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The eosimiid primates (Anthropoidea) of the Heti Formation, Yuanqu Basin, Shanxi and Henan Provinces, People's Republic of China

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Abstract

We describe the eosimiid primate fossils collected during the course of four field seasons in the late middle Eocene Heti Formation of central China. In addition to providing new information about the anatomy of *Eosimias centennicus*, the Heti Formation sample documents substantial taxonomic diversity in the Asian eosimiid radiation. One new genus and three new species of Eosimiidae are proposed here. These include *Eosimias dawsonae*, n. sp.; *Phenacopithecus xueshii*, n. gen. and sp.; and *Phenacopithecus krishtalkai*, n. sp.

The anatomy of the upper dentition of eosimiids is described in detail for the first time. As is the case for the lower dentition, a unique combination of primitive and derived traits characterizes the upper dentition of *Eosimias* and *Phenacopithecus*. Eosimiid upper molars bear many of the same derived features—including strong protocone cristae and the absence of a postprotocingulum—that have been cited as evidence for a special relationship between anthropoids and certain adapiforms. However, the upper molars of eosimiids further approximate those of other basal anthropoids in having reduced or absent conules and complete lingual cingula. These features are lacking in *Periconodon* and other adapiforms that have been regarded by some workers as being phylogenetically close to anthropoids. Given that similarities in upper molar anatomy are among the only derived features that can be cited in support of a possible adapiform ancestry for anthropoids, the occurrence of these same features in eosimiids significantly weakens the adapiform hypothesis of anthropoid origins.

The holotype maxillary fragment of *Phenacopithecus krishtalkai* reveals that eosimiids possessed a relatively small infraorbital foramen and a deep lower face between the inferior orbital margin and the alveolar border. Eosimiids therefore lacked the orbital hypertrophy characteristic of living tarsiers and many fossil omomyids and microchoerids. Eosimiids apparently had relatively small orbits, suggesting that they maintained a diurnal activity cycle.
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Keywords: Eosimiidae; *Eosimias*; *Phenacopithecus*; Anthropoid origins; Paleontology; Eocene; Heti Formation

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Introduction

The extinct primate family Eosimiidae was originally proposed on the basis of jaws and teeth recovered from middle Eocene fissure-fillings in southern Jiangsu Province, People's Republic of China (Beard et al., 1994). Despite the fragmentary condition of all eosimiid fossils known at that time, their unique combination of primitive and derived dental and mandibular characters suggested that eosimiids were basal members of the anthropoid clade. By 1994 several lines of evidence indicated that anthropoids must have diverged from other major primate lineages much earlier than had long been assumed (Beard et al., 1991; Godinot and Mahboubi, 1992, 1994; Beard and MacPhee, 1994; Dagosto and Gebo, 1994; Ford, 1994; Godinot, 1994). Accordingly, the discovery of anatomically primitive and phylogenetically basal anthropoids in rocks of middle Eocene age was hardly unexpected. Nevertheless, initial phylogenetic reconstructions interpreting *Eosimias* as a basal anthropoid met with considerable skepticism (Godinot, 1994; Godinot and Mahboubi, 1994; Simons and Rasmussen, 1994a,b; Simons, 1995).

Since their original description, basic knowledge regarding the anatomy, taxonomic diversity, and paleogeographic range of eosimiid primates has increased substantially. Aspects of eosimiid cranial and postcranial anatomy have been described for the first time (MacPhee et al., 1995; Gebo et al., 2000a,b, 2001, 2002), and new eosimiid taxa have extended the known stratigraphic and geographic ranges of the family (Beard et al., 1996; Jaeger et al., 1999). This expanded data set has forged a broader consensus among specialists regarding the phylogenetic position of eosimiids as basal members of the anthropoid clade (Beard et al., 1996; Kay et al., 1997; Ross et al., 1998; Jaeger et al., 1999; Gebo et al., 2000a, 2001; Ross, 2000; Beard, 2002). Despite these advances, a minority of scientists continues to doubt the anthropoid affinities of eosimiids (Gunnell and Miller, 2001; Ciochon and Gunnell, 2002a,b; Schwartz, 2003; Simons, 2003).

Here, we describe the eosimiid fossils recovered during four seasons (1994–1997) of paleontological fieldwork in the Yuanqu Basin of central China,

organized by personnel from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP, Chinese Academy of Sciences) and the Carnegie Museum of Natural History. These fossils further substantiate the anthropoid affinities of Asian eosimiids by revealing some intriguing new aspects of their anatomy. At the same time, the new material underscores the taxonomic diversity that was achieved by the Asian eosimiid radiation by the late middle Eocene. Although both tarsiid and sivaladapid primates have also been recovered from the Yuanqu Basin (Zdansky, 1930; Gingerich et al., 1994; Beard, 1998; Qi and Beard, 1998; Gebo et al., 1999; Tong et al., 1999), eosimiids are the most diverse and abundant primate group encountered there.

Geological setting

The Yuanqu Basin is a small graben located in the Zhongtiao Range along the border of Shanxi and Henan provinces in central China (Fig. 1). Sedimentary rocks of Tertiary and Quaternary age fill much of the basin. Chief among these are strata belonging to the Eocene Heti Formation, which is now known to be more than 1500 m thick (J.R. Kappelman, personal communication). Despite its great thickness, outcrops of the Heti Formation are often discontinuous owing to the local ubiquity of Plio–Pleistocene loess, which directly overlies the Heti Formation in the Yuanqu Basin.

Traditionally, the Heti Formation has been divided into three members. The lowermost of these, known as the Yuli Member, is dominated by relatively coarse clastic sediments, including both sandstones and conglomerates. It has so far proven to be poorly fossiliferous, although it has yielded specimens of the perissodactyls *Eomoropus quadridentatus* and *Breviodon minutus*, suggesting a middle Eocene age (Tong, 1997). The Rencun Member includes well-developed paleosols as well as relatively fine-grained floodplain sediments. In the Zhaili Member, relatively fine-grained floodplain sediments continue to dominate. Some of the most abundantly fossiliferous sites in the Zhaili Member, such as Locality 1, developed as abandoned channel-fills.
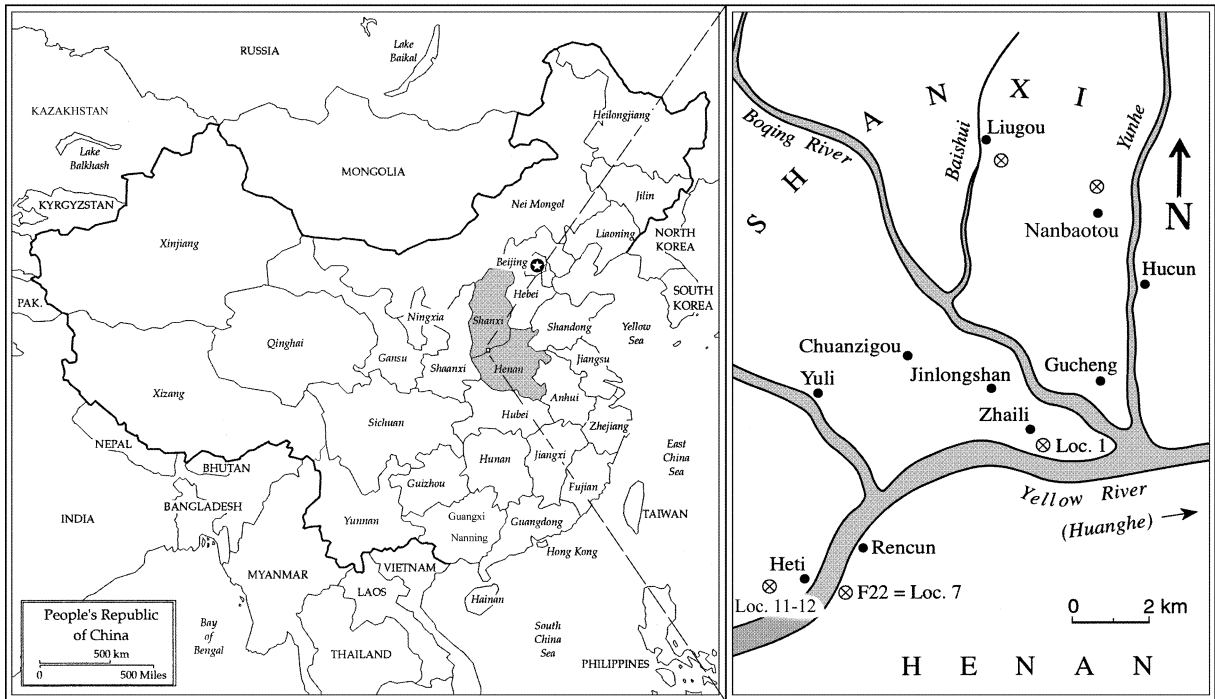
Fig. 1. Map of the Yuanqu Basin showing geographic locations of major primate-bearing fossil localities in the Eocene Heti Formation. Type localities for Yuanqu Basin Eosimiidae are as follows: *Eosimias centennicus*, Locality 1 on the northern bank of the Yellow River, just southeast of Zhaili village; *Eosimias dawsonae*, Locality 11–12 on the northern bank of the Yellow River, west of Heti village; *Phenacopithecus xueshii*, Nanbaotou locality north of Nanbaotou village; *Phenacopithecus krishtalkai*, Locality 7 on the southern bank of the Yellow River, directly opposite Heti village.

The mammalian faunas of both the Rencun and Zhaili members of the Heti Formation are often referred to the Sharamurunian Asian Land Mammal Age, which is thought to correlate with the latter part of the middle Eocene according to modern timescales (Russell and Zhai, 1987; Holroyd and Ciochon, 1994). Tong et al. (1995) follow most other workers in accepting a Sharamurunian age for the Rencun Member, but differ in advocating that the Zhaili Member correlates with their "Naduan" land mammal age, a contentious biostratigraphic interval that corresponds with the latest part of the middle Eocene and the late Eocene in their usage. Ongoing studies of the biostratigraphy and paleomagnetic reversal stratigraphy of the Heti Formation promise to clarify the relative and absolute ages

of its important mammalian faunas in the near future.

Systematic paleontology

Order Primates Linnaeus, 1758
Suborder Anthropoidea Mivart, 1864
Family Eosimiidae Beard et al., 1994

Type genus
    Eosimias Beard et al., 1994.

Included genera
    Eosimias Beard et al., 1994; *Bahinia* Jaeger et al., 1999; *Phenacopithecus*, new genus.

Emended diagnosis
    Lower molars with larger, more cuspidate paraconids than in other anthropoids. Upper molars

Fig. 2. *Eosimias centennicus*, holotype, IVPP V11000. Associated left and right dentaries preserving left C_1–M_3 and right I_1–M_3 (occlusal view; stereopairs).

without hypocones, in contrast to *Algeripithecus*, *Tabelia*, Parapithecidae, Proteopithecidae, and most Catarrhini and Platyrrhini. Differs from Oligopithecidae and undoubted Catarrhini in retaining three premolars in each jaw quadrant. P_4 metaconid situated distal and well inferior to protoconid, without strong transverse crest uniting these cusps, in contrast to Platyrrhini, Catarrhini, Oligopithecidae, and Proteopithecidae. Hypoconulids and entoconids on lower molars widely separated, in contrast to Catarrhini, Para-

pithecidae, Oligopithecidae, Proteopithecidae, and *Arsinoea*.

Eosimias Beard et al., 1994

Type species
  Eosimias sinensis Beard et al., 1994.

Included species
  Eosimias sinensis Beard et al., 1994; *Eosimias centennicus* Beard et al., 1996; *Eosimias dawsonae*, new species.

Emended diagnosis

Smaller than *Bahinia*. P^3 with small but distinct protocone, in contrast to *Bahinia*. Trigons of upper molars relatively shorter (mesiodistally) and wider (buccolingually) than in *Bahinia* and *Phenacopithecus*. Lingual cingula of upper molars weaker than in *Bahinia* and *Phenacopithecus*. Pre- and postprotocristae of upper molars less trenchant than in *Bahinia*. P_2 relatively smaller than in *Bahinia*. P_4 trigonid mesiodistally shorter in relation to talonid than in *Bahinia* and *Phenacopithecus*. M_2 paraconid larger and more lingual in position than in *Phenacopithecus*.

Discussion

The three species assigned here to *Eosimias* form a morphologically cohesive group in which features that appear to be diagnostic for *Bahinia* and *Phenacopithecus* are absent. However, most eosimiid species are documented by unique or fragmentary specimens. As such, the recovery of more nearly complete fossils may alter the generic allocation of certain eosimiid species in the future.

Eosimias centennicus Beard et al., 1996

Holotype

IVPP V11000, associated left and right dentaries preserving left C_1–M_3 and right I_1–M_3 (Figs. 2–4).

Hypodigm

The holotype; IVPP V10218.1–7, isolated upper cheek teeth (see Tong, 1997); IVPP V10219.1–5, isolated lower cheek teeth (see Tong, 1997); IVPP V11001.1, right dentary preserving P_3–M_3 (Fig. 5); IVPP V11001.2, right dentary preserving P_4–M_2; IVPP V11993, left maxilla preserving P^3, $M^{1–2}$ (Fig. 9); IVPP V11994, right dentary preserving P_2 and P_4–M_2; IVPP V11995, associated left C_1 (fragment), P_2, P_4 (fragment), M_1, and M_2 crowns (originally preserved in a single dentary that was severely damaged in the field); IVPP V11996.1, isolated left C^1 (Fig. 6); IVPP V11996.2, isolated right deciduous P^4 (Fig. 7); IVPP V11996.3, isolated right P^4 (Fig. 8).

Type locality

Locality 1, also known as the "River Section" locality or Tuqiaogou, Zhaili Member of Heti Formation, Yuanqu Basin, Shanxi Province, People's Republic of China. Exact geographic coordinates are as follows: 35°04.95′ North, 111°50.99′ East.

Known distribution

Late middle Eocene of Shanxi Province, People's Republic of China (type locality only).

