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New fossils of *Gaindatherium* (Rhinocerotidae, Mammalia) from the Middle Miocene of Pakistan

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Abstract: New isolated teeth with maxillary and mandibular fragments from the Chinji Formation of the Lower Siwaliks are described and determined as *Gaindatherium browni* and *Gaindatherium vidali*. This material comes from the Middle Miocene of Lava and Dhok Bun Ameer Khatoon localities, northern Pakistan, and significantly increases the number of remains previously known for this rhinocerotid genus. Specimens from the Lava site determined as *G. vidali* present morphological differences with respect to those of *G. browni*, being similar to those of *G. vidali* from the Nagri Formation, showing a greater size. Previously, *G. vidali* was reported only from the Nagri Formation of the Middle Siwaliks and the new material thus significantly widens the chronological distribution of this species in the continental deposits of the Siwaliks. This record implies that both species are not successive but rather coeval during the late Middle Miocene.

Key words: Rhinocerotinae, Chinji Formation, Siwaliks, Potwar Plateau, biostratigraphy

1. Introduction

Fossil vertebrates from Pakistan and particularly the Tertiary deposits of the Siwalik Group (Pakistan and India) have been studied for more than a century (e.g., Lydekker, 1883, 1884; Pilgrim, 1913, 1917; Matthew, 1929; Pilbeam et al., 1979, 1996; Flynn et al., 1995; Barry et al., 2002). Among mammals, fossil rhinocerotids from the Siwaliks and other Pakistani areas are very abundant and diversified (Lydekker, 1881, 1884; Colbert, 1934, 1935; Forster-Cooper, 1934; Heissig, 1972; Cerdeño and Hussain, 1997; Antoine and Welcomme, 2000; Antoine et al., 2003, 2010). The recent revision of unpublished specimens from the Siwaliks (Khan, 2009) revealed the presence of new material of *Alicornops*, *Chilotherium*, and *Gaindatherium* from different areas of the Potwar Plateau. *Chilotherium* and *Alicornops* remains have been already studied in detail (Khan MA et al., 2011; Khan et al. 2013), and this contribution presents the comparative description of the material identified as *Gaindatherium*, coming from the Chinji Formation at 2 different localities, Lava and Dhok Bun Ameer Khatoon. Two of the included specimens were preliminarily studied by Khan MA et al. (2011b) as part of the mammal assemblage recovered from the Lava site. The whole sample is a significant increase of known remains assigned to *Gaindatherium* since Heissig's (1972) work.

The genus *Gaindatherium* was described by Colbert (1934) with the species *G. browni* from the Chinji Formation. A second species was later added, *G. vidali*, characterizing the overlying Nagri Formation (Heissig, 1972); that author identified this species from one of the specimens included previously in *G. browni* by Colbert (1934), namely the mandible AMNH 19471 that also comes from the Nagri Formation. Antunes and Ginsburg (1983) recognized the genus *Gaindatherium* in West Europe, describing the new subgenus and species *Gaindatherium* (*Iberotherium*) *rexmanueli* from several localities in the Lisbon area (Portugal). Later, Ginsburg et al. (1987) assigned to the same species 8 isolated teeth from Beaugency-Tavers (France). However, Cerdeño (1996) considered *G. rexmanueli* as belonging to *Prosantorhinus*, a Miocene genus known from Germany and France and then extended to Spain and Portugal. She proposed the species *Gaindatherium rexmanueli* as synonymous with *Prosantorhinus douvillei*.

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Gaindatherium has a wide geographic as well as stratigraphic range in and outside Pakistan. In Baluchistan (Pakistan) it is known from the Early Miocene of the Vihowa and Chitarwata Formations and it was living in association with a diversified and exceptionally large rhinoceros assemblage, very rich in diceratheriines, rhinocerotines, elasmotheriines, and teleoceratines (Antoine and Welcomme, 2000; Metais et al., 2009). The Manchar Formation in Sindh has also yielded *Gaindatherium* sp. from strata equivalent to the Kamlial and Chinji Formations in the Potwar Plateau (Raza et al., 1984).

The Lower Siwaliks of the Ramnagar region, Jammu, India, have yielded *Gaindatherium browni*, *Brachypotherium perimense*, *and Chilotherium* sp., along with other mammals representing small- and medium-sized browsing forms, very similar to the Chinji mammalian fauna (Middle Miocene) of the Potwar Plateau, Pakistan (Basu, 2004). The assemblage indicates a woodland-type ecosystem having a substantial forest component and subordinately developed grassy subareas (Basu, 2004).

According to Chavasseau et al. (2009), in the Middle Miocene fossiliferous Li and Pong basins of northwestern Thailand, *Gaindatherium* lived in association with *Stegolophodon* (Tassy et al., 1992) as well as the anthracothere *Brachyodus* and the suid *Conohyus* (Ducrocq et al., 1994, 1997). *Gaindatherium* has also been collected from the Mae Moh basin of Thailand in association with *Stegolophodon*, the mustelid *Siamogale*, and the amphicyonid *Maemohcyon* (Ginsburg et al., 1983; Ginsburg and Tassy, 1985; Ducrocq et al., 1994, 1995; Peigné et al., 2006).

2. Geographic and stratigraphic context

The studied material comes from 2 fossil localities found nearby Lava and Dhok Bun Ameer Khatoon villages, Chakwal district, northern Pakistan (Figure 1). The geography and geology of the areas were described by Khan MA et al. (2008, 2011b).

The Lava locality (32°62′N, 71°98′E) is located 11 km southeast of Lava village; the fossiliferous section is characterized by sandstone and reddish shale characteristic of the Chinji Formation in the Siwaliks (Khan MA et al., 2011b).

Dhok Bun Ameer Khatoon (32°47′N, 72°55′E) is situated about 16 km northeast of Chua Saydan Shah (Figure 1). It constitutes one of the most famous fossiliferous localities of the Siwaliks, comprising a panorama of sedimentary exposures of all the 5 component formations (Kamlial, Chinji, Nagri, Dhok Pathan, and Soan) of the Siwalik group (Johnson et al., 1982; Cheema, 2003; Khan et al., 2008; Khan MA et al., 2011a). The stratigraphic and sedimentological details can be found in the works of Raza (1983) and Friend et al. (2001).

