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Rhinocerotid remains from Middle Siwalik Subgroup of Northern Pakistan

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ABSTRACT: A recent expedition in the Potwar Plateau of Pakistan has yielded dental material of three rhinocerotid species *Chilotherium intermedium*, *Alicornops complanatum*, and *Brachypotherium perimense*. The material came from the Nagri and Dhok Pathan formations of the Middle Siwalik Subgroup in Punjab, Pakistan. These specimens are good addition to provide additional morphological characters that show information about the variations in dental characters of theese already recorded species and contribute to recent work on Rhinocerotidae from the Middle Siwalik Subgroup of Pakistan. The studied remains of these three rhinocerotids species whose remains are relatively low in the Middle Siwaliks are good paleontological contribution with some more detailed work suggested here to understand about these genera. Presence of these Siwalik rhinocerotids indicates diverse habitats from forest to savanna environments.

KEY WORDS: *Alicornops*, *Brachypotherium*, *Chilotherium*, Miocene, Paleontology, Perissodactyla, Potwar Plateau.

INTRODUCTION

The Perissodactyla (Equidae, Chalicotheriidae and Rhinocerotidae) roamed in the fauna of the Sulaiman Range, Bugti Hills and the Siwalik Group during the Mio-Pleistocene (Antoine *et al*., 2003a, 2013; Flynn *et al*., 2013, 2016; Bibi and Métais, 2016). Among perissodactyls, rhinocerotids are commonly occurring and existing throughout the Neogene sediments of the entire region after equids (Heissig, 1972). The rhinocerotids are represented by many genera and species in South Asia, and quite well-diverse in the structure of nature (Lydekker, 1881; Colbert, 1935; Heissig, 1972; Khan A.M., 2009; Antoine *et al*., 2013; Rafeh *et al*., 2020). The Miocene was a time of maximum species richness and ecological diversity for Rhinocerotidae. It was also a time of evolutionary change, driven partly by changes in the physical and biotic environment and partly by palaeogeographic changes (Bernor *et al*., 1996; Fortelius *et al*., 1996).

Rhinocerotids are represented by many genera and species in the Siwalik Group that include; *Brachypotherium perimense*, *B. fatehjangense* *Aceratherium* sp., *Gaindatherium browni*, *G. vidali*, *Caementodon oettingenae*, *Rhinoceros* aff. *sondaicus*, *Alicornops* sp., *A. complanatum*, *A. laogouense*, *Chilotherium intermedium*, *Ch. blanfordi*, *Rhinoceros sivalensis*, *R. kendengindicus* and *Punjabitherium platyrhinus* (Heissig, 1972; Welcomme *et al*., 1997, 1999, 2001; Welcomme and Ginsburg, 1997; Marivaux *et al*., 1999; Antoine and Welcomme, 2000; Antoine *et al*., 2003a; Khan A.M., 2009; Khan M.A. *et al*., 2009, 2012, 2014; Khan A.M. *et al*., 2010, 2011, 2012, 2013: Rafeh *et al*., 2019, 2020).

The systematics of the Siwalik *Chilotherium* has been discussed by Matthew (1929), Colbert (1935), Heissig (1972, 1975, 1989) and Deng (2006a, b), and it is, however, little understood mainly because of the limited samples. For example, the status of *Chilotherium intermedium complanatum* described by Heissig (1972) from the Dhok Pathan Formation has been revised by Antoine (2003) on the basis of cladistic analysis and this species is now placed in the genus *Alicornops* as *Alicornops complanatum*. Colbert (1935) proposed that *Chilotherium intermedium* is a dominant species in the Middle Siwalik and tagged many specimens housed in the American Museum of Natural History, New York to this species. Heissig (1975) erected the subgenus *Subchilotherim intermedium intermedium* for the Siwalik subspecies, *Chilotherium intermedium intermedium*, and later, it was ranked to the genus (Heissig, 1989). Recently, Khan A.M. *et al*. (2011) considered that *Subchilotherium intermedium intermedium* is a junior synonym of *Chilotherium intermedium.*

Alicornops is well known rhinocerotid of the Eurasian middle and late Miocene (Cerdeño and Sánchez, 2000). The type species *A. simorrense* (Lartet, 1851) has been recovered from the middle Miocene of Turkey (Heissig, 1976), France (Ginsburg and Guérin, 1979) and Poland (Kubiak, 1981), the late Miocene of Moldova (Lungu, 1984), Romania (Codrea, 1992, 1996) and Spain (Cerdeño and Sánchez, 2000). Another species, *A.*

alfambrense (European), was described from the late Miocene of, France, Germany and Spain (Cerdeño and Alcalá, 1989; Cerdeño, 1995, 1997; Cerdeño and Sánchez, 2000). In Pakistan, *Alicornops complanatum* was documented by Antoine *et al*. (2003b) in the late Miocene of Sartaaf (Bugti hills, Baluchistan), on the basis of the subspecies *C. intermedium complanatum* Heissig, 1972. This locality has been correlated with the Dhok Pathan Formation of the Middle Siwaliks (Pilbeam *et al*., 1996). Another Asian species of *Alicornops* is *A. laogouense* Deng, 2004, described in Laogou, Linxia Basin, Gansu, China (Deng, 2004), and later by Khan A.M. *et al*. (2013) from Dhok Pathan Formation of Pakistan.

The genus *Brachypotherium* is an extinct rhinocerotid which has been found mostly from the Miocene deposits in Africa and Eurasia (Colbert, 1935; Guérin, 1980; Heissig, 1999; Geraads, 2010). In Europe, *Brachypotherium* has been well documented (Heissig, 1996, 1999; Becker *et al*., 2009). Fossil remains of the genus *Brachypotherium* were described by many researchers in the Siwaliks (Miocene) of northern Pakistan. Falconer and Cautley (1847) gave the genus name *Aceratherium* and species *Rhinoceros* (*Aceratherium*?) *perimensis* for the species *Brachypotherium perimense*. Later on, Lydekker (1881), Schlosser (1903), Pilgrim (1910, 1912), Colbert (1935), Heissig (1972), Cerdeño and Hussain (1997), Antoine *et al*. (2010), Antoine (2012), Khan A.M. *et al*. (2010, 2012), and Iqbal *et al*. (2013) discovered and analyzed the detailed morphometric characters for correlation, evolution and prediction of the paleoenvironment of the Siwaliks. More recently, Rafeh *et al*. (2019, 2020) made a detailed interspecific comparison of dental morphological features along with comprehensive discussion on paleoecology of this genus recovered from the Middle Miocene (Chinji Formation) of the Lower Siwalik Subgroup.

