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Significance of primate petrosal from Middle Eocene fissure-fillings at Shanghuang, Jiangsu Province, People's Republic of China

An isolated petrosal bone belonging to a diminutive primate is reported from Middle Eocene fissure-fills near Shanghuang (southern Jiangsu Province, People's Republic of China), the type locality of several newly described primates (*Eosimias sinensis*, a basal anthropoid; *Adapoides troglodytes*, a basal adapinid; *Tarsius eocaenus*, a congener of extant tarsiers; and *Macrotarsius macrorhysis*, the first Asian representative of an otherwise exclusively North American genus). Because of its fragmentary condition and unique combination of characters, the Shanghuang petrosal cannot be assigned unambiguously to any of the Shanghuang primate taxa known from dental remains. However, the possibility that the petrosal represents either an adapid or a tarsiid can be dismissed because it lacks defining basicranial apomorphies of these groups. By contrast, the clement does present arterial features consistent with its being haplorhine. Deciding between the likeliest candidates for its allocation—Omomyidae and Eosimiidae—is difficult, in part because it is not known what (or even whether) basicranial characters can be used to distinguish these clades. If the Shanghuang petrosal is that of an eosimiid, as both direct and indirect evidence appears to indicate, the following implications emerge: (1) as long suspected on other grounds, anthropoids share a closer evolutionary history with Omomyidae (and Tarsiiformes) than they do with Adapidae (and Strepsirhini); (2) the specialised basicranial anatomy of extant anthropoids and their immediate cladistic relatives is derived from a primitive precursor whose otic morphology was like that of omomyids in most known respects; (3) the evolution of the defining dental and basicranial apomorphies of extant Anthropoidea has been distinctly mosaic in pattern.

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Introduction

Our knowledge of the taxonomic diversity of primates inhabiting coastal regions of China during the Middle Eocene has been enhanced dramatically by discovery of a diverse primate fauna in the Shanghuang fissure-fillings, including at least two species of adapiforms, an omomyid, a tarsiid and several species of basal anthropoids or eosimiids (Qi *et al.*, 1991; Beard *et al.*, 1994). The mammalian fauna recovered from these fissures differs compositionally from better-known Middle Eocene faunas of Central Asia in several respects. In addition to a wide range of previously unrecorded species of placental mammals, the Shanghuang fauna also includes marsupials, a group not hitherto reported from the Eocene of Asia.

In contrast to many other Paleogene Asian fossil localities, the Shanghuang fissures preserve, in remarkable abundance, skeletal elements other than jaws and teeth. This by itself makes them of special interest for paleoprimatological studies. At present, teeth and jaws are all that are available to document the early phases of primate evolution in Asia (e.g. Ba Maw *et al.*, 1979; Russell & Gingerich, 1980, 1987; Ciochon *et al.*, 1985; Beard & Wang, 1991; Beard *et al.*, 1994). Because of the high endemicity of many early Asian primates, such material is often of limited value for assigning individual fossil taxa to their appropriate higher clades. For example, while their teeth indicate that *Hoanghoni*, *Amphipithecus*, *Pondaungia* and *Lushius* are primates of some sort, there is no consensus on their narrower cladistic relationships (e.g. Simons, 1971; Szalay, 1970, 1972; Gingerich, 1977, 1980; Ba Maw *et al.*, 1979; Ciochon *et al.*,

1985; Rasmussen & Simons, 1988). Given the numerous advances made in recent years in our understanding of character phylogeny within the major clades of primates, it is surely reasonable to believe that these and other problematic cases could be fully and finally resolved if more complete anatomical material were available for analysis.

The specimen providing the impetus for the present paper is an isolated petrosal bone of a small primate from Shanghuang Fissure D, CM 69728 (Figure 1; for a list of institutional acronyms, see legend of Table 2). This specimen constitutes the first fossil evidence pertaining to the primate basicranium to be recovered from the Eocene of Asia. As we discuss below, the evidence tends to favour the conclusion that the Shanghuang primate petrosal represents a species within the newly-named family Eosimiidae, here regarded as the sister group of undoubted anthropoids or "telanthropoids" (see Materials and methods; Beard *et al.*, 1994). If this taxonomic attribution is accurate (and if the reconstructed phylogenetic position of Eosimiidae is also correct), the new petrosal from Shanghuang sheds important new light on the evolution of basicranial characters among higher-level taxa of primates, including early anthropoids.

Materials and methods

We shall use the informal designator "telanthropoid(s)" (end-anthropoids) to refer to the higher-level grouping presently consisting of Oligopithecidae + Parapithecidae + Platyrrhini + Catarrhini. The term "basal anthropoids" can be used without prejudice to refer to taxa that have been proposed as close relatives or sister groups of telanthropoids, but whose relationships are not necessarily well clarified. Until these relationships are worked out, there is little reason to enter into extended debate over which basal anthropoid taxon is most closely related to the telanthropoids (which appear to be a monophyletic group).