3. Materials and methods

The fossils described herein were collected by some of the authors (AMK, MAK, MA) and are housed in the Dr Abu Bakr Fossil Display and Research Center of the Department of Zoology, University of the Punjab, Lahore, Pakistan. The specimens are cataloged into 2 series: the

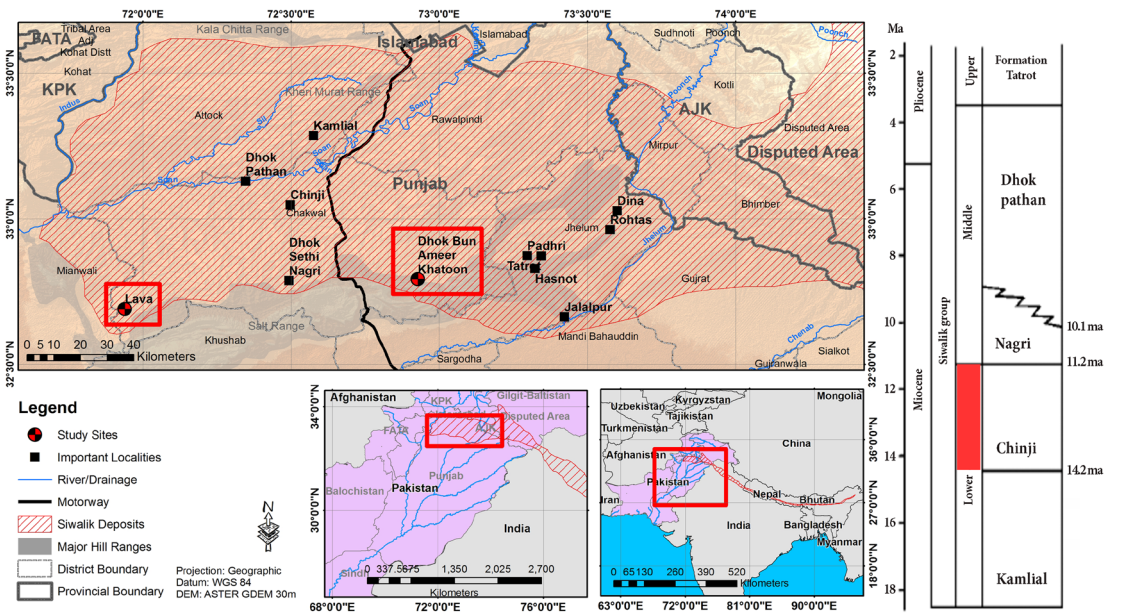

Figure 1. Geographic locations and chronostratigraphic correspondences of Lava and Dhok Bun Ameer Khatoon localities of the Chinji Formation (middle Miocene; 14.2–11.2 Ma) in northern Pakistan.

first figure denotes the collection year, while the second denotes the serial number of the respective specimen. They are detailed in Section 4.

For morphological descriptions, tooth cusp nomenclature follows Heissig (1972). Tooth length and width were measured at maximum level and dimensions are given in millimeters. The comparative study was mainly based on data from Colbert (1934, 1935) and Heissig (1972) for previous material from the Lower and Middle Siwalik localities. Suprageneric classification follows Antoine et al. (2003).

Abbreviations: AMNH – American Museum of Natural History; D – deciduous; Fm. – Formation; H – height; i – lower incisor; l – left; L – length; M – upper molar; m – lower molar; Ma – million years; P – upper premolar; p – lower premolar; Pl. – plate; PUPC – Punjab University Paleontological Collection; r – right; W – width.

4. Systematic paleontology

Order Perissodactyla OWEN, 1848
Family Rhinocerotidae GRAY, 1825
Subfamily Rhinocerotinae GRAY, 1821
Tribe Rhinocerotini GRAY, 1821
Subtribe Rhinocerotina OWEN, 1845
Genus *Gaindatherium* COLBERT, 1934
Type species: *Gaindatherium browni* COLBERT, 1934
Gaindatherium browni COLBERT, 1934
(Figures 2 and 3; Table 1)

1934 *Gaindatherium browni*. – Colbert, pp. 1–13; figures 1–5; tables 1 and 2.

1972 *Rhinoceros* (*Gaindatherium*) *browni*. – Heissig, pp. 18–24; plates 1 and 2; plate 4, figure 5.

Holotype. – AMNH 19409, an almost complete skull.

Stratigraphic Level. – Chinji Formation (14.2–11.2 Ma), the Lower Siwaliks.

Diagnosis [after Colbert (1934) and Heissig (1972)]. – An Upper Tertiary rhinoceros of medium size, with a saddle-shaped skull having a single horn on the nasals, and with brachydont, simple molar teeth. The orbit is located in an approximately central position above the first molar; the occiput is vertical; the postglenoid and posttympanic processes are fused, forming a closed tube for the external

