

Bramatherium (Artiodactyla, Ruminantia, Giraffidae) from the Middle Siwaliks of Hasnot, Pakistan: biostratigraphy and palaeoecology

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Abstract: We describe here new remains of the giraffid *Bramatherium*, from the late Miocene-early Pliocene of Hasnot, northern Pakistan. The fossil giraffid material from Hasnot represents 2 taxa of *Bramatherium*, *B. megacephalum* and *B. grande*. The Hasnot locality is characterised by high proportions of ruminants, namely Boselaphini, Antilopini, Sivatheriinae, Cervini, *Dorcotherium*, and *Dorcabune*. The Hasnot fossil ruminant assemblage is fairly typical for the Siwalik province and comparisons with the Greco-Iranian-Afghan and African palaeobiological provinces indicate a late Miocene-early Pliocene age. It is suggested that local Hasnot palaeoenvironments comprised wetlands to woodland biomes, perhaps devoid of expansive dense forests.

Key words: Vertebrates, Mammalia, Artiodactyla, late Miocene, Siwaliks, Hasnot

1. Introduction

Giraffoids with ossicones were first found in the early Middle Miocene in Africa or their likely ancestors were recorded in the Middle Miocene at Bugti in Pakistan (Barry *et al.* 2005). Giraffid history started in the Early Miocene of Zebel Zelten in northern Africa with *Zarafa* Hamilton, 1973 and *Prolibytherium* Arambourg, 1961. Giraffids have a fairly rich fossil record; approximately 30 species have been found throughout the Neogene of the Old World (Bohlin 1926; Hamilton 1978; Heintz *et al.* 1981; Geraads 1985, 1986; Janis & Scott 1987; Gentry & Hooker 1988; Gentry 1993; Geraads & Güleç 1999; Geraads *et al.* 2004, 2005; Kostopoulos & Saraç 2005; Khan & Akhtar 2005–2006). Today, the family Giraffidae is represented by only 2 species, the okapi [*Okapia johnstoni* (Sclater, 1901)] and the giraffe [*Giraffa camelopardalis* (Linnaeus, 1758)]. Both modern species are found in Africa. The okapi is present in a limited area of heavy forests in West Africa, whereas the giraffe is found in the more open parts of Sub-Saharan Africa (Solounias 2007; Harris *et al.* 2010).

In the Siwaliks (Figure 1A – chronostratigraphic context), the giraffids made their first appearance in the lower portion of the Chinji Formation (Matthew 1929; Colbert 1935; Bhatti 2004). The large or sivatheriine-sized giraffids were not present in the Chinji Formation. As indicated by the fossil record, the sivatheriines were definitely present in the Nagri Formation (Colbert 1935; Bhatti 2004). The Dhok Pathan Formation was

certainly the age of gigantic giraffids. Many species of the sivatheriine giraffes are known from the beds of this age (Khan *et al.* 2010). The Tatrot Formation (ca. 3.4–2.6 Ma) is still without any record of the giraffids (Bhatti 2004). The Pinjor Formation (ca. 2.5–0.6 Ma) is characterised by the presence of *Sivatherium giganteum* Falconer and Cautley, 1836 and *Giraffa punjabiensis* Pilgrim, 1911 (Nanda 2002; Dennell *et al.* 2006). The primary goal of this paper is to report new fossil material of *Bramatherium* from Hasnot in northern Pakistan (Figure 1) and discuss a provisional synonymy of *Hydasitherium* Lydekker, 1876 with *Bramatherium* Falconer, 1845, as suggested by Geraads & Güleç (1999) in the Greco-Iranian province. Based on the recorded ruminant faunal elements from Hasnot, the biostratigraphy and palaeoecology of this area are also discussed.

1.1. Locality

Hasnot is situated in the west of Jhelum district (32°49'N, 73°18'E), Punjab, northern Pakistan (Figure 1A). The locality of Hasnot yielded a rich mammalian fauna (Table 1), which provides the opportunity for high-resolution sampling and reconstruction of palaeoenvironments (Pilbeam *et al.* 1977; Barry *et al.* 2002; Bhatti 2004; Farooq *et al.* 2007a, 2007b, 2007c, 2007d, 2008; Khan 2007, 2008; Khan *et al.* 2007, 2008, 2009, 2010; Ghaffar *et al.* 2010, 2011). The fossiliferous localities around the village of Hasnot are stratigraphically situated in 3 different formations (Figure 1B), and they have yielded fossil

