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NEW BASAL PERISSODACTYLA (MAMMALIA) FROM THE LOWER EOCENE GHAZIJ FORMATION OF PAKISTAN

BY

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Abstract — Three new species of basal early Eocene perissodactyls are described from two stratigraphic intervals in the upper Ghazij Formation of Balochistan Province, Pakistan. *Perissobune intizarkhani,* n. gen. and sp., is confined to the lower part of the upper Ghazij Formation, where it is the most common perissodactyl. A closely related, larger species, *Perissobune munirulhaqi*, n. sp., ranges through the lower and upper parts of the upper Ghazij Formation, but it is much less common than *P. intizarkhani*. Both species are known from dentaries, maxillae, and isolated teeth. *Perissobune* has bunodont cheek teeth with well developed cusps and conules but limited development of lophs.

Ghazijhippus talibhasani, n. gen. and sp., is confined to the lower part of the upper Ghazij Formation, where it is relatively rare. *G. talibhasani* is known from a cranium, a dentary, and isolated teeth. *Ghazijhippus* has molars a little more lophodont than those of *Perissobune*, but dental and cranial characteristics are still very primitive for a perissodactyl. Cladistic analysis of forty cranial and dental characteristics shows that *Ghazijhippus* is intermediate between the generalized basal perissodactyl *Hallensia* and several primitive North American equids.

Early Eocene *Perissobune* and *Ghazijhippus* are the oldest and most primitive perissodactyls known from Pakistan. Ghazij Formation perissodactyls confirm that vertebrate faunas in Indo-Pakistan became progressively more cosmopolitan and more modern during the early Eocene: perissodactyls from the middle Ghazij, lower part of the upper Ghazij, and upper part of the upper Ghazij Formation number 0, 3, and 7 species, respectively. The lower part of the upper Ghazij Formation yields the three species described here as basal Perissodactyla, whereas the upper part of the upper Ghazij has a much more diverse fauna with a single basal species and six species representing four derived suborders of Perissodactyla.

INTRODUCTION

The Indian Subcontinent is important for the biogeography of late Paleocene and early Eocene mammals, as Krause and Maas (1990), Clyde et al. (2003), and others have emphasized. Late Paleocene mammals have not yet been found, but two sites, one in Pakistan and the other in India, are producing a diversity of early Eocene mammals.

The Pakistan sites are in Balochistan Province (Fig. 1) and include coal mine faunas near the city of Quetta that have yielded quettacyonids (Gingerich et al., 1997, 1998, 1999) and an anthracobunid (Ginsburg et al., 1999) from the paralic middle Ghazij Formation. The middle Ghazij is overlain by continental clastics of the upper Ghazij Formation. The upper Ghazij has yielded two faunas, one from the lower part of the upper Ghazij that is rich in quettacyonid condylarths, tillodonts, and perissodactyls (Gingerich et al., 1998; Gunnell and Gingerich, 2004), and the other from the upper part of the upper Ghazij with a more diverse fauna dominated by cosmopolitan taxa found on northern continents (e.g., artiodactyls, perissodactyls, and primates; Gingerich et al., 2001; Gunnell et al., 2008,

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FIGURE 1 — Pakistan location map showing the distribution of localities yielding the early Eocene basal perissodactyls described here (solid circles). A detailed map of basal perissodactyl localities in the vicinity of Kingri is shown in Figure 2. Coordinates and stratigraphic levels for all localities are given in Table 1. Abbreviations: *NWFP*, North-West Frontier Province; *Turkm*., Turkmenistan.

2012). Khan and Clyde (2013) provided an overview of Ghazij Formation stratigraphy and reviewed the tectonic setting.

The Indian sites are in Gujarat State, where the most productive is the Vastan coal mine in the Cambay Shale (Fig. 1; Rana et al., 2004, 2005; Bajpai et al., 2005, 2008; Rose et al., 2006, 2007, 2008, 2009, 2013, 2014a,b; Smith et al., 2007; Kumar et al., 2010; Missiaen et al., 2011b). Vastan mammals include extinct groups such as tillodonts and cambaytheres, and representatives of modern groups such as artiodactyls, bats, lagomorphs, primates, and rodents. Quettacyonid condylarths and true perissodactyls, which are important components of the middle Ghazij and lower part of the upper Ghazij faunas, have not been found at Vastan.

Relative ages of the oldest Pakistan and Indian mammal-bearing sites are equivocal. In Pakistan the middle Ghazij Formation cannot be older than planktonic foraminiferal zone P6A (E3; Gingerich et al., 1997) and cannot be younger than the transition from magnetochron 24R to 24N (Clyde et al., 2003), so it is in the range from 54.5 to 54 Ma (Vandenberghe et al., 2012). The lower part of the upper Ghazij Formation is younger than the 24R to 24N transition and older than the first appearance of *Eotitanops* (Missiaen et al., 2011a), so it is in the range from 54 to 52 Ma (Vandenberghe et al., 2012). The upper part of the upper Ghazij Formation is younger than the first appearance of *Eotitanops* and must be as old or older than planktonic foraminiferal zone P9 (E7; Afzal, 1996), so it is in the range of 52 to 50 Ma, based on the presence of *Eotitanops* (Missiaen et al., 2011a). On a North American time scale, the first two intervals are equivalent in time to the Wasatchian land-mammal age, and the third interval is equivalent to the early Bridgerian land-mammal age.

In India the lower part of the Vastan coal sequence with mammals is regarded as upper NP9 to lower NP12 based on dinoflagellates (Garg et al., 2008), in the range of 56 to 53 Ma (Vandenberghe et al., 2012). The age of the interval producing mammals at Vastan is possibly more narrowly near 54.0 Ma (Clementz et al., 2010). Paleomagnetic reversal stratigraphy would enable more precise correlation, and current interpretation of the carbon isotope record at Vastan (Samanta et al., 2013) seems highly questionable without an accompanying high-resolution paleomagnetic stratigraphy.

In previous studies we described brontotheriid and ceratomorph perissodactyls from the upper part of the upper Ghazij Formation near the town of Kingri in northeastern Balochistan (Fig. 2; Missiaen et al., 2011a; Missiaen and Gingerich, 2012). Here we increase the taxonomic diversity of the early Eocene perissodactyls known from Pakistan by describing two new genera and three new species of distinctly bunodont basal perissodactyls from the upper Ghazij Formation. Most come from sites near Kingri as well, but some come from the Sor Range near Quetta, from Pir Ismail Ziarat, and from Daghari (geographic coordinates are given in Table 1).

All three of the new species are found in the lower part of the upper Ghazij Formation, from which no perissodactyls were previously described, with only the largest form continuing into the upper part of the upper Ghazij Formation. These bunodont perissodactyls therefore represent the oldest modern mammals from Pakistan.

INSTITUTIONAL ABBREVIATION

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

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order PERISSODACTYLA Owen, 1848
Suborder PERISSODACTYLA *incertae sedis*

Family *incertae sedis*

Perissobune, new genus

Type species.— *Perissobune intizarkhani* new species.
Referred species.— *Perissobune munirulhaqi* new species.
Diagnosis.— Early Eocene perissodactyl characterized by strong development of cusps and conules on the cheek teeth, by

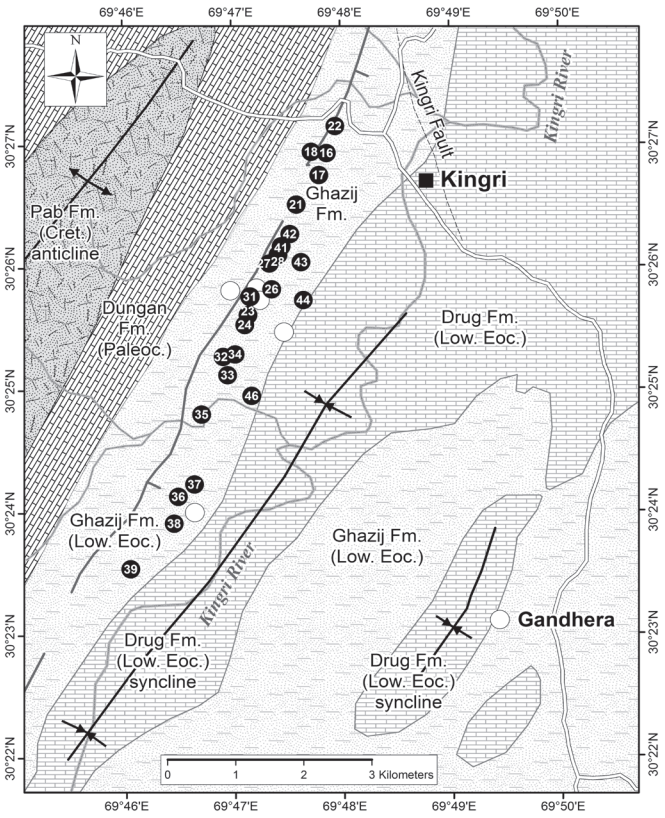

FIGURE 2 — Geological map showing Ghazij Formation outcrops in the vicinity of Kingri in eastern Balochistan (adapted from Jones et al., 1960; see Fig. 1 for location in Pakistan). Stratigraphic succession includes Upper Cretaceous Pab Formation sandstones, Paleocene Dungan Formation marine limestones and shales, lower Eocene Ghazij Formation marine shales overlain by continental sandstones and shales, and lower Eocene Drug Formation marine limestones. Numbered solid circles are Ghazij Formation localities yielding basal perissodactyls. Unnumbered open circles are localities lacking these. Coordinates and stratigraphic levels for all localities are given in Table 1. Abbreviations: *Cret*., Cretaceous; *Eoc*., Eocene; *Fm*, Formation; *Low*., Lower; *Paleoc*., Paleocene.

a distinct increase in size of the molars posteriorly, by a small upper molar parastyle, and by a distinctly twinned metaconid on lower molars. *Perissobune* differs from other perissodactyls in its limited lophodonty, with complete absence of dilambdodont features, an incomplete lingual cingulum on the upper molars, and no posthypocristid on lower molars. *Perissobune* shares some similarities with *Nakusia* and with early Eocene anthracobunids, but *Perissobune* differs from *Nakusia* in having transversely narrower upper cheek teeth, a relatively larger M^1, and a transversely compressed upper molar metacone. *Perissobune* differs from anthracobunids in having relatively lower cusps, a stronger upper molar parastyle and ectoloph, and a basined hypoconulid lobe on M_3. *Perissobune* differs from both *Nakusia* and other anthracobunids in having a less connate paracone and metacone on upper premolars.

Etymology.— *Perissobune* is so named because of the perissodactyl affinities of the genus and the distinctly bunodont morphology of its premolar and molar teeth.

Occurrence.— Early Eocene (Ypresian) Ghazij Formation of Balochistan Province, Pakistan. *Perissobune* is known from both the lower and upper parts of the upper Ghazij Formation. As reviewed above, the lower part of the upper Ghazij Formation is in the range from 54 to 52 Ma, and the upper part of the upper Ghazij Formation is in the range from 52 to 50 Ma (Clyde et al., 2003; Missiaen et al., 2011a; Vandenberghe et al., 2012). On a North American time scale, the first interval is equivalent in time to the middle or late Wasatchian land-mammal age, and the second interval is equivalent to the early Bridgerian land-mammal age.

Discussion.— Dental terminology is illustrated in Figure 3.

Perissobune intizarkhani, new species

Figs. 3–4

Holotype.— GSP-UM 4656 (Fig. 3A; Fig. 4S–T), right dentary with P_4–M_3. The specimen is a young individual with teeth only slightly worn and M_3 not fully erupted. Measurements of the holotype are included in Table 2.

Type locality.— The holotype is from locality GH-37 in the Kingri area, Balochistan Province, Pakistan (Fig. 2). This locality is in the lower part of the upper Ghazij Formation, early Eocene (Ypresian).

