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EOCENE MAMMAL FAUNAS FROM NORTHERN INDO-PAKISTAN

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ABSTRACT—We present a summary of the Eocene mammal faunas of Indo-Pakistan based on study of the known faunas and new collections. New taxa described here are the carpolestid *Parvocristes oligocollis,* the plesiadapid *Jattadectes mamikheli* (both new families for the subcontinent), the hyaenodontid *Paratritemnodon jandewalensis,* the arctocyonid *Karakia longidens,* the raoellid *Khirtharia aurea,* and the helaletid *Jhagirilophus chorgalensis.* Based on the faunal evidence and considering the geological setting, we also evaluate the uniformity of the Eocene faunas from northern Indo-Pakistan. Tentatively, we propose that three chronologically distinct faunas occur in Northern Indo-Pakistan. These are, from oldest to youngest, (1) the Banda Daud Shah Fauna, (2) the Ganda Kas Fauna, and (3) the Kalakot Fauna. Although there are broad similarities between these faunas and Eocene faunas of the Northern Hemisphere, the Indian subcontinent retained a highly distinctive fauna in that period.

INTRODUCTION

Eocene fossil mammals from northern Indo-Pakistan were first described by Pilgrim (1940) and Dehm and Oettingen-Spielberg (1958). Both studies were mainly based on fossils from the Ganda Kas Area (Fig. 1, Kuldana Formation), and this area was subsequently also studied by Hussain et al. (1978) and West (1980). To the east of the Kala Chitta Hills, Eocene mammal faunas are known from the Kalakot area (Subathu Formation) of Jammu in the Jammu and Kashmir Province of northwestern India (Ranga Rao, 1971, 1972; Kumar and Sahni, 1985; Kumar, 1991, 1992). Kumar (1998) presented the most recent faunal list for mammals from the Kalakot Eocene. To the west of the Ganda Kas Area, important faunas were discovered near Chorlakki (Kohat District; Gingerich et al., 1979; Thewissen et al., 1987) and Barbora Banda (H-GSP Locality 300 of the Banda Daud Shah Area of Karak District; Thewissen et al., 1983). These beds are identified as the Mami Khel Formation or Kuldana Formation.

Here, we report new fossil mammals from several additional sites in the Ganda Kas and Banda Daud Shah Area collected under the Howard University-Geological Survey of Pakistan (H-GSP) Project. We also describe new mammals from the Chorgali Formation of the Khair-e-Murat Range (Pakistani Punjab), from which no vertebrates have ever been described. Thewissen et al. (1998) described the old and new localities in detail. The new collections enhance our understanding of the relations among the Eocene Indo-Pakistani faunas, summarized in Table 1. This table provides a summary of Eocene mammal faunas of Indo-Pakistan, and emphasizes their distinctive character that is unlike that of any other continent.

Institutional Abbreviations—**GSP-UM**, Geological Survey of Pakistan, Islamabad, Pakistan, University of Michigan collections; **H-GSP**, Geological Survey of Pakistan, Howard University collections; **IVPP**, Institute for Vertebrate Paleontology and Paleoanthropology, Bejing, People's Republic of China; **USNM**, U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.; **WIHG**, the Wadia Institute of Himalayan Geology, Dehra Dun, India.

SYSTEMATIC PALEONTOLOGY

Order DIDELPHIMORPHIA Gill, 1872
Family DIDELPHIDAE Gray, 1821
Subfamily HERPETOTHERIINAE Trouessart, 1879

Gen. et sp. indet.
(Figs. 2A, B and 3)

Referred Specimen—H-GSP 92158, right lower molar, presumed m3, in a mandibular fragment containing the anterior root of subsequent molar, H-GSP Locality 62, Kuldana Formation of the Ganda Kas Area. H-GSP 92158 was found by sorting matrix derived from acid dissolution of blocks of sedimentary rock. Small teeth at this locality are rare, but further acid preparation yielded immediately an additional right lower molar (presumed m4) of similar morphology and size suggesting it came from the same jaw. This tooth presumably fitted on the root of the first specimen. This molar is included in H-GSP 92158 but was severely damaged. The fragmentary remains were used for the enamel microstructure study (Fig. 3).

Description—H-GSP 92158 is a small tribosphenic right lower molar (length: 1.38 mm; trigonid width: 0.81 mm; talonid width: 0.81 mm) with a large protoconid, somewhat lower metaconid, and smaller paraconid. The paraconid is directed anteriorly and gives rise to a wide trigonid basin that opens lingually. The paraconid is distinct and is positioned at the anterolingual corner of the tooth. Sharp crests join the protoconid with the two lingual trigonid cusps. The cristid obliqua meets the posterior wall of the trigonid buccal to the notch in the protocristid.

The talonid bears three cusps. The tip of the entoconid is broken, but the size of its base implies a height similar to the hypoconid. The hypoconulid is much lower than the other talonid cusps and is positioned on the posterior lingual side of the tooth. The hypoconulid and entoconid are twinned. Cingulids are present on the anterior, buccal, and posterior sides of the tooth.

Enamel prisms in the fragmentary molar are horseshoe shaped in cross section and are aligned in rows (Pattern 2 enamel of Boyde, 1971). The molar exhibits prismatic enamel, and the prisms do not decussate. Enamel tubules are also evident.

Discussion—H-GSP 92158 is identified as a marsupial based on the combination of two gross features: a small anterolingual positioned paraconid that creates a wide trigonid basin open lingually; and a twinned hypoconulid and entoconid. In addition, most marsupial enamel is characterized by the presence of parallel prisms that do not decussate (Tomes, 1906; Stern and Crompton, 1989; Wood et al., 1999) and enamel tubules (Lester et al., 1987) as seen in H-GSP 92158. Parallel prismatic enamel

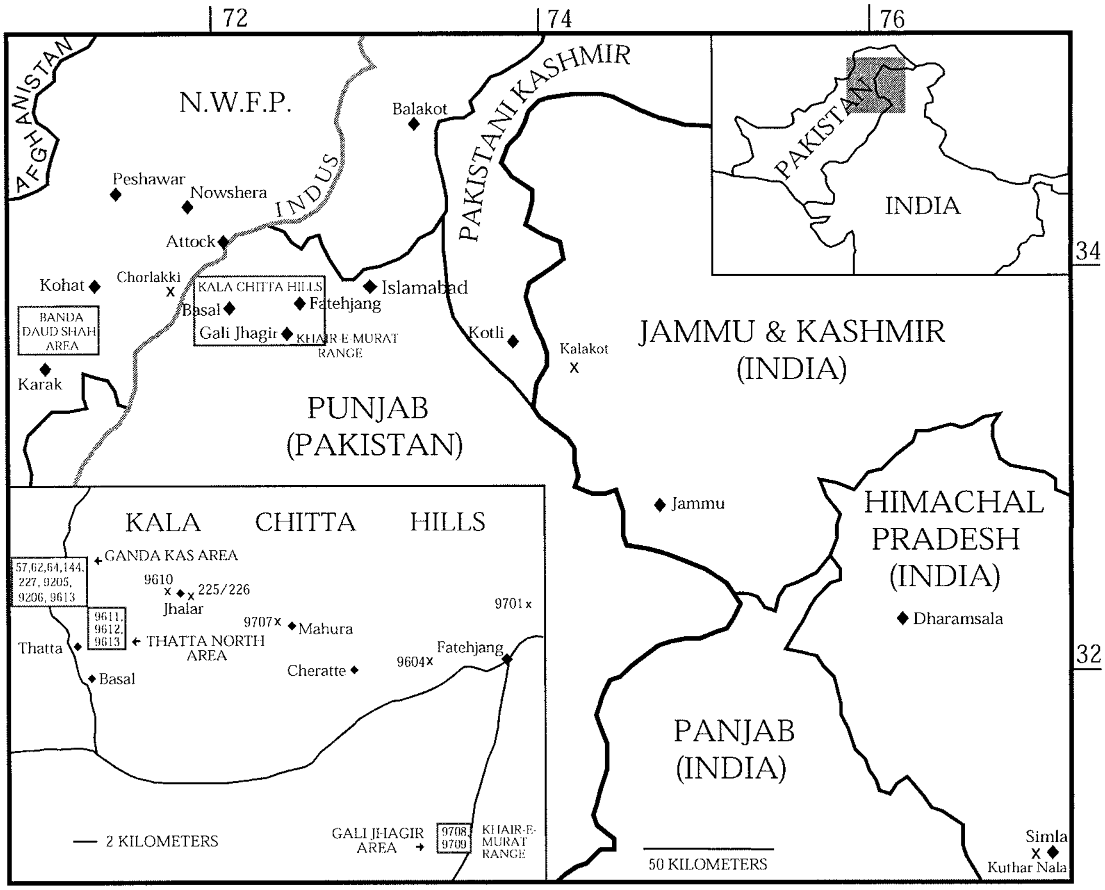

FIGURE 1. Map of northern Pakistan and India, with geographical names and numbered localities mentioned in text. Upper right corner is a locator map, and left lower corner shows an enlargement of the Kala Chitta Hills and Khair-e-Murat Range. See Thewissen et al. (1998) for further details on localities. Diamonds indicate towns, "x", a fossil locality.

is present in a number of tribosphenic placentals (bats, moles, shrews; Boyde, 1964 cited in Stern and Crompton, 1989). In tribosphenic bats, the tubules do not extend far into the enamel. While long tubules do occur in some megachiropterans (Lester and Hand, 1987), these bats do not have tribosphenic molars. It is unlikely that H-GSP 92158 represents a talpid or a soricid because these families are not known from the Eocene. These placentals are also different on a macroscopic level, their trigonid basin is narrow lingually and entoconid and hypoconid are not twinned.

Eocene marsupials with tribosphenic teeth are commonly classified as didelphids (e.g., McKenna and Bell, 1997) which contains two Old World Eocene subfamilies: Peradectinae and Herpetotheriinae (for alternate classifications see Crochet, 1980, and Marshall et al., 1990). Crochet (1980), Krishtalka and Stucky (1983), and Korth (1994) discuss the differences between these subfamilies. The primary difference concerns the cusps of the talonid of the lower anterior molars. In peradectines, the entoconid and hypoconulid are similar in height and not separated by a notch, whereas in herpetotheriines, the hypoconulid is much smaller than the entoconid, and these cusps are separated by a notch. H-GSP 92158 displays the herpetotheriine characters.

No Eocene didelphids have been described from central and eastern Asia. For post-Eocene Asian *Asiadidelphis* (see Emry et al., 1995) and *Siamoperadectes* (see Ducrocq et al., 1992) only parts of the upper dentition are known, and this makes direct comparison impossible. *Asiadidelphis* is considerably larger than the Pakistani specimen. Qi et al. (1991) mentioned a Chinese didelphid in an Eocene faunal list, but this specimen has not been described.

Crochet et al. (1992) described *Qatranitherium* from the Oligocene of Oman as a peradectine, but McKenna and Bell (1997) considered this genus synonymous with the herpetotheriine *Peratherium* following Simons and Bown (1984). The Omani specimen consists of a deciduous p3 and cannot be compared to the Pakistani specimen. *Kasserinotherium,* from the Eocene of Tunesia (Crochet, 1986), is known from upper molars only and, according to McKenna and Bell (1997), may not be a marsupial. It cannot be compared directly to our specimen.

Other Old World genera of Eocene herpetotheriines are: *Garatherium* (see Crochet, 1984), *Amphiperatherium,* and *Peratherium* (see Crochet, 1980, for a review). A single upper molar is known for African *Garatherium,* so the genus can not be compared to H-GSP 92158. *Peratherium* and *Amphiperatherium* are well known from Europe, but the main difference in the lower dentition between these two involves the relative size of molar cusps on subsequent molars. Because only one complete molar from H-GSP 92158 is preserved, a comparison of cusp sizes between molars cannot be made.