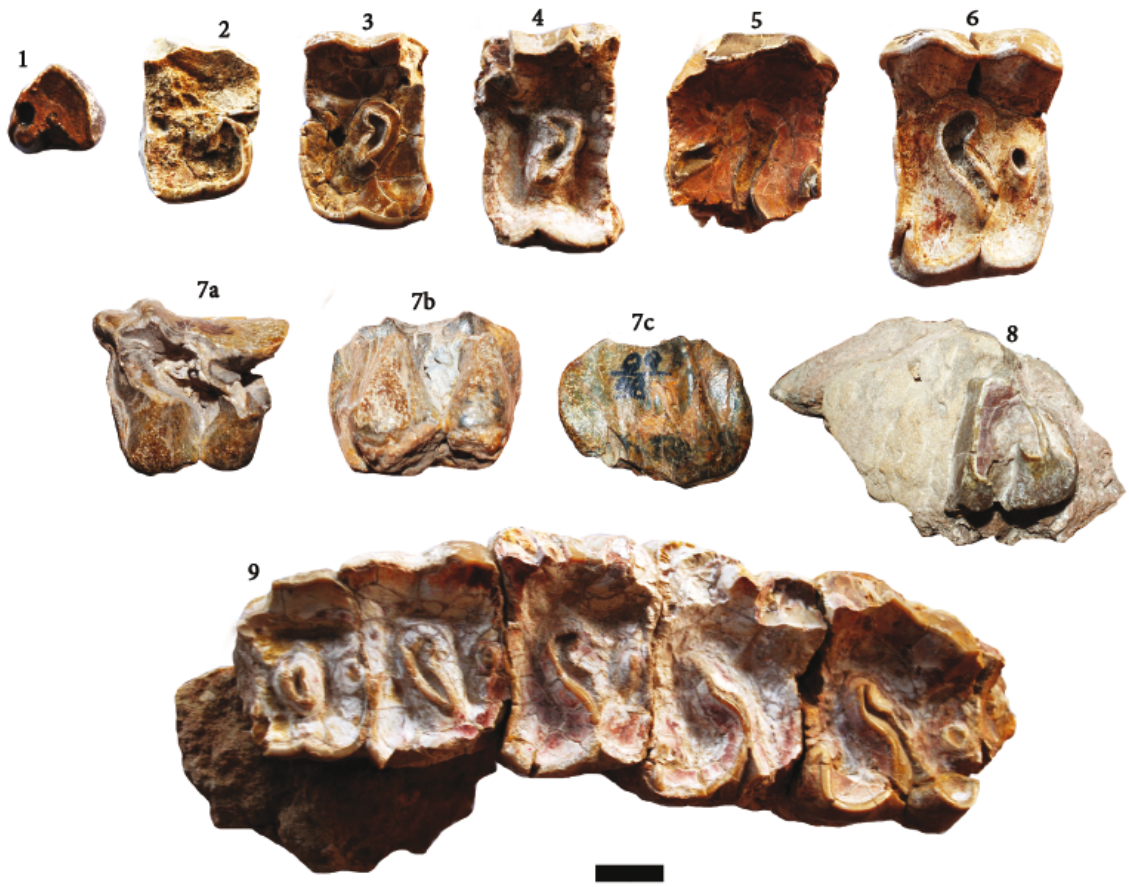

Figure 2. *Gaindatherium browni* (Rhinocerotini, Rhinocerotidae, Mammalia). 1, PUPC 02/146, rP1; 2, PUPC 08/122, lP2; 3, PUPC 08/123, rP3; 4, PUPC 08/124, rP4; 5, PUPC 86/146, rP4; 6, PUPC 02/08b, lP4; 7a–7c (a- occlusal, b- lingual, c- labial), PUPC 09/58, rM2; 8, PUPC 07/41, rM3; 9, PUPC 02/08a, lP2-M2.. Scale bar = 20 mm.

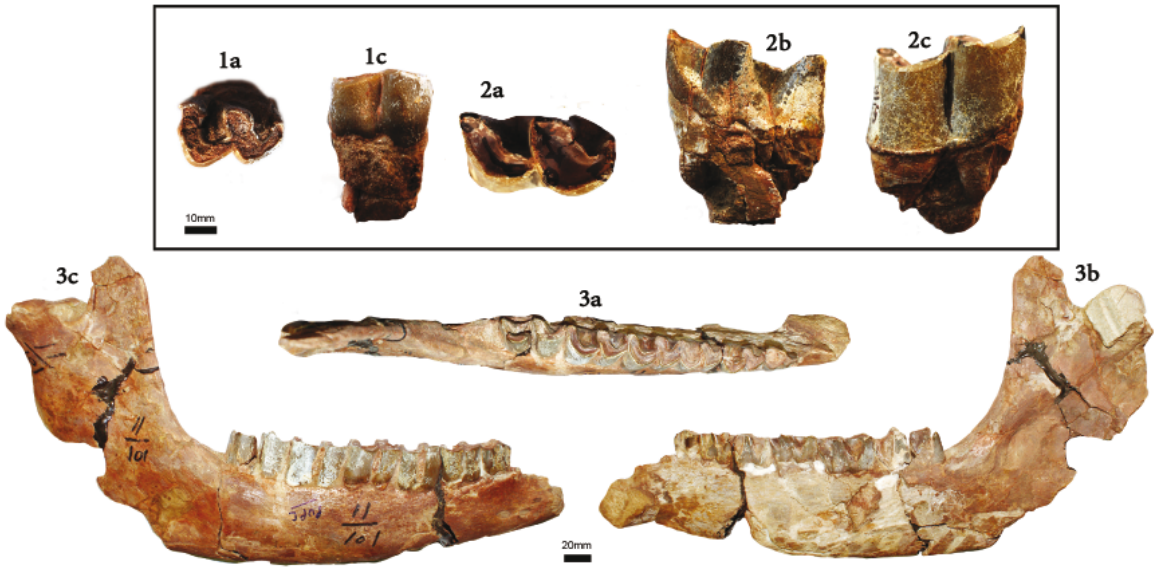

Figure 3. *Gaindatherium browni*. 1a and 1c, PUPC 02/11, rp2; 2a–2c, PUPC 02/155, rm3; 3a–3c, PUPC 11/101, right mandibular ramus with p2-m3. a- occlusal, b- lingual, c- labial. Scale bars = 10 mm (1 and 2) and 20 mm (3).

auditory meatus. There are 2 upper incisors, of which the lateral incisor is quite small; the upper molars do not present an antecrochet or crista, and the crochet is slightly developed.

Referred material. – Dhok Bun Ameer Khatoon , PUPC 02/146, rP1; PUPC 08/122, lP2; PUPC 08/123, rP3; PUPC 08/124, rP4; PUPC 86/146, rP4; PUPC 02/08b, lP4; PUPC 09/58, rM2; PUPC 07/41, rM3; PUPC 02/08a, lP2-M2; PUPC 02/11, rp2; PUPC 02/155, rm3. Lava, PUPC 11/101, mandibular fragment with rp2-m3.

Description.

