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EARLY-MIDDLE EOCENE KULDANA FORMATION OF KOHAT  
(PAKISTAN)**

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# ARTIODACTYLA AND PERISSODACTYLA (MAMMALIA) FROM THE EARLY-MIDDLE EOCENE KULDANA FORMATION OF KOHAT (PAKISTAN)

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J. G. M. THEWISSEN, P. D. GINGERICH AND D. E. RUSSELL

*Abstract.*—Chorlakki, yielding approximately 400 specimens (mostly isolated teeth and bone fragments), is one of four major early-to-middle Eocene mammal localities on the Indo-Pakistan subcontinent. On the basis of ungulates described in this paper we consider the Chorlakki fauna to be younger than that from Barbora Banda, older than the Kalakot fauna, and possibly comparable in age to the Ganda Kas/Lammidhan fauna.

Artiodactyls are abundant in the Chorlakki fauna. Two families are represented: Dichobunidae and Raoellidae. A new dichobunid, *Pakibune chorlakkiensis* n. gen. et sp., and a new raoellid, *Indohyus major* n. sp., are described. A new diagnosis of Raoellidae is given here. Perissodactyls are rare at Chorlakki. However a few elements identified as isctolophid tapiroids, brontotheriids, and hyracodontids are known.

Raoellidae is endemic to the Indo-Pakistan subcontinent and may be related to European Dacrytheriidae. Pakistan dichobunids too seem to have European affinities. The perissodactyls are possibly more closely related to Eocene taxa from the rest of Asia than to those from Europe.

## INTRODUCTION

The locality of Chorlakki in the Kohat District, North-West Frontier Province of Pakistan, is one of the few Eocene localities on the Indo-Pakistan subcontinent yielding fossil mammals. A description of the locality and preliminary faunal list were presented by Gingerich et al. (1979, 1983). Chorlakki is located about 4 km NNW of the village of that name. Its coordinates are 33° 37' 20" N latitude, 71° 55' 20" E longitude. Most of its vertebrate fauna has already been published (Gingerich et al., 1979; Russell and Gingerich, 1980; Gingerich and Russell, 1981; Russell and Gingerich, 1981; Hartenberger, 1982; Gingerich et al., 1983; Wells and Gingerich, 1983; de Broin, 1987; Gayet, 1987; Rage, 1987; Russell and Gingerich, 1987). Table 1 provides an updated faunal list.

Concerning the ungulates, only one new artiodactyl was described since the discovery of the locality in 1977 (Gingerich et al., 1979). The fauna contains several new artiodactyl taxa, and others merit a closer comparison with related forms. Perissodactyls are rare at Chorlakki, in contrast to other Eocene mammal localities from the Indian subcontinent, such as Barbora Banda in Kohat (de Bruijn et al., 1982; Thewissen et al., 1983; Russell and Gingerich, 1987) and Kalakot in Kashmir (Ranga Rao, 1971 and 1972; Sahni and Khare, 1972 and 1973; Kahn, 1973; Ranga Rao and Obergfell, 1973; Ranga Rao and Misra, 1983; Kumar and Sahni, 1985). Another difference between Chorlakki and these faunas is the preservation of the material: specimens from Chorlakki are almost all isolated teeth,

TABLE 1 — Mammalian faunal list for the early-to-middle Eocene locality Chorlakkii, Kohat District, North-West Frontier Province, Pakistan.

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Order	PROTEUTHERIA (?)
Family	<i>incertae sedis</i>
	<i>Pakilestes lathrius</i> Russell and Gingerich, 1981
Order	LIPOTYPHILA
Family	undetermined
	<i>Seia shahi</i> Russell and Gingerich, 1981
Order	CHIROPTERA
Family	undetermined
	Chiropteran indet. A of Russell and Gingerich, 1981
	Chiropteran indet. B of Russell and Gingerich, 1981
Order	PRIMATES
Family	OMOMYIDAE
	<i>Kohatius coppensi</i> Russell and Gingerich, 1980
Family	ADAPIDAE
	<i>Panobius afridi</i> Russell and Gingerich, 1987
	Cf. <i>Agerinia</i> sp.
Order	CREODONTA
Family	HYAENODONTIDAE
	<i>Paratritemnodon indicus</i> Ranga Rao, 1973
Order	CETACEA
Family	PROTOCETIDAE
	<i>Pakicetus inachus</i> Gingerich and Russell, 1981
Order	PROBOSCIDEA
Family	ANTHRACOBUNIDAE
	<i>Lammidhanianus wardi</i> (Pilgrim, 1940)
	<i>Pilgrimella pilgrimi</i> Dehm and Oettingen-Spielberg, 1958
Order	ARTIODACTYLA
Family	DICHOBUNIDAE
	<i>Diacodexis pakistanensis</i> Thewissen et al., 1983
	<i>Chorlakkia hassani</i> Gingerich et al., 1979
	<i>Pakibune chorlakkensis</i> n. gen. n. sp.
	<i>Dichobunidae</i> indet.
Family	RAOELLIDAE
	<i>Khirtharia dayi</i> Pilgrim, 1940
	<i>Indohyus indirae</i> Ranga Rao, 1971
	<i>I. major</i> n. sp.
Order	PERISSODACTYLA
Family	ISECTOLOPHIDAE
	Gen. and spec. indet.
Family	BRONTOTHERIIDAE
	<i>Eotitanops dayi</i> Dehm and Oettingen-Spielberg, 1958
Family	HYRACODONTIDAE?
	" <i>Forstercooperia</i> " <i>jigniensis</i> (Sahni and Khare, 1973)
Order	TILLODONTIA
Family	TILLOTHERIIDAE
	<i>Basalina basalensis</i> Dehm and Oettingen-Spielberg, 1958
Order	RODENTIA
Family	CHAPATTIMYIDAE
	<i>Birbalomys woodi</i> Sahni and Khare, 1973
	<i>B. sondaari</i> (Hussain et al., 1978)
	<i>B. ijlsti</i> (Hussain et al., 1978)
	<i>B. vandermeuleni</i> (Hussain et al., 1978)
	<i>Chapattimys wilsoni</i> Hussain et al., 1978
	<i>C. debruijni</i> Hartenberger, 1982
Family	YUOMYIDAE
	cf. <i>Petrokozlovina</i> sp. indet. 2 of Hartenberger, 1982

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while material from Barbora Banda and Kalakot often consists of more complete dentitions. Localities near the village of Ganda Kas in Punjab (Pilgrim, 1940b; Dehm and Oettingen-Spielberg, 1958; Gingerich, 1977; Hussain et al., 1978; West, 1980) resemble Chorlakkia in mode of preservation.

Specimens cited in this study are housed in the American Museum of Natural History, New York (AMNH); British Museum of Natural History, London (BMNH); Geological Survey of Pakistan, Islamabad (GSP-UM and H-GSP); Geology Department of Lucknow University, Lucknow (LUV and VPL/ K); Institut für Paläontologie und Historische Geologie, München (München); Directorate of Geology, Oil and Natural Gas Commission, Dehra Dun (ONG/K); Princeton University Museum of Natural History, Princeton (PU); and University of Michigan Museum of Paleontology, Ann Arbor (UM).

### SYSTEMATIC PALEONTOLOGY

Class MAMMALIA

Order ARTIODACTYLA

Family DICHOBUNIDAE Gill, 1872

Genus *Chorlakkia* Gingerich et al., 1979

*Chorlakkia hassani* Gingerich et al., 1979

Figure 1, 2A-G, 3C-H.

*Holotype*.—GSP-UM 66 (L dentary with  $M_1$ - $M_3$ ).

*Referred specimens*.—GSP-UM 106 (R  $M^3$ ), 153 (R  $M_2$ ), 272 (L  $P_4$ ), 691 (L  $M_1$  trigonid), 695 (L  $P^4$ ), 1408 (R  $P^4$  fragment), 1437 (L  $M^2$ ), 1488 (L  $M_1$  trigonid), 1505 (L  $M_2$ ), 1512 (L  $M_3$ ), and 1703 (L  $M^2$ ).

*Description*.—Specimens here referred add considerably to our knowledge of *Chorlakkia* because only the holotype was described previously. Trigonids of the anterior molars are heavily worn the holotype (Fig. 1), and it is not clear whether  $M_1$  and  $M_2$  retain a paraconid. The two preserved  $M_1$ s described here (GSP-UM 691 and 1488) indicate that the paraconid is absent. GSP-UM 691 (Fig. 2C-E) further shows that the paracristid is stronger than the metacristid.

GSP-UM 1505 (Fig. 2G-H) is an  $M_2$  that is less worn than  $M_2$  of the holotype. Here too the paraconid is absent, which seems to be characteristic of all molars of *Chorlakkia*. Both recovered  $M_2$ s are somewhat larger than that in the holotype (Table 2 summarizes dental measurements of dichobunids). A single  $M_3$  is referred to *Chorlakkia* (GSP-UM 1512). The specimen is badly damaged and most of the enamel is gone. This may have been caused by passage through the digestive tract of a predator. Features that remain match those of the holotype.

Among the referred elements that are not preserved in the holotype is a  $P_4$  (GSP-UM 272, Fig. 2A-B). It fits approximately the roots of the  $P_4$  of the holotype. It has a single trenchant cusp with a small anterior and somewhat larger posterior cingulum. A posterior ridge on the main cusp extends to a small bulge in the posterior cingulum.

Preservation of the recovered  $P^4$ s is not optimal; in GSP-UM 695 enamel is missing and the protocone of GSP-UM 1408 is broken off. The paracone is large and rounded with a weak crest extending between its tip and a small metastyle, and in GSP-UM 695 a weak crest joins the parastyle anteriorly. The parastyle is larger than the metastyle and forms a large anterior process of the tooth. The protocone is slightly larger than the parastyle and it is lingual to the paracone. The anterior border of GSP-UM 695 is concave in occlusal view and the posterior border is approximately straight.

The main differences between the two upper molars that are probably  $M^2$ s (GSP-UM 1437 and 1703, Fig. 3C-F) are the position of the protocone, which is more anterior in GSP-UM 1703, and a

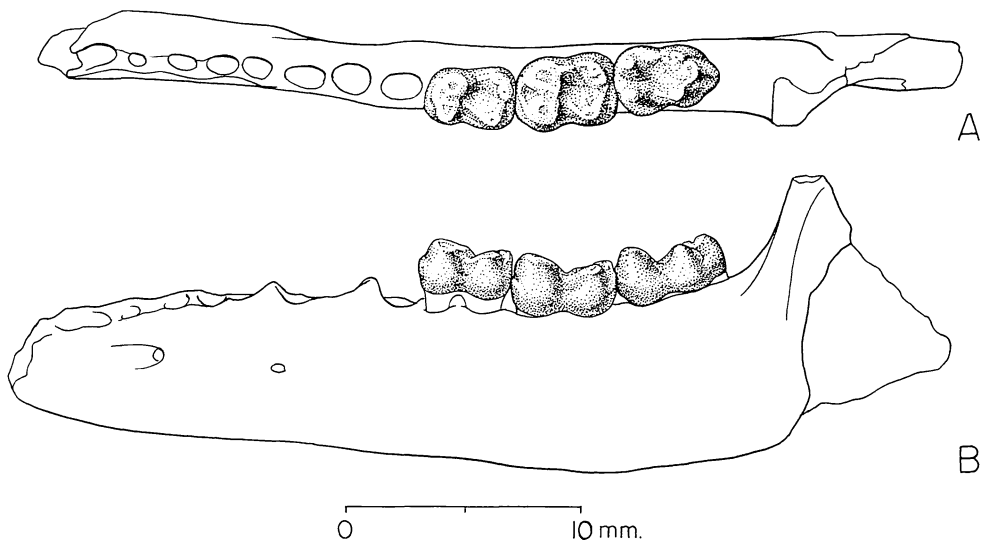


FIG. 1.— *Chorlakkia hassani* Gingerich et al., 1979 from Chorlakkii. A-B, holotype, left dentary with  $M_1$ - $M_3$  (GSP-UM 66, occlusal and lateral view). Notice the worn state of the molars; referred material in Fig. 2 is important because it shows characteristics obscured by wear in the holotype.

weaker postcingulum. In both molars the labial cingulum is broad and the lingual cingulum interrupted.

The only recovered  $M^3$  (GSP-UM 106, Fig. 3G-H) is not well preserved, much of the enamel being dissolved. The metacone is only slightly smaller than the paracone. Cingula are weak and crests are low, while the preprotocrista is missing. In contrast to the anterior molars, the cusps of  $M^3$  appear to be less bulbous.

*Discussion.*—New elements make a more detailed comparison with the closely related *Diacodexis pakistanensis* possible. Lower molars of *C. hassani* are most easily distinguished from those of *D. pakistanensis* by the absence of a paraconid. Cusps of *C. hassani* are more obtuse, and teeth of this species are slightly larger (all measurements of dichobunids are cited in Table 2). *Chorlakkia* differs from most other dichobunids by the absence of the paraconid in combination with its small size.  $P_4$  is broader and has a weaker cingulum than in *Diacodexis*. *Chorlakkia* is at present known only from the type locality, Chorlakkii.

