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New early Eocene tapiromorph perissodactyls from the Ghazij Formation of Pakistan, with implications for mammalian biochronology in Asia

PIETER MISSIAEN and PHILIP D. GINGERICH



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Early Eocene mammals from Indo-Pakistan have only recently come under study. Here we describe the first tapiromorph perissodactyls from the subcontinent. *Gandheralophus minor* gen. et sp. nov. and *G. robustus* sp. nov. are two species of Isectolophidae differing in size and in reduction of the anterior dentition. *Gandheralophus* is probably derived from a primitive isectolophid such as *Orientolophus hengdongensis* from the earliest Eocene of China, and may be part of a South Asian lineage that also contains *Karagalax* from the middle Eocene of Pakistan. Two specimens are referred to a new, unnamed species of Lophialetidae. Finally, a highly diagnostic M3 and a molar fragment are described as the new eomorpid chalicotheriid *Litolophus ghazijensis* sp. nov. The perissodactyls described here, in contrast to most other mammalian groups published from the early Eocene of Indo-Pakistan, are most closely related to forms known from East and Central Asia, where Eocene tapiromorphs are diverse and biochronologically important. Our results therefore allow the first biochronological correlation between early Eocene mammal faunas in Indo-Pakistan and the rest of Asia. We suggest that the upper Ghazij Formation of Pakistan is best correlated with the middle or late part of the Bumbanian Asian Land Mammal Age, while the Kuldana and Subathu Formations of Pakistan and India are best correlated with the Arshantan Asian Land Mammal Age.

Key words: Mammalia, Perissodactyla, Isectolophidae, Lophialetidae, Eomoropidae, biochronology, Eocene, Ghazij Formation, Pakistan.

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Introduction

The Indian subcontinent has a relatively poor fossil record for research on the origin and evolution of Eocene land mammals, despite the important role attributed to it in some biogeographic hypotheses (Krause and Maas 1990). Middle Eocene mammalian faunas have been known since 1940 (Pilgrim 1940; Dehm and Oettingen-Spielberg 1958; Ranga Rao 1972; Sahni and Khare 1971; Sahni and Jolly 1993; and others). However, early Eocene mammalian faunas from this region have only been found fairly recently (Gingerich et al. 1997, 1998, 2001; Clyde et al. 2003), and in the past five years a more detailed picture of these faunas has started to emerge (Rose et al. 2006, 2009a, b; Smith et al. 2007; Gunnell et al. 2008; Kumar et al. 2010; Missiaen et al. 2011).

Here we describe the first early Eocene tapiromorph perissodactyls from Indo-Pakistan. The specimens were col-

lected in 1999 in the Kingri area in Balochistan (Pakistan), at Gandhera Quarry and two nearby localities (Fig. 1). They were found in the upper part of the upper Ghazij Formation and are probably about 51.5 to 52.5 Ma in age, correlative with the start of the Bridgerian Land Mammal Age in North America (Gunnell et al. 2008; Missiaen et al. 2011).

Tapiromorpha contains the important perissodactyl groups Tapiroidea, Rhinoceroidea, and Chalicotheroidea, as well as a number of primitive taxa that have been allied with them, although their precise relationships are still ambiguous (see Hooker 2005). Tapiromorpha are especially abundant in the Eocene faunas of East Asia, where they play an important role in mammalian biochronology (Ting 1998; Wang et al. 2007a). The present study of the oldest tapiromorphs from Indo-Pakistan therefore allows the first biochronological correlation between early Eocene mammal faunas in Indo-Pakistan and East Asia.

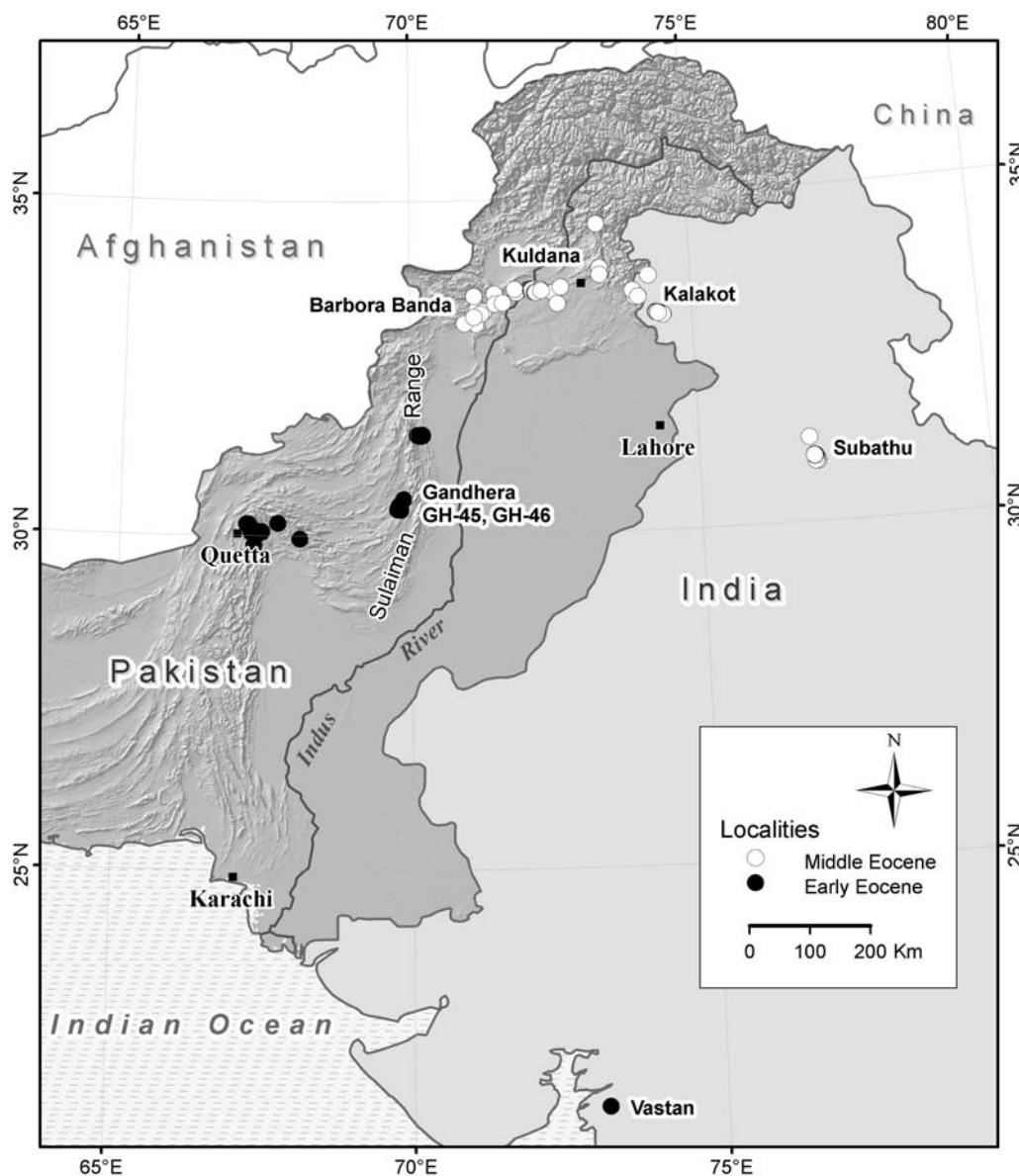


Fig. 1. Location map of Pakistan and western India showing the distribution of localities yielding early Eocene (solid circles) and middle Eocene (open circles) continental vertebrates. Tapiromorpha described here come from the Gandhera (GH-40), GH-45, and GH-46 localities in the upper part of the upper Ghazij Formation. All are near Kingri in Balochistan Province.

Institutional abbreviation.—GSP-UM, Geological Survey of Pakistan–University of Michigan collection, Quetta, Pakistan.

Other abbreviation.—ALMA, Asian Land Mammal Age.

Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Perissodactyla Owen, 1848

Suborder Tapiromorpha Haeckel, 1866

Family Isectolophidae Peterson, 1919

Genus *Gandheralophus* nov.

Type species: *Gandheralophus minor* sp. nov.; see below.

Etymology: *Gandhera*, referring to Gandhera Quarry, the locality from where this genus was first reported; and Greek *lophus*, crest, a common root in tapiromorph names.

Included species.—*Gandheralophus minor* sp. nov. and *G. robustus* sp. nov.

Diagnosis.—Small isectolophids with a robust dentition and a degree of lophodonty similar to *Homogalax* or *Karagalax*. Dental formula $?.?.?.3/3.1.3-4.3$; P3-4 with closely spaced paracone and metacone; upper molars relatively rectangular with only a weak labial projection of the parastyle, with a short and straight ectoloph, with a relatively transverse protoloph and metaloph, and with a very weak paraconule and no distinct metaconule; M3 with a rounded posterior border.