Description

The morphology of the lower dentition and dentary was described by Beard et al. (1996). Several additional isolated cheek teeth from the type locality were subsequently described by Tong (1997). The enlarged sample of *Eosimias centennicus* specimens now available from the type locality allows us to comment on intraspecific variation in the lower dentition and to clarify aspects of the upper dentition that were either unknown or inadequately known previously. Dental measurements for *E. centennicus* are provided in Table 1.

IVPP V11001.1 is a right dentary preserving P_3–M_3 (Fig. 5) that differs in some minor details from the holotype, owing mainly to the very light degree of wear in the new specimen. Superficial inspection suggests that P_3 is taller relative to P_4 than is the case in the holotype, with a lingual cingulid that is more inclined mesially. In fact, these apparent differences result from slight postmortem displacement of the P_3 crown in IVPP V11001.1. Actual differences include minor variation in the development of the paraconid on $P_{3–4}$ (stronger in IVPP V11001.1, weaker in the holotype) and in the position of the paraconid on M_2 (fully lingual in the holotype, more mesial in position in IVPP V11001.1). In IVPP V11001.2 (not figured), the P_4 paraconid is stoutly constructed, thereby matching the condition in IVPP V11001.1, but the M_2 paraconid is fully lingual, as is the case in the holotype. Given that all of these specimens were collected from the same stratum at the same locality and are similar in size, we regard these minor differences in morphology as reflecting normal intraspecific variation.
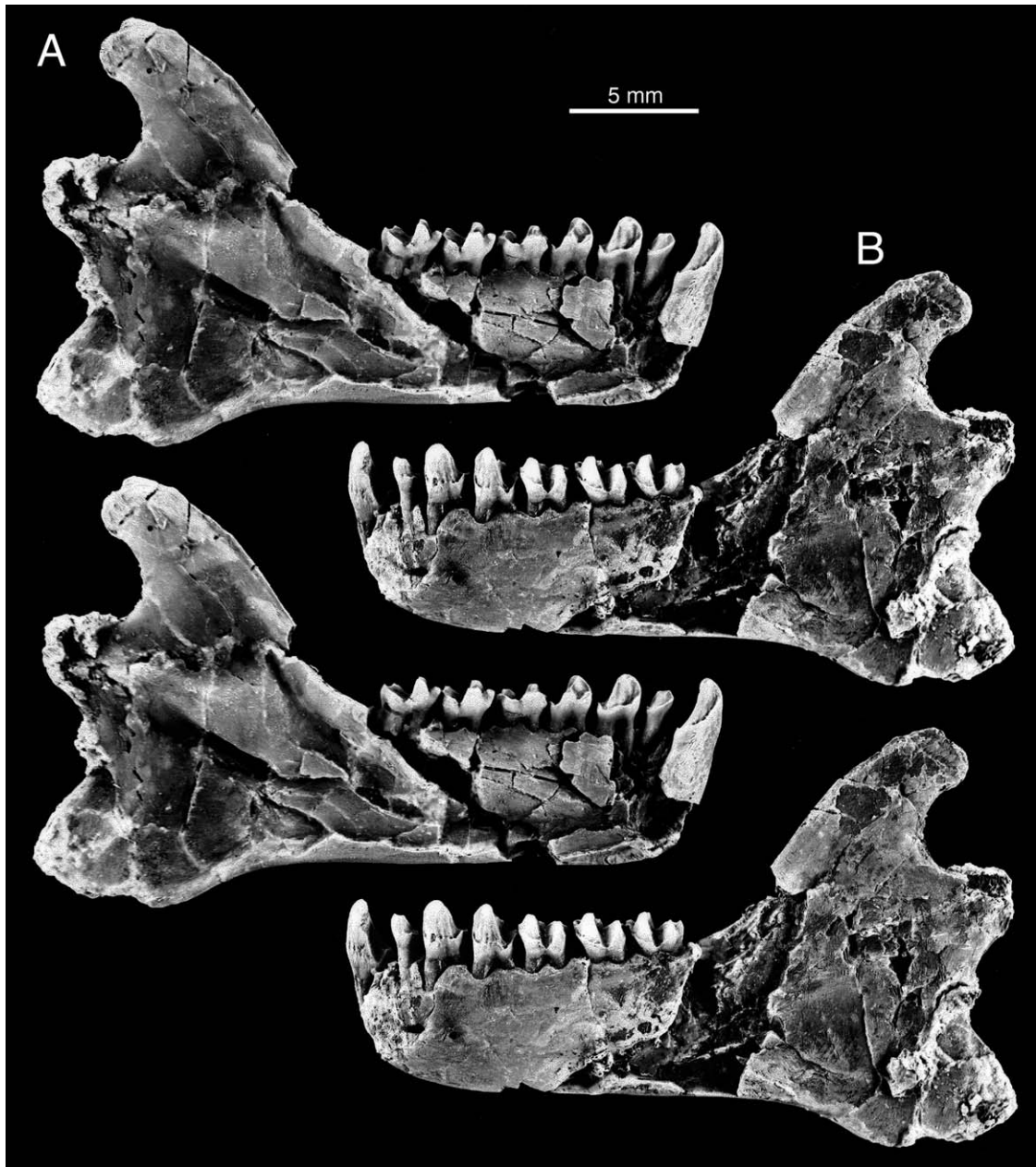
Fig. 3. *Eosimias centennicus*, holotype (in part), IVPP V11000. Left dentary preserving C_1–M_3 in lingual (A) and buccal (B) views. Both views are stereopairs.

IVPP V11996.1 is an isolated left C^1 (Fig. 6) that documents upper canine morphology for the first time in eosimiids. The tooth is imperfectly preserved, because much of the enamel has been

eroded from the crown. Given its small absolute size, the crown is surprisingly robust, being sub-triangular in cross-section. Neither mesial nor distal accessory tubercles or cuspules occur; rather, a
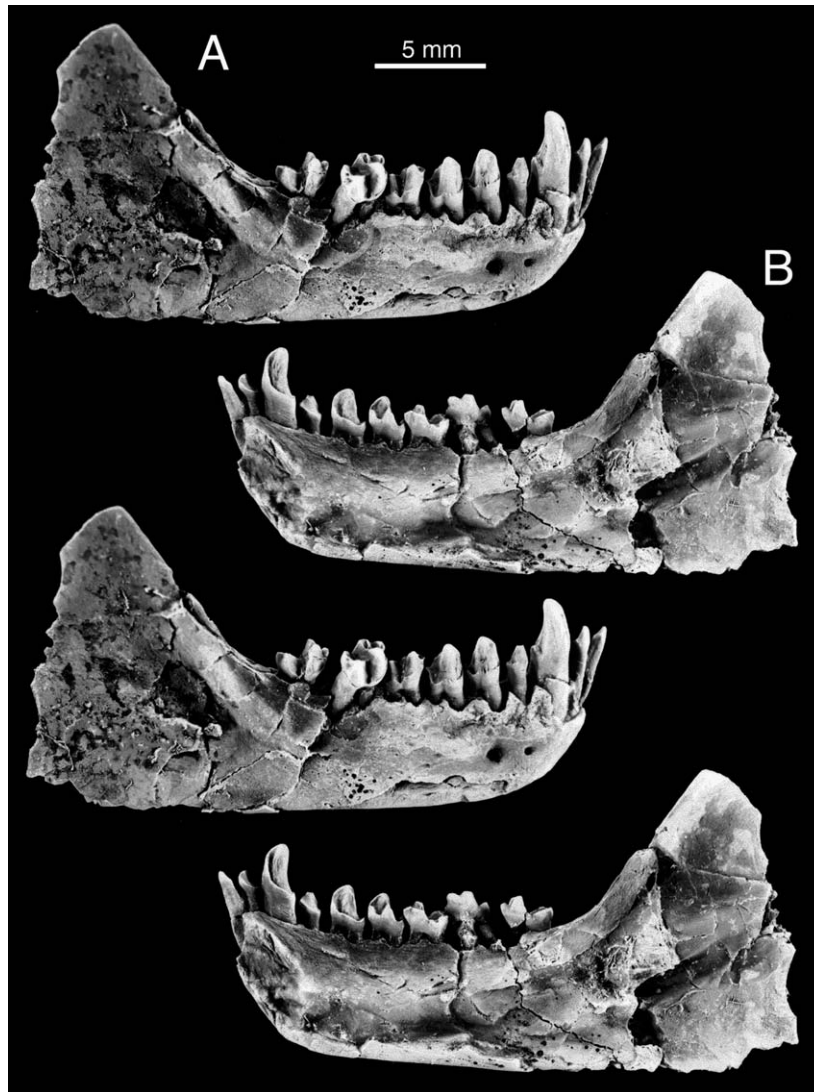
Fig. 4. *Eosimias centennicus*, holotype (in part), IVPP V11000. Right dentary preserving I_1–M_3 in buccal (A) and lingual (B) views. Both views are stereopairs.

single cusp dominates the simple crown morphology. The buccal side of the crown forms an evenly convex surface mesially, where there is no evidence of a cingulum. Farther distally, a cingulum does occur. This part of the buccal surface of the crown, immediately mesial to the distal crest, is slightly concave. The mesial and lingual sides of the crown are each rather flat. Their bases are lined by cingula. There is no

development of a vertically oriented mesial groove, as occurs in many living and fossil anthropoids. The distal crest, however, is well-developed, being among the most salient features of the crown. Crown height is roughly 2.75 mm, while the root is 4.00 mm long.

IVPP V11996.2 is an isolated right deciduous P^4 (Fig. 7). Buccally, the tooth bears three cusps: from mesial to distal these are the parastyle,
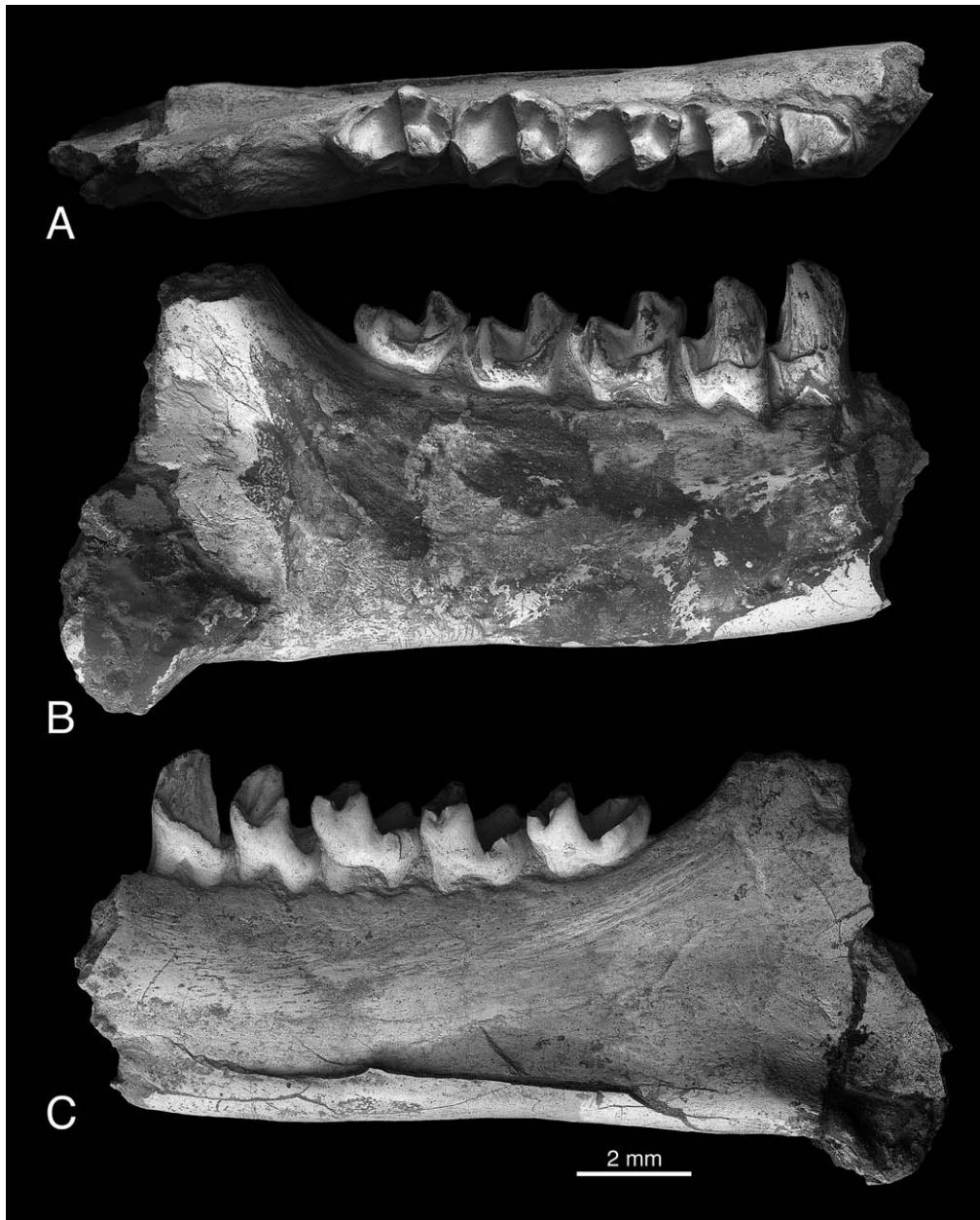
Fig. 5. *Eosimias centennicus*, IVPP V11001.1, right dentary preserving P_3–M_3 in occlusal (A), buccal (B), and lingual (C) views.