Kappelman et al. (1996) described a herpetotheriine from Turkey. A comparison with a cast of the Turkish AK 94-8 (Kappelman et al., 1996) shows that in the Pakistani specimen the paraconid is directed more anterolingually and closer to the metaconid, giving rise to a lingually more closed trigonid basin. In the Turkish specimen the paraconid is directed more anteriorly, and the trigonid basin is more open. While the metaconid and protoconid are similar in height and diverge in the Pakistani

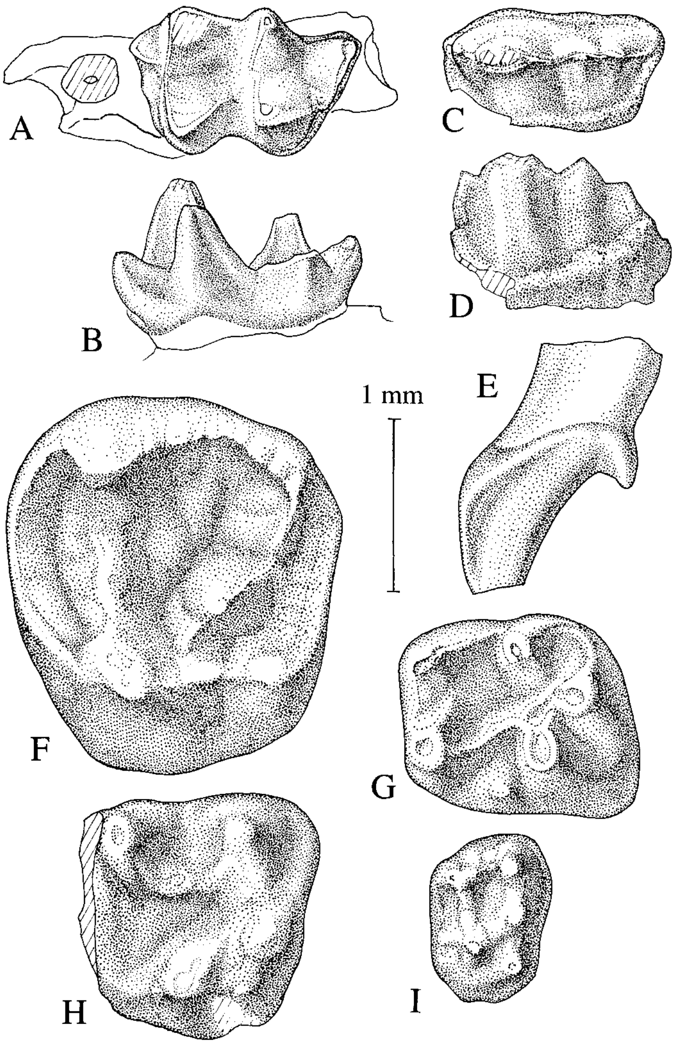

FIGURE 2. Marsupials, carpolestids, and rodents from the Kuldana and Chorgali formations. **A**, **B**, right mx of a herpetotheriinae indet. (H-GSP 92158), in occlusal and lingual views. **C**–**E**, *Parvocristes oligocollis,* sp. nov., holotype right p4 in occlusal and lingual view (C–D, H-GSP 92163), and presumed right I1 (E) in lingual view (H-GSP 92164). **F**, *Birbalomys sondaari,* right Mx in occlusal view (H-GSP 92161). **G**, *Birbalomys ijlsti,* left mx in occlusal view (H-GSP 91057). **H**, cf. *Saykanomys chalchae,* left mx fragment in occlusal view (H-GSP 97249). **I**, *Gumbatomys asifi,* left P4 in occlusal view (H-GSP 92160).

specimen, the protoconid is higher in the Turkish specimen, and the two cusps are parallel. The cristid obliqua touches the trigonid more lingually in the Pakistani specimen. Some of these differences could be due to the position of the teeth in the jaw (e.g., m1 versus m2), but we believe that the Pakistani specimen represents a different taxon than the Turkish specimens. We feel that, at present, there is insufficient material to name the Pakistani taxon.

Order PLESIADAPIFORMES Simons and Tattersall in Simons, 1972
Family CARPOLESTIDAE Simpson, 1935

Genus *PARVOCRISTES,* gen. nov.

Diagnosis—p4 with poorly developed plagiaulacoid blade, consisting of a row of cusps connected by a weak crest. Posterolingual side of p4 with broad cingulid.

Etymology—Combination of *parvo* (Latin: poor) and *cristes* (shortened from cristatus, Latin: crested) a reference to the poor development of the crest in this carpolestid.

PARVOCRISTES OLIGOCOLLIS, sp. nov.
(Fig. 2C–E)

Holotype—H-GSP 92163, unworn right p4 retrieved from screenwash matrix, H-GSP Locality 225, Kuldana Formation of the Jhalar Area.

Referred Specimen—H-GSP 92164, isolated incisor, presumed right I1, from the type locality, found in the same sample of screenwash matrix as the holotype.

Distribution—Early Eocene (Kuldana Formation) of Northern Pakistan.

Diagnosis—No distinction can be made between generic and specific diagnoses at this time.

Etymology—Combination of *oligos* (Greek: few) and *collis* (Latin: hill), referring to the low number of cusps on the plagiaulacoid tooth.

Description—The holotype is a two-rooted plagiaulacoid tooth (length: 1.2 mm; width: 0.7 mm), consisting of 4 large cusps connected by a central crest that is slightly lingually convex (Fig. 2C, D). The second of these cusps is the highest, followed by the third, first, and fourth, respectively. The labial side of the tooth is slightly concave and has a wide complete cingulid. The lingual side of the tooth is more or less flat and has a broad cingulid posteriorly. The anterolingual part of the tooth is damaged, and the presence of the cingulid here cannot be ascertained. The posterior edge of the cingulid is notched in occlusal view, apparently to accommodate the tooth posterior to it. Anteriorly, the central crest divides and is continued in the lingual and labial cingulid. The anterior margin of the tooth is strongly concave and apparently embraced the posterior part of the tooth anterior to it.

In order to investigate the size of the enamel prisms of H-GSP 92163, a small area near the tip of the highest cusp was exposed to 5% hydrochloric acid for 10 seconds. This area was then studied under a compound microscope with reflected light. This indicated that enamel prisms of this tooth are small, approximately 2 to 3 micrometers in size.

The referred specimen (H-GSP 92164, Fig. 2E) is a small pointed incisor (length: 0.9 mm; width: 0.5 mm). In lingual view, it bears a strongly anteriorly projecting, somewhat curved cusp. Near the posterior cingulum of the tooth there is a small secondary cusp. In anterior view, the crown is directed somewhat lingually. There is a weak medial cingulum, but no lateral cingulum.

Discussion—Plagiaulacoid teeth occur in several clades of mammals, including marsupials, multituberculates, and plesiadapiforms. The trenchant teeth of derived members of these groups are often hard to distinguish, possibly as a result of far reaching convergence relating to its function. For instance, Biknevicius (1986) noted a number of similarities between derived carpolestids such as *Carpodaptes* and the multituberculate *Ptilodus* (see Krause, 1982).

The holotype of *Parvocristes* shows a very low degree of plagiaulacoidy and retains several features not found in derived plagiaulacoid taxa. Important among these are that the blade is comprised of four clear cusps, that there are strong lingual and labial cingulids, and that the lingual cingulid is widened posteriorly. The referred specimen further strengthens the identification by the presence of an accessory cusp on a strongly projecting incisor.

The holotype of *Parvocristes* differs from caenolestoid marsupials in lacking a talonid basin (Bown and Fleagle, 1993), and from polydolopoids in retaining a cingulid on the lingual

TABLE 1. Mammalian faunal list for Eocene Indo-Pakistan. Numbers of specimens are indicated for important areas discussed in the text, only non-marine records (1; 2; 3; 4; >5, between 5 and 9; >10, 10 or more; p, present but number unknown). "Other sites" refers to all freshwater localities in the Ganda Kas Area except Locality 62 which has its own column.

Country	Pakistan					India
Formation	Mami Khel		Chorgali	Kuldana		Subathu
Area	Banda Daud Shah	Chorlakki	Gali Jhagir	Locality 62	Other Sites	Kalakot
TAXON						
DIDELPHIMORPHA						
HERPETOTHERIINAE	—	—	—	1	—	—
PROTEUTHERIA						
Pakilestes lathrius	—	2	—	—	—	—
LYPOTYPHLA						
Seia shahi	—	2	—	—	—	—
CHIROPTERA	2	—	—	—	—	—
PLESIADAPIFORMES						
CARPOLESTIDAE						
Parvocristes oligocollis	—	—	—	—	2	—
PLESIADAPIDAE						
Jattadectes mamikheli	1	—	—	—	—	—
RODENTIA						
CHAPATTIMYIDAE						
Birbalomys ijlsti	—	>10	—	5	>10	P
Birbalomys lavocati	—	—	—	—	>10	P
Birbalomys sondaari	—	>10	—	2	>10	P
Birbalomys vandermeuleni	—	—	—	—	>10	P
Birbalomys woodi	—	3	—	—	—	P
Chapattimys debruijni	—	1	—	—	1	P
Chapattimys ibrahimshahi	—	—	—	—	>10	P
Chapattimys wilsoni	—	2	—	1	>10	P
Gumbatomys asifi	—	3	—	1	—	P
cf. *Saykanomys chalchae*	—	—	1	—	>10	—
YUOMYIDAE						
Advenimus bohlini	—	—	—	—	—	P
cf. *Petrokoslovia sp. indet. 1*	—	1	—	—	1	P
cf. *Petrokoslovia sp. indet. 2*	—	1	—	—	—	P
FAMILY INDET.	2	—	—	—	—	—
PRIMATES						
ADAPIDAE	—	—	—	—	—	P
Panobius afridi	1	2	—	—	—	—
cf. *Agerinia* sp.	—	1	—	—	—	—
OMOMYIDAE						
Kohatius coppensi	—	3	—	—	—	—
Kohatius sp. A	—	—	—	—	1	—
cf. *Kohatius sp.*	1	—	—	—	—	—
CREODONTA						
HYAENODONTIDAE						
Paratritemnodon indicus	—	P	—	—	—	3
P. jandewalensis	1	—	—	—	2	—
ARCTOCYONIA						
ARCTOCYONIDAE						
Karakia longidens	1	—	—	—	—	—
QUETTACYONIDAE						
Obashtakaia aeruginis	—	—	—	—	—	—
Quettacyon parachai	—	—	—	—	—	—
Sororocyon usmanii	—	—	—	—	—	—
ARTIODACTYLA						
DICHOBUNIDAE						
Chorlakkia hassani	—	>10	—	—	—	—
Diacodexis pakistanensis	>10	1	—	—	—	—
Dulcidon gandaensis	—	—	—	—	1	—
Dichobunid indet. large	—	—	—	1	1	—
Pakibune chorlakkiensis	—	2	—	—	—	—
RAOELLIDAE						
Haqueina haquei	—	—	—	—	1	—
Indohyus indirae	—	2	—	—	—	>10
Indohyus major	—	1	—	—	—	—
Khirtharia aurea	—	—	3	—	—	—
Khirtharia dayi	—	>10	—	>5	>5	—
Khirtharia inflata	—	—	—	—	—	>10
Kunmunella kalakotensis	—	—	—	—	—	>10
Kunmunella transversa	—	—	2	—	—	1
Metkatius kashmirensis	—	—	—	—	—	1

TABLE 1. *(Continued)*

Country	Pakistan					India
Formation	Mami Khel		Chorgali	Kuldana		Subathu
Area	Banda Daud Shah	Chorlakki	Gali Jhagir	Locality 62	Other Sites	Kalakot
CETACEA						
PAKICETIDAE	1	—	—	—	—	—
Ichthyolestes pinfoldi	—	8	—	7	2	—
Nalacetus ratimitus	—	—	—	5	—	—
Pakicetus attocki	—	—	—	>10	—	1
Pakicetus inachus	—	>10	—	1	—	—
AMBULOCETIDAE						
Ambulocetus natans	—	—	—	—	—	—
Gandakasia potens	—	—	—	—	—	—
Himalayacetus subathuensis	—	—	—	—	—	—
REMINGTONOCETIDAE						
Andrewsiphius minor	—	—	—	—	—	—
Andrewsiphius kutchensis	—	—	—	—	—	—
Attockicetus praecursor	—	—	—	—	—	—
Dalanistes ahmedi	—	—	—	—	—	—
Kutchicetus minimus	—	—	—	—	—	—
Remingtonocetus harudiensis	—	—	—	—	—	—
Remingtonocetus sloani	—	—	—	—	—	—
PROTOCETIDAE						
Babiacetus mishrai	—	—	—	—	—	—
Babiacetus indicus	—	—	—	—	—	—
Indocetus ramani	—	—	—	—	—	—
Rodhocetus kasrani	—	—	—	—	—	—
Takracetus simus	—	—	—	—	—	—
BASILOSAURIDAE						
Basilosaurus drazindai	—	—	—	—	—	—
Basiloterus hussaini	—	—	—	—	—	—
Gaviacetus razai	—	—	—	—	—	—
MESONYCHIA						
MESONYCHIDAE	—	—	—	—	1	1
TILLODONTIA						
ESTHONYCHIDAE						
Basalina basalensis	—	1	—	—	1	—
PERISSODACTYLA						
BRONTOTHERIIDAE						
Eotitanops dayi	—	>5	—	—	>5	—
Pakotitanops latidentatus	—	—	—	—	3	—
Mulkrajanops moghliensis	—	—	—	—	—	1
ISECTOLOPHIDAE						
Karagalax mamikhelensis	>10	1?	—	—	—	—
Sastrilophus dehmi	—	—	—	—	—	1
LOPHIALETIDAE						
Kalakotia simplicidentata	—	—	—	—	—	>5
cf. *Kalakotia*	—	—	—	1	1	—
HELALETIDAE						
Hyrachyus asiaticus	—	—	—	—	—	2
Jhagirilophus chorgalensis	—		2	—	—	—
Triplopus kalakotensis	—	—	—	—	—	1
DEPERTELLIDAE						
Teleolophus daviesi	—	—	—	—	1	—
HYRACODONTIDAE						
‘‘Forstercooperia’’ jigniensis	—	1	—	—	—	3
PROBOSCIDEA						
ANTHRACOBUNIDAE						
Anthracobune pinfoldi	—	—	—	—	—	—
Anthracobune aijiensis	—	—	—	—	—	4
Jozaria palustris	—	—	—	—	—	—
Nakusia shahrigensis	—	—	—	—	—	—
Pilgrimella wardi	—	2	—	5	8	—
Pilgrimella n. spec.	—	1	—	3	1	—
SIRENIA						
PROTOSIRENIDAE						
Ishatherium subathuensis	—	—	—	—	—	—
Protosiren sattaensis	—	—	—	—	—	—
Order Indet.						
SORORYCTIDAE						
Sororyctes ghaznavii	—	—	—	—	—	—

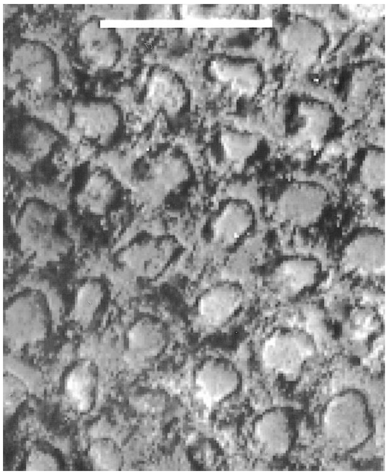

FIGURE 3. Scanning electron micrograph of enamel microstructure of herpetotheriine marsupial from Ganda Kas (H-GSP 92158). Scale bar equals 10 microns.

side of the tooth. Furthermore, no plagiaulacoid marsupials are known outside of South America and Australia.