CM 69728 was compared to specimens of *Tarsius bancanus*, *Microcebus murinus*, *Lemur fulvus*, *Otolemur crassicaudatus*, *Galago senegalensis*, *Cebuella pygmaea* and *Callithrix jacchus* in the collections of the AMNHM and the senior author. We have also examined specimens or casts of *Shoshonius cooperi* (CM 31366), *Necrolemur antiquus* (unnumbered cast in AMNHVP collection), *Smilodectes gracilis* (MPM 2612), *Notharctus* sp. (AMNHVP 11466) and *Rooneyia viejaensis* (TMM 40688-7).

Institutional acronyms used in text, figures, and tables: AMNHM, American Museum of Natural History, Department of Mammalogy; AMNHVP, American Museum of Natural History, Department of Vertebrate Paleontology; CM, Carnegie Museum of Natural History, Section of Vertebrate Paleontology; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology; MPM, Milwaukee Public Museum; TMM, Texas Memorial Museum.

The Shanghuang fissure-fillings

The Shanghuang localities, the first fossiliferous fissures of early Cenozoic age to be discovered on the Asian continent, occur in Triassic limestones belonging to the Shangqinglong Formation. The fossil-bearing deposits were formed as infillings in a karst landscape roughly 45 Ma ago. Five localities, identified by the letters A–E, have been sampled within the confines of a single working quarry operation. Fissure D is of special interest in the present context because it is the source of the Shanghuang primate petrosal. The faunal composition of Fissure D (as currently known) indicates that this fissure is somewhat older than some or all of the other sampled fissures, perhaps by as much as 1–2 Ma (Beard *et al.*, 1994; Wang & Dawson,

1994). For example, Fissure D has yielded the new basal cricetid rodent *Pappocricetodon antiquus*, which retains several primitive characters not found in other species of this genus (Tong, 1992; Wang & Dawson, 1994). More advanced species of *Pappocricetodon* occur in fissures A-C at Shanghuang, while *P. antiquus* has only been found in Fissure D. The primate fauna from Fissure D also differs from those found in other sampled fissures. Fissure D preserves adapiforms in much greater abundance than do the others, and Fissure D is the only locality at Shanghuang to have yielded fossils ascribable to Omomyidae. [Fissure D is the type locality of *Macrotarsius macrorhysis*, the only omomyid currently recorded from Shanghuang (Beard *et al.*, 1994).] Eosimiid primates also occur in relative abundance in Fissure D, but tarsiids have not been found there (see Discussion).

Morphology of Shanghuang petrosal (CM 69728)

The specimen is a left petrosal (Figure 1) of a small eutherian. The promontorium is largely intact, although the bony processes and canals extending from or attached to it are damaged to a greater or lesser extent. Dorsomedially, the area surrounding the internal acoustic meatus is well preserved, but posteriorly the mastoid and parts of the semicircular canals have been shorn off. Readily-recognisable landmarks include the fenestra vestibuli, fenestra cochleae, tegmen tympani and facial canal.

Ventral aspect: tympanic floor and roof

Arising in sutureless continuity from the medial, posterior and anterior sides of the cochlear housing [Figure 1(A)] is a fragmentary rampart of bone, interpretable as the remnant of a once more complete tympanic floor. The size and nature of this tympanic floor cannot, of course, be determined unequivocally from the evidence available. However, it is parsimonious to believe that the rampart was, ontogenetically speaking, an outgrowth of the petrosal bone, and that it must have been part of a relatively large structure, in view of the fact that its morphological origin runs around most of the non-tegmental part of the cochlear housing. These facts are consistent with, but do not constitute a proof of, the proposition that the floor was completely ossified (i.e. a bulla was present). Although a few non-primates (e.g. macroscelideans, some erinaceomorphs) possess some petrosal material in their tympanic floors (MacPhee *et al.*, 1988), primates are the only mammals in which the bulla is largely or completely formed by the petrosal, and the only ones in which bullar outgrowths produce a continuous petrosal plate that extends (in the adult) from most or all of the non-tegmental part of the cochlear housing. Of the ectotympanic there is no sign, unless the small ledge at the posterior terminus of the channel for the facial nerve represents the attachment site of the bone's posterior crus. Nothing concerning the relationships or position of the ectotympanic in life can be inferred from this fact.