paracone, and metacone. The parastyle, which is distinctly smaller than the paracone and metacone, is more buccal in position than the latter cusps. A weak buccal cingulum is present, but the apices of the paracone and metacone are located very near the buccal margin of the crown. In other words, the buccal walls of the paracone and metacone are nearly vertical, which contrasts markedly with the disposition of these cusps in the permanent upper molars (particularly M^2). The protocone is canted
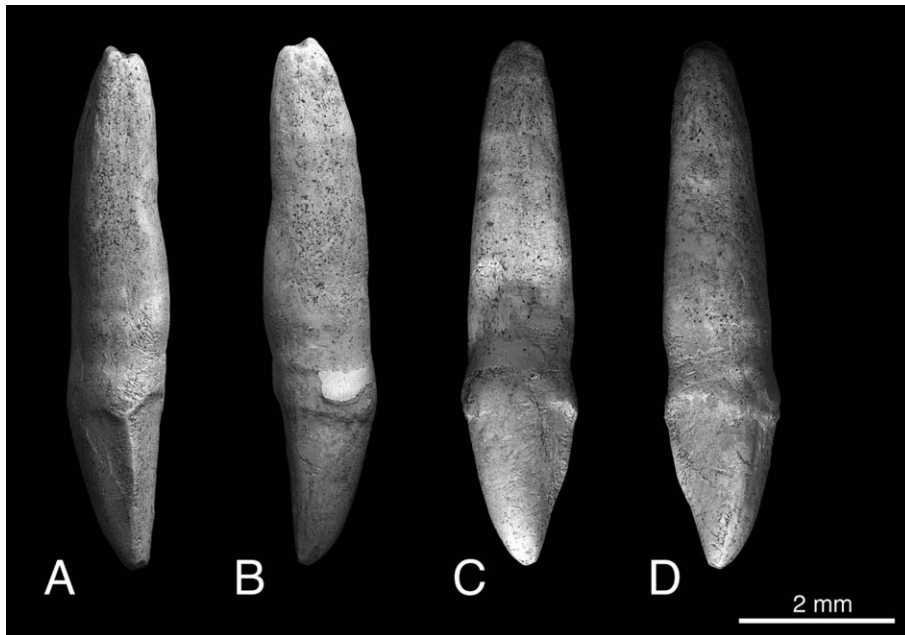
Fig. 6. *Eosimias centennicus*, IVPP V11996.1, isolated left C[1] in distal (A), mesial (B), buccal (C), and lingual (D) views.

mesially as is typically the case in primates. Well-developed pre- and postprotocristae are present, but there is no postprotocingulum or *Nannopithex* fold. A weak paraconule is evident on the pre-protocrista, but there is no metaconule. The postprotocrista bifurcates near the base of the metacone. The mesial branch of this bifurcation forms an arcuate crest that continues for a short distance up the lingual wall of the metacone, while the distal branch merges with the distal cingulum. There is a complete lingual cingulum, but this structure is best developed distally. A well-developed wear facet breaches the lingual cingulum immediately distal to the protocone.

IVPP V11996.3 is an isolated right P[4] (Fig. 8). Its crown exhibits simple morphology, being dominated by two main cusps. The larger of these is the paracone, which is a high, conical cusp situated near the midline of the crown's buccal margin. From its summit the preparacrista descends sharply to join a well-developed parastyle. In contrast, the postparacrista slopes more gradually toward the distobuccal corner of the tooth, where it merges with a swelling of enamel that may be an incipient metastyle. Two additional minor crests, both of which are less trenchant than the pre- and postparacristae, descend the lingual face of the paracone toward the protocone. The more mesial of these crests unites with the mesial cingulum, thereby delimiting a small mesial basin or fovea bounded also by the preparacrista and the mesial cingulum. The lingual part of the crown is dominated by the protocone, which is situated on the mesial margin of the crown, closer to the base of the paracone than to the lingual border of the tooth. Well-developed cingula line the mesial, distal and buccal margins of the crown.

IVPP V11993 is a left maxillary fragment preserving the crowns of P[3] and M[1–2] (Fig. 9). The maxillary fragment has been distorted post-mortem, such that its individual tooth crowns have been rotated and translated with respect to their positions in life. Presumably, bioturbation and/or trampling in the soft sediments in which the specimen was entombed caused this plastic deformation. Despite this nuisance, the three teeth clearly derive from a single individual. Furthermore, the homologies of the individual tooth loci
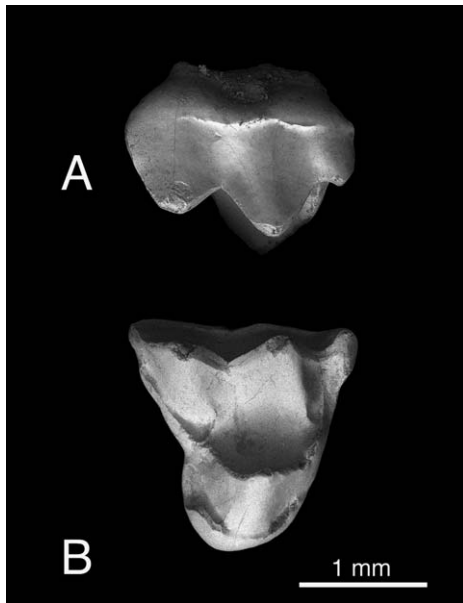
Fig. 7. *Eosimias centennicus*, IVPP V11996.2, isolated right deciduous P^4 in buccal (A) and occlusal (B) views.

are indisputable from comparison with other eosimiid maxillae.

The P^3 bears two cusps of markedly different size. The paracone is large and centrally located on the buccal margin of the crown. There is a strong postparacrista, but the mesial side of the paracone is primarily convex, aside from a small vertically oriented groove near the base of the cusp. The much smaller protocone is located near the mesial margin of the crown's lingual lobe, and the cusp as a whole is canted mesially. A distinctive feature is the presence of a crest on the mesial side of the protocone that connects the apex of this small cusp with the mesial cingulum. Cingula occur about the entire perimeter of the crown's base. Distal to the protocone, a well-developed wear facet scores the lingual cingulum.

The M$^{1–2}$ are simple, tritubercular molars that share a basic pattern of crown morphology. As such, they are described together here, although distinguishing features will be noted. The paracone and metacone are roughly equivalent in size, and are joined by mesiodistally oriented postparacrista and premetacrista. On M^2 these cusps are located more internally on the crown, because of the more
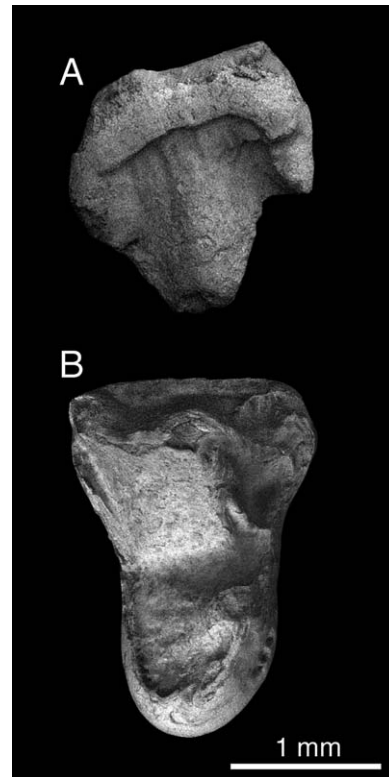

Fig. 8. *Eosimias centennicus*, IVPP V11996.3, isolated right P^4 in buccal (A) and occlusal (B) views.

gentle inclination of their buccal walls. The parastyle occurs as a well-developed and individualized cusp, connected to the paracone by the preparacrista. In contrast, the metastyle is a mere swelling of enamel marking the buccal termination of the postmetacrista. A buccal cingulum is present on both M$^{1–2}$, although this structure is somewhat stronger on M^2. The protocone is canted mesially, such that its apex lies nearer to the paracone than the metacone. Pre- and postprotocristae are remarkably well-developed, and conules are entirely absent. There is no postprotocingulum or *Nannopithex* fold. The postprotocrista continues buccally about halfway up the lingual wall of the metacone. This buccal extension of the postprotocrista is probably homologous with the hypometacrista found in many anthropoids. The lingual cingulum is continuous, but there is only very minor swelling in the areas that support the

Table 1
Dental measurements (in mm) for *Eosimias centennicus* (MD, maximum mesiodistal length; BL, maximum buccolingual width)

	V11000	V11001.1	V11001.2	V11993	V11994	V11995	V11996.1	V11996.2	V11996.3	Sample mean
I_1MD	0.55									
I_1BL	0.50									
I_2MD	0.80									
I_2BL	0.90									
C_1MD	1.75									
C_1BL	1.50									
P_2MD	1.15				1.10	1.15				1.13
P_2BL	0.85				0.90	0.90				0.88
P_3MD	1.60	1.80								1.70
P_3BL	1.05	1.05								1.05
P_4MD	1.70	1.45	2.00		1.90					1.76
P_4BL	1.20	1.10	1.40		1.30					1.25
M_1MD	1.55	1.60	2.10		2.10	2.10				1.89
M_1BL	1.25	1.15	1.50		1.35	1.40				1.33
M_2MD	2.10	2.05	2.05		2.10	2.05				2.07
M_2BL	1.75	1.60	1.65		1.45	1.55				1.60
M_3MD	2.35	2.25								2.30
M_3BL	1.60	1.45								1.53
C^1MD							1.45			
C^1BL							1.30			
P^3MD				1.75						
P^3BL				2.10						
P^4MD									1.65	
P^4BL									2.40	
M^1MD				2.15						
M^1BL				2.90						
M^2MD				1.95						
M^2BL				3.05						
dP^4MD								1.80		
dP^4BL								1.80		

hypocone and pericone in certain anthropoid taxa. The M^1 differs from the M^2 in being relatively longer mesiodistally and narrower buccolingually. The M^1 also differs in occlusal outline in showing a notable degree of "waisting" lingual to the metacone, whereas the occlusal outline of M^2 is more nearly rectangular.

Comparisons

The morphology of C^1 in *Eosimias* matches that of anthropoids more closely than any other primate group. Many living and fossil anthropoids, including the eosimiid *Bahinia*, differ from *Eosimias* in possessing a vertically oriented groove on the mesial surface of C^1, but in other respects the upper canine of *Eosimias* closely

resembles those of other anthropoids. Upper canine morphology is poorly documented among Omomyidae, but in the washakiin omomyid *Dyseolemur pacificus* (Rasmussen et al., 1995) this tooth differs substantially from that of *Eosimias*. The C^1 in *Dyseolemur* is buccolingually compressed and is therefore less triangular in cross-section than is the case in *Eosimias*. The C^1 is also shorter in crown height and not as stoutly constructed in *Dyseolemur*. In *Tarsius* C^1 bears well-developed mesial and lingual crests that are absent in *Eosimias*. In most, if not all, adapiforms (e.g., *Notharctus*, *Leptadapis,* and *Mahgarita*), the upper canines are buccolingually compressed relative to mesiodistal length. Accordingly, adapiform canines lack the stout, circular to triangular
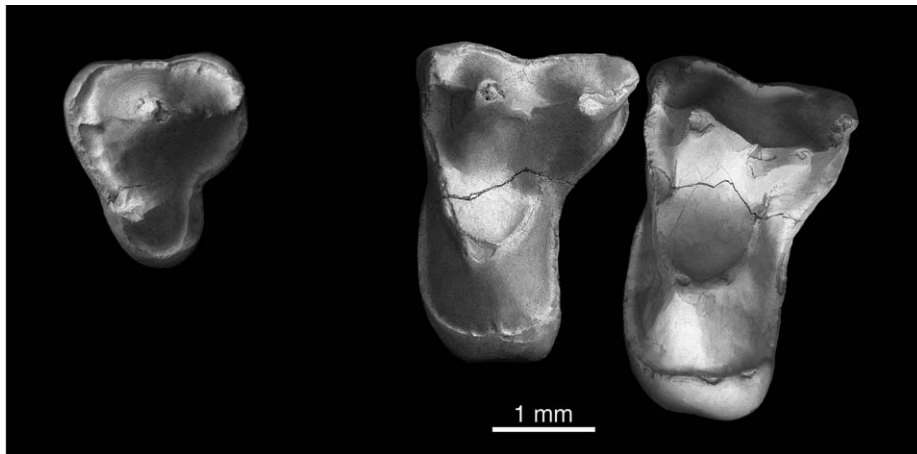
Fig. 9. *Eosimias centennicus*, IVPP V11993, left maxilla preserving P^3, M^{1-2} in occlusal view.

cross-sectional proportions that are found in *Eosimias* and other early anthropoids.

The deciduous P^4 of *Eosimias* differs markedly from this tooth in *Tarsius*, in which only a single major cusp, apparently homologous with the paracone on deciduous P^4 of *Eosimias*, is present (Luckett and Maier, 1982). We are unaware of any published descriptions of deciduous P^4 in omomyids. In early anthropoid taxa other than *Eosimias*, only rarely has deciduous P^4 been described or figured. An isolated tooth (GZC-7) from Glib Zegdou, Algeria attributed by Godinot and Mahboubi (1994) to *Algeripithecus minutus* is regarded here as deciduous P^4 of that species. Its morphology is generally similar to that of *Eosimias* in that the tooth is molariform, with the paracone and metacone located nearer the buccal margin of the crown than is the case in molars of either genus. The deciduous P^4 of *Algeripithecus* differs from its homologue in *Eosimias* in ways that mirror differences in the upper molars of these taxa. These include the presence of a well-developed hypocone and distinct conules in *Algeripithecus*, both of which are absent in *Eosimias*.

The P^3 in *Eosimias* closely resembles its homologue in *Bahinia*. In both of these early anthropoid taxa, the paracone of P^3 is a stoutly constructed cusp, especially in the buccolingual dimension. The reduced size and mesial location of the protocone on P^3 of *Eosimias* are characters that also occur in

Bahinia, in which the protocone is even more atrophied than in *Eosimias*. These aspects of P^3 protocone morphology differ from conditions in primitive omomyids (e.g., *Teilhardina*) and adapiforms (e.g., *Cantius*), in which this cusp is relatively much larger and located farther lingually and less mesially. In certain derived adapiforms, such as *Periconodon* and *Mahgarita*, the protocone of P^3 is reduced or even lost, but P^3 in these taxa differs from those of early anthropoids in possessing a mesiodistally elongated paracone that is much less inflated buccolingually. *Tarsius* also possesses a reduced protocone on P^3, but in *Tarsius* this tooth differs from the condition found in early anthropoids in bearing neomorphic crests on the mesial and lingual sides of the paracone.