Here, the dentitions of three rhinocerotid genera *Chilotherium*, *Alicornops* and *Brachypotherium* are reported. The remains of these Siwalik genera are still poorly known, leaving a great hiatus in the anatomical features of these genera.

Geology and Stratigraphy

Sethi Nagri. The Sethi Nagri village (Fig. 1) is present at the boundaries of district Chakwal, province Punjab (32°45′N, 72°14′E). The area in the vicinity of the village is designated as the stratotype of the Nagri Formation. It comprises sandstone with mud and associated conglomerates. The sandstone is gray-green, bluish gray, intermediate massive, cross-bedded and coarse-grained. The sandstone color in many places varies from reddish blue to dull red with deposition of salt and limestone and moderate to weak cement. The reddish, brown, pale orange-chocolate and grayish deposits vary in each section by proportion indicated by the glacial or sandy clay. The conglomerate bed has a diverse composition and thickness in different areas, consisting gravel of schists, quartzite, and other granite rocks (Pilgrim, 1913; Colbert, 1935; Barry *et al.*, 2002, 2013).

Northern Kundal Nala. Kund is a small village (Lat. 32°45' N, Long. 72°20' E), located at 2.5 km northwest of the Chinji village in Chakwal (Fig. 1). The area is characterized by sandstone with mud and associated conglomerates. In many places, the color of sandstone varies from light to dark gray with the deposition of salt and limestone, and moderate to weakly cement. The proportion varies from section to section indicates that there are sandy clay or glacial chocolate, brown, grayish, reddish and pale orange deposits.

Dhok Pathan. The Dhok Pathan village (Lat. 33°07′N, Long. 72°14′E) is in district Chakwal, Punjab, Pakistan (Fig. 1). This Formation is characterized by sandstone and loamy soil (Cotter, 1933). The sandstone is usually gray, light gray, glossy white or reddish-brown and occasionally rusty orange, yellow, greenish yellow, grayish yellow, brown chocolate, limestone and sand. The slight peeling of yellowish-brown sandstone is common (Cheema *et al*., 1977). The Formation is characterized by sandstone with discontinuous orange-brown clays, scattered conglomerates in the lower part and conglomerates with sandstone and clays in the upper part (Cheema *et al*., 1977; Pilbeam *et al*., 1977; Barry *et al*., 1982; Johnson *et al*., 1982).

Hasnot. Hasnot (Fig. 1) preserves a substantial fossil record among the known Late Miocene-Early Pliocene fossiliferous sites of the Siwalik Group (Pilbeam *et al*., 1977; Barry *et al*., 2002). The Hasnot village (Lat. 32°49′N, Long. 73°07′E) is situated about 54 km west of the Jhelum city in the Potwar Plateau, Punjab, Pakistan. Lithologically, the paleosols belong to the alternation of the sandstone by the clay blocks with occasional conglomerates and an aggregate of conglomerates. The sandstones contain orange-brown mud at the top (Barry *et al*., 2002; Khan M.A. *et al.*, 2013). These deposits are characterized by fine, granular, riverine and sedimentary environments (Barry and Flynn, 1990; Behrensmeyer *et al*., 1995; Wills and Behrensmeyer, 1995; Barry *et al*., 2002).

Padhri. Padhri (32°52′N, 73°18′E) is present in the northwest of Hasnot, Jhelum, Pakistan (Fig. 1). The paleosols consist of light ash sandstones and orange-red clay stones, and in the upper horizons, small conglomerates are present (Barry *et al*., 2002).

MATERALS AND METHODS

A total of 12 isolated dental elements which comprised 5 upper premolars, 3 upper molars, and 4 lower premolars.

Material collection and preparation

The rhinocerotid fossils were collected carefully from the fossiliferous locations of districts Jhelum and Talagang (Fig. 1). Various field visits were made for the fossil

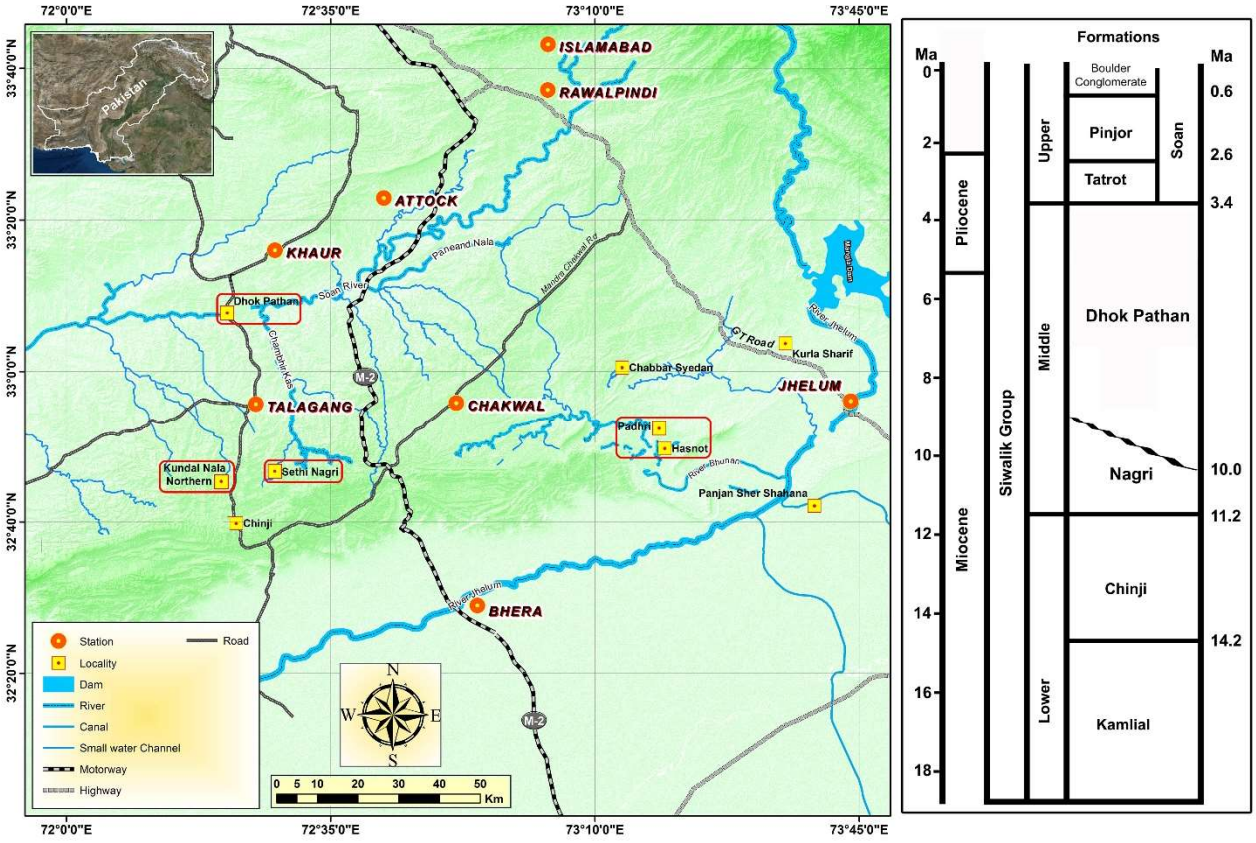

Fig. 1. Map showing the studied localities of Middle Siwalik Subgroup of Pakistan.

collection. The fossils were thoroughly washed and cleaned in the laboratory with the help of fine needles and brushes and prepared for the study. The damaged fossils were assembled with adhesive material.