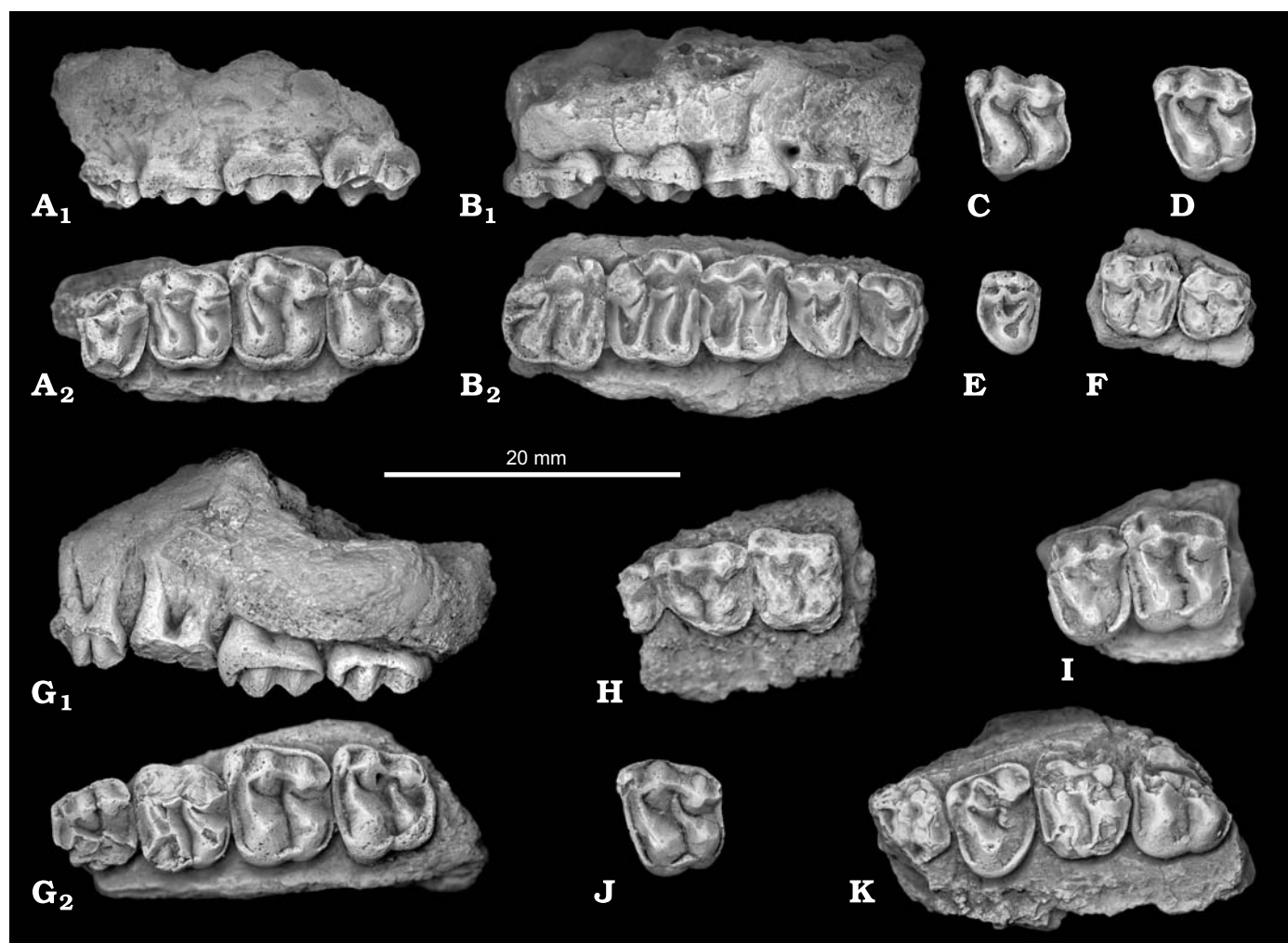


Fig. 2. Upper dentition of tapiromorph perissodactyls *Gandheralophus minor* gen. et sp. nov. (A–F) and *Gandheralophus robustus* gen. et sp. nov. (G–K) from the early Eocene upper Ghazij Formation in Pakistan. **A.** GSP-UM 4710, left P4–M3 in labial (A₁) and occlusal (A₂) views. **B.** GSP-UM 4716, right P3–M3 in labial (B₁) and occlusal (B₂) views. **C.** GSP-UM 5288, left M2 in occlusal view. **D.** GSP-UM 5284, left M2 in occlusal view. **E.** GSP-UM 4787, right P3 in occlusal view. **F.** GSP-UM 4696, right DP3–4 in occlusal view. **G.** GSP-UM 4722, left P4–M3 in labial (G₁) and occlusal (G₂) views. **H.** GSP-UM 4690, left DP2–4 in occlusal view. **I.** GSP-UM 4711, left P4–M1 in occlusal view. **J.** GSP-UM 5274, left M1 in occlusal view. **K.** GSP-UM 4709, left P3–M2 in occlusal view.

p3–4 with well-developed but not strongly anteriorly projecting paracristid; lower molars without a metastylid and with a weak hypoconulid. Differs from other isectolophids by smaller m1–2 hypoconulids, and from all isectolophids except *Orientolophus* by its smaller size and weaker upper molar parastyle. Differs from *Orientolophus* by stronger lophodonty, a stronger parastyle on the upper molars, and lower molars with a more abruptly angled paracristid and a stronger posterior size increase. Differs from *Cardiolophus* by stronger lophodonty and a smaller upper molar parastyle. Differs from *Homogalax* and *Chowliia* by less trapezoidal upper molars with weaker parastyles and conules and a relatively smaller M3. Differs from *Cardiolophus*, *Homogalax*, and *Chowliia* by weaker upper molar conules, a more molarized p3–4 trigonid and lower molars without a metastylid. Differs from *Karagalax* by a weaker posterior size increase of the molars and a more robust overall dentition, a more

closely spaced paracone and metacone on P3–4, less trapezoidal upper molars and a less developed paracristid on p3–4. Differs from *Isectolophus* by weaker lophodonty and a weaker posterior size increase, the presence of a small paracone on the upper molars, a larger angle between the ectoloph and the upper molar cross-lophs, a more lingually closed talonid basin on the lower molars and a labiolingually wider m3 hypoconulid lobe.

Stratigraphic and geographic range.—Late early Eocene (Ypresian); upper part of the upper Ghazij Formation; Gandhera Quarry, Balochistan (Pakistan).

Gandheralophus minor sp. nov

Figs. 2A–F, 3A–D; Table 1.

Etymology: From Latin *minor*, smaller, referring to the small size of the species, which is smaller than any other isectolophid currently known.

Holotype: GSP-UM 6770, a partial dentary with right p3–m3 in situ.

Table 1. Summary measurements (in mm) of *Gandheralophus minor* gen. et sp. nov. and *G. robustus* gen. et sp. nov. specimens from the early Eocene upper Ghazij Formation in Pakistan. Abbreviations: L, anteroposterior length; Max, maximum; Min, minimum; N, number of measurements; SD, standard deviation; W, labiolingual width.

	Upper dentition								Lower dentition							
	P4 L	P4 W	M1 L	M1 W	M2 L	M2 W	M3 L	M3 W	P4 L	P4 W	M1 L	M1 W	M2 L	M2 W	M3 L	M3 W
<i>Gandheralophus minor</i> gen. et sp. nov.																
N	3	4	5	6	11	11	9	9	6	5	8	7	7	7	8	9
Min	4.47	5.68	5.70	6.82	6.16	6.99	6.02	7.20	4.36	2.80	5.16	3.35	6.35	4.39	7.81	4.12
Mean	4.98	6.05	5.88	6.98	6.47	7.56	6.38	7.38	4.95	3.19	5.74	3.74	6.58	4.55	8.40	4.45
Max	5.38	6.29	6.14	7.20	6.70	7.99	6.60	7.62	5.39	3.89	6.13	3.99	6.97	4.76	8.92	4.88
SD	0.46	0.28	0.17	0.15	0.28	0.35	0.21	0.15	0.35	0.42	0.32	0.22	0.26	0.13	0.43	0.26
<i>Gandheralophus robustus</i> gen. et sp. nov.																
N	3	4	2	3	4	6	3	2	1	1	3	3	4	4	5	7
Min	5.55	6.66	6.81	7.34	7.02	8.03	6.97	7.72	—	—	6.76	4.31	7.12	4.93	9.72	5.01
Mean	5.70	7.41	6.90	7.99	7.32	8.39	7.36	8.30	5.33	3.89	6.85	4.44	7.36	5.06	10.36	5.42
Max	5.87	8.02	6.98	8.76	7.64	8.73	8.15	8.87	—	—	6.93	4.54	7.71	5.26	11.25	5.98
SD	0.16	0.69	0.12	0.72	0.25	0.29	0.68	0.81	—	—	0.09	0.12	0.25	0.15	0.55	0.36

Type locality: Gandhera Quarry, Balochistan Province, Pakistan. GPS coordinates of the type locality are: 30.3852° N, 69.8238° E.

Type horizon: Late early Eocene (Ypresian); upper part of the upper Ghazij Formation; Gandhera Quarry, Balochistan (Pakistan).

Referred material.—GSP-UM 4686, left p4-m2; GSP-UM 4692, left DP4-M1; GSP-UM 4696, right DP3-4; GSP-UM 4698, right m2-3; GSP-UM 4700, right p4-m3; GSP-UM 4701, left m1-3; GSP-UM 4710, left P4-M3; GSP-UM 4715, right M1-2; GSP-UM 4716, right P3-M3; GSP-UM 4719, left dp4-m1; GSP-UM 4720, left m2-3; GSP-UM 4721, right m2-3; GSP-UM 4724, left P4-M2; GSP-UM 4787, right P3; GSP-UM 4788, right p4; GSP-UM 4789, right p4; GSP-UM 4834, right m3; GSP-UM 4835, left m3; GSP-UM 4838, left p4-m1; GSP-UM 4915, right DP4; GSP-UM 4916, left M2; GSP-UM 5275, left M3; GSP-UM 5277, right M2; GSP-UM 5279, left M2; GSP-UM 5280, left M2; GSP-UM 5282, right M3; GSP-UM 5284, left M2; GSP-UM 5285, right M3; GSP-UM 5286, right M3; GSP-UM 5288, left M2; GSP-UM 5290, left M3; GSP-UM 5292, left M3; GSP-UM 5293, left M1; GSP-UM 5294, right M1; GSP-UM 5295, right M2; GSP-UM 5300, left M2; GSP-UM 5301, right M1; GSP-UM 5324, right M1; GSP-UM 5326, left Max. M1-2; GSP-UM 5329, right M1; GSP-UM 5352, right m1; GSP-UM 5353, left m2-3; GSP-UM 5354, left m2; GSP-UM 5355, right m3; GSP-UM 5359, left m3; GSP-UM 5361, left m3; GSP-UM 5379, left p4; GSP-UM 5380, left dp4; GSP-UM 5431, left P3-M2; GSP-UM 5433, right M2-3; GSP-UM 5439, left M1; GSP-UM 5440, left M2; GSP-UM 5442, right M1; GSP-UM 5444, right m3; GSP-UM 5445, right p4; GSP-UM 6222, left MX; GSP-UM 6256, right M1; GSP-UM 6257, left M3; GSP-UM 6258, right M1; GSP-UM 6259, left M2; GSP-UM 6261, left M2; GSP-UM 6263, left M2; GSP-UM 6264, left M2; GSP-UM 6266, right MX; GSP-UM 6267, left M1; GSP-UM 6268, left P4; GSP-UM 6269, left P4; GSP-UM 6270, left m1-2; GSP-UM 6271, left m1; GSP-UM 6273, right m3.

