Contributions

from the Museum of Paleontology, University of Michigan

Vol. 32, no. 1, pp. 1-14 December 15, 2008

NEW PRIMATES (MAMMALIA) FROM THE EARLY AND MIDDLE EOCENE OF PAKISTAN AND THEIR PALEOBIOGEOGRAPHICAL IMPLICATIONS

BY

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Abstract — Five early and middle Eocene primates, including three new adapiforms and one new omomyiform, are described from the Ghazij and Kuldana formations of northwestern Pakistan. These are among the oldest primates known from the Indo-Pakistan subcontinent. Two of the new adapiforms (*Panobius russelli* and *Panobius amplior*) and the omomyiform (*Indusius kaliae*) have European affinities and suggest faunal interchange between Asia and Europe in the early Eocene. One new adapiform (*Sulaimania arifi*) is similar to later-occurring (late Eocene and early Oligocene) primates from Pakistan and Europe suggesting that a distinct lineage representing the family Adapidae (s. s.) extended back into the early Eocene. An additional omomyiform of uncertain affinities (*Kohatius* cf. *K. coppensi*) is recorded from the Ghazij Formation in Balochistan. Comparison with Chinese faunas suggests that primates were not able to freely migrate between East and South Asia during most of the Eocene, perhaps because of the persistent presence of a wide Turgai Strait that blocked northern dispersal routes and/or initiation of Himalayan uplift, which may have blocked or restricted southern dispersal corridors.

INTRODUCTION

The Asian record of early Cenozoic Primates has grown dramatically in the past 30 years, beginning with the description of *Altanius* from Mongolia (Dashzeveg and McKenna, 1977; Gingerich et al., 1991). Many additional primates have been reported subsequently from Pakistan (Russell and Gingerich, 1980, 1987; Marivaux et al., 2001, 2002, 2005; Thewissen et al., 2001), China (Beard et al., 1994; Gingerich et al., 1994; Beard and Wang, 2004; Ni et al., 2004, 2007), Thailand (Chaimanee et al., 1997, 2000a; Ducrocq, 1998, 1999, 2001; Ducrocq et al., 1995, 2006; Marivaux et al., 2006), Myanmar (Chaimanee et al., 2000b; Gunnell et al., 2002; Jaeger et al., 1998, 1999; Takai et al., 2001, 2003; Beard et al., 2007), and India (Bajpai et al., 2005, 2007; Rose et al., 2007).

Here, we add to this diversity with the description of five new fossil primates from the early and middle Eocene of Pakistan. Included among this sample are three adapiforms (including a new genus and three new species), and two omomyiforms (one new genus and species). The majority of these specimens come from Gandhera Quarry (Fig. 1) in Balochistan Province, Pakistan, but we also describe a new adapiform species from Chorlakki in the North-West Frontier Province of Pakistan. Gandhera Quarry is stratigraphically situated near the top of the upper Ghazij Formation (Fig. 2) and is late early Eocene (Ypresian) in age (Clyde et al., 2003; Gingerich et al., 1997, 1998, 1999, 2001). Chorlakki is in the Kuldana Formation and is somewhat younger than the Ghazij Formation (latest Ypresian-earliest Lutetian; see Gingerich et al., 2001a,b).

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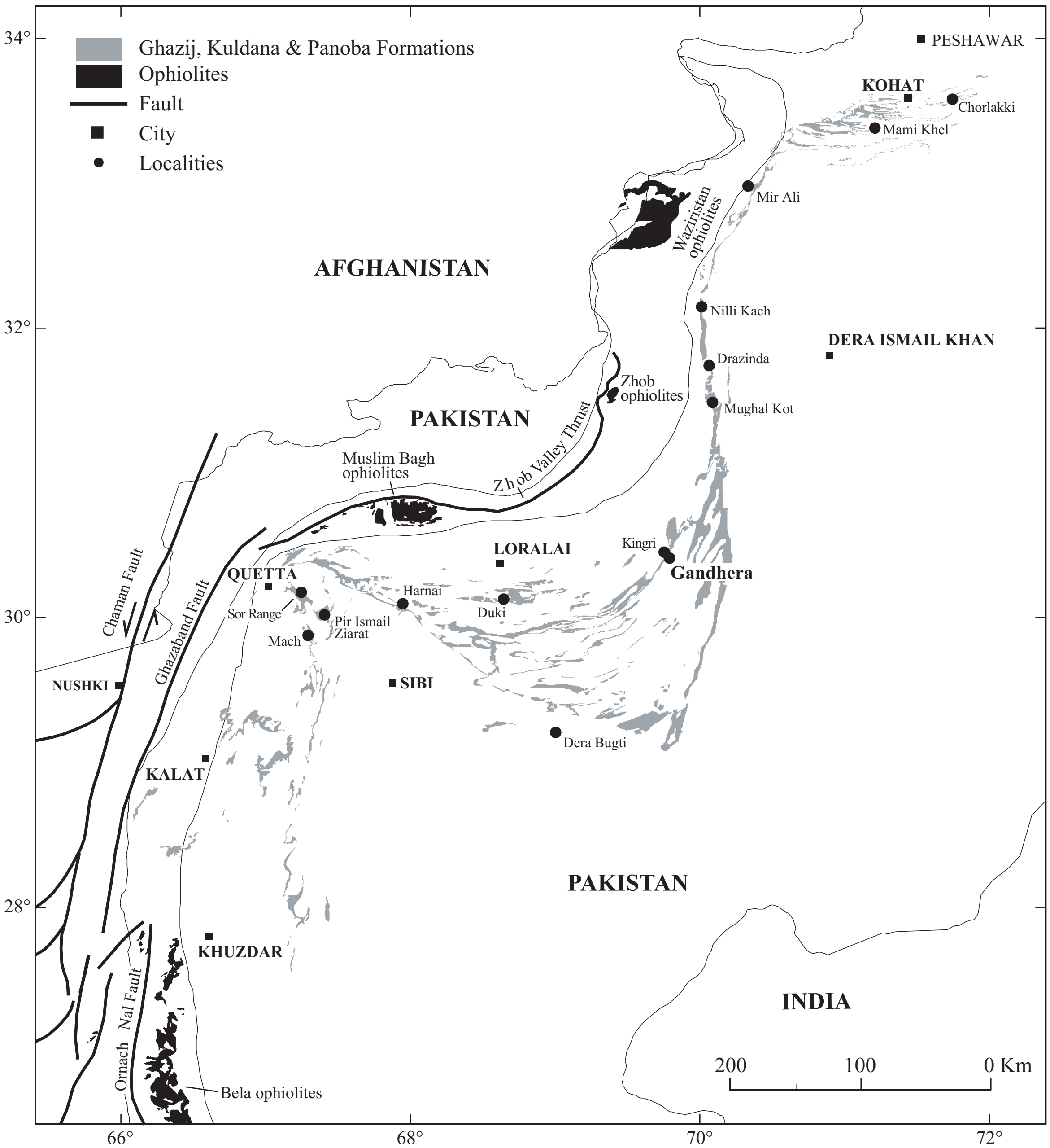

FIGURE 1 — Map of central Pakistan showing the suture zone and associated ophiolites, the distribution of primate-bearing Ghazij and Kuldana Formations, and the location of cities and fossil localities in Balochistan and the North-West Frontier Province. Gandhera is in the middle of the area shown, and Chorlakki is about 300 km northeast of Gandhera.