Cataloguing, measurements and dental terminology

The identifiable fossils from the gross collection were catalogued and nominated for the taxonomic study. The specimen inventory number consists of a yearly catalogue number and serially catalogue number, so numbers on the specimen represent collection year and serial number of that year (e.g., PUPC 15/38). Upper case letters stand for upper dentition and lower-case letters for lower dentition. The measurements were taken occlusally with digital calipers. The dental nomenclature follows Antoine *et al.* (2010, Fig. 3).

Abbreviations

M, upper molar; m, lower molar; P, upper premolar; p, lower premolar; L, length; W, width; PUPC, Punjab University Paleontological Collection, Lahore, Punjab, Pakistan; NRRU-RIN (hereafter abbreviated as RIN), Nakhon Ratchasima Rajabhat University, Nakhon Ratchasima, Thailand.

RESULTS

SYSTEMATIC PALEONTOLOGY

Order Perissodactyla Owen, 1848
Family Rhinocerotidae Owen, 1845
Subfamily Rhinocerotinae Dollo, 1885
Tribe Aceratheriini Dollo, 1885
Genus *Chilotherium* Ringström, 1924

Chilotherium cf. *intermedium* (Lydekker, 1884)

Fig. 2

***Diagnosis*:** A *Chilotherium* of medium size. Upper incisor absent; cheek teeth hypsodont; parastyle fold indistinct or lacking; protocone constricted; ectoloph greatly elongated.The trigonid is angularly V-shaped. On the lower molars the lingual and labial cingula are absent, the hypolophid reclines backward, and the entoconid have a flat lingual margin (Heissig, 1972).

Referred material. *Upper dentition*: PUPC 16/386, partial right P2 (Dhok Pathan); PUPC 13/274, partial left P3 (Dhok Pathan); PUPC 16/239, partial left M1(Padhri); PUPC 16/240, partial right M2 (Hasnot). *Lower Dentition*: PUPC 13/277, left p2 (Dhok Pathan); PUPC 17/13, partial p2 (Sethi Nagri).

***Description*:** *Upper dentition.* The material contains partial and well-preserved premolars and molars (Fig. 2

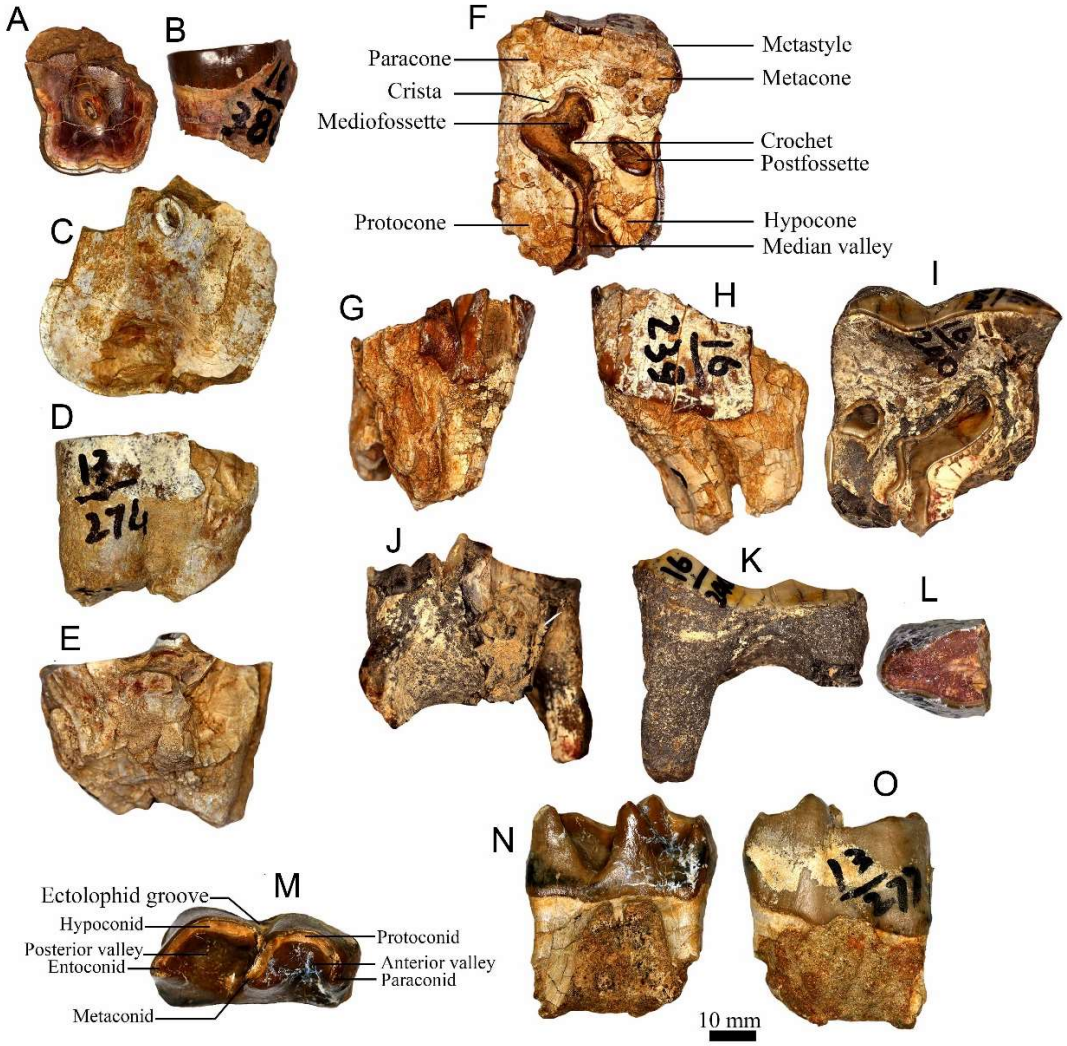

Fig. 2. Chilotherium cf. intermedium. **A-B**. PUPC 16/386, right P2; **C-E**. PUPC 13/274, left P3; **F-H**. PUPC 16/239, left M1; **I-K**. PUPC 16/240, right M2; **L**. PUPC 17/13, partial p2; **M-O**. PUPC 13/277, left p2 with roots. A, C, F, I, L, M. Occlusal view, B, D, G, J, N. Lingual view, E, H, K, O. Labial view.