We reconstruct the tympanic process as extending from the cochlear capsule at a relatively dorsal position, which means that there would have been significant exposure of the medial and anterior aspects of the cochlear housing within the tympanic cavity. Marked tympanic exposure of the cochlear housing is seen in many mammals with well-developed bullae. Among primates of modern aspect, such exposure is found in all lemuriform strepsirrhines and all known adapids and omomyids represented by adequate basicranial remains (see MacPhee & Cartmill, 1986; Ross, 1994). In extant lemurs, ontogenetic investigations have revealed that the petrosal plate (the bullar process) actually arises from the ventral aspect of the promontorium (midcapsular arc) in fetal life, but bone remodelling in the juvenile progressively

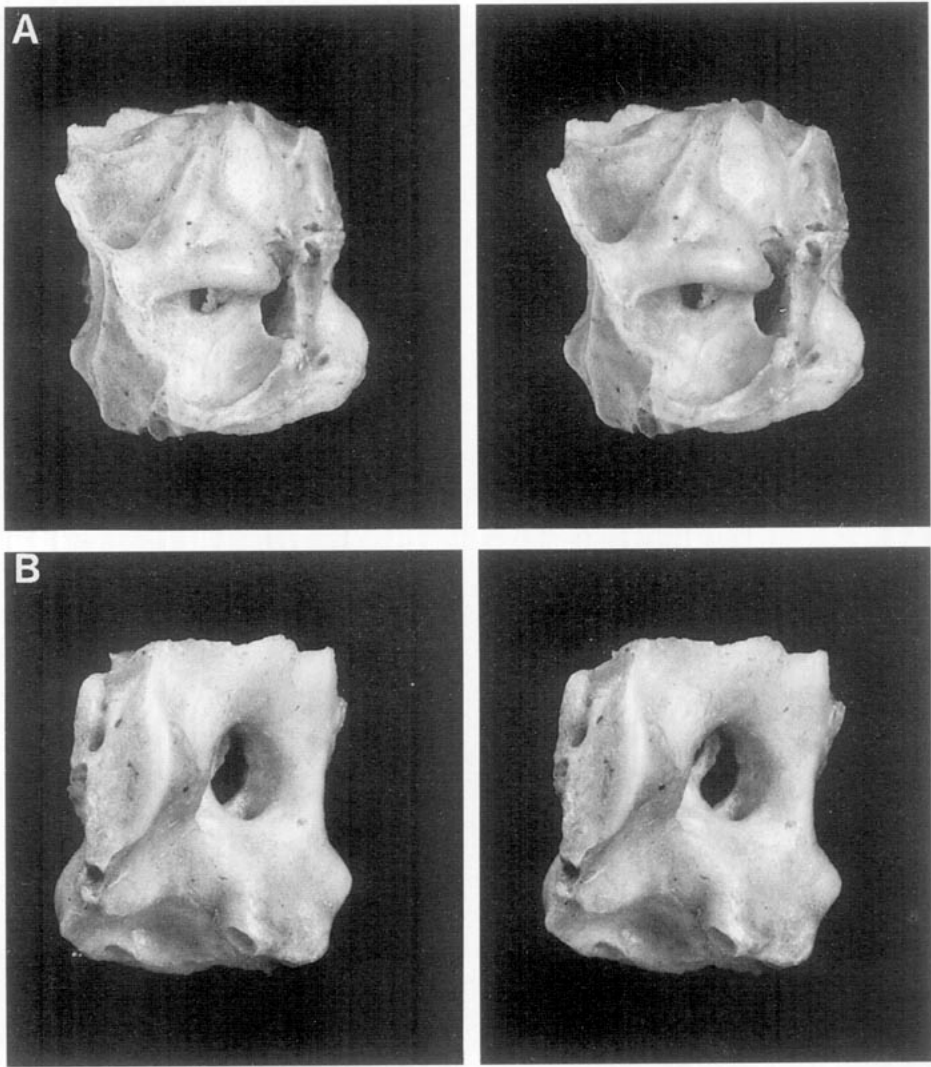
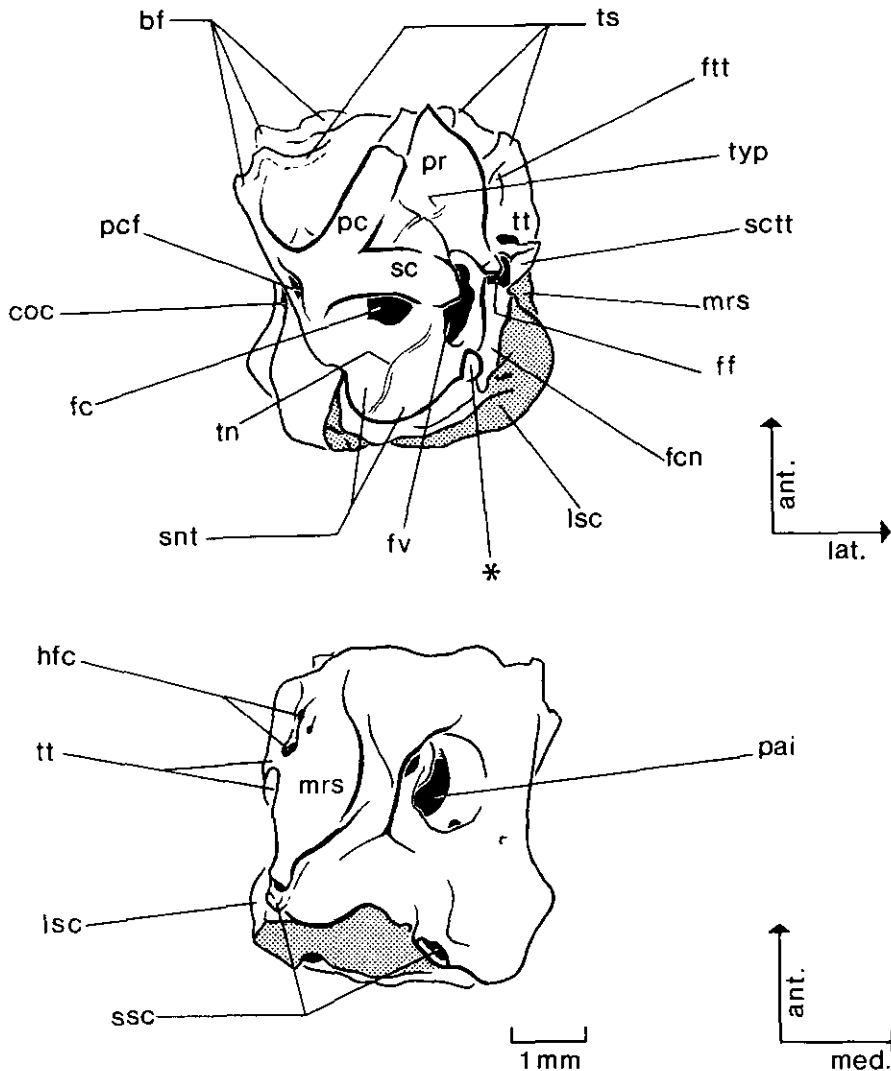