Upper dentition: The most complete specimen, PUPC 02/08a (Figure 2, number 9), bears the left P2-M2 series, some of the teeth incomplete but relatively well preserved (some cracks are present in the occlusal surfaces). The high degree of wear is reflected in the wide and short teeth (especially P3-M1). The entrance of the median valley is closed in premolars because of the fusion of the protocone (larger) and hypocone, leaving a shallow lingual groove between them. In P3 and P4, a short crochet projects into the transversely elongated central fossette. Enamel traces of the postfossette are present in the 3 premolars. The ectoloph, more complete in P3, is undulate with smooth paracone and metacone folds. The protocone is more lingually projected than the hypocone. Long double roots are observable in P2.

Among the isolated upper teeth, the right P1, PUPC 02/146 (Figure 2, number 1), is a small subtriangular, birooted tooth of middle wear. The enamel is thin and the crown is low. Owing to wear, the ectoloph is very thick. The parastyle is prominent. A very small fossette is present at the junction of metaloph and ectoloph. The protoloph is not developed; there is an anterolingual cingulum limiting the tooth in that area. The metaloph is straight and oblique, with the hypocone anterior to the metacone level. A posterolingual cingulum limits a deep posterior fossette. The other isolated premolars (Figure 2, numbers 2–6) are heavily worn and very similar in occlusal morphology to their corresponding teeth in the described maxillary fragment.

The M1 in PUPC 02/08a is very worn, with the protocone and hypocone in contact but not fused. The closed valley is reduced to a sinuous ridge that barely reflects the presence of a former little developed crochet. It is slightly more visible in the M2, where the median valley, though being very narrow, is still open. The M2 presents a small postfossette remnant, better preserved than that of M1.

The isolated M2 of PUPC 09/58 (Figure 2, numbers 7a–7c) is similar in morphology and occlusal outline. The crochet is well developed at the base and broken towards the apex. The M3 of PUPC 07/41 (Figure 2, number 8) is triangularly outlined, with moderate wear. The parastyle is narrow and well projected anterolabially. A wide, shallow depression separates it from the paracone fold, a little less prominent. Behind the paracone fold, the ectometaloph is straight labially. The crochet is prominent. A cingular border is present all around the molar base, better developed anteriorly. The protocone expands gradually towards the base.

Hemimandible: PUPC 11/101 is a well-preserved hemimandible with the cheek tooth series p2-m3 (Figure 3, numbers 3a–3c; Table 1). The horizontal ramus is high, with the ventral border a little convex anteroposteriorly and

Table 1. Comparative dental measurements (mm) of *Gaindatherium browni* from the Chinji Formation.

Inventory number	Nature	L	Ant. W	Post. W	H
PUPC 02/146	P1	24	22	23	
PUPC 02/08a	P2	29	37	43	
	P3	35	47	48	
	P4	40	58	54	
	M1	41	64	57,5	
	M2	45	52	50	
PUPC 07/41	M3	41	37,6		
PUPC 08/122	P2	28	38	41	
PUPC 08/123	P3	38	51	49	-
PUPC 08/124	P4	39	58	56,5	
PUPC 02/08b	P4	41	59		
PUPC 86/146	P4	42	X		
PUPC 09/58	M2	49	53,5	45	43
[1]AMNH 29838	P1	19	22,5	-	
	P2	28	34,5	-	
	P3	32	43	-	
[1]AMNH19409	M1	40	51	-	
	M2	42	52	-	
[2]CHK6	D3	40	43	42	-
[2]1956 II 239a	P1	21	17	19	-
[2]1956 II 241	P3	30	41	41	-
	P4	32	48	46	-
	M1	34	52	48	-
	M2	42	52	45	-
	M3	42	46	30	-
[3]China SBV84003	M3	53	65	-	37
PUPC 11/101	p2	20,5	14,4	-	
	p3	26	20	-	
	p4	26	23,4	-	
	m1	33,4	23	-	
	m2	38	24,6	-	
	m3	43	24,5	-	
PUPC 02/11	p3	28	15,5	19	
PUPC 02/155	m3	43	25,5	23	
[2]1956 II 247 & 249	p2	24	13	17	
	p3	30	18	21	
	p4	34	21	25	
	m1	36	24	26	
	m2	40	25	24	
	m3	46	25	25	
[1]AMNH29838	p2	28,5	21,5	-	
	m3	43	26	-	
[2]1956 II 253	p2	26	14	17	
	m3	46	25	25	

[1]Colbert (1934), *G. browni* from Siwaliks.
[2]Heissig (1972), *G. browni* from Siwaliks.
[3]Tang and Zong (1987), *G.* cf. *browni* from Pliocene of Yangjiawan, China.

Table 2. Comparative dental measurements (mm) of *Gaindatherium vidali* from the Chinji Formation.

Number	Nature	L	Ant. W.	Post. W.	H
PUPC 84/61	P2	24	28,5	28	-
PUPC 07/101	P4	38	48,5	42	45
PUPC 07/102	M1	35,5	46	39	39
PUPC 08/125	D3	37	38	33	-
[1]NG 354	P2	25	32		-
[1]NG 322	P4	-	46	44	-
[1]NG 350	M1	34	44	41	40
[1]NG 349	D3	31	34	32	-

[1]Heissig (1972). *G. vidali* from Siwaliks.

the maximum convexity at the level of m1; it is moderately wide, with its anterior region narrower than the posterior one. The alveolar border of the ramus is slightly concave in occlusal outline (Figure 3, number 3c). The symphysis is broken, but the depression representing the alveolus for i2 is conspicuous. The vertical ramus is almost at a right angle; the angular process hardly surpasses the condyle posteriorly. The condyle is inclined medially.

Lower dentition: The first premolar in the dentary PUPC 11/101 is absent. The premolar series is shorter than the molar series. In lower premolars, the faint cement deposition is observable only on the labial wall of premolars. The teeth are of early middle wear. The labial groove is deep and reaches the crown basis. The anterior valley is V-shaped and the posterior is U-shaped. The premolars are triangular in outline, with long double roots and without cingula. The hypolophid is long and transverse. The metaconid and entoconid are not constricted. Due to wear, the metaconid is larger than the entoconid and the trigonid valley is considerably smaller and narrower than the talonid valley. The transversal paralophid is markedly long in all teeth, lingually reaching the level of the metaconid and entoconid. It forms a right angle with the horizontal axis of the mandibular corpus, whereas the lingual branches of the metalophid and the hypolophid are inclined backwards, especially on the molars. Besides the shallower ectoflexid, p3 differs from p4 mainly by the smaller size of its anterior part, because the trigonid is narrower and the paralophid shorter. The isolated lower premolar (Figure 3, numbers 3a and 3c) is very similar in morphology and dimensions to the p3 of the dentary.