Diagnosis.— *Perissobune intizarkhani* differs from *P. munirulhaqi* in being about 20% smaller in size, in having weaker labial cingula on the lower cheek teeth, in having a relatively shorter P_3 with a less anteriorly projecting paraconid, and in having transversely narrower lower molars with a more limited posterior size increase, a weaker twinning of the metaconids, and a more prominent hypoconulid on $M_{1–2}$.

Etymology.— The species is named for Dr. Intizar Hussain Khan of the Geological Survey of Pakistan in recognition of his collaboration and synthetic sedimentological and stratigraphic studies of the Ghazij Formation in Pakistan (e.g., Clyde et al., 2003; Khan and Clyde, 2013).

Referred material.— All four-digit numbers are GSP-UM specimen numbers. Locality **GH-9**: 4045, left M_x fragment; 4046, right P^4; 4048, left M_x fragment; 4052, right M_x fragment; 4073, left M_x fragment. Locality **GH-10**: 4117, left P_4 fragment. Locality **GH-14**: 4165, left M_x fragment. Locality **GH-16**: 4257, right dentary with P_3–M_1; 4266, right maxilla with roots of $M^{2–3}$; 4267, left maxilla with $M^{1–3}$; 4282, right M_3 fragment; 4291, left M_3. Locality **GH-17**: 4260, left dentary with roots of $M_{2–3}$; 4312, right M_1 fragment. Locality **GH-18**: 4274, right M^2; 4275, left M_2. Locality **GH-21**: 4299, left P_4; 4300, left P_4; 6483, left M^x fragment. Locality **GH-22**: 4306, left P^4; 4479, right M^x; 4482, right P^4; 4483, left M_2. Locality **GH-23**: 4418, right M^x. Locality **GH-24**: 4433, left M^2. Locality **GH-26**: 4328, left M_x; 4332, right M_3; 4333, left M^3; 4342, right M^1. Locality **GH-27**: 4345, left maxilla with $M^{1–3}$; 4350, right M_x fragment; 4353, right M_3; 4360, left dentary with $M_{2–3}$; 4361, right M^2; 4363, right

M_3 fragment; 4364, right M^3; 4367, left P_4; 4376, left dentary with roots of $M_{1–3}$; 4452, left M_2; 4453, right dentary with $P_{3–4}$; 4494, left P_4; 4497, right P_3; 4498, left P^4; 6463, left maxilla with $M^{2–3}$. Locality **GH-28**: 4378, left M^2; 4380, left M^3; 4381, right M^3 fragment; 4464, right M_3 fragment; 4466, left maxilla with $M^{1–3}$. Locality **GH-31**: 4510, right dentary with $M_{1–2}$; 4513, right edentulous dentary. Locality **GH-32**: 4528, right M^3; 4536, associated right P^4 and M^3; 4544, left M^1. Locality **GH-33**: 4554, left M^3; 4561 left P^3; 4563, right P_4; 4565, edentulous dentary; 4566, left M_3; 4567, right M_x fragment; 4568, right M_x fragment P_4; 4569, right M_3; 4570, right P_3; 4571, right M_3 fragment; 4572, right M_x. Locality **GH-34**: 4587, left P_3; 4596, right P^4; 4616, left maxilla with $M^{2–3}$. Locality **GH-35**: 4625, left dentary with $M_{2–3}$; 6553, right dentary with P_4–M_2; 6554, left M^x fragment. Locality **GH-36**: 4636, right maxilla with $M^{2–3}$. Locality **GH-37**: 4643, right M_3; 4653, left M_x; 4655, left M^x fragment. Locality **GH-38**: 4662, left M^3; 4664, right M_x; 4666 right M^3. Locality **GH-39**: 4677, left dentary with P_3–M_1; 4679, right M_3. Locality **GH-41**: 6467, left dentary with $P_{3–4}$; 6473, right dentary with P_4–M_2; 6476, left M_x fragment. Locality **GH-42**: 6478, right P^2.

Description.— In the upper dentition P^2 is a transversely narrow tooth (Fig. 4A–B). The labial side is dominated by a paracone fused with the weaker metacone closely behind it. The lingual side features a protocone and a small talon shelf.

P^3 is transversely wider and more robust than P^2, and has more distinct cingula (Fig. 4C–D). The labial cusps are distinctly more robust, but the metacone is still completely fused with the larger paracone. The protocone is much better

TABLE 1 — Fossil localities yielding the early Eocene specimens described here, including their stratigraphic interval within the upper Ghazij Formation, source area within Balochistan, and geographic coordinates (GCS) in decimal degrees. '*P*' indicates the presence of a taxon in a locality, and '*Type*' indicates that this locality is the type locality for the taxon. Abbreviation: *U. Ghazij Fm*., upper Ghazij Formation. Note that all three basal perissodactyl species are present in the lower part of the upper Ghazij Formation, but *Perissobune munirulhaqi* is the only one present in the upper part of the upper Ghazij Formation.

Locality	Stratigraphic level	Area	GCS East	GCS North	*Perissobune intizarkhani*	*Perissobune munirulhaqi*	*Ghazijhippus talibhasani*
GH-4	Lower U. Ghazij Fm.	Sor Range	67.1923° E	30.1730° N	–	P	–
GH-8	Lower U. Ghazij Fm.	Sor Range	67.2080° E	30.1583° N	–	P	–
GH-9	Lower U. Ghazij Fm.	Pir Ismail Ziarat	67.4320° E	30.0607° N	P	–	–
GH-10	Lower U. Ghazij Fm.	Daghari	67.2542° E	30.0550° N	P	–	–
GH-14	Lower U. Ghazij Fm.	Sor Range	67.1945° E	30.1723° N	P	–	–
GH-16	Lower U. Ghazij Fm.	Kingri	69.7978° E	30.4488° N	P	P	–
GH-17	Lower U. Ghazij Fm.	Kingri	69.7967° E	30.4458° N	P	–	–
GH-18	Lower U. Ghazij Fm.	Kingri	69.7955° E	30.4490° N	P	P	–
GH-21	Lower U. Ghazij Fm.	Kingri	69.7932° E	30.4418° N	P	P	–
GH-22	Lower U. Ghazij Fm.	Kingri	69.7992° E	30.4525° N	P	–	–
GH-23	Lower U. Ghazij Fm.	Kingri	69.7857° E	30.4268° N	P	–	–
GH-24	Lower U. Ghazij Fm.	Kingri	69.7852° E	30.4255° N	P	–	–
GH-26	Lower U. Ghazij Fm.	Kingri	69.7893° E	30.4303° N	P	–	P
GH-27	Lower U. Ghazij Fm.	Kingri	69.7890° E	30.4338° N	P	P	–
GH-28	Lower U. Ghazij Fm.	Kingri	69.7903° E	30.4350° N	P	–	–
GH-31	Lower U. Ghazij Fm.	Kingri	69.7860° E	30.4293° N	P	P	P
GH-32	Lower U. Ghazij Fm.	Kingri	69.7818° E	30.4212° N	P	P	–
GH-33	Lower U. Ghazij Fm.	Kingri	69.7825° E	30.4187° N	P	–	P
GH-34	Lower U. Ghazij Fm.	Kingri	69.7837° E	30.4215° N	P	P	P
GH-35	Lower U. Ghazij Fm.	Kingri	69.7785° E	30.4133° N	P	–	P
GH-36	Lower U. Ghazij Fm.	Kingri	69.7748° E	30.4022° N	P	–	–
GH-37	Lower U. Ghazij Fm.	Kingri	69.7773° E	30.4038° N	Type	–	Type
GH-38	Lower U. Ghazij Fm.	Kingri	69.7742° E	30.3985° N	P	P	–
GH-39	Lower U. Ghazij Fm.	Kingri	69.7675° E	30.3923° N	P	–	P
GH-41	Lower U. Ghazij Fm.	Kingri	69.7908° E	30.4362° N	P	–	–
GH-42	Lower U. Ghazij Fm.	Kingri	69.7922° E	30.4378° N	P	–	–
GH-43	Lower U. Ghazij Fm.	Kingri	69.7938° E	30.4340° N	–	–	P
GH-44	Upper U. Ghazij Fm.	Kingri	69.7942° E	30.4288° N	–	Type	–
GH-46	Upper U. Ghazij Fm.	Kingri	69.7862° E	30.4158° N	–	P	–

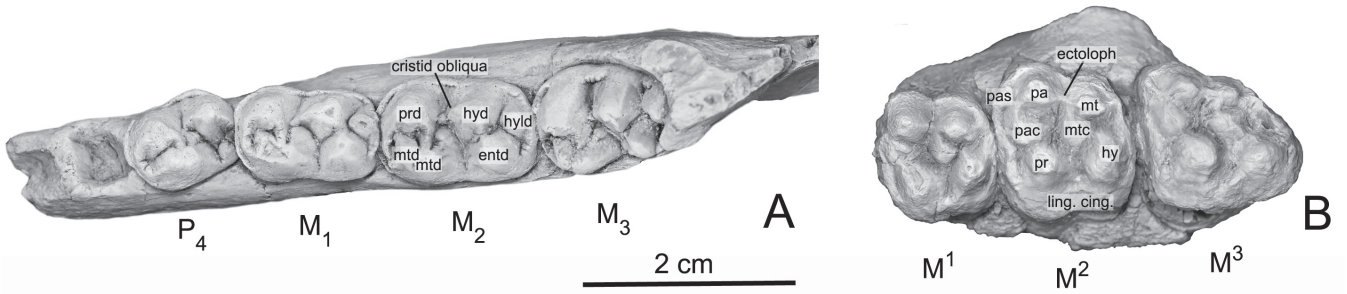

FIGURE 3 — Dental terminology illustrated on lower and upper molars of *Perissobune intizarkhani*, n. gen. and sp. **A**, GSP-UM 4656, right dentary with P_4–M_3 (holotype) in occlusal view. **B**, GSP-UM 4345, left maxilla with $M^{1–3}$ in occlusal view. Anterior is at the left, posterior at the right, labial and buccal at the top, and lingual at the bottom in both illustrations. The metaconid (*mtd*) is twinned and the cristid obliqua is weakly developed on lower molars. The ectoloph and lingual cingulum (*ling. cing.*) are weakly developed on upper molars. Abbreviations: *entd*, entoconid; *hy*, hypocone; *hyd*, hypoconid; *hyld*, hypoconulid; *ling. cing.*, lingual cingulum; *mt*, metacone; *mtc*, metaconule; *mtd*, metaconid; *pa*, paracone; *pac*, paraconule; *pas*, parastyle; *pr*, protocone; *prd*, protoconid.

developed than on P^2, and the trigon basin shows a weak protoloph but no metaloph or conules.

P^4 is anteroposteriorly shorter than P^3 and more rectangular (Fig. 4E–F). The labial side has a small parastyle. The metacone is only slightly smaller than the paracone, and more clearly separated from it than on more anterior premolars. The P^4 protocone is similar to the P^3 protocone. P^4 has a distinct paraconule and protoloph, but also a weaker metaconule and metaloph.

M^1 and M^2 are similar in shape and differ mostly by the larger size and slightly stronger cingula on M^2 (Fig. 4G–J). Both are subtrapezoidal and are distinctly bunodont, with the crowns dominated by strong inflated cusps and conules. The parastyle is weak, forming only a small swelling on the anterior cingulum directly anterior to the paracone. The paracone is slightly more robust than the more lingually placed metacone. Both cusps are separated at the base but are connected by a low, straight centrocrista. The subequal paraconule and metaconule are very distinct and positioned lingual to and somewhat anterior to the paracone and metacone respectively. The protocone and hypocone are also robust cusps, with the hypocone placed somewhat more labial than the protocone.