Figure 1. Stereopairs [(A) ventral; (B) dorsal] of CM 69728, an isolated petrosal provisionally assigned to *Eosimiidae*, from Shanghuang Fissure D, Jiangsu Province, People's Republic of China. In (A), the medial side of specimen is on the left of the image and the rostral is toward the top of the page. Key to abbreviations on interpretative drawing: bf, fragments of auditory bulla; coc, cochlear canaliculus; fc, fenestra cochleae; fcn, facial canal; ff, foramen faciale; ft, fossa for tensor tympani; fv, fenestra vestibuli; hlc, hiatuses for greater and lesser petrosal nn; lsc, lateral semicircular canal (prominence); mrs, margo superior (of petrosal); pai, porus acusticus internus; pc, promontorial canal; pcf, posterior carotid foramen; pr, promontorium; sc, stapedial canal; sctt, stapedial canal (fragments on tegmen tympani); snt, sinus tympani; ssc, superior semicircular canal (prominence); tn, tympanic nerve (groove for); ts, transbullar septum; tt, tegmen tympani; typ, tympanic plexus (grooves for). The asterisk identifies the small block of bone that may be part of an attachment site of the posterior crus of the ectotympanic. In (A), the shading identifies areas that would have been enclosed within the inflated mastoid cavity (e.g. lsc). In (B), shading identifies preserved part of parafloccular fossa.

shifts the bullar process medially. Bony remodelling of the tympanic floor also occurs in extant lorises, *Tarsius*, and teleranthropoids according to patterns characteristic for each group, as explained in detail by MacPhee & Cartmill (1986). Although disagreement continues



Key diagram to Figure 1.

concerning the homology of the pneumatic patterns seen in extant *Tarsius* and Anthropoidea (cf. MacPhee & Cartmill, 1986; Simons & Rasmussen, 1989; Ross, 1994; Rasmussen, 1994; Beard & MacPhee, 1994), for present purposes it suffices to note that in both of these taxa the section of the bullar process that borders the tympanic cavity per se (as opposed to the anterior accessory cavity) is in the midcapsular position in the adult. CM 69728 is therefore unlike both tarsiers and telanthropoids in having a markedly inflated tympanic floor. The modern anthropoid pattern of pneumaticisation is notably ancient, occurring in more or less its present condition in the petrosal of *?Apidium* described by Cartmill *et al.* (1981).

There are at least four low crests or transbullar septa that run between the promontorium and the inner aspect of the bullar process, some of which can be seen in Figure 1(A). The bullar excursion of these septa cannot, of course, be determined. The rostral-most septum

[middle *ts* in Figure 1(A)] is continuous with the promontorial canal; the remaining septa do not seem to have conducted anything. Transbullar septa are distributed diversely among primates, erinaceomorphs, and many other mammalian taxa with auditory bullae (Cartmill *et al.*, 1981).