In multituberculates, the plagiaulacoid tooth is commonly a high blade with its summit posteriorly, and lacking cingulids (e.g., Krause, 1980, 1982; Kielan-Jaworowska and Nessov, 1992), and *Parvocristes* differs from multituberculates in all these respects. Furthermore, no unambiguous multituberculates have been described from Indo-Pakistan. A tooth fragment of a late Cretaceaous gondwanathere is known from India and may represent a multituberculate (Krause et al., 1997), but the taxonomic status of gondwanatheres is unclear, and the only known jaw for the family lacks plagiaulacoid teeth (Pascual et al., 1999). *Parvocristes* lacks the large prisms that occur in Asian multituberculates (Carlson and Krause, 1985).

H-GSP 92163 is most similar to the p4 of the carpolestid *Elphidotarsius* in its retention of cingulids (e.g., USNM 9411), in the presence of four cusps (serrations) that constitute the blade (Rose, 1975), and in having the highest part of the blade in the anterior part of the tooth. *Parvocristes* differs from *Elphidotarsius* (as well as *Carpolestes, Carpodaptes,* and *Carpocristes*) in having a poorly developed blade, with clearly distinct cusps.

The p4 of *Parvocristes* is similar to *Carpocristes* (IVPP 10697.1), but differs from *Elphidotarsius* in having a flat labial and concave lingual side and in its widened cingulum on the posterolingual side of the tooth. This concavity occurs in all species referred to *Carpocristes* as well as in *Carpolestes dubius* (see Beard and Wang, 1995). *Chronolestes,* from the early Eocene Wutu Basin of China, has also been described as a carpolestid (Beard and Wang, 1995), but this taxon lacks a plagiaulacoid tooth and is thus unlike *Parvocristes.* The referred incisor of *Parvocristes* is similar to those referred to *Chronolestes* by Beard and Wang (1995), in projecting anteriorly, and in the presence of a small accessory cusp.

H-GSP 92163 is the only plagiaulacoid tooth known from Indo-Pakistan and the first record of plesiadapiforms from the subcontinent. *Parvocristes* lacks the derived characters of other carpolestids. As such, it is consistent with the biogeographical scenario for plesiadapiform migrations proposed by Beard and Wang (1995) which holds that the origin of the carpolestid radiation occurred in Asia. Although more primitive, *Parvocristes* is much younger than the oldest North American carpolestids, which are of Torrejonian age.

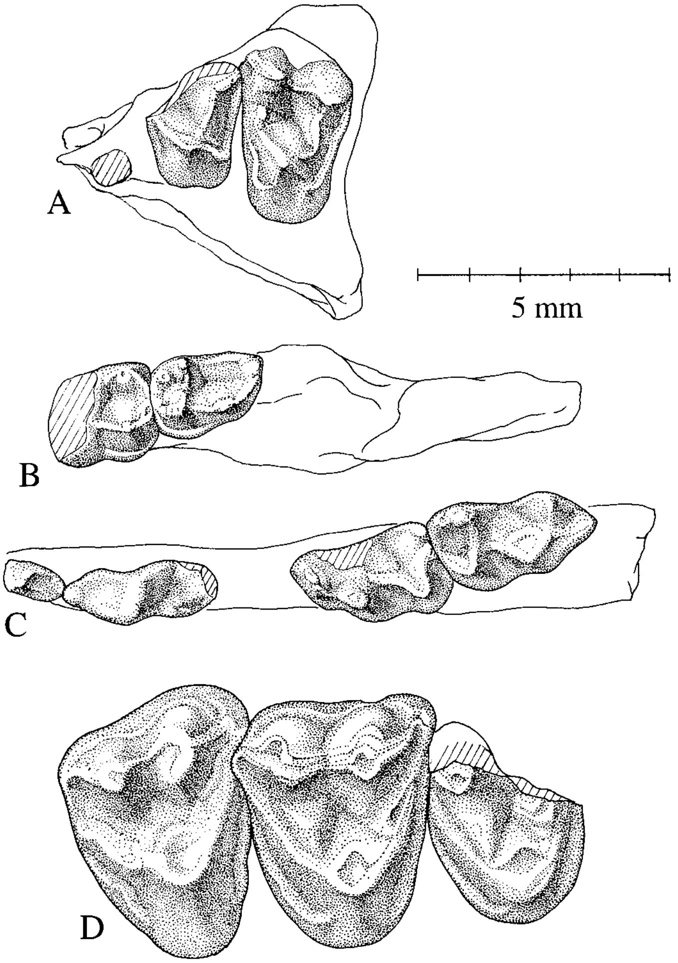

FIGURE 4. Plesiadapids, primates, arctocyonids, and artiodactyls from the Mami Khel Formation. **A**, *Jattadectes mamikheli,* gen. et sp. nov., occlusal view of left M2–3 (H-GSP 97203). **B**, *Panobius afridi,* occlusal view of left m2–3 (H-GSP 97205). **C**, *Karakia longidens,* gen. et sp. nov., occlusal view of left posterior p3, p4, m2, and m3 (H-GSP 97199). **D**, *Diacodexis pakistanensis,* occlusal view of right M1–3 (H-GSP 97212).

Family PLESIADAPIDAE Troussart, 1897

Genus *JATTADECTES,* gen. nov.

Diagnosis—M3 with strong preprotocrista, very weak postprotocrista, and a protocone fold intermediate in strength between the two. M3 larger than M2.

Etymology—Combination of Jatta, village near the type locality (see Thewissen et al., 1998) and dectes, after *Pronothodectes,* a similar genus.

JATTADECTES MAMIKHELI, sp. nov.

(Fig. 4A)

Holotype and Only Specimen—H-GSP 97203, left maxillary fragment with M2–3. The labial side of the M2 is missing and that of the M3 is slightly damaged. We interpret these teeth as M2–3 because the posterior edge of the palate shows that no roots were present posterior to the second tooth in the specimen. The enamel of H-GSP 97203 is very thin due to postmortem geochemical weathering. The specimen was found at H-GSP Locality 9712 (Jatta Salt Mine in the Banda Daud Shah Area).

Diagnosis—No distinction can be made between generic and specific diagnosis at this time.

Distribution—Early Eocene (Mami Khel Formation) of Northern Pakistan.

Description—A lingual alveolus is all that remains of the M1. Its position suggests that the M1 was slightly narrower than the M2. The lingual part of the M2 bears a protocone from which a strong preprotocrista and a much weaker postprotocrista extend labially. The paraconule and metaconule are small and similar in size. The protocone fold is stronger than the postprotocrista and extends basally where it joins the postcingulum. The cingulum is somewhat enlarged at the posterolingual margin of the tooth creating a small ledge. Only a small portion of the metacone is preserved, and the paracone is missing. There is a weak precingulum.

The last molar is larger than the M2. It is short anteroposteriorly (2.1 mm) and wide buccolingually (width cannot be measured because the labial side is damaged). Similar to the M2, the preprotocrista is stronger than the postprotocrista, and the conules are weak. The protocone fold is stronger than the postprotocrista. The ledge formed where the protocone fold joins the cingulum is more distinct in M2 than M3. The preparacrista extends anterolabial from the paracone. The labial edge of the tooth is not preserved.

Discussion—No plesiadapids are known from Indo-Pakistan, and no upper molars of Indo-Pakistani primates have been described. A specimen attributed to *Diacodexis pakistanensis* (see Kumar and Jolly, 1986) probably represents an adapid and differs from *Jattadectes* in being much larger and having sharper cusps and crests. We have not seen the remainder of the specimens described by Kumar and Jolly (1986).

We use the ordinal taxonomy of archontans as summarized by Rose (1995). We consider H-GSP 97203 to be a plesiadapiform and not a primate based on the size relations between the M2 and M3. In *Jattadectes*, the M3 is larger than the M2, as in plesiadapiformes, whereas in Eocene primates the M3 is usually much smaller than the M2. In addition, *Jattadectes* has short and wide upper molars as in Plesiadapiformes. Rose (1995) discussed general differences between plesiadapiformes and primates.

The present specimen resembles plesiadapids more than the other plesiadapiform families. Carpolestids are much smaller and have large conules, and paromomyids have low blunt cusps with a large hypocone. Most described genera of plesiadapids are distinguished on the basis of their incisors and lower cheekteeth (Gingerich, 1975), therefore comparison with other plesiadapids is limited. We consider *Jattadectes* to be relatively similar to *Pronothodectes* based on the triangular shape of the teeth and small size, but it differs in the size relations between the upper molars and the difference in size between the preprotocrista and postprotocrista.

Order RODENTIA Bowdich, 1821
Family CHAPATTIMYIDAE Hussain et al., 1978

BIRBALOMYS SONDAARI (Hussain et al., 1978)
(Fig. 2F)

Referred Specimens—H-GSP 91053 (M3) and H-GSP 92161 (Mx) from H-GSP Locality 62 in the Ganda Kas Area.

Description—H-GSP 92161 (length: 1.9 mm; width: 2.3 mm) has four large cusps. These are, in order of decreasing size, protocone, paracone, hypocone, and metacone. The protocone is connected to the hypocone by a crest, and conules are present. Pre- and postcingula are strong. H-GSP 91053 (length: 2.0, width 2.1 mm) has a large protocone and paracone, but lacks a metacone and hypocone. The area of the metacone is covered with small crenulations. This tooth has a strong paraconule and metaconule.

Discussion—Among the rodents known from the Ganda Kas Area (Hussain et al., 1978), these specimens match only *Birbalomys sondaari* in size and morphology. These specimens are the first rodents to be described from Locality 62.

BIRBALOMYS IJLSTI (Hussain et al., 1978)
(Fig. 2G)

Referred Specimens—H-GSP 91054 (D4), H-GSP 91057 (mx), H-GSP 91059 (Mx), H-GSP 96540 (mx), and H-GSP 30226 (P3) from H-GSP Locality 62 in the Ganda Kas Area.

Description—The most diagnostic of these teeth is the upper molar (H-GSP 91059). This tooth (length: 1.3 mm; width: 1.5 mm) has four cusps, in order of decreasing size: protocone, paracone, hypocone, and metacone. There is a pronounced metaconule (mesocone) on this upper molar as well as on the dP4 (H-GSP 91054, length: 1.5 mm, width 1.5 mm). Both teeth lack a paraconule. One of the lower molars (H-GSP 91057, length: 1.3 mm, width 1.1 mm) lacks the entolophid, whereas its ectolophid is strongly concave labially. This specimen and a second, heavily worn, lower molar (H-GSP 96540, length: 1.2 mm, width: 1.1 mm) are smaller than the lower molars in the type sample of the species.

Discussion—The small size of the hypocone of the upper teeth suggests that they pertain to *Birbalomys* and not to *Chapattimys* (Hussain et al., 1978). In size they are similar to Indo-Pakistani ''*Saykanomys*'' *chalchae* and *Birbalomys ijlsti*. Hussain et al. (1978) considered the presence of a mesocone (metaconule) to be diagnostic of *B. ijlsti*, but their figures show the presence of this cusp in both taxa. The large size of this cusp in our specimens is consistent with their identification as *B. ijlsti*. *B. ijlsti* is the most common rodent at Locality 62.

cf. *SAYKANOMYS CHALCHAE* Shevyreva, 1972
(Fig. 2H)

Referred Specimen—H-GSP 97249 (mx) from H-GSP Locality 9709 in the Chorgali Formation near Gali Jhagir.

Description—H-GSP 97249 is a bunodont lower molar (length: 1.6 mm; width 1.3 mm) with a weak ectolophid. Part of the trigonid of this specimen is missing, but the large protoconid is preserved. The hypoconid, entoconid, and hypoconulid are similar in size to eachother. The only crest on the talonid is a very weak ectocristid that is concave lingually.

Discussion—Hussain et al. (1978) were the first to recognize cf. *Saykanomys chalchae* from Indo-Pakistan, but their specimens were referred to *Birbalomys ijlsti* by Hartenberger (1982). We consider our specimen conspecific with Ganda Kas cf. *S. chalchae* and distinct from *B. ijlsti*. The Indo-Pakistan material of cf. *S. chalchae* may have to be separated specifically from the Central Asian type material and transferred to the genus *Birbalomys*. Our specimen of cf. *S. chalchae* differs from those of *B. ijlsti* in the weaker development of its crests and its larger size, consistent with the description of Hussain et al. (1978).