The upper teeth referred here are fairly homogeneous in morphology. They are the most abundant dichobunid upper cheek teeth in the fauna, which, in addition to the blunt cusps, suggests that they represent the upper molars of the most abundant dichobunid taxon represented by lower teeth: *Chorlakkia hassani*.

Upper molars of *Chorlakkia* resemble the holotype of *Dulcidon gandaensis* (Dehm and Oettingen-Spielberg, 1958). Not since its initial description in 1958 has any material been referred to *Dulcidon*. The single problematic tooth has been thought to be a condylarth (Dehm and Oettingen-Spielberg, 1958; Crusafont and Russell, 1967), an insectivore (Van Valen, 1965), and an artiodactyl (Gingerich and Russell, 1981). Part of this confusion is certainly due to the poor preservation of the specimen, which is heavily worn, lacks enamel in several places and is cracked. Overall morphology of the upper molars described as *C. hassani* agrees with the holotype of *D. gandaensis*; the main difference is that the latter is smaller and shorter. The cusps of teeth here referred to *Chorlakkia* are more bulbous than those of the holotype of *Dulcidon*. When better material of *Dulcidon* becomes available, it may well prove to be congeneric with *Chorlakkia*.

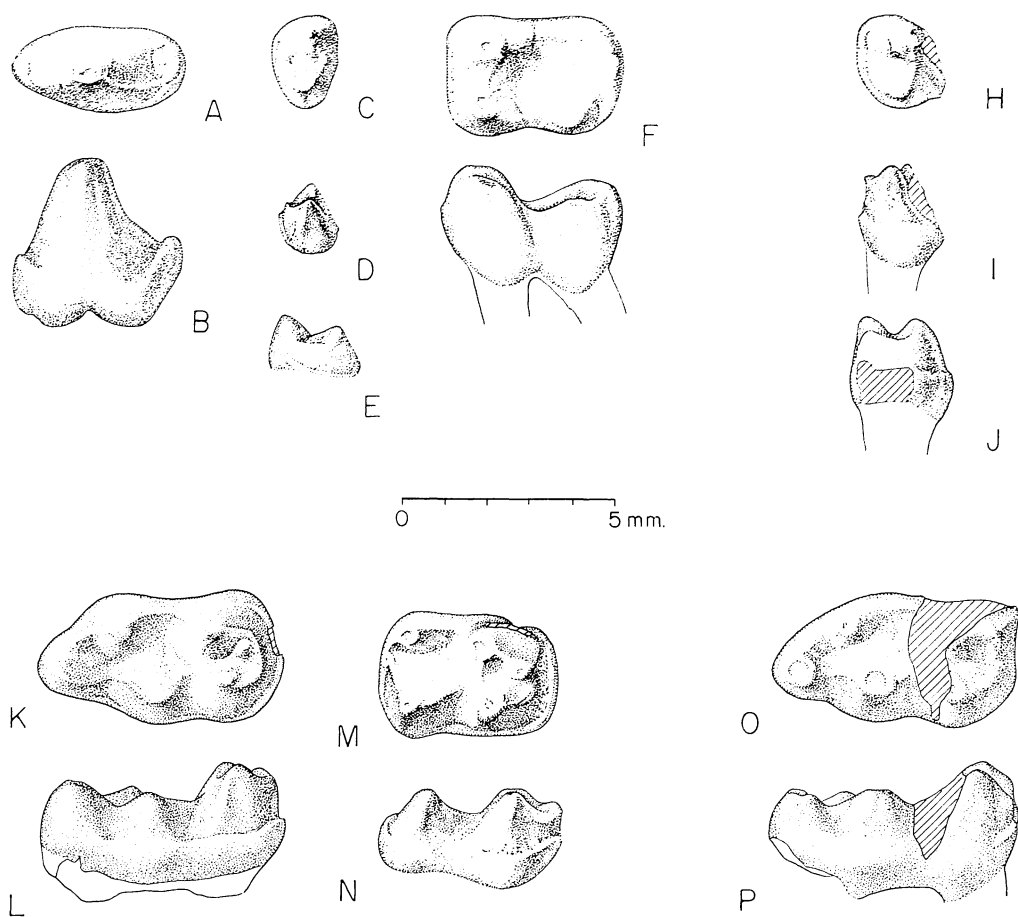


FIG. 2— Lower cheek teeth of dichobunids from Chorlakkia (except for GSP-UM 690, Fig. 2M-N, which is from Lammidhan). A-B, left  $P_4$ , *Chorlakkia hassani* Gingerich et al., 1979 (GSP-UM 272, occlusal and labial view). C-E, left  $M_1$  trigonid, *Chorlakkia hassani* (GSP-UM 691, occlusal, labial, and anterior view). F-G, left  $M_2$ , *Chorlakkia hassani* (GSP-UM 1505, occlusal and labial view). H-J, left  $M_1$  trigonid, *Diacodexis pakistanensis* Thewissen et al., 1983 (GSP-UM 1483, occlusal, labial, and anterior view). K-L, right  $M_3$ , *Pakibune chorlakkensis* n. gen. n. sp., holotype (GSP-UM 259, occlusal, and labial view). M-N, right  $M_2$ , *Pakibune chorlakkensis* n. gen. n. sp. from Lammidhan (GSP-UM 690, occlusal and labial view). O-P, right  $M_3$ , Dichobunidae indet. (GSP-UM 1476, occlusal and labial view). Notice the reduction of the paraconid in all *Chorlakkia* molars, while this cusp is present in *Diacodexis*. The paraconid is central in *Pakibune*, but not in other dichobunids. *Pakibune* and the dichobunid indet. (Fig. 2O-P) are larger than *Chorlakkia* and *Diacodexis pakistanensis*.

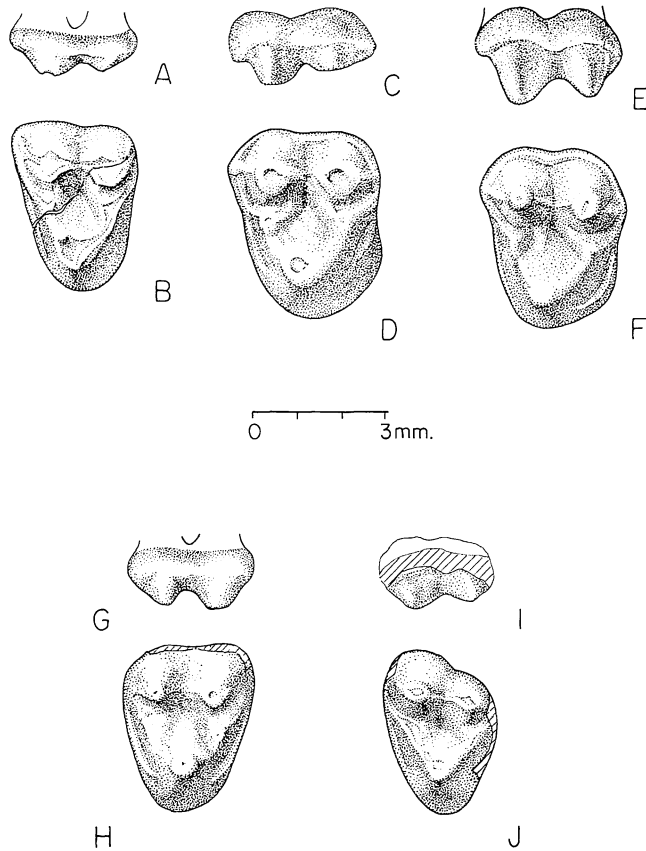


FIG. 3.— Upper molars of Dichobunidae and ?Dichobunidae from Chorlakkii (except for München 1, Fig. 3A-B, which is from Ganda Kas). A-B left  $M^2$ ?, *Dulcidon gandaensis* (Dehm and Oettingen-Spielberg, 1959), holotype from Ganda Kas (München 1, labial and occlusal view). C-D, left  $M^2$ , *Chorlakkia hassani* (GSP-UM 1703, labial and occlusal view). E-F, left  $M^2$ , *Chorlakkia hassani* (GSP-UM 1437, labial and occlusal view). G-H, right  $M^3$ , *Chorlakkia hassani* (GSP-UM 106, labial and occlusal view). I-J, left  $M^3$ , ?Dichobunidae (GSP-UM 274, labial and occlusal view). We refer most of the dichobunid upper molars from Chorlakkii to *Chorlakkia*, the most abundant dichobunid in the fauna. *Chorlakkia* may prove to be a junior synonym of *Dulcidon*, but until more material of *Dulcidon* becomes available, this cannot be substantiated. We refer GSP-UM 274 to ?Dichobunidae because of its reduced metacone, a feature usually not present in small dichobunids.

*Remarks.*—The specimen number mentioned for the holotype of *C. hassani* in the type description is its field number; its museum number is GSP-UM 66.

Genus *Diacodexis* Cope, 1882  
*Diacodexis pakistanensis* Thewissen et al., 1983  
 Figure 2H-J

*Referred specimen.*—GSP-UM 1483 (L  $M_1$  trigonid).

*Description and discussion.*—The trigonid matches the size of an  $M_1$  trigonid. The paraconid is strong, although weaker than the metaconid; all cusps on the trigonid are acute. The paracristid is sharp. These are the major differences between *Diacodexis* and *Chorlakkia*.



TABLE 2— Length (L) and width (W) of dichobunid molars (in mm) from Chorlakkia and Lammidhan (only GSP-UM 690). Upper molars measured perpendicular (L) or parallel (W) to protocone - paracone axis.

GSP-UM	P4		M1		M2		M3	
	L	W	L	W	L	W	L	W
<i>Chorlakkia hassani</i> , lower dentition								
66			3.5	2.6	3.9	3.0	4.1	2.8
153					4.0	3.2		
272	3.9	1.8						
1505					4.1	2.7		
1512							4.5	2.8
<i>Pakibune chorlakkensis</i> , lower dentition (GSP-UM 690 from Lammidhan)								
259							5.8	3.1
690					4.3	2.8		
Dichobunidae <i>indet.</i> , lower dentition								
1476							6.9	3.6
<i>Chorlakkia hassani</i> , upper dentition								
106							3.2	4.1
695		3.0						
1408	3.4							
1437					3.6	4.3		
1703					3.6	4.4		

*Diacodexis pakistanensis* is rare at Chorlakkia and it is more primitive than *Chorlakkia* in retaining the paraconid. *D. pakistanensis* was originally described from Barbora Banda, an Eocene locality about 80 km southwest of Chorlakkia, where it is the only artiodactyl known. *Diacodexis pakistanensis* is the most primitive artiodactyl from the Indo-Pakistan subcontinent and a likely ancestor of later Eocene dichobunids from Indo-Pakistan.

*Diacodexis pakistanensis* is also known from Lammidhan in Potwar (GSP-UM 217). The locality of Lammidhan is near Ganda Kas, east of Chorlakkia, in the Kala Chitta Hills of Punjab (see description in Gingerich, 1977).

### Pakibune new genus

*Type and only species.*—*Pakibune chorlakkensis* new species.

*Diagnosis.*—Dichobunid of moderate size, larger than Asian *Diacodexis*, *Chorlakkia*, and *Dulcidon*, but smaller than European *Cuisitherium* and *Bunophorus*. Similar in size to the North American *Diacodexis metsiacus*. Differs from all other Dichobunidae in having a labially situated paraconid and strong hypoconulid on M<sub>3</sub>.

*Etymology.*—*Paki* abbreviation of Pakistan and *bune* common suffix of dichobunids.

**Pakibune chorlakkensis** new species

Figure 2K-N

*Holotype*.—GSP-UM 259 (R M<sub>3</sub>).

*Referred material*.—GSP-UM 690 from Lammidhan (R M<sub>2</sub>).

*Type locality*.—Chorlakki, about 4 km NNW of Chorlakki-village, Kohat district, Northwest Frontier Province, Pakistan, 33° 37' 20" N latitude, 71° 55' 20" E longitude.

*Age and distribution*.—Continental red beds of the Kuldana Formation (see, e.g., Wells, 1983). These are also called Mami Khel Clay (Meissner et al., 1974). Early to middle Eocene of Chorlakki (Kohat) and Lammidhan (Potwar).

*Diagnosis*.—As for the genus, see above.

*Etymology*.—Named for type locality, Chorlakki.

*Description*.—The type, an M<sub>3</sub> (Fig. 2K-L), has an anteroposteriorly elongated trigonid. The protoconid is slightly larger than the metaconid, but not as high. The protoconid and metaconid are connected by a weak metaclistid. The paracristid is stronger than the metaclistid. The paracristid bends sharply lingually and then posteriorly from the anterior side of the protoconid; it is less distinct anterior to the metaconid. The paraconid is a small cusp situated on the paracristid close to the midline of the tooth. The cristid obliqua is concave labially and contacts the trigonid below the metaconid-protoconid notch. The hypoconid is larger than the entoconid but approximately the same height. The hypoconulid is the largest cusp on the talonid; it is connected to the entoconid and hypoconid by weak crests. A cingulum is present on the anterior and labial sides of the tooth; it is interrupted labial to the hypoconid.