The distinct protoloph of M^1 and M^2 runs anterolabially from the protocone to the paraconule, joining the ectoloph between the parastyle and the paracone. The metaloph is shorter than the protoloph. It runs from the hypocone to the anterolingual corner of the metacone, forming a distinctive step at the level of the metaconule. The prehypocrista portion of the metaloph is somewhat variably developed, with some specimens having the appearance of a doubled hypocone.

Narrow cingula are present on the anterior, labial, and posterior sides of M^1 and M^2, with a distinct swelling on the anterior cingulum near the base of the paraconule. The labial cingulum is interrupted posterolabial to the paracone. The posterior cingulum is continuous with the labial cingulum, and lingually it forms a ridge rising onto the back of the hypocone. A small separate shelf is also present posterolingual to the hypocone.

M^3 is larger than M^2 but is markedly tapering posteriorly. On M^3 the metacone is reduced, and it is followed by a small metastyle. The M^3 hypocone is placed more posteriorly and M^3 has a well-developed posterior cingulum delimited by a raised posterior crest on which a series of small cuspules is developed.

In the lower dentition, P_1 was small, with two fused roots, whereas P_2 was more similar in size to P_3 and had two distinct roots. Crowns are not preserved. Specimen GSP-UM 4257 (Fig. 4M–N) shows the presence of long diastemata (12.4 mm) anterior and posterior to P_1. There is a marked deepening of the jaw at the level of P_2.

P_3 is robust and ovoid in occlusal view (Fig. 4K–L). There is a small paraconid placed directly in front of the large protoconid. The metaconid is weakly separated from the protoconid and it is rapidly obliterated by wear. A weak crest descends posteriorly from the protoconid to a single, centrally placed talonid cusp.

P_4 is similar in size to P_3 but it is more rectangular in occlusal view (Fig. 4K–L). P_4 has a distinct, twinned metaconid that is placed directly lingual to the protoconid. The anterior part of the P_4 trigonid is rounded, and it lacks a real paraconid. The P_4 talonid has a short cristid obliqua, a marked, labially-placed hypoconid, and a small entoconid

Molars of *Perissobune intizarkhani* are shown in Figure 4O–T. M_1 has a weak paracristid that runs anteriorly and lingually from the protoconid and then rises onto the metaconid. The protoconid is connected to the metaconid by a distinctly notched protolophid. The metaconid is strongly twinned and has a short crest running anteriorly and joining the paracristid. The back of the metaconid has a weak lingual metastylid and a strong metaconid buttress (Hooker, 1994). The hypoconid and entoconid are very robust, and subequal in size with the entoconid occupying a slightly more posterior position. The hypoconulid is weaker than the hypoconid or entoconid, but it is still very well developed. The strong swelling of the talonid cusps leaves little room for the development of lophs, but a notched hypolophid is present between the entoconid and hypoconid, and a low cristid obliqua runs anteriorly and somewhat lingually to the back wall of the trigonid.

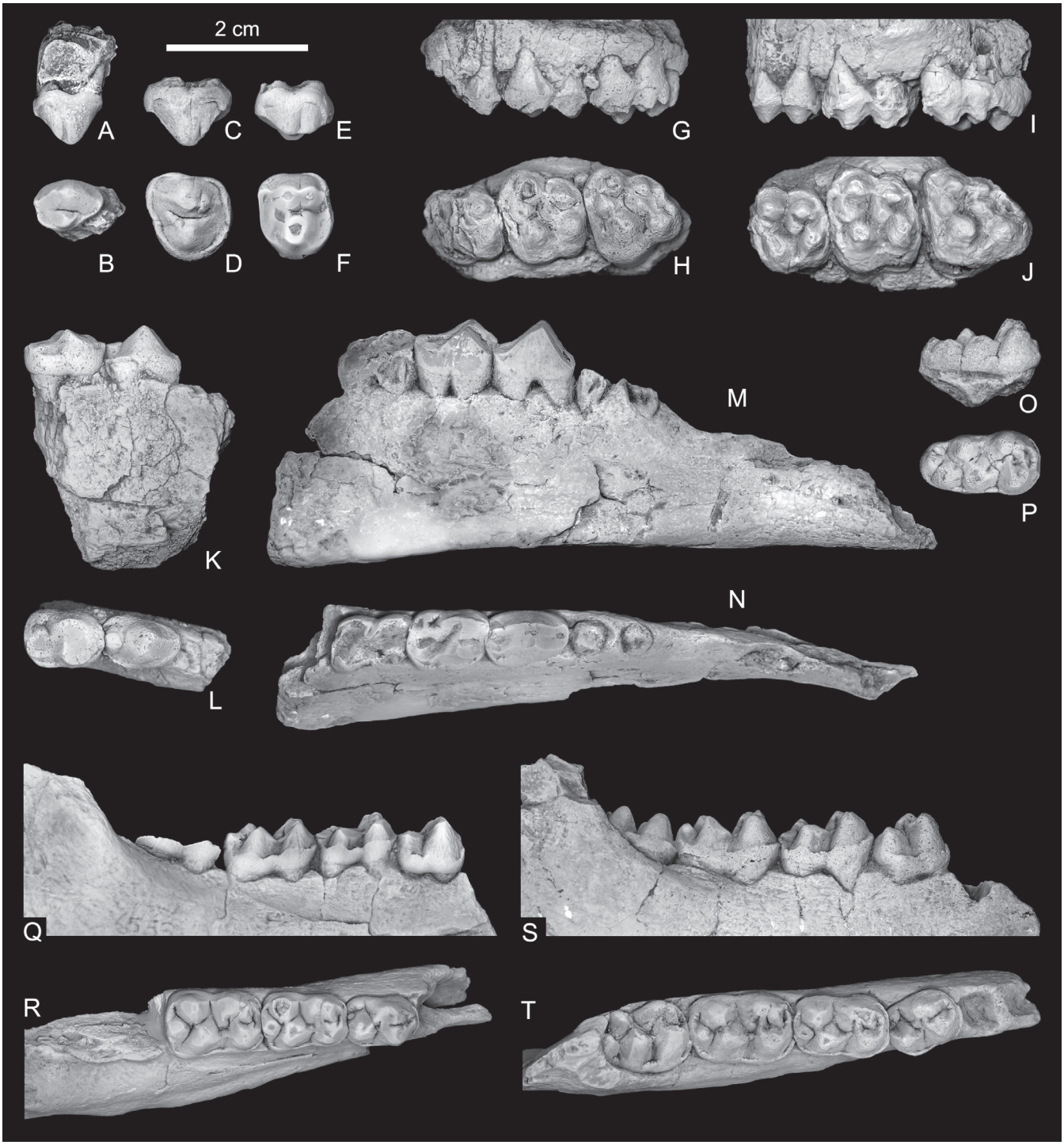

FIGURE 4 — Dentition of *Perissobune intizarkhani*, n. gen. and sp., from the upper Ghazij Formation in Pakistan, early Eocene in age. **A–B**, GSP-UM 6478, right P^2 in labial (A) and occlusal (B) view. **C–D**, GSP-UM 4561 left P^3 in labial (C) and occlusal (D) view. **E–F**, GSP-UM 4498, left P^4 in labial (E) and occlusal (F) view. **G–H**, GSP-UM 4466, left maxilla with $M^{1–3}$ in labial (G) and occlusal (H) view. **I–J**, GSP-UM 4345, left maxilla with $M^{1–3}$ in labial (I) and occlusal (J) view. **K–L**, GSP-UM 4453, right dentary with $P_{3–4}$ in labial (K) and occlusal (L) view. **M–N**, GSP-UM 4257, right dentary with P_3–M_1 in labial (M) and occlusal (N) view. **O–P**, GSP-UM 4643, right M_3 in labial (O) and occlusal (P) view. **Q–R**, GSP-UM 6553, right dentary with P_4–M_2 in labial (Q) and occlusal (R) view. **S–T**, GSP-UM 4656, right dentary with P_4–M_3 (holotype) in labial (S) and occlusal (T) view.

TABLE 2 — Measurements of teeth of *Perissobune intizarkhani*, n. gen. and sp., from the upper Ghazij Formation, early Eocene, of Pakistan. GSP-UM 4656 is the holotype. Molars marked with a superscript or subscript 'x' could be first or second molars. Measurements are in mm, and asterisks indicate estimates where measurements could not be determined due to wear or damage. Abbreviations: *L*, anteroposterior length; *W*, labiolingual width.

Upper Dentition

GSP-UM	Site	P^1L	P^1W	P^2L	P^2W	P^3L	P^3W	P^4L	P^4W	M^1L	M^1W	M^xL	M^xW	M^2L	M^2W	M^3L	M^3W
4046	GH-09	–	–	–	–	–	–	10.05	12.82	–	–	–	–	–	–	–	–
4267	GH-16	–	–	–	–	–	–	–	–	11.95*	15.48	–	–	13.10	16.20	14.56	16.53
4274	GH-18	–	–	–	–	–	–	–	–	–	–	–	–	14.79	16.96	–	–
4291	GH-16	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16.04	16.16
4333	GH-26	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12.54*	13.23*
4342	GH-26	–	–	–	–	–	–	–	–	11.94	13.30	–	–	–	–	–	–
4345	GH-27	–	–	–	–	–	–	–	–	11.59*	12.89	–	–	13.59	14.72	15.32	14.02
4361	GH-27	–	–	–	–	–	–	–	–	–	–	–	–	12.81	15.24	–	–
4378	GH-28	–	–	–	–	–	–	–	–	–	–	–	–	14.81	–	–	–
4418	GH-23	–	–	–	–	–	–	–	–	–	–	12.17	13.82	–	–	–	–
4433	GH-24	–	–	–	–	–	–	–	–	–	–	–	–	11.81*	13.73*	–	–
4466	GH-28	–	–	–	–	–	–	–	–	–	–	–	–	12.01	13.67	13.43	13.77
4479	GH-22	–	–	–	–	–	–	–	–	–	–	12.99*	13.91*	–	–	–	–
4498	GH-27	–	–	–	–	–	–	10.28	12.07	–	–	–	–	–	–	–	–
4528	GH-32	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16.34	16.80
4536	GH-32	–	–	–	–	–	–	10.70*	13.70*	–	–	–	–	–	–	16.26*	16.82*
4544	GH-32	–	–	–	–	–	–	–	–	13.05	14.64	–	–	–	–	–	–
4554	GH-33	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12.28	13.26
4561	GH-33	–	–	–	–	12.08	12.53	–	–	–	–	–	–	–	–	–	–
4587	GH-34	–	–	–	–	11.60	12.20	–	–	–	–	–	–	–	–	–	–
4596	GH-34	–	–	–	–	–	–	–	12.63	–	–	–	–	–	–	–	–
4616	GH-34	–	–	–	–	–	–	–	–	–	–	–	–	13.19*	13.89	15.18	14.22
4636	GH-36	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13.33	13.58
4662	GH-38	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13.34	14.16
4666	GH-38	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12.59	12.96
6463	GH-27	–	–	–	–	–	–	–	–	–	–	–	–	14.49	15.55	14.84	14.09