CHAPATTIMYS DEBRUIJNI Hartenberger, 1982

Referred Specimen—H-GSP 97110 (m3) from H-GSP Locality 9205 in the Kuldana Formation of the Ganda Kas Area.

Description—This m3 (length: 2.4 mm; width 2.2 mm) is weathered, but retains most of its enamel. It has two large cusps on the trigonid, but only a single large cusp on the talonid: a worn hypoconid. The hypoconulid and entoconid are small, and the only crest that is strong is the ectocristid. This crest is lingually concave and ends posterior to the protoconid.

Discussion—The size of H-GSP 97110 suggests that it is one of the three large rodent species in Indo-Pakistan: *Birbalomys woodi*, *Chapattimys ibrahimshahi*, and *C. debruijni*. H-GSP 97110 pertains to *Chapattimys* because it has wide lower molars. The crenulations in its talonid basin (Hartenberger, 1982) imply that it is referable to *C. debruijni* because the enamel of the talonid basin of *C. ibrahimshahi* is smooth (Hussain et al., 1978). There appears to be some morphological overlap between the larger Eocene rodent species from Indo-Pakistan, although Srivastava and Kumar (1996) recognized all three species at Kalakot. The study of chapattymyids is severely limited by the absence of jaws with multiple teeth for most species.

CHAPATTIMYS WILSONI Hussain et al., 1978

Referred Specimen—H-GSP 30412 (Mx) from H-GSP Locality 62 in the Kuldana Formation of the Ganda Kas Area.

Description—This upper molar (length: 1.7 mm; width 2.0 mm) is complete and hardly worn. It has a hypocone that is similar in size to the protocone and is placed more lingual than the protocone. The protocristid is sharp and continuous. The metacristid extends between metacone and metaconule, but does not reach the protocone.

Discussion—This tooth represents a medium-sized chapattimyid. The position and size of the hypocone suggest that it pertains to *Chapattimys,* and its size implies that it is the smaller of the two species: *C. wilsoni.*

GUMBATOMYS ASIFI Hartenberger, 1982
(Fig. 2I)

Referred Specimen—H-GSP 92160 (P4) from H-GSP Locality 62.

Description—H-GSP 92160 is small and very narrow (length: 0.7 mm, width: 0.9 mm). The tooth bears a large protocone and a paraconule labial to it. Posterolingual to the paraconule is the metaconule. The conules are similar in size to the paracone and metacone, and each conule is connected to the cusp labial to it by a crest. There are no connections between the protocone and paraconule. The cusps are high, making the tooth somewhat hypsodont.

Discussion—*Gumbatomys asifi* is a rare rodent and is known only from Chorlakki (no locality data are given for the three specimens referred to this species by Hartenberger, 1982, but GSP-UM locality records indicate that they were found at the type locality). It is the only chapattimyid that is somewhat hypsodont, and hypsodonty is the basis for attributing H-GSP 92160 to this species.

Order PRIMATES Linnaeus, 1758
Family ADAPIDAE Trouessart, 1879

PANOBIUS AFRIDI Russell and Gingerich, 1987
(Fig. 4B)

Referred Specimen—H-GSP 97205, left mandible with m2–3, in a mandibular fragment that includes part of the ascending ramus. The trigonid of the m2 and the hypoconulid of the m3 are severely damaged. The specimen is from H-GSP Locality 9712 of the Banda Daud Shah Area.

Description—The talonid (width: 1.9 mm) of the m2 has a large hypoconid and a much smaller but distinct entoconid. The cristid obliqua reaches the posterior side of the trigonid just lingual to the protoconid. There is a strong labial cingulid. The trigonid basin of the m3 (width: 1.6 mm) is small, and the protoconid and metaconid are low. The paraconid is smaller and is placed anterolabial to the metaconid. The largest cusp on the talonid (width: 1.4 mm) is the hypoconid. The area of the hypoconulid is damaged, and the entoconid is barely discernible. The labial cingulid is strong. The mandibular foramen lies at the level of the tooth row, and the depth of the mandible below the trigonid of the m3 is 3.3 mm.

Discussion—The m3 of H-GSP 97205 closely resembles the referred m3 of *Panobius afridi* (GSP-UM 689). These specimens are similar in the presence of a labially placed paraconid, a strong cingulid labial to the protoconid, and a weak entoconid. The holotype of *P. afridi* is an isolated m1 (GSP-UM 688). The main feature used to characterize the genus is the anterolabial extension of the trigonid basin as seen in the holotype (Russell and Gingerich, 1987). However, this feature is not present in either the referred m3 or the H-GSP specimen. It is likely that GSP-UM 689 and H-GSP 97205 are conspecific, but they may not pertain to *Panobius afridi.* More material is necessary to evaluate the status of *Panobius.* This is only the tenth specimen of an Eocene primate described from Indo-Pakistan, and the only specimen consisting of more than a single tooth (all other specimens are reviewed by Thewissen et al., 1997). It is also likely that several of the specimens described by Kumar and Jolly (1986) as *Diacodexis pakistanensis* are actually adapid primates.

Order CREODONTA Cope, 1875
Family HYAENODONTIDAE Leidy, 1869
PARATRITEMNODON Ranga Rao, 1973

PARATRITEMNODON JANDEWALENSIS, sp. nov.
(Fig. 5A–C)

Holotype—H-GSP 96140, left lower molar, H-GSP Locality 9205, Kuldana Formation of the Ganda Kas Area. The paraconid is broken at its base, and the tip of metaconid is missing.

Referred Specimen—H-GSP 96135, maxilla with one preserved root of P4, base of M1, and M2, found at the type locality.

Diagnosis—Nearly twice as large as *Paratritemnodon indicus* in linear dimensions. The metastyle of the M2 of *P. jandewalensis* is relatively larger than in *P. indicus* and the talonid is longer.

Distribution—Early Eocene (Kuldana Formation) of Northern Pakistan.

Etymology—Species indication refers to the main dry river (nala in Punjabi) of the Ganda Kas Area, Jandewala Nala. This nala is located approximately 1 km south of the type locality.

Description—The holotype is a lower molar (length: 12.4 mm; width: 7.2 mm) with a trigonid that is longer than the talonid. The protoconid is high and vertical, and the paracristid descends steeply down its anterior edge. The paracristid probably formed a V-shaped cutting blade, but the part that ascends the paraconid is not preserved. The cross-section of the base of the paraconid is large and suggests that this cusp was tall. The protocristid descends the lingual face of the protoconid and fuses into the metaconid. The tip of the latter cusp is not preserved, but its size can be estimated from its basal cross section. The cusp was small, probably only half as high as the protoconid.

The talonid is strong and has a deep central basin. The hypoconid is the largest cusp and the cristid obliqua extends anteriorly from it to the posterior side of the protoconid. The entoconid is small and fused to the hypoconulid. The tip of the hypoconulid is missing. The base of the hypoconulid is connected to the entoconid by a small intervening cusp.

The M2 of *Paratritemnodon jandewalensis* (H-GSP 96135, length: 10.4 mm; width: 12.4 mm) is triangular in outline, with a large crescentic protocone, large paraconule and metaconule, and a connate paracone and metacone. The latter cusps are broken off at their base. The stylar shelf is extensive, and the parastyle is small and lies on an anterior extension of the tooth. No enamel is present on the posterobuccal corner of the tooth, but this corner projects labially beyond the anterobuccal corner. The posterior edge of the tooth forms one shearing edge that includes both the postprotocrista and the postmetacrista.

No crown is preserved for M1, but its basal outline suggests that it was similar in shape to the M2 but smaller in size. A single, rounded root is present anterior to the M1, representing the posterior root of the P4. The palate is excavated anterior and posterior to the protocone of the M2. These excavations are embrasure pits for the trigonids of the m2 and m3.

Discussion—*Paratritemnodon jandewalensis* retains three lower molars, as evidenced by the embrasure pits. The holotype retains a metaconid and lacks hypercarnassial specializations. This suggests that it represents a taxon within the proviverrine grade of hyaenodontids (Polly, 1996). Proviverrines are a diverse group of basal hyaenodontids, and many of them are not diagnosed on the basis of elements present in the *P. jandewalensis* (e.g., Gingerich and Deutsch, 1989; Crochet, 1991; Polly, 1996).

Paratritemnodon jandewalensis has a high trigonid, unlike many other proviverrines, such as *Arfia, Paracynohyaenodon, Proviverra,* and *Quercytherium.* The shearing edge on the posterior side of the molars of the new species is mainly developed from the postmetacrista, unlike *Prototomus* and *Paracynohyaenodon. P. jandewalensis* lacks the high parastyle of *Koholia* (see Crochet, 1988). The M1 and M2 are similar in outline, and both teeth have a strong posterior shearing edge, unlike *Prolimnocyon.*

A single creodont, *Paratritemnodon indicus,* has been described from Indo-Pakistan. Specimens of this species are only described from the Subathu Formation of Kalakot (Ranga Rao, 1973; Kumar, 1992). They include the holotype mandible (Ranga Rao, 1973) and an additional mandible and maxilla (Kumar, 1992). Casts of the latter specimens (WIF/A 1102 and WIF/A 103) indicate that *P. jandewalensis* and *P. indicus* are similar in most respects. The differences mentioned in the diagnosis probably do not merit naming of a separate genus. Thus, we refer the new species to *Paratritemnodon.*

In addition to *Paratritemnodon indicus* from Kalakot, the species has also been mentioned in faunal lists for the Ganda Kas Area (West, 1980) and the Locality Chorlakki (Thewissen et al., 1987). West (1980) referred a mandible fragment with one premolar to *Paratritemnodon indicus.* He did not provide an illustration, did not state at which locality in Ganda Kas the specimen (H-GSP 1003) was found, and the specimen is now lost. We are unable to evaluate this record. Several fragmentary teeth of a creodont smaller than *P. jandewalensis* are known from Chorlakki, and these are best identified as *P. indicus* at present.

Order ARCTOCYONIA Van Valen, 1969
Family ARCTOCYONIDAE Giebel, 1855

KARAKIA, gen. nov.

Diagnosis—Elongate p4 with large lingual metaconid. Tribosphenic molars with low cusps, a low trigonid, and a moderately-sized hypoconulid on m3.

Etymology—*Karakia* is named for the town closest to the type locality, Karak.

Discussion—*Karakia* combines ungulate molar morphology (low, bunodont molars, relatively large m3 hypoconulid, elongate p4) with molarized premolars, and its ordinal affinities most likely lie with primitive ungulates, such as arctocyonids (see discussion below).

KARAKIA LONGIDENS, sp. nov.
(Fig. 4C)

Holotype and Only Specimen—H-GSP 97199, mandibular fragment with posterior part of p3, complete p4, m2, and m3, found at H-GSP Locality 9710, Mami Khel Formation of the Banda Daud Shah Area. The crown and roots of the m1 are missing, and its alveoli are resorbed. This leaves a diastema of 1.7 mm between the p4 and m2, which is clearly shorter than the m1 would have been, suggesting that the bone of the mandible was remodelled in life after the loss of the m1. All teeth are worn, and the trigonid of m2 is distorted by crushing. It is unlikely that the elongated tooth (interpreted as p4) is a d4 because the specimen is old (as evidenced by its worn teeth), and the jaw shows that no germ of a tooth is present below the tooth in question.

Diagnosis—No distinction can be made at present between the generic and specific diagnoses.

Distribution—Early Eocene (Mami Khel Formation) of Northern Pakistan.

Etymology—The species indication is based on the main feature that differentiates *Karakia* from other arctocyonids: the length of the premolars (*longus,* long; *dens,* tooth).

Description—Only a small, posterior fragment of the p3 is preserved (width: 0.6 mm). This tooth was double rooted, narrow, and lacked labial and lingual cingula. Only the posterior base of the tooth, the protoconid is preserved, but the cusp was apparently large and triangular and dominated the lateral profile of the tooth. A crest extends distally from its tip, traverses the postcingulid and ends on the posterior edge of the tooth. Lingual to this crest is the metaconid, which is set low on the side of the base of the protoconid.

The p4 (length: 2.7 mm; width 1.0 mm) has a large but low, triangular protoconid. A small cusp occurs on the anterior part of the tooth, and from it a crest ascends the protoconid. This crest reaches the tip of the protoconid and extends lingually from there, ending in a low metaconid. The posterior side of the trigonid is steep and ends in a strongly worn talonid. A large exposed area of dentin indicates that there was a large hypoconid. The posterior side of the p4 shows a clear interdental facet for m1. There are no cingula.

The m2 (width: 1.6 mm) is a low-crowned tooth with the trigonid somewhat higher than the talonid. The trigonid is also somewhat obliquely worn. The protoconid and metaconid are worn, and the latter cusp is damaged. Exposed dentin suggests that these cusps were similar in size. The paraconid is distorted, but it was smaller than the protoconid. Weak crests connect the protoconid to the lingual cusps. The hypoconid was probably the highest cusp on the talonid. The cristid obliqua is weak and extends directly lingual to the trigonid. Another crest extends to the posterolingual side of the tooth, where there is a small facet for the hypoconulid. Immediately anterolingual to this facet is a large facet for the entoconid, which may have matched the hypoconid in size in an unworn tooth. The only cingulum present occurs on the posterior side of the tooth. This cingulum ascends the side of the hypoconulid.