A-O). The P2 (PUPC 16/386, Fig. 2 A-B) is a worn tooth. The tooth is too much worn that the height of crown is minimum. Only mediofossette is present which is very narrow and eye shaped. Protocone and hypocone are well-preserved while metacone is only partially preserved. The hypoloph is slightly pinched centrally. Roots are partially preserved and united.

The P3 (PUPC 13/274, Fig. 2C-E) is in late wear and heavily broken. The protocone is fully preserved, hypocone is slightly broken, and para- and metacones are partially preserved. The enamel of proto- and hypoconeis partially preserved and mediofossette can be identified easily. Roots are partially conserved.

PUPC 16/239 represents an M1 (Fig. 2F-H) that is highly worn and due to heavy weathering, enamel of proto- and paracone is almost completely lost, similarly that of hypo- and metacone is partially lost. As a result of heavy wear, protocone and hypocone are in contact resulting in partial closure of median valley. The protocone is slightly constricted posteriorly and hypocone is constricted anteriorly. The mediofossette is broad and deep while postfossette is small and oval shaped. Ectoloph is straight. Crista or cristella is absent. A prominent crochet, and a small crista is also present. Roots are partially preserved, lingual are united and labial are separate.

PUPC 16/240 represents an isolate M2 (Fig. 2I-K) that is highly worn and partially broken, resulting is loss of some part of proto- and hypocone (Fig. 2I-K). Only a small amount of crown is preserved which indicate that tooth belongs to a very old individual. The protocone show slight constriction at its posterior side while hypocone is slightly more constricted anteriorly. Mediofossette is has become very narrow due to wear while postfossette is small, deep and compressed from lingual side. Crochet is slightly developed. No Crista or cristella is present. Roots

Table 1. The comparative measurements of the cheek teeth of ***Chilotherium*** cf. ***intermedium***, ***Alicornops complanatum*** and ***Brachypotherium perimense***. *Studied specimens. Referred data taken from Khan A.M. *et al*. (2009, 2011, 2012) and Handa *et al*. (2020).

Taxa /Number	Position	Length	Width	L/W
Chilotherium cf. *intermedium*				
PUPC 16/386*	rP2	24.04**	30.92**	-
PUPC 17/16*	rP3	50.58	-	-
PUPC 13/274*	lP3	42.74	46.55	0.64
PUPC 16/239*	lM1	36.60	53.66	0.55
PUPC 16/240*	rM2	49.14	52.41	0.73
PUPC 13/277*	lp2	37.00	18.69	0.55
PUPC 97/84	P2	31.0	42.0	1.35
PUPC 07/93	P3	41.00	49.00	0.83
PUPC 07/93	M1	60.00	71.0	0.84
PUPC 07/93	M2	64.20	72.0	0.89
PUPC 08/02	p2	35.00	29.50	0.11
Alicornops complanatum				
PUPC 16/253*	lP3	43.33	43.36	0.99
PUPC 16/241*	lP4	36.20	31.60	1.14
PUPC 07/46	P3	42.00	46.0	0.91
PUPC 07/47	P4	37.80	46.20	0.81
Brachypotherium perimense				
PUPC 13/276*	rP4	55.90	66.53	0.84
PUPC 14/216*	rp2	30.17	20.71	0.45
PUPC 17/14*	rp3	44.08	30.71	1.43
PUPC 07/126	P4	61.5	60.0	0.98
NRRU-RIN 1220	P4	63.84	83.47	1.31
NRRU-RIN 395	P4	59.46	90.24	1.52
NRRU-RIN 1201	P4	57.84	63.81	1.10
NRRU-RIN 1228	P4	58.77	86.41	1.47
NRRU-RIN 355	p2	33.54	21.31	0.64
	p3	50.65	26.20	0.52

are also preserved especially the root under the paracone. Lingual roots are united while labial roots are separate. Median valley is very narrow and pinched centrally.

Lower Dentition. The recovered material in the lower dentition includes partial p2 (PUPC 17/13, Fig. 2L) and well-preserved p2 (PUPC 13/277). PUPC 17/13 represents paraconid, and some part of preserved paralophid, protoconid and metaconid. All structures are highly worn. Roots are partially preserved (Fig. 2.L). PUPC 13/277 is fully preserved(Fig. 2M-O). It is in early stage of wear, and brachydont. Paraconid is well-developed with its very thin paralophid. Protoconid is highest and pointed while metaconid is higher than the paraconid, hypoconid and entoconid. Anterior valley is small and narrow, sharply V-shaped while the posterior valley is very broad and deep and elongate U-shaped. Anterior cingulid is incipient lingually and transversely, and more developed labially. Posterior cingulid is more developed and is present almost in the center of hypolophid. The entoconid has well-developed cristid making it flat lingually. Ectolophid groove is also well-developed. Anterior roots are less preserved and are narrower than posterior one.

Comparison

The upper dentition has well-developed flat and broad ectoloph and slightly constricted protocone. The present material is comparable to Chilotherium intermedium described by Colbert (1935) and figured by Matthew (1929) from the Middle Siwaliks of Pakistan in having a broad and flat ectoloph, a somewhat oblique protoloph and metaloph, moderately strong crochet, absence of crista or cristella and moderate constriction of protocone. The upper dentition (PUPC 16/386, PUPC 13/274, PUPC 16/239 and PUPC 16/240) show strong affinities to the typical *Chilotherium intermedium* in having slightly constricted protocone, moderate crochet, and bulbous hypocone in the upper molars. The lower dentition in the present study has also close resemblance in morphology to the juvenile dental material of *C. intermedium* described by Colbert (1935) from the Middle Siwaliks, characterizing V-shaped trigonid, absence of lingual and labial cingulum, the backwardly reclining hypolophid and flat lingual margin of the entoconid. This Siwalik fossil material is rigorously identical morphometrically. Consequently, the studied rhinocerotid material is ascribed to *Chilotherium* cf. *intermedium* due to breakage of the specimens (Fig. 2, Table 1). As far as the specimens referred to *C. intermedium* by Heissig (1972), most of the material attributed to this species/subspecies (described as *Chilotherium intermedium complanatum*) has been reassessed and attributed to genus *Alicornops* as described above. The specimens described by Khan A.M. *et al*. (2011), PUPC 07/93, a right maxillary fragment with P3-M3 (Fig. 2) can be partially compared with the studied material, because our material is either fragmentary or extremely worn. Both have large and flat ectoloph prominent crochet and medio- and posterior fossette.