Diagnosis.—*G. minor* differs from *G. robustus* in being ap-

proximately 15% smaller; in having a P4 with a complete metaloph; in having upper molars with a larger, more rounded parastyle cusp, a more closely placed paracone and metacone, and a more posteriorly directed metaloph; in having an M3 with a more reduced posterior region that sometimes presents accessory cusps or crests; in having a p1, a larger p2 and a more molariform p3; and in having an open trigonid on p4 and the lower molars.

Description.—P3 is a small, premolariform tooth. The labial side bears the small but distinct parastyle and the larger, closely spaced paracone and metacone. The lingual part of P3 bears a protocone, a distinct protoloph with a faint paraconule, and a weak metaloph. There is also a small anterior cingulum, and a large, rounded posterior cingulum without a hypocone.

P4 is larger than P3 and differs from it by a less closely spaced and slightly anteroposteriorly compressed paracone and metacone, and by a relatively larger protocone.

M1 is rectangular to somewhat trapezoidal in shape and slightly wider than long. The parastyle is placed anterior to the paracone and smaller than the latter. The metacone is slightly lower than the paracone, and is placed posterolingual to and clearly separated from the latter. The protoloph often presents a reduced paraconule and attaches to the ectoloph between the parastyle and the paracone. The metaloph attaches to the anterolingual corner of the metacone and lacks a metaconule. Labial and lingual cingula are variably developed, ranging from almost absent (Fig. 2C) to complete and continuous (Fig. 2A, D).

M2 is similar to M1, but markedly larger and slightly more trapezoidal.

M3 is similar in size to M2, but tapers strongly posteriorly and has a rounded posterior border. The M3 metacone is much smaller in size than on M1–2 and transversely compressed. The hypocone has a less lingual position than on M1 or M2. On the posterior part of M3, accessory structures are variably developed, including small cusps on the metaloph or the posterior border, or even a crest running

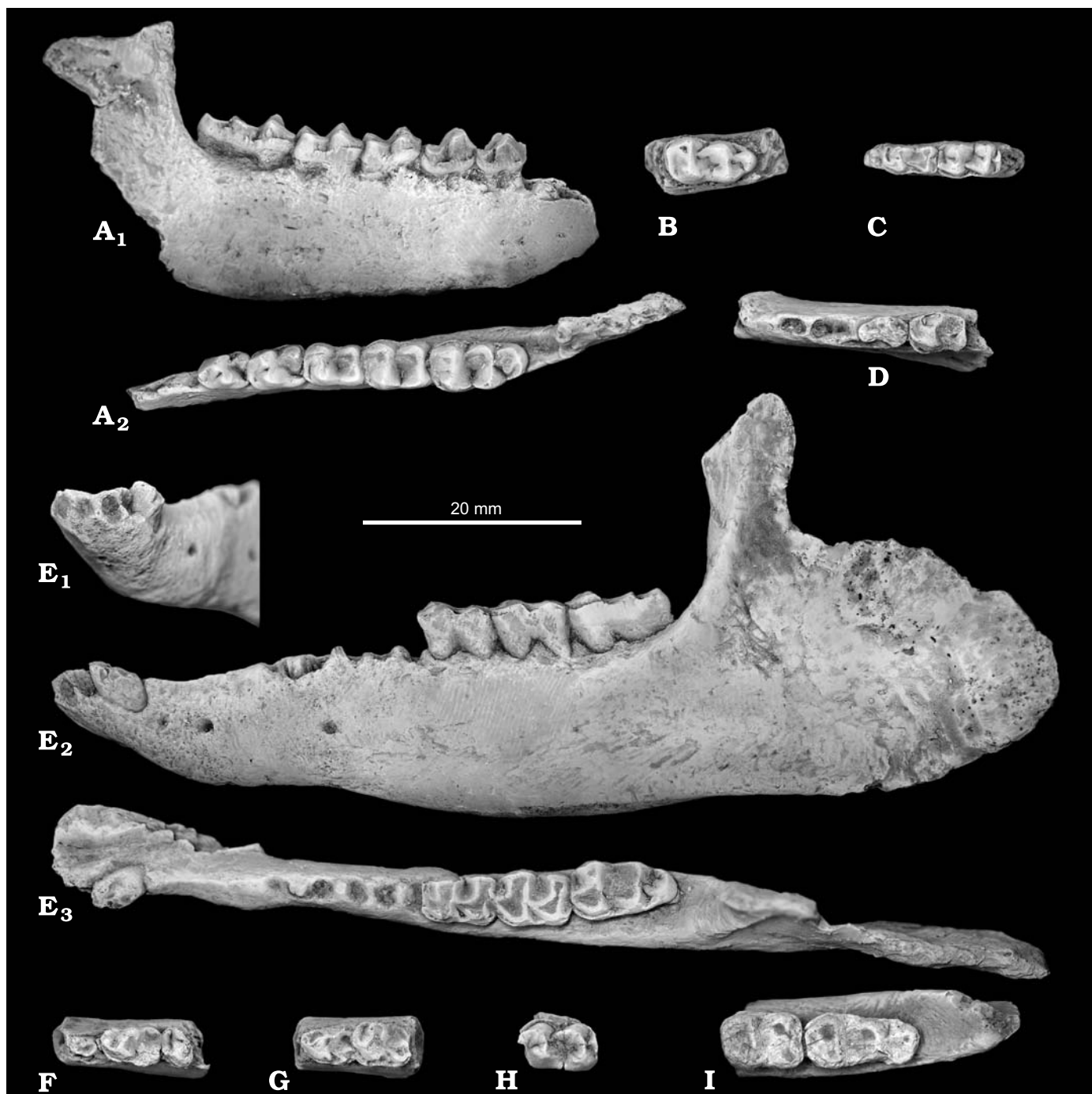


Fig. 3. Lower dentition of tapiromorph perissodactyls *Gandheralophus minor* gen. et sp. nov. (A–D) and *Gandheralophus robustus* gen. et sp. nov. (E–I) from the early Eocene upper Ghazij Formation in Pakistan. A. GSP-UM 6770, holotype, right p3–m3 in labial (A₁) and occlusal (A₂) views. B. GSP-UM 5355, right m3 in occlusal view. C. GSP-UM 4719, left dp4–m1 in occlusal view. D. GSP-UM 5445, left p3–4 and alveoli of p1–2 in occlusal view. E. GSP-UM 6768, holotype, left m1–3 and alveoli of right i1–left p4 in anterior (E₁), labial (E₂) and occlusal (E₃) views. F. GSP-UM 5360, left p3–4 and roots of p2 in occlusal view. G. GSP-UM 5446, left p3–4 in occlusal view. H. GSP-UM 6275, right m1 in occlusal view. I. GSP-UM 4717, right m2–3 in occlusal view. Note the difference in size and in reduction of the anterior dentition between both species.

from the middle of the metaloph to the posterior border of M3 (Fig. 2B).

DP3 is subquadrate with the anterior half transversely narrower than the posterior half, and with a well-separated paracone and metacone (Fig. 2F). A short protoloph runs anterolabially from the protocone, and a second, incomplete

crest runs posterolingually from the protocone to the base of the metacone. The hypocone of DP3 is clearly developed, but does not form a metaloph.

DP4 is fully molariform, mainly differing from M1 in being smaller and relatively narrower transversely.

The anterior lower dentition of *G. minor* is unknown, but

the holotype GSP-UM 6770 (Fig. 3A) and specimen GSP-UM 5445 (Fig. 3D) show the presence of a diastema, one large alveolus and two smaller alveoli in front of p3. These can be interpreted as the postcanine diastema, the large single root of p1 and the two roots of p2, which means that there was no diastema between p1 and p2. Based on the alveoli in GSP-UM 5445, p2 was about 10 percent shorter than p3.

The p3 is subrectangular and premolariform. The paracristid is short and placed anterolingual to the strong protoconid. The metaconid is slightly smaller than the protoconid and placed posterolingual to it. The talonid has one labially placed cusp that is connected to the base of the protoconid.

The p4 paracristid is much better developed than on p3, forming a crest that descends anteriorly from the protoconid and then curves lingually. The p4 protoconid and metaconid are subequal in size, with the metaconid placed directly lingual and only slightly posterior to the protoconid. The p4 talonid is slightly basined, but usually presents only a single, large and labially placed cusp.

The m1 is rectangular, with the protoconid and hypoconid subequal to or slightly more robust than the metaconid and entoconid. Wear is stronger on the labial side, lowering the labial cusps and crests faster than their lingual counterparts. The trigonid is short, with the paracristid running down only a little from the protoconid before abruptly turning lingually. The protolophid and hypolophid are distinct, but somewhat notched, and are oriented transversely or just slightly obliquely. The hypoconulid is strongly reduced, forming only a small cusp pressed against the middle part of the hypolophid.

The m2 is very similar to m1, mainly differing from it by its larger size and more robust appearance.

The m3 is similar in width to m2, but is distinctly longer and tapers strongly behind the trigonid. m3 has a distinct, basined hypoconulid lobe. The hypoconulid is usually robust and placed on the midline of the tooth or somewhat labial to it, with a posthypocristid running anteriorly towards the hypolophid. The hypoconulid lobe is variable in its development (Fig. 3A, B). In specimens where it is more strongly developed, it is more clearly basined, with a more labially placed hypoconulid and often an accessory cuspule lingual to the latter.

The dp4 is similar to m1, but transversely narrower, with a more anteriorly projecting paracristid and a smaller hypoconulid (Fig. 3C).

Gandheralophus robustus sp. nov.

Figs. 2G–K, 3E–I; Table 1.

Etymology: From Latin *robustus*, solid, referring to the larger size and more robust aspect of the dentition in comparison with *G. minor*.

Holotype: GSP-UM 6768, a partial jaw with left m1–3 in place, and alveoli of the right i1 and the left i1–p4.

Type locality: Gandhera Quarry (GSP-UM locality GH-40), Balochistan Province, Pakistan. GPS coordinates of the type locality are: 30.3852° N, 69.8238° E.

Type horizon: Late early Eocene (Ypresian); upper part of the upper Ghazij Formation; Gandhera Quarry, Balochistan (Pakistan).