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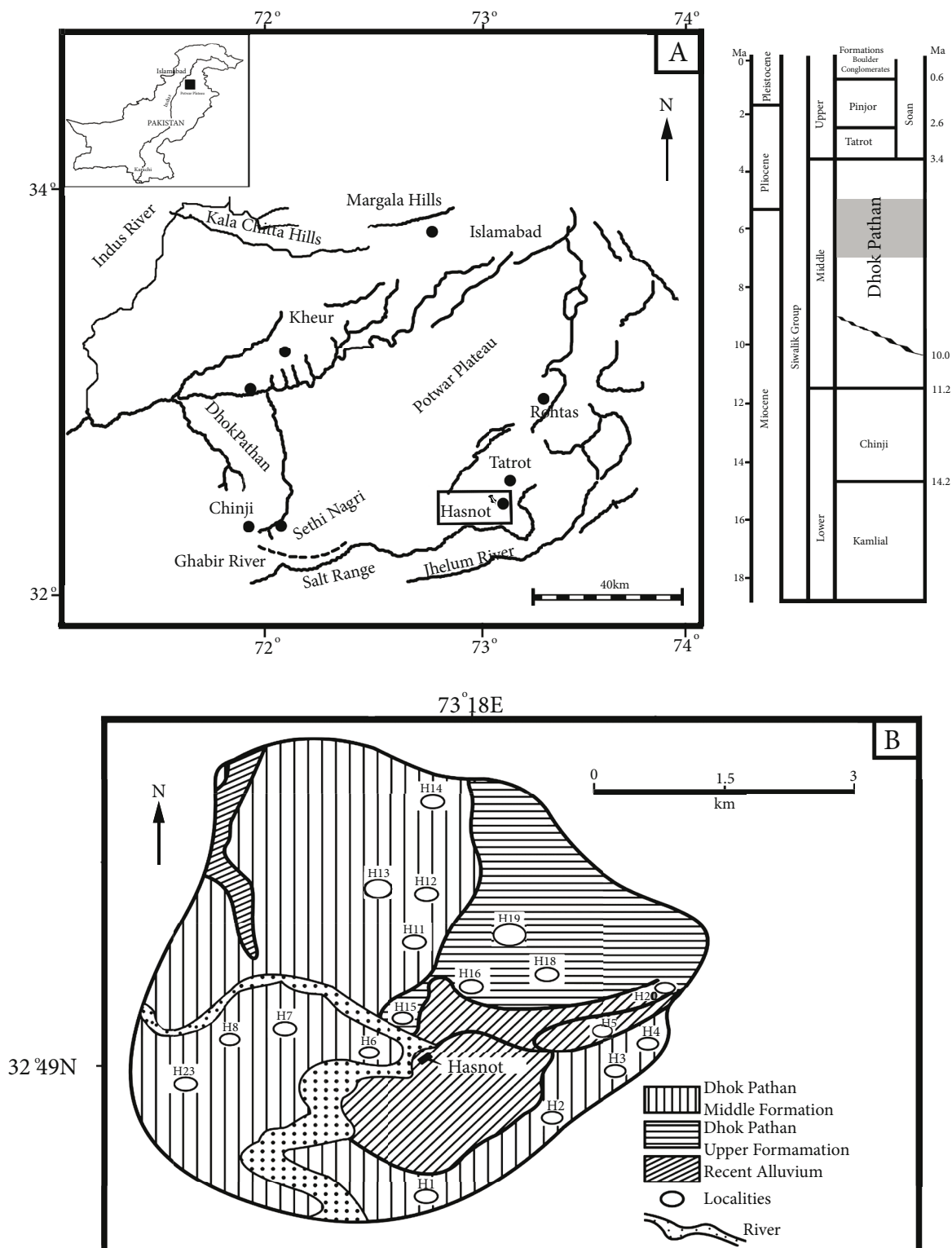


Figure 1. A) A simplified map of the Potwar Plateau in northern Pakistan, with chronostratigraphic context of the Siwaliks Neogene-Quaternary deposits (data from Behrensmeier & Barry 2005; Dennell 2008; Nanda 2008); reference localities of the Siwaliks are shown with circles. **B)** A simplified geologic map of the Hasnot area with indicated localities around the village Hasnot (H = Hasnot), from where the studied material was recovered.

Table 1. Mammalian faunas of Hasnot (referred data are taken from Colbert 1935; Pilgrim 1937, 1939; Hussain 1971; Sarwar 1977; Bernor & Hussain 1985; Pickford 1988; Akhtar 1992; Farooq *et al.* 2007a, 2007b, 2007c, 2007d; Khan *et al.* 2009; Ghaffar *et al.* 2010, 2011; Khan 2010). Many species are under taxonomic revision.

Cercopithecidae	
<i>Cercopithecus hasnoti</i>	<i>Macacus sivalensis</i>
Rodentia	
<i>Rhizomys sivalensis</i>	<i>Rhizomys</i> sp.
<i>Hystrix sivalensis</i>	
Carnivora	
<i>Amphicyon lydekkeri</i>	<i>Indarctos punjabiensis</i>
<i>Promellivora punjabiensis</i>	<i>Enhydriodon falconeri</i>
<i>Sivaonyx bathygnathus</i>	<i>Vishnuictis salmontanus</i>
<i>Ictitherium sivalense</i>	<i>Hyaenictitherium indicum</i>
<i>Lycyaena macrostoma</i>	<i>Lycyaena macrostoma-cinayaki</i>
<i>Precrocuta carnifex</i>	<i>Precrocuta gigantea</i>
<i>Precrocuta gigantean-latro</i>	<i>Adcrocuta eximia</i>
<i>Mellivorodon palaeindicus</i>	<i>Acluropsis annectans</i>
<i>Paramachairodus orientalis</i>	<i>Felis</i> sp.
<i>Propontosmilus sivalensis</i>	
Proboscidea	
<i>Dinotherium indicum</i>	<i>Paratetralophodon hasnotensis</i>
<i>Tetralophodon falconeri</i>	<i>Tetralophodon punjabiensis</i>
<i>Zygodolophodon chinjiensis</i>	<i>Choerolophodon corrugatus</i>
<i>Anancus perimensis</i>	<i>Stegolophodon latidens</i>
<i>Stegolophodon cautleyi</i>	<i>Stegodon bombifrons</i>
<i>Stegodon cliftii</i>	<i>Stegodon elephantoides</i>
Equidae	
<i>Cormohipparion antelopinum</i>	<i>Cormohipparion theobaldi</i>
<i>Sivalhippus perimense</i>	<i>Hipparion</i> sp.

Table 1. (continued).