The paraconid and metaconid of the referred M<sub>2</sub> (GSP-UM 690, Fig. 2M-N) are closer together than in the holotype, and the lingual surface between these cusps is concave. The cristid obliqua is strong and straight, and the hypoconid is placed near the posterolabial corner of the tooth. The postcristid is weak and the hypoconulid is a small cusp at the lingual extremity of the postcingulum. The entoconid is much smaller than the hypoconid and it is situated near the posterolingual corner of the tooth. A cingulum is present on the anterior, labial, and posterior side of the tooth; it is interrupted at the base of the hypoconid.

*Discussion*.—With the exception of Barbora Banda, dichobunids are never abundant in Asian and Indo-Pakistan faunas and, because of this, few elements are known for many species. This makes direct comparison of taxa difficult or impossible. *Pakibune* cannot be compared with the taxa for which only upper teeth are known, such as *Dulcidon* Van Valen, 1965, *Aksyria* Gabunia, 1973, and *Dichobune?* of Zdansky (1930).

*Pakibune chorlakkensis* is different from all other dichobunids in having a labially positioned paraconid. It differs from *Diacodexis pakistanensis*, *Chorlakkia*, and *Dulcidon* in being larger. With respect to the development of crests and the position of the hypoconid, *Pakibune* resembles *Diacodexis* more than *Chorlakkia*. A metaclistid is present, and the hypoconulid and entoconid are well separated. *Pakibune* is smaller than the enigmatic genus *Haqueina*, and it also differs from that taxon in the position of the paraconid, the weak entoconid, and the less oblique postcrista.

## Dichobunidae indet.

Figure 2O-P

*Referred specimen*.—GSP-UM 1476 (R M<sub>3</sub>).

*Description and discussion*.—An indeterminate dichobunid is represented by a single isolated M<sub>3</sub> (GSP-UM 1476, Fig. 2O-P) in which the posterior side of the trigonid is damaged. The paracristid is

somewhat angular and ends at a small lingual paraconid. The hypoconid is much larger than the entoconid and it is more centrally placed than in *Pakibune*. All preserved cusps are bulbous, and crests are weak. The cristid obliqua is apparently absent, a weak crest extends from the hypocone posteriorly to the base of the hypoconulid. Cingula are present on the trigonid portion of the tooth and on a small area anterior to the hypoconid.

This tooth was referred to *Diacodexis pakistanensis* by Thewissen et al. (1983; field no. 78184), but it differs from that taxon and from *Chorlakkia hassani* in being larger (see Table 2) and in the virtual absence of all cristids on the talonid. An additional difference from *Chorlakkia* is the presence of a paraconid, while it differs from *Pakibune* in the position of the paraconid.

#### Family ?DICHOBUNIDAE

Gen. et sp. indet.

Figure 3I-J

*Referred material.*—GSP-UM 274 (L M<sup>3</sup>).

*Description and discussion.*—This tooth is an M<sup>3</sup> of uncertain affinities. The specimen lacks much of its enamel, mainly on the labial and posterior sides. Its cusps are low and bulbous, the metacone is much smaller than the paracone. The cingulum is only preserved on the labial and anterior sides, and the parastyle is broken off. The conules are weak. The specimen has been exposed to abrasion and to enamel dissolution. Length is 2.8 mm, width is 3.4 mm.

Possibly this specimen is referable to Dichobunidae. Usually, however, dichobunid M<sup>3</sup>s have a more subequal paracone and metacone, as in *Dulcidon*. Possibly also the tooth represents a hypsodontid condylarth, with which it agrees in metacone reduction. Hypsodontids have not yet been reported from the Indo-Pakistan subcontinent. Only more material can bring a solution.

#### Family RAOELLIDAE Sahni et al., 1981

?Helohyidae (in part). Pilgrim, 1940b, p. 141.

Dichobunidae (in part), Dehm and Oettingen-Spielberg, 1958, p. 26; Ranga Rao, 1972, p. 3; Sahni and Khare, 1973, p. 44; Gingerich, 1977, p. 192.

?Choeropotamidae (in part), Ranga Rao, 1971, p. 126.

Anthracotheriidae (in part), Sahni and Khare, 1972, p. 47.

Helohyidae (in part), M. C. Coombs and W. P. Coombs, 1977, p. 292; W. P. Coombs and M. C. Coombs, 1977, p. 292; West, 1980, p. 522.

Raoellidae Sahni et al., 1981, p. 629; Sahni et al., 1983, p. 81; Kumar and Sahni, 1985, p. 157.

*Type genus.*—*Indohyus* Ranga Rao, 1971 (including *Raoella* Sahni and Khare, 1972, and *Kunmunella* Sahni and Khare, 1972).

*Referred genera.*—*Khirtharia*, *Bunodentus*, *Metkatius*, and possibly *Haqueina*.

*Diagnosis.*—Upper molars bilophodont (or incipiently bilophodont); anterior cusps and loph stronger than posterior ones; postprotocrista absent; paraconule weak or absent; P<sup>3</sup> lacks protocone. On lower molars, as far as known, paraconid and metacristid absent; no hypoconulid on M<sub>1</sub> and M<sub>2</sub>; postcristid usually strong.

*Age and distribution.*—Early to middle Eocene of northwestern India and Pakistan.

*Discussion.*—Genera of Raoellidae were shifted among Dichobunidae, Helohyidae, Choeropotamidae, and Anthracotheriidae until Sahni et al. (1981) proposed the family Raoellidae for

a number of them. The exact contents of the family, as described, is not clear, but at least "*Raoella*", "*Kunmunella*," and *Khirtharia* (a senior synonym of *Bunodentus* in their view) seem included. Sahni et al. (1983) referred *Pilgrimella* and *Lammidhanja* to Raoellidae, but Wells and Gingerich (1983) identified these genera as proboscideans.

According to Sahni et al. (1981) bunolophodont upper molars are characteristic of the family. A single crest extends labially from both lingual cusps of the upper molars. The anterior crest (preprotocrista) divides at the paraconule into a preparaconule crista that meets the cingulum anterior to the paracone, and a postparaconule crista that contacts the base of the paracone. The latter crests may be very weak. The posterior crest contacts the base of the middle of the metacone, sometimes ascending that cusp partially. A centrocrista is sometimes present, but no postprotocrista ever occurs (contra M. C. Coombs and W. P. Coombs, 1977, pp. 301–302). This pattern of crests is well developed in *Indohyus* and it is weak (but still recognizable) in *Khirtharia* and *Bunodentus*. In addition to their crest pattern, upper molars of *Indohyus*, *Khirtharia*, and *Bunodentus* all have a metacone that is smaller than the paracone, and a protocone that is stronger than the posterior lingual cusp. Length and width increase from  $M^1$  to  $M^3$  (*Khirtharia* is an exception to this,  $M^3$  being narrower anteroposteriorly than  $M^2$ ).

Lower molars of all four genera of raoellids are similar in the weak development of crests on the trigonid, absence of a paraconid, presence of an equally large protoconid and metaconid, absence of a hypoconulid on the anterior molars (unknown in *Metkatius*), and presence of a single cusp on the third lobe of  $M_3$ . Besides this, a crest links the hypoconid and entoconid of *Indohyus* and *Khirtharia*. This crest is absent in *Bunodentus* and *Metkatius*; the transverse crests of the upper molars is absent in *Bunodentus* as a result of the great bunodonty of its cusps.

The position of another Indian Eocene genus, *Haqueina*, remains problematical because only lower molars are described for it; these differ from raoellid molars in having a third lobe developed into a loop-like crest with two cusps and in having a more oblique cristid obliqua. Material referred to *Haqueina* by Sahni and Khare (1973) was later referred to *Indohyus* by Kumar and Sahni (1985).

Raoellidae seems to be a morphologically coherent, endemic artiodactyl family of the Indo-Pakistan subcontinent. Before the unity of the family was recognized, different hypotheses were put forward for the origin of individual genera by several authors.

Sahni and Khare (1972) assigned "*Raoella*" and "*Kunmunella*" to the Anthracotheriidae, a family well diagnosed by W. P. Coombs and M. C. Coombs (1977). Raoellids differ from primitive anthracotheres in having a small paraconule, a straight centrocrista (the only anthracothere that lacks a W-shaped, selenodont centrocrista is *Anthracohyus*), and a third lobe on  $M_3$ , which only has a single cusp. The inner cusps, or at least the metaconule, of the upper molars of anthracotheres are selenodont, while in raoellids a single crest from both lingual cusps contacts the middle of both labial cusps. The protoconid of anthracotheres is also somewhat selenodont, a feature not present in raoellids.

Anthracotheriidae are similar to Haplobunodontidae, a family of European artiodactyls that traditionally has been considered a subfamily of anthracotheres. Sudre (1978) raised it to familial status following a suggestion of Pilgrim (1940b). Haplobunodontidae differ from Anthracotheriidae mainly in the mastoid exposure on the lateral side of the skull (Pearson, 1927). The family is only known from Europe ("*Rhagatherium*" *aegypticum* Andrews 1906 from the Fayum depression of Egypt may not be a haplobunodontid according to Sudre, 1978). Dentally haplobunodontids resemble anthracotheres closely, and differ from raoellids in the same features that anthracotheres do. An additional character is the degree of molarization of  $P^4$ : a distinct metacone is developed in haplobunodontids (except *Haplobunodon*, see Stehlin, 1908), but never in raoellids.

Ranga Rao (1971) referred *Indohyus* to Choeropotamidae. This monogeneric European family is also morphologically similar to anthracotheres and differs from Raoellidae in the same diagnostic upper molar characters.  $M_3$  has a bicuspid hypoconulid according to Casanovas Cladellas (1975).

M. C. Coombs and W. P. Coombs (1977) revised the family Helohyidae, including of North American *Helohyus* and Asian *Gobiohyus*. They also included *Indohyus*, *Bunodentus*, "*Kunmunella*," and "*Raoella*." These authors left *Khirtharia* incertae sedis, although Pilgrim (1940b) had earlier assigned it to ?Helohyidae. Raoellid genera differ from *Gobiohyus* (AMNH 20249, 26278, 26279) and *Helohyus* (AMNH 11673, 12151, 13128) in having a more pronounced size difference between the paracone and metacone, weaker conules, and weak postparaconule and postmetaconule cristae. In the lower molars, raoellids lack a metacristid and paraconid (the latter is sometimes lost in helohyids as well, according to M. C. Coombs and W. P. Coombs, 1977), and they have a weak crest linking the entoconid and hypoconid. Additional differences between raoellids and *Gobiohyus* are the weaker parastyle, absence of a postprotocrista, and absence of a metaconid on P<sub>4</sub>.

In general, Helohyidae resemble closely Dichobunidae, the stem family of artiodactyls, and Helohyidae have been considered a subfamily of Dichobunidae (e.g., Gazin, 1955). The generalized nature of helohyid dentition differs from the "bunolophodonty" of raoellid molars, a fact that was already noted by Sahni et al. (1981). West (1980) referred a partial upper molar (HGSP 1974b from Ganda Kas) to late Eocene *Gobiohyus* cf. *G. orientalis*, which would be the only helohyid known from the Indo-Pakistan subcontinent. We think that the specimen is too fragmentary to be diagnostic.

The most diagnostic feature distinguishing raoellids from dichobunids is the development of transverse crests on the upper molars. Other features do occur in some genera of other families. We here note some differences and some exceptions. The metaconule is hypertrophied in raoellids, and takes the position of the hypocone. This is not the case in most dichobunids, but *Buxobune* also has an enlarged metaconule. No hypocone is ever present in raoellids; the same is true for certain diacodexines but not for dichobunines and homacodontines. The postprotocrista is absent in raoellids but present in dichobunids, except for *Buxobune* and *Dichobune*. The paracristid and metacristid are reduced in raoellids, as in *Aumelasia*, *Bunophorus*, and *Wasatchia*, but in contrast to many other dichobunids. The paraconid is completely reduced, as it is in the dichobunine *Homacodon* and, often the diacodexine *Bunophorus*, but not in many other diacodexines. The hypocristid is enlarged in raoellids; it is present in many dichobunids (*Dichobune*, *Homacodon*, *Hexacodus*), but it is usually not so large as in raoellids and may be missing completely.

Raoellidae resemble the European genus *Tapirulus* to some extent. Sudre (1978) has described the evolution of the only *Tapirulus* lineage known; its most conspicuous feature is its increasingly "tapiroid" morphology (Sudre, 1978; p. 109), principally the development of transverse crests. Raoellidae are similar to *Tapirulus* in this derived feature. It is possible that Raoellidae are closely related to the more primitive species of *Tapirulus*, such as *T. majori* and *T. depereti*. Later species of that lineage have a W-shaped centrocrista, a character not present in raoellids. More material is known for the supposed ancestor of *Tapirulus*: *Cuisitherium* Sudre et al., 1983. *Cuisitherium* has a weak hypocristid and a single cusp on the third lobe of M<sub>3</sub>; the hypocone is absent and the metaconule is hypertrophied but *Cuisitherium* lacks the tapiroid morphology of *Tapirulus* and Raoellidae. Some specimens have a W-shaped centrocrista, unlike raoellids. A close relationship between *Tapirulus* and Raoellidae seems probable, but cannot be proven yet.

#### Genus *Khirtharia* Pilgrim, 1940

*Type and only species*.—*Khirtharia dayi* Pilgrim, 1940b.