Referred material.—GSP-UM 4690, left DP3–4; GSP-UM 4709, left P4–M2; GSP-UM 4711, left P4–M1; GSP-UM 4717, right m2–3; GSP-UM 4722, left P4–M3; GSP-UM 5273, left M2; GSP-UM 5274, left M1; GSP-UM 5276, left M1; GSP-UM 5278, left M2; GSP-UM 5281, left M2; GSP-UM 5283, left M3; GSP-UM 5287, left M2; GSP-UM 5289, left M1; GSP-UM 5291, right DP4; GSP-UM 5296, left M1; GSP-UM 5297, right M1; GSP-UM 5298, left M2; GSP-UM 5302, left M2; GSP-UM 5323, left M1–2; GSP-UM 5325, right M2–3; GSP-UM 5327, right M1; GSP-UM 5328, left M1–2; GSP-UM 5356, right m3; GSP-UM 5357, left m3; GSP-UM 5358, right m3; GSP-UM 5360, left p2–4; GSP-UM 5362, left m3; GSP-UM 5363, right m2; GSP-UM 5364, right m2; GSP-UM 5378, left m3; GSP-UM 5381, left m2; GSP-UM 5382, left m2; GSP-UM 5432 P4–M2; GSP-UM 5434 right M1; GSP-UM 5435, left DP4; GSP-UM 5436, left M1; GSP-UM 5437, left M2; GSP-UM 5438, right P4; GSP-UM 5441, left M2; GSP-UM 5443, left m3; GSP-UM 5446, left p3–4; GSP-UM 6255, right P4–M3; GSP-UM 6260, left M2; GSP-UM 6262, right M2; GSP-UM 6265, left M1; GSP-UM 6272, right m1; GSP-UM 6275, right m1.

Diagnosis.—*G. robustus* differs from *G. minor* in being larger in size and more robust in appearance; in having a P4 with a metaconule but without a complete metaloph; in having upper molars with an anteroposteriorly compressed parastyle cusp, a slightly stronger labial cingulum and a more anteriorly directed metaloph; in lacking p1, having a smaller p2 and having a p3 with a smaller metaconid; in having a closed trigonid on p4 and on the lower molars; and in having a relatively larger m3.

Description.—The P4 of *G. robustus* has a variably developed, anteroposteriorly compressed parastyle which it is clearly separated from the subequal, closely spaced paracone and metacone. The robust protocone is the largest cusp on P4, and is connected to the ectoloph by a distinct protoloph. There is no continuous metaloph on P4, but a premetaconule crista runs from the metaconule to the premetacrista.

M1 is rectangular to somewhat trapezoidal in shape and slightly wider than long. The small, anteroposteriorly compressed parastyle is positioned directly anterior to the paracone. The metacone is somewhat lower than the paracone and clearly separated from it in a more posterolingual position. The protoloph has a strongly reduced paraconule and attaches to the ectoloph between the parastyle and the paracone. The metaloph attaches to the ectoloph just anterior to the metacone. Labial and lingual cingula are variably developed, ranging from weakly developed to strongly developed and continuous.

M2 is similar to M1 but larger and more trapezoidal.

The dimensions of M3 are similar to those of M2, but M3 is distinctly more trapezoidal with a rounded posterior border. No accessory structures have been observed on the posterior part of M3.

A partial DP2 preserved on specimen GSP-UM 4690

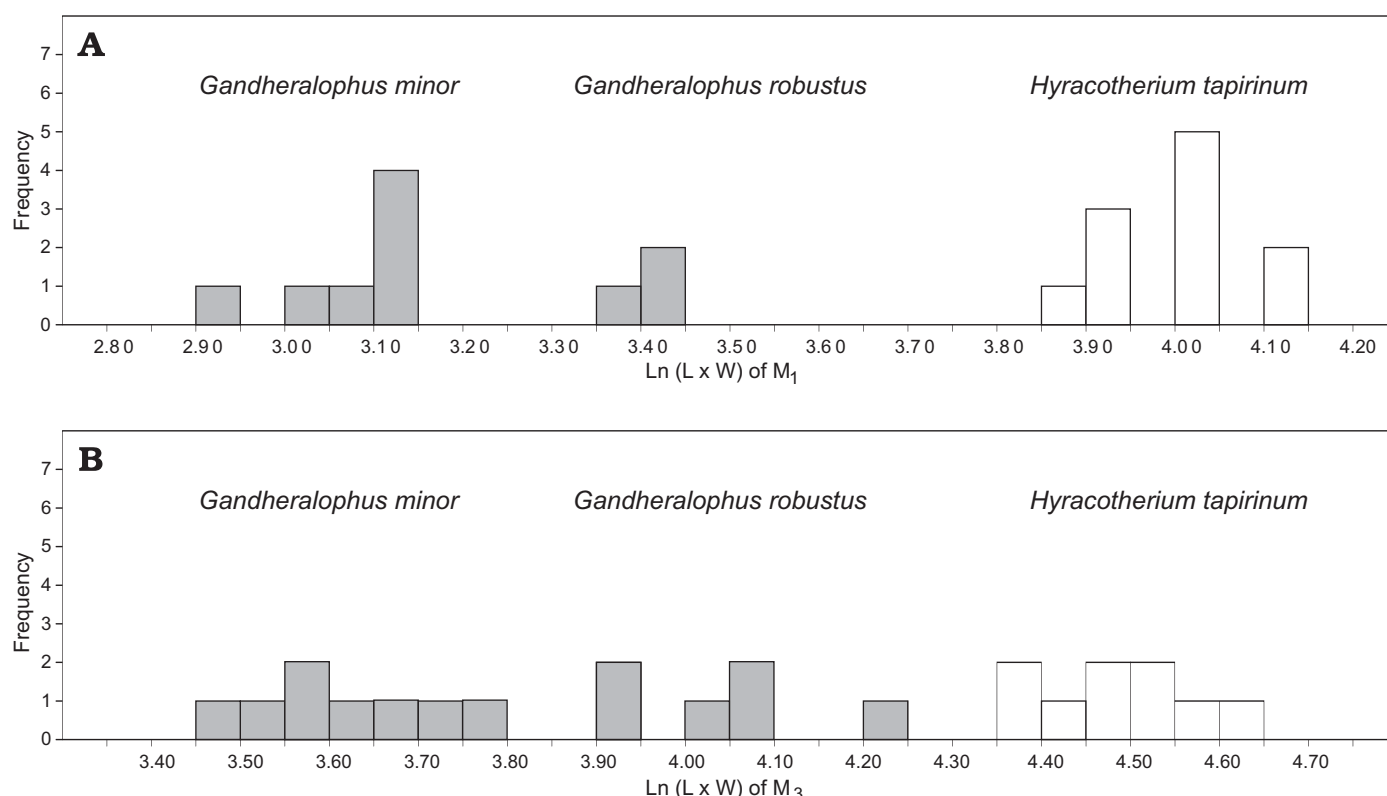


Fig. 4. Histograms showing the distribution of m1 (A) and m3 (B) size in *Gandheralophus* gen. nov. specimens of the two Pakistan species described here: *G. minor* and *G. robustus* (solid bars). The holotype of each species falls in the modal class. Comparison to a mixed male and female sample of the North American reference species, *Hyracotherium tapirinum* (Cope, 1875) (open bars; after Gingerich 1981) shows that the variability of *Gandheralophus* specimens is too great to represent a single species. Empirically, mammalian species have natural-log (length × width) ranges of 0.4 units (mean ± 2 standard deviations; Gingerich 1981). Each species shown here fits within a 0.4-unit range. Distributions of size of *G. minor* and *G. robustus* are strongly bimodal. Taken together they would have a range of 0.55 units (2.90 to 3.45) for m1 and of 0.80 units (3.45 to 4.25) for m3. Thus *G. minor* and *G. robustus* represent separate species.

(Fig. 2H) shows the presence of a metacone and a distinct hypocone.

DP3 is subtriangular with a well-developed parastyle, paracone and metacone which are all clearly anteroposteriorly separated. The protoloph is short and connects the well-developed protocone to the preparacrista. There is no real metaloph, but a distinct metaconule is placed between and slightly anterior to the metacone and hypocone.

P4 is fully molariform, mainly differing from M1 by its more anteriorly projecting parastyle and better developed paraconule and metaconule.

The anteriormost lower dentition of *G. robustus* is unknown, but the holotype specimen shows the closely appressed alveoli of a small i1, a moderately sized i2 and i3, and the root of a strong canine. The canine is followed by a diastema of 10.5 mm, followed in turn by two small, partially fused alveoli and then by four larger alveoli. This shows that p1 is absent in *G. robustus*, and that p2 is reduced. The symphysis was not constricted and its posterior margin is situated just before the alveoli of p2.

The p3 is subrectangular and premolariform (Fig. 3F–G). The paracristid projects strongly anteriorly and bears a marked paraconid. The strong protoconid is placed centrally on the trigonid, while the much smaller metaconid is placed postero-

lingual to it. The talonid presents a cusp that is placed just labial to the midline, with a crest running anteriorly towards the back of the protoconid.

The p4 is much wider than p3, with a metaconid that is subequal in size to the protoconid. The p4 paracristid is less anteriorly projecting than on p3 and does not have a paraconid. Instead, it forms a curved crest that runs down anteriorly from the protoconid, curves rather sharply into a transverse orientation and then curves again, running up the metaconid and forming a closed trigonid basin.

The m1 is rectangular (Figs. 3E, H) with a trigonid similar to that on p4. The transversely oriented protolophid and hypolophid are distinct, but clearly notched. The hypoconulid is strongly reduced, forming a small, low cusp pressed against the back of the hypolophid.

The m2 is very similar to m1, mainly differing from it by its larger size, more robust appearance, and shorter paracristid (Fig. 3I).

The m3 is distinctly larger than m2. The hypoconulid lobe is somewhat variable in development, but always forms a distinct basin with a posthypocristid directed towards the center of the hypolophid and usually a small, accessory lingual cusp.

Comparison.—The molars of *Gandheralophus minor* and *G.*

robustus show only few distinct morphological differences, and both species are therefore placed in the same genus *Gandheralophus*. The two species differ most distinctly in size (Fig. 4), and in the anterior dentition. *G. robustus* differs from *G. minor* in lacking p1, in having a smaller p2 and a morphologically simplified, more premolariform p3. These features can all be considered derived features, suggesting an evolutionary reduction of the anterior premolars in *G. robustus*. In this light, the weaker P4 metaloph in *G. robustus* might also be interpreted as a derived trait, and part of the same evolutionary tendency. Additionally, the relatively larger size of m3, and especially of the hypoconulid lobe, has also been considered a derived character in perissodactyls (Hooker 1994; Froehlich 2002). Combined, these observations suggest that *G. minor* is closer to the ancestral morphotype of the genus *Gandheralophus*, whereas *G. robustus* is characterized by its reduced anterior dentition, as well as its larger size and more robust teeth.