The P^4 in *Eosimias* shares a basic overall design with P^3. Both teeth have a buccolingually robust and basally inflated paracone that is central in position, and a much smaller, mesially canted protocone on the mesial margin of the lingual lobe. The P^4 differs from P^3 in having a more extensive lingual lobe. As a result, the occlusal outline of P^4 is nearly rectangular (with the long axis being buccolingual), while that of P^3 is more nearly triangular. The left and right P^4 crowns in the holotype and only known specimen of *Bahinia pondaungensis* are not well preserved, largely precluding detailed comparisons with *Eosimias*. However, the different occlusal outlines of P^{3-4} in *Eosimias* also characterize these
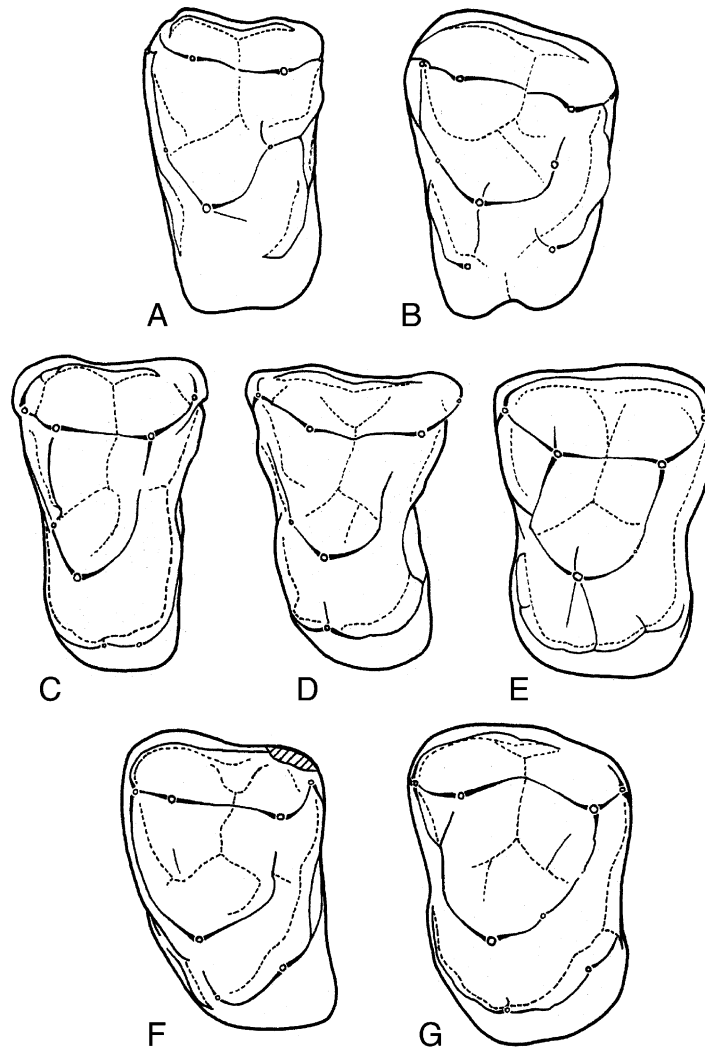
Fig. 10. Schematic drawings of M^2 structure in some Paleogene primates, scaled to have equal buccolingual width. Taxa depicted are as follows: the omomyid *Teilhardina belgica* (A), the adapiform *Periconodon helveticus* (B), the eosimiid *Eosimias centennicus* (C), the eosimiid *Phenacopithecus krishtalkai* (D), the eosimiid *Bahinia pondaungensis* (E), the proteopithecid *Proteopithecus sylviae* (F), and the oligopithecid *Catopithecus browni* (G).

teeth in *Bahinia*. Among primates other than Eosimiidae, *Proteopithecus* is particularly similar to *Eosimias* in P^4 morphology. The primary distinction between these taxa is the presence of a stronger distal cingulum or talon with a small hypocone in *Proteopithecus*. The upper premolars of oligopithecids differ from those of eosimiids and *Proteopithecus* in having relatively larger protocones that are more distal in position.

The M$^{1–2}$ of *Eosimias* are remarkably similar to those of other early anthropoids, particularly other eosimiids and *Proteopithecus* (Fig. 10). Detailed similarities to *Oligopithecus* and *Catopithecus* also exist, although here the resemblance is less than to the taxa cited earlier. In all of these early anthropoids, M$^{1–2}$ lack even rudimentary development of a postprotocingulum or *Nannopithex* fold, have reduced or absent conules, show strong

development of pre- and postprotocristae (the latter crest often extends up the lingual face of the metacone), and bear complete lingual cingula. With the exception of *Catopithecus* and *Proteopithecus*, early anthropoids lack cuspate hypocones on M^{1-2}, although the talon region can be expanded distolingually. The M^{1-2} of most omomyids differ from those of *Eosimias* and other early anthropoids in retaining well-developed conules, in having much weaker pre- and postprotocristae, in lacking a continuous lingual cingulum, and in possessing a postprotocingulum. Within Omomyidae, exceptions to this generalization can certainly be found. For example, M^{1-2} of *Omomys*, *Chumashius,* and *Macrotarsius* lack a postprotocingulum, and in certain specimens of *Teilhardina* these teeth bear a complete lingual cingulum (e.g., Kay and Williams, 1994: Fig. 10e). Nevertheless, we are unaware of any omomyid in which all (or even most) of the diagnostic character states found in M^{1-2} of early anthropoids occur together. Like those of *Eosimias* and other early anthropoids, the M^{1-2} of *Tarsius* lack postprotocingula, possess complete lingual cingula, and bear relatively well-defined pre- and postprotocristae. *Tarsius* differs from early anthropoids in retaining conules on its upper molars. The upper molars of certain adapiforms also resemble those of early anthropoids in some key features. Among these adapiform taxa, *Periconodon* has been cited as being particularly close to early anthropoids in upper molar morphology (Rasmussen, 1994). The M^{1-2} in *Periconodon* lack postprotocingula and show relatively well-developed protocone cristae, as is the case in early anthropoids. However, the upper molars of *Periconodon* differ from those of *Eosimias* and other early anthropoids in lacking complete lingual cingula and in retaining molar conules. *Periconodon* further differs from *Eosimias*, *Bahinia*, *Proteopithecus*, and *Oligopithecus rogeri* in having upper molars that are relatively less extensive in the buccolingual dimension.

Discussion

On the basis of M_1 dimensions in the holotype lower jaw, Beard et al. (1996) calculated several estimates of mean adult body mass for *Eosimias centennicus*, using regression equations developed by Conroy (1987). Those estimates (which ranged between 91 and 179 grams) now appear to be too high, based on mean M_1 dimensions in the current sample of this species from its type locality (see Table 1). Our revised estimates of adult body mass in *Eosimias centennicus* range between 64 and 131 g.

Eosimias dawsonae, new species

Holotype

IVPP V11999, left dentary fragment bearing the crowns of M_{2-3} and the roots or alveoli for P_3–M_1 (Fig. 11); only known specimen. Collected by K. C. Beard on May 9, 1995.

Type locality

Locality 11–12, Rencun Member of Heti Formation, Yuanqu Basin, Shanxi Province, People's Republic of China. Exact geographic coordinates are as follows: 35°02.18′ North, 111°47.96′ East.

Known distribution

Late middle Eocene of Shanxi Province, People's Republic of China (type locality only).

Diagnosis

Largest known species of *Eosimias*.

Etymology

For Dr. Mary R. Dawson, in recognition of her numerous contributions to knowledge of the Eocene vertebrates of the Northern Hemisphere.

Description

The configuration of the preserved roots and alveoli for P_4 in the holotype demonstrate that this tooth would have been oriented obliquely with respect to the rest of the tooth row, as is typical for *Eosimias*. The crowns of the two remaining molars are riddled with microfractures, but the morphology of these teeth closely resembles that of *Eosimias sinensis* and *Eosimias centennicus*. The preserved part of the dentary is notable for its great depth (depth of dentary below M_2, 6.30 mm) and relative robusticity. Measurements of the holotype of *E. dawsonae* are as follows: M_2 mesiodistal length (MD), 2.40 mm; M_2 buccolingual
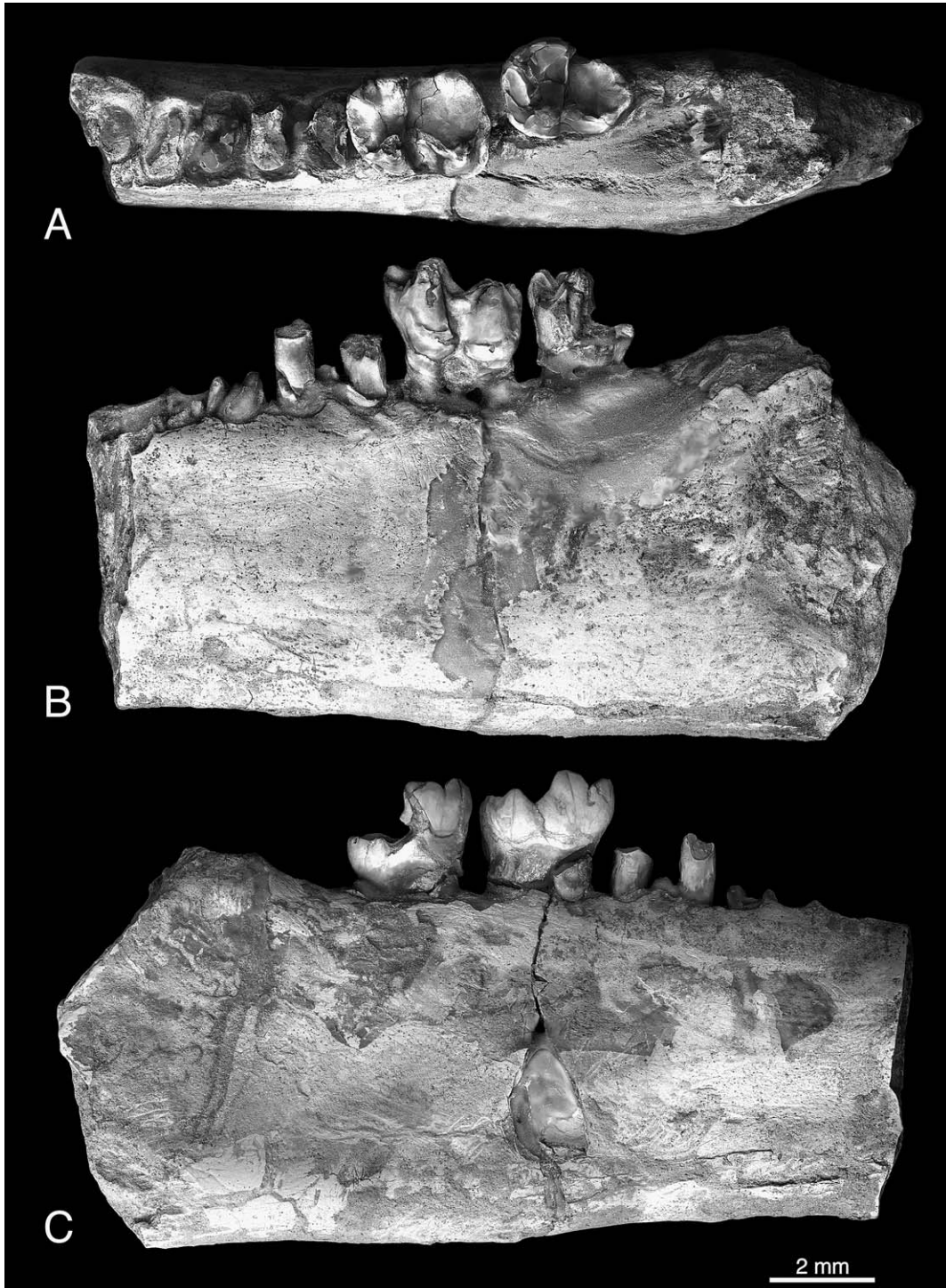
Fig. 11. *Eosimias dawsonae*, new species, holotype, IVPP V11999. Left dentary fragment bearing the crowns of M_{2-3} and the roots or alveoli for P_3–M_1 in occlusal (A), buccal (B), and lingual (C) views.
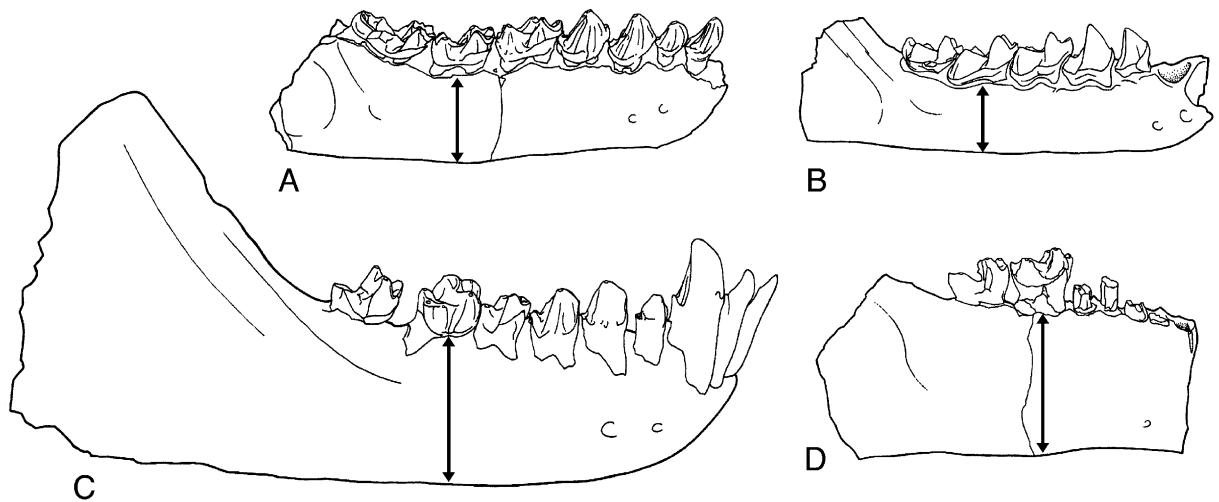
Fig. 12. Schematic drawings of the lower jaws of some Paleogene primates, scaled to have equal M_2 lengths. Taxa depicted are as follows: the omomyid *Shoshonius cooperi* (A), the tarsiid *Xanthorhysis tabrumi* (B), the eosimiid *Eosimias centennicus* (C), and the eosimiid *Eosimias dawsonae* (D). Note the great depth and robusticity of the dentary in eosimiids (see arrows beneath M_2 crowns), which contrasts with the shallow dentaries found in the tarsiiforms *Shoshonius* and *Xanthorhysis*.

width (BL), 1.90 mm; M_3MD, 2.45 mm; M_3BL, 1.65 mm.