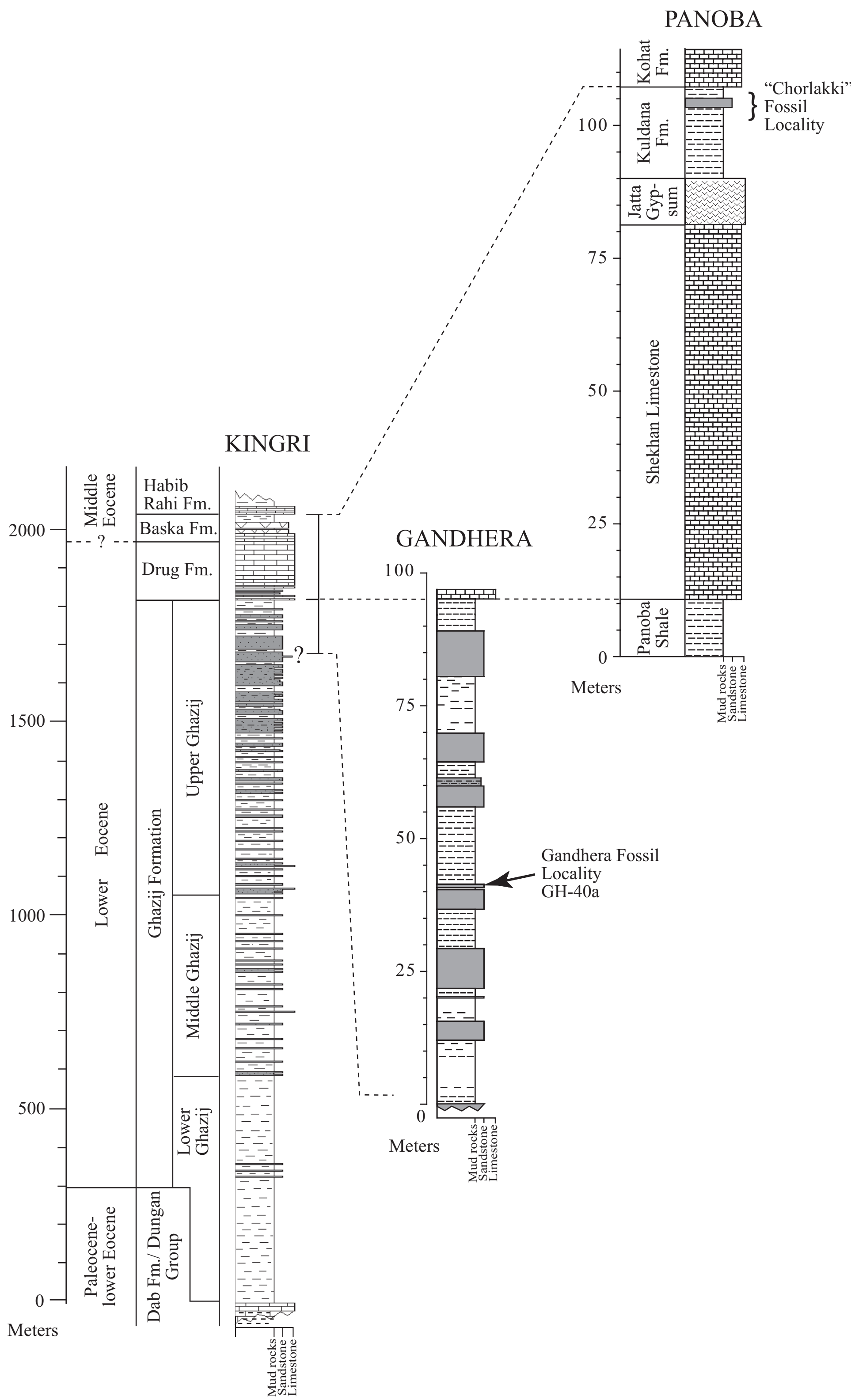

FIGURE 2 — Fence diagram showing the stratigraphic relationships of the Ghazij and Kuldana Formations, and the relative positions of Gandhera Quarry and the Chorlakki locality.

ABBREVIATIONS

Dental Nomenclature.— L = maximum crown length; W = maximum crown width; all measurements recorded in millimeters; lower teeth indicated by upper case lettering with subscript, upper teeth by upper case lettering with superscript.

GSP-UM — Geological Survey of Pakistan (Quetta), University of Michigan
H-GSP — Howard University, Geological Survey of Pakistan

Class MAMMALIA Linnaeus, 1758
Order PRIMATES Linnaeus, 1758
Infraorder ADAPIFORMES Szalay and Delson, 1979
Family NOTHARCTIDAE Trouessart, 1879
Subfamily CERCAMONIINAE Gingerich, 1975

PANOBIUS Russell and Gingerich, 1987

Panobius russelli, sp. nov.
Fig. 3, 4A-B,D-F

Holotype.— GSP-UM 5073, right dentary P_4-M_2.

Hypodigm.— GSP-UM numbers 6768, left M_1; 6769, right M_2; 6770, left M_1 (Fig. 4D); 6771, right M_2; 6772, right M_1 (broken); 6773, left dentary M_1; 6774, left M_1; 6775, left P_4 (Fig. 4A-B); 6776, right M_2; 6777, left M_2; 6778, right M_2; 6779, left M_2; 6780, right M_3; 6781, right M_3; 6782, left M_3; 6783, right dentary M_{1-2}; 6784, left M^1 or M^2; 6785, left M^1 or M^2 (Fig. 4E); 6786, left M^1 or M^2; 6787, left M^3; 6788, right M^3; 6789, left M^3; 6790, right M^3 (Fig. 4F); 6791, right M^1 or M^2; 6792, right M^1 or M^2; 6793, right M_2; 6798, left M_2; 6799, right M_2.

Type locality.— Gandhera Quarry, Balochistan Province, Pakistan.

Age and distribution.— Late early Eocene (Ypresian); all known specimens from type locality only.

Diagnosis.— *Panobius* differs from all other known cercamoniines except *Donrussellia* in retaining paraconids on all lower molars. Differs from *Donrussellia* in having a simpler P_4 lacking distinct paraconid, a weaker metaconid, and a less transverse talonid that is distolingually extended; M_{1-2} with higher paraconids, higher para- and protocristids, and straight cristid obliquae; M_1 with trigonid more open lingually. *Panobius russelli* differs from *P. afridi* in being larger (20% in comparable tooth dimensions; see Table 1), in having a smaller M_3 relative to M_2, and in having a more distinct and slightly more distally positioned lower molar hypoconulid. *P. russelli* differs from *P. amplior* in being 30% smaller in P_4 dimensions and in having a less distinct metaconid on P_4.

Etymology.— Specific name honors Donald E. Russell, for his many contributions to the understanding of Asian mammal faunas.

Description.— P_4 has a relatively tall protoconid with a convex and rounded buccal flank and a flat lingual surface. The paracristid is sharply defined, oriented anteroposteriorly, and continuous with a weak anterior cingulid. There is no paraconid development. The postprotocristid extends about two-thirds the way down the postvallid, where it divides into a buccal branch that continues to the posterior margin of the tooth and a lingual branch which forms a weak enamel bulge in the position of the metaconid. These branches of the postprotocristid enclose a small, distolingually distended talonid. Weak buccal and lingual cingulids are present but these are not continuous distally.