Lower Dentition

GSP-UM	Site	P_1L	P_1W	P_2L	P_2W	P_3L	P_3W	P_4L	P_4W	M_1L	M_1W	M_xL	M_xW	M_2L	M_2W	M_3L	M_3W
4045	GH-09	–	–	–	–	–	–	–	–	–	–	11.37*	8.23*	–	–	–	–
4257	GH-16	–	–	–	–	11.63	7.76	11.71	8.39	11.69*	8.37*	–	–	–	–	–	–
4299	GH-21	–	–	–	–	–	–	11.65*	8.36	–	–	–	–	–	–	–	–
4328	GH-26	–	–	–	–	–	–	–	–	–	–	13.03	8.24*	–	–	–	–
4332	GH-26	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16.07	8.23
4353	GH-27	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16.40	9.95
4360	GH-27	–	–	–	–	–	–	–	–	–	–	–	–	14.36	9.95*	18.63	10.39
4367	GH-27	–	–	–	–	–	–	10.05*	7.90*	–	–	–	–	–	–	–	–
4452	GH-27	–	–	–	–	–	–	–	–	–	–	–	–	13.27	9.07	–	–
4453	GH-27	–	–	–	–	11.00	7.22	11.51	8.26	–	–	–	–	–	–	–	–
4483	GH-22	–	–	–	–	–	–	–	–	–	–	–	–	14.98	10.17	–	–
4494	GH-27	–	–	–	–	–	–	9.97*	7.41	–	–	–	–	–	–	–	–
4510	GH-31	–	–	–	–	–	–	–	–	11.59	7.60*	–	–	13.37	8.98*	–	–
4563	GH-33	–	–	–	–	–	–	10.83	7.28	–	–	–	–	–	–	–	–
4566	GH-33	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16.45*	7.97*
4569	GH-33	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16.39	9.41
4570	GH-33	–	–	–	–	10.69	7.11	–	–	–	–	–	–	–	–	–	–
4625	GH-35	–	–	–	–	–	–	–	–	–	–	–	–	12.39	8.10*	16.55	8.45
4643	GH-37	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16.89	9.02
4653	GH-37	–	–	–	–	–	–	–	–	–	–	12.21*	8.85	–	–	–	–
4656	GH-37	–	–	–	–	–	–	10.66	8.03	13.17	8.76	–	–	14.62	10.03	–	9.70*
4679	GH-39	–	–	–	–	–	–	–	–	–	–	–	–	–	–	15.72*	7.94
6473	GH-41	–	–	–	–	–	–	–	–	10.19	7.26*	–	–	–	8.64*	–	–
6553	GH-35	–	–	–	–	–	–	9.76	6.68	11.37	7.89	–	–	12.74	9.08	–	–

M_2 is generally similar in morphology to M_1, differing mainly in its larger size.

M_3 differs from M_2 in having strong expansion of the hypoconulid region and in having a slightly more posterior entoconid. The M_3 hypoconulid lobe generally consists of a large labial cusp, a somewhat smaller posterior cusp, and a small lingual cusp.

Measurements of individual specimens of *Perissobune intizarkhani* are listed in Table 2, and a statistical summary is provided in Table 3.

Discussion.— Perissobune intizarkhani presents a number of important features that have often been considered to be characteristic or typical of primitive perissodactyls. These include: (1) the presence of diastemata anterior and posterior to the first premolar; (2) partially molarized last premolars; (3) a distinct π-shaped crown pattern on upper molars, with a labial ectoloph; (4) an anterior protoloph; (5) a posterior metaloph with an anteriorly shifted metaconule; (6) a transverse protolophid and hypolophid on lower molars; and (7) enlarged last molars with a large hypocone on M^3 and a distinct hypoconulid lobe on M_3 (Radinsky, 1969; McKenna et al., 1989; Froehlich, 1996; Hooker, 2005).

The molars of *Perissobune* are not strongly lophodont, and the conules and cusps are not reduced as in tapiroids and rhinocerotoids. Neither does the *Perissobune* dentition show a tendency towards the dilambdodont dentition of chalicotheres, brontotheres or palaeotheres. The retention of distinct molar cusps and conules and the strong twinning of the metaconid are similar to the condition seen in hippomorph perissodactyls, but because the former may be a primitive condition and the latter character is difficult to interpret (Radinsky, 1969; Froehlich, 2002), their phylogenetic value is unclear and limited.

Among basal perissodactyls, *Perissobune* partially resembles *Hallensia* in having bunodont teeth, an incomplete upper molar lingual cingulum, and the reduction of the parastyle on upper cheek teeth and the paracristid on lower cheek teeth. However, *Perissobune* differs from *Hallensia* in having stronger development of molar cusps and conules, stronger twinning of the metaconid, absence of a posthypocristid, and a stronger posterior size increase of the molars. We consider *Perissobune* to represent a basal perissodactyl of uncertain familial affinities.

Molars of *Perissobune intizarkhani* from the upper Ghazij Formation resemble those of *Nakusia* from the middle Ghazij Formation (Ginsburg et al., 1999) and those of *Cambaytherium* Bajpai et al. (2005) and *Indobune* Rose et al. (2006) in their overall bunodont morphology and in their general cusp pattern.

Nakusia, described as an anthracobunid, is based on a single specimen from the middle Ghazij Formation, with many morphological features obscured by wear. *Perissobune intizarkhani* is similar in size to *Nakusia*, but *P. intizarkhani* has transversely narrower cheek teeth, with a width/length ratio that is about 20% smaller than that of *Nakusia. P. intizarkhani* further differs from *Nakusia* in having an M^1 that is on average 16% larger in area than P^4, whereas in *Nakusia* teeth at both positions are identical in size (Ginsburg et al., 1999). *P. intizarkhani* differs morphologically from *Nakusia* in having a more molarized P^4, with better separated and more equal paracone and metacone and with a relatively larger paraconule. *P. intizarkhani* differs morphologically from *Nakusia* too in having upper molars that are more trapezoidal in outline, with a transversely compressed metacone. Therefore, within the limitations set by the limited fossil evidence available for *Nakusia*, we consider *P. intizarkhani* to be distinctly different from *Nakusia*.

Cambaytherium and *Indobune* were described and named by research teams working independently at the early Eocene Vastan site in India (Bajpai et al., 2005, 2006; Rose et al., 2006). *Cambaytherium* was initially considered to be a perissodactyl close to the European middle Eocene *Hallensia* (Bajpai et al., 2006), and *Indobune* was described as an anthracobunid most similar to *Nakusia* (Rose et al., 2006), but *Cambaytherium* and *Indobune* are very similar in morphology and probably represent the same taxon (Missiaen et al., 2011b). *Cambaytherium* and *Nakusia* are now considered sister taxa of Perissodactyla (Rose et al., 2014a,b).

Perissobune intizarkhani differs from *Cambaytherium* in having more salient transverse lophs on P^4–M^3, better developed parastyles on upper molars, and lower molars with more distinctly twinned metaconids, a more strongly developed protolophid and hypolophid, and a more centrally placed hypoconulid. Most importantly, *Perissobune intizarkhani* differs from the Vastan taxon in having more molariform last premolars, with a better developed paraconule and metacone on P^4, and a stronger paraconid, more anterior and lingual metaconid, and more labial hypoconid on P_4.

Perissobune intizarkhani resembles to some degree the possible anthracobunid *Nakusia*, but *P. intizarkhani* differs markedly from typical anthracobunids (Wells and Gingerich, 1983) in having a much lower-cusped dentition, less connate paracone and metacone cusps on upper premolars, and a stronger parastyle and ectoloph, with weaker cingula, on upper molars. Differences in the lower dentition include absence of a metaconid on P_3, a more labially oriented cristid oblique on lower molars, and a distinct, basined hypoconulid lobe on M_3.

The molars of *Perissobune* resemble molars of *Nakusia* and *Cambaytherium* to some degree, with a number of clear differences, but the premolars of *Perissobune* are very different from premolars of those taxa. We therefore doubt that the molar similarities are indicative of any close phylogenetic tie. In this regard, it might also be noteworthy that although *Perissobune* differs from quettacyonid condylarths in virtually every aspect of its dental morphology, the *Perissobune* dentition resembles that of quettacyonids in being bunodont. It is therefore possible that during the early Eocene, ecological conditions on the Indian subcontinent favored bunodonty in medium sized herbivores, leading to convergent evolution and dental similarities.

Perissobune munirulhaqi, new species
Fig. 5

?Isectolophidae, gen. et sp. indet., Gingerich et al., 1998, p. 12, fig. 11 f–g.

Holotype.— GSP-UM 6498 (Fig. 5A–B), right dentary with P_3–M_3. This specimen preserves a high ascending ramus and moderately worn premolars and molars. Measurements of individual specimens of *Perissobune munirulhaqi* are listed in Table 4.

Type locality.— The holotype is from locality GH-44 in the Kingri area, Balochistan Province, Pakistan (Fig. 2). This is in the upper part of the upper Ghazij Fm, early Eocene (Ypresian).

Diagnosis.— *Perissobune munirulhaqi* resembles *P. intizarkhani* but differs in being larger (Fig. 6), in having stronger labial cingulids on the lower teeth, in having a relatively longer P_3, in having relatively wider lower molars with a more marked posterior size increase, with stronger twinning of the metaconids and a relatively smaller hypoconulid on $M_{1–2}$.

TABLE 3 — Summary statistics for measurements of *Perissobune intizarkhani*, n. gen. and sp., from the lower part of the upper Ghazij Formation, early Eocene, of Pakistan. Original measurements are listed in Table 2. Abbreviations: *L*, anteroposterior length; *W*, labiolingual width; *N*, number of individuals; *Min*., minimum value; *Max*., maximum value; *SD*, standard deviation; *CV*, coefficient of variation.

Measurement		N	Min.	Max.	Mean	SD	CV
Upper dentition							
P^4	L	3	10.05	10.70	10.34	0.330	0.03
	W	4	12.07	13.70	12.81	0.676	0.05
M^1	L	4	11.59	13.05	12.13	0.634	0.05
	W	4	12.89	15.48	14.08	1.197	0.09
M^2	L	9	11.81	14.81	13.40	1.123	0.08
	W	8	13.67	16.96	15.00	1.215	0.08
M^3	L	14	12.28	16.34	14.22	1.448	0.10
	W	14	12.96	16.82	14.56	1.388	0.10
Lower dentition							
P_4	L	8	9.76	11.71	10.77	0.793	0.07
	W	8	6.68	8.39	7.79	0.611	0.08
M_1	L	5	10.19	13.17	11.60	1.062	0.09
	W	5	7.26	8.76	7.98	0.598	0.07
M_2	L	7	12.39	14.98	13.68	0.987	0.07
	W	8	8.10	10.17	9.25	0.734	0.08
M_3	L	8	15.72	18.63	16.64	0.875	0.05
	W	9	7.94	10.39	9.01	0.906	0.10

Etymology.— The species is named for Dr. Munir ul Haq of the Geological Survey of Pakistan in recognition of his collaboration in organizing field work and paleontological study of the Ghazij Formation and its faunas in Pakistan (e.g., Gingerich et al., 2001; Gunnell et al., 2008).

Referred material.— All four-digit numbers are GSP-UM specimen numbers. Locality **GH-4**: 4004, right M_1 fragment. Locality **GH-8**: 4040, left M^2 fragment. Locality **GH-16**: 4247, left P^4 fragment; 4269, left M^2. Locality **GH-18**: 4272, right M_1 fragment; 4273, right M_1 fragment. Locality **GH-27**: 4346, left M_1; 4365, left M^3 fragment; 4373, left M_3 fragment. Locality **GH-31**: 4516, right dentary with $P_{3–4}$; 4517, right edentulous dentary with roots of P_3–M_1. Locality **GH-34**: 4588, right P_4. Locality **GH-38**: 4661, right dentary with broken P_3–M_2. Locality **GH-46**: 6536, left M_x fragment.

Description.— GSP-UM 4247 (Fig. 5G) is identified as a partial left P^4 of *Perissobune munirulhaqi*. This specimen preserves only the lingual margin of the distinct, partially fused paracone and metacone. The lingual part of the tooth shows a strong protocone and paraconule, and a slightly weaker metaconule.

GSP-UM 4040 (Fig. 5J) and GSP-UM 4365 (Fig. 5I) are the only upper molars known for *Perissobune munirulhaqi*, and both are poorly preserved, showing few morphological details. These specimens are markedly larger than their homologues in *P. intizarkhani*, but do not seem to differ from them morphologically.