*Amended diagnosis*.—Raoellid with weakly developed bunolophodont upper molars; transverse crests are weaker than in *Indohyus* but stronger than in *Bunodentus*. M<sup>3</sup> is anteroposteriorly narrower than M<sup>2</sup>. Lower molars with low bunodont cusps and crests that are weaker than those of *Indohyus* but stronger than in *Bunodentus*.

*Age and distribution.*—Early to middle Eocene of northwestern India and Pakistan.

*Discussion.*—Synonymy of *Bunodentus* and *Khirtharia* was formally proposed by West (1980) and followed by Kumar and Sahni (1985). *Bunodentus* is based on the type material of *B. inflatus* Ranga Rao, 1972, and on material described by Ranga Rao and Misra (1983) and by Kumar and Sahni (1985). *Bunodentus* differs from *Khirtharia* in the proportions of  $M_2$  and  $M_3$  (see Fig. 4, all measurements on raellids are summarized in Table 3). In *Bunodentus* there is an increase in size from  $M_1$  to  $M_3$ , and the size difference between  $M_2$  and  $M_3$  is much greater than in *Khirtharia*. The hypoconulid of  $M_3$  is larger in *Bunodentus*.

In the upper molars of *Bunodentus*,  $M^3$  is larger than  $M^2$  and the posterior part of  $M^3$  is unreduced (ONG/K 9), while in *Khirtharia* the paracone of  $M^3$  is larger than the metacone and the posterior transverse diameter is much less. Upper molars of *Bunodentus* are more or less quadrangular, while those of *Khirtharia* are transversely elongated. In our view, these features and the main distinctive character, the bulbous cusps of *Bunodentus*, merit generic distinction between these taxa.

*Khirtharia dayi* Pilgrim 1940

Figure 5A-J

*Referred specimens.*—From Chorlakk:  $P_3$ , GSP-UM 1510;  $P_4$ , GSP-UM 1412;  $P_x$ , GSP-UM 1644;  $M_1$  or  $M_2$ , GSP-UM 88, 116, 1466, 1470, 1487, 1520, 1537, and 1733; dentary with partial  $M_1$  and  $M_2$ , GSP-UM 1711;  $M_1$ , GSP-UM 115;  $M_2$ , GSP-UM 1404, and 1559;  $M_3$ , GSP-UM 68, 74, 87, 142, 272, 1428, 1514, 1536, 1538, 1558, 1644, 1700, 1707, 1708, and 1730;  $P^x$ , GSP-UM 80, 86, 317, and 1455;  $M^1$  or  $M^2$ , GSP-UM 70, 89, 90, 141, 263, 1403, 1421, 1459, 1463, 1467, 1481, 1485, 1501, 1507, 1525, 1558, 1706, and 1866;  $M^3$ , GSP-UM 114, 117, 133, 283, 694, 1414, 1418, 1475, 1477, 1513, 1548, and 1554;  $M_x$  fragments, GSP-UM 71, 142, 698, 1400, 1405, 1500, 1552, 1555, 1654, 1665, 1674, 1676, 1679, 1710, 1713, 1720, 1862, 1863, 1876, 1878, 1880, 1890, and 1895. From Panoba: GSP-UM 240 (L  $M_x$ ).

*Description and discussion.*—The holotype of *Khirtharia dayi* is an  $M_2$  (BMNH.M 15796, Fig. 5A-B) from Lammidhan; it is larger than most *Khirtharia* from Chorlakk (Fig. 4A). The paratype  $M_3$  (BMNH.M 15797), an  $M_2$  and  $M_3$  described by Dehm and Oettingen-Spielberg (1958), and three Chorlakk specimens (GSP-UM 1559, 1711, and 1730) are all large. Many other Chorlakk specimens, specimens described by West (1980) from Ganda Kas (see West and Lukacs, 1979), and a specimen described by Sahni and Khare from Kalakot (1973; LUVF 15014) are smaller than these.

Length versus width diagrams for all published lower molars of *Khirtharia* and the Chorlakk sample are presented in Fig. 4, based on measurements in Table 3. Three clusters of *Khirtharia* specimens are apparent in the  $M_1/M_2$  plot, the largest teeth representing the second molars of large individuals (such as the holotype of *K. dayi*) and the smallest the first molars of small individuals. The middle cluster represents probably a mixed sample of  $M_1$ 's of large *K. dayi* and  $M_2$ 's of smaller specimens; at the moment we are unable to distinguish between these (except of course for the molars in jaws). Only few specimens can be identified in this way and until more complete material becomes available we are unable to evaluate if these specimens are all part of a single (sexually dimorphic?) population, or if two species are present.

The smaller morph is about four times as abundant as the larger at Chorlakk, and the genus *Khirtharia* is the most abundant artiodactyl. *Indohyus* is only represented by three specimens. At Kalakot, the reverse is true: many specimens of *Indohyus* are known, but only two specimens of *Khirtharia* have been described (Sahni and Khare, 1973).

Figure 5E-F is a composite cheek tooth dentition of the smaller *Khirtharia*. Only one upper cheek tooth series (HGSP 1979, see West, 1980) is known for the genus. In this specimen,  $M^3$  differs from

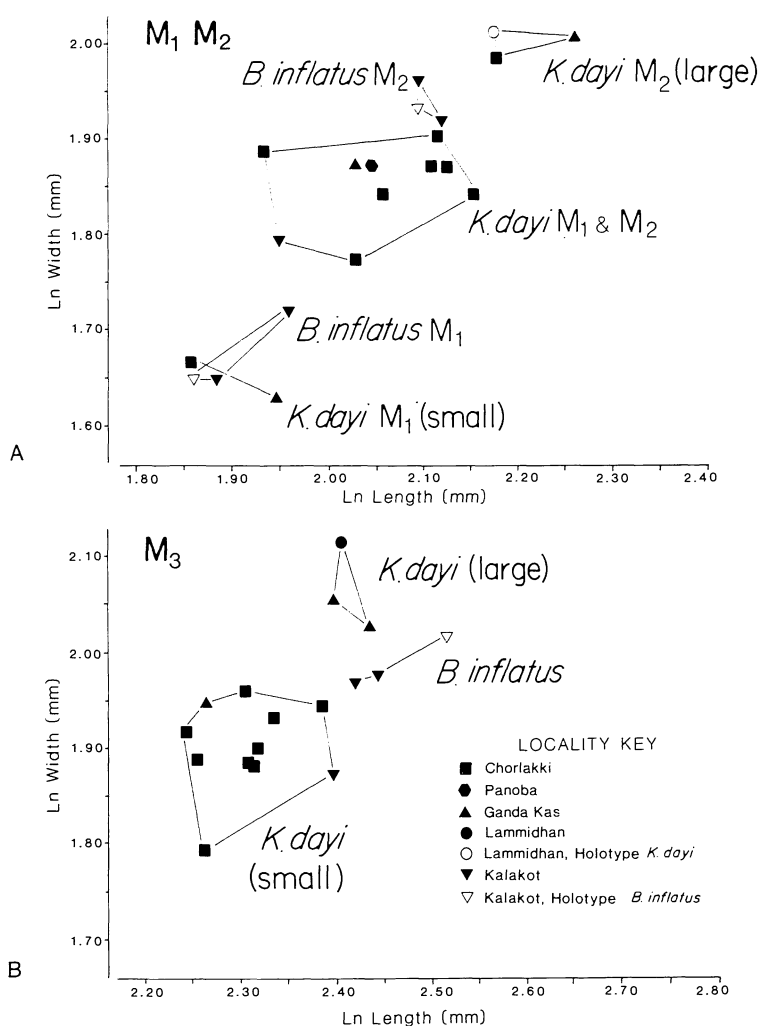


FIG. 4— Diagrams of log length versus log width for all published lower molars of *Bunodentus* and *Khirtharia*, including the sample from Chorlakkki described here. A. Diagram for M<sub>1</sub> and M<sub>2</sub>. B. diagram for M<sub>3</sub>. *Bunodentus* differs in morphology but not in size from *Khirtharia*. Within the *Khirtharia* M<sub>1</sub> and M<sub>2</sub> sample, three clusters are apparent. The holotype of *K. dayi* is in the cluster of largest specimens and it is almost certainly an M<sub>2</sub>. The cluster of smallest specimens is assumed to consist only of the M<sub>1</sub>s. The middle cluster is a mixed sample of M<sub>1</sub>s of large individuals and M<sub>2</sub>s of small individuals. Two groups of different sizes are also recognizable in Fig. 4B. The cluster of large M<sub>3</sub>s includes the paratype of *K. dayi*.

M<sup>2</sup> in having a strongly reduced metacone, a somewhat reduced hypocone, and a lower L/W ratio. Isolated M<sup>3</sup>s of the Chorlakkki sample were identified based on these differences, but because M<sup>1</sup> and M<sup>2</sup> are so similar, it was not possible to distinguish these teeth.

Several morphologies are apparent in the Chorlakkki sample, GSP-UM 1463 resembles M<sup>2</sup> in HGSP 1979, it is quadrangular and it has a large metacone (Fig. 5G). GSP-UM 1467 (Fig. 5J) is a molar of about equal length and width, but with a strongly reduced metacone suggesting that it may be M<sup>3</sup>. It has, however, a strong interdental wear facet on its posterior side, indicating that it was either not M<sup>3</sup> or that there was another (supernumerary?) tooth behind it. Other *Khirtharia* molars are short with

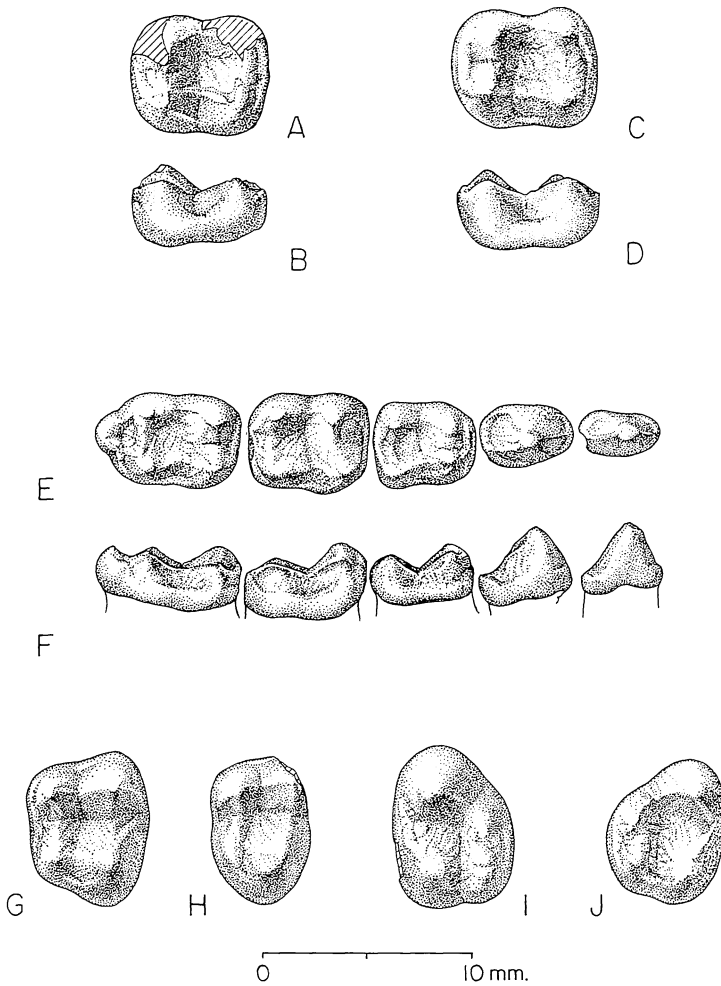


FIG. 5.— Cheek teeth of *Khirtharia dayi* from Chorlakkki (except for BMNH.M 15790, Fig. 5A-B, which is from Lammidhan). A-B, left  $M_2$ , *Khirtharia dayi* Pilgrim, 1940, holotype from Lammidhan (GSP-UM BMNH.M 15790, occlusal and labial view). C-D, left  $M_2$  (GSP-UM 1559, occlusal and labial view). E-F, right  $P_3$ - $M_3$ , composite dentition (GSP-UM 1412, 1510, 115, 1404, and 87, occlusal and labial view). G, right  $M^2$  (GSP-UM 1463, occlusal view). H, right  $M^1$  or  $M^2$  (GSP-UM 1485, occlusal view). I, left  $M^3$  (GSP-UM 114, occlusal view). J, right  $M^3$  (GSP-UM 1467, occlusal view). Notice the size difference between the holotype of *K. dayi* and the specimens of the composite dentition, see also Fig. 4. GSP-UM 1463 resembles  $M^2$  of the dentition described by West (HGSP 1979), while GSP-UM 1485 does not resemble any molar or premolar of that specimen. GSP-UM 114 and 1467 both resemble the  $M^3$  of HGSP 1979, but GSP-UM 1467 has a posterior interdental wear facet, which indicates that it is either not a  $M^3$  or that the jaw had a supernumerary tooth.



TABLE 3 — Length (L) and width (W) of *Khirtharia* and *Indohyus* molars from Chorlakkki (in mm).