Although the condition of the specimen precludes a detailed assessment of the nature and position of principal pneumatic spaces, there are some pneumatisation-related features that are worth a brief mention. Comparisons of CM 69728 to dissections of extant primates indicate that there was significant inflation in the mastoid region. The discreteness and smooth exterior surface of the lateral semicircular canal [Figure 1(A)] establish that much of it was exposed within a pneumatic space, which by virtue of its position can be homologised with the mastoid cavity. In small mammals that lack any sort of mastoid inflation (e.g. *Tupaia*), the lateral semicircular canal is actually buried in the exterior sidewall of the skull (MacPhee, 1981). In such cases the limbus of the canal is not discrete and its cortex is rough rather than smooth.

The position of broken borders on the lateral aspect of the specimen shows that the mastoid cavity originally extended into the crest (margo superior) on the endocranial surface of the petrosal that lies immediately dorsal to the porus acusticus internus [Figure 1(B)]. However, this extension ended blindly, without passing into the petrosal plate, and therefore we see no reason to separately designate this space as a supracochlear cavity (cf. MacPhee, 1981). Cellule development, so characteristic of telanthropoid mastoid cavities, is not in evidence. The area where the mastoid aditus would have communicated with the epitympanic recess is not preserved.

The rostral wall of the tympanic cavity is largely absent and the degree of pneumatisation in this region cannot be assessed. Thus we cannot determine whether the wall incorporated an anterior accessory cavity like that of telanthropoids or *Tarsius*, or simply ended as a blind pocket as in other primates.

The only parts of the tympanic roof [Figure 1(A)] that remain are the tegmen tympani and the area posterior to the fenestra cochleae (sinus tympani). The tegmen tympani, although incomplete laterally, is nevertheless comparatively large, as is typical for primates and a few other eutherian taxa (including erinaceomorphs). The tegmen's ventral surfaces bear the remains of tubes for the stapedia artery and facial nerve (see below). A small depression on the tegmen tympani is in the correct position to be the fossa for the tensor tympani.

The sinus tympani, the space situated behind the fenestra cochleae, is defined posteriorly by the broken-off base of the bullar process. We infer that the lateral portion of the sinus contained the origin of the stapedia muscle, which was therefore intratympanic as in most primates of modern aspect except certain tarsiiforms (see discussion in Beard & MacPhee, 1994).

In almost all eutherians the lateral aspect of the tympanic roof is completed by an epitympanic wing of the squamosal that communicates broadly with the tegmen tympani. This was presumably also the case in the present specimen, although no portion of this wing remains.

Dorsal aspect: endocranial surface

Noteworthy features of the endocranial surface include the porus acusticus internus [Figure 1(B)] and the cochlear canaliculus for the perilymphatic duct [because of the tilt of the specimen, this latter feature is better seen in Figure 1(A)]. The stapedia artery (see below) presumably had its exit foramen on the missing lateral portion of the tegmen tympani. Although almost all of the superior semicircular canal is missing, it is clear from bone textures

that this specimen originally possessed a commodious parafloccular fossa, as is typical for most Recent primates of modern aspect (Gannon *et al.*, 1988). A subarcuate canal (Cartmill *et al.*, 1981) was not identified.

Vascular and neural canals

Conspicuous canals, identified here as the internal carotid, promontorial and stapedia [Figure 1(A)], adorn the ventral surface of the promontorium. The canals are “complete” in the sense that they form closed tubes for the greater part of their intratympanic courses. The internal carotid and its dependencies are partly enclosed by bone in several eutherian groups, but complete encapsulation of these vessels by bone is quite rare (primates, scandentians, some macroscelideans, some erinacomorphs).

Despite the loss of almost all of the bulla, the posterior carotid foramen is preserved intact. It is situated in what is described conventionally as the posteromedial position, more or less at the same transverse level as the fenestra cochleae. Among primates, this constitutes a resemblance to certain omomyids (e.g. *Necrolemur* and *Rooneyia*) and also to lorises, although in this latter group the internal carotid system is involuted in the adult stage. In adapids, *Shoshonius*, and those lemuriforms that preserve the internal carotid artery, the posterior carotid foramen is located posterolaterally. In telanthropoids and *Tarsius* the artery enters either medially or centrally, in advance of the transverse level of the fenestra cochleae (cf. Cartmill *et al.*, 1981). There is much disagreement regarding whether the telanthropoid and tarsier conditions are homologous (cf. Beard & MacPhee, 1994); however, it is unarguable that they differ from the posteromedial and posterolateral conditions, which is all we wish to point out here.