Discussion

Available stratigraphic and biostratigraphic evidence indicates that *Eosimias dawsonae* from the Rencun Member is older than *Eosimias centennicus* from the Zhaili Member of the Heti Formation (Tong et al., 1995). However, the type locality for *Eosimias dawsonae* is not laterally contiguous with other fossiliferous sites in the Heti Formation, so that it cannot be tied directly to them.

The depth and robusticity of the eosimiid dentary has been briefly discussed by Beard et al. (1996), who contrasted the dorsoventrally deep symphyseal region of *Eosimias centennicus* with the much more gracile and procumbent symphyses of omomyids and adapiforms. Here, we emphasize that the entire dentary of eosimiids, including the portion beneath the cheek teeth, is much more robust than is the case in omomyids, tarsiids, and adapiforms of similar body size (Fig. 12). For example, the depth of the dentary of *E. dawsonae* beneath M_2 (6.30 mm) is far greater than that of the omomyid *Shoshonius cooperi* (3.80 mm), although the lower molars of *Shoshonius* are sub-

stantially larger than those of *Eosimias dawsonae*. The early tarsiid *Xanthorhysis tabrumi*, which has lower molars that are only slightly smaller than those of *Eosimias dawsonae*, also possesses a much shallower dentary (3.75 mm). Most adapiforms are so much larger than *Eosimias* that meaningful comparisons of mandibular depth in these taxa are difficult. However, in the relatively small adapiform *Adapoides troglodytes* the depth of the dentary beneath M_2 is only 5.00 mm, despite the fact that the cheek teeth of this species are much larger than those of *Eosimias dawsonae*. The great depth of the dentary in *Eosimias* compared with early tarsiiform and adapiform primates of roughly similar body size further substantiates the anthropoid affinities of *Eosimias*, because anthropoid dentaries are relatively deeper and more robust than those of prosimians (Ravosa, 1991, 1996; Ravosa and Hylander, 1994).

Previous estimates of body mass for species of *Eosimias* have relied on regressions of body mass versus M_1 area and various tarsal dimensions in living species of primates (Beard et al., 1994, 1996; Gebo et al., 2000a). Depending on the nature of the regression model that is chosen (see Conroy, 1987), mean estimates of body mass based on M_1

area range from 67–137 g in *Eosimias sinensis* and 64–131 g in *Eosimias centennicus*. Strictly speaking, the same estimates cannot be generated for *Eosimias dawsonae*, because the only known specimen lacks the crown of M_1. However, assuming that the ratio between M_1 area and M_2 area in *E. dawsonae* tracks that shown by *E. sinensis* and *E. centennicus*, we can estimate M_1 area in *E. dawsonae* and then proceed to calculate its body mass. This procedure yields mean estimates of body mass for *E. dawsonae* ranging from 107–276 g.

Phenacopithecus, new genus

Type species
Phenacopithecus xueshii, new species.

Included species
Phenacopithecus xueshii, new species; *Phenacopithecus krishtalkai*, new species.

Diagnosis
Larger than *Eosimias*, smaller than *Bahinia*. P_2 relatively smaller than in *Bahinia*. P_4 trigonid mesiodistally longer in relation to talonid than in *Eosimias*. P_4 with only a weak mesiolingual cingulid, in contrast to *Eosimias* and *Bahinia*, which have either a crestiform or cuspidate paraconid on P_4. Paraconid on M_2 smaller and more buccal in position than in *Eosimias*.

Etymology
Greek *phenakos*, impostor; and Greek *pithekos*, ape.

Discussion
Because the upper dentition of the type species is inadequately known and the lower dentition of the referred species remains unknown, future discoveries may demonstrate that the two species now included in *Phenacopithecus* actually belong in separate genera. We are confident that neither species can be referred to either *Eosimias* or *Bahinia*, however. Rather than propose a fourth genus of Eosimiidae at this stage, we tentatively allocate both species to *Phenacopithecus* here.

Phenacopithecus xueshii, new species

Holotype
IVPP V11998.4, right P_4 (Fig. 16A–D).

Hypodigm
The holotype; IVPP V11998.1, right M_2 (Fig. 19); IVPP V11998.2, left M_1 (Fig. 18D–F); IVPP V11998.3, right M_3 (Fig. 20); IVPP V11998.5, right P_3 (Fig. 15); IVPP V11998.6, left P_2 (Fig. 14); IVPP V11998.7, left deciduous P_4 (Fig. 17); IVPP V11998.8, right M_1 trigonid; IVPP V11998.9, right M^1 fragment (Fig. 21A); IVPP V11998.10, left P_4 (Fig. 16E–H); IVPP V11998.11, left P_4 (Fig. 16I–L); IVPP V11998.12, right M_1 (Fig. 18A–C); IVPP V11998.13, left P_2; IVPP V11998.14, left M^3 fragment (Fig. 21B); IVPP V11998.15, left M^3 fragment (Fig. 21C); IVPP V11998.16, right I_2 (Fig. 13).

Type locality
Nanbaotou locality, Zhaili Member of Heti Formation, Yuanqu Basin, Shanxi Province, People's Republic of China. Exact geographic coordinates are as follows: 35°08.14′ North, 111°51.80′ East.

Known distribution
Late middle Eocene of Shanxi Province, People's Republic of China (type locality only).

Diagnosis
Differs from *P. krishtalkai* in having less extensive lingual cingulum and talon on M^1.

Etymology
For our colleague, Professor Huang Xueshi, in recognition of his many contributions to knowledge of early Cenozoic mammals in China and his tireless dedication to recovering the Nanbaotou fauna in the field.

Description and comparisons
The available sample consists of isolated teeth obtained by screen-washing the microvertebrate site of Nanbaotou. Fortunately, most of the lower tooth loci (I_2 and P_2–M_3) are represented, although much less is known of the upper dentition of this species. Dental measurements for *Phenacopithecus xueshii* are provided in Table 2.

We tentatively identify IVPP V11998.16 as a right I_2 of *Phenacopithecus xueshii* on the basis of comparisons with other early anthropoids,

Table 2
Dental measurements (in mm) for *Phenacopithecus xueshii* (MD, maximum mesiodistal length; BL, maximum buccolingual width)

	1[a]	2	3	4	5	6	7	10	11	12	13	16	Sample mean
I_2MD												1.40	
I_2BL												1.65	
P_2MD						1.40					1.25		1.33
P_2BL						1.10					0.95		1.03
P_3MD					2.20								
P_3BL					1.55								
P_4MD				2.35				2.30	2.25				2.30
P_4BL				1.85				1.75	1.70				1.77
M_1MD		2.40								2.45			2.43
M_1BL		1.80								1.90			1.85
M_2MD	2.70												
M_2BL	2.30												
M_3MD			2.80										
M_3BL			2.00										
dP_4MD							2.05						
dP_4BL							1.40						

[a]All specimen catalog numbers are shown in abbreviated form as follows: 1=IVPP V11998.1, 2=IVPP V11998.2, etc.
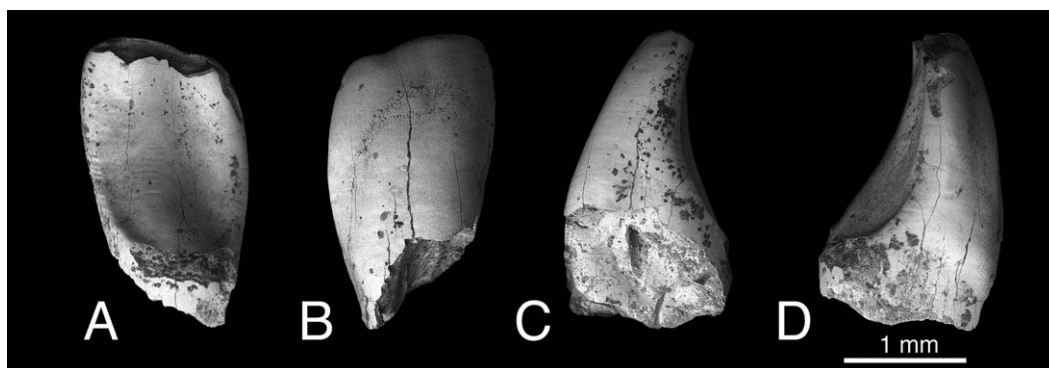
Fig. 13. *Phenacopithecus xueshii*, new genus and species, IVPP V11998.16, isolated right I_2 in lingual (A), buccal (B), mesial (C), and distal (D) views.

especially *Eosimias centennicus*, *Arsinoea kallimos*, and *Catopithecus browni*. The crown is tall and spatulate, with a smoothly convex buccal surface (Fig. 13). Its lingual surface bears a central, vertically oriented pillar of enamel that is flanked both mesially and distally by concavities. Basally, there is a weakly developed lingual cingulid. The base of the crown is much broader buccolingually than its apex. In lingual view, the crown is slightly asymmetrical because of its relatively narrower mesial side.

Compared to that of *Eosimias centennicus*, the I_2 of *Phenacopithecus xueshii* is notably larger relative to the cheek teeth. In this respect, *Phenacopithecus* resembles other anthropoids (including *Arsinoea* and *Catopithecus*) more closely than it does *Eosimias*. Morphologically, the very spatulate shape of the I_2 crown in *Phenacopithecus* differs from the more pointed I_2 crown in *Eosimias*. Indeed, the crown of I_2 in *Phenacopithecus* is more nearly spatulate than that of *Arsinoea*, which is conspicuously asymmetrical due to the strong
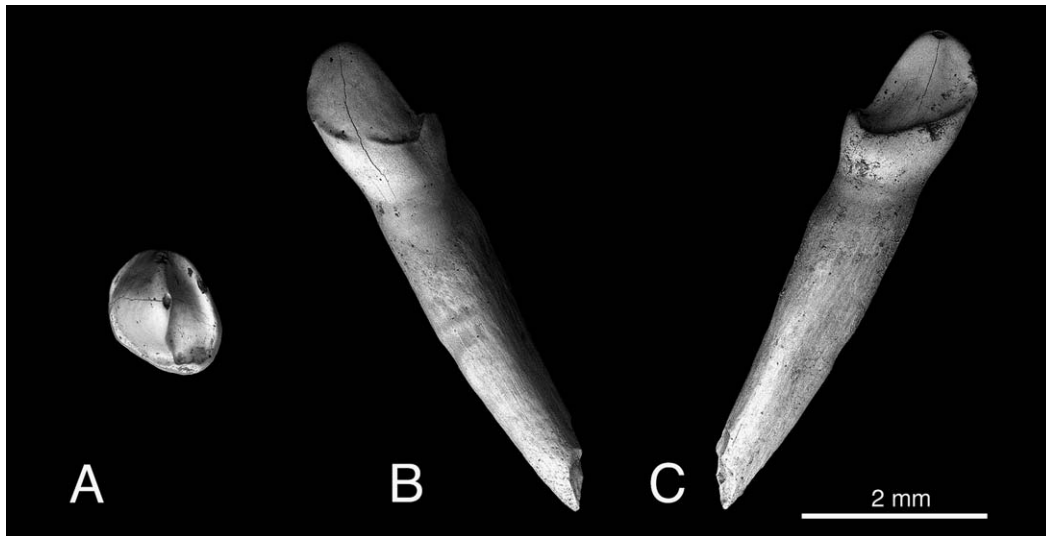
Fig. 14. *Phenacopithecus xueshii*, new genus and species, IVPP V11998.6, isolated left P_2 in occlusal (A), buccal (B), and lingual (C) views.

mesial inclination of its central lingual pillar, which may have supported an apical cuspule not unlike that found in *Eosimias*.

The P_2 is represented by two specimens, of which IVPP V11998.6 is the more nearly complete (Fig. 14). The tooth is single-rooted and relatively simple in morphology. Its crown is dominated by the mesially canted protoconid, which is the only distinct trigonid cusp. The buccal surface of the tooth is evenly convex, while the lingual surface is excavated, especially distally. Cingulids line the entire periphery of the crown. Crests emanate from the mesial and distal sides of the protoconid. The preprotocristid is confluent basally with the relatively well-developed lingual cingulid. The postprotocristid also terminates near the base of the trigonid, just buccal to the location of the tiny talonid cuspule. The root is remarkably stout and long, measuring at least 4.30 mm in length (the entire root is not preserved). Given the oblique orientation of the crowns and roots of P_{3-4} in all eosimiids, it is interesting to note that the root of P_2 is not circular in cross-section. Rather, the root is strongly reinforced in the mesiobuccal–distolingual dimension, which is the same orientation shown by the more posterior premolars.

The P_2 in *Phenacopithecus* clearly resembles that of *Eosimias* in being small relative to the other premolars. In this respect, *Phenacopithecus* and *Eosimias* differ from *Bahinia*, most living and fossil platyrrhines, and those Fayum anthropoids in which P_2 is retained.