GSP-UM	M1 or 2		M3	
	L	W	L	W
<i>Khirtharia dayi</i> , lower dentition				
68			10.3	6.9
74			10.1	6.7
87			9.6	6.0
115	6.4	5.3		
1466	8.6	6.3		
1467			10.1	6.6
1470	7.5			
1482	7.8	6.3		
1514			10.9	7.0
1520	7.6	5.9		
1536			9.5	6.6
1538			10.1	6.6
1558	8.3	6.5		
1559	8.8	7.3		
1644			10.0	7.1
1708			9.4	6.8
1711				7.4
1730			10.7	
1733	8.4	6.5		
<i>Khirtharia dayi</i> , upper dentition				
70	7.5	9.4		
89		7.1		
114			7.5	10.4
133			7.1	9.8
141	7.6	9.0		
283	7.3	9.6		
694			7.5	8.2
1414			9.0	8.2
1418			6.6	8.7
1421	7.1	8.8		
1463	7.6	9.4		
1475			7.6	9.5
1477			7.7	
1485	6.4	8.9		
1501	7.6	9.3		
1507	7.8	10.0		
1513			7.3	9.2
1548			7.3	9.0
1554			8.6	8.1
1706	6.8			
<i>Indohyus indirae</i> , lower dentition				
102	8.9	5.8		
696		5.4		
<i>Indohyus major</i> , lower dentition				
1435		10.0		

reduced posterior cusps (e.g., GSP-UM 114, Fig. 5I), resembling the  $M^3$  of HGSP 1979. A single molar is anteroposteriorly narrow and has no reduced metacone (GSP-UM 1485, Fig. 5H); it is not an  $M^3$  since it has a posterior wear facet, and does not resemble the quadrangular  $M^1$  of HGSP 1979. Identification of these different types has to await the recovery of more complete dentitions.

#### Genus *Indohyus* Ranga Rao, 1971

*Indohyus* Ranga Rao, 1971, p. 126, Pl. 1-4, Pl. 5:1, Pl. 6:1, 1a, and 1b. Kumar and Sahni, 1985, p. 164, Pl. 5:G-O, Pl. 6:A-J, Pl. 7:A-R.

*Indohyus*(?), Ranga Rao, 1971, p. 131, Pl. 5:2, 2a, and 2b, Pl. 6:2, 2a, and 2b.

*Raoella* Sahni et Khare, 1972, p. 47, Pl. 1:3-4, fig. 3.

*Kunmunella* Sahni et Khare, 1972, p. 50, Pl. 1:5, fig. 4; Kumar and Sahni, 1985, p. 160, Pl. 4:I-M, Pl. 5:A-F.

*Discussion.*—The type description of “*Raoella*” (Sahni and Khare, 1972) indicates the possibility that “*Raoella*” is synonymous with *Indohyus*. This synonymy was later proposed by Kumar and Sahni (1985).

Originally only  $M^3$  was known for “*Kunmunella*”, while no  $M^3$  was known for *Indohyus* and “*Raoella*”. The type description of “*Kunmunella*” (Sahni and Khare, 1972) does not compare the taxon with either *Indohyus* or *Raoella*. M. C. Coombs and W. P. Coombs (1977) state by implication that “*Kunmunella*” differs from both *Indohyus* and “*Raoella*” in its smaller and less labial metaconule (the posterolingual cusp of the upper molars).

In material referred to “*Kunmunella*” by Kumar and Sahni (1985), the metaconule of  $M^3$  is much smaller than that of the anterior molars, and it is similar to the metaconule of the type  $M^3$ . The anterior molars of *Kunmunella* do not differ from those of *Indohyus*.

In their amended diagnosis of *Kunmunella*, Kumar and Sahni (1985) state that this genus has more transverse upper molars, a smaller and more labial hypocone, a stronger cingulum in  $M^3$ , a weaker  $M_3$  hypoconulid, and a less oblique cristid obliqua than *Indohyus*. Some of these differences, such as the transverse upper molars and oblique ectolophid, are due to distortion caused by tectonic deformation.

The lingual cingulum of the holotype  $M^3$  of *Kunmunella rajauriensis* is only interrupted at the most lingual point of the protocone, as in the  $M^3$  of the specimens referred to *Indohyus indirae* by Kumar and Sahni (1985, VPL/K 512 and 514). It is continuous, but very weak, in the type specimens of *K. transversa* (VPL/K 526, Kumar and Sahni, 1985), and in a specimen referred to *K. kalakotensis* by Kumar and Sahni (1985, VPL/K 525). This characteristic obviously cannot serve as a diagnostic character.

Size of the  $M_3$  hypoconulid is a variable character and although the only  $M_3$  of *Kunmunella* figured by Kumar and Sahni (1985; VPL/K 572) lacks a large part of this cusp, the remaining part does not indicate that the cusp was any smaller than in *Indohyus*. One other  $M_3$  has been referred to *Kunmunella*, VPL/K 502, but no cast of this specimen is available.

*Kunmunella* seems little different from *Indohyus* and we therefore synonymize the genera, but until a larger sample of *Indohyus* becomes available it is not possible to evaluate the deformation and variation of the sample.

*Indohyus indirae*  
Figure 6A-E

*Indohyus indirae* Ranga Rao, 1971, p. 129, Pl. 1-4, Pl. 5:1, Pl. 6:1, 1a, and 1b.

*Indohyus(?) kalakotensis* Ranga Rao, 1971, p. 131, Pl. 5:2, 2a, and 2b; Pl. 6:2, 2a, and 2b.

*Raoella dograi* Sahni and Khare, 1972, p. 47, Pl. 1:3 and 4, fig. 3.

*Kunmunella rajauriensis* Sahni and Khare, 1972, p. 50, Pl. 1:5, fig. 4.

*Kunmunella transversa* Sahni and Khare, 1985, p. 160, Pl. 4:I-M, Pl. 5:A-F.

*Referred specimen*.—GSP-UM 102 (L M<sub>2</sub>), and GSP-UM 696 (R M<sub>2</sub> trigonid).

*Discussion*.—We doubt the validity of the many species of this small *Indohyus* and the genera synonymized with it; their similarity was already discussed in the preceding section. We synonymize *Indohyus? kalakotensis* Ranga Rao, 1971, *Raoella dograi* Sahni and Khare, 1972, *Kunmunella rajauriensis* Sahni and Khare, 1971, and *Kunmunella transversa* Kumar and Sahni, 1985, with their senior synonym *Indohyus indirae* Ranga Rao, 1971.

*Indohyus indirae* is the best known raoellid, numerous partial jaws have been described from the type locality, Kalakot, where it is the most abundant artiodactyl. Chorlakkhi is the second locality where it has been found, and here it is much less abundant than *Khirtharia*.

***Indohyus major*** new species  
Figure 6F-H

*Holotype and hypodigm*.—GSP-UM 1435 (isolated L trigonid).

*Type locality*.—Chorlakkhi, Kohat District, North-West Frontier Province of Pakistan (see description above).

*Age and distribution*.—Early to middle Eocene, type locality only.

*Etymology*.—*major*, latin for "larger", as the species is much larger than the known species of *Indohyus*.

*Diagnosis*.—About twice as large as *Indohyus indirae* (see Table 3).

*Description*.—Isolated trigonid with pointed protoconid and metaconid placed close together. Paraconid absent, protoconid and metaconid are connected by a continuous U-shaped paracristid. Medially the paracristid has a sharp angle at the level of the metaconid. The anterior portion of the cristid obliqua is low and contacts the trigonid labial to the level of the notch in the metacristid. A cingulum is only present on the anterior and labial side of the tooth as far as known.

*Discussion*.—In size this specimen resembles *Gobiohyus yanghuensis* Young, 1937, from China, which was referred to *Indohyus* by M. C. Coombs and W. P. Coombs (1977). Judging from the figures in Young (1937), we think that the upper molars lack transverse crests, and are bunodont. This indicates that *Gobiohyus yanghuensis* is a dichobunid or helohyid rather than a raoellid.

*Indohyus major* is the largest artiodactyl known from Chorlakkhi from dental remains. It bridges the gap in the sizes of herbivores, lying between the small tapiroids and artiodactyls and the larger brontotheres and anthracobunids.

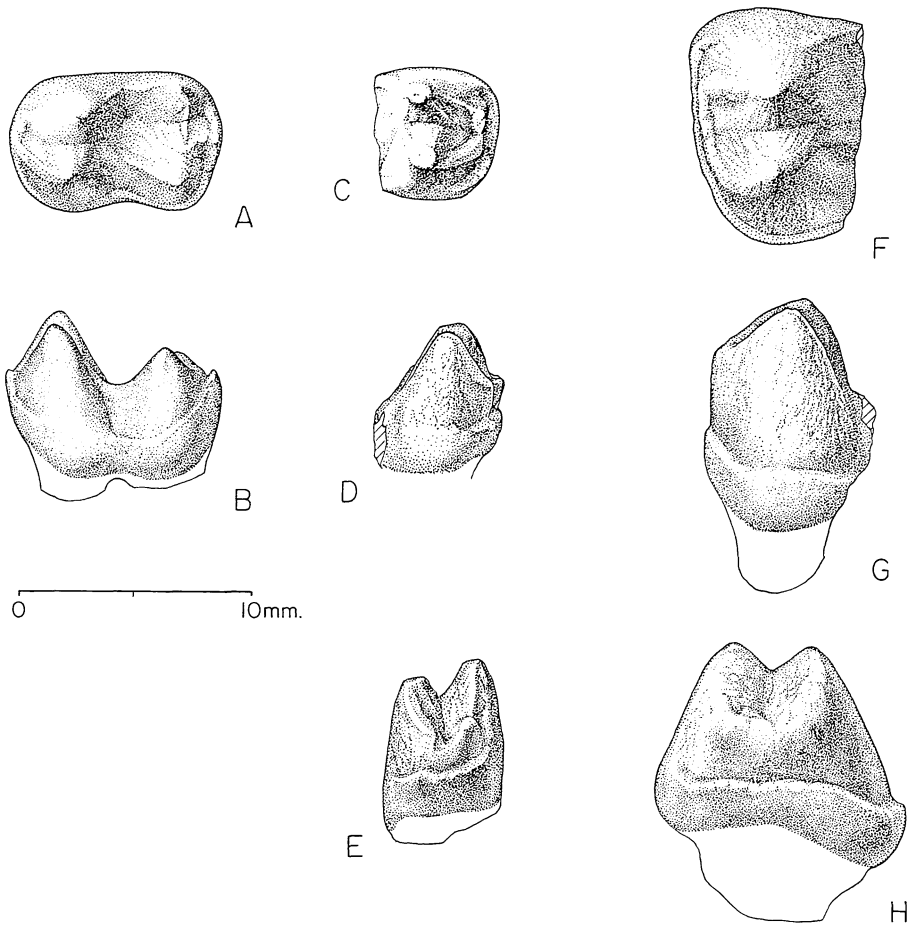


FIG. 6— Lower molars of *Indohyus* from Chorlakkki. A-B, left  $M_2$ , *I. indirae* (GSP-UM 102, occlusal and labial view). C-E, right  $M_2$  trigonid, *I. indirae* (GSP-UM 696, occlusal, labial, and anterior view). F-H, left  $M_2$  trigonid, *I. major* n. sp., holotype (GSP-UM 1435, occlusal, labial, and anterior view). The main difference between *Indohyus* and *Khirtharia* (Fig. 5) is the acuteness of the cusps in the former. Only two specimens of the smaller *Indohyus* were recovered at Chorlakkki. These are referred to *I. indirae*, until more material makes revision of the many species of this genus possible. The only specimen known for *I. major* is the holotype. It is about twice the size of the small species of *Indohyus*.

#### Artiodactyla indet.

#### Figure 7

*Referred specimens.*—GSP-UM 1413 (L astragalus), 1736 (R calcaneum), and 1897 (R calcaneum).