Lower teeth of *Perissobune munirulhaqi* are shown in Figure 5A–F and 5H. Figure 5A–B shows the holotype with P_3–M_3. P_3 is robust and roughly triangular in occlusal view. The paraconid is distinctly anterior to the strong protoconid. The metaconid is much smaller than the protoconid and placed posterolingual from it. A weak crest descends posteriorly from the protoconid to a single, slightly labially displaced talonid cusp.

P_4 is anteroposteriorly shorter than P_3 and more rectangular in occlusal view. P_4 has a distinct, twinned metaconid that is slightly smaller than the protoconid and situated posterolingual to it. The rounded paracristid runs anteriorly and lingually from the protoconid and lacks a paraconid. The P_4 talonid has a short cristid obliqua, a marked hypooconid, slightly offset labially, and a small entoconid.

M_1 has a very weak paracristid forming the anterior border of the tooth. The metaconid is posterior to the protoconid. The metaconid is strongly twinned and has a distinct crest descending from its anterolingual corner to join the paracristid. The hypoconid and entoconid are very robust and subequal in size, with the entoconid being more posterior in position. Both are stronger than the posteriorly-placed hypoconulid. A notched hypolophid connects the entoconid to the hypoconid, and a low cristid obliqua runs from the hypoconid to the posterolingual corner of the protoconid.

M_2 is generally similar in morphology to M_1, differing mainly in its much larger size.

M_3 differs from M_2 in being larger, in having a strongly projecting hypoconulid lobe, and in having a slightly more posterior entoconid.

FIGURE 5 — Dentition of *Perissobune munirulhaqi*, n. gen. and sp., from the upper Ghazij Formation in Pakistan, early Eocene in age. **A–B**, GSP-UP 6498 (holotype), right dentary with P_3–M_3 in labial (A) and occlusal (B) view. **C–D**, GSP-UM 4588, right P_4 in labial (C) and occlusal (D) view. **E–F**, GSP-UM 4273, right M_1 fragment in labial (E) and occlusal (F) view. **G**, GSP-UM 4247, left P^4 fragment in occlusal view. **H**, GSP-UM 4004, right M_1 fragment in occlusal view. **I**, GSP-UM 4365, left M^3 fragment in occlusal view. **J**, GSP-UM 4040, left M^2 fragment in occlusal view.

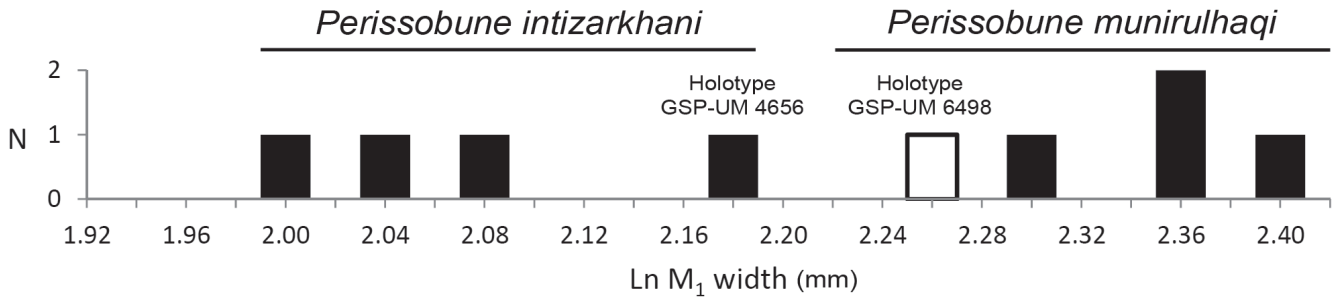

FIGURE 6 — Histogram comparing molar size in *Perissobune intizarkhani* and *P. munirulhaqi*. M_1 width (mm) is chosen for comparison because the measurement is represented by a reasonable number of specimens, central in the tooth row, and not affected by interproximal wear during life. Measurements are given in Tables 2 and 4. Solid black bars represent specimens from the lower part of the upper Ghazij Formation, and the open bar is a specimen from the upper part of the upper Ghazij Formation. Horizontal lines under each species name show the 0.2-natural-logarithm-unit range of variation expected for a linear measurement of tooth size in a large sample of a single mammalian species (Gingerich, 1981). There are clearly two species of *Perissobune* present in the lower part of the lower Ghazij Formation. Holotypes were chosen for their completeness and preservation. Note that the holotype of *P. munirulhaqi* comes from the upper part of the upper Ghazij Formation, but the species is well represented in the lower part of the upper Ghazij as well.

Measurements of individual specimens of *Perissobune munirulhaqi* are listed in Table 4.

Discussion.— *Perissobune munirulhaqi*, represented by 14 specimens, is much less common in the Ghazij Formation than *P. intizarkhani*, represented by 83 specimens. The small sample size and poor preservation of specimens with upper cheek teeth limits the possibilities for detailed comparison. *P. munirulhaqi* is significantly larger than *P. intizarkhani* (Fig. 6), differing by about 23% in linear dimensions. *P. munirulhaqi* further differs from *P. intizarkhani* in having stronger labial cingulids on the lower teeth, a relatively longer P_3, relatively wider molars with a more marked posterior size increase, stronger twinning of the molar metaconids, and a relatively smaller hypoconulid on $M_{1–2}$.

Both species co-occur in the lower part of the upper Ghazij Formation, but only the rare *P. munirulhaqi* has been found in the upper part of the upper Ghazij Formation, possibly indicating a difference in stratigraphic range.

GSP-UM 4004, from the lower part of the upper Ghazij Formation in the Sor Range, was originally reported as a possible isectolophid perissodactyl (Gingerich et al., 1998), but based on the size, development the cusps, and strong labial cingulum, this specimen is here re-identified as *P. munirulhaqi*. Isectolophidae therefore seem to be absent from the lower part of the upper Ghazij Formation, and only make their appearance in the upper part of the upper Ghazij Formation where they are known from two much smaller forms from Gandhera Quarry (Missiaen et al., 2011a).

Ghazijhippus, new genus

Type and only species.— *Ghazijhippus talibhasani* n. sp.

Diagnosis.— *Ghazijhippus* is an early Eocene perissodactyl characterized by a limited degree of lophodonty, robust molar cusps and conules, a long diastema in front of P_1 and a short diastema behind P_1, and twinned metaconids on the lower molars. It differs from primitive hippomorphs in lacking a metaconule on P^3, in having more distinct upper molar parastyles, in having relatively shorter trigonids, and in having weaker cristid obliquae on lower molars. *Ghazijhippus* differs from contemporary *Perissobune* in having stronger lophs and weaker cusps on both upper and lower molars, in lacking a protocone on P^2, in having stronger parastyles on upper cheek teeth, in having less anteriorly placed paraconules and metaconules on upper molars, and in having a shorter P_1–P_2 diastema.

Etymology.— Named for the Ghazij Formation of Pakistan, where the specimens described here were found; and *hippus* (Gr., masc., 'horse'), a common root in perissodactyl names.

Occurrence.— Lower Eocene (Ypresian) Ghazij Formation of Balochistan Province, Pakistan. *Ghazijhippus* is known only from the lower part of the upper Ghazij Formation. As reviewed above, the lower part of the upper Ghazij Formation is in the range from 54 to 52 Ma (Clyde et al., 2003; Missiaen et al., 2011a; Vandenberghe et al., 2012). On a North American time scale, this is equivalent in time to the middle or late Wasatchian land-mammal age.

Discussion.— Dental terminology is illustrated in Figure 3.

Ghazijhippus talibhasani, new species
Figs. 7–8

Holotype.— GSP-UM 4638 (Figs. 7, 8A–B), cranium with left P^2–M^3 and right P^4–M^3. Measurements of the holotype are included in Table 5.

Type locality.— The holotype is from locality GH-37 in the Kingri area, Balochistan Province, Pakistan (Fig. 2). It came from the lower part of the upper Ghazij Fm, early Eocene (Ypresian).

Diagnosis.— As for the genus.

Etymology.— Named for Mirza Talib Hasan, former Director of Palaeontology and Stratigraphy at the Geological

Survey of Pakistan, whose interest and support made fieldwork in the Ghazij Formation possible.

Referred material.— All are GSP-UM numbers. Locality **GH-26**: 4335, right M_3. Locality **GH-31**: 4504, left M^3 fragment; 4505, right M_3 fragment. Locality **GH-33**: 4585, left M^3. Locality **GH-34**: 4589, right M_3. Locality **GH-35**: 4632, left M^2. Locality **GH-39**: 4678, left M_3 fragment; 4681, left dentary with P_1–P_3 and $M_{2–3}$. Locality **GH-43**: 6486, left M^2.

Description.— The holotypic cranium of *Ghazijhippus talibhasani*, GSP-UM 4638, is illustrated in Figure 7. It is relatively complete, but somewhat deformed obliquely by compression. Premaxillae on both sides are missing, and the left squamosal and jugal are missing. The cranium measures 173 mm in length as preserved, from the front of the canine alveoli to the occipital condyles. Adding the missing premaxillae yields an estimate for total condylobasal length of about 180 mm. The bizygomatic breadth of the cranium is 86 mm.

Salient features of the cranium are a broad, flat frontoparietal shield tapering from the breadth of the orbits to midline convergence with the narrow nuchal crest. Temporal fossae do not extend onto the skull roof, and there is no sagittal crest like that seen in primitive equids (e.g., *Hyracotherium* and/or *Eohippus*). Alveoli for the upper canine teeth are relatively large and the zygomatic arches are robust, which together with conformation of the frontoparietal shield suggest that the cranium is probably male. There is a 12 mm diastema between the upper canine and P^1, and a shorter diastema following P^1.

Sutures are poorly preserved, but the cranium appears to show nasals that have broad contact with the frontals. Premaxillae are missing, but these appear to have contacted the nasals as in other early perissodactyls. Both supraorbital processes of the frontals are well preserved, and there is no trace of a supraorbital notch or foramen. There is no preglenoid process and the anterior border of the mandibular fossa is relatively flat. The postglenoid process faces more laterally than anteriorly, and there is no postglenoid foramen. The post-tympanic process is short relative to the postglenoid process, and mastoid exposure is narrow on the lateral surface of the cranium. There is no tympanic bulla attached to the skull.

The dentary, GSP-UM 4681 (Fig. 8K–L), is gracile, with a shallow mandibular ramus and relatively small canine alveoli, suggesting it may be female. The mandibular symphysis is solidly fused. Fusion extends posteriorly as far as the posterior edge of P_1, and the jaw deepens substantially between the canine and P_1. There is a 22 mm long diastema between alveoli for the lower canine and P_1, with a shorter 5.7 mm diastema following P_1.

The dentition of *Ghazijhippus talibhasani* is illustrated in Figure 8A–J. Alveoli in the holotypic cranium show that the upper canine of was moderate in size, vertically implanted, and separated from P^1 by a diastema of about 12 mm. P^1 has two large alveoli and was probably ellipsoidal in outline. A short diastema of about 2.5 mm separates the roots of P^1 and P^2.

P^2 is transversely narrow and again ellipsoidal in occlusal view, having a strong labial paracone. There is no metacone on P^2. This tooth has no cusp medial to the paracone, but there is a weak lingual cingulum.

P^3 is transversely much wider, and more triangular in occlusal view, than P^2. The labial side bears a small parastyle anterior to the paracone, and a strong paracone and metacone. The metacone is not much smaller than the paracone and relatively well separated from it. The lingual side of P^3 shows

TABLE 4 — Measurements of teeth of *Perissobune munirulhaqi*, n. gen. and sp., from the upper Ghazij Formation, early Eocene, of Pakistan. GSP-UM 6498 is the holotype. Molars marked with a superscript or subscript 'x' could be first or second molars. Measurements are in mm, and asterisks indicate estimates where measurements could not be determined due to wear or damage. Abbreviations: *L*, anteroposterior length; *W*, labiolingual width.