The only known P_3 of *Phenacopithecus xueshii* is double-rooted and moderately exodaenodont (Fig. 15). Although both roots are broken near the base of the crown, it is apparent that in life the mesial root would have been more buccal in position than the distal root. The crown is morphologically simple. Like that of P_2, the trigonid of P_3 is dominated by the protoconid, which is its only distinct cusp. Pre- and postprotocristids adorn the mesial and distal flanks of this cusp, but neither of these crests are particularly trenchant. Cingulids occur about the entire undamaged periphery of the crown, and the lingual cingulid is particularly strongly developed. Minor damage on the distobuccal part of the crown's base makes it impossible to determine the degree of completeness of the buccal cingulid. The talonid is low and extremely simple in morphology, being abbreviated both mesiodistally and labiolingually. There are neither distinct cusps nor crests on the talonid,
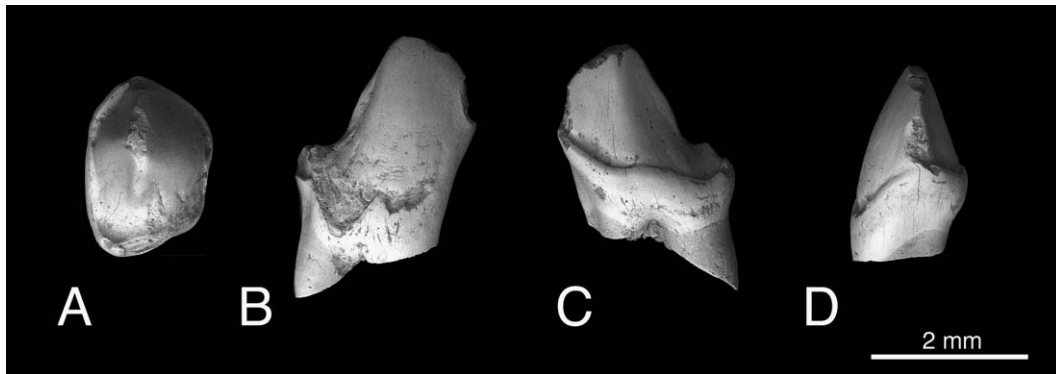
Fig. 15. *Phenacopithecus xueshii*, new genus and species, IVPP V11998.5, isolated right P_3 in occlusal (A), buccal (B), lingual (C), and mesial (D) views.

although this structure is slightly damaged distally, where a tiny hypoconid would occur if one were present.

In all known eosimiids P_3 is remarkably uniform (the crown of P_3 is damaged in the only specimen of *Bahinia pondaungensis* in which this tooth locus is preserved). All possess a low, simple talonid; a trigonid that lacks paraconid and metaconid cusps; relatively complete cingulids that are particularly strong lingually; a mesial root that is more buccally situated than the distal root; and slight to moderate exodaenodonty. This combination of conditions also occurs in *Siamopithecus* (Chaimanee et al., 2000a) and Fayum proteopithecids (*Proteopithecus* and *Serapia*), suggesting that this type of P_3 morphology approximates the anthropoid morphotype.

The P_4 of *Phenacopithecus xueshii* is documented by three specimens, the most pristine of which has been designated the holotype (Fig. 16). Like P_3, P_4 is double-rooted and the mesial root is offset buccally with respect to the distal root. The crown, which is more strongly exodaenodont than that of P_3, is dominated by the trigonid, which is mesiodistally longer in relation to the talonid than is the case in *Eosimias*. In part, this mesiodistal elongation derives from the less vertical orientation of the preprotocristid in *Phenacopithecus*, but the talonid also appears to be relatively shorter mesiodistally than is the case in *Eosimias*. There is no development whatsoever of a paraconid. Rather, the preprotocristid simply merges with the

modestly developed lingual cingulid at the point where a cuspidate (*Eosimias centennicus*) or crestiform (*Eosimias sinensis* and *Bahinia pondaungensis*) paraconid occurs in other eosimiids. The metaconid is well-developed and situated inferior and distal to the protoconid. The postprotocristid joins the protoconid with the metaconid. A continuation of this crest runs inferiorly and distally from the metaconid to merge with the distolingual cingulid. The buccal cingulid is moderately developed and variably complete in the three specimens at hand. In all three specimens, this structure is roughly W-shaped in buccal view, because the cingulid is prolonged inferiorly where the dual exodaenodont bulges of enamel occur, just above the two roots. The talonid is more strongly developed than that of P_3, but this structure remains relatively short mesiodistally. It bears a single cusp, the hypoconid, which is united with the postvallid by a distinct cristid obliqua. Together, the cristid obliqua, the hypoconid, and thedistolingual cingulid completely surround a small talonid basin.

As is the case in other primitive haplorhine primates (e.g., Bown and Rose, 1987), P_4 appears to be a particularly diagnostic tooth locus among eosimiids. At the same time, shared P_4 characters form some of the most compelling evidence from the dentition that eosimiids are closely related to each other and to other basal anthropoids. In all eosimiids P_4 is slightly to moderately exodaenodont; the mesial root is situated farther buccally
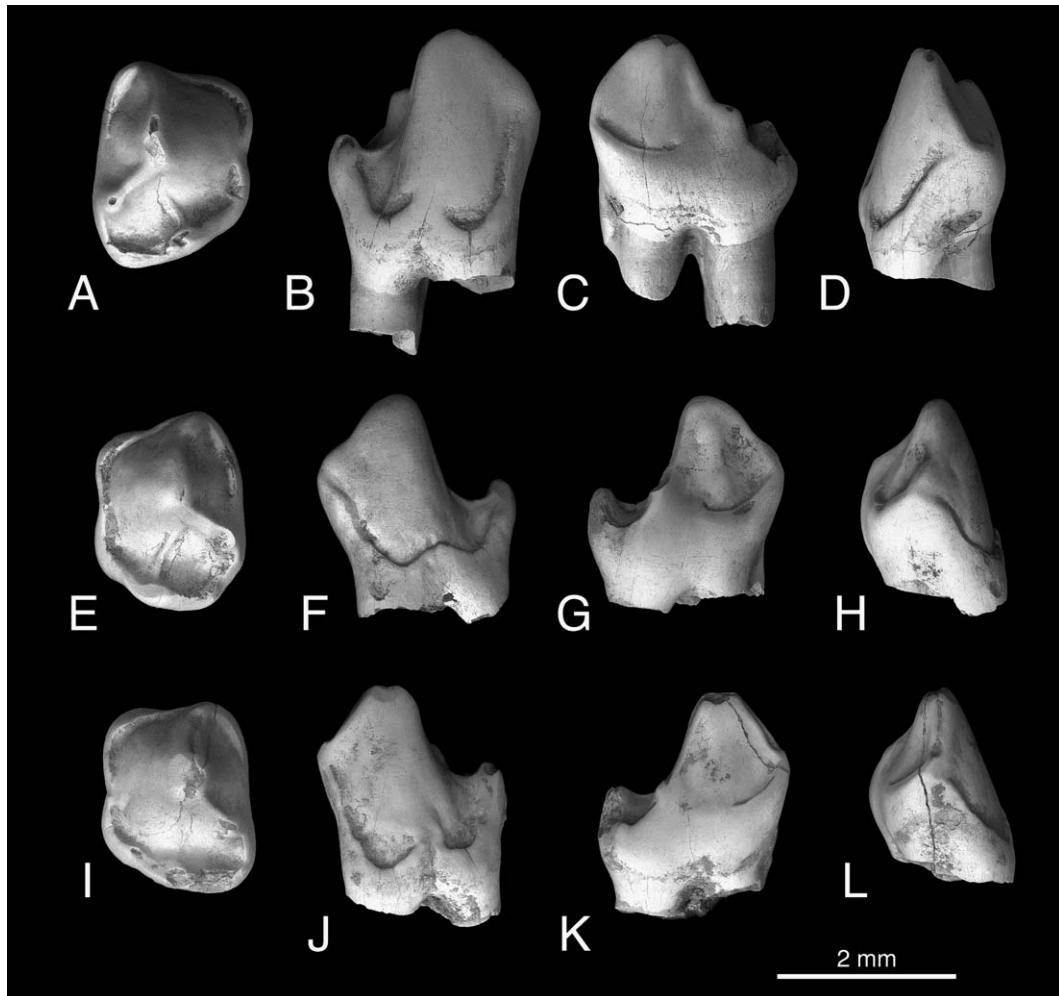
Fig. 16. *Phenacopithecus xueshii*, new genus and species, isolated lower fourth premolars. (A–D) IVPP V11998.4, holotype right P$_4$ in occlusal (A), buccal (B), lingual (C), and mesial (D) views. (E–H) IVPP V11998.10, left P$_4$ in occlusal (E), buccal (F), lingual (G), and mesial (H) views. (I–L) IVPP V11998.11, left P$_4$ in occlusal (I), buccal (J), lingual (K), and mesial (L) views.

than the distal root; the talonid is low and simply constructed; the metaconid is present and situated inferiorly and distally with respect to the protoconid; a strong, transverse crest uniting metaconid and protoconid is lacking; and the paraconid is absent or only weakly developed. This combination of characters is replicated in the primitive amphipithecid *Siamopithecus eocaenus* (Chaimanee et al., 2000a). With slight modifications, such as enlargement and/or mesial displacement of the metaconid, a very similar P$_4$ morphology characterizes more advanced amphi-

pithecids, such as *Amphipithecus* and *Pondaungia* (Jaeger et al., 1998; Chaimanee et al., 2000b), and the proteopithecids *Proteopithecus* and *Serapia* (Simons, 1992; Miller and Simons, 1997). Given the widespread distribution of these characters among basal anthropoid taxa, the anatomy of P$_4$ among eosimiids probably approximates that of the anthropoid morphotype.

Gunnell and Miller (2001) recently argued that P$_4$ in *Eosimias* is not exodaenodont, based in part on their novel methods for quantifying exodaenodonty in primates. We reject Gunnell and Miller's
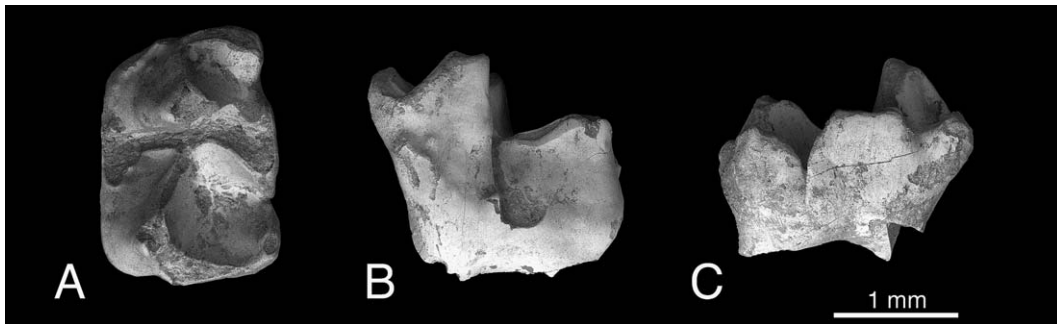
Fig. 17. *Phenacopithecus xueshii*, new genus and species, IVPP V11998.7, isolated left deciduous P$_4$ in occlusal (A), buccal (B), and lingual (C) views.

(2001) simple metrical definition of exodaeno-donty, whereby such classical examples of exodae-nodonty as that of the P$_4$ in carpolestid plesiadapoids fail to qualify. Rather, following Hürzeler's (1944: 7) original definition of the term, we consider lower premolar crowns to be exodae-nodont whenever the buccal enamel protrudes buccally and inferiorly beyond the inferior margins of the lingual sides of the same teeth. By this definition, P$_{3-4}$ in *Phenacopithecus xueshii* (and other eosimiids) are quite exodaenodont (see mesial views of specimens illustrated in Figs. 15 and 16).

A single deciduous P$_4$ of *Phenacopithecus xueshii* is known (Fig. 17). As is typically the case among placental mammals, this tooth is funda-mentally molariform in morphology, although it is relatively longer and narrower than the adult molars. The crown is moderately worn, especially the hypoflexid and the major crests of the trigonid and postcristid. The metaconid appears to have been particularly long mesiodistally. Although its apex is obscured by wear, the metaconid was likely positioned farther distally in relation to the protoconid than is the case on the lower molars.

The morphology of M$_1$ does not depart dra-matically from that of other eosimiid primates (Fig. 18). All three trigonid cusps are distinctly cuspidate. In terms of both basal volume and height, the protoconid is the largest of the trigonid cusps. The paraconid and metaconid are propor-tionally similar, and the paraconid is mesiolingual

(but not fully lingual) in position. The largest cusp on the talonid is the hypoconid. From the latter cusp, the cristid obliqua runs mesio-lingually, joining the postvallid near the base of the protoconid. As a result, the hypoflexid is relatively shallow. The entoconid is relatively mesial in pos-ition, and the hypoconulid is centrally located, near the midline of the postcristid. The buccal cingulid is weakly developed and seemingly discon-tinuous, being most apparent in the region of the hypoflexid.

Despite the overall similarity shared by all eosimiids in M$_1$ morphology, a few minor anatomical differences are known. For example, in *Phenacopithecus xueshii* the protoconid of M$_1$ is not as enlarged relative to the metaconid as is the case in *Eosimias sinensis*. In contrast, these trigo-nid cusps are roughly the same size in *Eosimias centennicus*. This condition is difficult to ascertain in *Bahinia pondaungensis*, because the metaconid is broken on the only M$_1$ known for this taxon. The centrally located hypoconulid does not project distally beyond the postcristid in *Phenacopithecus*, whereas this cusp is offset both buccally and distally in *Eosimias*, especially *E. sinensis*. In *Bahinia* and amphipithecids the hypoconulid is relatively smaller and less distinct from the post-cristid than is the case in either *Eosimias* or *Phenacopithecus*. Among most Fayum anthro-poids, including *Arsinoea*, proteopithecids, and oligopithecids, the hypoconulid and entoconid on M$_1$ are "twinned"; that is, the hypoconulid is shifted strongly linguad. In most platyrrhines the
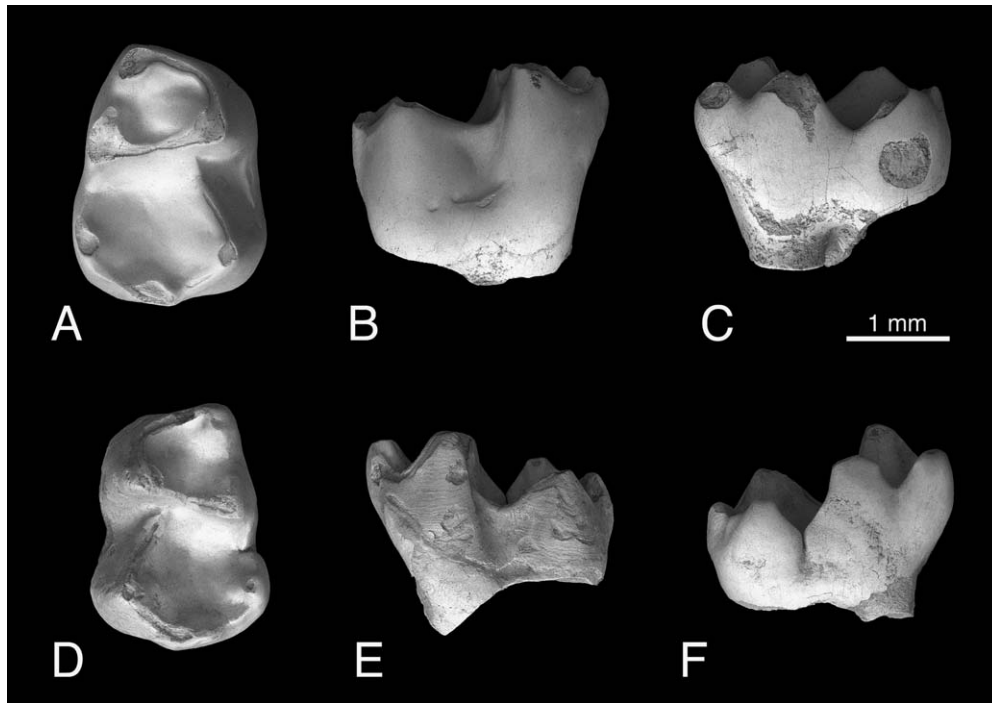
Fig. 18. *Phenacopithecus xueshii*, new genus and species, isolated lower first molars. (A–C) IVPP V11998.12, right M_1 in occlusal (A), buccal (B), and lingual (C) views. (D–F) IVPP V11998.2, left M_1 in occlusal (D), buccal (E), and lingual (F) views.

hypoconulids on $M_{1–2}$ are greatly reduced or absent.