Rhinocerotidae	
<i>Chilotherium blanfordi</i>	<i>Chilotherium intermedium</i>
<i>Subchilotherium intermedium</i>	<i>Alicornops</i> sp.
<i>Brachypotherium perimense</i>	
Suidae	
<i>Tetraconodon magnus</i>	<i>Propotamochoerus ingens</i> (?)
<i>Propotamochoerus hysudricus</i>	
<i>Hippopotamodon sivalense</i>	<i>Hippopotamodon vagus</i>
<i>Sivalhyus punjabiensis</i>	<i>Hippohyus lydekkeri</i>
Anthracotheriidae	
<i>Microbunodon silistrensis</i>	<i>Merycopotamus dissimilis</i>
Tragulidae	
<i>Dorcabune anthracotherioides</i>	<i>Dorcabune nagrii</i>
<i>Dorcatherium majus</i>	<i>Dorcatherium minus</i>
<i>Dorcatherium minimus</i>	
Cervidae	
<i>Rucervus simplicidens</i>	<i>Cervus triplidens</i>
<i>Cervus sivalensis</i>	<i>Cervus punjabiensis</i>
<i>Cervus rewati</i>	
Giraffidae	
<i>Bramatherium megacephalum</i>	<i>Bramatherium perimense</i>
<i>Giraffa punjabiensis</i>	
Bovidae	
<i>Taurotragus latidens</i>	<i>Tragoportax salmontanus</i>
<i>Tragoportax punjabicus</i>	<i>Tragoportax browni</i>
<i>Proleptobos birmanicus</i>	<i>Selenoportax vexillarius</i>
<i>Selenoportax lydekkeri</i>	<i>Pachyportax latidens</i>
<i>Pachyportax giganteus</i>	<i>Gazella lydekkeri</i>
<i>Gazella padriensis</i>	<i>Elaschistoceras khauristanensis</i>
<i>Eotragus</i> sp.	? <i>Tragoportax curvicornis</i>

material of Giraffidae, including *B. megacephalum* and *B. grande*. The lithostratigraphy of the area was described in detail by Pilbeam *et al.* (1977) and Barry *et al.* (2002). It consists of sandstones with alternate clays and scattered conglomerates in the lower part and conglomerates with sandstones and orange-brown clays in the upper part.

2. Materials and methods

The studied material is stored at the Palaeontology Laboratory of the Zoology Department of the University of Punjab in Lahore, Pakistan, and the Palaeontology Laboratory of the Government College University in Faisalabad, Pakistan. The material was discovered by a team of members from the Palaeontology Laboratories of the Government College University, Faisalabad, and the University of Punjab, Lahore, Pakistan, during the past few years from outcrops near Hasnot, northern Pakistan (Figure 1A). The ascribed material comes from the 4 fossiliferous sites corresponding to a single horizon of Hasnot (H7, H8, H11, and H23) (Figure 1B). Various field trips were carried out to the Hasnot locality of the district Jhelum, Punjab, northern Pakistan. Emphasis was placed on collecting fossils of large vertebrates. A systematic surface survey was the primary means of collecting the fossil remains, although minor excavations were also carried out at a few sites having relatively larger surface concentrations of fossils. This produced additional fossils that supplemented the collection made through the surface search.

The specimens were catalogued and given a number that consisted of a year and a serial catalogue number, such that numbers on the specimen represent the collection year and the serial number of that year (e.g., 09/17 for the seventeenth item collected in 2009). Uppercase letters identify samples of upper dentition and lowercase letters are used for lower dentition. Comparisons of specimens were made with those at the American Natural History Museum (AMNH); the Geological Survey of Pakistan (GSP); the Geological Survey of India (GSI); the Palaeontological Collection of the Zoology Department of Punjab University, Lahore, Pakistan (PUPC); and the Palaeontological Collection of Government College University Faisalabad (PC-GCUF). The morphological and metrical characters of the specimens are described and their systematic determination is discussed. The terminology of the tooth crown elements and manners of measurements follow Gentry and Hooker (1988) and Gentry *et al.* (1999). The discussion in Section 4 is based on the published and unpublished ruminant fossil assemblage from Hasnot.

3. Systematic palaeontology

Family GIRAFFIDAE Gray, 1821

Subfamily SIVATHERIINAE Zittel, 1893

Genus *Bramatherium* Falconer, 1845

Synonymy: *Hydasphitherium* Lydekker, 1877

? *Helladotherium* Gaudry, 1860

Vishnutherium Lydekker, 1876

Type species. *Bramatherium perimense* Falconer, 1845.

Diagnosis. Colbert, 1935: 348.

Geographic distribution. Late Miocene to Early Pliocene of the Pakistan-Indian Subcontinent and the Greco-Iranian province (Lydekker 1876; Pilgrim 1910; Matthew 1929; Colbert 1935; Geraads & Güleç 1999; Sehgal & Nanda 2002; Bhatti 2004; Khan 2007).

Bramatherium megacephalum (Lydekker, 1876)

Figure 2; Table 2

Synonymy: *Hydasphitherium megacephalum* Lydekker, 1876

Vishnutherium iravaticum Lydekker, 1876

Hydasphitherium birmanicum Pilgrim, 1910

Type specimen. GSI D150 – a skull, figured in Lydekker (1876, p. 154).

Stratigraphic range. Nagri–Dhok Pathan formations (Matthew 1929; Colbert 1935; Sehgal & Nanda 2002; Bhatti 2004; Khan & Akhtar 2005–2006; Khan 2007).

Abbreviated diagnosis. The parastyle of *Bramatherium megacephalum* is prominent as compared to the mesostyle and the metastyle. The anterior median rib is moderately developed, whereas the posterior median rib is weakly developed. The enamel is rugose. The stylids are present and the prefossette is transversely compressed. Those of *Bramatherium megacephalum* are smaller than those of *B. grande* (Colbert 1935; Khan 2007).

Studied material. PC-GCUF 10/46 (right p4), PC-GCUF 10/47 (right p4), PUPC 68/242 (left m1), PC-GCUF 10/48 (right mandibular ramus with m1-2), PUPC 06/10 (left m2), PUPC 06/11 (broken left m3).

Locality. Hasnot (Dhok Pathan Formation), Jhelum district, Punjab province, Pakistan.