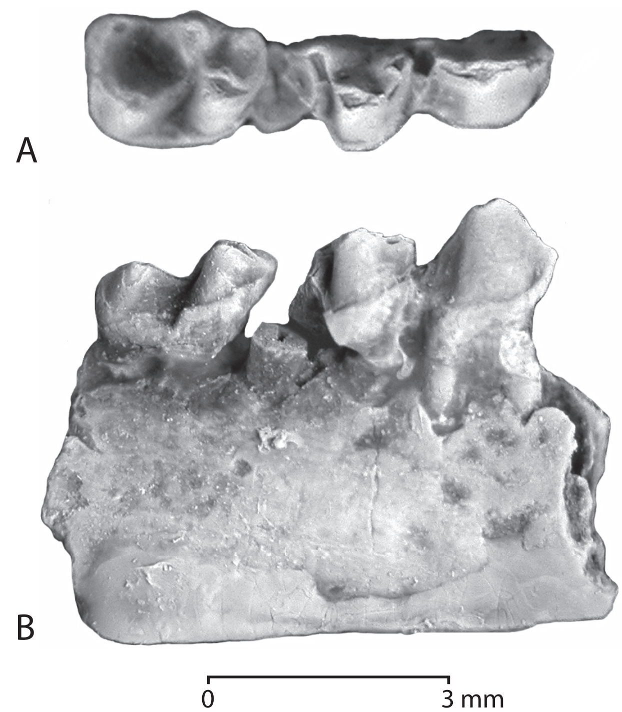

FIGURE 3 — Holotype dentary of *Panobius russelli* (GSP-UM 5073), showing right P_4-M_2 in occlusal (top) and lateral (bottom) views.

The protoconid of M_1 is the tallest and most prominent of the trigonid cusps, with the paraconid and metaconid being lower and of equal height. The paraconid is centered on the trigonid and connected to the protoconid by a short, high, and curving paracristid. The metaconid is distal to the protoconid and slightly lingual of the paraconid, and it is separated from the protoconid by a v-shaped notch. All of the trigonid cusps are bulbous and basally inflated and the trigonid is widely open lingually. The hypoconid and entoconid are not as bulbous as the trigonid cusps and are placed along the margins of the talonid, with the hypoconid being slightly higher than the entoconid. The hypoconulid is small, buccal of center, connected to the hypoconid by a well developed hypocristid, and connected to the entoconid by a sharply defined postcristid. The cristid obliqua joins the postvallid buccal of center and it is continuous with the metaconid. The entocristid is short but closes off the shallow talonid basin lingually. A weak cingulid is developed anterobuccally, but

TABLE 1 — Tooth measurements of Gandhera Quarry *Panobius russelli* specimens.

GSP-UM #	Description	P_4L	P_4W	M_1L	M_1W	M_2L	M_2W	M_3L	M_3W	$M^{1/2}L$	$M^{1/2}W$	M^3L	M^3W
5073	R dent. P_4-M_2	1.9	1.3	—	—	2.1	1.5	—	—	—	—	—	—
6768	L M_1	—	—	2.1	1.5	—	—	—	—	—	—	—	—
6769	R M_2	—	—	—	—	2.0	1.4	—	—	—	—	—	—
6770	L M_1	—	—	2.2	1.4	—	—	—	—	—	—	—	—
6771	R M_2	—	—	—	—	2.0	1.4	—	—	—	—	—	—
6773	L dent. M_1	—	—	2.1	1.3	—	—	—	—	—	—	—	—
6774	L M_1	—	—	2.2	1.4	—	—	—	—	—	—	—	—
6775	L P_4	2.2	1.3	—	—	—	—	—	—	—	—	—	—
6776	R M_2 (worn)	—	—	—	—	2.0	1.4	—	—	—	—	—	—
6777	L M_2	—	—	—	—	2.0	1.5	—	—	—	—	—	—
6778	R M_2	—	—	—	—	2.0	1.5	—	—	—	—	—	—
6779	L M_2	—	—	—	—	2.0	1.4	—	—	—	—	—	—
6780	R M_3	—	—	—	—	—	—	1.9	1.4	—	—	—	—
6781	R M_3	—	—	—	—	—	—	2.1	1.4	—	—	—	—
6782	L M_3	—	—	—	—	—	—	2.2	1.4	—	—	—	—
6784	L M^1 or M^2	—	—	—	—	—	—	—	—	2.1	2.9	—	—
6785	L M^1 or M^2	—	—	—	—	—	—	—	—	1.9	2.9	—	—
6786	L M^1 or M^2	—	—	—	—	—	—	—	—	2.0	3.0	—	—
6787	L M^3	—	—	—	—	—	—	—	—	—	—	1.4	2.5
6788	R M^3	—	—	—	—	—	—	—	—	—	—	1.4	2.2
6790	R M^3	—	—	—	—	—	—	—	—	—	—	1.4	2.4
6791	R M^1 or M^2	—	—	—	—	—	—	—	—	2.2	2.8	—	—
6792	R M^1 or M^2	—	—	—	—	—	—	—	—	2.1	3.0	—	—
6793	R M_2	—	—	—	—	2.3	1.3	—	—	—	—	—	—
6798	L M_2	—	—	—	—	2.0	1.5	—	—	—	—	—	—
6799	R M_2	—	—	—	—	2.0	1.5	—	—	—	—	—	—
6789	L M^3	—	—	—	—	—	—	—	—	—	—	1.1	2.2

there is no other cingular development. M_2 is similar to M_1 except that the paraconid is smaller and more closely appressed to the metaconid, producing a narrowly open trigonid lingually. The paracristid on M_2 is longer and more curving than that on M_1. The cristid obliqua is not continuous with the metaconid, and the hypoconid and hypoconulid are somewhat more prominent compared to these cusps on M_1. The anterobuccal cingulid is more prominent on M_2.

The trigonid of M_3 is compressed anteroposteriorly. The paraconid is very small and placed along the anterior margin of the trigonid between the protoconid and metaconid. The hypoconid is low and the entoconid is indistinct. The hypoconulid is single-lobed and centered, and a shallow talonid basin continues onto the hypoconulid. There is a weak anterobuccal cingulid but no other cingular development.

$M^{1\text{-}2}$ have an anteriorly placed protocone that is lower than the paracone and metacone, which are of equal height. The protocone has a sloping and extended lingual flank. The preprotocrista is continuous with a small parastyle, while the postprotocrista terminates at the base of the metacone. There is a weak paraconule present, but no metaconule. There is no postprotocingulum. There is a moderate anterior cingulum restricted to the lingual half of the teeth, while a heavier posterior cingulum extends to a small metastyle. There is no mesostyle, and the stylar shelf is undeveloped. There is no distinct hypocone developed on the posterior cingulum, and the cingula are not continuous lingually. M^3 is similar to the other molars but the paracone is larger than the metacone, the parastylar region is enlarged and buccally extended, the protocone is anteroposteriorly restricted, and the anterior and posterior cingula are weaker.

Discussion.— *Panobius* is a relatively primitive cercamoniine that resembles *Donrussellia* more closely than any other known adapiform. Depending on the polarity of premolar character states, *Panobius* could be interpreted as a more primitive taxon than *Donrussellia* (if simple premolars are primitive). If cercamoniines arose from a notharctid ancestry (relatively molariform and complex posterior premolar), as seems probable, then *Panobius* may instead represent a derived taxon as part of a lineage that developed simplified posterior premolars.

New adapiforms recently described from Vastan lignite mine in India (Bajpai et al., 2005, 2007; Rose et al., 2007) all appear to differ from *Panobius*. *Marcgodinotius* (Bajpai et al., 2005) differs from *Panobius* in having relatively shorter and broader molars with weaker paraconids (absent on M_3), having the protoconid and metaconid aligned (metaconid not distally placed), and having a centrally placed hypoconulid on M_2 (not buccal and connected to hypoconid by strong hypocristid). *Suratius* (originally described as an omomyid by Bajpai et al., 2007, but surely an adapiform) differs from *Panobius* in having a large and low paraconid and a relatively large talonid on P_4, and in having M_2 with aligned protoconid and metaconid and lacking a hypoconulid. *Asiadapis* (Rose et al., 2007) differs from *Panobius* in having a P_4 with a more complex and better developed talonid, M_2 lacking a paraconid, and M_2 with aligned protoconid and metaconid. *Asiadapis* does share the buccally shifted hypoconulid with *Panobius*, and its lower molars are somewhat more rectangular as in the Pakistan primate. Both *Suratius* and *Asiadapis* are relatively large, with only *P. amplior* (see below) approaching the size of either of these Vastan adapiforms.