Another important matter is that, in telanthropoids and *Tarsius* alone, the internal carotid is morphologically walled up in the medial portion of the bulla or in a related septum. This is the fundamental basis for describing their arterial tracks as “perbullar” (Cartmill *et al.*, 1981). In all other primates of modern aspect, the canals housing the internal carotid and its intratympanic dependencies pass through the bulla and travel across the ventral surface of the promontorium (“transpromontorial” condition). The arterial track of CM 69728 clearly corresponds to the transpromontorial routing, and, when account is also taken of the position of the posterior carotid foramen, the resemblance to such omomyids as *Necrolemur* and *Rooneyia* is manifest.

The stapedia and promontorial tubes appear to be roughly equal in calibre and both are incomplete distally. The stapedia tube seems to terminate at the aperture of the fenestra vestibuli, but its continuation—reduced to a fragmentary gutter—can be identified more laterally on the tegmen tympani, crossing the facial canal. Although the gutter is incomplete, there is no sign of a bifurcation and therefore no indication that the proximal stapedia released a ramus inferior. It cannot be ruled out that a split occurred more distally along the stapedia’s route, on a part of the middle ear roof that is not preserved, but this is considered unlikely.

The promontorial tube appears to become a hemicanal distally, but inspection of edges shows that this is due to breakage. Mental reconstruction of the trajectory of the promontorial tube indicates that the rostral part of the canal did not follow the contour of the anterior pole of the promontory, but instead must have continued on as a discrete “free” tube. A similar morphology is seen in adapids (e.g. *Smilodectes*) as well as omomyids (e.g. *Rooneyia*).

Broken edges along the conduit for the facial nerve indicates that it was probably a complete canal in life. The facial track ends under the prominence of the lateral semicircular canal at the

position indicated in Figure 1(A), which would be typical for most eutherians. (The stylomastoid foramen would presumably have been situated immediately ventral to this point in the intact skull.) The apparent continuation of the canal as seen in the illustration is misleading; the continuation is the ledge described previously as a possible articular surface for the ectotympanic. On the endocranial surface there are small foramina [Figure 1(B), hfc] that lead backward into the facial track, presumably for the greater and lesser petrosal nerves. A very clearly marked groove for the tympanic nerve of the glossopharyngeal [Figure 1(A), tn] crosses the sinus tympani, passes through (or under) the stapedial canal on the promontorium, and then disappears into the tensor tympani fossa. This course has also been identified for ?*Apidium* (Cartmill *et al.*, 1981); it differs very little from the standard eutherian pattern (MacPhee, 1981). Faint traces of grooves for the caroticotympanic branches and other elements of the tympanic nerve plexus may also be seen.

Discussion

The feature that we regard as decisive for the allocation of CM 69728 to Primates is the long, plate-like continuation of the otic capsule in the plane of the tympanic cavity. It is probable but not demonstrable with this material that the plate was petrosal in origin. This character occurs in a very small number of other eutherian taxa, and of these, Erinaceomorpha is the only one whose presence at Shanghuang is confirmed. However, no Cenozoic erinaceomorph described to date has petrosal-derived tympanic outgrowths that arise from the anterior as well as the medial aspect of the otic capsule. [For detailed comparison of erinaceomorph/primate basicranial features, see MacPhee *et al.* (1988).] In short, there is no group other than Primates to which CM 69728 can be reasonably assigned.

Allocation to a major clade within Order Primates is more complex. As noted above, the faunal list for the Shanghuang fissure-fillings includes several species of adapids, tarsiids and eosimiids, but only one omomyid (*Macrotarsius macrorhysis*). Fissure D, the source of CM 69728, has not yielded any tarsiid dental fossils, which are currently known only from Fissures A and C. Variation in the taxon complements of individual fissures at Shanghuang may be pertinent, since there is some evidence for heterochroneity among these features (see above). In any case, for CM 69728 to represent *Tarsius eocaenus*, the Shanghuang tarsier, one would have to infer a degree of morphological variation within *Tarsius* that is not encountered in any other primate genus. As to Adapidae, the Shanghuang petrosal has no attributes in common with known members of this family, except for characters that are either primitive for primates of modern aspect (e.g. intact stapedial ramus superior), or ones that are primitive at a higher level (e.g. transpromontorial internal carotid). By default, this leaves either Eosimiidae or Omomyidae as the most probable seating for the species represented by the Shanghuang petrosal.