Description. The material consists of mainly isolated teeth (Figure 2). The teeth are well preserved and their enamel is strongly rugose. Only PUPC 06/11 is broken posteriorly. The fourth premolars are strongly molarised with an anteroposteriorly lengthened metaconid, as in all giraffids [Figure 2(1 and 2)]. The second molars are large relative to the first molar. There is a small basal pillar on m1, but it is usually absent on the remaining molars [Figure 2(3 and 4)]. A weak cingulid is present anterolingually. The praeprotocristid is connected to the metaconid, whereas the postprotocristid is not connected to the metaconid in unworn teeth. The praehypocristid is free, while the posthypocristid is connected to the postentocristid [Figure 2(5)]. The medial valley between the anterior conids is slightly shallower than the one between the posterior conids. The molars have strong meta-, meso-, and entostylids. The metaconid and entoconid ribs are

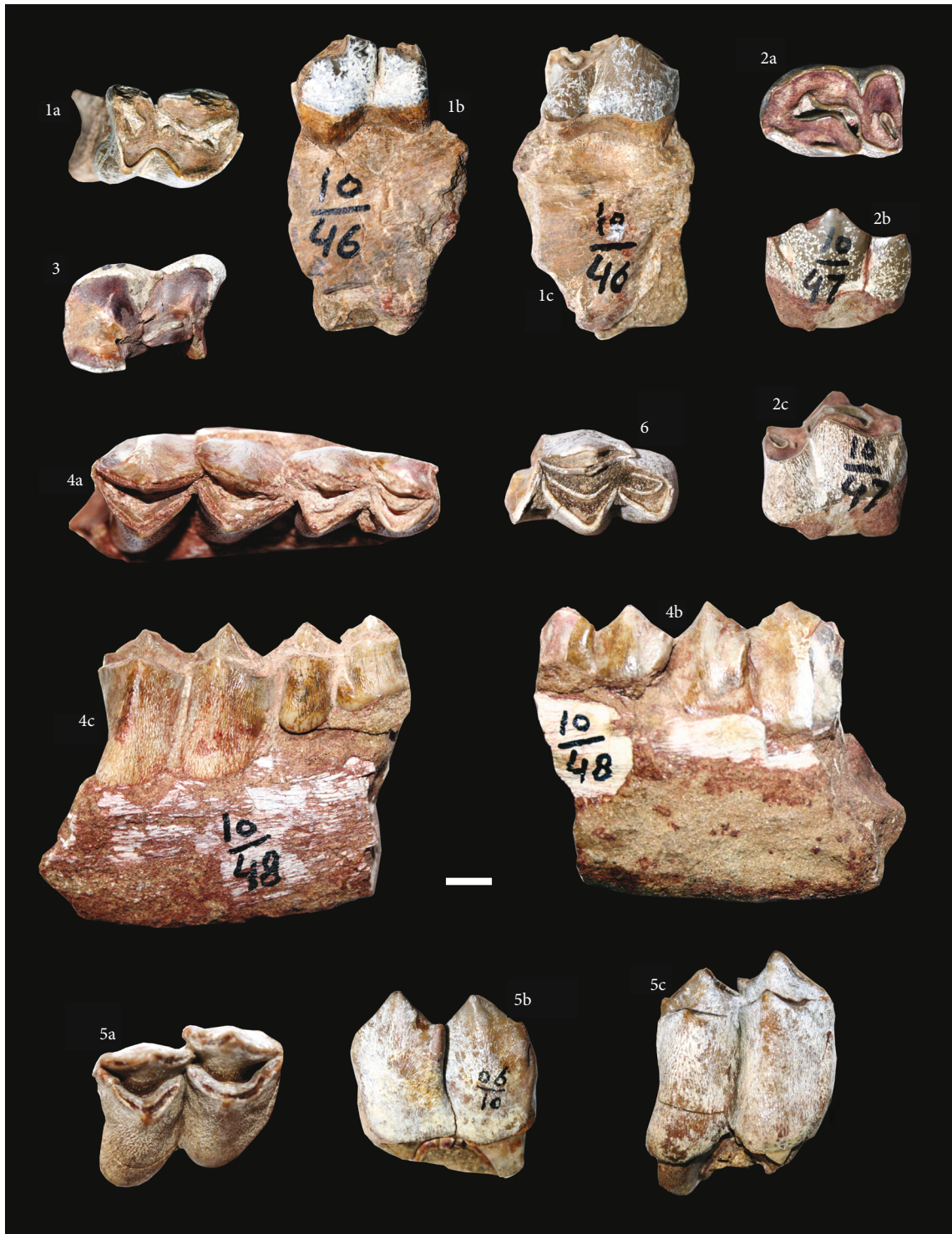


Figure 2. *Bramatherium megagephalum*. 1. PC-GCUF 10/46 - rp4, 2. PC-GCUF 10/47 - rp4, 3. PUPC 68/242 - lm1, 4. PC-GCUF 10/48 - mandibular ramus with rm1-2, 5. PUPC 06/10 - lm2, 6. PUPC 06/11 - broken lm3. a = occlusal view, b = lingual view, c = labial view. Scale bar = 10 mm.

Table 2. Comparative measurements of the studied cheek teeth of the Siwalik *Bramatherium* in millimetres. *: Studied specimens. Referred data are taken from Matthew (1929), Colbert (1935), Bhatti (2004), and Khan *et al.* (2010).

Taxa	Number	Nature/position	Length	Width	W/L ratio	
<i>B. megacephalum</i>	PC-GCUF 10/46*	rp4	30.0	21.0	0.70	
	PC-GCUF 10/47*	rp4	32.0	22.0	0.68	
	PUPC 68/242*	lm1	36.0	26.0	0.72	
	PC-GCUF 10/48*	rm1	33.0	20.0	0.60	
		rm2	39.0	25.0	0.64	
	PUPC 06/10*	lm2	42.0	32.0	0.76	
	PUPC 97/17	rm2	32.5	19.0	0.58	
		rm3	44.0	19.0	0.43	
	AMNH 19669	rp4	31.0	24.0	0.77	
		rm1	38.0	27.0	0.71	
		rm2	38.0	28.0	0.73	
		rm3	50.0	28.5	0.57	
		PUPC 95/24	lm3	44.0	20.0	0.45
		AMNH 19488	rM3	38.5	39.0	1.01
	<i>B. cf. megacephalum</i>	PUPC 09/78	lm1	32.0	19.5	0.60
lm2			39.0	25.0	0.64	
lm3			-	-	-	
<i>B. grande</i>	PUPC 69/156*	LM3	46.0	46.0	1.00	
	Ind. Mus. B135	M3	64.0	55.0	0.85	
	GSI B514	M3	56.0	57.0	1.02	
	PUPC 09/17*	rm3	58.0	29.0	0.50	
	PUPC 67/195	rm2	50.0	34.0	0.68	
rm3		68.0	32.0	0.47		
<i>B. cf. grande</i>	PUPC 09/77	rm2	37.0	28.0	0.75	
		rm3	54.5	27.0	0.49	
? <i>B. sp.</i>	PUPC 83/267	rm2	38.7	30.6	0.79	
		rm3	58.0	27.5	0.47	

well developed. The third lobe of m3 forms a complete loop that is relatively small and elliptical [Figure 2(6)].