In general, *Chilotherium intermedium* can be distinguished from *C. blanfordi* by its moderately prominent parastyle fold and slight constriction of the protocone (Forster-Cooper 1934). *Chilotherium intermedium* shows some affinities with *C. wimani* described by Deng (2001) from Fugu, Shanxi and Linxia basin, China, in the presence of weakly constricted protocone and unconstricted hypoconid, well-developed parastyle fold and paracone ribs, weaker development of crochet, and small antecrochet broad. However, *C. wimani* differs greatly from *C. intermedium* due to low crown and wavy labial wall in the upper cheek teeth. *C. intermedium* differs from *C. anderssoni* from China in having flat labial wall and the absence of the mediofossette (Deng, 2006b). In the upper premolars of *C. anderssoni*, the lingual cingulum is weak and discontinuous, while in *C. intermedium*, the lingual cingulum is well developed and continuous in the upper premolars. In upper molars of *C. anderssoni*, the lingual cingulum and the crista are completely absent, and the antecrochet is large enough to fill the whole median valley (Deng, 2006b). The presence of a prominent crista,

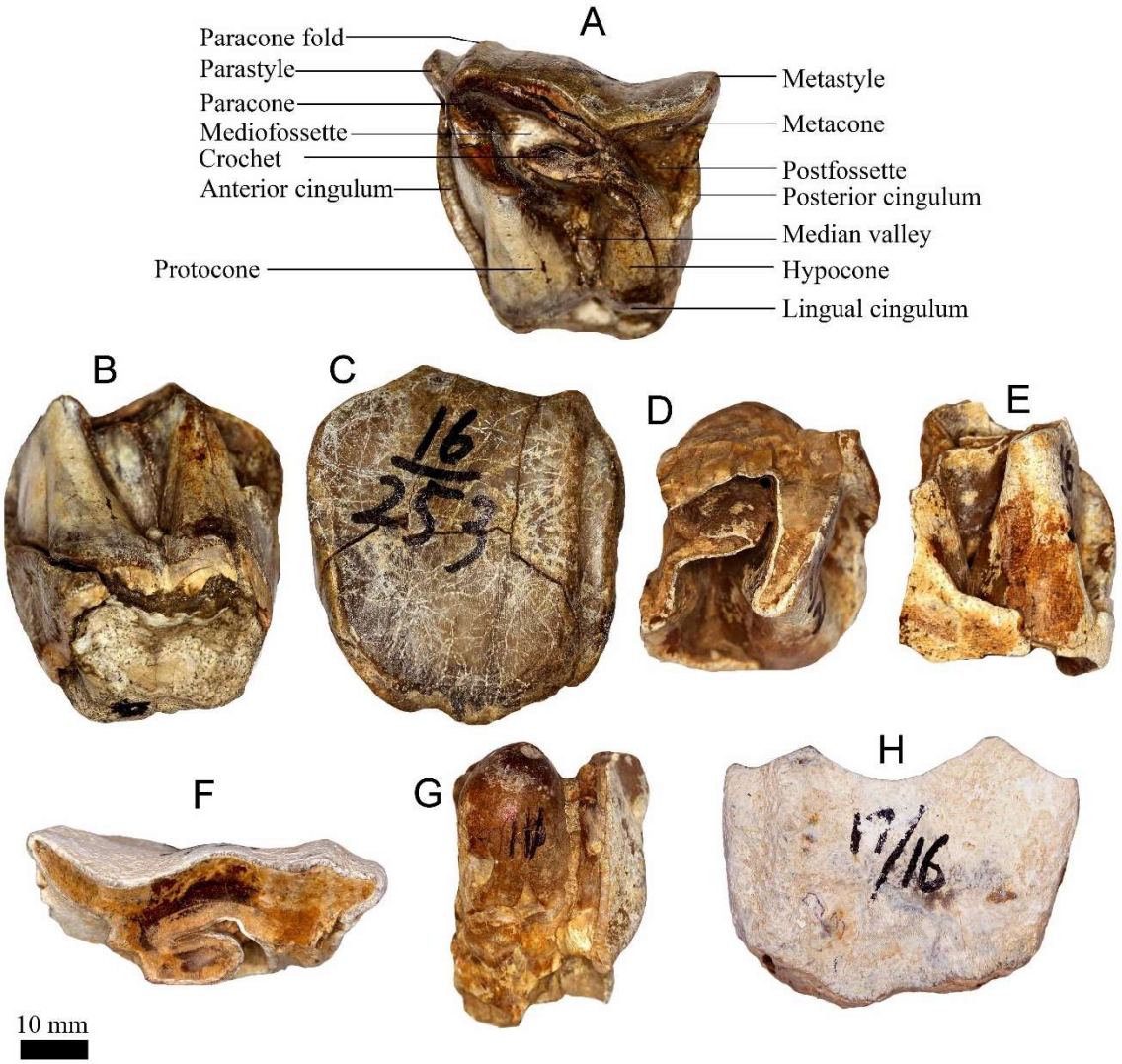

Fig. 3. ***Alicornops complanatum*** **A-C**. PUPC 16/253, P3 and **D-E**. PUPC 16/241, partial right P4; **F-H**. PUPC 17/16, partial right P4. A, D, F. Occlusal views, B, G, E. Lingual views, C, H. Labial views.

a well-developed crochet, a moderate antecrochet and a lingual bridge between the protoloph and ectometaloph of third upper molar in the Siwalik specimens distinguish them from *C. anderssoni* (Khan A.M. *et al*., 2011). *Chilotherium intermedium* upper dentition markedly differs from *C. licenti* Sun, Li, and Deng, 2018 (Fig. 2) in terms of much reduced constriction of the protocone as this structure is very pronounced in the *C. licenti* antero-posteriorly. Moreover, the mediofossette, crochet and median valley are broader and more pronounced in *C. licenti* as compared to *C. intermedium*.

Tribe Rhinocerotini Gray, 1821

Genus *Alicornops* Ginsburg and Guérin, 1979

Alicornops complanatum **(Heissig, 1972)**

Fig. 3

Diagnosis**:** *Alicornops* differing from the type species by the presence of a sometimes double crochet in P2-P4, mesostyle in D2, simple paralophid in d2; I1 absent; absence of antecrochet in P2-P3, of median fossette in P3-P4, of crista in P3 and upper molars; labial cingulum of lower premolars reduced; usual absence of antecrochet in P4; usual presence of lingual cingulum in upper molars; and small dimensions of p2 and d1. (Antoine *et al*., 2003b).