The low-crowned molars of *Gandheralophus*, together with its distinct protoloph and metalophs on the upper molars, upper molars with short, straight ectolophs and very small paraconules, and distinct hypolophids on the lower molars are typical of a group of basal tapiroids often placed in the probably paraphyletic family Isectolophidae (Radinsky 1963; Schoch 1989; Gingerich 1991; Ting 1993; Froehlich 1999; Lucas et al. 2003; Maas et al. 2001; Holbrook et al. 2004). *Gandheralophus* can be characterized as moderately lophodont, having relatively rectangular upper molars without a strongly projecting parastyle and with very weak upper molar conules, lacking a diastema between p1 and p2, having a p3–4 with a well-developed, molariform trigonid, and having lower molars with weak m1–2 hypoconulids and lacking a metastylid.

Its smaller size, the shape of the upper molars, the absence of a diastema between p1 and p2, the more molariform p3–4 and the absence of a metastylid clearly differentiate *Gandheralophus* from *Cardiolophus* and *Homogalax* from the early Eocene of North America (Gingerich 1991) and from similar taxa such as *Homogalax wutuensis* and *Chowliia laoshanensis* (Tong and Wang 2006) from the early Eocene of East Asia. The absence of a p1–2 diastema and of a metastylid are shared with *Isectolophus*, known from North America and Asia (Radinsky 1963; Lucas et al. 2003). However, *Gandheralophus* differs from *Isectolophus* by its less advanced lophodonty, upper molars with a small paraconule and more oblique cross-lophs, by lower molars with a more lingually closed talonid basin, and a labiolingually wider m3 hypoconulid lobe.

The more rectangular, less trapezoidal shape of the upper molars and the absence of a metastylid or twinned metacone make *Gandheralophus* morphologically closer to *Orientolophus* and *Karagalax*. The poorly known *Orientolophus* was described from the earliest Eocene Lingcha Formation in South China (Ting 1993). *Orientolophus* is generally considered to be the most primitive isectolophid known (Froehlich 1999; Hooker and Dashzeveg 2004), and is more primitive

than *Gandheralophus* in terms of a weaker parastyle and a weaker metaloph and hypolophid, as well as stronger upper molar conules and m1–2 hypoconulids. *Karagalax* was described by Maas et al. (2001) from the Barbora Banda locality in Pakistan, and is probably early middle Eocene in age (Gingerich 2003). *Karagalax* shares the absence of a diastema between p1 and p2 and a similar degree of lophodonty with *Gandheralophus*, but differs from the latter by a slightly more projecting upper molar parastyle, a transversely narrower lower dentition, and a strongly projecting paracristid on p3–4.

These observations may suggest that *Gandheralophus* and *Karagalax* formed a separate, South Asian isectolophid lineage that was possibly derived from a taxon close to *Orientolophus* from the earliest Eocene of South China. This southern lineage would then differ from other isectolophids from East and Central Asia and from North America by a smaller, less projecting parastyle, a more transverse metaloph and a smaller hypoconulid. This southern lineage would additionally differ from *Cardiolophus*- and *Homogalax*-like forms by the absence of a p1–2 diastema and lower molars with a more transverse hypolophid and lacking a metastylid, as well as possibly a stronger P3 postprotocrista. Finally, it would differ from *Isectolophus* by its less advanced lophodonty and a lingually less open lower molar talonid. The possibility of this southern isectolophid lineage is biogeographically significant, but it may require a more exhaustive phylogenetic analysis beyond the scope of this paper, as well as a better morphological knowledge of *Orientolophus* to be confirmed.

Infraorder Ceratomorpha Wood, 1937

Family Lophialetidae Matthew and Granger, 1925

Lophialetidae gen. et sp. indet.

Fig. 5A, B.

Referred material.—GSP-UM 6505, an isolated right M3; GSP-UM 6540, a left dentary with m2–3.

Description.—Specimen GSP-UM 6505 was found at GSP-UM locality GH-45 about 3 kilometers southeast of Kingri, and is a well-preserved, strongly lophodont M3 with a length of 14.6mm and a width of approximately 16.2mm. The parastyle is rounded and distinct, separated from the paracone but placed close to it (Fig. 5B). The paracone is the highest cusp of the tooth, with a markedly convex labial side and a flat lingual side. The metacone is strongly reduced, almost completely flat and barely higher than the rest of the ectoloph, forming an anteroposteriorly directed flange. The protoloph and metaloph are well-developed, unnotched and as high as the ectoloph. The protoloph is distinctly longer and slightly more robust than the metaloph. The protocone and hypocone are distinct and equal in height, but the protocone is more robust. The anterior cingulum is distinct but narrow and there is a small, short posterior cingulum. There are no labial or lingual cingula.

Specimen GSP-UM 6540 was collected from GSP-UM locality GH-46, in the same horizon as specimen GSP-UM 6505, about 500 meters southeast of locality GH-45. This

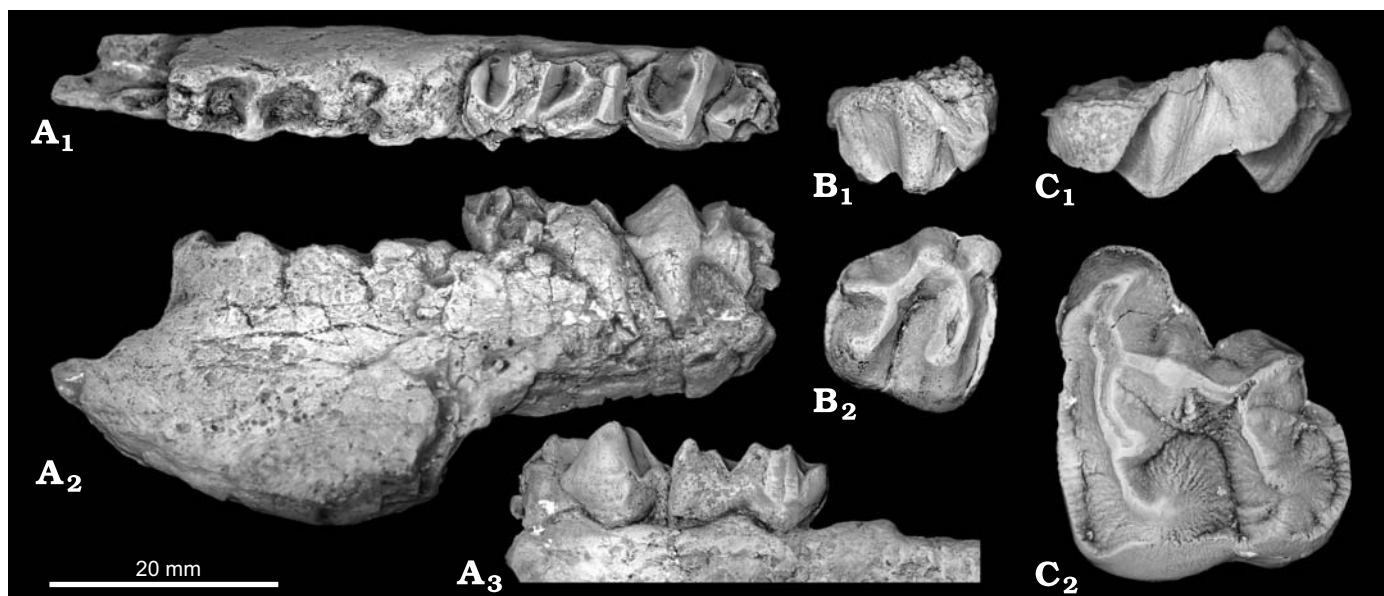


Fig. 5. Lower dentition of Lophialetidae and Eomoropidae from the early Eocene upper Ghazij Formation in Pakistan. **A, B.** Lophialetidae gen. et sp. indet. **A.** GSP-UM 6540, left m2–3 in occlusal (A₁), labial (A₂), and lingual (A₃) views. **B.** GSP-UM 6505, right M3 in labial (B₁) and occlusal (B₂) views. **C.** Eomoropid *Litolophus ghazijensis* sp. nov., GSP-UM 6519, left M3 in labial (C₁) and occlusal (C₂) views.

specimen consists of a partial dentary with strongly lophodont m2–3 in place, preceded by five alveoli for the posterior root of p3 and the roots of p4 and m1 (Fig. 5A). Both molars are severely damaged, but m2 was approximately 14.6 mm long with an estimated trigonid width of 8.6 mm, while the width of the m3 trigonid was about 8.8 mm. Both molars have a well-developed but relatively low paracristid that descends anterolingually from the protocone in a smooth curve. The protoconid is distinct and more robust than the metaconid, but is fully integrated into the paracristid and protolophid. The metaconid is positioned posterolingual to the protoconid and has a distinct anterolabial rib jutting out of the protolophid. The talonid is not well preserved on either of the molars, but the hypolophid was high and distinct, and oriented parallel to the protolophid. The cristid obliqua runs anterolingually from the hypoconid towards the posterolingual corner of the protoconid, but shows a distinct notch at the point of attachment to the protolophid.

Comparison.—Based on size and morphological compatibility, GSP-UM 6505 and GSP-UM 6540 can be readily assigned to the same taxon, which is characterized by strong lophodonty, with the upper molars being marked by a prominent parastyle, a lack of conules and a metacone that is reduced to an anteroposteriorly directed flange, at least on M3. The lower molars show a similarly distinct lophodonty with a prominent but low paracristid and cristid obliqua. The strongly lophodont condition is typical of ceratomorph perissodactyls, and within this group the flat metacone and the distinct but not strongly developed paracristid and cristid obliqua are found only in the Asian endemic family Lophialetidae and in primitive rhinocerotoids such as *Hyrachyus* (Radinsky 1969).

The wear pattern on GSP-UM 6505, with the protoloph wearing down from the top and the metaloph wearing down

from the front, supports this assignment to either lophialetids or rhinocerotoids (Radinsky 1965). Both groups can be unequivocally distinguished based on the upper premolars and the development of the m3 hypoconulid lobe, but this information is unfortunately missing for the taxon from the Ghazij Formation. The Ghazij material however differs from *Hyrachyus* by an uncompressed and less labial parastyle, a paracone with a more convex labial side and a flat lingual side, the absence of an anterolingual rib on the lower molar protoconid, and possibly the absence of an upper molar labial cingulum.