Remarks. The Eurasian palaeotragines are characterised by small size, brachydonty, and a flat entoconid wall, which are characters that are absent in the studied teeth. The teeth are reminiscent of sivatheriines in having narrowly pointed labial lobes, transversely compressed prefossette, hypsodonty, and outward-facing lingual ribs. These dental features resemble those of *Bramatherium* (Pilgrim 1911; Matthew 1929; Colbert 1935; Bhatti 2004), a sivatheriine from the upper Miocene Siwalik. *Giraffa* differs from the studied sample because of its brachydont teeth and lower molars with ectostylids set less obliquely to the axis of the jaw and not elongated. The material differs from *Sivatherium*, which displays more pointed labial lobes (protoconid and hypoconid), more outbowing lingual ribs, and a strong mesostylid (Gentry 1997). The absolute

dimensions of the available specimens are smaller than those of *B. grande* (Table 2; Figure 2), and their proportions and morphological characters (narrowly pointed labial lobes, transversely compressed prefossette, hypsodonty, and outward-facing lingual ribs) clearly display the features of *B. megacephalum* (Colbert 1935; Bhatti 2004).

Bramatherium grande (Lydekker, 1878)

Figure 3; Table 2

Synonymy: *Hydasphitherium magnum* Pilgrim, 1910

Helladotherium grande Pilgrim, 1910

Type specimen. GSI B155 – a left upper molar, figured in Lydekker (1878, p. 93).

Stratigraphic range. Dhok Pathan Formation (Matthew 1929; Colbert 1935; Bhatti 2004).

Abbreviated diagnosis. A large species, considerably larger than *B. megacephalum*, but otherwise similar to it (Colbert 1935). Cheek teeth are large and heavy, with

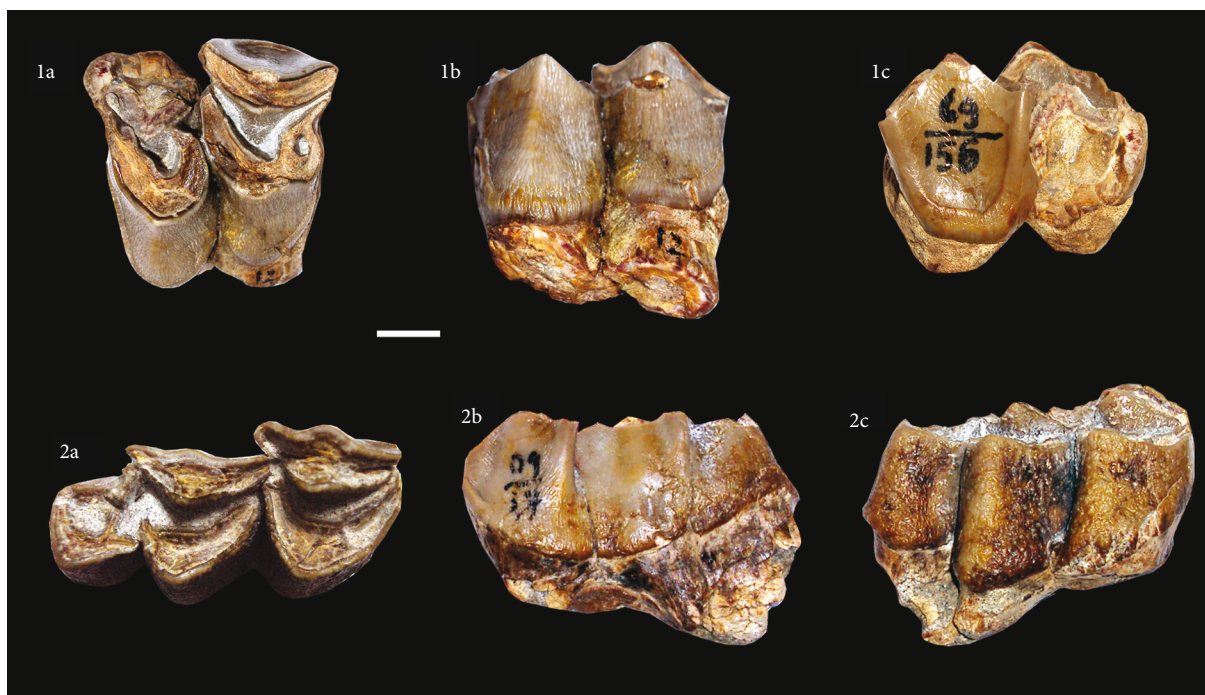


Figure 3. *Bramatherium grande*. 1. PUPC 69/156 – IM3, 2. PC-GCUF 09/17 – rm3. a = occlusal view, b = lingual view, c = labial view. Scale bar = 10 mm.

rugose enamel. The mandible is relatively short and has a mandibular groove beneath the teeth. The lower molars are broader and somewhat larger (Khan *et al.* 2010).

Studied material. PUPC 69/156 (left M3), PC-GCUF 09/17 (right m3).

Locality. Hasnot (Dhok Pathan Formation), Jhelum district, Punjab province, Pakistan.