In the original description of *Panobius afridi* from Chorlakki (Russell and Gingerich, 1987), the holotype (GSP-UM 688) was described as a left M_1. Now that more complete specimens are available it can be determined that this tooth is, in fact, a left M_2.

Panobius is the most common primate known from the early and middle Eocene of Pakistan, but it is still a very rare taxon. The type sample of *Panobius russelli* from Gandhera Quarry is represented by 29 specimens, including three jaw fragments, and this is by far the largest sample of *Panobius* yet known.

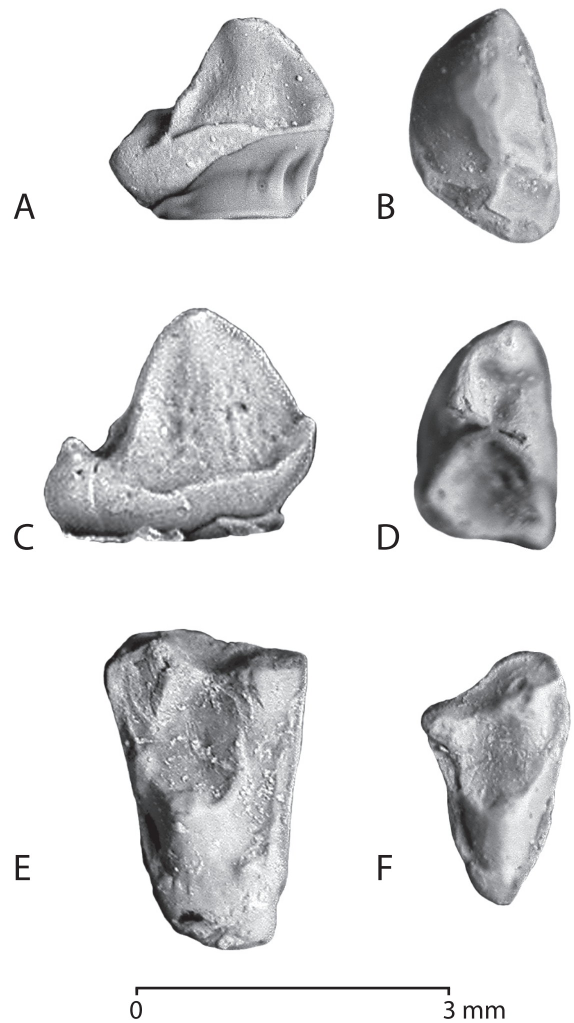

FIGURE 4 — Photographs of representative teeth of *Panobius russelli* (A-B, D-F) and *P. amplior* (C). A-B, left P_4 of *P. russelli* (GSP-UM 6775) in medial and occlusal views. C, left P_4 of *P. amplior* (GSP-UM 101, holotype) in medial view. D, left M_1 of *P. russelli* (GSP-UM 6770) in occlusal view. E, left M^1 or M^2 of *P. russelli* (GSP-UM 6785) in occlusal view. F, right M^3 of *P. russelli* (GSP-UM 6790) in occlusal view.

Panobius amplior, sp. nov.
Fig. 4C

Adapidae indet., Russell and Gingerich, 1987, p. 213.
Panobius afridi, Thewissen et al., 2001, p. 354.

Holotype.— GSP-UM 101, left P_4.

Referred Specimen.— H-GSP 97205, left dentary with partial M_2 and compete M_3.

Type locality.— Chorlakki, North-West Frontier Province, Pakistan.

Age and distribution.— Early middle Eocene (Lutetian); only known specimen, from type locality only.

Diagnosis.— Very similar to the P_4 of *P. russelli*, but differs in being 30% larger in tooth dimensions and in having a more distinct metaconid. *P. amplior* differs from *P. afridi* in being much larger.

Etymology.— Specific name from Latin 'amplus' meaning large, in reference to the relatively large size of this species.

Discussion.— The type specimen of *P. amplior* was originally described as Adapidae indet. (Russell and Gingerich, 1987). Now that the P_4 of *Panobius* is known (GSP-UM 5073), GSP-UM 101 can be assigned to that genus but it clearly belongs to a species larger than either *P. afridi* or *P. russelli*. Dimensions of the type specimen of *P. amplior* are $P_4L = 2.5$, $P_4W = 1.7$.

The presence of a larger species of *Panobius* is also documented by Thewissen et al. (2001). These authors described a left dentary with a broken M_2 and complete M_3 from Banda Daud Shah as representing *P. afridi*. However, the width of M_2 (1.9 mm) is much too large to represent either *P. afridi* or

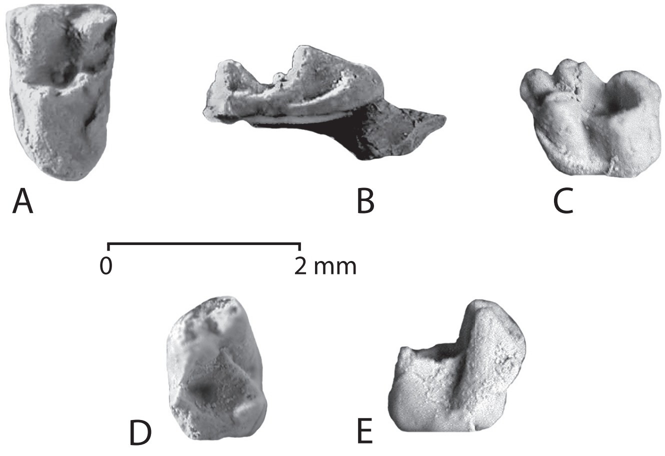

FIGURE 5 — Photographs of *Indusius* and *Sulaimania*. A-B, left M^2 of *I. kaliae* (GSP-UM 6795), in occlusal and anterior views. Note the strongly lingually-angled lingual root in anterior view. C, left M_2 of *I. kaliae* (GSP-UM 6794, holotype), in oblique buccal view. D-E, right M_2 of *S. arifi* (GSP-UM 6796, holotype), in occlusal and buccal views. Scale bar represents 2 mm.

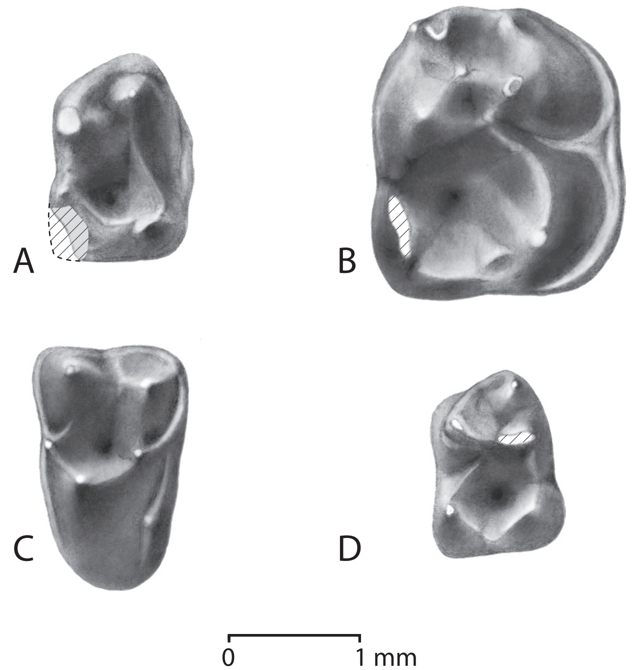

FIGURE 6 — Drawings of primate teeth from Gandhera Quarry, all in occlusal view. A, *Sulaimania arifi*, right M_2 (GSP-UM 6796, holotype). B, *Kohatius* cf. *K. coppensi*, right M_2 (GSP-UM 6797). C, *Indusius kaliae*, left M^2 (GSP-UM 6795). D, *Indusius kaliae*, left M_2 (GSP-UM 6794, holotype).