The Ghazij taxon differs from more derived rhinocerotoids by a subquadrangular M3, an unreduced parastyle, and by a low paracristid and cristid obliqua (Prothero et al. 1989). Within Lophialetidae, the morphology of the Ghazij taxon seems to be intermediate between *Schlosseria* on the one hand and *Lophialetes* and *Eoletes* on the other (Matthew and Granger 1925; Radinsky 1965; Lucas et al. 1997), most markedly because of the shape of the M3 metacone and the height of the lophs. The Ghazij taxon resembles *Schlosseria magister* in its parastyle morphology and a less triangular M3 with a more transverse metaloph. The Ghazij taxon is, however, closer to *Lophialetes* and *Eoletes* in size, as well as in terms of its flat lingual side of the paracone.

Kalakotia simplicidentata from the middle Eocene of India and Pakistan is sometimes placed in the family Lophialetidae (Ranga Rao 1972; Russell and Zhai 1987; Thewissen et al. 2001). Other studies of perissodactyl evolution do, however, show that *Kalakotia* is not a lophialetid, most clearly by the absence of a complete lophoid loop on P3–4 (Hooker 1989; Schoch 1989). Although there are some similarities between the Ghazij material described here and *Kalakotia*, the Ghazij taxon differs from *Kalakotia* by its larger size and less anteroposteriorly elongated shape, as well as by higher lophs of the

upper and lower molars. The Ghazij taxon additionally differs from *Kalakotia* by an M3 with a weaker parastyle, a more flattened paracone and metacone, and a different wear pattern, as well as by lower molars with an anterolingually flat paracone and a notched cristid obliqua.

Based on the similarities and differences noted above, we suggest that GSP-UM 6505 and GSP-UM 6540 represent a new, previously unknown species of Lophiaetidae. The phylogenetic relationships within this family are, however, unclear, even for taxa where many specimens are available (see Lucas et al. 1997). We therefore refrain from suggesting more detailed affinities or formally naming a new taxon.

Stratigraphic and geographic range.—Late early Eocene (Ypresian); upper part of the upper Ghazij Formation; Kingri area, Balochistan (Pakistan).

Infraorder Ancylopoda Cope, 1889

Superfamily Chalicotherioidea Gill, 1872

Family Eomoropidae Gill, 1872

Genus *Litolophus* Matthew and Granger, 1925

Type species: *Litolophus gobiensis* Matthew and Granger, 1925; Arshantan (middle? Eocene), Arshanto Formation, Nuhetingboerhe, Inner Mongolia.

Included species.—*Litolophus gobiensis* and *L. ghazijensis* sp. nov.

Stratigraphic and geographic range.—Early to middle Eocene of Asia and Indo-Pakistan.

Litolophus ghazijensis sp. nov.

Fig. 5C.

Etymology: Referring to the Ghazij Formation in Pakistan, where the specimen was found.

Holotype: GSP-UM 6519, an isolated left M3.

Type locality: GSP-UM locality GH-46, Balochistan Province, Pakistan. GPS coordinates of the type locality are: 30.4158° N, 69.7862° E.

Type horizon: Late early Eocene (Ypresian); upper part of the upper Ghazij Fm; Kingri area, Balochistan (Pakistan).

Referred material.—GSP-UM 6534, right upper molar fragment.

Diagnosis.—Chalicotherioid similar to *Litolophus gobiensis* in size, in lacking a mesostyle, and in having a posterolabially rotated metacone; differing from *L. gobiensis* in having a more posterior paracone, in having a stronger posterolabial rotation of the metacone, and in having a metaloph that is parallel to the protoloph and not posterolabially rotated and in line with the ectoloph as in *L. gobiensis*.

Description.—Specimen GSP-UM 6519 is an isolated M3 with a length of 27.3 mm and a width of 28.3 mm. The parastylar lobe is prominently projecting anterolabially, but the parastyle cusp itself is mostly flattened. The paracone is distinct and bears a marked labial rib. There is no mesostyle. The metacone is positioned posterior to the paracone and is not much higher than the ectoloph, but still clearly visible. The metacone is flattened, with an anterolingual-postero-

labial orientation roughly parallel to the parastyle. The strong protoloph attaches high onto the ectoloph, but is distinctly notched lingual to the paraconule. The paraconule is situated at the labiolingual midpoint of the protoloph, but is markedly posteriorly displaced from the main axis of the latter. The protocone is a robust cusp that extends posteriorly from the protoloph. The distinct metaloph has no sign of a metaconule and is slightly higher than the protoloph and roughly parallel to it. The hypocone is placed directly posterior to the protocone and is slightly higher than the protocone, but much less robust. GSP-UM 6519 has distinct anterior and posterior cingula and no real lingual cingulum. There is some minor damage to the labial edge of the tooth, but the labial cingulum was probably weak.

Specimen GSP-UM 6534 is a partial hypocone of a right upper molar found at locality GH-45, and is identical to GSP-UM 6519 in all preserved features.

Comparison.—A molar protoloph interrupted by a paraconule, and a high molar metaloph without a metaconule are considered two typical and diagnostic traits of the superfamily Chalicotherioidea (Radinsky 1964). Within this group, the absence of a mesostyle is seen only in the genera *Litolophus*, *Lophiaspis*, *Paleomoropus*, and *Protomoropus*, although the chalicotherine affinities of the latter three genera have been questioned (Fischer 1977; Lucas and Kondrashov 2004). *Litolophus ghazijensis* differs from *Paleomoropus* and *Protomoropus* by its significantly larger size, stronger lophs, and more projecting parastyle. *L. ghazijensis* differs from *Lophiaspis* in having a less labial paracone.

Litolophus ghazijensis differs from these three genera and resembles *L. gobiensis* by a posteriorly displaced paraconule and protocone, and by a posterolabially rotated metacone. In addition, it resembles *L. gobiensis* in having a relatively deeply notched protoloph lingual to the paraconule, in having a high hypocone with posterolabial and anterolingual flanges, and in having an indistinct accessory crest that is present posterolingual to the paracone of GSP-UM 6519 and in some *L. gobiensis* specimens (Bai et al. 2010). *L. ghazijensis*, however, differs from *L. gobiensis* by a more vertical parastyle with a less convex anterolabial side and by a stronger posterior displacement of the paraconule. Additionally, in *L. ghazijensis* the metacone is more strongly rotated and is parallel to the parastyle, whereas the metaloph is not rotated as in *L. gobiensis* but remains parallel with the protoloph as in other Eocene chalicotheres.

Although the chalicotherine material from the Ghazij Formation is currently very limited, the morphology of GSP-UM 6519 is highly diagnostic, clearly indicating affinities with the genus *Litolophus* and differences from *L. gobiensis*.

Discussion

Biogeography.—From the comparisons above, it is clear that the tapiromorph perissodactyls from the upper part of the

upper Ghazij Formation are most closely linked to fossil taxa from Pakistan and Asia. Although this might seem an obvious conclusion, it is remarkable, because primates from the Ghazij formation are thought to be related to European taxa, and to be isolated from East Asian or Burmese taxa (Gunnell et al. 2008). Similarly, the Vastan fauna, the only other early Eocene mammal fauna currently known from Indo-Pakistan, also mainly displays similarities to European faunas (Smith et al. 2007, Rose et al. 2009a, b; Kumar et al. 2010), and only very few similarities to Asian faunas (Rose et al. 2008).

The study of both Ghazij and Vastan mammals is not yet completed, but preliminary faunal lists (Gingerich et al. 2001; Rose et al. 2006) and published data on fossil primates (Gunnell et al. 2008, Rose et al. 2009a) seem to indicate that the two faunas are not very similar. In this respect, it is interesting to note that the Ghazij Formation sediments are thought to be of deltaic origin, shed eastward by an oceanic island chain called the Ghazij Islands (Gingerich et al. 1997; Clyde et al. 2003). As such, the Ghazij Islands were seemingly separated from the main Indo-Pakistan subcontinent by a sea strait. This geographic separation, paleo-environmental differences, and differences in age may account for the faunal differences between the Ghazij and Vastan faunas.

Biochronology.—Few attempts have been made to correlate the early Eocene mammal faunas of Indo-Pakistan with those from elsewhere in Asia, mainly because of the limited knowledge of the early Eocene of Indo-Pakistan and the lack of shared taxa. Our results are the first to allow such a biochronological correlation, especially since tapiromorph perissodactyls play an important role in Eocene mammal biochronology in East Asia (Ting 1998; Wang et al. 2007a; Missiaen 2011).

The Ghazij Formation of Pakistan has yielded three distinct mammal faunas. The mammal fauna from the middle Ghazij Formation consists of quettacyonids and the anthracobunid *Nakusia*, while the lower part of the upper Ghazij Formation is characterized by an abundance of tillodonts and quettacyonids (Gingerich et al. 1997, 1998, 2001; Clyde et al. 2003).

Quettacyonids and tillodonts are absent from the upper part of the upper Ghazij Formation, while tapiromorph perissodactyls are only present from this level onwards. Because of these changes in faunal composition, the faunas from the middle Ghazij Formation and from the lower part of the upper Ghazij Formation can be considered as markedly more archaic and endemic (Clyde et al. 2003), and a biochronological correlation is only possible for the fauna from the upper part of the upper Ghazij Formation.