Referred material. PUPC 16/253, left P3 (Northern Kundal Nala), PUPC 16/241, partial right P4 (Hasnot); PUPC 17/16, partial right P4 (Dhok Pathan).

Description**:** The P3 (PUPC 16/253; Fig. 3A-C) reflects well-preserved cusps. The anterior cingulum is heavy and thick whereas the posterior cingulum is thick, covering the postfossette. The mediofossette is broad and deep. The protocone constriction is weak. A well developed crochet blocks the median valley. The postfossette is open posteriorly. The median valley has a small tubercle. The parastyle and paracone fold are well-developed whereas the mesostyle and metastyle are less developed. The ectoloph is

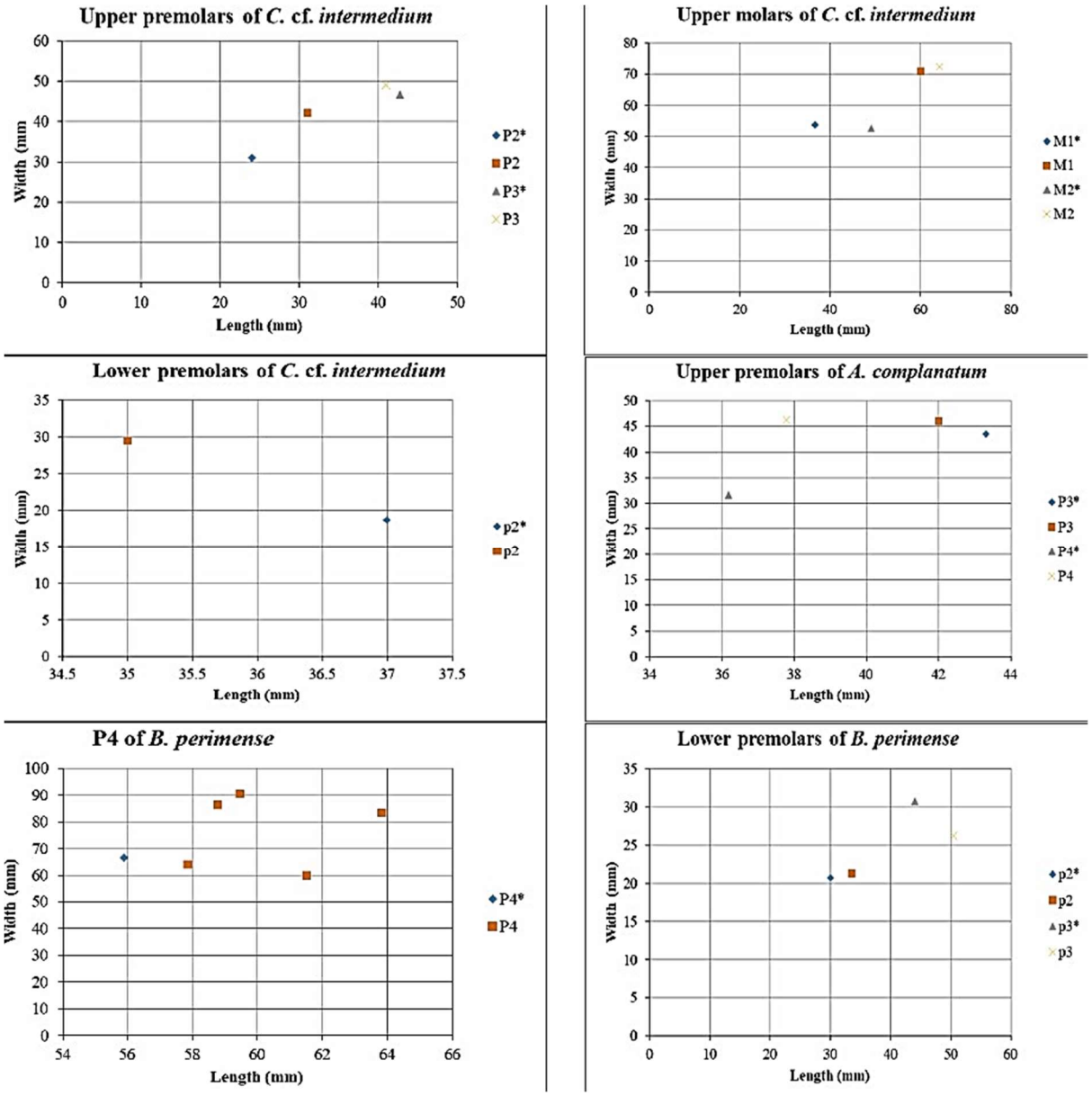

Fig. 4. Bivariate showing size variations of the cheek teeth of ***Chilotherium*** cf. ***intermedium***, ***Alicornops complanatum*** and ***Brachypotherium perimense***. *Studied specimens. Referred data taken from Khan *et al*. (2009, 2011, 2012) and Handa *et al*. (2020).

large and broad (Fig. 3A-C). The P4 (PUPC 16/241) is a partial tooth with lingual heavy cingulum, protocone, mediofossette, strong crochet, moderately deep median, and moderately developed postfossette (Fig. 3D-E).

PUPC 17/16, P4, is highly worn and lingual cusps are totally missing. Paracone, parastyle, paracone fold, metacone, metastyle and crochet are completely preserved. The crochet is extremely long and thick. Traces of cement are present on the labial surface. Enamel is whitish (Fig. 3F-H).

Comparison

The described upper premolars have hardly constricted protocone, projecting parastyle, well-pronounced anteroposterior and lingual cingula, different width of the proto- and metaloph, triangular postfossette, and very large and thick crochet. The lingual faces of the protocone and hypocone are alike in the P3 of PUPC 16/253 and PUPC 17/16. These specimens from the Nagri and Dhok Pathan formations show similarities in the characters described above with the dentition of *Chilotherium intermedium complanatum* (= *Alicornops complanatum* after Antoine *et al*., 2003b) described by Heissig (1972), hence, the material is assigned to *A. complanatum*. The metric values have been provided in Table 1 and a bivariate graph (Fig. 4) covers the size variations of the rhinocerotids.