P. russelli but it would be an appropriate size to represent the same species as the P_4 from Chorlakki.

Two recently described adapiform primates from Vastan mine (Bajpai et al., 2007; Rose et al., 2007) have P_4s of similar size and morphology to that of *P. amplior*. Of these, *Suratius* (Bajpai et al., 2007) is more easily distinguished from *P. amplior* by the presence of a distinct metaconid on P_4, a cusp lacking on P_4 of *P. amplior*. *Asiadapis* (Rose et al., 2007) has a P_4 that resembles *P. amplior* quite closely but the latter taxon can be distinguished by possession of a complete P_4 cingulid (non-continuous both buccally and lingually in *A. cambayensis*); and possession of a relatively shorter talonid that is basally distended posterolingually, lacks a distinct hypoconid cusp, and lacks an expanded lingual surface and basin development (*A. cambayensis* has a more elongated talonid with a distinct hypoconid and an expanded, basined lingual half). *P. amplior* also has P_4 with more distinct and sharply defined pre- and postprotocristae.

Family Uncertain

Sulaimania arifi, gen. et sp. nov.

Figs. 5D-E, 6A

Holotype.— GSP-UM 6796, right M_2.

Type locality.— Gandhera Quarry, Balochistan Province, Pakistan.

Age and distribution.— Late early Eocene (Ypresian); type specimen only.

Diagnosis.— Among Paleogene primates *Sulaimania* most closely resembles late middle Eocene (Bartonian) *Anchomomys* and *Adapis*, and Oligocene *Bugtilemur*. *Sulaimania* differs from *Anchomomys* in being smaller; in having a complete paracristid continuous with premeta- and preprotocristids that closes trigonid anteriorly; in having a stronger preprotostylid; higher and shorter entocristid and anteriorly placed entoconid; a relatively shorter and broader talonid basin that is closed in its entirety by a relatively high cristid obliqua, postcristid, and entocristid; in having a cristid obliqua that does not extend to the crown of the metaconid; and in having the trigonid relatively taller compared to the talonid; *Sulaimania* differs from *Adapis* in being much smaller; in having a less robust and low paracristid; trigonid fovea closed anteriorly; cristid obliqua narrower and more sharply defined and does not extend to crown of metaconid; talonid notch only very narrowly open (unlike the broad U-shaped notch in *Adapis*); trigonid taller than talonid; and lacking the robust buccal cingulid found in some *Adapis* species; *Sulaimania* differs from *Bugtilemur* in being smaller; in having a more lingually angled cristid obliqua that joins the postvallid centrally not buccally; in having a preprotostylid, a weaker, incomplete protocristid, and a weaker hypoconulid; in lacking a paraconid (very weakly developed in *Bugtilemur*); in having a more posteriorly angled paracristid; and in having a taller trigonid relative to talonid.

Etymology.— Generic name for the Sulaiman Range in western Pakistan. Specific name for Muhammad Arif, in recognition of his many contributions that enabled the joint GSP-UM project to be so successful over the course of many years of collaboration.

Description.— M_2 is a small tooth (L = 1.4 mm, W = 1.0 mm). The trigonid is mesiodistally compressed and taller than the talonid and the talonid is relatively broad and deep lingually and is slightly broader than the trigonid. The protoconid and metaconid are of equal height with the latter more robust and positioned distal to the former. There is no paraconid but a low and well developed paracristid is present that is continuous lingually with a robust premetacristid and buccally with a short and straight preprotocristid. A small but distinct cusplet is formed just inferior to the paracristid on the anterobuccal aspect of the protoconid, here termed the preprotostylid. A smaller and less distinct preprotostylid is present in *Anchomomys*, especially on M_1. The protocristid is short and notched.

The hypoconid is relatively tall and marginally placed and appears to be distal to the entoconid but neither the entoconid nor hypoconulid are preserved on the tooth. The entocristid is tall and slightly notched at the base of the metaconid and is continuous with the postmetacristid. The cristid obliqua curves slightly lingually, joins the postvallid buccal of center, and is tall, closing off the talonid buccally. The most mesial aspect of the cristid obliqua joins a weakly elevated postmetaconid ridge but does not extend to the tip of the metaconid as it does in *Anchomomys* and *Adapis*. There are no cingulids developed but the base of the hypoflexid is expanded as in many omomyids and adapiforms.

Discussion.— *Sulaimania arifi* is most similar to *Anchomomys* and primitive *Adapis sciureus* among known primates. It is a plausible ancestral form for the later occurring *Adapis* lineage. It also shares affinities with the purported lemuriform *Bugtilemur* from Oligocene deposits near Dera Bugti in Pakistan (Marivaux et al., 2001). Among the features shared in common between *Bugtilemur* and *Sulaimania* are talonids nearly closed completely by continuous entocristid, postcristid, and cristid obliqua; a high entocristid that extends nearly to posterior border of metaconid, producing a very narrow and shallow talonid notch; lack of cingulids; trigonids closed; straight and distinct preprotocristid present; and presence of a postmetaconid ridge on postvallid (*Sulaimania* lacks a postprotoconid ridge that is present in *Bugtilemur*).

It appears that *Bugtilemur* may have had an adapiform ancestry that can be traced into the early Eocene. If so, this suggests that it is not a lemuriform but instead represents part of yet another adapiform lineage in southern Asia (also see Godinot, 2006). Given the growing evidence of a primate fauna dominated by adapiforms in the Eocene of Asia (Ciochon and Gunnell, 2002), and survival of sivaladapid adapiforms into the Asian Miocene (Gingerich and Sahni, 1979, 1984), it is not surprising that additional, previously unknown adapiforms, would be discovered in South Asia.

Infraorder OMOMYIFORMES Schmid, 1982
Family OMOMYIDAE Trouessart, 1879
Subfamily Uncertain

Kohatius cf. *K. coppensi*
Fig. 6B

Referred specimen.— GSP-UM 6797, right M_2.
Locality.— Gandhera Quarry, Balochistan Province, Pakistan.
Age and distribution.— Late early Eocene (Ypresian); referred specimen only.

Description.— Based on a comparison with the holotype of *Kohatius coppensi*, a slightly damaged M_1 (Russell and Gingerich, 1980), GSP-UM 6797 represents an M_2 of an animal very similar in size ($M_2L = 2.3$, $M_2W = 1.9$) and morphology. In general, the outline of M_2 is squared and is slightly flared buccally. The protoconid and metaconid are of equal size, height, and proportions. The metaconid is positioned posterior to the protoconid and the two are separated by a U-shaped notch (that is, the protocristid is absent). The paraconid is smaller but distinct, appressed to the anterior flank of the metaconid, and connected to the protoconid by a short but well-defined paracristid.

The hypoconid is distinct, tall, laterally compressed, and set in from the tooth margin (aligned with, but shorter than, the protoconid). The hypoflexid is relatively shallow, but there is a distinct buccal cingulid present that extends from the paracristid to a small, slightly buccally placed hypoconulid. At the base of the hypoflexid, the buccal cingulid extends into a distinct shelf. The cristid obliqua is relatively tall, sharply defined, and curves to join the apex of the metaconid while the posthypocristid is short, poorly defined and extends to the hypoconulid. The entoconid is lower than the hypoconid, less distinct, more basally inflated, and set on the tooth margin. The entocristid is low and indistinct, leaving the talonid notch shallowly open. The talonid is closed posteriorly by the postcristid and the vaguely defined hypoconulid, and the talonid basin is relatively shallow. The enamel is smooth on all crown surfaces.