Description and remarks. PUPC 69/156 is moderately worn with thick and fairly rugose enamel [Figure 3(1)]. The cingulum is present anteroposteriorly. The isolation of protocone, paracone, metacone, and metaconule is visible occlusally. The protocone is larger transversally than the metaconule. The lingual wall of the protocone is rounded, while the metaconule is slightly narrow and angular lingually. The protocone is elongated transversely and shortened longitudinally. A dentinal islet and weak spur are present in the metaconule. The anterior half of the crown is comparatively higher than the posterior half of the molar.

The lower tooth PC-GCUF 09/17 [Figure 3(2)] resembles *B. megacephalum* in enamel rugosity, its transversely compressed prefossette, pointed labial lobes, outbowing of the lingual ribs, and the structure of the crown, which is oblique with respect to the axis of the jaw, but metrically the sample is considerably larger than that of *B. megacephalum* (Table 2; Figure 3). Morphometrically, the studied molars are a good match for *B. grande* (Matthew 1929; Colbert 1935; Khan *et al.* 2010) and have been assigned to *B. grande*.

3.1. Synonymy

The taxonomy and validity of the Siwalik giraffids have not been fully resolved yet (Matthew 1929; Colbert 1935; Gentry 1997). Lydekker (1876) described the genus *Hydaspitherium* based on a collection from different localities of the Siwaliks. Further collection of this genus was done by Pilgrim (1910), Matthew (1929), Colbert (1935), Bhatti (2004), Khan (2007), and Khan *et al.* (2010). These collections comprise cranial and postcranial elements. They identified 4 *Hydaspitherium* species, namely *H. megacephalum* Lydekker, 1876; *H. grande* Lydekker, 1878; *H. magnum* Pilgrim, 1910; and *H. birmanicum* Pilgrim, 1910 from the Siwaliks (Lydekker 1876, 1878; Pilgrim 1910; Matthew 1929; Colbert 1935).

Colbert (1935) synonymised *Helladotherium grande* with *Hydaspitherium grande*. Matthew (1929, p. 550) and Hamilton (1978, p. 218) suggested a synonymy of *Helladotherium* with *Bramatherium*. Geraads and Güleç (1999) suggested a synonymy of *Hydaspitherium* Lydekker, 1876 with *Bramatherium* Falconer, 1845, based on the skull recovered from Kavakdere in central Turkey. Nevertheless, there is much variation in the Siwalik giraffid dentition and the earlier researchers did not consider the variability of the species owing to insufficient material and incomplete information. As the spectrum of intraspecific variability in the Siwalik giraffids is large, this synonymy is now formally founded, and following Geraads and Güleç (1999), we shall now continue to use *Bramatherium* as a valid taxon in the Siwaliks.

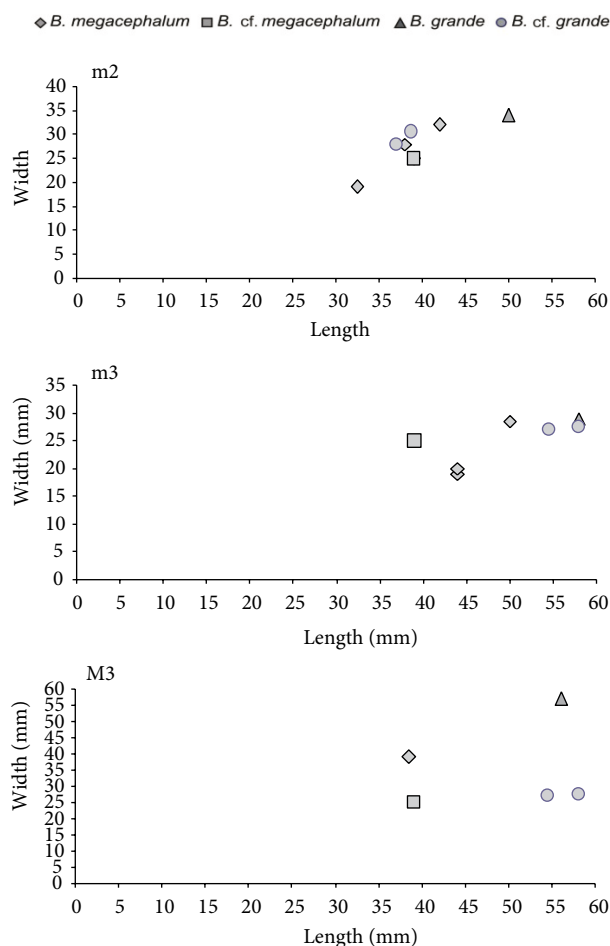


Figure 4. Size variation in the described species of the Hasnot giraffids.

The description of *B. birmanicum* (Pilgrim 1910) and *Vishnutherium iravaticum* Lydekker, 1876 was simply based on a few fragmentary specimens. These species were only erected to display minor variations in tooth size, though the authors discussed the resemblance of these species to *B. megacephalum* (Lydekker 1876; Pilgrim 1910). These species are considered to be invalid by Matthew (1929) and Colbert (1935). Nevertheless, the fossil record for *B. megacephalum* has increased (Bhatti 2004; Khan et al. 2010) and it shows that the size variation is now better understood for this species (Table 2; Figure 4). The size variation of *B. birmanicum* and *Vishnutherium iravaticum* probably represents either sexual dimorphism or immature individuals, since the rest of their morphological features are close to those of *B. megacephalum*. In our opinion, the systematic positions of *B. birmanicum* (Pilgrim 1910) and *Vishnutherium iravaticum* Lydekker, 1876 are doubtful and should be synonymised with *B. megacephalum*.

Bramatherium grande (Lydekker 1878) and *B. magnum* (Pilgrim 1910) are the large-sized Siwalik sivatheriines.

They were only erected to display minor variations in size (Matthew 1929; Colbert 1935). Similarly, *B. grande* has the same characteristics as *B. magnum* and both of them are larger in size than *B. megacephalum* (Figure 4). Dental size variation (Table 2) of *B. grande* and *B. magnum* suggests interspecific variability. The difference is probably due to sexual dimorphism, subject to interspecific variability in the late Miocene Siwalik Sivatheriinae. This is especially true if one considers the range of variation observed within the species of extinct Eurasian sivatheriines (e.g., see Geraads & Güleç 1999; Gentry et al. 1999).