The m3 (length: 3.0 mm; width: 1.8 mm) is low-crowned, with a large protoconid. The paracristid extends lingually from the protoconid. It bends posteriorly on the lingual half of the tooth and reaches the wear facet that indicates the presence of a small paraconid. The paraconid and metaconid may have been similar in size, as suggested by their wearfacets. The hypoconid and entoconid were also similar in size. The cristid obliqua is very weak and extends anterolingually from the hypoconid in the direction of the metaconid. A crest connects the posterior sides of the hypoconid and entoconid. From the approximate midpoint of this crest a second crest extends posteriorly, descending to the hypoconulid. The hypoconulid is low and small, positioned on the posterior side of the tooth. There are no cingula.

Discussion—*Karakia* can be recognized as an ungulate because its molar cusps and trigonids are low, the premolars elongate, and the m3 hypoconulid well developed. *Karakia* is bunodont, and its overall molar morphology resembles arctocyonids, hyopsodontids, and dichobunids. *Karakia* shares with arctocyonids and hyopsodontids the presence of a metaconid on the premolars, and the moderate size (for an ungulate) of the hypoconulid on m3 (this cusp is relatively larger in derived ungulates). In these respects it is unlike dichobunid artiodactyls.

However, unlike condylarths and similar to Eocene artiodactyls, the p3 and p4 are unusually long. The most conservative interpretation of *Karakia* is that it represents an arctocyonid, but it remains possible that it is an extremely primitive artiodactyl.

Condylarths are rare in Indo-Pakistan, and only three quettacyonids, closely related to arctocyonids, have been described. These taxa, *Quettacyon, Sororocyon,* and *Obashtakaia,* appear to all have a short and bulbous p4 (Gingerich et al., 1998a, b), which is very unlike the p4 of *Karakia.* The overall morphology of *Karakia* approximates the Eocene artiodactyls of Indo-Pakistan very well, but it retains a metaconid on the premolars; the loss of this cusp is one of the diagnostic features of early Eocene artiodactyls.

When more material becomes available, comparison of *Karakia* with dichobunids such as *Diacodexis pakistanensis, Chorlakkia hassani,* and *Dulcidon gandaensis* will be especially significant in determining primitive artiodactyl dental morphology. Some Indo-Pakistani dichobunids are known from fragmentary material only and cannot be directly compared to *Karakia.* This makes the identification of these taxa, such as *Dulcidon,* uncertain, and the taxon has previously been thought to be a hyopsodontid (Dehm and Oettingen-Spielberg, 1958), a paroxyclaenid (Van Valen, 1965) and a dichobunid (Thewissen et al., 1987). *Karakia* is not conspecific with any of the described condylarths or dichobunids from Indo-Pakistan, as it is substantially smaller than any of them.

Order ARTIODACTYLA Owen, 1848
Family DICHOBUNIDAE Gill, 1872
Genus *DIACODEXIS* Cope, 1882

DIACODEXIS PAKISTANENSIS Thewissen et al., 1983
(Fig. 4D)

Referred Specimens—H-GSP 97148, left partial p3 and p4–m3 from H-GSP Locality 9710; and H-GSP 97212, right M1–3 from H-GSP Locality 9712, Mami Khel Formation of Banda Daud Shah Area.

Description—In H-GSP 97148, the anterior portion of the p3 is missing, but its width can be measured (1.6 mm). The p4 has a deep groove on the anterolingual side exposing dentine, and there is a small cusp on the anterolingual part of the cingulid (length: 3.6, width: 2.2). The molars are similar to the type material (Thewissen et al., 1983) in the small size of the paraconid (decreasing from m1 to m3), the well-developed talonid basin, and the long and narrow talonid of m3 with a distinct hypoconulid lobe (m1 length: 3.5 mm; width: 2.4 mm; m2 length: 3.7 mm, width: 3.0 mm; m3 length: 5.0 mm; width: 3.3 mm). The labial cingulid is weak on all teeth.

In H-GSP 97212, the paracone and labial portion of the metacone are missing in the M1 (length: 3.0 mm). The M2 and M3 are similar in size and shape (M2 length: 4.0 mm, width: 4.9 mm; M3 length: 3.9 mm, width: 5.2 mm). The metacone is smaller than the paracone and decreases in size from the M1 to the M3. All conules except the paraconule on the M3 are worn. The parastyle of the M3 is stronger than that of the M2, and there is a small metastyle on the posterolabial side of the M3.

Discussion—H-GSP 97148 and 97212 were collected at two new localities of the Mami Khel Formation in the Banda Daud Shah Area. Previously *Diacodexis pakistanensis* was known from H-GSP Locality 300 (Barbora Banda) of the Banda Daud Shah Area (Thewissen et al., 1983) and GSP-UM Locality Chorlakki of Kohat District (Thewissen et al., 1987). *D. pakistanensis* has not been found east of the Indus River in Pakistan. Specimens attributed to *Diacodexis* have been described from Kalakot, India (Kumar and Jolly, 1986), but these are more likely to represent an adapid (see under discussion of *Panobius*).

Thewissen et al. (1983) compared Pakistani *Diacodexis* to North American and European forms. The Pakistani specimens are generally similar to European taxa with the exception of *D. gazini,* but differ from North American *Diacodexis* in the narrow width of the lower molars and the distinct triangular shape of the upper molars. Further studies will determine whether Pakistani and (some) European *Diacodexis* should be separated generically from North American species.

There is evidence of a large dichobunid in the Eocene of the Ganda Kas Area. Two specimens, each consisting of a partial upper tooth, are known for this species. One partial upper molar was described by West (1980) as *Gobiohyus* (H-GSP 1974D). This specimen bears sharp, well-defined crests, unlike *Gobiohyus,* and is in most respects similar to large North American dichobunids such as *Wasatchia* and *Bunophorus.* A newly recovered specimen (H-GSP 96487 from Locality 9613, width 8.7 mm; Fig. 4I) is a partial left P4 with well-defined and sharp crests. At present, we consider this specimen conspecific with H-GSP 1974D.

Family RAOELLIDAE Sahni et al., 1981
Genus *KHIRTHARIA* Pilgrim, 1940

KHIRTHARIA DAYI Pilgrim, 1940
(Fig. 5D)

Referred Specimens—H-GSP 92009, right maxillary fragment with P3–M3; H-GSP 92036, right m3 used for stable isotope analysis (an epoxy cast replaces the specimen); H-GSP 96350, right maxillary fragment with lingual margin of M1 and M2–3; and H-GSP 96360, right partial mandible with m1–3, including the ascending ramus. All specimens are from H-GSP Locality 62, Kuldana Formation of the Ganda Kas Area.

Description—The anterolingual margin of H-GSP 92036 is missing (width: 6.3 mm). The metaconid is slightly larger than the protoconid and the two cusps are joined by the protocristid. The hypoconid is larger than the entoconid and joined by the postcristid. There is a distinct hypoconulid lobe. The enamel is slightly crenulated, and there is a pronounced labial cingulid below the junction of the protoconid and hypoconid.

In H-GSP 96350, only a lingual enamel fragment of the M1 is preserved, and the remaining molars are damaged labially. The M2 (length: 7.3 mm) and the M3 (length: 7.8 mm) are slightly bilophodont and square in outline. The M2 is slightly smaller than the M3. In the M3, the protocone is larger than the hypocone, and the paracone is larger than the metacone (as seen in the M3). The cingulum is weak; it is best developed on the posterior margin of the M3 and on the lingual margin between the protocone and hypocone. The enamel is slightly crenulated.

The molars of H-GSP 96360 increase in size from the m1 to the m3 (m1 length: 7.2 mm, width: 5.6 mm; m2 length: 8.3 mm, width: 6.9 mm; m3 length: 11.9 mm, width: 8.0 mm). The metaconid is larger and higher than the protoconid, and these cusps are joined by the protocristid. The cristid obliqua, postcristid, and entocristid outline a square talonid basin. The hypoconid is larger than the entoconid, and in the m3, there is a distinct hypoconulid lobe. There is a labial cingulid on all molars, and the enamel is crenulated.

Discussion—West (1980) synonymized the species *Bunodentus inflatus* with *Khirtharia dayi,* and this synonymy was followed by Russell and Zhai (1987). Alternatively, Kumar and Sahni (1985) proposed the combination *Khirtharia inflatus* for Indian artiodactyls described as *Khirtharia dayi* by Sahni and Khare (1973) and *Bunodentus inflatus* by Ranga Rao (1972). Kumar and Sahni (1985) retained the Pakistani type material of *K. dayi* as distinct from the Indian material. We agree with the latter opinion and recognize two described species of *Khirtharia*: *K. dayi* and *K. inflata.*

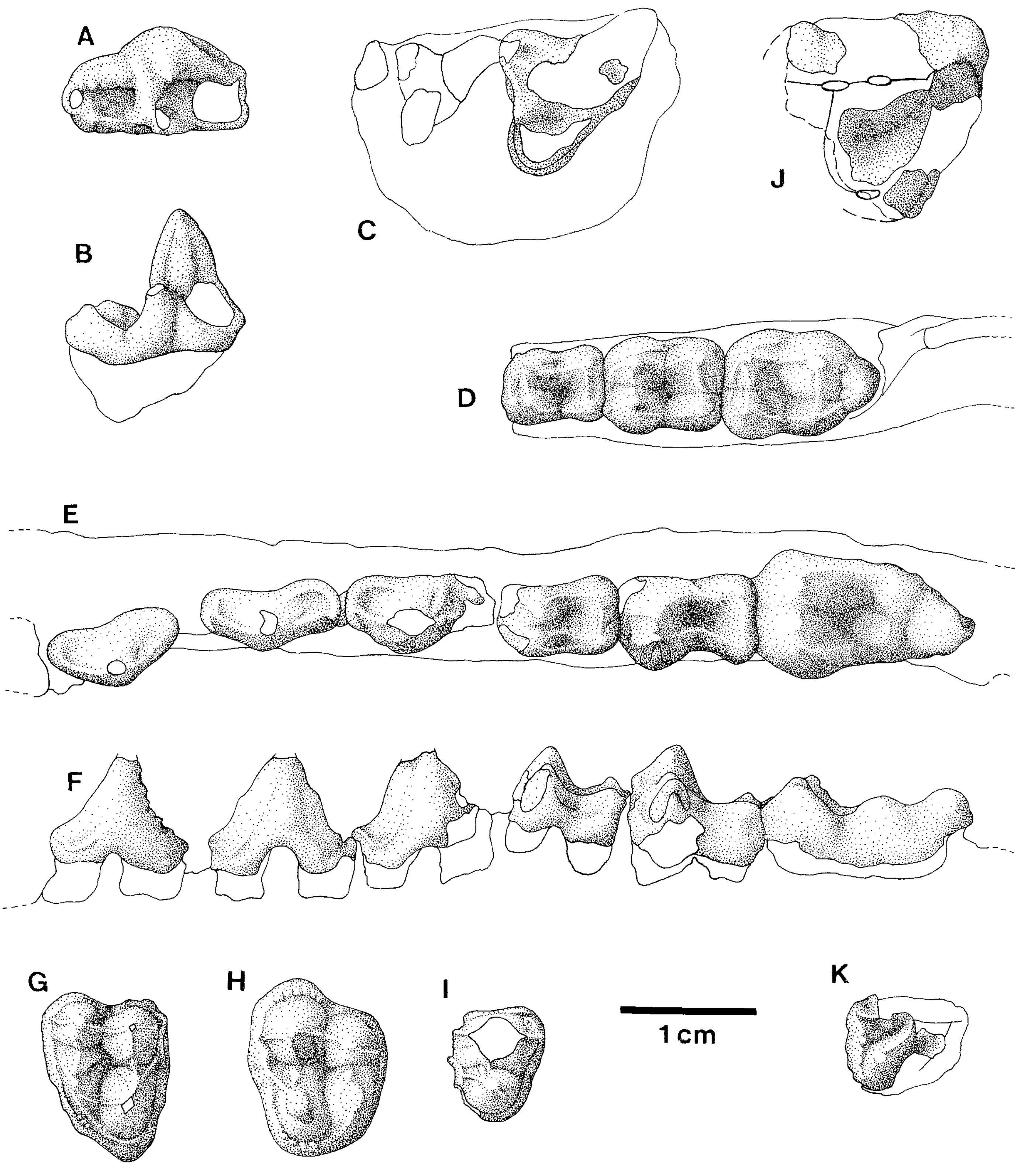

FIGURE 5. Creodonts, artiodactyls, and perissodactyls from the Kuldana and Chorgali formations. **A**, **B**, *Paratritemnodon jandewalensis*, sp. nov., holotype left mx (H-GSP 96140) in occlusal and lingual view. **C**, *P. jandewalensis*, occlusal view of left maxilla with base of M1 and M2 (H-GSP 96135). **D**, *Khirtharia dayi*, occlusal view of right m1–3 (H-GSP 96360). **E**, **F**, *Kunmunella transversa*, occlusal and labial view of left p2–m3 (H-GSP 97187). **G**, *Kunmunella transversa*, occlusal view of right M2 (H-GSP 97184). **H**, *Khirtharia aurea*, sp. nov., occlusal view of holotype left M3 (H-GSP 97192). **I**, Occlusal view of left P4 of an unidentified large dichobunid (H-GSP 96487). **J**, Occlusal view of left Dx of an unidentified large perissodactyl (H-GSP 96456). **K**, cf. *Kalakotia*, occlusal view of right Mx (H-GSP 96455), enamel is only preserved on the posterolingual side.