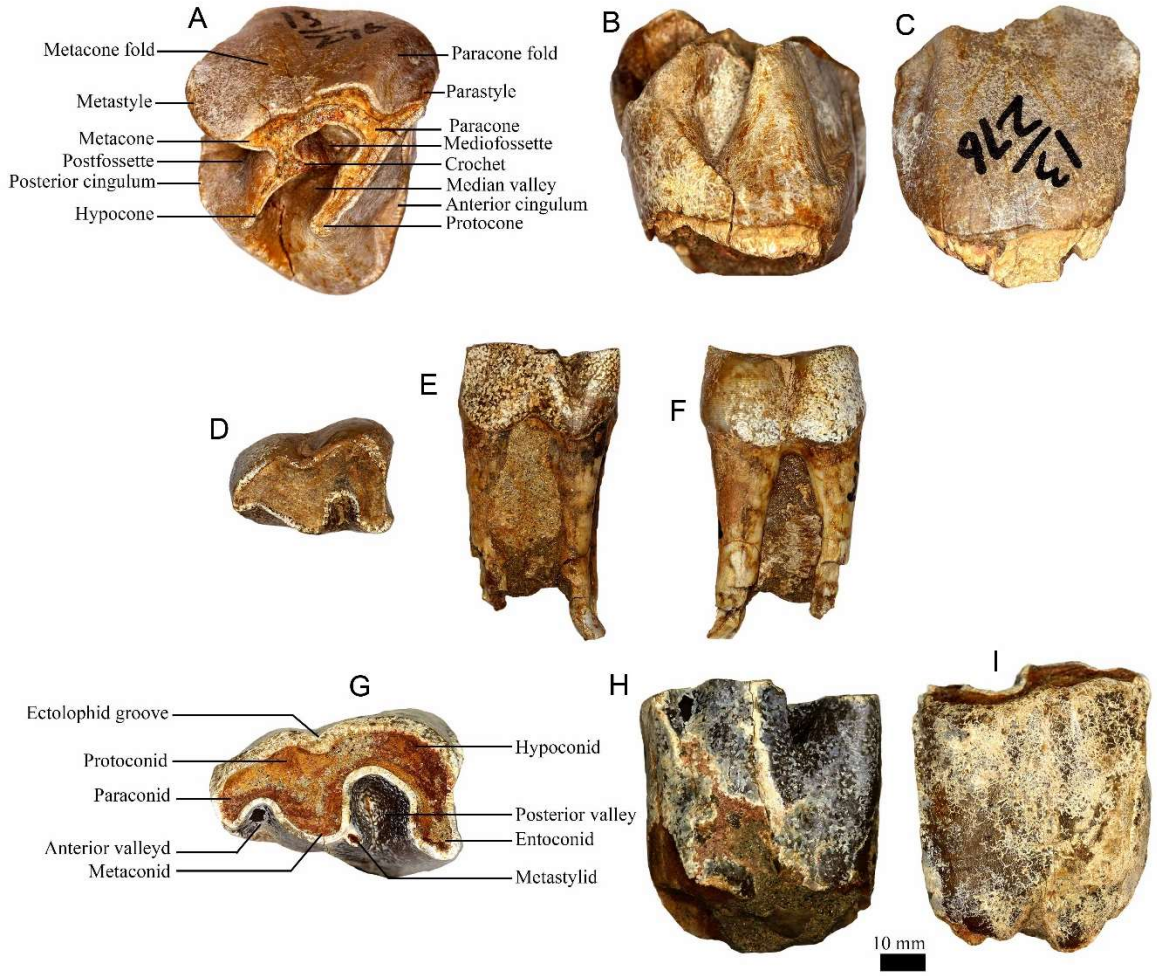

Fig. 5. ***Brachypotherium perimense***. **A-C**. PUPC 13/276, right P4; **D-F**. PUPC 14/216, right p2; **G-I**. PUPC 17/14, right p3. A, D, G. Occlusal views, B, E, H. Lingual views, C, F, I. Labial views.

Tribe Rhinocerotini Gray, 1821
Subtribe Teloceratina Roger, 1902
Genus *Brachypotherium* Roger, 1904

Brachypotherium perimense (Falconer and Cautrey, 1847) **Fig. 5**

***Diagnosis*:** A rhinoceros of gigantic size with hypsodont teeth. Upper incisor present and well developed. Nasals shorter and hornless. Upper premolars molariform with strong convex outer wall. Molars with moderately developed crochet, weaker antecrochet and rudimentary crista. Upper molars with weak constriction of the inner cusp. Protocone somewhat constricted. Lower molars narrow and compressed and almost without labial groove. Cingula reduced and short (Heissig, 1972).

Referred material. PUPC 13/276 right P4 (Dhok Pathan); PUPC 14/216, right p2 (Sethi Nagri); PUPC 17/14, right p3 (Sethi Nagri).

***Description*:** The P4 (PUPC 13/276, Fig. 5A-C) is in early wear. The cusps are oriented posteriorly. The apices of protocone and hypocone are thin, and protocone show a slight constriction. The paracone with its parastyle is smaller and more worn than the metacone and metastyle. The hypocone and metacone are more elevated than the protocone and paracone. The paracone fold is heavier than the metacone fold. The mediofossette is deeper and smaller than the postfossette. Crochet is visible. The anterior cingulum is heavy and flanked, covering the tooth antero-transversely. The posterior cingulum is thin. The median valley is deep and U-shaped and is blocked by tubercle corresponding to lingual cingulum (Fig. 5B). The p2 (PUPC 14/216, Fig. 5D-F) is heavily worn. The paraconid and paralophid are small whereas other cusps are more developed. The anterior valley is small and narrow whereas the posterior valley is broad, tending to U-shaped. The anterior cingulid is incipient lingu-transversely. The ectolophid groove is well-developed and deep. Hypolophid is very compressed anteriorly due to contact with third premolar. Roots are well-preserved, anterior roots are slightly smaller. The p3 (PUPC 17/14, Fig. 5G-I) is well preserved and moderately worn. Tooth possesses all typical features of premolar like all lophids,

cusps, and both valleys. The anterior valley is small whereas the posterior valley is broad, moderately deep and U-shaped. A small metastylid (like spur) is present. The ectolophid groove is narrow and shallow. The cingulid is present postero-labially at hypoconid.