Matthew (1929, p. 243) and Colbert (1935, p. 360) already proposed close affinities between *B. grande* and *B. magnum*. Moreover, both species are restricted to the Dhok Pathan Formation. Following nomenclature rules, it is obvious that *B. grande* (Lydekker 1878) has priority over *B. magnum* (Pilgrim 1910). Therefore, we consider here that there are 2 species of *Bramatherium* in the late Miocene of the Siwaliks: a small species *B. megacephalum* and a large species *B. grande*. However, further fossil material (including nondental) is needed to test this hypothesis of synonymy.

4. Discussion

4.1. Age and correlation

The ruminant species identified from Hasnot on the basis of published and unpublished work (Pilgrim 1937, 1939; Akhtar 1992; Farooq et al. 2007a, 2007b, 2007c, 2007d; Khan 2007; Khan et al. 2007, 2008, 2009; Ghaffar et al. 2010, 2011) are as follows:

Family Bovidae

Tribe Boselaphini *Selenoportax vexillarius*, *S. lydekkeri*
Pachyportax latidens, *Eotragus* sp. *Tragoportax punjabicus*,
T. salmontanus, *T. browni* *Elaschistoceras khauristanensis*

Tribe Bovini *Vishnucobus patulicornis*

Tribe Reduncini *Kobus porrecticornis*

Tribe Antilopini *Prostrepsiceros vinayaki*, *Gazella lydekkeri*

Family Tragulidae *Dorcatherium majus*, *Dt. minus*
Dorcabune anthracotherioides, *Db. nagrii*

Family Cervidae *Rucervus simplicidens*, *Cervus triplidens*, *C. sivalensis* *C. rewati*

Family Giraffidae *Bramatherium megacephalum*, *B. grande* *Giraffa punjabiensis*

Thus, this makes the recovered ruminant fauna from the Hasnot localities respectable enough to provide an indication of the age of the Hasnot localities. The age of the Hasnot ruminants is clearly later than the Middle Miocene, and also they appear to be earlier than the middle of the Pliocene, because boselaphines are part of the ruminant fauna, and thus they are likely to be the end representatives of the Upper Miocene (Khan et al. 2009, 2010).

Biostratigraphically, the ruminant taxa can be clearly divided into 3 groups, based on the presence of these taxa at different stratigraphic levels in the Hasnot sedimentary succession. *Eotragus* sp., *Cervus rewati*, and *C. triplidens* appear in localities H15 and H20, which are located at the top of the Hasnot sedimentary succession (Figure 1B). The top sedimentary succession is represented by localities H21 to H15, as shown in Figure 1B, whereas *S. lydekkeri* and *Dt. majus* appear in the middle of the succession coming from localities H6 to H1. *Rucervus simplicidens* and *S. vexillarius* appear in the lower (H14 to H7) and middle (H6 to H1 and H20 to H21) parts of the succession while *C. sivalensis* covers the top and middle of the succession. Other taxa like *Dt. minus*, *G. lydekkeri*, and *P. latidens* can be found in the whole range of the Hasnot succession.

The cervids are mostly found at the top of the succession of Hasnot, which is very close to the Tatrot Formation (Upper Siwaliks), containing abundant cervid fauna. The absence of *S. lydekkeri* in the top succession of Hasnot proves that the succession can be considered closer to the Tatrot Formation (Upper Siwaliks) than to the Dhok Pathan Formation (Middle Siwaliks), as *S. lydekkeri* is absent in the Tatrot Formation. The middle succession of Hasnot has a similar fauna as the Dhok Pathan Formation, whereas the giraffids, which are present in the lower succession of Hasnot, are very common in the Dhok Pathan village localities (Khan *et al.* 2010). Furthermore, *Eotragus* sp. is found for the first time in the top succession of Hasnot, which is hitherto absent in the Dhok Pathan Formation (Khan *et al.* 2009).

Bramatherium agrees better with the Late Miocene sivatheres than with those of the Pliocene or later. *Giraffa punjabiensis* comes from the Dhok Pathan in the time span between 7.1 and 5.0 Ma (Colbert 1935; Barry *et al.* 1991) and it is abundant in the Hasnot localities (Colbert 1935; Bhatti 2004) with a size similar to that of *Palaeotragus coelophrys* from Maragheh (Iran). Based on the fossil record, it seems that sivatheres do not appear before the Late Miocene (Gentry 1999).

The suid *Propotamochoerus* sp. (10.2–6.5 Ma), the sivathere *Bramatherium* sp. (10.3–7.1 Ma), *Selenoportax* (7.4 to ca. 4.0 Ma), and the antilopines (8.6–7.4 Ma) suggest an age of 7–5 Ma for the localities H5 to H14 (north-west) of Hasnot (Pickford 1988; Barry *et al.* 2002). The cervids are very common in Hasnot (Khan 2007; Ghaffar *et al.* 2010, 2011). It is most likely that they entered the Siwaliks in the Early Pliocene. The tragulids (*Dorcatherium* and *Dorcabune*) that appear in the Siwalik sequences are dated as 18–6.4 Ma (Barry & Flynn 1989). Thus, it is clear that 3 phases characterise the Hasnot ruminants, the first from 7 to 6.2 Ma, the second from 6.2 to 5.3 Ma, and the third from 5.3 to 5 Ma. Therefore, the Hasnot ruminants support a Late Miocene to Early Pliocene age for the Hasnot localities, perhaps equivalent to MN 13 (late Turolian to

late Vellasian) in terms of the European Mammal Neogene zone scale and around 7.0–5.0 Ma in terms of dating.