Khirtharia dayi can be distinguished from *K. inflata* by the change in the quadrate shape of its upper molars: from M1 to M3 the hypocone decreases in size giving the molars an increasingly rectangular shape. The hypocone remains prominent in *K. inflata* and the molars remain square. Secondly, *K. dayi* material exhibits weak parallel proto- and metacristae; these are absent in *K. inflata.* The most striking distinction between these species is the inflation of individual cusps in *K. inflata.* Distinctions in the lower molars are minor. In general, the cusps of *K. inflata* are more inflated. Other discriminating features include the greater size difference in the protoconid and metaconid in *K. dayi;* the presence of a labial cingulid in *K. dayi* (absent in *K. inflata*); and the stronger crenulation of enamel in *K. dayi.*

KHIRTHARIA AUREA, sp. nov.

(Fig. 5H)

Holotype—H-GSP 97192, left M3 found at H-GSP Locality 9709, Chorgali Formation, Gali Jhagir Area.

Referred Material—H-GSP 97188 left M1, paracone missing; and H-GSP 97191, m3 talonid, from the type locality.

Range and Distribution—Middle Eocene (Chorgali Formation) of Northern Pakistan.

Diagnosis—*K. aurea* differs from *K. dayi* and *K. inflata* in being larger and in having stronger cingula. Hypocone smaller than the protocone. Cusps well-developed, but less inflated than in *K. inflata.*

Etymology—*aureus* (fem: aurea) is Latin for golden, and refers to the color of the sediment at the type locality.

Description—The two upper molars are large, subtriangular, and bunodont. In H-GSP 97192 (length: 10.5 mm; width: 14.0 mm), the paracone is the largest cusp and is slightly labial to the metacone. Very weak crests extend from the lingual to the labial cusps and between the para- and metacone. A weak preparacrista is also present. On the lingual side, the protocone is more lingual than the much smaller hypocone. While similar in basal outline to the paracone, the protocone is lower in height. The cingulum is continuous except at the postero-lingual margin of the hypocone.

In H-GSP 97188, the metacone is slightly smaller in basal outline than the protocone but is greater in height. There is a slight postmetacrista that terminates in a cingulum. The cingulum is nearly continuous. The cingulum thickens and is crenulated between the proto- and hypocone, and between hypo- and metacone. The cingulum is barely distinguishable on the posterolingual side of the hypocone. The protocone is the largest cusp that is preserved. There is considerable wear on the tip of the protocone and on the postprotocrista. The hypocone is significantly smaller than the protocone and set labially, which gives the tooth a slightly subtriangular shape. There are two conules labial to the hypocone, the metaconule and another anterior to the metaconule. A pronounced wear facet is visible on the posterior margin of the protocone and the anterior margin of the hypocone. This tooth is smaller than H-GSP 97192 (width: 9.6 mm) and may represent a M1.

The lower molars are known only from a talonid, but it shows that lower molars are as bunodont as the upper molars. H-GSP 97191 (width: 7.0 mm) preserves the posterior margin of the hypoconid, entoconid, and the hypoconulid lobe. The hypoconid appears to be significantly larger than the entoconid. The hypoconulid lobe is distinct, with a single cusp that is placed close to the entoconid and hypoconid. A weak crest connects the entoconid and hypoconid, but the hypoconulid lacks any crests to the more anterior cusps.

Discussion—Few specimens of *Khirtharia aurea* are available, but they clearly indicate the presence of a *Khirtharia* species different from the known taxa in the Chorgali Formation. At present, size distinguishes the new species best from the two other species. *K. aurea* is approximately 30% larger than the two other species in its genus. An important difference from *K. inflata* is the lack of inflated cusps.

The three species of *Khirtharia* and the monotypic *Metkatius* represent a small, bunodont radiation of raoellids. The remaining genera of raoellids (*Haquiena, Indohyus,* and *Kunmunella*) are discussed below.

Genus *KUNMUNELLA* Sahni and Khare, 1971

KUNMUNELLA TRANSVERSA Kumar and Sahni, 1985

(Fig. 5E–G)

Referred Specimens—H-GSP 97184 right M2; and H-GSP 97187 left mandible with p2–m3. The dentary, the m3, and the trigonid of m2 have undergone chemical alteration to a soft ‘‘chalky’’ mineral that makes the morphology difficult to discern; H-GSP locality 9709, Chorgali Formation, Gali Jhagir Area.

Description—H-GSP 97184 (Fig. 5G) is subtriangular in shape and somewhat bilophodont with crests running from the protocone to the paracone, and from the hypocone to the metacone. The paracone and metacone are approximately equal in size with the metacone slightly labial to the paracone. There is a small parastyle on the anterolabial part of the cingulum, and the metastyle is virtually absent. The paraconule is weak, and the metaconule is barely distinguishable. The protocone is larger in basal outline but lower in height than the paracone and metacone. The hypocone is the smallest cusp, and its small size gives the tooth an overall subtriangular shape. A crest extends between the posterior cingulum below the metaconule to the hypocone and terminates at the lingual cingulum.

The premolars of H-GSP 97187 increase in size and complexity of the cingulid morphology posteriorly (p2 length: 9.1 mm, width: 3.9 mm; p3 length: 9.7 mm, width: 4.3 mm; p4 length: 11.1 mm, width: 5.1 mm). The p2 has a weak labial cingulid, while p3 and, in particular, p4 have a distinct labial cingulid with a small cusp on the anterolabial margin. This cusp is completely worn on p3. The posterolabial cingulid is also well developed. There is a distinct lobe on the posterior margin of the p4, and it includes a small metaconid. Each of the premolars exhibits apical wear. There is also a wear facet on the posterolingual side of the p4 adjacent to the crest that extends between the protoconid and the metaconid.

Like the premolars, the molars increase in size posteriorly (m1 length: 7.9 mm, trigonid width: 4.8 mm, talonid width: 5.6 mm; m2 length: 9.4 mm, trigonid width: 6.2 mm, talonid width: 6.2 mm; m3 length: 14.9 mm, trigonid width: 8.4 mm; talonid width: 6.7 mm). On the trigonid, the metaconid is the largest cusp. The protoconid is smaller than the metaconid and is deeply worn on the m1 and m2; wear cannot be determined on the m3. The metaconid and protoconid are poorly separated. The trigonid is much higher than the talonid, especially on the m2. On the talonid, the hypoconid is the largest cusp. The hypoconid and entoconid are connected by a crest. The cristid obliqua terminates medially below the junction of the protoconid and metaconid. The m3 is similar to the m2 but shows a distinct hypoconulid lobe.

Discussion—In order of increasing size, the lophodont genera of raoellids are: *Haquiena, Kunmunella,* and *Indohyus. Haquiena* is known from a single jaw from the Ganda Kas Area (Dehm and Oettingen-Spielberg, 1958). *Haquiena* can be identified as a raoellid and not a dichobunid because it lacks a paraconid and has somewhat connate proto- and metaconid. Two isolated molars referred to this taxon by Sahni and Khare (1973) are larger than *Haquiena* and are more likely referable to *Indohyus* or *Kunmunella.*

Indohyus and *Kunmunella* differ mainly in the shape of M2 and M3: square in the former, rectangular (short anteroposteriorly) in the latter. The rectangular shape of H-GSP 97184 leads us to refer the Chorgali material to *Kunmunella.* According to Kumar and Sahni (1985), there are two species of *Kunmunella, K. kalakotensis* and *K. transversa.* These are best distinguished on the basis of the shape of P4. Molar differences that can be used to identify the Chorgali material are minor, but suggest that this material is best identified as *K. transversa.*

Indohyus is known mainly from Kalakot where a single species appears to be present (Russell and Zhai, 1987). Thewissen et al. (1987) described fragmentary material from Chorlakki that is probably referable to *Indohyus indirae* and named a new species of this genus, *I. major,* based on very fragmentary material of greater size.

Order PERISSODACTYLA Owen, 1848
Family BRONTOTHERIIDAE Marsh, 1873

EOTITANOPS DAYI Dehm and zu Oettingen-Spielberg, 1958

Referred Specimens—H-GSP 92089, right maxilla with badly damaged M2 and M3, H-GSP Locality 64; H-GSP 96457, mandibular fragment with symphysis, root of left p1 and crown of p2, H-GSP Locality 9613. H-GSP 97028, paralophid of lower molar, H-GSP Locality 227. Kuldana Formation of the Ganda Kas and Thatta areas.

Description—The new specimens are fragmentary and do not add to our knowledge of the morphology of *Eotitanops.*

Discussion—Brontotheres are some of the most common fossils in Eocene deposits of northern Pakistan. The largest sample comes from the Ganda Kas Area where 11 fragmentary specimens of *Eotitanops* have been described (Dehm and Oettingen-Spielberg, 1958; West, 1980). Thewissen et al. (1987) described *Eotitanops* from Chorlakki.

PAKOTITANOPS LATIDENTATUS West, 1980

Referred Specimens—H-GSP 96034, right maxilla with worn M2 and small root fragment of M3, H-GSP Locality 9206; H-GSP 97114, left P3 with labial cusps missing, and fragments of DP4 and P4, attached to the maxilla, H-GSP Locality 9205. Kuldana Formation of the Ganda Kas Area.

Description—P3 (length: 17 mm) has a strong protocone from which the paracrista extends anterolabially. There is no metacrista. The anterior wall of the protocone slopes more than the posterior wall, causing the protocone to be located on the anterior part of the tooth. Anterior and posterior cingula are strong.

Most of the morphology of the upper molar (H-GSP 97114, length 36 mm, approximate width 41 mm) is obscured by damage or wear, but it is clear that the ectoloph was strong and W-shaped and that the protocone was higher than the hypocone.

Discussion—West (1980) listed a number of features that distinguish *Pakotitanops latidentatus* from *Eotitanops dayi.* All were based on a single specimen of the former (H-GSP 1050), a damaged and very worn M2. Given that the material of *Eotitanops dayi* is also poorly preserved, we cannot evaluate most of these characters. It is clear that *Pakotitanops* is distinctly larger than *Eotitanops dayi* and that its teeth are wider. The third Indo-Pakistani brontothere, *Mulkrajanops moghliensis* Kumar and Sahni (1985) is also known from a single specimen only. *Mulkrajanops* is smaller than *Eotitanops dayi.* The new P3 of *Pakotitanops* does differ morphologically from *Eotitanops* (GSP-UM 2579, Thewissen et al., 1987) in being longer lingually.

Family LOPHIALETIDAE Matthew and Granger, 1925

cf. *KALAKOTIA*
(Fig. 4K)

Referred Specimen—H-GSP 91046, right maxilla with P4, H-GSP Locality 62 (Ganda Kas Area); H-GSP 96455, right upper molar, H-GSP Locality 9613 (Thatta Area). Kuldana Formation.

Description—H-GSP 91046 is a maxilla with three roots for P3, and the base of a worn P4. Of this tooth only a rim of enamel remains, and the entire surface of the tooth is worn flat (length: 6.6 mm, width: 8.6 mm).

The posterior part of an upper molar (H-GSP 96455) represents another specimen of a small tapir (approximate width: 7.9 mm) with enamel lacking on the anterior part of the tooth. This specimen shows a sharp metaloph and lacks a metaconule. The metaloph is oriented strongly obliquely and reaches the ectoloph anterior to the metacone. Fragments of the paraloph are preserved anterior to the metaloph, and the paraloph may be shorter than the metaloph. The paracone and metacone are damaged, but it is clear that they were labial in position. The metacone is not lingually displaced. A short crest extends from the posterolingual corner of the paracone to the center of the tooth, and another short crest descends in a similar position from the ectoloph posterior to the metacone. This part of the ectoloph bends labially and reaches the base of the tooth. A cingulum is present on the posterior side of the tooth.

Discussion—Two families of small tapiromorphs have been described from Indo-Pakistan. Isectolophids are known from Kalakot (Sahni and Khare, 1971), Chorlakki (Thewissen et al., 1987) and from Barbora Banda (Maas et al., 2001). Ranga Rao (1972) described the lophialetid *Kalakotia simplicidentata* from Kalakot. The Kalakot sites also yielded taxa that we consider junior synonyms of *Kalakotia* (following Russell and Zhai, 1987, and Thewissen et al., 1987): *Aulaxolophus quadrangularis, Chasmotherium mckennai,* and *Schlosseria radinskyi.* Larger perissodactyl taxa (discussed below) have been referred to helaletids, hyrachyids, and hyracodontids.

H-GSP 96455 has a strong ectoloph with poorly defined paracone and metacone, lacks conules, and retains sharp transverse lophs. This indicates that the specimen is not an isectolophid. The posterior part of the ectoloph of depertellids is weak and the metacone lingually displaced, unlike H-GSP 96455. The metaloph of helaletid molars touches the centrocrista close to the metacone, giving rise to a long metacone and postmetacrista. This is unlike H-GSP 96455.