The M_2 is documented by a single specimen (Fig. 19). The three trigonid cusps are almost completely linked with one another by crests; only the paraconid and metaconid remain separated by a small valley immediately mesial to the premetacristid. The paraconid is smaller and situated farther buccally than is the case in *Eosimias sinensis* and most individuals of *E. centennicus*, although some specimens of the latter species (e.g., IVPP V11011.1; see Fig. 5) document intraspecific variation for these characters. The talonid is noticeably wider than the trigonid. Dual hypoconulid cuspules are relatively centrally placed on the postcristid. The entoconid is mesial in position, lying just distal to the postvallid. The buccal cingulid is moderately developed, especially in the region of the hypoflexid. This structure appears to be lacking near the base of the hypoconid.

The M_3 (Fig. 20) closely resembles M_2 in most aspects of trigonid morphology. Its talonid is appreciably narrower than its trigonid. The hypoconulid lobe is abbreviated both mesiodistally and buccolingually, barely projecting distally beyond the remainder of the talonid. Two tiny cuspules, either or both of which may be homologous with the entoconid, occupy the lingual crest on the talonid. Mesially, the buccal cingulid is fairly strong until its termination at the distal end of the hypoflexid.

Three isolated upper molars are known, none of which is complete (Fig. 21). IVPP V11998.9 consists of roughly the lingual two-thirds of a right upper molar crown, identified here as M^1 on the basis of comparisons with the holotype maxilla of *P. krishtalkai* (see below). The entire lingual part of the crown is preserved, including the protocone, the pre- and postprotocristae, the lingual cingulum and talon, and most of the trigon. The lingual part of the paracone is also preserved, including part of the apex of this cusp and the adjacent postparacrista. Missing are the parastyle, the metacone, and the entire buccal margin of the crown. Notable

Fig. 19. *Phenacopithecus xueshii*, new genus and species, IVPP V11998.1, isolated right M_2 in occlusal (A), buccal (B), and lingual (C) views.
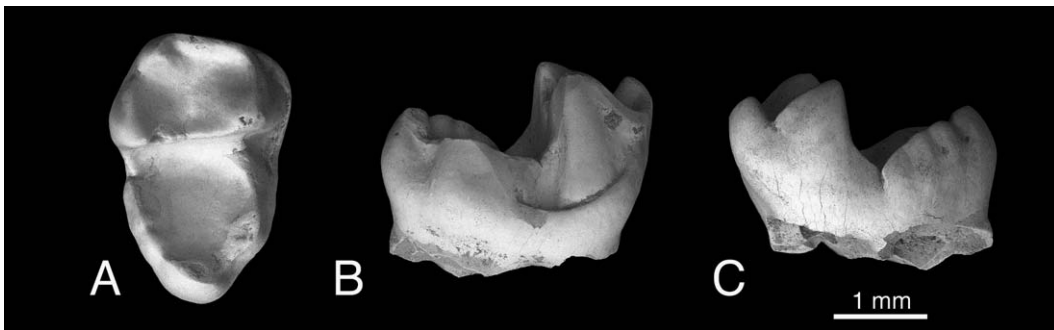

Fig. 20. *Phenacopithecus xueshii*, new genus and species, IVPP V11998.3, isolated right M_3 in occlusal (A), buccal (B), and lingual (C) views.

features include the mesially canted protocone with well-developed pre- and postprotocristae, the absence of a postprotocingulum or *Nannopithex*-fold, the loss or significant reduction of conules, and the complete lingual cingulum, which is moderately enlarged distolingual to the protocone, forming a presumptive talon.

Two morphological features that support our identification of IVPP V11998.9 as a fragmentary M^1 rather than M^2 are the relatively narrow trigon (as suggested by the short distance between the paracone and protocone) and the relatively slender lingual cingulum and talon. In *P. krishtalkai*, M^1 differs from M^2 in having a less expansive trigon (particularly buccolingually) and in having a less

extensive talon. Differences in the occlusal outlines of M^1 and M^2 are possibly more diagnostic in distinguishing between these upper molars in various eosimiids. For example, in both *Eosimias centennicus* and *Phenacopithecus krishtalkai*, M^1 shows significantly more "waisting" lingual to the metacone, because the metacone projects distally well beyond the level of the crown's protocone lobe. In contrast, the occlusal outline of M^2 is more nearly rectangular in these taxa. This difference in the occlusal outlines of M^1 and M^2 is less apparent in *Bahinia pondaungensis*. Unfortunately, because the metacone is completely broken away in IVPP V11998.9, this criterion does not apply in this case.
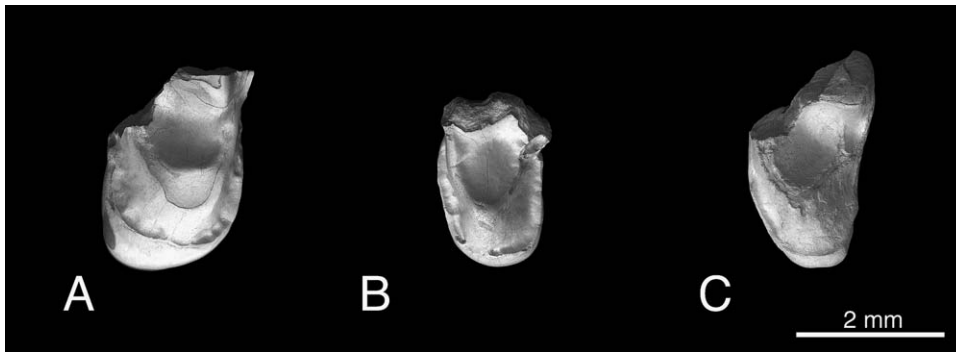
Fig. 21. *Phenacopithecus xueshii*, new genus and species, isolated upper molar fragments in occlusal view. (A) IVPP V11998.9, lingual fragment of right M^1; (B) IVPP V11998.14, lingual fragment of left M^3; (C) IVPP V11998.15, left M^3 missing the paracone and surrounding region.

Two additional upper molar fragments are currently known for *P. xueshii*, both of which are partial left M^3 crowns (Fig. 21B, C). Both specimens exhibit the same suite of upper molar features that characterize M^1 and M^2 in Eosimiidae. That is, they each have mesially canted protocones, relatively trenchant pre- and postprotocristae, and complete (or nearly so, in the case of IVPP V11998.14) lingual cingula. In addition, they each lack any trace of a postproto-cingulum or *Nannopithex*-fold, and their conules are highly reduced or absent. Curiously, the post-protocrista divides into two distinct branches in the vicinity of the region where a metaconule would occur if one were present. Although there is no metaconule per se, the more distal of the two crests emanating from the postproto-crista might be regarded as a postmetaconule crista.

Discussion

Of the specimens included in the hypodigm of *P. xueshii*, only the fragmentary M^1 is directly comparable with the holotype and only known specimen of *P. krishtalkai*. This problem is reflected in the terse diagnoses for the two species. Estimates of mean adult body mass in *P. xueshii* using Conroy's (Conroy, 1987) regression equations range from 163–316 g.

Phenacopithecus xueshii occurs in the strati-graphically highest fossil locality currently known in the Heti Formation, while *P. krishtalkai* is known from a single site in the Rencun Member. We do not yet know how much time is represented by this stratigraphic disparity, but it is likely to be substantial based on preliminary studies of the associated faunas and paleomagnetic reversal stratigraphy.

Phenacopithecus krishtalkai, new species

Holotype

IVPP V11997, right maxilla fragment preserving P^4–M^2 (Fig. 22); only known specimen.

Type locality

Locality 7, Rencun Member of Heti Formation, Yuanqu Basin, Henan Province, People's Republic of China. Exact geographic coordinates are as follows: 35°03.01′ North, 111°48.82′ East.

Known distribution

Late middle Eocene of Henan Province, People's Republic of China (type locality only).

Diagnosis

M^1 with more extensive lingual cingulum and talon than in *P. xueshii*.

Etymology

For Dr. Leonard Krishtalka, who discovered the only known specimen of this species on May 11, 1994.

Description

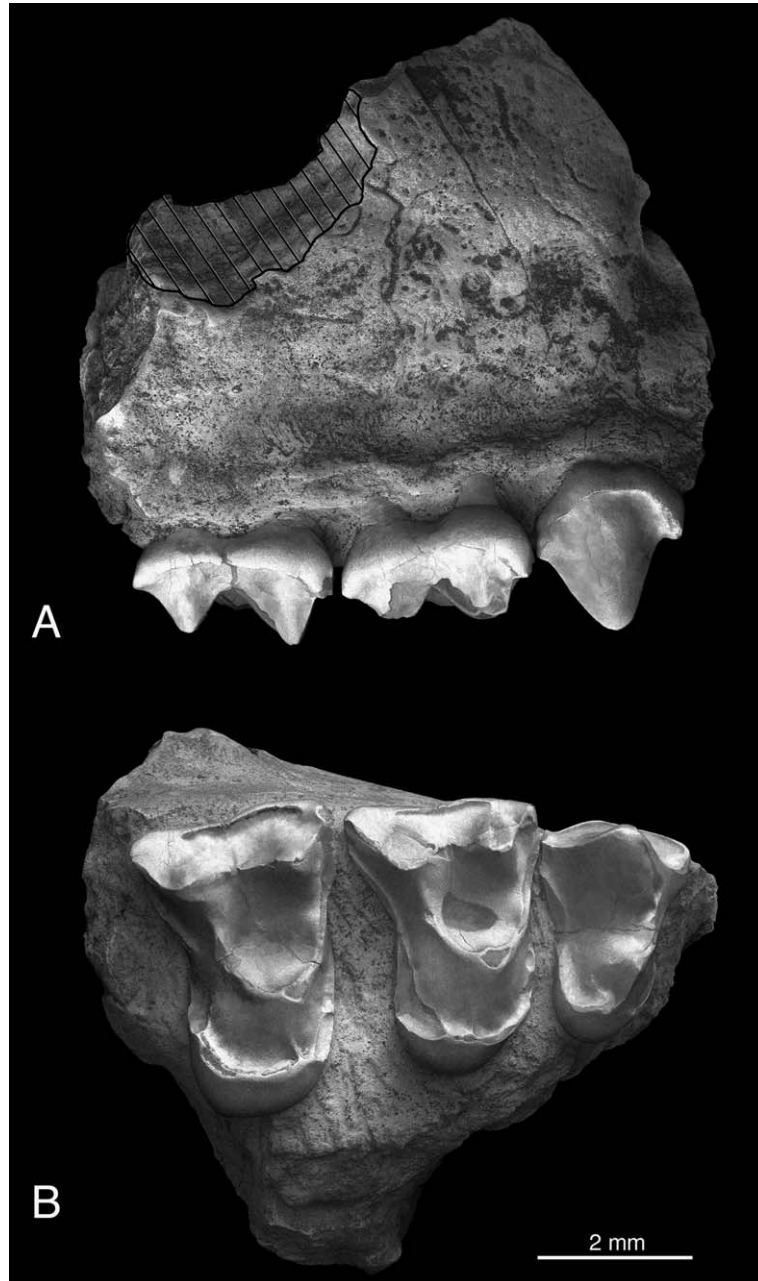The holotype of *P. krishtalkai* is among the few eosimiid maxillae currently known. It preserves

Fig. 22. *Phenacopithecus krishtalkai*, new species, holotype, IVPP V11997. Right maxilla fragment bearing the crowns of P^4–M^2 in buccal (A), and occlusal (B) views. The broken root of the zygomatic process is highlighted by hatchmarks in buccal view.

some notable aspects of the upper dentition and face that are otherwise undocumented among Eosimiidae.

