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

BY

GREGG F. GUNNELL1, PHILIP D. GINGERICH1, MUNIR UL-HAQ2, JONATHAN I. BLOCH3, INTIZAR H. KHAN4, AND WILLIAM C. CLYDE5

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).
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.

Holotype.— GSP-UM 5073, right dentary P4-M2.

Hypodigm.— GSP-UM numbers 6768, left M1; 6769, right M2; 6770, left M1 (Fig. 4D); 6771, right M2; 6772, right M1 (broken); 6773, left dentary M1; 6774, left M1; 6775, left P4 (Fig. 4A-B); 6776, right M2; 6777, left M2; 6778, right M2; 6779, left M2; 6780, right M1; 6781, right M1; 6782, left M1; 6783, right dentary M1,2; 6784, left M1 or M2; 6785, left M1 or M2 (Fig. 4E); 6786, left M1 or M2; 6787, left M2; 6788, right M1; 6789, left M1; 6790, right M1 (Fig. 4F); 6791, right M1 or M2; 6792, right M1 or M2; 6793, right M2; 6794, left M2; 6795, left M2; 6796, right M2; 6797, left M2; 6798, right M2; 6799, right M2; 6800, left M2.

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 P4 lacking distinct paraconid, a weaker metaconid, and a less transverse talonid that is distolinguually extended; M1,2 with higher paraconids, higher para- and protocristids, and straight cristid obliquae; M1 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 M1 relative to M2, and in having a more distinct and slightly more distally positioned lower molar hypoconulid. Panobius russelli differs from P. amplior in being 30% smaller in P4 dimensions and in having a less distinct metaconid on P4.

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

Description.— P4 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.

The protoconid of M1 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...
there is no other cingular development. M₂ is similar to M₁ except that the paraconid is smaller and more closely appressed to the metaconid, producing a narrowly open trigonid lingually. The paracristid on M₂ is longer and more curving than that on M₁. The cristid obliqua is not continuous with the metaconid, and the hypoconid and hypoconulid are somewhat more prominent compared to these cusps on M₁. The anterobuccal cingulid is more prominent on M₂.

The trigonid of M₃ 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.

M₁₋₂ 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 parastylar, while the postprotocrista terminates at the base of the metacone. There is a weak paracristid 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. M₃ is similar to the other molars but the paracone is larger than the metacone, the parastylar region is enlarged and bucally extended, the protocone is anteroposteriorly restricted, and the anterior and posterior cingula are weaker.

<table>
<thead>
<tr>
<th>GSP-UM #</th>
<th>Description</th>
<th>P₄L</th>
<th>P₄W</th>
<th>M₁L</th>
<th>M₁W</th>
<th>M₂L</th>
<th>M₂W</th>
<th>M₃L</th>
<th>M₃W</th>
<th>M₁/₂L</th>
<th>M₁/₂W</th>
<th>M₃L</th>
<th>M₃W</th>
</tr>
</thead>
<tbody>
<tr>
<td>5073</td>
<td>R dent. P₄-M₂</td>
<td>1.9</td>
<td>1.3</td>
<td></td>
<td></td>
<td>2.1</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6768</td>
<td>L M₁</td>
<td></td>
<td></td>
<td>2.1</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6769</td>
<td>R M₂</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.0</td>
<td>1.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6770</td>
<td>L M₁</td>
<td></td>
<td></td>
<td>2.2</td>
<td>1.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6771</td>
<td>R M₂</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.0</td>
<td>1.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6773</td>
<td>L dent. M₁</td>
<td></td>
<td></td>
<td>2.1</td>
<td>1.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6774</td>
<td>L M₁</td>
<td></td>
<td></td>
<td>2.2</td>
<td>1.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6775</td>
<td>L P₄</td>
<td>2.2</td>
<td>1.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6776</td>
<td>R M₂ (worn)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.0</td>
<td>1.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6777</td>
<td>L M₂</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.0</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6778</td>
<td>R M₂</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.0</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6779</td>
<td>L M₂</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.0</td>
<td>1.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6780</td>
<td>R M₃</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.9</td>
<td>1.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6781</td>
<td>R M₃</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.1</td>
<td>1.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6782</td>
<td>L M₁</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.2</td>
<td>1.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6784</td>
<td>L M¹ or M²</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.1</td>
<td>2.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6785</td>
<td>L M¹ or M²</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.9</td>
<td>2.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6786</td>
<td>L M¹ or M²</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.0</td>
<td>3.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6787</td>
<td>L M³</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.4</td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td>6788</td>
<td>R M³</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.4</td>
<td>2.2</td>
</tr>
<tr>
<td>6790</td>
<td>R M³</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.4</td>
</tr>
<tr>
<td>6791</td>
<td>R M¹ or M²</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.2</td>
<td>2.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6792</td>
<td>R M¹ or M²</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.1</td>
<td>3.0</td>
<td></td>
</tr>
<tr>
<td>6793</td>
<td>R M₂</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.3</td>
<td>1.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6798</td>
<td>L M₂</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.0</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6799</td>
<td>R M₂</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.0</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6789</td>
<td>L M³</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.1</td>
<td>2.2</td>
</tr>
</tbody>
</table>
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. Maregodinotius (Bajpai et al., 2005) differs from Panobius in having relatively shorter and broader molars with weaker paraconids (absent on M3), having the protoconid and metaconid aligned (metaconid not distally placed), and having a centrally placed hypoconulid on M2 (not buccal and connected to hypoconid by strong hypocristid). Suratius (originally described as an omnomyid 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 P4, and in having M2 with aligned protoconid and metaconid and lacking a hypoconulid. Asiadapis (Rose et al., 2007) differs from Panobius in having a P4 with a more complex and better developed talonid, M2 lacking a paraconid, and M3 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 M1. Now that more complete specimens are available it can be determined that this tooth is, in fact, a left M2.