The molars are considerably larger than the premolars. The m1 length is smaller, but its maximal width is greater than that of the m2, which is the longest tooth. The trigonid and talonid valleys of m2-m3 have a V-shaped lingual transverse profile. The talonid valley of m3 is more rounded, though without being U-shaped. On the m3, the hypoconulid forms a faint but distinct fold in the hypolophid, projecting slightly into the talonid valley. The hypolophid is oblique but transverse in occlusal view. The paralophid is narrow and short; the metaconid is slightly constricted; and the entoconid has a posterior groove. The isolated m3 PUPC 02/155 (Figure 3, numbers 2a–2c), little worn, is similar to the m3 in the dentary.

Comparison. – The studied remains from the Chinji Formation present close similarities to those described by Colbert (1934) as *Gaindatherium browni*. Particularly, the premolars coincide with those of specimen AMNH 29838 (Colbert, 1934, figure 4), with 2 marked labial folds, protocone and hypocone fused with wear, and a poorly developed crochet. The holotype (AMNH 19409) of *G. browni* does not have preserved premolars, and the molars have no trace of crochet; however, the paratype AMNH 29838 presents a small crochet, more evident in M2, thus being closer to our material. The M3, better preserved in the holotype than in AMNH 29838, coincides with PUPC 07/41 with the presence of a small crochet, slightly more labially placed in the holotype. On the other hand, Heissig (1972, plate 1) figured several M1-M2 of *G. browni* that present short but developed, and even multiple, crochets. He also included an M3 that differs by its convex ectometaloph, rather different from both the holotype and PUPC 07/41. The P3 figured by Heissig (1972) also differs from AMNH 29838 in the lack of a metacone fold and the presence of a relatively less developed crochet.

The Chinese M3 assigned to *Gaindatherium* cf. *browni* by Tang and Zong (1987) has the paracone fold less developed than in the original material described by Colbert (1935) and PUPC 07/41. It is greater in dimensions than the Pakistani remains (Table 2).

The lower dentition has a great resemblance to the characteristic morphology of *Gaindatherium browni* as proposed by Colbert (1934, 1935) and Heissig (1972). The slight difference in size of the present specimens (table 2) with respect to that material is interpreted as intraspecific variation, maybe due to ontogenetic differences or even to sexual dimorphism.

Gaindatherium vidali HEISSIG, 1972

(Figure 4; Table 3)

1881 *Aceratherium perimense.* – Falconer and Cautley-Lydekker, table 3, figure 2.

1934 *Gaindatherium browni.* – Colbert, figure 5.

1935 *Gaindatherium browni.* – Colbert, figure 84.

1972 *Rhinoceros* (*Gaindatherium*) *vidali.* – Heissig, plate 3, figures 1–7; plate 4, figures 6–9 and 12.

Holotype. – GSP 1956 II 260 – left mandibular ramus with p3-m3, collection of the Geological Survey of Pakistan, Quetta; right ramus with p4 and m3; and the left p2, Bayer. Staatslg, palaont. hist. Geol. München. Nagri Formation, the Middle Siwaliks.

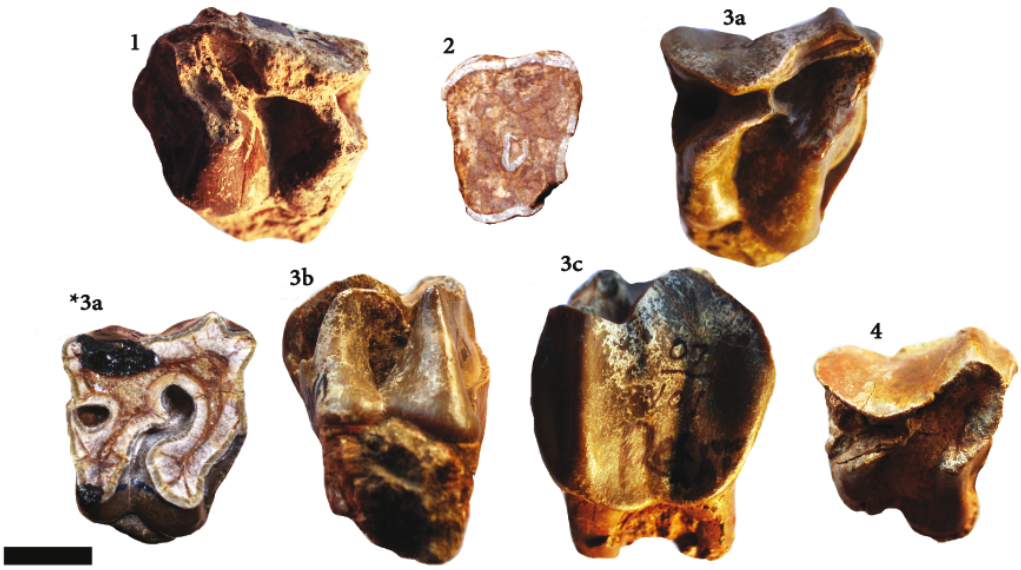

Figure 4. *Gaindatherium vidali* (Rhinocerotini, Rhinocerotidae, Mammalia). 1, PUPC 08/125, lD3; 2, PUPC 84/61, rP2; 3 (a- occlusal, b- lingual, c- labial), PUPC 07/101, rP4; 4, PUPC 07/102, rM1.. Scale bar = 20 mm.

Diagnosis (after Heissig 1972). – Small species of *Gaindatherium*, with weakly curved i2 contrary to *G. browni*. Upper premolars with strong metacone fold and upper molars without it. Mesostyle very weak. Secondary folds also weak, simple, just the anterior groove of the protocone is basally insinuated. Neither lingual nor labial cingula are present. The M3 talon is weak; the posterior roots are completely fused. Lower premolars with obtuse labial groove; lower molars with narrow fossettes.