In lateral view the root of the zygomatic process is marked by an area of broken bone (outlined by hatchmarks in Fig. 22). From that which remains,
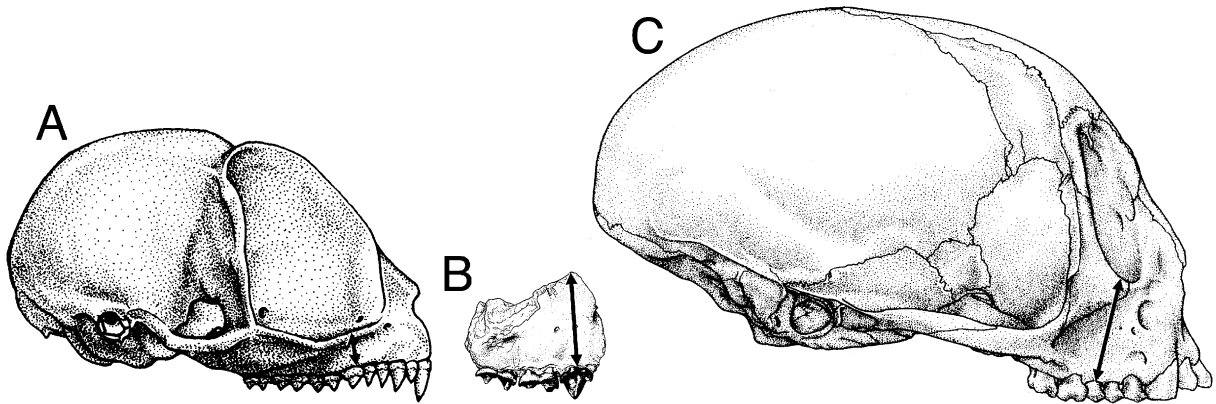
Fig. 23. Schematic drawings illustrating the divergent facial and orbital proportions of a living tarsier (A) and a living squirrel monkey (C). Note the qualitatively greater depth of the lower face (the region between the inferior orbital margin and the alveolar border; see arrows) in the squirrel monkey compared to the tarsier. Although the inferior orbital margin is not preserved in the holotype maxilla fragment of *Phenacopithecus krishtalkai* (B), it is apparent that this fossil would have had a deep lower face in life. The tarsier and the *Phenacopithecus* fossil are shown at the same scale, while the squirrel monkey is reduced to 67% of its actual proportions relative to the other specimens.

it is clear that the root of the zygomatic process was relatively superior in position with respect to the maxillary alveolar margin. For example, the inferiormost point on the broken root of the zygomatic process lies 1.90 mm above the alveolar border in the holotype of *P. krishtalkai*, whereas the same point protrudes lateral to the alveolar margin in *Shoshonius cooperi*, an omomyid primate with large, tarsierlike orbits. Although the inferior orbital rim is not preserved, it is clear that the maxilla was deep in the region between the alveolar margin and the orbit (Fig. 23). A minimum estimate of maxillary depth in this region is 5.80 mm, based on the specimen as it is now preserved. For comparison, the same measurement in the adapiform primate *Mahgarita stevensi* (holotype) is 6.05 mm, although *Mahgarita* was obviously much larger than *Phenacopithecus krishtalkai*.

Most of the circumference of a small infraorbital foramen is preserved superior to the mesial part of P^4, 2.75 mm above the alveolar margin. The height of the infraorbital foramen is 0.50 mm; the breadth of the foramen cannot be measured directly due to breakage, but it probably did not exceed 0.65 mm.

The P^4 (MD, 2.05 mm; BL, 2.85 mm) bears two main cusps. The paracone is large and basally inflated. There is a trenchant postparacrista, but

the preparacrista is much weaker. Near the base of the paracone on its mesial side is a vertically oriented groove. The apex of the paracone is located near the midline of the buccal side of the tooth. The much smaller protocone, in contrast, lies on the mesial edge of the tooth's lingual lobe. Buccal and lingual crests emanate from the apex of the protocone. The lingual crest extends to the lingual margin of the crown, where it turns distally to become confluent with the raised distal cingulum or talon. At the mesial culmination of the buccal cingulum lies a small parastyle.

The upper molars of *Phenacopithecus krishtalkai* share numerous features with those of *Eosimias centennicus*. Because $M^{1–2}$ of *E. centennicus* were described in detail above, here we focus on the distinctive aspects of upper molar morphology in *P. krishtalkai*. The $M^{1–2}$ of *P. krishtalkai* (M^1MD, 2.50 mm; M^1BL, 3.40 mm; M^2MD, 2.60 mm; M^2BL, 3.90 mm) differ most notably from these teeth in *E. centennicus* in having a much stronger lingual cingulum and talon. Together, these structures form an extensive, raised lip that is most prominent distolingually. There is no development of a cuspate hypocone. Prominent wear facets occur on the lingual cingulum and talon both mesially and distally, slightly lingual to the protocone. Of these, the distal wear facet is more

conspicuous. The trigons of the upper molars are relatively more expansive in *P. krishtalkai* than in *Eosimias*, because the paracone and metacone cusps are more widely spaced and the protocone cristae diverge from the protocone at a larger angle. *Phenacopithecus krishtalkai* also bears weaker parastyles on its upper molars than does *Eosimias*.

Comparisons

The P^4 in *Phenacopithecus krishtalkai* shares the same basic design as that found in *Eosimias centennicus*. Minor differences are observed in crown proportions (P^4 is mesiodistally narrower in relation to buccolingual breadth in *Eosimias*) and the presence or absence of the small mesial fovea that occurs in the only known P^4 of *Eosimias centennicus* but not on the holotype of *Phenacopithecus krishtalkai*. Given current sample sizes, it is impossible to know whether these minor differences are taxonomically diagnostic.

The upper molars of *P. krishtalkai* are intermediate in size and certain aspects of morphology between those of *Eosimias* and *Bahinia*. *Phenacopithecus krishtalkai* shares with the latter genus more expansive molar trigons and stronger lingual cingula and talons than occur in *Eosimias*. *Bahinia* bears more trenchant crests on all sides of its upper molar trigons and possesses more uniform development of the lingual cingula, whereas in *P. krishtalkai* the lingual cingula are stronger distally than mesially. As noted above, the upper molars of all of these eosimiid taxa are remarkably similar to those of other early anthropoids, especially *Proteopithecus*.

Phylogenetic implications of the Yuanqu Basin eosimiids

It is now widely, though not universally, accepted that Asian eosimiids lie near the base of the anthropoid evolutionary radiation (MacPhee et al., 1995; Beard et al., 1994, 1996; Kay et al., 1997; Ross et al., 1998; Jaeger et al., 1999; Gebo et al., 2000a, 2001; Ross, 2000; Beard, 2002). The additional eosimiid material reported here strengthens this view, because the new sample documents further shared derived characters link-

ing eosimiids with other early anthropoids. New evidence, mainly from the morphology of the upper dentition and the anatomy of the lower face, therefore complements previous evidence from the lower dentition and tarsal region indicating that eosimiids are basal anthropoids.

Upper molar anatomy has figured prominently in recent iterations of the hypothesis that anthropoids evolved from Eocene adapiforms (Rasmussen and Simons, 1988; Simons, 1989, 1995; Rasmussen, 1994; Simons and Rasmussen, 1996). The new material described here shows that *Eosimias* and *Phenacopithecus* possess many of the upper molar characters that have been cited as putative synapomorphies linking anthropoids to cercamoniine adapiforms. In particular, all of these taxa share upper molars bearing relatively strong protocone cristae, with the buccal part of the postprotocrista frequently being continuous with the hypometacrista, while the postprotocingulum is lacking. In addition, the upper molars of eosimiids share a number of characters with other early anthropoids that are lacking in adapiforms. These traits include the loss of conules, the presence of complete lingual cingula, and the mesial position of the protocone, which is also strongly canted mesially.

Certain species of oligopithecids, such as *Oligopithecus savagei* from the Fayum region of Egypt, are more similar to cercamoniine adapiforms than to *Eosimias* in the basic proportions of their upper molars. In *O. savagei* and many cercamoniine adapiforms, the upper molars are relatively narrow buccolingually (Rasmussen and Simons, 1988). However, the upper molars of other oligopithecids, especially *O. rogeri* from the locality of Taqah in Oman (Gheerbrant et al., 1995), are relatively broader than is the case in *O. savagei* and cercamoniine adapiforms. *Proteopithecus* also resembles *Oligopithecus rogeri* and eosimiids in having relatively broad upper molars (Miller and Simons, 1997). Given this taxonomic distribution, we conclude that basal anthropoids possessed upper molars with occlusal outlines similar to those of eosimiids, *Proteopithecus*, and *O. rogeri*, and that the buccolingually narrow upper molar proportions shared by *O. savagei* and certain cercamoniine adapiforms are due to convergence.

In general, oligopithecids appear to have figured too prominently in some recent attempts to ascertain morphotypic conditions for Anthropoidea and to reconstruct the broader relationships of this clade (Rasmussen and Simons, 1988; Simons, 1989, 1990, 1995; Rasmussen, 1994; Simons and Rasmussen, 1996). Paradoxically, the same workers who champion similarities between certain oligopithecids and adapiforms as evidence of an adapiform ancestry for anthropoids also posit that oligopithecids are nested deep within the anthropoid radiation, as basal members of the Catarrhini (Simons and Rasmussen, 1996; Seiffert et al., 2000; Seiffert and Simons, 2001). Without necessarily endorsing catarrhine affinities for oligopithecids, we agree that these primates are likely to be nested deep within the anthropoid radiation. If such a phylogenetic reconstruction for oligopithecids is accurate, robust hypotheses concerning anthropoid origins will need to rely on taxa—such as eosimiids—that occupy more basal positions on the anthropoid evolutionary tree.

New information regarding the facial anatomy of eosimiids can be gleaned from the holotype of *P. krishtalkai*. Though fragmentary, this specimen shows that eosimiids possessed a dorsoventrally deep maxilla between the inferior orbital rim and the alveolar margin. The depth of the lower face in *P. krishtalkai* differs markedly from the condition in omomyids and tarsiids, in which the root of the zygomatic process and the inferior orbital rim closely approximate the alveolar margin (Fig. 23). Clearly, *Phenacopithecus* lacked the hypertrophied orbits that are characteristic of living tarsiers and many omomyids and microchoerids. This anatomical fact poses a major challenge to those who persist in advocating a special phylogenetic tie between eosimiids and living and fossil tarsiiform primates (Rasmussen et al., 1998; Simons, 2003). At the same time, the presence of relatively small orbits in *Phenacopithecus* suggests that eosimiids probably resembled living anthropoids (with the exception of *Aotus*) in having a diurnal activity pattern. Quantitative data on orbit diameter and are currently available remain highly suggestive.

The small size of the infraorbital foramen in the holotype of *Phenacopithecus krishtalkai* also carries functional and phylogenetic implications. *Phenacopithecus krishtalkai* probably resembled living haplorhine primates in having a small infraorbital foramen relative to skull length (cf. Kay and Cartmill, 1977). In life, *P. krishtalkai* presumably lacked the extremely well-innervated and highly irrigated rhinarial region that is characteristic of living strepsirhines and inferred for fossil adapiforms and microchoerids (Kay and Cartmill, 1977; Beard, 1988).

Summary and conclusions

Eosimiid primates occur at most of the well-sampled fossil vertebrate sites in the Eocene Heti Formation of central China. The numerical abundance and stratigraphic range of eosimiids in the Heti Formation demonstrate that these animals were a relatively common and temporally persistent component of late middle Eocene mammalian faunas in this part of central China. Establishing the geochronological significance of the stratigraphic distribution of eosimiids in the Heti Formation will depend on analyses of paleomagnetic reversal stratigraphy that are currently in progress.

The Asian eosimiid radiation generated a substantial amount of taxonomic diversity. Four eosimiid species—*Eosimias centennicus*, *Eosimias dawsonae*, *Phenacopithecus xueshii*, and *Phenacopithecus krishtalkai*—have been documented to date in the Heti Formation alone. The stratigraphic ranges of *Phenacopithecus* and *Eosimias* appear to overlap throughout much of the Heti Formation. Indeed, the two genera co-occur at Locality 7 in the Rencun Member, in the form of the holotype of *Phenacopithecus krishtalkai* (described here) and isolated teeth of *Eosimias* described and illustrated by Tong (1997: Fig. 23). Additional eosimiid taxa are known from the Shanghuang fissure-fillings of Jiangsu Province near the central Chinese coastline and the Pondaung Formation of central Myanmar.

Although several workers continue to challenge the anthropoid affinities of Eosimiidae, new anatomical evidence presented here further substantiates the anthropoid status of these fossils. To our knowledge, no one has ever claimed that eosimiids are closely related to adapiform or strepsirhine

primates. Rather, those who question whether eosimiids are anthropoids have often argued that eosimiids are related to living and fossil tarsiiform primates in some manner, although the details of this putative relationship typically remain unspecified (Rasmussen et al., 1998; Ciochon and Gunnell, 2002a,b; Simons, 2003). These same workers routinely neglect to cite potential synapomorphies linking eosimiids with tarsiiforms, relying instead on primitive characters to cast doubt on the anthropoid affinities of eosimiids. For example, Simons (2003:28–29) recently expressed the opinion that, "*Eosimias* anatomy is not convincingly anthropoidean. It is tarsierlike or omomyidlike, *possibly only due to primitiveness.* The possible affinities [of *Eosimias*] with tarsiids should be further analyzed to ascertain whether it is [*sic*] real or due to shared primitive features" (italics added for emphasis). While we applaud further efforts to elucidate the phylogenetic position of *Eosimias* and its close relatives, we suggest that workers who continue to advocate tarsiiform affinities for eosimiids do so on the basis of anatomical characters that are at least purported to be shared and derived.

In contrast to tarsiiform primates, eosimiids share the following derived traits with other basal anthropoids: dorsoventrally deep dentaries, dorsoventrally deep maxillae in the region between the alveolar border and the inferior orbital rim, protocones on P^{3-4} that are reduced in size and mesiobuccal in position, upper molar conules that are reduced in size or entirely absent, complete lingual cingula on upper molars, absence of post-protocingula on upper molars, lower incisors that are implanted nearly vertically, P_{3-4} crowns that are obliquely oriented and moderately exodaenodont, and an M_3 hypoconulid lobe that is reduced in size both mesiodistally and buccolingually. While these features link eosimiids with other basal anthropoids, eosimiids retain several primitive characters (such as well-developed paraconids on all lower molars) that readily distinguish them from proteopithecids and most other living and fossil anthropoids. This unique combination of primitive and derived character states documents the mosaic evolution of modern anthropoid features, a pattern that is also apparent—though to a lesser degree—in the Fayum sample of basal anthropoid taxa. With the possible exception of such poorly known African taxa as *Altiatlasius* and *Afrotarsius*, eosimiids are the most basal group of anthropoids currently known.

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