The late Miocene (Vellasian and mainly Turolian) fauna of the Greco-Iranian province was evidenced by many earlier authors (e.g., De Bonis *et al.* 1992; Iliopoulos 2003). Knowledge of these faunas originated from the discovery and study of the major localities of Pikermi (Greece), Samos (Greece), and Maragheh (Iran), known since the 19th century (Solounias 1981; Gentry 1999). The Hasnot localities can be compared with those Late Miocene to Early Pliocene faunas in adjacent continental regions. Except for *G. lydekkeri*, the much greater abundance of spiral-horned Antilopini is also noteworthy in the Greco-Iranian-Afghan province (Solounias 1981; Bernor 1986; Kohler 1987; Gentry & Heizmann 1996).

Caprini, Reduncini, Bovini, Boselaphini, and Antilopini are present in the Turolian of the Greco-Iranian province as well as in the Late Miocene-Early Pliocene of Hasnot. Cervidae occur sparingly in the Greco-Iranian Turolian, and there are even rare records of Tragulidae. Gentry (1999) identified ?*Bramatherium* sp., *Tragoportax cyrenaicus*, *Pachyportax latidens*, *Prostrepsiceros* aff. *vinayaki*, and *Gazella* aff. *lydekkeri* from the Late Miocene of the Baynunah Formation (Abu Dhabi), which are also common in the Hasnot localities.

In Langebaanweg (South Africa), a boselaphine *Tragoportax acrae* has a resemblance to species *Tragoportax salmontanus* from Hasnot and this is likely to reflect that both species are Late Pliocene (Gentry 1978, 1999, 2010; Harris 1991, 2003). In East Africa, at Mpesida, Lukeino, and the Manonga Valley, Cephalophini, Hippotragini, and *Aepyceros* are additional constituents (Thomas 1984; Gentry 1997, 2010). The only resemblance to the Hasnot ruminants seems to be the presence of a sivatherine giraffid at a comparable stage of evolutionary development in East Africa. According to Gentry, this ?*Sivatherium* sp. could easily belong to *Bramatherium* (Gentry 1999), a genus common in Hasnot. There are no Boselaphini or spiral-horned Antilopini, although boselaphines were present earlier in the East African Miocene and *Tragoportax* at Lothagam 1 (Kenya). Additionally, Nakaya *et al.* (1984, p. 109) recorded a possible spiral horned antelope (as *Palaeoreas* sp.) in the earlier Namurungule Formation, and Smart (1976) listed *Antilope* sp. for Lothagam 1 (Kenya). The North African pecorans, as known from Bled ed-Douarah, Sahabi, and Wadi Natrun (Saudi Arabia), are Boselaphini (*Tragoportax cyrenaicus*), Bovini (“*Leptobos*” *syrticus*), Reduncini (*Kobus* sp.), Hippotragini (*Hippotragus* sp.), Alcelaphini (*Damalacra* sp.), Neotragini (*Raphicerus* sp.), Antilopini (*Prostrepsiceros libycus*, *Gazella* sp.), and Giraffidae (*Sivatherium* aff. *hendeyi*) (Geraads 1989; Harris 1987; Lehmann & Thomas 1987; Gentry 2010).

The African ruminant faunas from Langebaanweg and Chad are very close to the Hasnot ruminants with a conspecific boselaphine, a spiral-horned antilopini (*Prostrepsiceros vinayaki*), and 2 giraffids (*Bramatherium megacephalum*, *Sivatherium* sp.), but they differ in the presence of several exclusively African tribes such as Cephalophini and Hippotragini. The Hasnot ruminants are different from those of the Greco-Iranian Turolian province. The Hasnot fauna shows some affinity with the Baynunah Formation (Abu Dhabi) and the North African faunas. The Hasnot ruminant fossil record provides evidence of faunal interchange for a limited number of species between Africa and Eurasia by the Late Miocene and earliest Pliocene (Gentry 1999; Bibi 2007, 2011).

4.2. Palaeoecology

The presence of giraffines, boselaphines, antilopines, and a gazelle at Abu Dhabi, North Africa, and the Siwaliks could indicate a rather parkland-like landscape (Gentry 1999, 2010; Khan *et al.* 2009). The presence of a southern or hot climate is plausible, but without any substantial development of aridity. The gazelle might have had a lifestyle more like that of the present day West African *Gazella rufifrons* than the lifestyle of the desert gazelles of North Africa and Arabia. The presence of the tragulids in the Late Miocene of the Siwaliks (Khan *et al.* 2012, 2013) and their absence from North Africa and Abu Dhabi suggests that the range contraction of this family had proceeded further, and that suitable habitats were unavailable in the Arabian Peninsula.

Bramatherium megacephalum and *B. grande* may have been sufficiently adapted to semiarid conditions to persist in the Late Miocene Arabian fossil record and the Siwaliks (Matthew 1929, Colbert 1935; Geraads & Güleş 1999;

Gentry *et al.* 1999; Bhatti 2004; Khan *et al.* 2010). The age range for this species is quite broad, potentially as old as the base of the Nagri Formation up until 3.4 Ma (Bhatti 2004). Fauna of the Hasnot locality that are associated with *Bramatherium*, particularly *Pachyportax*, *Selenoportax*, and *Gazella*, may indicate the presence of drier and more open habitats (Khan 2007; Khan *et al.* 2009). The abundance of *Dorcatherium* sympatric with bovids reflects a humid landscape (Farooq *et al.* 2008; Khan *et al.* 2012; Khan & Akhtar 2013). If taxa such as *Pachyportax*, *Selenoportax*, and *Gazella* inhabited relatively more arid and more open environments (Khan *et al.* 2009), *Dorcatherium* was confined to wetlands (Khan *et al.* 2012; Khan & Akhtar 2013).

The recovered giraffid material with the mammalian remains (Table 1) fits well with the Siwalik Late Miocene to Early Pliocene fauna, indicating the Upper Dhok Pathan Formation (Middle Siwaliks) (isochronous to the European Late Turolian age) (Pilbeam *et al.* 1977; Barry *et al.* 2002; Khan *et al.* 2009). The palaeoecological attributes of the extinct *Bramatherium* with associated fauna suggest a wetland to woodland environment for Hasnot, probably devoid of any wide open grasslands.

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