Discussion.— *Kohatius* remains very poorly known. In addition to the tooth described here, the remainder of the hypodigm includes the holotype of *K. coppensi* (M_1, GSP-UM 139) and two broken tooth fragments (GSP-UM 144 & 145) from Chorlakki also assigned to that species (Russell and Gingerich, 1980), a dentary fragment with P_4 from Barbora (GSP-UM 212) in the North-West Frontier Province, Pakistan assigned to cf. *Kohatius* sp. (Russell and Gingerich, 1987), and an isolated P_4 (H-GSP 92166) from near Jhalar in Punjab, Pakistan referred to as *Kohatius* species A (Thewissen et al., 1997).

When *Kohatius* was originally described (Russell and Gingerich, 1980) it was questionably assigned to the subfamily Omomyinae, while in a later paper the same authors chose not to place it in a subfamily (Russell and Gingerich, 1987). Thewissen et al. (1997) assigned *Kohatius* to the subfamily Anaptomorphinae, while Gunnell and Rose (2002) felt *Kohatius* was too poorly known to assign to a specific omomyid subfamily. Until more complete material is found, the systematic position of *Kohatius* will remain unresolved.

Subfamily MICROCHOERINAE Lydekker, 1887

Indusius kaliae, gen. et sp. nov.
Figs. 5A-C, 6C-D

Holotype.— GSP-UM 6794, left M_2 (Figs. 5C, 6D).
Referred specimen.— GSP-UM 6795, left M^2 (Figs. 5A-B, 6C).

Type locality.— Holotype and referred specimen from Gandhera Quarry, Balochistan Province, Pakistan.

Age and distribution.— Late early Eocene (Ypresian); both known specimens from type locality only.

Diagnosis.— Smaller than other known omomyiforms, with the exception of the enigmatic *Altanius*. Differs from *Altanius* in having M^2 with broader and deeper trigon basin; conules relatively smaller and lacking or having only poorly developed postpara- and premetaconule cristae; having protocone more anteriorly placed with a lingually extended flank, lacking a postprotocingulum; having a small and indistinct cingular hypocone; and in lacking a central anteroposterior constriction of the trigon (across the conules). M_2 differs from *Altanius* in having the trigonid nearly as wide as the talonid; an inflated paraconid that is more distinctly separated from the metaconid which is also larger than in *Altanius*; and in lacking the distinct, posteriorly extended hypoconulid found in *Altanius*. *Indusius* differs from most omomyiforms except primitive *Teilhardina*, *Steinius*, *Melaneremia*, *Omomys*, and *Chumashius* in lacking a postprotocingulum on upper molars. Further differs from *Teilhardina* in having a less basally inflated M_2, with the cristid obliqua joining postvallid more lingually; a less distinct hypoconulid; a taller entoconid; and a relatively narrower talonid basin. Further differs from *Melaneremia* in having a buccally curved postmetacrista on M^2; an M^2 protocone placed farther buccally which extends lingual slope and produces a relatively narrower trigon basin buccolingually; M_2 entocristid that slopes anteriorly; and a relatively shorter M_2. Further differs from the other taxa in lacking elevated and robust pre- and postprotocristae on M^2 and in having a relatively more constricted trigon basin.

Etymology.— Generic name for the Indus River which flows north-south through western Pakistan. Specific name for Kali, the Hindu Goddess of time and the transformation of death.

Description.— *Indusius kaliae* was a very small primate ($M_2L = 1.3$, $M_2W = 1.0$; $M^2L = 1.1$, $M^2W = 1.7$), smaller than all other known euprimates except for the possible omomyid *Altanius*. M_2 has a trigonid only slightly taller than the talonid with the talonid being slightly broader than the trigonid. All three trigonid cusps are distinct, the paraconid being basally inflated, centrolingually placed, anteriorly extended, and larger than the protoconid and metaconid. The latter two cusps are about the same size, less basally inflated, with the metaconid positioned only slightly posterior to the protoconid. All three trigonid cusps are separated from each other by distinct notches. There is a weak and low paracristid connecting the base of the paraconid to the anterior base of the protoconid. The protocristid is deeply notched between the protoconid and metaconid. The talonid is relatively short, broad, and deep.

The hypoconid and entoconid are marginal, less distinct than the trigonid cusps, and positioned opposite one another. The hypoconid is slightly larger than the entoconid. The hypoconulid is centrally placed, extended posteriorly and confluent with the postcristid. The cristid obliqua is short and high and joins the postvallid buccal of center closing off the talonid buccally. The entocristid is straight, steep and short leaving a distinct talonid notch. The hypoflexid is moderately deep and there is a weak buccal cingulid present.

The M^2 of *I. kaliae* (GSP-UM 6795) has sharply defined protocone, paracone, and metacone. The protocone is anteriorly placed and slightly shorter than the other two cusps, which are about equal in height. The protocone is extended lingually into a rounded lobe. There is no distinct hypocone, but a small enamel swelling is formed at the lingual end of a moderate postcingulum. There is no postprotocingulum or mesostyle developed. A relatively weak precingulum is present, but it does not join the postcingulum lingually. Para- and metaconules are distinct and low. The pre- and postprotocristae are steeply sloping but well defined; these close off a centrally placed and relatively deep trigon basin. The preparaconule crista is continuous with the small parastylar region, while the postmetaconule crista wraps around the base of the metacone but does not reach the slightly better developed metastylar region. The centrocrista are sharply defined and steeply angled, forming a distinct notch. There is a low and weak buccal cingulum that carries no cuspules. The lingual root of the tooth is sharply angled lingually.

Discussion.— It is difficult to place *I. kaliae* taxonomically. It vaguely resembles *Altanius* from the Bumbanian of Mongolia, but differs substantially from that taxon. It appears to be primitive in lacking an upper molar postprotocingulum, as do some species of *Teilhardina*, but *Indusius* differs from this taxon as well. *Indusius* also shares some features in common with *Tarsius*, and could conceivably be a member of Tarsiiformes rather than Omomyiformes. It is smaller than other tarsiiforms, including all species of *Tarsius* (Musser and Dagosto, 1987; Ginsberg and Mein, 1987; Beard et al., 1994), *Xanthorhysis* (Beard, 1998), and the unnamed tarsiiform recently described from Krabi in Thailand (Ducrocq et al., 2006).

Perhaps surprisingly, among all omomyid taxa now known, *Indusius* seems most similar to the recently described primitive microchoerine *Melaneremia bryanti*, known from the early Eocene locality of Abbey Wood, Blackheath Beds, United Kingdom (Hooker, 2007). Among the features held in common between *Indusius* and *Melaneremia* are the following: relatively small to extremely small size; very low crowned molars; upper molar trigon basins elongate anteroposteriorly; upper molars with relatively robust pre- and postcingula; small upper molars conules; upper molars lacking a postprotocingulum or mesostyle; upper molars lacking or having a very weak hypocone; lower molars with straight entocristids; and lower molars with distinct paraconids (where known). *Indusius* lacks an accessory cuspule anterior to the metaconid that is sometimes developed in *Melaneremia*, and it also has a relatively more robust M_2 paraconid. Low crowned molars and anteroposteriorly elongated upper molar trigon basins have been interpreted as synapomorphies of Microchoerinae (Hooker, 2007), suggesting that *Indusius* may well be a small microchoerine. More complete specimens are needed to determine character polarities between *Indusius* and *Melaneremia*, but the presence of a microchoerine-like omomyid on the Indo-Pakistan subcontinent in the early Eocene is intriguing paleobiogeographically.