							Upper Dentition										
GSP-UM	Site	P1L	P^1W	P^2L	P^2W	P^3L	P^3W	P^4L	P^4W	M^1L	M^1W	M^xL	M^xW	M^2L	M^2W	M^3L	M^3W
4365	GH-27	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16.52*	18.59*
							Lower Dentition										
GSP-UM	Site	P_1L	P_1W	P_2L	P_2W	P_3L	P_3W	P_4L	P_4W	M_1L	M_1W	M_xL	M_xW	M_2L	M_2W	M_3L	M_3W
4004	GH-04	–	–	–	–	–	–	–	–	–	10.46*	–	–	–	–	–	–
4272	GH-18	–	–	–	–	–	–	–	–	–	10.54*	–	–	–	–	–	–
4273	GH-18	–	–	–	–	–	–	–	–	–	10.95	–	–	–	–	–	–
4346	GH-27	–	–	–	–	–	–	–	–	13.15*	9.79*	–	–	–	–	–	–
4516	GH-31	–	–	–	–	13.49	8.51	12.94	9.38	–	–	–	–	–	–	–	–
4588	GH-34	–	–	–	–	–	–	12.35	8.95	–	–	–	–	–	–	–	–
6498	GH-44	–	–	–	–	14.92	9.05	12.55	9.19	12.26*	9.52*	–	–	15.2	12.04	22.27	12.39

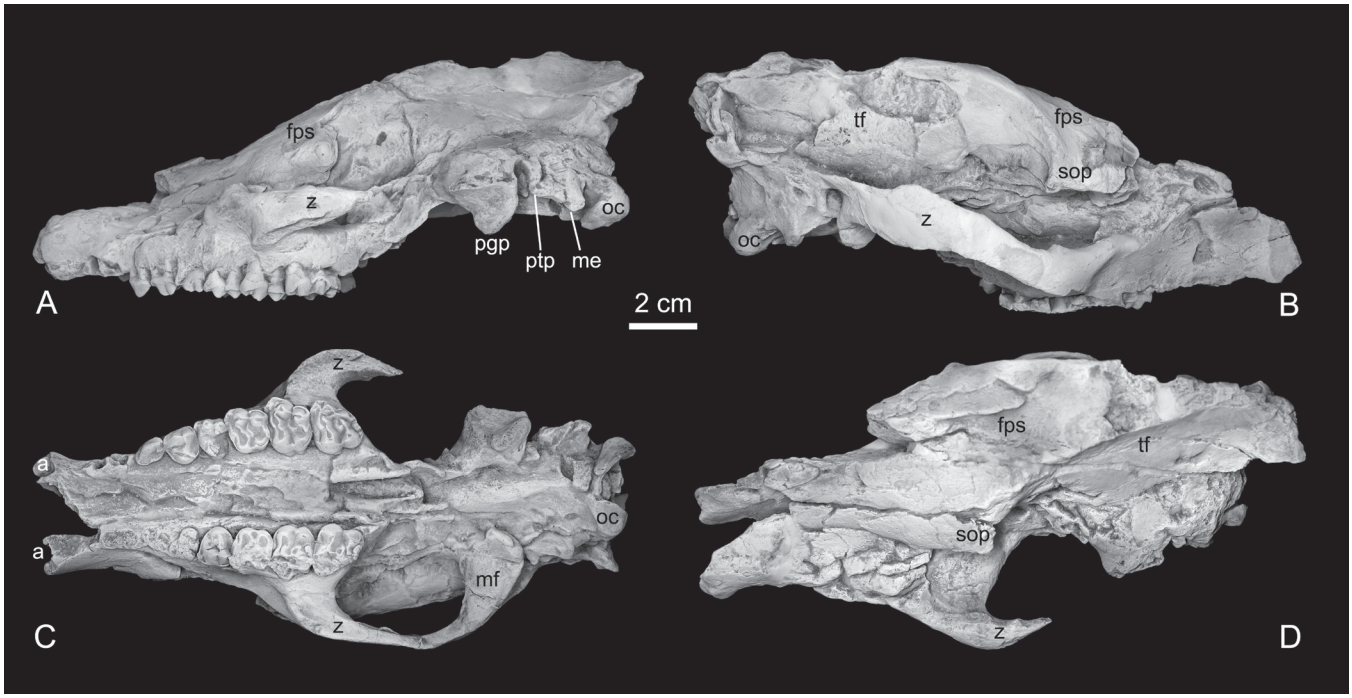

FIGURE 7 — Holotypic skull (GSP-UM 4638) of *Ghazijhippus talibhasani*, n. gen. and sp., from the upper Ghazij Formation in Pakistan, early Eocene in age. Skull is shown in **A**, left; **B**, right; **C**, ventral; and **D**, dorsal views. Abbreviations: *a*, canine alveolus; *fps*, fronto-parietal shield; *me*, mastoid exposure; *mf*, mandibular fossa; *oc*, occipital condyle; *pgp*, postglenoid process; *ptp*, post-tympanic process; *sop*, supraorbital process; *tf*, temporal fossa; *z*, zygomatic arch.

a distinct protocone, a protoloph with a paraconule, a metaloph and a weak talon shelf.

P^4 is larger than P^3 and morphologically differs from it by the more strongly developed cusps and lophs, with better separated paracone and metacone, a higher protocone, a distinct paraconule, and a stronger metaloph with a metaconule. Cross lophs on P^3 and P^4, to the extent that these are developed, do not meet.

All three upper molars are trapezoidal in occlusal outline, with the anterior margin of the crown being longer than the posterior margin. The difference in length of the anterior margin compared to the posterior margin is greatest on M^2 and M^3. Protocone, paracone, metacone, and hypocone cusps are all well developed on all three molars, with no connecting centrocristae. The metacone on M^3 is in a labial position like those on M^1 and M^2. Upper molars retain distinct paraconules and metaconules. There is no distinct preparaconule crest. Paracones and metacones on upper molars are all convex labial bulges, and there are moderately large parastyles, but no mesostyles. The parastyles are more or less in line with the paracones and metacones on all three upper molars, and the parastyles have simple uncurved apices. The metaloph on upper molars joins the ectoloph anterior to the metacone, with a premetaconule crista curving toward the metacone.

M^1 has a distinct parastyle on the ectoloph that projects anterolabially from the paracone. The metacone is slightly smaller than the paracone and clearly separated from it. Both cusps are connected by a low, straight centrocrista and a short postmetacrista runs posterolabially from the metacone. The protoloph is relatively high and runs anterolabially from the protocone to the somewhat anteroposteriorly compressed paraconule and then attaches to the ectoloph between the parastyle and paracone. The hypocone is similar in development to the protocone but situated slightly more labially. The metaconule is more robust than the paraconule and situated anterolingual to the metacone. The metaloph is shorter than the protoloph, and reaches the ectoloph about midway between the paracone and metacone. The anterior cingulum is distinct and bears a swelling at the level of the paraconule. The narrow posterior cingulum is continuous labially with an incomplete labial cingulum. Lingually it curves around the posterolingual corner of the hypocone.

M^2 is larger than M^1 and more trapezoidal in occlusal view, with a more labially placed and more distinct parastyle and paracone. Both the paraconule and metaconule are robust and inflated. There is a well-developed labial cingulum, an anterior cingulum, and a narrow posterior cingulum.

M^3 differs from M^2 in having a narrower crown posteriorly, with a reduced metacone, and metaconule, a more posterior hypocone, and a stronger posterior cingulum but one that does not curve around the base of the hypocone.

GSP-UM 4681 is the only specimen preserving lower premolars (Fig. 8K–L). P_1 is a transversely narrow, two-rooted tooth, consisting of a distinct protoconid and a small talonid

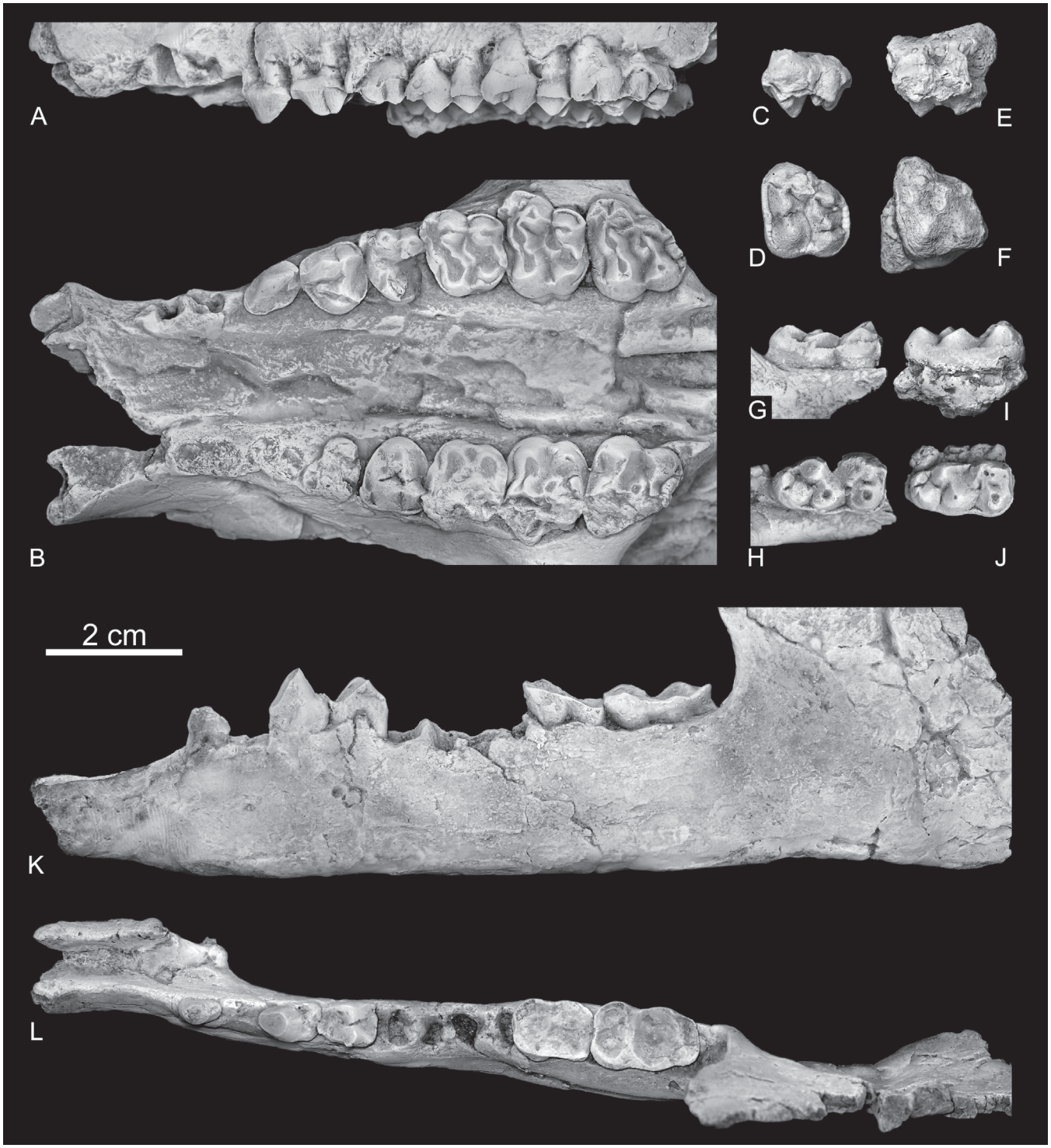

FIGURE 8 — Dentition of *Ghazijhippus talibhasani*, n. gen. and sp., from the early Eocene upper Ghazij Formation in Pakistan. **A–B**, GSP-UM 4638 (holotype), left P^2–M^3 and right P^4–M^3 in left labial (A) and occlusal (B) view. **C–D**, GSP-UM 6486, left M^2 in labial (C) and occlusal (D) view. E–F, GSP-UM 4585, left M^3 in labial (E) and occlusal (F) view. **G–H**, GSP-UM 4589, right M_3 in labial (G) and occlusal (H) view. **I–J**, GSP-UM 4335, right M_3 in labial (I) and occlusal (J) view. **K–L**, GSP-UM 4681, left dentary with P_1–P_3 and M_2–$_3$ in labial (K) and occlusal (L) view.