Microfossils and paleomagnetic studies indicate a late early Eocene age for the upper part of the upper Ghazij Formation (Gingerich et al. 1997, 2001; Clyde et al. 2003), suggesting an initial correlation with the Bumbanian or Arshantan Asian Land Mammal Age (ALMA) in East and Central Asia. The Bumbanian and Arshantan are often correlated to

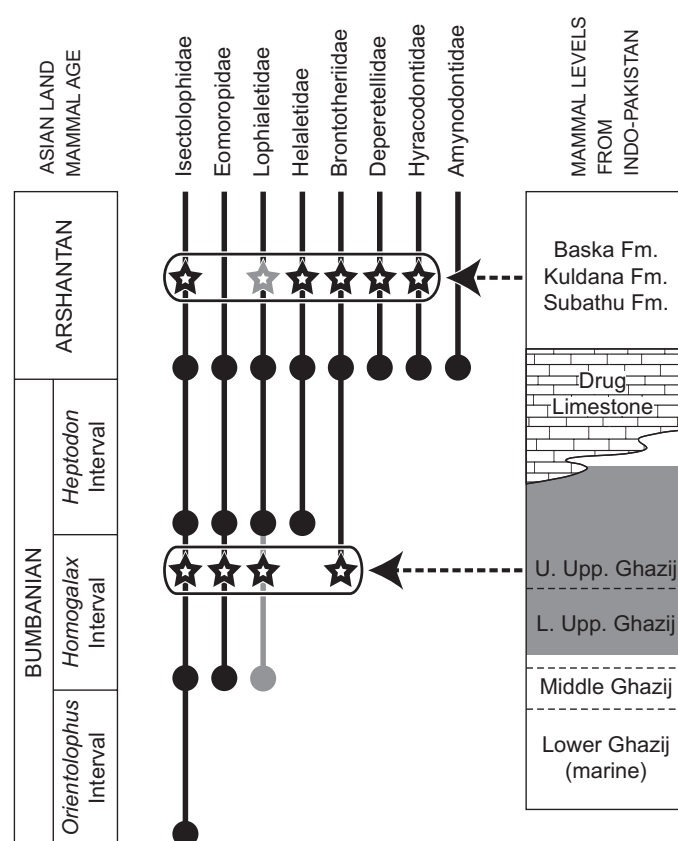


Fig. 6. Biochronological correlation of early and middle Eocene mammal levels from Indo-Pakistan (right) to the Asian Land Mammal Age (left) defined in East and Central Asia. Circles indicate the presence of perissodactyl families in a biochronological interval in East and Central Asia, stars indicate their presence in Indo-Pakistan. Gray symbols indicate taxonomic uncertainties. The faunas from the middle Ghazij Formation and from the lower part of the upper Ghazij Formation lack tapiromorphs and other biochronologically informative taxa, and are characterized by an abundance of Quettacyonidae and Tillodontia. Asian mammal biochronology is based on Tsubamoto et al. (2004) and Missiaen (2011). Abbreviations: U. Upp. Ghazij, upper part of the upper Ghazij Formation; L. Upp. Ghazij, lower part of the upper Ghazij Formation.

the early and middle Eocene respectively, but the boundary between both is poorly known and their correlation is rather tentative (Russell and Zhai 1987; Ting 1998).

The Bumbanian period has been divided into three intervals, called the *Orientolophus*, *Homogalax* and *Heptodon* interval zones (Ting 1998; Missiaen 2011). Of the three tapiromorph families found in the upper part of the upper Ghazij Formation, Isectolophidae appear in the *Orientolophus* interval and Eomoropidae in the *Homogalax* interval (Fig. 6). Lophialetidae have been reported in the *Heptodon* interval, but *Ampholophus* described from the Wutu fauna in the *Homogalax* interval has also been tentatively placed in this family (Tong and Wang 2006; Wang et al. 2007b; Missiaen 2011). Overall, the tapiromorph assemblage from the upper part of the upper Ghazij Formation is most similar to that from the Wutu fauna in the *Homogalax* interval, suggesting a potentially similar age for both faunas.

The faunas from the *Orientolophus* interval contain very primitive taxa such as the isectolophid *Orientolophus* and the basal chalicotheriid *Protomoropus* (Ting 1993; Hooker and Dashzeveg 2004). These forms are clearly more primitive than any of the Ghazij taxa and possibly ancestral to them, suggesting that the fauna from the upper part of the upper Ghazij Formation is decidedly younger than the early Bumbanian *Orientolophus* interval. The late Bumbanian faunas from the *Heptodon* interval are characterized by the appearance of the family Helaletidae, which is absent in the upper part of the upper Ghazij Formation, potentially suggesting that the Ghazij fauna is older than the *Heptodon* interval. However, the limited number of tapiromorph specimens from the Ghazij fauna, as well as the tentative referral of *Ampholophus* to the family Lophialetidae means that such an interpretation is only weakly supported.

The new unnamed species of Lophialetidae and the new eomorpid *Litolophus ghazijensis* are similar to taxa best known from the Arshantan ALMA. Nevertheless, Arshantan faunas are typically characterized by the presence of more derived perissodactyls, such as *Hyrachyus*, *Helaletes*, Deperetelidae, Hyracodontidae, Amynodontidae, and Brontotheriidae (Tsubamoto et al. 2004; Wang et al. 2007b, but see Meng et al. 2007). Of these, only brontotheres have been recorded in the mammal fauna from the upper Ghazij Formation, and both brontothere genera from the Ghazij Formation are distinctly smaller and more primitive than the Arshantan forms (Misiaen et al. 2011). The absence of any of these evolved forms therefore clearly suggests that the upper Ghazij fauna is older than the Arshantan ALMA.

Most of these evolved taxa are, however, present in the stratigraphically higher Kuldana and Subathu Formations in Pakistan and India (Fig. 6), suggesting a correlation of these faunas with the Arshantan period (Dehm and Oettingen-Spielberg 1958; Ranga Rao 1972; Khan 1973; Ranga Rao and Obergfell 1973; Sahni and Khare 1973; West 1980; Kumar and Sahni 1985; Maas et al. 2001; Thewissen et al. 2001).

Correlation of mammal faunas over long distances will always cause uncertainties and require considerable caution. Nevertheless, current evidence favors the correlation of the late early Eocene fauna from the upper part of the upper Ghazij Formation with the faunas from the *Homogalax* or *Heptodon* intervals of the Bumbanian ALMA. The early middle Eocene faunas from the Kuldana and Subathu Formation are best correlated with the Arshantan ALMA (Fig. 6). This means that the fauna from the upper Ghazij Formation is older than the Arshantan faunas, although the exact age difference can currently not be estimated because of the limited biochronological knowledge of this period in both regions.

Conclusions

The late early Eocene upper part of the upper Ghazij Formation in the Kingri area has yielded four new species of

tapiromorph perissodactyls. The new genus *Gandheralophus* contains two new species of primitive isectolophids, *G. minor* and *G. robustus*. *Gandheralophus* is probably derived from a highly primitive isectolophid such as *Orientolophus hengdongensis* from the earliest Eocene of South China and may be part of a southern isectolophid lineage also containing *Karagalax* from the early middle Eocene of Pakistan. Two Ghazij specimens are referred to a new, unnamed species of Lophialetidae. A single, well-preserved and highly diagnostic M3 allows the description of *Litolophus ghazijensis*, a new species of eomorpid Chalicotherioidea. Affinities of the tapiromorph perissodactyls described here clearly lie with Asian mammal faunas. This is intriguing, because so far the primates, bats, artiodactyls, rodents and tillodonts that have been described from the early Eocene of Indo-Pakistan have mostly shown affinities with European faunas, rather than Asian ones.

The present study allows the first biochronological comparison of mammalian faunas from Indo-Pakistan with those from East and Central Asia, where the biochronology for this period has been mostly based on tapiromorph perissodactyls. Isectolophidae, Lophialetidae and Eomoropidae all appear in the Bumbanian Asian Land Mammal Age. The tapiromorph perissodactyls from the upper part of the upper Ghazij Formation are more derived than those from the early Bumbanian *Orientolophus* interval, but the general assemblage is similar to that from the Bumbanian *Homogalax* and *Heptodon* intervals. The derived perissodactyl groups that are typical for the Arshantan faunas are all absent from the upper Ghazij Formation of Pakistan, but they are present in the younger Kuldana and Subathu Formation in Indo-Pakistan. Current evidence therefore suggests the correlation of the upper Ghazij Formation with the middle to late Bumbanian ALMA, and of the Kuldana and Subathu Formations with the Arshantan ALMA.