Table 3. Measurements (mm) of the hemimandible PUPC 11/101 of Gaindatherium browni.

Depth of the horizontal ramus at p2	50.0
Depth of the horizontal ramus at p3	51.0
Depth of the horizontal ramus at p4	56.0
Depth of the horizontal ramus at m1	60.0
Depth of the horizontal ramus at m2	61.0
Depth of the horizontal ramus at m3	78.0
Width of the horizontal ramus at p2	29.0
Width of the horizontal ramus at p4	33.0
Width of the horizontal ramus at m3	39.0
Length of the premolar series p2-4	73.0
Length of the molar series m1-3	114.0
Length of the ascending ramus posterior to m3	165.0
Total length of the horizontal ramus	265.0
Complete length of the ascending ramus	135.0
Width of the condyle	64.0
Height of the condyle	45.0
Total length from anterior tip to condyle level	382.0

Referred material. –PUPC 08/125, lD3; PUPC 84/61, rP2; PUPC 07/101, rP4; PUPC 07/102, rM1, Lava, Chakwal district, Punjab, Pakistan, Chinji Formation, Lower Siwaliks.

Description. – PUPC 08/125 is an incomplete D3 (Figure 4, number 1), with thin enamel. Anterior and posterior cingula are well developed, but lingual and labial cingula are absent. The median valley is open lingually. The postfossette is rounded, deep, and funnel-shaped. The crochet emerges from the apex of the metaloph, just beneath the ectoloph; it is long, almost reaching the protoloph. Parastyle and paracone fold are broken. Overall morphology is similar to the permanent premolars, except by the absence of the metacone fold in the D3.

The P2 of PUPC 84/61 (Figure 4, number 2) is a much worn tooth; a small median fossette is still visible, quite centered on the occlusal surface. A rudimentary anterior cingulum is present, but there is no trace of posterior cingulum. The paracone and metacone folds are moderately developed. Protocone is broken lingually.

The P4 of PUPC 07/101 (Figure 4, numbers 3a–3c) is a barely worn premolar. There is no lingual or labial cingulum. The anterior cingulum is well developed and serrated. The posterior cingulum limits the postfossette, which is deep and funnel-shaped. The median valley is widely open lingually. The protocone and hypocone are conical, the former well developed and more rounded than the latter. There is no trace of antecrochet or crista. Instead, a delicate crochet extends into the median valley from

the apex of the metaloph. A weak mesostyle is present. The parastyle and paracone fold are well developed and prominent, especially the latter. The metacone fold is weak, while the metastyle is well developed. The protoloph and metaloph are oriented diagonally to the ectoloph.

PUPC 02/102 (Figure 4, number 4) is a complete, unworn M1. The ectoloph is concave behind the strongly developed paracone fold. There is no antecrochet or crista. Traces of anterior and posterior cingula are visible. The median valley has a wide and deep lingual opening.

Comparison. – When compared to the material of *Gaindatherium* described by Colbert (1935) and Heissig (1972) from the Chinji and Nagri Formations, respectively, the specimens from Lava resemble *G. vidali* both in morphology and dimensions (Table 2). The similarities are due to the presence of strongly developed labial folds and a deep notch of the inner wall in P2; the great distance between the paracone and metacone folds; strong anterior cingulum in molars; anterior protocone fold; and well-developed funnel-shaped postfossette. Other differences from *G. browni* are the absence of lingual cingulum, median valley more widely open, and crochet strongly developed and angled against the metaloph; the premolars of *Gaindatherium vidali* in the present collection are also wider and shorter than those of *Gaindatherium browni.*

Dental wear can significantly alter the morphology of various dental features, such as the shape and size of the crochet and antecrochet, shape and opening of the median valley, presence and absence of crista and cingula, etc. For the purpose of a better comparison, a cross-section was made of the unworn P4 PUPC 07/101 of *G. vidali* (Figure 4, number 3a), at the same level of the occlusal surface on P4 PUPC 02/08b (Figure 2, number 6), referred to *G. browni*. The comparison showed that the profile of the postfossettes is different; the crochet is still visible in the sectioned tooth of *G. vidali*; the protocone and hypocone are separate in *G. vidali* even at this stage of wear, whereas they join much higher from root level in *G. browni*, closing the median valley; the angle between parastyle and paracone fold is more acute; and the anterior labial profile is wavy in *G. vidali* whereas it is rather straight in *G. browni*.

5. Discussion and conclusion

As expressed among the descriptions and comparisons, the studied specimens are comparable to the homologous dental elements of both species of *Gaindatherium* known from the Siwaliks, *G. browni* and *G. vidali*. At the same time, they show marked morphological and metrical differences with respect to other rhinocerotids recognized in the Chinji Formation and its equivalents in other areas, such as the Manchar Formation, Sindh (Cerdeño and Hussain, 1997; Khan et al., 2013; see the latter for a summary).

Among these other species, *Chilotherium intermedium* is strikingly dissimilar in dental morphology. Contrary to both species of *Gaindatherium*, *C. intermedium* bears hypsodont teeth with a greatly elongated ectoloph and greatly projected parastyle; protocone constricted; trigonid in lower molars angularly V-shaped; hypolophid reclined backward; and entoconid with flattened lingual margin (Matthew, 1929; Colbert, 1935; Heissig, 1972; Khan et al., 2011). *Brachypotherium fatehjangense* is somewhat similar to *Gaindatherium* in the absence of crista and a conspicuous and deep labial groove in the lower dentition. However, it differs from *G. browni* in the presence of subhypsodont cheek teeth; the wide and evenly flat or slightly concave ectoloph behind a rather insignificant paracone fold; and the absence of lingual cingulum in the upper premolars. In turn, *Hispanotherium matritense* differs from both species of *Gaindatherium* in its subhypsodont condition, the presence of a constricted protocone in P3 and P4, a closed median valley of the premolars, well-developed secondary folding of the enamel, a lingual wall on D2, and a constricted entoconid on lower milk teeth (Cerdeño and Iñigo, 1997; Deng, 2002).