Overall, H-GSP 96455 is similar to the lophialetid *Kalakotia,* but differs in having narrower teeth, and in having accessory crests that descend from the lingual side of the ectoloph. These are minor differences, and the specimens belong to a species that is closely related to *Kalakotia.* The material at hand is too incomplete to merit formal diagnosis of a new species or an evaluation of its generic status.

Family HELALETIDAE Osborn, 1892

JHAGIRILOPHUS, gen. nov.

Diagnosis—Large tapiromorph (sensu Froelich, 1999) with lingually displaced metacone, complete cingulum labial to the metacone, and well-developed protoloph, metaloph, ectoloph, and parastyle. *Jhagirilophus* lacks conules and a cingulum labial to the paracone. The paracone and metacone are not merged into the ectoloph.

Etymology—Named for the type locality, which is near the village of Gali Jhagir in the Khair-e-Murat Range. The genus name combines this geographic designation with -lophus, a common suffix for lophodont tapiroids.

Discussion—*Jhagirilophus* is a large tapiromorph perisso-

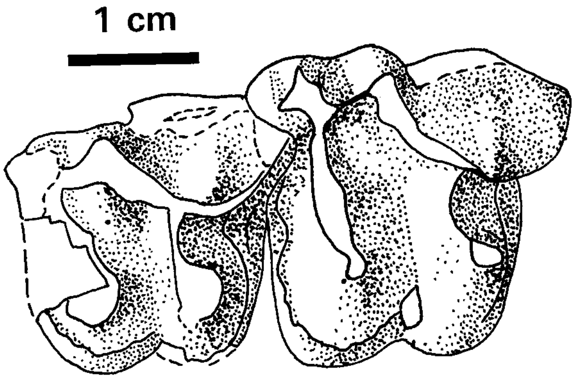

FIGURE 6. *Jhagirilophus chorgalensis,* sp. nov., occlusal view of holotype left M1–2 (H-GSP 97193) from the Chorgali Formation.

dactyl. It is similar to North American *Hyrachyus* in most respects but differs in the presence of a cingulum labial to the metacone. Absence of this cingulum was considered an important feature in diagnosing *Hyrachyus* from helaletids by Radinsky (1963). Presence of this cingulum in *Jhagirilophus* leads us to classify it, conservatively, as a helaletid.

JHAGIRILOPHUS CHORGALENSIS, sp. nov.

(Fig. 6)

Holotype—H-GSP 97193, left M1–2, and several enamel fragments of the same specimen. Locality 9709, Chorgali Formation, near Gali Jhagir, Khair-e-Murat Range.

Referred Specimen—H-GSP 97142, fragments of upper molar, possibly M3 (as based on its high crown), H-GSP Locality 9709.

Diagnosis—No distinction can be made at present between the generic and specific diagnoses.

Distribution—Middle Eocene (Chorgali Formation) of Northern Pakistan.

Etymology—The species indication is derived from the name of the formation that yielded the specimens, the Chorgali Formation.

Description—The M1 bears four cusps and lacks conules (length: 20.7 mm; width: 19.2 mm). The protocone is worn, but similar in size to the hypocone. From these lingual cusps, two crests extend labially. The anterior of these, the protoloph, reaches the labial side of the tooth anterior to the paracone. The metaloph reaches the centrocrista just anterior to the metacone. The M1 preserves the base of a large parastyle. The paracone is a large cusp, with convex sides that do not blend into the ectoloph. The metacone is more lingual on the tooth than the paracone. Just like the paracone, the metacone is not subsumed into the ectoloph. The ectoloph extends posterolabially from the metacone. The ectoloph of the M1 is continuous with the ectoloph of the M2. The cingula of the M1 are partly damaged; they are retained lingual to the protocone, labial to the metacone, and posterior to the hypocone. There was no cingulum labial to the paracone.

M2 is similar to M1 in all respects but is larger and more complete (length: 23.4 mm; width: 24.2 mm). The protoloph reaches the ectoloph approximately halfway between the parastyle and paracone, and the parastyle consists of a U-shaped crest that extends labially from the M1 and then bends lingually to continue as the ectoloph. The ectoloph then bends labially again crossing the paracone. The M2 has cingula in the same position as the M1 and also has a complete anterior cingulum. It lacks a cingulum lingual to the hypocone.

Discussion—The larger ceratomorph perissodactyls of the Indian continent that we consider valid are: *Teleolophus daviesi, Triplophus kalakotensis, ''Fostercooperia'' jigniensis,* and *Hyrachyus asiaticus.* Currently, the familial attribution of these is disputed.

Dehm and Oettingen-Spielberg (1958) described a single lower molar as ?*Teleolophus daviesi* and referred it to Helaletidae. This taxon is now generally considered a deperetellid (e.g., Russell and Zhai, 1987; Prothero and Schoch, 1989) and is probably not generically distinct from *Teleolophus* (Radinsky, 1965). Large ceratomorph perissodactyls are rare in the vicinity of Ganda Kas, but a deciduous premolar (H-GSP 96456, Fig. 4J) probably pertains to a ceratomorph.

Khan (1973) described a mandible with two teeth as the hyracodontid *Prothyracodon kalakotensis,* a genus previously synonymized with *Triplopus* by Radinsky (1967). Sahni and Khare (1973) described *Fostercooperia jigniensis* and referred it to the hyracodontids. Lucas et al. (1981) doubted the generic attribution of this species, and Russell and Zhai (1987) doubted its familial relation. Thewissen et al. (1987) referred some poorly preserved material from Chorlakki to this species.

Ranga Rao and Obergfell (1973) described *Hyrachyus asiaticus* from Kalakot and referred it to the Helaletidae. This generic attribution is followed by most authors, but *Hyrachyus* is sometimes placed in Hyrachyidae, Hyracodontidae, or Rhinocerotoidea (Prothero and Schoch, 1989; McKenna and Bell, 1997). Russell and Zhai (1987) attributed some unspecified Pakistani material to cf. *Hyrachyus asiaticus,* but we cannot evaluate this claim.

Direct comparisons of upper molars can be made between *Jhagirilophus* and two of these large ceratomorphs: *''Fostercooperia'' jigniensis* and *Hyrachyus asiaticus.* In both species the paracone and metacone are fused into the ectoloph, unlike *Jhagirilophus.* The other two large Indo-Pakistani ceratomorphs are, or are similar to, hyracodontids. *Jhagirilophus* differs from hyracodontids and other rhinocerotoids, in being low crowned and having weakly developed lophs (Prothero et al., 1986).

Gabunia (1999) described *Subhyrachyus tshakpaktasensis* from the early to middle Eocene of the Zaisan Basin of Kazakhstan as a hyrachyid. Unlike other *Hyrachyus* and *Jhagirolophus,* the metacone of *Subhyrachyus* is not lingually displaced, casting some doubt on its familial attribution.

DISCUSSION

Our knowledge of the Eocene mammals of Indo-Pakistan has gradually increased from the time when Pilgrim described the first specimens in 1940. In spite of this, fewer than 70 land mammal species are known (Table 1), and our understanding of these communities does not come close to our knowledge of the Eocene faunas of Europe and North and South America. The composition of the Indo-Pakistani faunas differs greatly from that of Eocene faunas from the rest of Asia (Russell and Zhai, 1987; Meng and McKenna, 1998; Ting, 1998), suggesting that Indo-Pakistan was faunally not a part of Asia in the early to middle Eocene. New collections, such as those described here, can be used to address the faunal dynamics of Indo-Pakistan in comparison with the rest of the world.

Early Tertiary Indo-Pakistani land mammals are known mainly from a band of outcrops that extends east to west across the following regions (Fig. 1): Karak and Kohat District in North-West Frontier Province (NWFP) of Pakistan, Pakistani Punjab, and the Indian state of Jammu and Kashmir (J&K). Here, we discuss and correlate temporally faunas from the following areas: the Mami Khel Formation of the Banda Daud Shah Area (Karak District), the Mami Khel Formation of the Locality Chorlakki (Kohat District), the Kuldana Formation of the Ganda Kas Area (Punjab), the Chorgali Formation of H-

GSP Locality 9709 near Gali Jhagir (Punjab), and the Subathu Formation of the Kalakot Area (J&K).

Means of Correlation—Most of the Paleogene sedimentary sequences of western Indo-Pakistan consist of a series of interbedded non-marine and marine strata. Unfortunately, the marine units that bracket the terrestrial deposits lack important biostratigraphic markers such as planktonic Foraminifera (e.g., Fatmi, 1973). Therefore, most attempts to correlate deposits and infer a chronology for the Eocene localities of Indo-Pakistan have been based on lithostratigraphy, biostratigraphy (benthic Foraminifera and mammals), or comparison of local sea level change with global eustacy.

Benthic Foraminifera abound in some of the marine rocks and have been used extensively in chronological correlations of these deposits. Concerning the formations that are the subject of this paper, Bajpai and Gingerich (1998) used benthos to determine the age of the cetaceans *Himalayacetus* (from the Subathu Formation of Himachal Pradesh, India) and *Pakicetus*. They based their conclusions on the benthic identifications of Mathur (1980 for 1978) and the benthic stratigraphic framework of the Western Tethys published by Serra-Kiel et al. (1998). According to Bajpai and Gingerich (1998), *Himalayacetus* was recovered from Subathu Formation subzone IIIc of Mathur (1980 for 1978). This zone is bracketed by beds containing *Nummulites atacicus* (Mathur, 1980 for 1978). Bajpai and Gingerich (1998) use this occurrence to constrain the age of *Himalayacetus* to fall within Serra-Kiel's (1998) Shallow Benthic Zone (SBZ) 8 (early Ypresian). For *Pakicetus*, found in the Kuldana Formation (our Mami Khel Formation) at the Locality Chorlakki, Bajpai and Gingerich (1998) cite the presence of *Orbitolites complanatus* (?SBZ 12–16: latest Ypresian to early Lutetian) in the Shekhan Formation (which underlies the Kuldana at Chorlakki) and of *Assilina exponens* (SBZ 14: middle Lutetian) in the Kuldana Formation near the town of Murree (Fig. 1, more than 50 km from Chorlakki) as evidence that *Pakicetus* is Lutetian in age, and therefore younger than the Indian *Himalayacetus*.

The use of these benthic Foraminifera for biostratigraphy is problematic. According to Fatmi (1973) *Nummulites atacicus* and *Orbitolites complanatus* are found in association in the Shekhan Formation, and Cotter (1933) found *Assilina exponens* and *Nummulites atacicus* together in the Kohat Formation (which overlies the Kuldana Formation in the Kala Chitta Hills). Furthermore, Mathur's recent paper (1997) omits *N. atacicus* altogether as an age marker in the Subathu Formation, and the benthic assemblage listed in that paper implies an SBZ 10 (middle to late Ypresian) age for *Himalayacetus*. Comparison of Mathur's Subathu benthic biozonation (1997) with Serra-Kiel's et al. (1998) biochronology shows other problems, such as the occurrence of *Miscellanea miscella* (SBZ 4–5) in beds overlying *Daviesina ruina* (SBZ 7–8). These discrepancies may have been caused by a variety of problems that we cannot evaluate at present. However, the occurrence of benthos is a better proxy for local depositional environments than for chronological correlations (Van Gorsel, 1988; Emery and Meyers, 1996). Taken together, these considerations lead us to be wary of chronological correlations based on benthos in subhimalayan deposits.

Gingerich and co-workers (Gingerich et al., 1995, 1997; Bajpai and Gingerich, 1998) attempted to constrain the ages of Eocene formations of Indo-Pakistan by interpreting documented transgressive-regressive sequences in the context of the global eustatic sea level chart (Vail et al., 1977; Haq et al., 1987, 1988). However, identification of global change in small depositional basins is dependent on the consideration of local factors (such as tectonism, subsidence, and climate) apart from global eustacy (Miall, 1997). Pivnik and Wells (1996) proposed that the Early Tertiary record of transgressions and regressions in northern Pakistan and India is more controlled by Himalayan tectonism than by global eustacy. This calls into question the use of the sea level charts for determining the chronology of these depositional sequences.

We feel that benthic Foraminifera and the pattern of transgressions and regressions do not yield reliable means of chronologic correlation of the Eocene sediments south of the Himalayas, and consider the mammals as the best guide to the relative age of the rocks. Ours is not the first attempt to correlate Eocene Indo-Pakistani rocks on the basis of their mammal faunas. Based on much smaller samples, previous authors have arrived at very different correlations. With our improved dataset, we will develop a working model for temporal correlations based on mammals by discussing each of the faunas individually and integrating them into a growing biostratigraphic framework. It is clear that temporal differences are not the only factors that influence presence or absence of mammal taxa, and that ecological factors play an important role. Below, we will interpret the differences between Locality 62 and other Ganda Kas localities as a result of the local environment, not time. Furthermore, we believe that it is possible to interpret several specific faunal differences among areas as the result of faunal evolution over time. These faunas can thus be used for biochronology.

