 1995), suggesting that the taxonomic contents of the other fissures are not relevant for the attribution of the petrosal. In addition to the petrosal, Fissure D has yielded eosimiid material “in relative abundance” (MacPhee *et al.*, 1995), one omomyiform, *Macrotarsius macrorhysis* (Beard *et al.*, 1994), and several taxa of adapiforms. The petrosal preserves no features that would link it to adapiforms to the exclusion of other primates, and tarsiiids are not found in Fissure D. Therefore, if the petrosal derives from one of the taxa represented in the fissure by dental material, *Macrotarsius* and eosimiids are possible originators of the petrosal.

In many ways the Shanghuang petrosal resembles those of omomyiforms, particularly the *Omomyys* petrosals described here. Indeed, the Shanghuang petrosal differs

from that of *Omomyys* only in having relatively larger arterial canals. It resembles anthropoids and *Necrolemur* in having a posterior carotid foramen that may have been slightly further forward leaving the foramen rotundum unshielded ventrally. The only omomyiform from Shanghuang, *Macrotarsius macrorhysis*, is known from two teeth recovered from the same fissure as the petrosal. There is, therefore, good morphological and associational evidence that the Shanghuang petrosal belongs to an omomyiform.

Arguing against the attribution of the petrosal to *Macrotarsius* is its small size (MacPhee *et al.*, 1995). To make this point, MacPhee *et al.* compared measures of promontorium length and body mass in seven species of extant primates. The measures of promontorium length were made on single specimens of the seven species and the body masses were obtained from the literature. They then compared body mass estimates for *Eosimias sinensis* (67–137 g) and *Macrotarsius macrorhysis* (900–1646 g). The three specimens of extant primates in the body size range of *E. sinensis* have petrosals measuring 3.00–4.11 mm and the two specimens in the body size range of *Macrotarsius* have petrosals measuring 5.23 and 5.31 mm. The Shanghuang petrosal measures 3.26 mm, suggesting to MacPhee *et al.* (1995) that the petrosal most probably belongs to *Eosimias* rather than *Macrotarsius*.

While these data are indeed suggestive, they are far from conclusive. The sample of seven promontorium lengths only ranges over 2.31 mm, measurement error is not documented, and the measurement of promontorium length used by MacPhee *et al.* (1995) is of unknown intraspecific variability and unknown relationship to body mass. It would be difficult to gather such data, requiring either dissection of osteological specimens or micro-CT. However, it should be done before the assignment of the Shanghuang petrosal to

Eosimias is accepted, particularly in light of recent reports of 15 haplorhine species from Shanghuang ranging in body mass from 12–23 g (Gebo *et al.*, 2000). These recent discoveries raise the possibility that the petrosal belongs to a nonanthropoid, non-tarsiid haplorhine that would not be expected to possess an anterior accessory cavity anyway.

The debate over the taxonomic status of the Shanghuang petrosal may be moot with respect to the phylogenetic placement of *Eosimias* and *Tarsius*. These taxa fall out as successive sister taxa to the Anthroipoidea whether the petrosal belongs to *Eosimias* or not (Ross *et al.*, 1998). In this tree structure, *Eosimias*' lack of the tarsier–anthropoid otic synapomorphies is equally parsimoniously viewed as either a gain of these features in the tarsier–anthropoid stem lineage and their loss in the Eosimiidae, or their parallel evolution in tarsiers and anthropoids.

Summary and conclusions

The morphology of the first petrosals from an omomyine are described: those of *Omomyys carteri*. These *Omomyys* petrosals exhibit a generic omomyiform morphology. The monophyly of Omomyiformes is based on other cranial characters (as well as dental and postcranial characters assessed elsewhere). The similarity of the Shanghuang petrosal to those of omomyiforms, and the presence of other small haplorhines in the Shanghuang fissures, suggest that an anthropoid affinity for that petrosal cannot be definitively established at present.

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