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References

- Bai, B., Wang, Y., and Meng, J. 2010. New craniodental materials of *Litolophus gobiensis* (Perissodactyla, "Eomoropidae") from Inner Mongolia, China, and phylogenetic analyses of Eocene chalicotheres. *American Museum Novitates* 3688: 1–27.
- Clyde, W.C., Khan, I.H., and Gingerich, P.D. 2003. Stratigraphic response and mammalian dispersal during initial India-Asia collision: evidence from the Ghazij Formation, Balochistan, Pakistan. *Geology* 31: 1097–1100.
- Dehm, R. and Oettingen-Spielberg, T. zu 1958. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 2. Die mitteleocänen Säugetiere von Ganda Kas bei Basal in Nordwest-Pakistan. *Abhandlungen der Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, München, Neue Folge* 91: 1–54.
- Fischer, K.H. 1977. Neue Funde von *Rhinocerotophiodon* (n. gen.), *Lophiodon*, und *Hyrachyus* (Ceratomorpha, Perissodactyla, Mammalia) aus dem Eozän des Geiseltals bei Halle (DDR). 1. Teil. *Rhinocerotophiodon*. *Zeitschrift für geologische Wissenschaft, Berlin* 5: 909–919.
- Froehlich, D.J. 1999. Phylogenetic systematics of basal perissodactyls. *Journal of Vertebrate Paleontology* 19: 140–159.
- Froehlich, D.J. 2002. Quo vadis eohippus? The systematics and taxonomy of the early Eocene equids (Perissodactyla). *Zoological Journal of the Linnean Society* 134: 141–256.
- Gingerich, P. D. 1981. Variation, sexual dimorphism, and social structure in the early Eocene horse *Hyracotherium* (Mammalia, Perissodactyla). *Paleobiology* 7: 443–455.
- Gingerich, P.D. 1991. Systematics and evolution of early Eocene Perissodactyla (Mammalia) in the Clarks Fork Basin, Wyoming. *Contributions from the Museum of Paleontology, University of Michigan* 28: 181–213.
- Gingerich, P.D. 2003. Stratigraphic and micropaleontological constraints on the Middle Eocene age of the mammal-bearing Kuldana Formation of Pakistan. *Journal of Vertebrate Paleontology* 23: 643–651.
- Gingerich, P.D., Abbas, S.G., and Arif, M. 1997. Early Eocene *Quettacyon parachai* (Condylarthra) from the Ghazij Formation of Baluchistan (Pakistan): oldest Cenozoic land mammal from South Asia. *Journal of Vertebrate Paleontology* 17: 629–637.
- Gingerich, P.D., Arif, M., Khan, I.H., and Abbas, S.G. 1998. First early Eocene land mammals from the upper Ghazij Formation of the Sor Range, Baluchistan. In: M.I. Ghaznavi, S.M. Raza, and M.T. Hasan (eds.), *Siwaliks of South Asia. Proceedings of the Third GEOSAS Workshop held at Islamabad, Pakistan, March 1997*, 1–17. Geological Survey of Pakistan, Islamabad.
- Gingerich, P.D., Arif, M., Khan, I.H., ul-Haq, M., Bloch, J.I., Clyde, W.C., and Gunnell, G.F. 2001. Gandhera Quarry, a unique mammalian faunal assemblage from the early Eocene of Baluchistan (Pakistan). In: G.F. Gunnell (ed.), *Eocene Vertebrates: Unusual Occurrences and Rarely Sampled Habitats*, 251–262. Plenum, New York.
- Gunnell, G.F., Gingerich, P.D., ul-Haq, M., Bloch, J.I., Khan, I.H., and Clyde, W.C. 2008. New euprimates (Mammalia) from the early and middle Eocene of Pakistan. *Contributions from the Museum of Paleontology, The University of Michigan* 32: 1–14.
- Holbrook, L.T., Lucas, S.G., and Emry, R.J. 2004. Skulls of the Eocene perissodactyls (Mammalia) *Homogalax* and *Isectolophus*. *Journal of Vertebrate Paleontology* 24: 951–956.
- Hooker, J.J. 1989. Character polarities in early Eocene perissodactyls and their significance for *Hyracotherium* and infraordinal relationships. In: D.R. Prothero and R.M. Schoch (eds.), *The Evolution of Perissodactyls*, 79–101. Oxford University Press, New York.
- Hooker, J.J. 1994. The beginning of the equoid radiation. *Zoological Journal of the Linnean Society* 112: 29–63.
- Hooker, J.J. and Dashzeveg, D. 2004. The origin of chalicotheres (Perissodactyla, Mammalia). *Paleontology* 47: 1363–1386.
- Hooker, J.J. 2005. Perissodactyla. In: K.D. Rose and J.D. Archibald (eds.), *The Rise of Placental Mammals*, 199–214. Johns Hopkins University Press, Baltimore.
- 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: 296–301.
- Krause, D.W. and Maas, M.C. 1990. The biogeographic origins of the late Paleocene–early Eocene mammalian immigrants to the Western Interior of North America. In: T.M. Bown and K.D. Rose (eds.), *Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior, North America. Geological Society of America, Special Paper* 243: 71–105.
- Kumar, K. and Sahni, A. 1985. Eocene mammals from the upper Subathu group, Kashmir Himalaya, India. *Journal of Vertebrate Paleontology* 5: 153–168.
- Kumar, K., Rose, K.D., Rana, R.S., Singh, L., Smith, T., and Sahni, A. 2010. Early Eocene artiodactyls (Mammalia) from Western India. *Journal of Vertebrate Paleontology* 30: 1245–1274.
- Lucas, S.G. and Kondrashov, P. 2004. Early Eocene (Bumbanian) perissodactyls from Mongolia and their biochronological significance. *New Mexico Museum of Natural History and Science Bulletin* 26: 215–220.
- Lucas, S.G., Emry, R.J., and Bayshashov, B.U. 1997. Eocene Perissodactyla from the Shinzaly River, Eastern Kazakhstan. *Journal of Vertebrate Paleontology* 17: 253–246.
- Lucas, S.G., Holbrook, L.T., and Emry, R.J. 2003. *Isectolophus* from the Eocene of the Zaysan basin, Kazakstan, and its biochronological significance. *Journal of Vertebrate Paleontology* 23: 238–243.
- Maas, M.C., Hussain, S.T., Leinders, J.J.M., and Thewissen, J.G.M. 2001. A new isctolophid tapiroid (Mammalia) from the early Eocene of Pakistan. *Journal of Paleontology* 75: 407–417.
- Matthew, W.D. and Granger, W. 1925. The smaller perissodactyls of the Irdivan Manha Formation, Eocene of Mongolia. *American Museum Novitates* 199: 1–9.
- Meng, J., Wang, Y., Ni, X., Beard, K.C., Sun, C., Li, Q., Jin, X., and Bai, B. 2007. New stratigraphic data from the Erlian Basin: implications for the division, correlation, and definition of Paleogene lithological units in Nei Mongol (Inner Mongolia). *American Museum Novitates* 3570: 1–31.
- Missiaen, P. 2011. An updated mammalian biochronology and biogeography for the early Paleogene of Asia. *Vertebrata Palasiatica* 49: 29–52.
- Missiaen, P., Gunnell, G.F., and Gingerich, P.D. 2011. New Brontotheriidae (Mammalia, Perissodactyla) from the early and middle Eocene of Pakistan with implications for mammalian paleobiogeography. *Journal of Paleontology* 85: 665–677.
- Pilgrim, G.E. 1940. Middle Eocene mammals from northwest India. *Proceedings of the Zoological Society of London, Series B* 110: 127–152.
- Prothero, D.R., Guéri, C., and Manning, E. 1989. The history of Rhinocerotidae. In: D.R. Prothero and R.M. Schoch (eds.), *The Evolution of Perissodactyls*, 322–340. Oxford University Press, New York.
- Radinsky, L.B. 1963. Origin and early evolution of North American Tapiroidea. *Peabody Museum of Natural History, Yale University, Bulletin* 17: 1–106.
- Radinsky, L.B. 1964. *Paleomoropus*, a new early Eocene chalicotheres (Mammalia, Perissodactyla), and a revision of Eocene chalicotheres. *American Museum Novitates* 2179: 1–28.
- Radinsky, L.B. 1965. Early Tertiary Tapiroidea of Asia. *Bulletin of the American Museum of Natural History* 129: 181–264.
- Radinsky, L.B. 1969. The early evolution of the Perissodactyla. *Evolution* 23: 308–328.
- Ranga Rao, A. 1972. Further studies on the vertebrate fauna of Kalakot, India. New mammalian genera and species from the Kalakot Zone of Himalayan foot hills near Kalakot, Jammu & Kashmir State, India. *Directorate of Geology, Oil & Natural Gas Commission, Dehra Dun, India, Special Paper* 1: 1–22.
- Ranga Rao, A. and Obergfell, F.A. 1973. *Hyrachyus asiaticus*, new species of an upper Eocene tapiroid (Mammalia, Perissodactyla) from Kalakot, India. *Directorate of Geology, Oil & Natural Gas Commission, Dehra Dun, India, Special Paper* 3: 1–8.
- Rose, K.D., DeLeon, V.B., Missiaen, P., Rana, R.S., Sahni, A., Singh, L., and Smith, T. 2008. Early Eocene lagomorph (Mammalia) from west-

- ern India and the early diversification of Lagomorpha. *Proceedings of the Royal Society of London B* 275: 1203–1208.
- Rose, K.D., Rana, R.S., Sahni, A., Kumar, K., Missiaen, P., Singh, L., and Smith, T. 2009a. Early Eocene primates from Gujarat, India. *Journal of Human Evolution* 56: 366–404.
- Rose, K.D., Rana, R.S., Sahni, A., Kumar, K., Singh, L., and Smith, T. 2009b. First tillodont from India: Additional evidence for an early Eocene faunal connection between Europe and India? *Acta Palaeontologica Polonica* 54: 351–355.
- Rose, K.D., Smith, T., Rana, R.S., Sahni, A., Singh, H., Missiaen, P., and Folie, A. 2006. Early Eocene (Ypresian) continental vertebrate assemblage from India, with description of a new anthracobunid (Mammalia, Tethytheria). *Journal of Vertebrate Paleontology* 26: 219–225.
- Russell, D.E. and Zhai, R. 1987. The Paleogene of Asia: mammals and stratigraphy. *Memoires du Museum National D'Histoire Naturelle Serie C, Sciences de la Terre* 52: 1–488.
- Sahni, A. and Jolly, A. 1993. Eocene mammals from Kalakot, Kashmir Himalaya: community structure, taphonomy and palaeobiogeographical implications. *Kaupia, Darmstädter Beiträge zur Naturgeschichte, Darmstadt* 3: 209–222.
- Sahni, A. and Khare, S.K. 1971. Three new Eocene mammals from Rajauri District, Jammu and Kashmir. *Journal of the Palaeontological Society of India* 16: 41–53.
- Sahni, A. and Khare, S.K. 1973. Additional Eocene mammals from the Subathu Formation of Jammu and Kashmir. *Journal of the Palaeontological Society of India* 17: 31–49.
- Schoch, R.M. 1989. A review of the tapiroids. In: D. Prothero and R.M. Schoch (eds.), *The Evolution of Perissodactyls*, 298–320. Oxford University Press, New York.
- Smith, T., Rana, R., Missiaen, P., Rose, K.D., Sahni, A., Singh, H., and Singh, L. 2007. High bat (Chiroptera) diversity in the early Eocene of India. *Naturwissenschaften* 94: 1003–1009.
- Thewissen, J.G.M., Williams, E.M., and Hussain, S.T. 2001. Eocene mammal faunas from northern Indo-Pakistan. *Journal of Vertebrate Paleontology* 21: 347–366.
- Ting, S. 1993. A preliminary report on an Early Eocene mammalian fauna from Hengdong, Hunan Province, China. *Kaupia* 3: 201–207.
- Ting, S. 1998. Paleocene and early Eocene Land Mammal Ages of Asia. *Bulletin of the Carnegie Museum of Natural History* 34: 124–147.
- Tsubamoto, T., Takai, M., and Egi, N. 2004. Quantitative analyses of biogeography and faunal evolution of Middle to Late Eocene Mammals in East Asia. *Journal of Vertebrate Paleontology* 24: 657–667.
- Tong, Y. and Wang, J. 2006. Fossil mammals from the early Eocene Wutu Formation of Shandong Province. *Palaeontologia Sinica, new series C* 192 (28): 1–195.
- Wang, Y., Meng, J., Ni, X., and Li, C. 2007a. Major events of Paleogene mammal radiation in China. *Geological Journal* 42: 415–430.
- Wang, Y., Meng, J., Ni, X., and Beard, K.C. 2007b. Early Eocene Bumbanian fauna from the Erlian Basin, Inner Mongolia, China, and its biochronological implications. *Journal of Vertebrate Paleontology* 27: 163A.
- West, R.M. 1980. Middle Eocene large mammal assemblage with Tethyan affinities, Ganda Kas Regio, Pakistan. *Journal of Paleontology* 54: 508–533.