The Ganda Kas Fauna—Vertebrates are found in a number of lithologies in the Kuldana Formation at the localities near Ganda Kas (and the geographically proximate areas of Jhalar and Thatta North, Thewissen et al., 1998). Lithologies differ, but all generally represent channel and floodplain deposits that were part of the same depositional system. One of the most important sites is H-GSP Locality 62. This locality is comprised of one thick channel-form conglomerate that has abundant vertebrate fossils. Sedimentological data suggest that Locality 62 probably sampled an abandoned channel with standing water (Aslan and Thewissen, 1996). This differs from other sites which represent a mix of fluvial environments. Differences in fauna are caused by differences in depositional environment, and we have treated Locality 62 separately in Table 1. Unlike all other localities, pakicetid cetaceans and anthracobunid proboscideans are the most abundant mammal taxa and fish (catfish, channids) and aquatic trionychid turtles abound.

Following West (1980), we consider that Locality 62 and the other Ganda Kas sites with terrestrial mammals have all sampled the same time interval and assume that minor differences in faunal composition at different localities are the results of differences in habitat of the mammals and sampling. Excluded from this generalization are the faunas from nearshore marine facies of the Ganda Kas Area, including those that yield *Ambulocetus* (see Thewissen et al., 1996). These facies overlie the freshwater beds and fall outside the scope of this review, which is mainly an attempt to correlate areas yielding land mammals.

The Kalakot/Gali Jhagir Fauna—The Kalakot mammal fauna of the Subathu Formation consists of taxa that are recovered from a series of localities in Jammu, close to the Pakistani border. Kumar (1998) published the most recent faunal list for these sites. Srivastava and Kumar (1996) discussed the taphonomy, concluding that minor differences in faunal composition between localities are probably due to taphonomic factors, and that all localities represent a coeval fauna.

At the familial level, the Ganda Kas Fauna and the Subathu fauna are similar: raoellids and chapattymyids dominate, and anthracobunids are also common. Lophialetids and brontotheres occur in both areas, with the former more common in Kalakot and the latter more common in Ganda Kas. Pakicetids are rare in Kalakot, as they are in all Ganda Kas localities except for Locality 62. Small dichobunids are rare or absent from both faunas.

At the generic and specific level, there are few similarities

TABLE 2. Working hypothesis for faunal succession in Indo-Pakistan, and suggested correlations to other continents. Only taxa critical to determine temporal relations are listed. Common taxa in Indo-Pakistani faunas are indicated with an asterisk.

Indo-Pakistan	Asian Mainland	North America
KALAKOT/GALI JH. FAUNA	IRDINMANHAN	BRIDGERIAN
*Raoellidae (*Indohyus, Kunmunella, Khirtharia inflata*)	Helohyidae	Helohyidae
*Chapattimyidae		
Hyracodontidae	Hyracodontidae	
Jhagirilophus	*Hyrachyus*	*Hyrachyus*
*Lophialetidae	Lophialetidae	
	Deperetellidae	Isectolophidae
Isectolophidae (rare)		
Brontotheriidae	Brontotheriidae	Brontotheriidae
GANDA KAS FAUNA	HEPTODON INTERVAL ZONE	LATE WASATCHIAN
*Raoellidae (*Khirtharia dayi*)		BUMBANIAN
small Dichobunidae (rare)		*Bunophorus, Wasatchia*
*Chapattymyidae		
Lophialetidae	Helaletidae	Helaletidae
Deperetellidae		Deperetellidae
	Isectolophidae	Isectolophidae
*Brontotheriidae		Brontotheriidae
BANDA DAUD SHAH FAUNA	HOMOGALAX/ORIENTOLOPHUS	EARLY/MIDDLE WASATCHIAN
	INTERVAL ZONE	BUMBANIAN
**Diacodexis*		*Diacodexis*
*Isectolophidae	Isectolophidae	Isectolophidae
Plesiadapidae	Plesiadapidae	

between the Ganda Kas and Kalakot faunas (Table 2). The raoellids *Indohyus, Kunmunella* and *Khirtharia inflata* are common at Kalakot. *Indohyus* and *Kunmunella* do not occur at Ganda Kas, and *Khirtharia dayi* (from Ganda Kas) differs clearly from *K. inflata* (and is sometimes considered different at the generic level). Different species of anthracobunids occur at Ganda Kas and Kalakot, clearly differing in size. The pakicetid *Pakicetus attocki* is found in both areas, and it is possible that a rare lophialetid at Ganda Kas represents *Kalakotia simplicidentata.* A number of chapattymyid species also occur in both areas, but since nearly all rodent specimens are isolated teeth, it is hard to judge dental variation and the generic status of some chapattymyids. Most significantly, *Hyrachyus*-like perissodactyls are present at Kalakot but absent at Ganda Kas.

The faunal differences at the generic and specific levels suggest to us that the Kalakot and Ganda Kas fauna are different in age. However, samples from these areas are similar at higher taxonomic levels, suggesting that they both sampled a long period of relative stability with no major changes in faunal composition above the generic level. Most of the families in common between Kalakot and Ganda Kas are endemics. This suggests that at the time when these fossils were buried, the Indo-Pakistani continent was isolated from neighboring areas, possibly separated by a shallow epicontinental sea allowing limited faunal interchange. This endemism complicates an effort to determine the temporal relations between the Indo-Pakistan faunas and those from the Asian mainland.

At present, the Gali Jhagir fauna consists of a few taxa only, but it is important because the raoellids and the helaletid *Jhagirilophus* are closely related to taxa from the Kalakot Subathu Formation. The two raoellids at Gali Jhagir match Kalakot taxa and not Ganda Kas taxa. *Jhagirilophus* represents a very derived tapiroid that is best classified as a helaletid but is also intermediate in morphology between large helaletids and *Hyrachyus.* A large helaletid and *Hyrachyus asiaticus,* are known from the Kalakot fauna, but do not occur in the Ganda Kas fauna. We find this convincing evidence that the Gali Jhagir Fauna and the Kalakot Fauna are similar in age.

The distinction between the Kalakot/Gali Jhagir and Ganda Kas Faunas mirrors that in both the Asian Mainland (Russell and Zhai, 1987; Ting, 1998) and North America (Krishtalka et al., 1987), where *Hyrachyus* indicates a younger age (Irdinmanhan and Bridgerian, Table 2). We therefore tentatively consider the Ganda Kas Faunas to predate the Kalakot/Gali Jhagir Faunas.

This observation appears to run counter to published lithostratigraphic observations showing that the Chorgali Formation underlies the Kuldana Formation (Fatmi, 1973). However the sites that yield mammals from these formations are 50 km apart, and further the Ganda Kas Area lacks any exposures of the Chorgali Fm., and the Gali Jhagir Area lacks exposures of the Kuldana Formation. The Chorgali Formation underlies the Kuldana Formation near Cheratte, northwest of Fatehjang (Pascoe, 1920; Cotter, 1933). However, the structural complexity of this area and the radical facies changes make lithologies a poor guide to the interpretation of temporal relationships between Kuldana and Chorgali mammal faunas. The paleontology of the Chorgali Formation has only been studied in detail in the Salt Range (Gill, 1952), far south of the areas of interest.

The Banda Daud Shah Fauna—In broad terms the redbed deposits of the Ganda Kas Area, in particular Locality 62, and the Karak Area are similar. Both represent fluvial deposition in an arid climate (Wells, 1983; Aslan and Thewissen, 1996). Both are comprised of thick red mudstone units with channel deposits of carbonate nodule conglomerates and sandstones. Field observation has shown that in Ganda Kas the lenticular conglomerates and sandstones are dispersed throughout the mudstones, while the coarser units in the Karak Area are concentrated along one horizon near the top of the redbeds. Aslan and Thewissen (1996) point out that channel deposition of conglomerates and sandstone occurred at a much faster rate at the Karak localities than at Ganda Kas, on the order of one to ten years as opposed to 10^3 years in Ganda Kas. As a result, articulated specimens of *Diacodexis pakistanensis* are preserved at the Barbora Banda Locality (H-GSP Locality 300) in the Karak Area, and vertebrate remains at Ganda Kas are unsorted and isolated (Wells, 1984). While these taphonomic factors may influence preservation, we suspect that they do not account for the differences in faunal composition.

The Banda Daud Shah Fauna at present consists of ten mammalian taxa, and all are distinct generically from mammals at the sites east of the Indus (Ganda Kas, Kalakot, and Gali Jhagir). The Banda Daud Shah Fauna is dominated by *Diacodexis pakistanensis,* a small and primitive dichobunid, which is commonly considered to be near the base of the artiodactyl phylogenetic tree (Gentry and Hooker, 1988; Theodor, 1996), and similar taxa are considered early Eocene on other continents. In the Ganda Kas Area, small dichobunids are nearly absent, with only a single tooth reported (*Dulcidon gandaensis*). The second most abundant taxon in the Banda Daud Shah Fauna is the primitive tapiroid *Karagalax mamikhelensis* (Maas et al., 2001), an isectolophid close to *Homogalax*. It is near the base of the tapiroid radiation, unlike more derived lophialetid tapiroids that are common at the sites east of the Indus. The occurrence of these primitive artiodactyls and perissodactyls suggest that the Banda Daud Shah Fauna predates the faunas from the sites east of the Indus.

No other comparisons can be made within low-rank clades of the Banda Daud Shah and Ganda Kas/Kalakot Faunas. However, two of the Banda Daud Shah families, plesiadapids and arctocyonids, represent orders which attained their greatest diversity in the Paleocene and undergo a steep decline in diversity and abundance in the early Eocene. Their presence at Banda Daud Shah and absence at sites east of the Indus is consistent with an older age of the Banda Daud Shah Fauna. Similar relative ages were previously suggested by de Bruijn et al. (1982), Thewissen et al. (1987), Russell and Zhai (1987), Thewissen and McKenna (1992), and Leinders et al. (1999). Finally, this interpretation is supported by two rodent teeth described from the Karak sites. These were interpreted as predating the radiation of chapattymids (de Bruijn et al., 1982).

Given the lack of magnetostratigraphic and adequate micropaleontological data, as well as the endemism of the mammal faunas of Indo-Pakistan, our assessment of the absolute age of these faunas is preliminary. Based on its mammal fauna, the Banda Daud Shah Fauna matches those from the early Eocene Bumbanian of China (Ting, 1998) and Wasatchian of North America (Krishtalka et al., 1987). We consider the Banda Daud Shah Fauna to be early Eocene in age.

Chorlakki—One of the largest Indo-Pakistani mammal faunas was collected at the Locality Chorlakki, located geographically between Banda Daud Shah and Ganda Kas. The most recent faunal list from this locality was published by Thewissen et al. (1987), this faunal list includes small dichobunids, the raoellids *Khirtharia* and *Indohyus*, isectolophids, brontotheres, *Paratritemnodon indicus* and a single tooth referred to ‘‘*Fostercooperia*.’’ As such, it is a mix of faunal elements from the Banda Daud Shah, Ganda Kas, and Kalakot Faunas.

Wells (1984) described the fossiliferous section at Chorlakki and noted that most fossils were found in granulestones, similar to those at H-GSP Locality 62 and the Karak Area. However, nearly all specimens of Chorlakki fossils are isolated teeth or bone fragments, suggesting extensive reworking. Fossils were mainly collected at two beds, Granulestone II and III of Wells (1984). These two beds are not part of the same section and could not be correlated convincingly given that the area is structurally strongly deformed and that no part of the longer section (with Granulestone II) resembles that of the shorter section (with Granulestone III).

Reworking of buried fossils may have mixed faunas from different times. Fossils collected from the different fossiliferous sections were not separated, and it is thus possible that two distinct faunas are represented. Until more fieldwork is done at Chorlakki, it is not possible to investigate whether this site contains one or more faunal assemblages.

CONCLUSIONS

Based on mammalian fossils, we distinguish three faunal zones in the Eocene of Indo-Pakistan, all known from multiple localities. The oldest fauna is from the Banda Daud Shah Area and contains primitive dichobunids, isectolophid tapirs, and archaic mammals such as plesiadapids and arctocyonids. Based on comparisons with Asia and North America (Table 2), this fauna may be equivalent in age to the Wasatchian faunas of North America.

The remaining faunas are from the Ganda Kas and Kalakot areas. These faunas display a degree of endemism and are dominated by chappatimyids and raoellids. These faunas contain artiodactyls and perissodactyls that are more derived than those from the Banda Daud Shah Area, such as raoellids, lophialetids, and brontotheres. At present, we consider the Ganda Kas Fauna to predate the Kalakot Fauna. This is mainly based on the presence of hyracodontids and *Hyrachyus*-like taxa at the latter sites.

Most geologic evidence (e.g., Beck et al., 1995) now supports the hypothesis that the Indian and Asian blocks underwent continental collision around the Cretaceous–Tertiary Boundary. The faunas discussed in this paper clearly postdate this initial docking of the plates. However, initial collision was unlikely to establish a land contact between the continents, since the shallow seas of the continental shelves covered the areas near the collision zone. Consistent with this, the unique character of the Indo-Pakistani faunas suggests endemism and relative isolation. Relating these faunas to plate tectonic events will require more detailed quantitative studies of coeval faunas in Indo-Pakistan, Asia, Africa, and Europe. Most important for this will be the recovery of Paleocene land mammal faunas from Indo-Pakistan. At present there is at least a 10 million year gap between faunas near the K-T boundary (e.g., Prasad et al., 1994) and those of the early Eocene (Gingerich et al., 1998b; this paper).

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