Concerning the phylogenetic relationships of *Gaindatherium*, Colbert (1934) defined *G. browni* as a species from the Chinji Formation showing several resemblances to the extant *Rhinoceros* and considered it as a possible direct ancestor. Many years later, Heissig (1972) described a second species as *Rhinoceros* (*Gaindatherium*) *vidali* from the Nagri Formation, and, since then, both species have been considered stratigraphically successive in the Siwaliks (Heissig, 1972; Sehgal and Nanda, 2002). Considering this background, both assumptions are, however, debatable. On the one hand, the relationship with the extant *Rhinoceros* does not appear so close according to modern phylogenetic analyses (Cerdeño, 1995; Antoine et al., 2003, 2010), in which it appears in a more basal position. On the other hand, the present study allows the recognition of both species of *Gaindatherium* as cooccurring within the Chinji Formation, which implies that they were not successive in either a stratigraphic or phylogenetic context.

In summary, the present study has allowed us: a) to provide significant new material for the genus *Gaindatherium* from Pakistan; b) to identify *Gaindatherium vidali* in the Chinji Formation, which increases the stratigraphic range of this species from the Middle Siwalik Nagri Formation to the Lower Siwaliks; and c) to establish that both *G. browni* and *G. vidali* are coeval species during the late Middle Miocene instead of successive taxa as previously proposed by Heissig (1972).

The new data together with those presented by Khan et al. (2013) lead us to establish the rhinoceros fauna of

the Chinji Formation as composed of *Gaindatherium browni*, *Gaindatherium vidali*, *Caementodon oettingenae*, *Chilotherium intermedium*, *Chilotherium blanfordi*, *Brachypotherium fatehjangense*, *Brachypotherium perimense*, *Dicerorhinus* aff. *sumatrensis*, *Dicerorhinus* aff. *abeli*, *Aceratherium* sp., and *Eurhinoceros* sp. inc. sed.

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References

Antoine PO, Downing KF, Crochet JY, Duranthon F, Flynn LJ, Marivaux L, Métais G, Rajpar AR, Roohi G (2010). A revision of *Aceratherium blanfordi* Lydekker, 1884 (Mammalia; Rhinocerotidae) from the Early Miocene of Pakistan: postcranials as a key. Zool J Linn Soc 160: 139–194.

Antoine PO, Duranthon F, Welcomme JL (2003). *Alicornops* (Mammalia, Rhinocerotidae) dans le Miocene superieur des collines Bugti (Balouchistan, Pakistan): implications phylogenetiques. Geodivestas 25: 575–603 (in French).

Antoine PO, Welcomme JL (2000). A new rhinoceros from the Lower Miocene of the Bugti Hills, Baluchistan, Pakistan: the earliest Elasmotheriine. Palaeontology 795–816.

Antunes MT, Ginsburg L (1983). Les rhinocerotides du Miocene de Lisbonne-systematique, ecologie, paleobiogeographie, valeur stratigraphique. Cienc da Terra (UNL) 7: 17–98 (in French).

Barry J, Morgan M, Flynn L, Pilbeam D, Behrensmeyer AK, Raza S, Khan I, Badgely C, Hicks J, Kelley J (2002). Faunal and environmental change in the Late Miocene Siwaliks of Northern Pakistan. Paleobiology 28: 1–72.

Basu PK (2004). Siwalik mammals of the Jammu Sub-Himalaya, India: an appraisal of their diversity and habitats. Quatern Int 117: 105–118.

Cerdeño E (1995). Cladistic analysis of the Family Rhinocerotidae (Perissodactyla). Am Mus Novitate 3143: 1–25.

Cerdeño E (1996). *Prosantorhinus*, the small teleoceratine rhinocerotid from the Miocene of Western Europe. Geobios-Lyon 29: 111–124.

Cerdeño E, Hussain ST (1997). On the Rhinocerotidae from the Miocene Manchar Formation, Sind, Pakistan. Pak J Zool 29: 263–276.

Cerdeño E, Iñigo C (1997). *Hispanotherium matritense* (Rhinocerotidae) de la ciudad de Madrid (España) y su relatión con el paleoambiente del Aragoniense medio (Mioceno Medio). Rev Espñ Paleontol 12: 80–90 (in Spanish).

Chavasseau O, Chaimanee Y, Yamee C, Tian P, Rugbumrung M, Marandat B, Jaeger JJ (2009). New Proboscideans (Mammalia) from the middle Miocene of Thailand. Zool J Linn Soc-Lond 155: 703–721.

Cheema IU (2003). Phylogeny and evolution of Neogene murine rodents from the Potwar Plateau of Pakistan and Azad Kashmir with special emphasis on zoogeographic diversification and stratigraphic implications. PhD, University of the Punjab, Lahore, Pakistan.

Colbert EH (1934). A new rhinoceros from the Siwalik beds of India. Am Mus Novitates 749: 1–13.

Colbert EH (1935). Siwalik mammals in the American Museum of natural History. T Am Philos Soc New Series 26: 1–401.

Deng T (2002). Limb bones of *Chilotherium wimani* (Perissodactyla, Rhinocerotidae) from the Late Miocene of the Linxia Basin in Gansu, China. Vertebrat Palasiatic 40: 305–316.

Ducrocq S, Chaimanee Y, Suteethorn V, Jaeger JJ (1994). Age and paleoenvironment of Miocene mammalian faunas from Thailand. Palaeogeogr Palaeocl Palaeoecol 108: 149–163.

Ducrocq S, Chaimanee Y, Suteethorn V, Jaeger JJ (1995). Mammalian faunas and the ages of the continental Tertiary fossiliferous localities from Thailand. J Southe Asian Earth 12: 65–78.

Ducrocq S, Chaimanee Y, Suteethorn V, Jaeger JJ (1997). A new species of *Conohyus* (Suidae, Mammalia) from the Miocene of northern Thailand. Neues Jahrb Geol P M 6: 348–360.