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.

Panobius amplior, sp. nov.
Fig. 4C

Adapidae indet., Russell and Gingerich, 1987, p. 213.

Holotype.— GSP-UM 101, left P4.
Referred Specimen.— H-GSP 97205, left dentary with partial M2 and complete M3.

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 P4 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 P4 of Panobius is known (GSP-UM 6775), 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 P4L = 2.5, P4W = 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 M2 and complete M3 from Banda Daud Shah as representing P. afridi. However, the width of M2 (1.9 mm) is much too large to represent either P. afridi or
**Sulaimania arifi**, gen. et sp. nov.  
Figs. 5D-E, 6A

**Holotype.**— GSP-UM 6796, right M2.  

**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 preprotoctistsids 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 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 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 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 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 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 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 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 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 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 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 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 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 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 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 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 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 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 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 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 the metaconid; and in having the trigonid relatively taller compared to the talonid; Sulaima
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 preprototyloidal. A smaller and less distinct preprototyloidal is present in Anchomomys, especially on M1. The protoconid 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 entoconid 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 postmetacristid 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 sciuereus 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 postmetacristid 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 M2.
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 M1 (Russell and Gingerich, 1980), GSP-UM 6797 represents an M2 of an animal very similar in size (M2L = 2.3, M2W = 1.9) and morphology. In general, the outline of M2 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 protoconid 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 entoconid is low and indistinct, leaving the talonid notch shallowly open. The talonid is closed posteriorly by the posterostyloidal 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 (M1, 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 P4 from Barbora (GSP-UM 212) in the North-West Frontier Province, Pakistan assigned to cf. Kohatius sp. (Russell and Gingerich, 1987), and an isolated P4 (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 unquestionably assigned to the subfamily Omomyiinae, 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 M2 (Figs. 5C, 6D).
Referred specimen.— GSP-UM 6795, left M2 (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 M2 with broader and deeper trigon basin; conules relatively smaller and lacking or having only poorly developed postpara- and premetacone cristae; having protocone more anteriorly placed with a lingually extended flank, lacking a postprotocristid; having a small and indistinct cingular hypococone; and in lacking a central anteroposterior constriction of the trigon (across the conules). M2 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 hypocoilid found in *Altanius*. *Indusius* differs from most omomyiforms except primitive *Teilhardina*, *Steinius*, *Melaneremia*, *Omomyx*, and *Chnumshius* in lacking a postprotocristid on upper molars. Further differs from *Teilhardina* in having a less basally inflated M2, with the cristid obliqua joining postvallid more lingually; a less distinct hypocoilid; a taller entocoilid; and a relatively narrower talonid basin. Further differs from *Melaneremia* in having a buccally curved postmetaconid on M2; an M2 protocone placed farther buccally which extends lingual slope and produces a relatively narrower trigon basin buccolingually; M2 entocristid that slopes anteriorly; and a relatively shorter M2. Further differs from the other taxa in lacking elevated and robust pre- and postprotocristae on M2 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 (M2L = 1.3, M2W = 1.0; M2L = 1.1, M2W = 1.7), smaller than all other known euprimates except for the possible omomyid *Altanius*. M2 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 protoconid 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 entoconid is straight, steep and short leaving a distinct talonid notch. The hypoflexid is moderately deep and there is a weak buccal cingulid present.

The M2 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 hypocoine, but a small enamel swelling is formed at the lingual end of a moderate postcingulum. There is no postprotocristid 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 cusplets. 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 Bambanian of Mongolia, but differs substantially from that taxon. It appears to be primitive in lacking an upper molar postprotocristid, 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 postprotocristid or mesostyle; upper molars lacking or having a very weak hypocone; lower molars with straight entocristids; and lower molars with distinct paranodes (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 M2 paracristid. Low crowned molars and anteroposteriorly elongated upper molar trigon basins have been interpreted as synapomorphies of Microchoerinidae (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 linguually-angled lingual root of M2 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.
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 sivuladapids 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.
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 M2 upon which Bajpai et al. (2008) base their discussion of shearing crest development in *Anthrasimias* is clearly an M3 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., 1991, 2008) are also similar to North American taxa.
et al., 1994) have close relatives in the Uinta-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 Myanmarepithecus. 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 notharctid s 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). Myanmarepithecus 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 eosimiiids 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 eosimiiids) but these phylogenetic hypotheses have yet to be convincingly demonstrated. Relict populations of sivaladapids, amphipithecids, and eosimiiids apparently did move from East Asia into South Asia by the Miocene. No firm evidence is available yet to suggest that one or more of them may have relatives outside of Asia (Afrotarsius in the case of eosimiiids) but these phylogenetic hypotheses have yet to be convincingly demonstrated. Relict populations of sivaladapids, amphipithecids, and eosimiiids apparently did move from East Asia into South Asia by 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).

LITERATURE CITED