The strongly lingually-angled lingual root of M^2 in *Indusius* suggests that this tiny primate had a very shallow maxilla and a relatively large orbit. As with most other known omomyiforms, this indicates that *I. kaliae* was probably nocturnal.

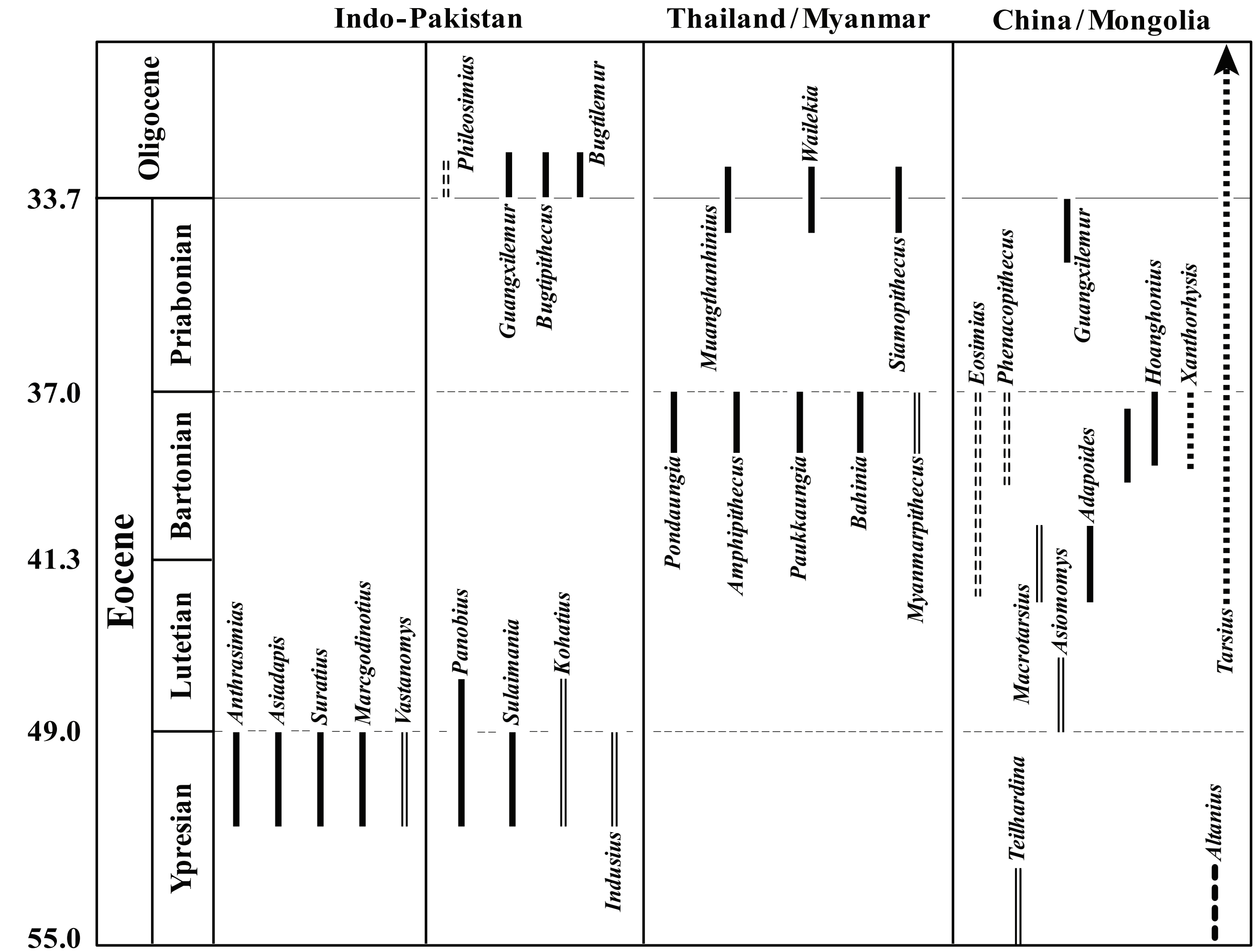

FIGURE 7 — Distribution of Paleogene Asian primate genera, including south Asian forms from Indo-Pakistan and East Asian forms from Thailand, Myanmar, China, and Mongolia. Positions within epochs and stages are relative, and are not meant to suggest precise stratigraphic position. Solid black lines represent adapiforms, solid parallel lines represent omomyiforms, dotted lines represent tarsiiforms, dashed parallel lines represent eosimiids, and dashed line represents *Altanius*.

DISCUSSION

The new taxa described here add to the growing diversity of early Cenozoic (Paleogene) euprimates now known from Asia (Fig. 7). The vast majority of this diversity is represented by adapiforms (59% of known genera), with omomyiforms (22%), tarsiiforms (9%), and the enigmatic eosimiids (9%) being much less diverse. Among adapiforms, 37% represent endemic sivaladapids while there are apparently no endemic omomyiforms in Asia (unless early Eocene *Altanius* is an omomyiform). No Asian primate taxon is particularly abundant, with most being represented by one or a few specimens.

An interesting paleobiogeographic pattern is slowly developing as more and more primate taxa are discovered in Asia. This pattern, as it is now known, is summarized in Figure 8 for Asian non-endemic primates. In the earliest Eocene, the omomyiform genus *Teilhardina* is ubiquitous across the northern continents with an apparent origin that may be traced to somewhere in eastern Asia, followed shortly thereafter by nearly synchronous appearances in Europe and North America (Smith et al., 2006; Beard, 2008; Gingerich et al., 2008). This appears to have been the only time in the Eocene when migratory routes capable of allowing primates passage were open across all of the northern continents.

Beginning at the Paleocene-Eocene carbon isotope excursion (CIE) demarcating the start of the Paleocene-Eocene Thermal Maximum (PETM), dispersal routes became more restricted in the northern continents, at least for arboreal taxa like primates. These changing dispersal patterns probably were due to both climatic (PETM) and tectonic causes (collision of the Indo-Pakistan subcontinent with central Asia producing the onset of Himalayan uplift and restricting southern dispersal routes). From the CIE onward, two distinct faunal interchange patterns develop, one represented by European-south Asian interchange