Flynn LJ, Barry JC, Morgan ME, Pilbeam D, Jacobs LL, Lindsay EH (1995). Neogene Siwalik Mammalian Lineages: Species longevities, rates of changes, and modes of speciation. Palaeogeogr Palaeocl 115: 249–264.

Forster-Cooper C (1934). The extinct rhinoceroses of Baluchistan. Philos T Roy Soc B 223: 569–616.

Friend PF, Raza SM, Geehan G, Shiekh KA (2001). Intermediate-scale architectural features of the fluvial Chinji Formation (Miocene), Siwalik Group, Northern Pakistan. J Geol Soc London 158: 163–177.

Ginsburg L, Ingavat R, Tassy P (1983). *Siamogale thailandica*, nouveau Mustelidae (Carnivora, Mammalia) Néogène du Sud-Est asiatique. B Soc Geol FR 7: 953–956 (in French).

Ginsburg L, Maubert F, Antunes MT (1987). Découverte d'*Hispanotherium* et de *Gaindatherium* (Rhinocerotidae, Mammalia) dans le Miocène de France. B Mus Natl Hist Nat 9: 303–311 (in French).

Ginsburg L, Tassy P (1985). The fossil mammals and the age of the lignite beds in the intramontane basins of Northern Thailand. J Geol Soc Thailand 8: 13–27.

Heissig K (1972). Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. Bayer Akad der Wiss Math Naturw Kla Abhan Neu Fol 152: 1–112 (in German).

Johnson NM, Opdyke ND, Johnson GD, Lindsay EH, Tahirkheli RAK (1982). Magnetic polarity stratigraphy and ages of Siwalik group rocks of the Potwar Plateau, Pakistan. Palaeogeogr Palaeocl 37: 17–42.

Khan AM (2009). Taxonomy and distribution of rhinoceroses from the Siwalik Hills of Pakistan. PhD, University of the Punjab, Lahore, Pakistan.

Khan AM, Cerdeño E, Khan MA, Akhtar M (2013). New *Alicornops* (Rhinocerotidae) remains from Lower and Middle Siwaliks, Pakistan: Rhinocerotid Palaeobiogeography in Pakistan. Ann Paleontol 99: 131–155.

Khan AM, Cerdeño E, Khan MA, Akhtar M, Ali M (2011). *Chilotherium intermedium* (Rhinocerotidae, Mammalia) from the Siwaliks of Pakistan: Systematic Implications. Pak J Zool 43: 651–663.

Khan MA, Akhtar M, Ghaffar A, Iqbal M, Khan AM, Farooq U (2008). Early ruminants from Dhok Bin Mir Khatoon (Chakwal, Punjab, Pakistan): Systematics, Biostratigraphy and Paleoecology. Pak J Zool 40: 457-463.

Khan MA, Akhtar M, Roohi G, Iqbal M, Samiullah K (2011a). *Sivaceros gradiens* Pilgrim 1937 (Mammalia, Bovidae, Boselaphini) from the Lower Siwaliks of Dhok Bun Amir Khatoon, Chakwal, Pakistan: systematics and biostratigraphy. Turk J Zool 35: 281–286.

Khan MA, Khan AM, Ghaffar A, Iqbal M, Akhtar M (2011b). New fossil locality in the Neogene of Lava. Pak J Zool 43: 61–72.

Lydekker R (1881). Siwalik Rhinocerotidae. Pal Indica 10: 1–62.

Lydekker R (1883). Synopsis of the fossil Vertebrata of India. Rec Geol Surv India 16: 61–93.

Lydekker R (1884). Additional Siwalik Perissodactyla and Proboscidea. Pal Indica 3: 1–34.

Matthew WD (1929). Critical observations upon Siwalik Mammals. B Am Mus Nat Hist 56: 435–560.

Metais G, Antoine PO, Baqri SRH, Crochet JY, Franceschi DD, Marivaux L, Welcomme JL (2009). Lithofacies, depositional environments, regional biostratigraphy and age of the Chitarwata Formation in the Bugti Hills, Balochistan, Pakistan. J Asian Earth Sci 34: 154–167.

Peigné S, Chaimanee Y, Yamee C, Tian P, Jaeger JJ (2006). A new amphicyonid (Mammalia, Carnivora, Amphicyonidae) from the late middle Miocene of northern Thailand and a review of the amphicyonine record in Asia. J Asian Earth_Sci 26: 519–532.

Pilbeam DR, Behrensmeyer AK, Barry JC, Shah SMI (1979). Miocene sediments and faunas of Pakistan. Postilla 179: 1–245.

Pilbeam D, Morgan M, Barry JC, Flynn L (1996). European MN units and the Siwalik faunal sequence of Pakistan. In: Bernor RL, Fahlbusch V, Mittmann HW, editors. The Evolution of Western Eurasian Neogene Mammal Faunas. New York, NY, USA: Columbia University Press, pp. 96–105.

Pilgrim GE (1913). The correlation of the Siwaliks with the mammalian horizons of Europe. Rec Geol Surv India 43: 264–326.

Pilgrim GE (1917). Preliminary note on some recent mammal collections from the basal beds of the Siwaliks. Rec Geol Surv India 48: 98–101.

Raza SM (1983). Taphonomy and paleoecology of middle Miocene vertebrate assemblages, southern Potwar Plateau, Pakistan. PhD, Yale University, New Haven, CT, USA.

Raza SM, Barry JC, Meyer GE, Martin LD (1984). Preliminary report on the geology and vertebrate fauna of the Miocene Manchar Formation, Sind, Pakistan. J Vertebr Paleontol 4: 584–599.

Sehgal AK, Nanda AC (2002). Age of the fossiliferous Siwalik sediments exposed in the vicinity of Nurpur, district Kangra, Himachal Pradesh. Curr Sci India 82: 392–395.

Tang Y, Zong G (1987). Mammalian remains from the Pliocene of the Hanshui River Basin, Shaanxi. Vertebrat Palasiatic 25: 222–235.

Tassy P, Anupandhanant P, Ginsburg L, Mein P, Ratanasthien B, Suteethorn V (1992). A new *Stegolophodon* (Proboscidea, Mammalia) from the Early Miocene of Northern Thailand. Geobios-Lyon 25: 511–523.