*Description.*—The astragalus (GSP-UM 1413, Fig. 7A and B) lacks the dorsal portion of the trochlea and the distolateral part of the head. It is double pulleyed and the trochlear facet is elongated and strongly curved with a deep groove. The axis of the trochlea is offset from the axis of the distal pulley and the lateral side between the two pulleys is deeply notched. The distal pulley has a strong ridge over its whole length on the lateral side. The sustentacular facet is slightly convex and medially

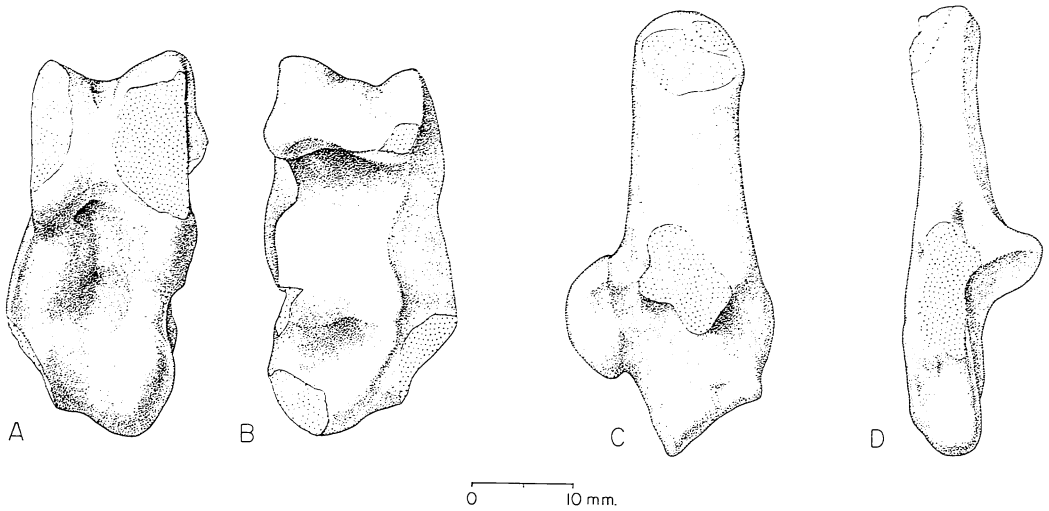


FIG. 7— Tarsal bones of a large artiodactyl. A-B, left astragalus (GSP-UM 1413, dorsal and plantar view). C, right calcaneum (GSP-UM 1736, medial view). D, right calcaneum (GSP-UM 1897, dorsal view). The calcanea may be of the same species, since they agree in size and morphology. Note the strong fibular facet and process, which may indicate the presence of a strong fibula. If the proportions of *Indohyus* are the same as those of the *Khirtharia dayi* teeth and astragalus that Pilgrim (1940b) described, then the described calcanea are too large to represent *I. major*. The astragalus is too large to go with the calcanea. Note its primitive morphology, offset pulleys, medio-lateral convex sustentacular facet, and a keel on the distal pulley, indicating that the cuboid and navicular were unfused.

bounded by a strong ridge. The proximal and distal side of the sustentacular facet is deeply excavated. The proximal calcaneal facet extends as far distally as the trochlea does, but its proximal part is indistinguishable as a result of breakage. Its length is 39.2 mm and its proximal width 16.3 mm.

Both calcanea (GSP-UM 1736 and 1897, Figure 7C and D) are damaged, but the remaining portions are complementary. GSP-UM 1736 is the most complete, it lacks only the sustentaculum tali, while GSP-UM 1897 lacks the tip of the tuber, the fibular process, and part of the distoplantar side.

The cuboid facet of the calcaneum is narrow and oriented obliquely dorsoplantarly. Medially it is continuous with the distal astragalal facet. The fibular facet is on a large process and has the shape of half a disc, with a midline length of 1.3 cm (GSP-UM 1736). The sustentaculum tali is small and its facet concave, matching the mediolaterally convex sustentacular facet of the astragalus. The lateral side of the calcaneum has a deep depression running proximo-distally. The length of GSP-UM 1736 is 49.0 mm.

*Discussion.*—Few postcranial bones were discovered at Chorlakkı and the find of large artiodactyl tarsals is therefore surprising. The described bones are without doubt too large for any dichobunid, *Khirtharia*, or the smaller *Indohyus*. *Indohyus major* is the largest artiodactyl represented by dental material, but even this species may be too small for such robust tarsals. Therefore we refer the tarsals to Artiodactyla indet., not claiming that the astragalus and calcanea are of the same species, since the calcanea are from a smaller individual than the astragalus.

Pilgrim (1940b) referred some postcranial material to *Khirtharia dayi* (BMNH.M 15800). The astragalus among this material is damaged proximally and plantarly, but the remaining morphology resembles that of the Chorlakkı astragalus. The relative proportions of teeth and astragalus of *Khirtharia* do not differ much from those of recent *Pecari angulatus* (UM R1626). The index of  $M_2$  width/distal astragalal width is 0.77 in *P. angulatus* and 0.82 in *K. dayi* (BMNH.M 15796 and 15800). The Chorlakkı astragalus (GSP-UM 1413), however, is much different from these; if it goes

with the holotype of *I. major*, the index  $M_2$  width/proximal astragalus width is 0.61, while it is 0.86 in *P. angulatus*. Gingerich (1977) referred an astragalus (UM 65871) from the Kuldana Formation of Lammidhan to ?*Haqueina*. In size and shape it matches the specimen that Pilgrim (1940b) referred to *Khirtharia*, but can not yet be identified with certainty. Gingerich (1977) also described an artiodactyl astragalus from the Kuldana Formation (UM 65872) as probably pertaining to *Lammidhan* or *Pilgrimella*. Both these genera were later identified as Proboscidea by Wells and Gingerich (1983). The only larger artiodactyls known from Ganda Kas are *Khirtharia* and *Haqueina*, and both are too small to go with the astragalus. UM 65872 is somewhat smaller than the astragalus from Chorlakki (length, 34.5 mm; proximal width, 14.3 mm), but morphologically it is similar. We assume that it is from an unidentified raoellid.

Raoellid astragali are generalized for artiodactyls. Among extant families, offset pulleys and a convex sustentacular facet with a medial ridge are retained in Tayassuidae and Suidae (Hussain et al., 1983), while these features also occur in the ancestral artiodactyl *Diacodexis* (e.g., UM 75147).

The most striking characteristic of the calcaneum is the strong process for the fibular facet. This feature is not matched in any recent families of artiodactyls and it is also stronger than that of *Diacodexis metsiacus*. A large fibular process may indicate the presence of a large fibula, a situation that is present in such graviportal artiodactyls as entelodonts. This is not a primitive trait, since the ancestral artiodactyl was slenderly built (Rose, 1982 and 1985).

Order PERISSODACTYLA  
 Superfamily TAPIROIDEA Gill, 1872  
 Family ISECTOLOPHIDAE Peterson, 1919  
 Gen. et Spec. indet.  
 Fig. 8A-B

*Referred material*.—GSP-UM 107 (R P<sup>3</sup> or P<sup>4</sup>).

*Description*.—Upper premolar in which the paracone, metacone, and metastyle are preserved (Fig. 8A-B). The labial cingulum is notched between the paracone and metacone. The preprotoconule crista extends to the anterior, and the postprotoconule crista to the posterior side of the paracone. The lingual side of the tooth is broken, and the tooth is heavily worn. Length is 5.2 mm, width is 5.9 mm.

*Discussion*.—Several small perissodactyls have been described from the middle Eocene of the Indo-Pakistan subcontinent: *Kalakotia simplicidentata* Ranga Rao, 1972; *Aulaxolophus quadrangularis* Ranga Rao, 1972; *Sastrilophus dehmi* Sahni and Khare, 1972; *Chasmotherium mckennai* Sahni and Khare, 1973; *Schlosseria radinskyi* Sahni and Khare, 1973. These have been assigned to a variety of families by different authors (Helaletidae, Hyracodontidae, Hyrachidae, and Lophialetidae; Ranga Rao, 1972; Sahni and Khare, 1972 and 1973; Ranga Rao and Obergfell, 1973; West, 1980). We consider all of these species, with the exception of *Sastrilophus dehmi*, to be synonymous.

Upper permanent premolars are known only for *Kalakotia* and *Sastrilophus*; we assume that the holotype of *Chasmotherium mckennai*, while described as having fully molarized posterior premolars (Sahni and Khare, 1973), actually preserves only deciduous premolars: its  $M^3$  is not fully erupted yet.

*Sastrilopus dehmi* was described as an isectolophid by Sahni and Khare (1972). Its primitive features include retention of a paraconule and metaconule. The metacone is not lingually deflected, making the angle between the ectoloph and metaloph more or less straight. In these characters it is close to the ancestral tapiroid *Homogalax*, and represents an isectolophid. It may be closely related to an undescribed tapiroid from Barbora Banda, with which it agrees in all of these features, although the Chorlakki specimen is smaller.

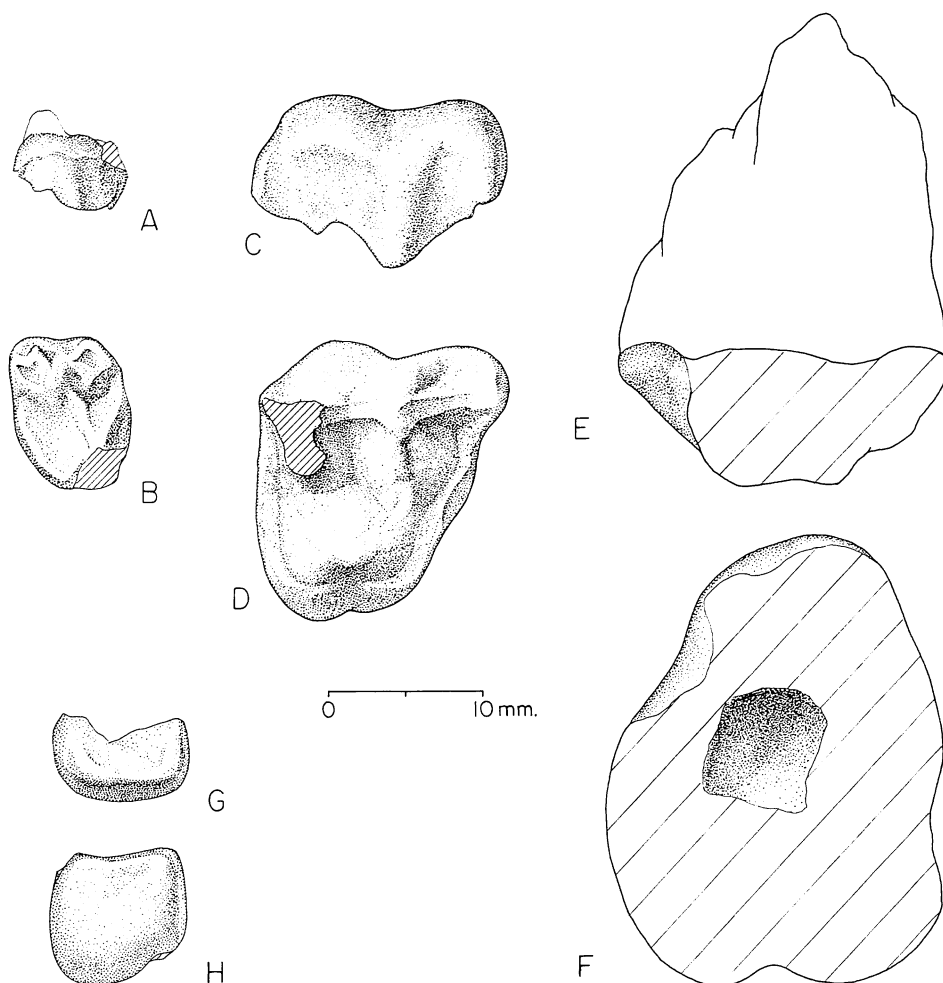


FIG. 8— Perissodactyla from Chorlakkhi. A-B, right  $P^3$  or  $P^4$ , Isectolophidae gen. et sp. indet. (GSP-UM 107, labial and occlusal view). C-D, left  $P^3$ , *Eotitanops dayi* Dehm and Oettingen-Spielberg, 1959 (GSP-UM 155, labial and occlusal view). E-F, right  $M^3$ , "*Forstercooperia*" *jigniensis* (Sahni and Khare, 1973), (GSP-UM 1446, labial and occlusal view). G-H, labial part of L trigonid of an anterior premolar, "*Forstercooperia*" *jigniensis* (GSP-UM 1446, occlusal and labial view). Although preservation of the tapiroid premolar is poor, it can be identified as an isectolophid on the basis of the presence of paraconule and postparaconule crista. Both structures are absent in lophialetids and helaletids. The large premolar is referred to Brontotheriidae on the basis of the presence of a strong parastyle and a weak metacrista. It matches in size only *Eotitanops dayi* and is the first premolar known for an Indo-Pakistan brontothere. The hyracodontid  $M^3$  is poorly preserved, but the dentine-enamel boundary is visible, indicating the outline of the tooth. Roots occur below all four major cusps. Identification of the premolar trigonid as a hyracodontid is mainly on the basis of size. Among the known Indian perissodactyl species only the hyracodontids and the brontothere *Mulkrajanops* match it in size. Brontothere premolars lack a metalophid, which is present in this specimen.

*Kalakotia simplicidentata* is less primitive than *Sastrilophus*: it lacks a paraconule and metaconule and its metacone has shifted lingually. Ranga Rao (1972) and West (1980) referred it to Lophialetidae. Lophialetidae, Helaletidae, and Lophiodontidae are morphologically similar. *Kalakotia* resembles lophialetids in the shape of the metacone and the position of the metaloph, but it lacks a metacone on P<sup>2</sup> and a protoloph-metaloph loop on P<sup>2</sup> and P<sup>3</sup> (see Radinsky, 1956 and 1969). P<sub>2</sub> and P<sub>3</sub> are less molarized in *Kalakotia* than in lophialetids.

The specimen from Chorlakki (GSP-UM 107) shows a well differentiated paracone and metacone, and a thickening in the paracrista, indicating the presence of the paraconule. This and the postparaconule crista indicate that it is not a lophialetid (see Matthew and Granger, 1925; Radinsky, 1965). It may represent an isectolophid premolar, but is too small to belong to any of the known species of this family.

Superfamily TITANOTHEROIDEA Osborn, 1898

Family BRONTOTHERIIDAE Marsh, 1873

*Eotitanops* Dehm and Oettingen-Spielberg, 1958

*Eotitanops dayi* Dehm and Oettingen-Spielberg, 1958

Fig. 8C-D

*Referred material*.—GSP-UM 104 (third lobe L M<sub>3</sub>), 155 (LP<sup>3</sup>), 156 (partial LM<sup>x</sup>), 1642 (partial LP<sup>3</sup>?), and possibly GSP-UM 1526 (partial L protocone) and 1692 (partial R paracone).