Since many of the features identified in the morphological description are known to occur in omomyids, it might be argued that CM 69728 should be assigned *faute de mieux* to *Macrotarsius*. There are at least four good reasons for hesitancy, however:

1. *Prima facie*, the estimated body size of *Macrotarsius* (Table 1 and Figure 2) does not correlate well with the diminutive size of CM 69728, suggesting that they cannot represent the same taxon. In order to quantify the relationship between body size and optic capsule size, we measured the Shanghuang petrosal and a small number of specimens of extant primates of known body weight for the dimension "long axis of promontorium" (PLA), defined in Table 2. Although the measurement points can be clearly defined, in some taxa they are obscured by other features (e.g. size and location of internal carotid canal in *Lemur*; elongation of sill of

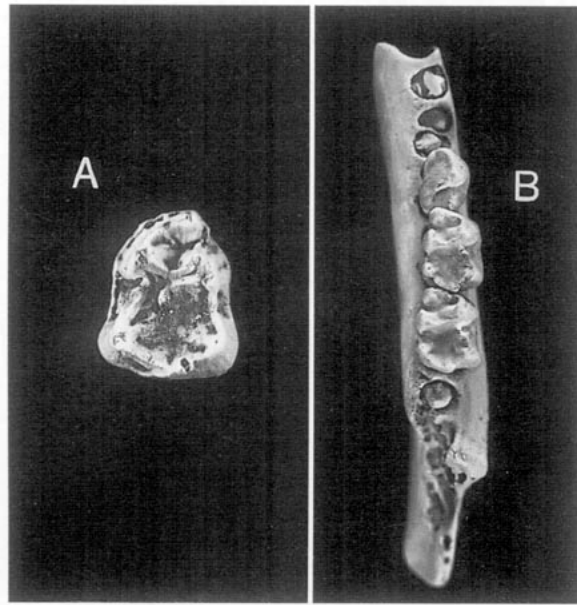


Figure 2. (A) Mandibular M1 of *Macrotarsius macrorhysis* (IVPP V11024, Fissure D) compared with (B) jaw of *Eosimias sinensis* (holotype, IVPP V10591, Fissure B). Note marked difference in size (dimensions provided in Table 1).

Table 1 Predicted body weights (g) for *Eosimias sinensis* and *Macrotarsius macrorhysis*, using the method of Conroy (1987)

Regression equation model	<i>Macrotarsius macrorhysis</i> predicted body wt	<i>Eosimias sinensis</i> predicted body wt
All primates	1221	69
Prosimians	900	67
Monkeys	1646	134
Anthropoids	1635	130
Female anthropoids	1382	137

Conroy's (1987) regression models predict body weight from M1 area; for discussion of correlation coefficients and errors of estimates for each model, consult original source. M1 of *Macrotarsius macrorhysis* (IVPP V11024): length, 3.91 mm; width, 3.32 mm. M1 of *Eosimias sinensis* IVPP V10591: length, 1.85 mm; width 1.40 mm.

fenestra cochleae in *Callithrix*), making it difficult to employ consistently the same plane of measurement. This is important because, in mammals generally, the size of the cochlear housing shows a strong negative correlation with body weight (Fleischer, 1973; Spoor, 1993). Thus although our PLA measurements for specimens of *Galago senegalensis* and *Lemur fulvus* differ by little more than 1 mm, there is a ten-fold difference in the average body weights of these taxa (Table 2). Nevertheless, we take it to be meaningful that promontorial length in CM 69728 is as small as in the smallest extant primates (Table 2). Our cautious conclusion, therefore, is that it would be unexpected for an animal in the apparent size range of

Table 2 Long axis of promontorium (PLA) in CM 69728 and some extant primates (mm), compared with body weights (g)

Taxon/catalogue no.	PLA	Body weight
? <i>Eosimias</i> sp. CM 69728 (petrosal)	3.26	NA
<i>Eosimias sinensis</i> IVPP V10591 (holotype)	NA	67–137
<i>Microcebus murinus</i>	3.00	60
<i>Tarsius bancanus</i>	4.11	125
<i>Cebuella pygmaea</i>	3.60	135
<i>Galago senegalensis</i>	4.03	215
<i>Callithrix jacchus</i>	4.80	570
<i>Otolemur crassicaudatus</i>	5.23	1150
<i>Lemur fulvus</i>	5.31	2495

PLA dimension: in ventral view, minimum distance from ventral sill of fenestra cochleae to rostral pole of promontorium, measured with ocular reticule and converted to mm. Because PLA can only be taken on specimens with broken or dissected auditory regions, sample per species is limited to $n=1$ (specimens from AMNHM). For extant primates, average body weight data are empirical values reported by Jungers (1985); value for *L. fulvus* is average of subspecies averages. For *Eosimias sinensis*, body weight is expressed as range of estimates of mean body weight as derived from predictive equations published by Conroy (1987). NA, not applicable.

Macrotarsius to have a petrosal as small as CM 69728. Equally, while *Tarsius eocaenus* from Fissures A and C is certainly small enough to have had a petrosal bone in the size range of CM 69728, the Shanghuang element lacks all features distinctive of tarsiers among primates (e.g. small, caudally directed stapedia artery; posterior carotid foramen situated in ventrum of bulla; large septum on promontorial anterior pole).