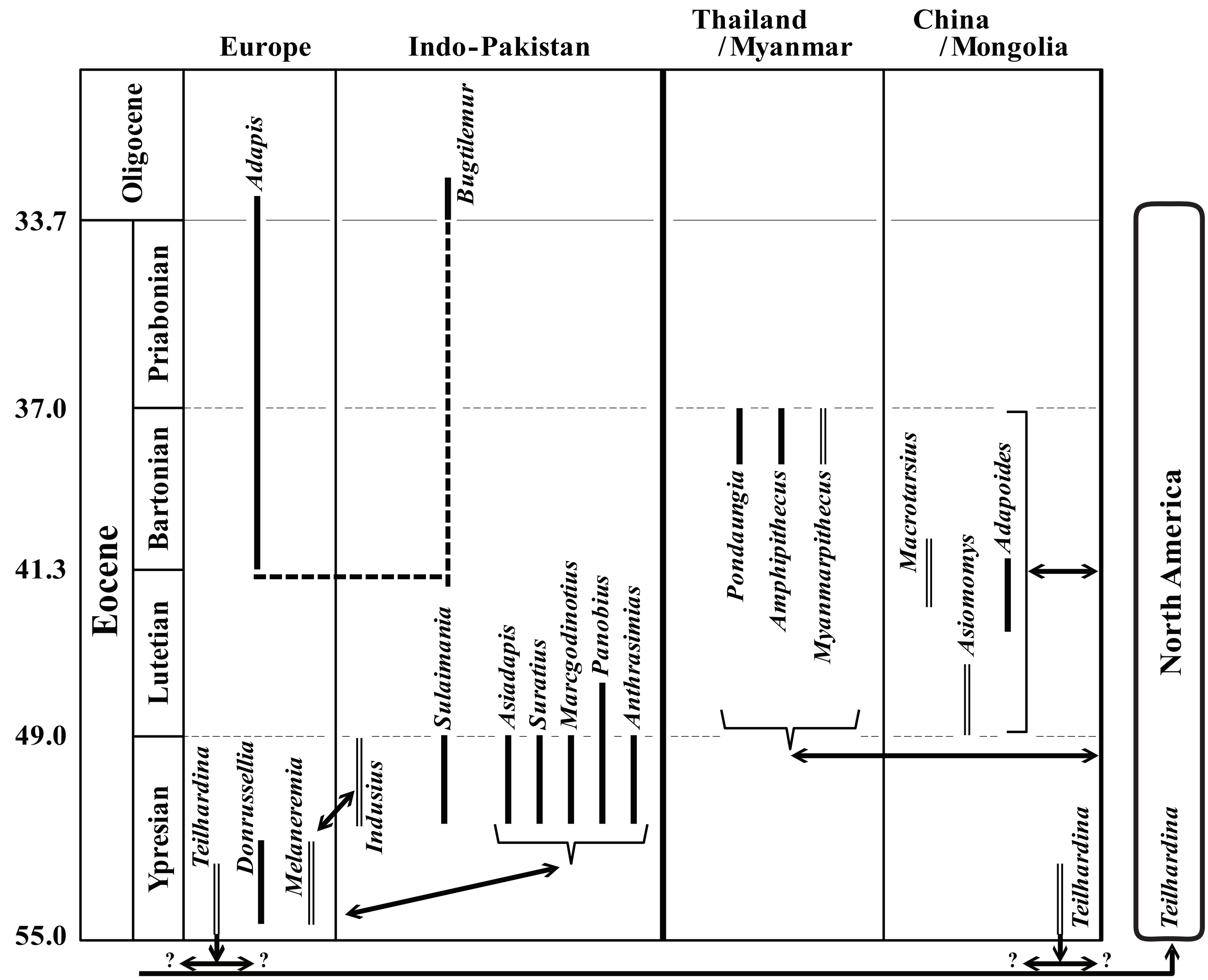

FIGURE 8 — Distribution of Paleogene Asian primates, with probable endemic forms (sivaladapids, tarsiids, eosimiids, and some adapiforms) removed, and probable phylogenetic and geographic connections indicated. Note: (1) *Sulaimania* represents a plausible ancestral morphotype for the purported lemuriform *Bugtilemur* as well as European Adapidae; (2) biogeographic connections of South Asian Indo-Pakistan primates after the beginning of the Eocene are with European forms; and (3) biogeographic connections of East Asian primates after the beginning of the Eocene are with North American forms. Solid lines indicate adapiforms, parallel lines indicate omomyiforms.

on the west side of the newly forming Himalayas, the other by east Asian-North American interchange on the east side of the nascent Himalayas and the Turgai Strait. The early Eocene European euprimates *Donrussellia* and *Melaneremia* have very close sister taxa in Pakistan in the form of *Panobius* and *Indusius*, respectively. The rest of the Pakistan and Indian early to early middle Eocene primate fauna also resembles European cercamoniine and microchoerine euprimates much more than any East Asian or North American forms.

Bajpai et al. (2008) recently described four isolated teeth from the early Eocene at Vastan mine in India as *Anthrasimias*, a possible anthropoid primate. Among the referred material of *Anthrasimias*, the upper molars appear nearly identical to the European adapiform *Anchomomys*, and almost certainly represent the Vastan adapiform *Marcgodinotius* (Bajpai et al., 2005; Rose et al., in press). The supposed M^2 upon which Bajpai et al. (2008) base their discussion of shearing crest development in *Anthrasimias* is clearly an M^3 instead as plainly can be seen when comparisons are made with *Anchomomys*. The unassociated lower molars included in the *Anthrasimias* hypodigm are comparable to *Marcgodinotius* in nearly every detail and also probably represent that genus.

The post-*Teilhardina* early Eocene of East Asia contains no primates to date, but in the middle Eocene some taxa do begin to appear, most of which seem to have relatives in North America. Lutetian aged *Asiomomys* is very similar to the Uintan California primate *Stockia* (Beard and Wang, 1991), while the late Lutetian *Macrotarsius* and *Adapoides* from Shanghuang (Beard et al., 1994) have close relatives in the Uintan-Duchesnean of North America (*Macrotarsius* occurs in both China and North America while *Adapoides* is very similar to the Texas adapiform *Mahgarita*).

Late middle Eocene primates from Myanmar include the amphipithecids *Pondaungia* and *Amphipithecus*, the enigmatic probable adapiform *Bahinia*, and the probable omomyiform *Myanmarpithecus*.

Pondaungia and *Amphipithecus* have been much discussed (Jaeger et al., 1998; Chaimanee et al., 2000b; Ciochon et al., 2001; Ciochon and Gunnell, 2002, 2004; Marivaux et al., 2003; Takai et al., 2003; Beard et al., 2005) but appear to be very similar in known dental, cranial, and postcranial morphology to notharctid adapiforms and can be easily matched in size and morphology by North American taxa such as *Pelycodus* and *Hesperolemur*. Even seemingly incongruous morphology, such as that documented by the controversial astragalus of a presumed amphipithecid (Marivaux et al., 2003; Gunnell and Ciochon, 2008), doesn't seem that difficult to encompass given that amphipithecids and notharctids do represent two distinct families of adapiforms.

Among other Burmese euprimates, *Bahinia* was originally described as a possible eosimiid (Jaeger et al., 1999), but a recent analysis of facial and palatal morphology of *Bahinia* (Rosenberger and Hogg, 2007) suggest that it is better interpreted as an adapiform (= strepsirrhine in the usage of Rosenberger and Hogg, 2007). The North American euprimate *Notharctus* was used in comparisons with *Bahinia*. When rescaled to the same tooth dimensions, these taxa were found to be very similar to one another (Rosenberger and Hogg, 2007). *Myanmarpithecus* was tentatively described as a possible anthropoid by Takai et al. (2001), but the authors noted that this taxon was very similar to some omomyiforms as well. Work now underway (Gunnell and Ciochon, in preparation) seems to support the latter idea.

Other Asian primates, including sivaladapids, tarsiids, and eosimiids appear to have been endemic forms. It is possible that one or more of them may have relatives outside of Asia (*Afrotarsius* in the case of tarsiiforms, and perhaps Fayum anthropoids in the case of eosimiids) but these phylogenetic hypotheses have yet to be convincingly demonstrated. Relict populations of sivaladapids, amphipithecids, and eosimiids apparently did move from East Asia into South Asia by the Oligocene, based on evidence from the Bugti Hills in Pakistan (Marivaux et al., 2005), but only sivaladapids survived into the Miocene. No firm evidence is available yet to suggest that East Asian primates were capable of moving westward into South Asia, Europe, or Africa at any time in the post-CIE Eocene.

ACKNOWLEDGMENTS

J. J. Hooker and T. Smith provided comparative casts. B. Miljour drew the specimens shown in Figure 6. W. J. Sanders expertly prepared all specimens. We thank K. D. Rose for helpful discussions. Field work was supported by the Office of Vice President for Research at the University of Michigan, the National Geographic Society (grant 5537-95 to PDG), and the National Science Foundation (grants EAR 0517773 and EAR 9714923 to PDG and EAR 9902905 to WCC).

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ISSN 0097-3556