*Description*.—The entoconid, part of the postcristid, and the whole third lobe are preserved in GSP-UM 104. A strong crest extends from the hypoconulid anteriorly and contacts the postcristid slightly lingual to its midpoint. Another crest runs along the medial side of the tooth and ends abruptly at the point where it contacts the entoconid.

GSP-UM 155 is a virtually complete P<sup>3</sup> (Fig. 8C-D). It has a strong parastyle and a well separated paracone and metacone connected by a straight ectoloph. The protocone is connected to the paracone by a weak preprotocrista and there are strong anterior and posterior cingula. The metastyle and the conules are absent. Its length is 28 mm, its width 18 mm.

GSP-UM 1526 is the anterior side of a protocone. The cingulum is strong and ascends the protocone on the lingual side.

GSP-UM 1642 is a partial premolar. The parts that are preserved are the labial and anterior parts of the paracone and parts of the lateral side of the metacone and anterior cingulum. The paracone has a strong rib laterally, which fuses distally with the parastyle. The anterior cingulum runs medially from the parastyle, enclosing a broad basin anterior to the paracone. This morphology resembles that of GSP-UM 155 closely.

GSP-UM 1692 is a small tooth fragment preserving the labial parts of the paracone and parastyle. Both these cusps have a thickened rib as in GSP-UM 155, but the furrow between the ribs is less pronounced than in GSP-UM 155.

*Discussion*.—GSP-UM 155 is the main evidence for referring the cited material to *Eotitanops dayi*. It differs from deperetellids and hyracodontids in the presence of a strong parastyle, the absence of a metacrista, and the weakness of the paracrista. Additional evidence that the Chorlakki material is not a rhinocerotoid or a tapiroid comes from GSP-UM 104: the third lower molar does not have a third lobe in these taxa.

Three brontotheres have been described from the middle Eocene of the Indian subcontinent: *Eotitanops dayi* Dehm and Oettingen-Spielberg, 1958, *Pakotitanops latidentatus* West, 1980, and *Mulkrajanops mogliensis* Kumar and Sahni, 1985. Of these, *Mulkrajanops* is smaller than the



Chorlakkii species and more advanced in that it has a folded ectoloph on the premolars (Kumar and Sahni, 1985).

Known material of the two other genera, *Pakotitanops* and *Eotitanops*, is very incomplete and cannot be compared directly. On the basis of size, GSP-UM 155 resembles *Eotitanops* most closely. Known brontothere material from the Indian subcontinent is very fragmentary, and thus we are unable to compare it to the early and middle Eocene brontotheres from central Asia (Kramarenko, 1974; Gabounia, 1977; Li and Ting, 1983), or with those from Europe (Osborn, 1929).

Superfamily RHINOCEROTOIDEA Gill, 1872  
 Family ?HYRACODONTIDAE Cope, 1879  
 “*Forstercooperia*” Wood, 1939  
 “*Forstercooperia*” *jigniensis* (Sahni and Khare, 1973)  
 Fig. 8E-H

*Referred material.*—GSP-UM 753 (fragment of a lower molar), 1446 (fragment of L trigonid), and 1542 (R M<sup>3</sup>).

*Description.*—GSP-UM 1446 (Fig. 8G-H) is the labial part of a premolar trigonid. The paralophid extends anteriorly from the protoconid; it is slightly convex on the labial side. At its most anterior extension, the paraconid is only slightly lower than the protoconid. Anteriorly, the tooth is narrow, a clear indication that it is one of the anterior premolars. Part of the metalophid is preserved lingual to the protocone; it is somewhat worn posteriorly and a weak cingulum is present anteriorly. The length of the trigonid on the labial side is 8.5 mm.

GSP-UM 1542 is a poorly preserved M<sup>3</sup> (Fig. 9C-D). Enamel is only present on an outline of the tooth and on either side of the centrocrista. Remnants of the maxillary bone are preserved, roots are present below the protocone, paracone, metacone, and hypocone. The metacone is lingually displaced. Length is 27.5 mm and width 37 mm.

*Discussion.*—The premolar fragment is larger than in isectolophids and helaletids known from the Indo-Pakistan subcontinent. It is smaller than *Pakotitanops*, *Eotitanops*, *Hyrachyus asiaticus*, and *Teleolophus*. The only perissodactyls from the Eocene of the Indo-Pakistan subcontinent that it may match in size are the Indian hyracodontids and the brontothere *Mulkrajanops*. It does not resemble the anterior premolars of brontotheres, because these lack a transverse metalophid. Assuming that the specimen is from one of the perissodactyl families that are known from Indo-Pakistan, we refer it to Hyracodontidae.

The lingual position of the metacone in the described M<sup>3</sup> is a hyracodontid feature unlike other large perissodactyls from Indo-Pakistan, such as brontotheres (Dehm and Oettingen-Spielberg, 1958; West, 1980; Kumar and Sahni, 1985) and *Hyrachyus* (Ranga Rao and Obergfell, 1973).

Two hyracodontids have been described from Indo-Pakistan: “*Prothyracodon*” *kalakotensis* Kahn, 1973 (this genus was synonymized with *Triplophus* by Radinsky, 1967) and “*Forstercooperia*” *jigniensis* Sahni and Khare, 1973. Lucas et al. (1981) indicate that *F. jigniensis* may not be referable to *Forstercooperia*, and we therefore place the name in quotation marks. The last upper molar is not known in either “*Forstercooperia*” *jigniensis* nor “*Prothyracodon*” *kalakotensis*, but GSP-UM 1542 matches the holotype P<sup>3</sup>-M<sup>2</sup> of “*Forstercooperia*” *jigniensis* (LUVF 15009) in size. GSP-UM 1446 agrees in size with both the paratype of “*Forstercooperia*” *jigniensis* (P<sub>3</sub>-M<sub>2</sub>; LUVF 15008) and the holotype of “*Prothyracodon*” *kalakotensis* (ONG/JK/1), being slightly smaller than both. We refer it provisionally to “*Forstercooperia*” *jigniensis*.

## CONCLUSIONS

Early to middle Eocene fossil mammal localities from the Indo-Pakistan subcontinent are rare; the most important ones occur along the southwest border of the Himalayas in Pakistan and northwest India. These are, from west to east: Barbora Banda, Chorlakkhi, Ganda Kas, and Kalakot. The red beds in which these faunas occur may be diachronous (Gingerich and Russell, 1981; de Bruijn et al., 1982).

Faunal composition differs markedly from west to east between these localities: Barbora Banda, the most western locality, has the most primitive fauna. Artiodactyls are only represented by a single dichobunid, *Diacodexis pakistanensis*, which is the most primitive of the continent. Only one perissodactyl is known, and it is a primitive isectolophid slightly larger than the isectolophid from Chorlakkhi. It may be more primitive than the other known Indo-Pakistan isectolophids, but no detailed comparison has been made. A few rodents are known from Barbora Banda; these may form the initial stock of the continent (de Bruijn et al., 1982). Russell and Gingerich (1987) described an omomyid primate, cf. *Kohatius* sp., from Barbora Banda.

Chorlakkhi is about 80 km northeast of Barbora Banda. It has a greater diversity of artiodactyls and perissodactyls than the latter locality. The fauna is also more diverse in that it has insectivores and bats (Russell and Gingerich, 1981), Primates (Russell and Gingerich, 1980 and 1987), Hyaenodontidae, Cetacea (Gingerich et al., 1983), Anthracobunidae (Wells and Gingerich, 1983), and Tillodontia. The rodents are more diverse than those of Barbora Banda (Hartenberger, 1982). Hussain et al. (1978) concluded that the species occurring at Chorlakkhi are endemic to the Indo-Pakistan subcontinent. The artiodactyls and perissodactyls of Chorlakkhi are more derived than those from Barbora Banda. The localities share primitive *Diacodexis* and isectolophids, but more evolved dichobunids, such as *Chorlakkia* and *Pakibune* occur at Chorlakkhi, besides endemic raoellids and derived perissodactyls such as brontotheres and hyracodontids. We suggest that this fauna is younger than that of Barbora Banda and that it indicates a period of relative isolation of the continent in which endemic forms developed.

A third fauna is not well known; it is found at a number of separate localities near the village of Ganda Kas, about 30 km east of Chorlakkhi. Separate localities have been named Lammidhan (Pilgrim, 1940b and Gingerich, 1977), Basal (Dehm and Oettingen-Spielberg, 1958), Jhalar (Pilgrim, 1940b and Hussain et al., 1978) and Ganda Kas (Dehm and Oettingen-Spielberg, 1958; West, 1980). In most respects the fauna from Ganda Kas resembles the Chorlakkhi fauna. Concerning the ungulates, the faunas differ in rare forms, such as the absence of *Indohyus* from Ganda Kas, and the presence of *Haqueina* there. These differences may reflect sampling rather than faunal differences. Possibly the single partial upper molar referred to *Gobiohyus* cf. *G. orientalis* by West from Ganda Kas (1980) is actually part of the upper dentition of *Haqueina*. An  $M_3$  originally referred to *Lammidhanian* (BMNH 32168) by Gingerich (1977) is from a selenodont anthracothere. No anthracotheres have been collected at Lammidhan or Ganda Kas. It is likely, as mentioned by Wells and Gingerich (1983), that this species came from the Miocene Murree Formation. The Ganda Kas localities may be contemporaneous with Chorlakkhi or slightly younger.

The fourth and most eastern major fauna is Kalakot, over 200 km east of Ganda Kas. It is known from a number of localities that are closely spaced on a 6 km section of the Kalakot-Rajauri road in northwestern India. Only the larger mammals of this fauna are well known; dichobunids are absent, lophialetids are present and are more abundant than isectolophids, and *Indohyus* dominates over *Khirtharia*. This is in contrast to the Chorlakkhi and Ganda Kas assemblages, where *Khirtharia* is more abundant than *Indohyus*. The absence of dichobunids and the dominance of the evolved lophialetids over primitive isectolophids could mean that this fauna postdates the Chorlakkhi and Ganda Kas faunas.

Dichobunids from the Indo-Pakistan subcontinent have little in common with the Eocene dichobunids that were described from central Asia. *Aksyiria oligostus* is based on a single upper molar (or

deciduous molar) described by Gabunia (1973). It resembles *Lantianius xiehuensis*, a form referred to Dichobunidae by Gingerich (1976), in that its cingula extend far lingually (they are even complete lingually in the case of *Lantianius*), making the molars more or less quadrate.

A jaw fragment referred to *Hoanghonius stehlini* by Woo and Chow (1957), was considered to be a possible artiodactyl by Gingerich et al. (1979); P<sub>4</sub> has a very distinct metaconid, a feature unlike small dichobunids (it is present in certain larger bunodont forms like the holotype of *Bunophorus sinclairi*, PU 13448, and *Hyperdichobune*, see Sudre, 1978).

Zdansky (1930) described a few forms from the Eocene of China that are sometimes considered artiodactyls. The tooth of *Haplomyilus?* sp. is probably a dP<sub>4</sub> and may or may not be an artiodactyl. *Heptacodon dubium* is represented by a single upper molar. It may be a dichobunid but it is a much more advanced form with a large hypocone. Zdansky's *Dichobune?* sp. was thought to be related to anthracotheres by Gingerich et al. (1979). The P<sub>4</sub> of the specimen has a large metaconid, unlike primitive anthracotheres. Its affinities are not yet clear, but the selenodonty of its cusps indicates that it was certainly not a dichobunid. The Indian dichobunids are, with the exception of *Diacodexis*, endemic to the Indo-Pakistan subcontinent, just as the raoellids are.

Many authors have commented on the resemblances between the early and middle Eocene faunas from the Indian subcontinent and those of Asia and Europe (Pilgrim, 1940a; West, 1980; Sahni et al. 1981; de Bruyn et al., 1982; Hartenberger, 1982; Buffetaut, 1978; Thewissen et al., 1983; Kumar and Sahni, 1985). We suggest that only *Diacodexis pakistanensis* is closely related to non-Indo-Pakistan dichobunids, it compares well with European *Diacodexis* (Thewissen et al., 1983). Other Indo-Pakistan dichobunids and raoellids are endemic, but the latter family may be related to the European dacrytheriid *Tapirulus*. Thus we consider think that the early to middle Eocene artiodactyls of the Indo-Pakistan subcontinent have European rather than Asiatic affinities.

Three of the four families of perissodactyls are only weakly indicative of affinities to forms of other continents. Tapiroids and hyracodontids are known from Indo-Pakistan, Europe, and Asia. Although genera described for the Indo-Pakistan subcontinent are often the same as those from Asia (*Hyrachyus*, *Teleolophus*, and *Triplopus*), we doubt that the material for these is complete enough to be absolutely diagnostic. The fourth family, Brontotheriidae, suggests affinity of the faunas of Indo-Pakistan and Asia. No brontotheres are known from Europe (except for *Diplacodon* from Rumania, see Osborn, 1929, but the locality from which it comes from is paleogeographically on the Asian and not on the European continent).

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#### LITERATURE CITED

- ANDREWS, C. W. 1906. A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt. British Museum (Natural History). London. pp. 1-324. 26 pl.