2. There are dozens of identified eosimiid teeth and jaws in the existing collections from Shanghuang, but only two teeth of *Macrotarsius*. This collection ratio could change with time, of course, although it is pertinent to note that almost 5 tons of Shanghuang matrix have now been processed (to mid-1994) without recovery of any additional material certifiably belonging to acknowledged omomyids.

3. CM 69728 is unusual among early haplorhines in that its stapedia and promontorial canals are large and subequal. In *Shoshonius* (Beard & MacPhee, 1994) canal proportions are similar, but—uniquely within Omomyidae—the posterior carotid foramen is posterolateral in position. In other omomyid taxa represented by basicranial remains (*Necrolemur*, *Microchoerus* and *Rooneyia*), the stapedia canal is consistently smaller than the promontorial canal, although the posterior carotid foramen is posteromedial in position, as in the Shanghuang specimen. Marked canal disproportion has long been construed as a critical morphological difference between adapids and omomyids [in adapids the stapedia canal is usually as large as, or larger than, the promontorial canal; see MacPhee & Cartmill (1986)].

4. The fact that the Shanghuang petrosal does not match exactly the morphology of any known omomyid, together with the absence in Fissure D of omomyids of the correct size to be likely candidates for its attribution, support the inference that the petrosal belongs to something else. By elimination, this means that it probably represents an eosimiid. If Eosimiidae is the sister-taxon of telanthropoids, as argued by Beard *et al.* (1994), one might infer that their basicranial anatomy ought to be more anthropoid-like than adapid- or

omomyid-like. But since the basicrania of the earliest accepted telanthropoids already have all of the specialisations found in extant members of the suborder (Cartmill *et al.*, 1981), there is in fact no empirical basis for predicting the morphology of their sister group from in-group evidence.

Of the above, point 1 is not completely decisive because Palaeogene Asia harboured omomyids other than *Macrotarsius*, some of which were smaller (Russell & Gingerich, 1980; Beard & Wang, 1991). Likewise, the fact that omomyid dental material has shown up at all in the Shanghuang fissure-fillings encumbers the probabilistic argument framed in point 2. On the other hand, CM 69728 exhibits a large, fully functional stapedia (point 3), a feature that is neither typically omomyid nor telanthropoid. Given these circumstances, we feel justified in concluding that this petrosal must represent some other clade, which, in our view, is more likely than not to be Eosimiidae. Eosimiids may simply have been primitive for the character under discussion, but this could mean that their basicranial anatomy may have been grossly similar to that of the last common ancestor of all haplorhines.

Conclusions

The isolated petrosal from the Eocene Shanghuang fissure-fillings described in this paper is probably, but not certainly, that of an eosimiid. Accepting this, several interesting implications emerge:

1. If eosimiids are indeed basal anthropoids, then on the evidence of CM 69728 it appears that the anthropoid basicranial morphotype may not be readily distinguishable from that of omomyids. But is this actually problematic? To a considerable extent, the view that anthropoids and omomyids are specially related is predicated on otic features (e.g. Szalay, 1976; Szalay & Delson, 1979; Rosenberger & Szalay, 1980). Accordingly, for omomyophiles at least (cf. MacPhee & Cartmill, 1986), animals having the combination of characters found in eosimiids merely fulfil the presumption that the most primitive cladistic anthropoids would have a basicranium organised something like that of an omomyid. Conversely, the expectation that basal anthropoids would have an adapid-like auditory region (Gingerich, 1973; Rasmussen, 1990) is starkly incongruent with eosimiid anatomy.

2. Eosimiid otic features as interpreted here, coupled with those of the recently described ear region of the omomyid *Shoshonius* (Beard *et al.*, 1991; Beard & MacPhee, 1994), cast new doubts on the tarsiiphile hypothesis of anthropoid origins (Cartmill, 1980; MacPhee & Cartmill, 1986). Just as the cranial anatomy of *Shoshonius* is inconsistent with putative tarsier-anthropoid synapomorphies of the basicranial and orbital regions (by making the tarsiiform morphotype considerably more primitive than shown by conditions in *Tarsius* itself), so the eosimiid ear region lacks the derived attributes once thought to define the *Tarsius*+Anthropoidea clade. Ironically, while the hypothesis of a strict *Tarsius*+Anthropoidea clade is greatly weakened by palaeontological evidence derived from *Shoshonius* and eosimiids, the argument for the monophyly of an expanded version of Haplorhini (including a wealth of fossil tarsiiform and basal anthropoid taxa) is augmented correspondingly.

3. Finally, the combination of dental and basicranial characters attributed to eosimiids (cf. Beard *et al.*, 1994) helps to reduce and make sense of the morphological gulf separating living anthropoids from other primates: the transformations defining the anthropoid clade evidently did not occur all at once, but in a mosaic fashion. In particular, it now seems at least moderately likely that a number of derived anthropoid dental and gnathic features preceded the reorganisation of the anthropoid ear region.

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