TABLE 5 — Measurements of teeth of *Ghazijippus talibhasani*, n. gen. and sp., from the upper Ghazij Formation, early Eocene, of Pakistan. GSP-UM 4638 is the holotype. Molars marked with a superscript or subscript 'x' could be first or second molars. Measurements are in mm, and asterisks indicate estimates where measurements could not be determined due to wear or damage. Abbreviations: *L*, anteroposterior length; *W*, labiolingual width.

Upper Dentition

GSP-UM	Site	P^1L	P^1W	P^2L	P^2W	P^3L	P^3W	P^4L	P^4W	M^1L	M^1W	M^xL	M^xW	M^2L	M^2W	M^3L	M^3W
4504	GH-31	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14.34*	13.58*
4585	GH-33	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14.31	15.12
4632	GH-35	–	–	–	–	–	–	–	–	–	–	–	–	14.64	15.26	–	–
4638-L	GH-37	–	–	8.83	5.74	9.78	9.89	9.53	10.51*	12.14	12.40	–	–	13.42	15.16	14.81	14.67
4638-R	GH-37	–	–	–	–	–	–	9.39	11.02	11.96*	–	–	–	12.60*	15.23*	14.11*	14.96*
6486	GH-43	–	–	–	–	–	–	–	–	–	–	–	–	13.10	14.21*	–	–

Lower Dentition

GSP-UM	Site	P_1L	P_1W	P_2L	P_2W	P_3L	P_3W	P_4L	P_4W	M_1L	M_1W	M_xL	M_xW	M_2L	M_2W	M_3L	M_3W
4335	GH-26	–	–	–	–	–	–	–	–	–	–	–	–	–	–	15.61	8.63
4589	GH-34	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16.31	9.08
4681	GH-39	6.01	3.19	8.55	5.29	–	6.12	–	–	–	–	–	–	10.99*	8.33*	15.65	9.17

heel. P_2 is dominated by the strong protoconid, with a short crest extending anteriorly from it and a weak crest descending posteriorly towards a small centrally located talonid cusp. P_3 is severely worn and damaged in GSP-UM 4681, but the trigonid region of this tooth suggests the presence of distinct paracristid and a relatively well developed metaconid placed posterolingual to the protoconid.

P_4 and M_1 are missing in GSP-UM 4681 (Fig. 8K–L), but alveoli suggest both were similar in size. The crown of M_2 is heavily worn, providing little information except that it was larger than M_1 and smaller than M_3.

M_3 is the only lower molar position showing the lower molar crown pattern (Fig. 8G–J). M_3 has a short, anterolingually directed paracristid, and a protoconid that is subequal to the weakly or moderately twinned metaconid. The protolophid is deeply notched, and the metalophid (crista obliqua), which is mesially reduced, joins the protolophid near its midpoint. The hypoconid is larger than the entoconid and placed more anteriorly. Both are connected by a low, notched hypolophid. The hypoconulid lobe is moderately developed and bears a large hypoconulid cusp that is connected to the midpoint of the hypolophid by a low posthypocristid as well as a smaller posterolingual accessory cusp.

Measurements of individual specimens of *Ghazijhippus talibhasani* are listed in Table 5.

Discussion.— No directly associated upper and lower teeth of *Ghazijhippus* have been found, but upper and lower teeth were found at the same locality. Their association is further supported by the compatible morphology of upper and lower teeth and the reasonably good occlusion of the molars.

Ghazijhippus talibhasani displays typical perissodactyl morphology, including a transverse nasal-frontal suture on the dorsal surface of the cranium, a characteristic π –shaped loph pattern on upper molars, a matching transversely-oriented protolophid and hypolophid on lower molars, and a distinct hypoconulid lobe on M_3. Within Perissodactyla, the dentition of *Ghazijhippus* seems closest to primitive hippomorph taxa such as *Hyracotherium* or *Eohippus*, based on the distinct upper molar conules and twinned lower molar metaconids, and the lack of features associated with evolution toward a more advanced hypsodont, lophodont or dilambdodont dentition (Froehlich, 1996, 2002).

Ghazijhippus is similar to primitive North American equids such as *Hyracotherium grangeri*, *H. aemulor* and *H. pernix* (Kitts, 1956; Gingerich, 1991) in the degree of lophodonty, the size of postcanine and premolar diastemata, the molarization of P^3, the strong upper molar conules, and the twinned lower molar metaconid. *Ghazijhippus,* however, differs from these forms in being larger, having more bunodont cusps, lacking a P^3 metaconule, having a more labially projecting upper molar parastyle, and in having lower molars with a relatively shorter trigonid, a weaker cristid oblique, and a stronger metaconid buttress (Hooker, 1994).

The strong cusps and conules of *Ghazijhippus* are reminiscent of the European basal perissodactyl *Hallensia* (Franzen and Haubold, 1986; Franzen, 1990), but *Ghazijhippus* differs from *Hallensia* in having longer postcanine diastemata, having more triangular upper premolars, having a stronger upper molar parastyle, and in having relatively larger last molars.

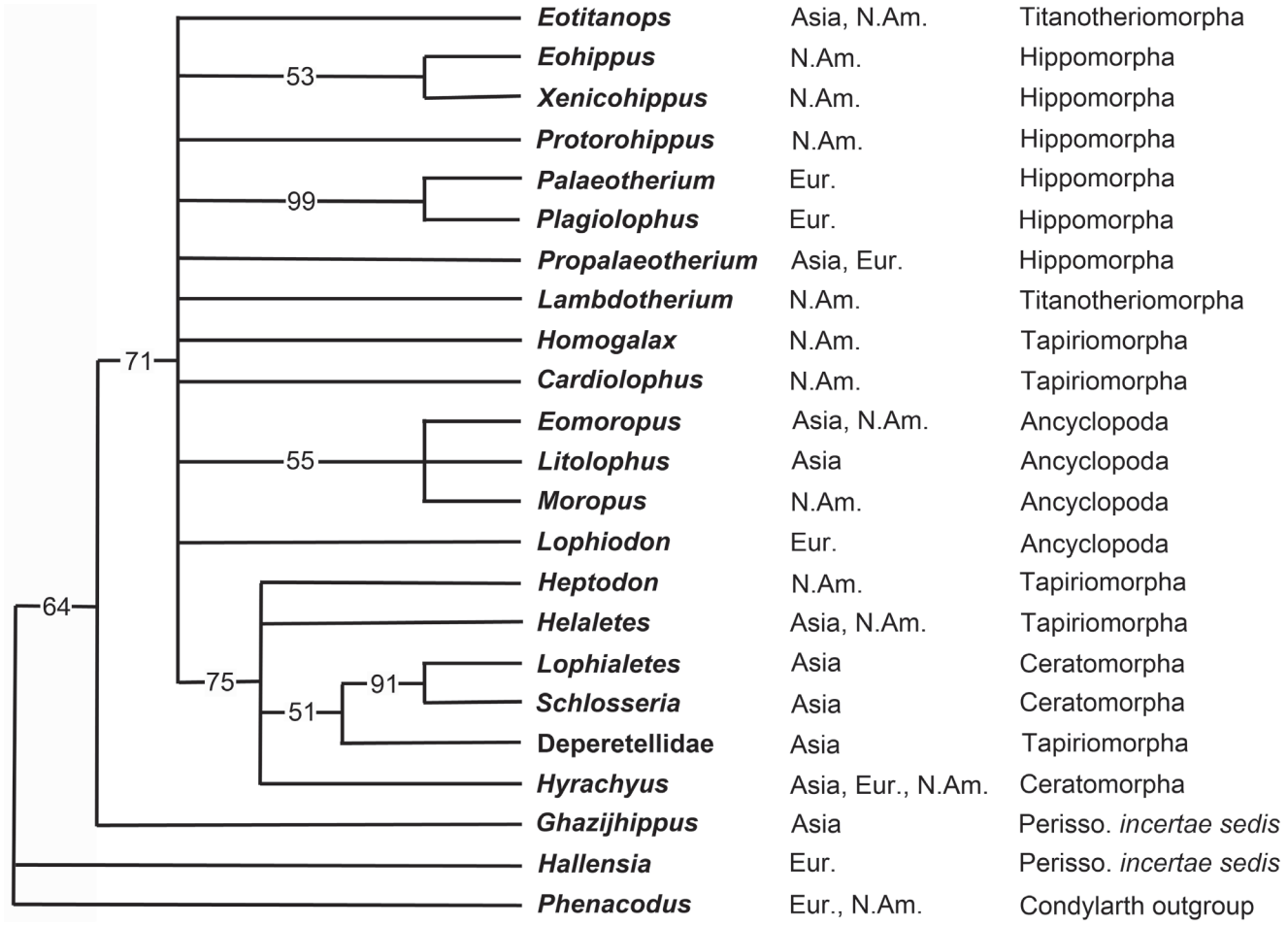

FIGURE 9 — Phylogenetic relationships of *Ghazijhippus talibhasani*, n. gen. and sp., based on cranial and dental characteristics described here, analyzed in the context of characters, taxa, and methods reported by Holbrook (2009). *Perissobune*, n. gen., is not included because it is known only from teeth. Analysis of 60 characters in 23 taxa yielded eight shortest trees of length 176 steps, with a consistency index of 0.443 (PAUP* branch and bound; Swofford, 2001). Condylarthran outgroup *Phenacodus* was used to root the trees. Tree shown here is a 50% majority-rule consensus. Bootstrap support values from 51 to 99 are frequencies of recovery of clades in 100 bootstrap replications. Note that *Ghazijhippus* lies within a clade of perissodactyls excluding *Hallensia* (a clade with 64% bootstrap support) and outside a clade of more derived perissodactyls (a clade with 71% bootstrap support). The geographic distribution of operational taxonomic units is shown in the central column of text, and the present classification of genera is shown in the right-hand column. This analysis was run to explore how *Ghazijhippus* is related to previously described perissodactyls, not to resolve conflicting phylogenetic relationships in the overall classification of perissodactyls.

Ghazijhippus talibhasani is similar in size to *Perissobune intizarkhani*, but *Ghazijhippus* differs distinctly from *Perissobune* in having stronger lophs with weaker cusps, in lacking a P^2 hypocone, in having a more individualized metacone on P^{3-4}, in having a stronger parastyle on all upper cheek teeth, in having a less anteriorly placed paraconule and metaconule on the upper molars, in having a shorter P_1–P_2 diastema, and probably also in having a less twinned metaconid and a weaker hypoconulid.

Cladistic analysis of forty cranial and dental characteristics (Fig. 9) confirms that *Ghazijhippus talibhasani* lies within Perissodactyla. We compared *Ghazijhippus* to the condylarth *Phenacodus* and to the range of perissodactyls studied by Holbrook (2009). Character coding for *Ghazijhippus* is included in the data block of the second Nexus file in the Appendix. The characters included here and the coding are both explained in Holbrook (2009). Missing data for *Ghazijhippus* are generally postcranial characteristics that are not yet known for the genus. *Perissobune* was not included because it is known only from dental specimens. Our analysis indicates that *Ghazijhippus* is a basal perissodactyl like *Hallensia* (Franzen, 1990), more basal than the primitive North American hippomorphs *Eohippus* (*Hyracotherium*), *Xenicohippus*, and *Protorohippus*. *Perissobune* probably occupies a similarly basal position within Perissodactyla.