- BROIN, F. de. 1987. Lower vertebrates from the early-middle Eocene Kuldana Formation of Kohat (Pakistan): Chelonia. Contributions from the Museum of Paleontology, University of Michigan, 27(7):169–185.
- BRUYN, H. de, S. T. HUSSAIN, and J. J. M. LEINDERS. 1982. On some early Eocene rodent remains from Barbara Banda, Kohat, Pakistan, and the early history of the order Rodentia. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, 85(3):249–258.
- BUFFETAUT, E. 1978. Crocodylian remains from the Eocene of Pakistan. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 156:262–315.
- CASANOVAS CLADELLAS, L. 1975. Estratigrafía y paleontología del yacimiento ludiense de Roc de Santa (area del Noguera-Pallaresa). Paleontología y Evolución, 10:1–158.
- COOMBS, M. C., and W. P. COOMBS Jr. 1977. Dentition of *Gobiohyus* and a reevaluation of the Helohyidae (Artiodactyla). Journal of Mammalogy, 58(3):291–315.
- COOMBS Jr., W. P., and M. C. COOMBS. 1977. The origin of anthracotheres. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 10:584–599.
- CRUSAFONT-PAIRÓ, M., and D. E. RUSSELL. 1967. Un nouveau paroxyclaenide de l'Eocène d'Espagne. Bulletin du Muséum National d'Histoire Naturelle, Série 2, 38(4):757–773.
- DEHM, R., and T. zu OETTINGEN-SPIELBERG. 1958. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 2. Die mitteleocänen Säugetiere von Ganda Kas bei Basal in Nordwest-Pakistan. Abhandlungen der Bayerischen Akademie der Wissenschaften, neue Folge, 91:1–54, 3 pl.
- GABOUNIA, L. 1977. Contribution à la connaissance des mammifères paléogènes du bassin de Zaïssan (Kazakhstan central). Geobios, Mémoire Spécial 1:29–37, 1 pl.
- GABUNIA, L. K. 1973. On the presence of a diacodexid (Diacodexinae) in the Eocene of Asia. Bulletin of the Academy of Sciences of the Georgian SSR, 71(3):741–744. [Russian]
- GAYET, M. 1987. Lower vertebrates from the early-middle Eocene Kuldana Formation of Kohat (Pakistan): Holostei and Teleostei. Contributions from the Museum of Paleontology, University of Michigan, 27(7):151–168.
- GAZIN, C. L. 1955. A review of the upper Eocene Artiodactyla of North America. Smithsonian Miscellaneous Collections, 128(8):1–96, 18 pl.
- GINGERICH, P. D. 1976. Systematic position of the alleged primate *Lantianius xiehuensis* Chow, 1964, from the Eocene of China. Journal of Mammalogy, 57(1):194–198.
- GINGERICH, P. D. 1977. A small collection of fossil vertebrates from the middle Eocene Kuldana and Kohat Formations of Punjab (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 24(18):190–203.
- GINGERICH, P. D., and D. E. RUSSELL. 1981. *Pakicetus inachus*, a new archaeocete (Mammalia, Cetacea) from the early-middle Eocene Kuldana Formation of Kohat (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 25(11):235–246.
- GINGERICH, P. D., D. E. RUSSELL, D. SIGOGNEAU-RUSSELL, and J.-L. HARTENBERGER. 1979. *Chorlakkia hasani*, a new middle Eocene dichobunid (Mammalia, Artiodactyla) from the Kuldana Formation of Kohat (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 25(6):117–124.
- GINGERICH, P. D., N. A. WELLS, D. E. RUSSELL, and S. M. I. SHAH. 1983. Origin of whales in epicontinental remnant seas: new evidence from the early Eocene of Pakistan. Science, 220(4595):403–406.
- HARTENBERGER, J.-L. 1982. A review of Eocene rodents of Pakistan. Contributions from the Museum of Paleontology, University of Michigan, 26(2):19–35.
- HUSSAIN, S. T., H. de BRUIJN, and J. J. M. LEINDERS. 1978. Middle Eocene rodents from the Kala Chitta Range (Punjab, Pakistan). Part I and II. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, 81(1):74–112.
- HUSSAIN, S. T., P. Y. SONDAAR, S. M. I. SHAH, J. G. M. THEWISSEN, E. F. H. M. COUSIN, and C. F. SPOOR. 1983. Fossil mammal bones of Pakistan, a field atlas. Part I: The artiodactyl astragalus. Memoirs of the Geological Survey of Pakistan, 14:1–17, 7 pl.
- KRAMARENKO, N. N. (ed.). 1974. Zoogeography of Paleogene of Asia. Treatise of the Academy of Sciences of USSR, Paleontological institut (Moskou), 146:1–302. [Russian]
- KHAN, A. 1973. A new mammalian fossil from the lower Murree of Kalakkot, Jammu and Kashmir State, India. Journal of the Geological Society of India, 14(3):296–301.
- KUMAR, K., and A. SAHNI. 1985. Eocene mammals from the Subathu Group, Kashmir Himalaya, India. Journal of Vertebrate Paleontology, 5(2):153–168.
- LUCAS, S. G., R. M. SCHOCH, and E. MANNING. 1981. The systematics of *Forstercooperia*, a middle to late Eocene hyracodontid (Perissodactyla: Rhinocerotoidae) from Asia and Western North America. Journal of Paleontology, 55(4):826–841.
- LI C.-K., and TING S.-Y. 1983. The Paleogene mammals of China. Bulletin of the Carnegie Museum of Natural History, 21:1–93. 4 app.

- LUCAS, S. G., R. M. SCHOCH, and E. MANNING. 1981. The systematics of *Forstercooperia*, a middle to late Eocene hyracodontid (Perissodactyla, Rhinocerotoida) from Asia and Western North America. *Journal of Paleontology*, 55(4):826–841.
- MATTHEW, W. D., and W. GRANGER. 1925. The smaller perissodactyls of the Irdin Manha Formation, Eocene of Mongolia. *American Museum Novitates*, 199:1–9.
- MEISSNER, C. R., J. M. MASTER, M. A. RASHID, and M. HUSSAIN. 1974. Stratigraphy of the Kohat Quadrangle, Pakistan. U.S. Geological Survey, Professional Papers, 716-D:1–30.
- OSBORN, H. F. 1929. The titanotheres of ancient Wyoming, Dakota, and Nebraska. U. S. Geological Survey, Monograph 55:pp. 1–953, 229 pl.
- PEARSON, H. S. 1927. On the skulls of Early Tertiary Suidae, together with an account of the otic region in some other primitive Artiodactyla. *Philosophical Transactions of the Royal Society of London. Series B*, 215:389–460.
- PILGRIM, G. E. 1940a. The dispersal of the Artiodactyla. *Biological Review*, 16:134–163.
- PILGRIM, G. E. 1940b. Middle Eocene mammals from North-West India. *Proceedings of the Zoological Society of London*, 110:127–152, 1 pl.
- RADINSKY, L. B. 1965. Early Tertiary Tapiroidea of Asia. *Bulletin of the American Museum of Natural History*, 129(2):181–263, 4 pl.
- RADINSKY, L. B. 1967. A review of the rhinocerotoid family Hyracodontidae (Perissodactyla). *Bulletin of the American Museum of Natural History*, 136(1):1–45.
- RADINSKY, L. B. 1969. The early evolution of the Perissodactyla. *Evolution*, 23:308–328.
- RAGE J. C. 1987. Lower vertebrates from the early-middle Eocene Kuldana Formation of Kohat (Pakistan): Squamata. *Contributions from the Museum of Paleontology, University of Michigan* 27(7):187–193.
- RANGA RAO, A. 1971. New mammals from Murree (Kalakot Zone) of the Himalayan foot hills near Kalakot, Jammu and Kashmir State, India. *Journal of the Geological Society of India*, 12(2):125–134.
- RANGA RAO, A. 1972. New mammalian genera and species from the Kalakot Zone of Himalayan foot hills near Kalakot, Jammu and Kashmir state, India. *Directorate of Geology, Oil, and Natural Gas Commission, Special Paper 1*:1–22, 4 pl.
- RANGA RAO, A., and V. N. MISRA. 1983 (for 1981). On the new Eocene mammal localities in the Himalaya foot-hills. *Himalayan Geology*, 11:422–428.
- RANGA RAO, A., and F. A. OBERGFELL. 1973. *Hyrachyus asiaticus*, new species of an upper Eocene tapiroid (Mammalia, Perissodactyla) from Kalakot India. *Directorate of Geology, Oil, and Natural Gas Commission, Special Paper 3*:1–8, 1 pl.
- ROSE, K. D. 1982. Skeleton of *Diacodexis*, oldest known artiodactyl. *Science*, 216:621–623.
- ROSE, K. D. 1985. Comparative osteology of North American dichobunid artiodactyls. *Journal of Paleontology*, 59(5):1203–1226.
- RUSSELL, D. E., and P. D. GINGERICH. 1980. Un nouveau primate omomyide dans l'Eocène du Pakistan. *Comptes Rendus de l'Académie des Sciences de Paris, Série 2*, 291: 621–624.
- RUSSELL, D. E. and P. D. GINGERICH. 1981. Lipotyphla, Proteutheria (?), and Chiroptera (Mammalia) from the early-middle Eocene Kuldana Formation of Kohat (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan*, 25(14):277–287.
- RUSSELL, D. E. and P. D. GINGERICH. 1987. Nouveaux primates de l'Eocène de Pakistan. *Comptes Rendus de l'Académie des Sciences de Paris, Série 2*, 304:209–214.
- SAHNI, A., S. B. BHATIA, J.-L. HARTENBERGER, J.-J. JAEGER, K. KUMAR, J. SUDRE, and M. VIANEY-LIAUD. 1981. Vertebrates from the Subathu Formation and comments on the biogeography of Indian subcontinent during the early Paleogene. *Bulletin de la Société Géologique de France*, 23(7):689–695.
- SAHNI, A., S. B. BHATIA, and K. KUMAR. 1983. Faunal evidence for the withdrawal of the Tethys in the Lesser Himalaya, Northwestern India. *Bollettino della Società Paleontologica Italiana*, 22(1–2):77–86.
- SAHNI, A., and K. KHARE. 1972 (for 1971). Three new Eocene mammals from Rajauri District, Jammu and Kashmir. *Journal of the Paleontological Society of India*, 16:41–53.
- SAHNI, A., and K. KHARE. 1973 (for 1972). Additional Eocene mammals from the Subathu Formation of Jammu and Kashmir. *Journal of the Paleontological Society of India*, 17:31–49.
- STEHLIN, H. G. 1908. Die Säugetiere des schweizerischen Eocäns. *Abhandlungen der schweizerischen Paleontologischen Gesellschaft*, 35:690–837.
- SUDRE, J. 1978. Les artiodactyles de l'Eocène moyen et supérieur d'Europe occidentale. *Memoirs et Travaux de l'Ecole Pratique des Hautes Etudes de l'Institut de Montpellier*, 7:1–229, 23 fig., 20 tab., 11 pl.
- SUDRE, J., D. E. RUSSELL, P. LOUIS, and D. E. SAVAGE. 1983. Les artiodactyles de l'Eocène inférieur d'Europe (Deuxième partie). *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 5, Section C*, (4):339–365.
- THEWISSEN, J. G. M., D. E. RUSSELL, P. D. GINGERICH, and S. T. HUSSAIN. 1983. A new dichobunid artiodactyl (Mammalia) from the Eocene of North-West Pakistan. *Dentition and Classification*. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Serie B*, 86(2):153–180.

- VAN VALEN, L. 1965. Paroxyclaenidae, an extinct family of Eurasian mammals. *Journal of Mammalogy*, 46(3):388–397.
- WELLS, N. A. 1983. Transient streams in sand-poor redbeds: early-middle Eocene Kuldana Formation of northern Pakistan. *Special publications of the International Association of Sedimentologists* 6:393–403.
- WELLS, N. A., and P. D. GINGERICH. 1983. Review of the Eocene Anthracobunidae (Mammalia, Proboscidea) with a new genus and species, *Jozaria palustris*, from the Kuldana Formation of Kohat (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan*, 26(7):117–139.
- WEST, R. M. 1980. Middle Eocene large mammal assemblage with Tethyan affinities, Ganda Kas region, Pakistan. *Journal of Paleontology*, 54(3):508–533.
- WEST, R. M., and J. R. LUKACS. 1979. Geology and vertebrate-fossil localities. Tertiary continental rocks, Kala Chitta Hills, Attock District, Pakistan. *Contributions in Biology and Geology, Milwaukee Public Museum*, 26: pp. 1–20.
- WOO J.-K. and CHOW M.-C. 1957. New materials of the earliest primate known in China, *Hoanghoniuss stehlini*. *Vertebrata Palasiatica*, 1(4):267–272, 2 pl.
- YOUNG, C. C. 1937. An early Tertiary vertebrate fauna from Yuanchu. *Bulletin of the Geological Society of China*, 17(3–4):413–438.
- ZDANSKY, O. 1930. Die alttertiären Säugetiere Chinas nebst stratigraphischen Bemerkungen. *Palaeontologia Sinica, Serie C*, 6(2):1–87, 5 pl.