Comparison

The present material collected from the Nagri and Dhok Pathan formations include only premolars. These are similar to *Brachypotherium perimense* described by Colbert (1935) and Heissig (1972) in having constricted protocone, well developed anterior cingulum and well-developed paracone fold (characteristic feature of *Brachypotherium* according to Colbert, 1935), and moderately developed crochet. The lower premolar in the present collection is very much similar to those described by West *et al*. (1978) in having well developed anterior cingulum, presence of tubercles corresponding to lingual cingulum, V-shaped valley present between entoconid and metaconid, and well developed metalophid and hypolophid (Fig. 4). The specimens in the present study are comparable to *B. perimense* described by Cerdeño and Hussain (1997) from the Manchar Formation in Sindh. According to them, the lower teeth in *B. perimense* have smooth external/ectolophid groove in buccal wall. Recently, Rafeh *et al*. (2020) describe some *Brachypotherium* remains from Chinji Formation (Lower Siwaliks), but none of the material described by them as *B. perimensis* is comparable to described specimens because they have described M3 in upper dentition and p4-m3 in lower dentition. However, we can compare P4 (PUPC 13/276) in our specimens with the PUPC07/170 described as P4 of *B. fatehjangense*. PUPC07/170 is smaller (51.8 mm in length) than our specimen (55.90 mm), the crochet is less developed and median valley is smaller. The specimens described by Khan A.M. *et al*. (2010) as *B. fatehjangense* are mostly broken, and picture quality is poor, hence, no comparison can be made. Similarly, the teeth in the specimen (PUPC 69/680, a fragment of left maxilla having P4-M1-3), described by Iqbal *et al*. (2013) are too weathered and deformed. However, from the provided description, the P4 in PUPC 69/680 of Iqbal *et al*. (2013) show similar characters like PUPC 13/276 in having hypsodonty, rather flat and long ectolophid, well-developed parastyle and paracone fold, and somewhat constricted protocone.

DISCUSSION

Since the establishment of the genus *Chilotherium* by Ringstrom (1924), 19 other species have been referred and assigned to this genus (Deng, 2006a). Geologically, *C. intermedium* has a long range and persistence with a medium-sized body bovid community and appeared in the Chinji Formation through the Middle Siwaliks, while *C. blanfordi* appeared in the Bugti beds and disappeared in the Middle Siwaliks (Colbert, 1935). The palaeomagnetic dating indicates that *C. intermedium* remained in the Siwaliks from 16.3 Ma to 7.6 Ma (Flynn *et al*., 1995).

Alicornops is one of the rarest reported genera of Rhinocerotidae in the Siwaliks. This genus is recognized by the two species from the Siwaliks of Pakistan. *A. complanatum* is identified from the Late Miocene of Dhok Pathan Formation whereas *A. laogouens* from late early Miocene to the Middle Miocene of Kamlial Formation (Khan A.M., 2009; Khan A.M. *et al*., 2013). The occurrence of *A. complanatum* in the Potwar plateau of Siwaliks extends its geographic distribution in Pakistan, previously reported from the Late Miocene of Sartaaf, Bugti hills, Baluchistan (Antoine *et al*., 2003b). The absence of *Alicornops* in the Chinji and Nagri formations might be due to its scarce fossil record, as other rhinocerotids are recognized from Kamlial to Dhok Pathan formations (Khan A.M. *et al*., 2013). The early Late Miocene fauna of the Siwaliks bearing *Alicornops* also have *Pachyportax*, *Selenoportax* and *Gazella* with hipparionines (Khan A.M. *et al*., 2013). Species richness decline in the Late Miocene and there were disappearances of many species including *Alicornops*, around 3.7 Ma. in Tatrot Formation (Pilbeam *et al*., 1996; Barry *et al*., 2002). Antoine *et al*. (2003b), based on phylogenetic studies, considered *A. complanatum* as the sister group of the type species *A. simorrense*, both included within the subtribe Aceratheriina, while *Chilotherium intermedium* belongs to Teleoceratina.

The first hypsodont rhinoceros appeared in the late Early Miocene (Antoine *et al*., 2003a), and the Late Miocene saw the radiation of forms adapted to increasingly open habitats, evidently by increasing body size and hypsodonty (Khan A.M. *et al*., 2011, 2013). This trend was particularly marked in Asia, and the rhinoceros communities of the Late Miocene, represent some of the westernmost occurrences of typical Asian taxa, especially Aceratheriini of the *Chilotherium* clade (Geraads and Saraç, 2003).

The diversity of Siwalik rhinoceroses is clearly dependent on climatic conditions. The change in climatic conditions has resulted in shrinkage and growing of dry and wet areas and their special vegetation (Heissig, 2003). The hypsodonty and brachydonty are also directly related to species environment. The hypsodont species could eat coarse grasses, so lived in open habitat where environmental conditions are intermediate (Lacombat, 2005). The high crowned genera i.e., *Chilotherium* and *Brachypotherium* are abundant in those areas of Chinji, Nagri and Dhok Pathan formations where the climatic conditions are intermediate. In the Nagri Formation, *B. perimense* is most common in times of transition and rare during most humid and most arid times (Heissig, 2003). Colbert (1935) recognized *B. perimense* in the Chinji, Nagri and Dhok Pathan formations while Heissig (1972) indicated that this species is also found in rocks of the Kamlial Formation. West *et al*. (1978) described lower dentition of *B. perimense* from the Dang valley in Nepal.

During the Late Miocene-Early Pliocene of the Siwaliks, based on the faunal studies (Heissig, 1972; Bernor and Hussain, 1985; Pilbeam *et al*., 1996; Kaiser *et al*., 2000; Barry *et al.,* 2002; Badgley *et al*., 2005; Khan A.M. *et al*., 2010, 2011, 2012, 2013; Wolf *et al*., 2013), it can be inferred that there was better-vegetated and considerably more humid environment than it is today in the Siwalik Group. Drier and open habitats are assessed by the presence of associated fauna like bovid taxa, *Pachyportax*, *Selenoportax* and *Gazella* along with rhinocerotids in the studied localities. In Miocene of the Siwaliks, *Alicornops*, *Chilotherium* and *Brachypotherium* lived together with *Gaindatherium* in open woodland with associated lakes and swamps (Khan A.M. *et al*., 2010, 2011, 2012, 2013). *Brachypotherium* is a conservative and long-lived genus with a wide geographic range in western Eurasia (Heissig, 1996). It is one of several rhinoceros' lineages to develop short legs and relatively high crowned teeth, but its paleoecology remains enigmatic. A hippopotamus-like life-style is possible, but this suggestion lacks direct support. Judging by dental wear, the animal seems to have been a mixed feeder (Fortelius, 1990; Fortelius and Solounias, 2000). *Brachypotherium,* like other elasmotherines, were the earliest hypsodont rhinoceroses in the Old World, and show grazer like dental wear (Fortelius, 1990). They were also relatively cursorial animals that first evolved in the open habitats that were beginning to appear in central Asia (Bernor *et al*., 1996).

CONCLUSIONS

Chilotherium, *Alicornops* and *Brachypotherium* present simultaneously in the Late Miocene-Early Pliocene of the Middle Siwalik Subgroup of Pakistan. The specimens are typical of the early Late Miocene to Early Pliocene age. Occurrence of these rhinocerotid genera with allied fauna in the Middle Siwalik Subgroup suggests a diversity of environment, indicating woodlands, shrubs and savannah in the Late Miocene-Early Pliocene of the Siwaliks.

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