TABLE 6 — Perissodactyl species known from the lower and upper parts of the upper Ghazij Formation, early Eocene, of Pakistan, summarizing results in Missiaen et al. (2011a), Missiaen and Gingerich (2012), and this study. Asterisks mark species whose type specimens come from the stratigraphic interval in the column heading.

Lower part of upper Ghazij Formation	Upper part of upper Ghazij Formation
PERISSODACTYLA	PERISSODACTYLA
Perissodactyla *incertae sedis*	Perissodactyla *incertae sedis*
Family *incertae sedis*	Family *incertae sedis*
Perissobune intizarkhani*	***Perissobune munirulhaqi****
Perissobune munirulhaqi	Tapiromorpha
Ghazijhippus talibhasani*	Isectolophidae
	Gandheralophus minor*
	Gandheralophus robustus*
	Ceratomorpha
	Lophialetidae
	Lophialetidae indet.
	Ancyclopoda
	Eomoropidae
	Litolophus ghazijensis*
	Titanotheriomorpha
	Brontotheriidae
	Balochititanops haqi*
	Eotitanops pakistanensis*

DISCUSSION

Addition of *Perissobune intizarkhani*, *P. munirulhaqi*, and *Ghazijhippus talibhasani* brings to nine the number of perissodactyl species known from the upper Ghazij Formation, early Eocene, of Pakistan (Table 6). *Perissobune* and *Ghazijhippus* are found in the lower part of the upper Ghazij Formation and therefore represent the oldest perissodactyls from Pakistan, and the oldest representatives of any modern order of mammals found in Pakistan. Planktonic foraminifera and paleomagnetic studies suggest a late early Eocene age for the upper Ghazij Formation (Gingerich et al., 1997; Clyde et al., 2003), and mammalian biochronology suggests that the boundary between the lower and upper parts of the upper Ghazij Formation is more or less equivalent to the Wasatchian-Bridgerian boundary in North America (Missiaen et al., 2011a). The geographic origin of Perissodactyla is not yet clear, but perissodactyls, represented by *Perissobune* and *Ghazijhippus*, were present in Indo-Pakistan in strata older than the North American Wasatchian-Bridgerian mammalian faunal transition.

The overlying upper part of the upper Ghazij Formation has a much more diverse perissodactyl fauna, yielding specimens of *Perissobune* but also of brontotheres, isectolophids, lophialetids and eomoropids (Missiaen et al., 2011a; Missiaen and Gingerich, 2012). Consistent with this observation, primates, artiodactyls, and hyaenodontid creodonts are known from the upper part of the upper Ghazij Formation but not from the lower part of the upper Ghazij (Gingerich et al., 2001; Gunnell et al., 2008). Vertebrate faunas in Indo-Pakistan became progressively more cosmopolitan and more modern during the early Eocene, probably involving dispersal across transient land connections (Clyde et al., 2003).

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APPENDIX

Nexus f iles used to generate the cladogram shown in Figure 9. The first file is a command file. The second is a data file. Character list and character coding follows Holbrook (2009), with the addition of cranial and dental character coding for *Ghazijhippus*, n. gen., described here. *Perissobune*, n. gen., was not included because it is known only from teeth and jaws.

```
#NEXUS
begin PAUP;
log start file=Ghazijhippus.log replace;
execute Ghazijhippus.nex;
set maxtrees=100 increase=auto;
set root=outgroup;
outgroup Phenacodus;
BandB;
roottrees;
contree all/strict=yes majrule=no treefile=Ghazij_Strict.tre;
contree all/strict=no majrule=yes treefile=Ghazij_MajRule.tre;
pscores /tl ci ri rc;
bootstrap nreps=100 treefile=boot.tre search=BandB;
END;
```

```
#NEXUS
[PAUP* 4.0b10 reg. Philip D. Gingerich, University of Michigan]
BEGIN TAXA;
DIMENSIONS NTAX=23;
TAXLABELS
Eotitanops Eohippus Protorohippus Xenicohippus Palaeotherium Plagiolophus Hallensia Propalaeo. Lambdotherium
Homogalax Cardiolophus Eomoropus Litolophus Moropus Lophiodon Heptodon Helaletes Lophialetes Schlosseria
Deperetellidae Hyrachyus Ghazijhippus Phenacodus;
END;

BEGIN CHARACTERS;
TITLE 'Ghazijhippus';
DIMENSIONS NCHAR=60;
FORMAT DATATYPE=STANDARD RESPECTCASE MISSING=? GAP=- SYMBOLS="0123";
CHARSTATELABELS
 1 'Nasals'/narrow_suture_intruding broad_suture_transv.,
 2 'Premaxilla'/contacting_nasal not_contacting_nasal,
 3 'Incisive foramen'/paired single_and_median,
 4 'Sphenopalatine foramen'/middle_of_orbit anterior_near_max._foram.,
 5 'Lacrimal'/facial_exposure exposure_in_rim,
 6 'Supraorbital notch'/distinct absent_or_shallow,
 7 'Optic foramen'/anteriorly_position posterior,
 8 'Foramen ovale'/separate confluent_w._mid._Lacerate,
 9 'Preglenoid process'/absent present,
10 'Postglenoid process'/facing_anteriorly facing_anterolaterally,
11 'Postglenoid foramen'/present absent,
12 'Posttympanic process'/equal_to_postglenoid short,
13 'Mastoid exposure'/posterior narrow_and_lateral,
14 'Ectotympanic'/not_attached attached,
15 'Acromion process on scapula'/present absent,
16 'Bicipital groove on humerus'/facet_absent distinct_facet,
17 'Lateral shelf on humerus'/absent present_and_tapered present_without_taper,
18 'Entepicondylar foramen'/present absent,
```

APPENDIX (CONT.)

19 ‘Manual digits’/five four fewer,
20 ‘Fovea capitis of femur’/central marginal absent,
21 ‘Greater trochanter of femur’/distal_to_head even_with_head higher_than_head,
22 ‘Supracondylar fossa of femur’/absent present,
23 ‘Med. troch. ridge of femur’/both_ridges_equal expanded,
24 ‘Sustentacular facet of astrag.’/separate confluent_with_dist._facet J-shaped,
25 ‘Navicular facet of astrag.’/hemispherical saddle-shaped,
26 ‘Entocuneiform’/tibial_side_of_tarsus posterior absent,
27 ‘Cuboid’/no_Mt_III_contact contacts_3rd_metatarsal,
28 ‘Postcanine diastema’/short long absent,
29 ‘First upper premolar’/short present_w._no_diastema absent,
30 ‘Metacone on upper P2’/absent present_and_small equal_to_paracone,
31 ‘Medial cusps on upper P2’/absent one two,
32 ‘Paraconule on upper P3’/absent present,
33 ‘Paraconule on upper P4’/present absent,
34 ‘Metaconule on upper P4’/present very_small_or_absent,
35 ‘Upper P3 and P4 cross lophs’/V-shaped U-shaped,
36 ‘Upper molar centrocrista’/absent present_and_flexed present_not_flexed,
37 ‘Upper molar mesostyle’/absent weak_and_angular strong,
38 ‘Upper molar paracone’/convex_labial_bulge flattened_labially pinched,
39 ‘Upper molar metacone’/convex_labial_bulge flattened_labially part_of_convex_ectoloph,
40 ‘Upper molar paraconules’/distinct_paraconules merged_into_protoloph,
41 ‘Upper molar metaconules’/present_and_distinct absent_or_very_small,
42 ‘Upper molar parastyles’/small_like_Phenacodus large_teardrop-shaped pinched lophoid,
43 ‘Main mass of parastyle’/more_lingual_less_in_line labial_to_para-meta_line,
44 ‘Upper molar parastyles’/apices_not_curving_distally distally_recurved,
45 ‘Parastyle of upper M3’/similar_to_M1M2_parastyles projecting_labially,
46 ‘U. molar preparaconule crista’/absent to_paracone_but_no_join joins_paracone,
47 ‘U. molar ectoloph-metaloph’/no_junction junction_ant._To_metacone joins_at_metacone,
48 ‘Metacone of upper M3’/as_on_M1M2 shifted_lingually,
49 ‘Upper molars M1M2’/roughly_square broader_than_long,
50 ‘Distal cusp on lower I3’/absent present,
51 ‘Lower P1’/absent present_without_post_diastema,
52 ‘Metaconid of lower P3’/absent present,
53 ‘Entoconid of lower P4’/absent present,
54 ‘Metaconids of lower M1M2M3’/not_twinned twinned,
55 ‘Lower molar protolophids’/absent_or_deeply_notched lophoid_and_not_notched,
56 ‘Lower molar metalophids’/reach_midpoint_of_protol. oblique_and_contacting longitudinal,
57 ‘Lower molar metalophids’/prominent reduced_mesially,
58 ‘Hypolophid of lower M3’/interrupted_by_notch complete,
59 ‘Hypoconulid of lower M3’/large small absent,
60 ‘Hypoconulid of lower M3’/joins_distal_hypolophid_only joins_posthypocristid joins_posthy._and_postent.;

MATRIX

Eotitanops	10?1010000	1010?01111	????1??002	1011012000	111101000?	000(01)110102
Eohippus	10????1100	00?0001?1	200?11?012	1100020000	010002101?	0110000001
Protorohippus	10??001100	0010001111	????0110002	1100021000	110002101?	011??00000
Xenicohippus	10?1?11(01)00	0010001111	200?1?0012	1100020000	11000(12)101?	1111100001
Palaeotherium	1110000110	0011?11121	1012111012	2100012110	1210020100	1111110100
Plagiolophus	1111000110	1010?11121	20121??120	1100012110	0210020101	2111110100
Hallensia	1010010?00	?0100??11?	??0011?001	0100001000	000011000	0111000000
Propalaeo.	10??000100	0010001111	200011?11(01)	1101012000	100001010	1111100100
Lambdotherium	?0????0?100	1000??????	?????1?0101	1001012000	110021010	0101110100
Homogalax	10??01?000	0010?01111	2?001?0001	(01)00(01)020000	1100021011	0101120100

APPENDIX (CONT.)

```
Cardiolophus    100?01?000   0010??????   ???01??000   0001020000   1100021O1?   0101120100
Eomoropus       1???000000   0111?????1?  ???0110??1   1011012210   1111122O1?   ?101110100
Litolophus      1?????0?000  ?111?????1?  ??????1?001  1011020210   1111122O1?   0111110100
Moropus         1100000000   1111102120   0000110121   1011022110   1111122101   2111110120
Lophiodon       100?01?001   1010000110   0000120121   1011020011   1100122100   2000100100
Heptodon        1000110001   0010001111   2100110112   1011020001   1100021010   11(01)0121110
Helaletes       1100110001   0010001111   2100111112   1011020001   1100021110   1110121110
Lophialetes     110??1?00?   ?01?00212?   ?100111112   1011120011   1100021011   2110120100
Schlosseria     ??????????   ?????????2?  ???0111112   1011120011   1100021O1?   2110120100
Deperetellidae  ??????????   ???????212?  ???0111002   2011020021   1100022011   1110121120
Hyrachyus       1000010001   0010101111   2101111112   1011020001   1100021010   1110121120
Ghazijhippus    10???1??01   1110??????   ???????100   0100000000   0100001O1?   01?1001000
Phenacodus      0000010000   0000?01101   1000000000   0000002000   0000000100   0000010010;
END;

BEGIN ASSUMPTIONS;
OPTIONS DEFTYPE=UNORD;
END;

BEGIN TREES;
END;
```