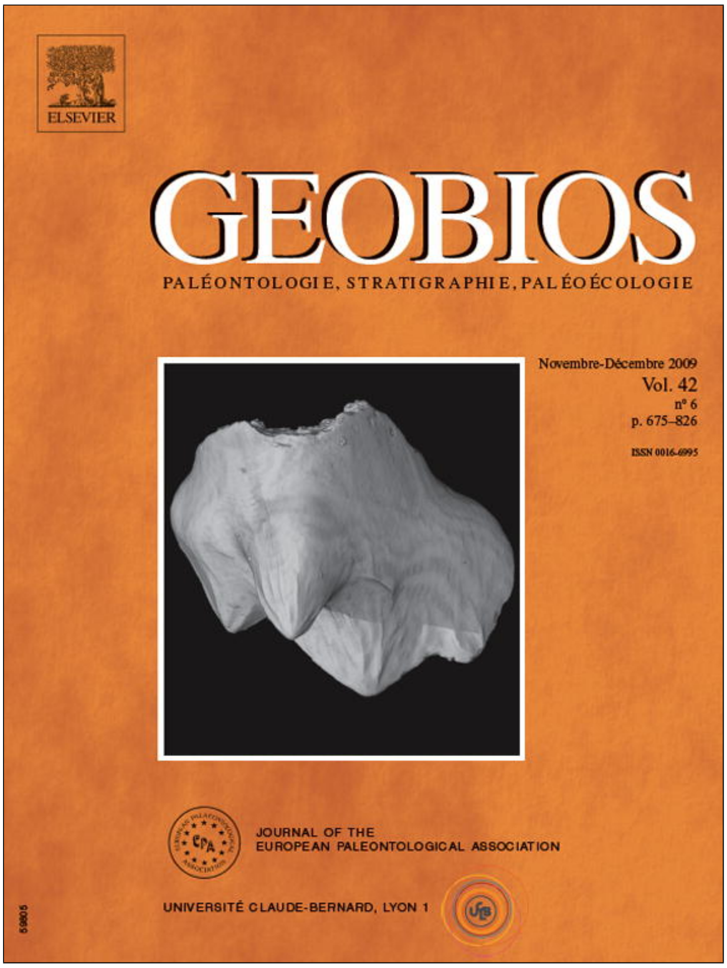
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Original article

Boselaphines (Artiodactyla, Ruminantia, Bovidae) from the Middle Siwaliks of Hasnot, Pakistan ☆

Bosélaphinés (Artiodactyla, Ruminantia, Bovidae) des Siwaliks moyens d'Hasnot, Pakistan

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Abstract

In this paper, boselaphine material from several localities in the area of the Hasnot Pakistan, is described, identified, and discussed. Four species that belong to three different genera of the tribe Boselaphini have been found: *Selenoportax vexillarius*, *S. lydekkeri*, *Pachyportax latidens* and *Eotragus* sp. *Eotragus* sp. is reported for the first time from the Hasnot and consequently from other Upper Middle Siwalik sediments of Pakistan and equivalent strata of the world, extending the range of the genus from the Lower to the Middle Siwaliks. Reviewing the Siwaliks' *Selenoportax* species, *S. dhokpathanensis* Akhtar and *S. tatrotensis* Akhtar are synonymized with *S. lydekkeri* and *S. vexillarius*, respectively.

Keywords: *Selenoportax*; *Pachyportax*; *Eotragus*; Bovidae; Late Miocene; Siwaliks; Hasnot

Résumé

Dans cet article, les Boselaphini de plusieurs localités de la région d'Hasnot, Pakistan, sont décrits, identifiés et discutés. Quatre espèces appartenant à trois genres différents ont été retrouvées : *Selenoportax vexillarius*, *S. lydekkeri*, *Pachyportax latidens* et *Eotragus* sp. *Eotragus* sp. est rapporté pour la première fois dans la région étudiée ainsi que dans les sédiments des Siwaliks moyens supérieurs ; il atteste de la présence du genre *Eotragus* dans les Siwaliks inférieurs et moyens. La révision des espèces de *Selenoportax* des Siwaliks amène à la mise en synonymie des espèces *S. dhokpathanensis* Akhtar et *S. lydekkeri*, d'une part, et *S. tatrotensis* Akhtar et *S. vexillarius*, d'autre part.

Mots clés : *Selenoportax* ; *Pachyportax* ; *Eotragus* ; Bovidae ; Miocene supérieur ; Siwaliks ; Hasnot

1. Introduction

During the Late Miocene, regional differentiation of ruminants became more intense; therefore, their territories were expanded from those of their evolutionary origins in the Middle Miocene (Gentry, 1970; Fortelius et al., 1996; Gentry and Heinzmann, 1996). Siwalik Hills' faunas were not an exception: following the above-mentioned trend, ruminant diversity in the Siwalik increased. Several bovid species have been identified in the Neogene of the Siwaliks (Colbert, 1935; Pilgrim, 1937, 1939; Thomas, 1984; Akhtar, 1992, 1995, 1996; Barry et al., 2002; Khan and Farooq, 2006, Khan et al., 2008a, 2008b). The number of these determined species has already been considered as exaggerated; nevertheless the taxonomy and the validity of the bovid species in the Siwaliks have not been fully resolved yet (Bibi, 2007). In 1935, Colbert mentioned 26 bovid species (Appendix A). He determined only 7 in the Middle Siwalik and 20 in the Upper Siwalik deposits, so it is clear that in both formations there is only one common species. Pilgrim in his legendary work on the Siwalik bovids (1937, 1939), described 75 bovid species of which 17 were let as indet. species and 28 were new to science (Appendix A). The descriptions of some new species were simply based on single

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specimens, and some of them were only erected to display minor variations, despite the fact that in the descriptions of some holotypes (e.g., *Strepsiportax gluten*, *Helicoportax tragelaphoides*), the author was not even confident about their validity (Pilgrim, 1937; p. 758). In 1992, Akhtar determined 33 species of bovids of which 11 were newly erected species, based on slight variations in their styles/stylids, median ribs and crests (Appendix A).

By the late Middle Miocene, it is apparent that the Siwaliks was inhabited by various boselaphines, caprines and gazelles. Many new forms of bovids, especially boselaphines appeared, while their diversification was reduced in the Early Pliocene. Although definite boselaphines are known from the Middle and Late Miocene, Solounias et al. (1995) described a new species, *Eotragus noyei,* from the Lower Siwaliks (Kamlial Formation, Lower Miocene) which they considered as the oldest bovid found until then. *Eotragus* sp. from Hasnot (Middle Siwaliks) is described in this paper for the first time. In addition, two species of the boselaphine genus *Selenoportax* erected by Akhtar in 1992 are reviewed and synonymised in this paper.

2. Siwalik Boselaphines

Boselaphini are represented today by a small group consisting of two species: Nilgauy (*Boselaphus tragocamelus*) and Tetracere (*Tetracerus quadricornis*). Boselaphine fossils extend appreciably in the Miocene of the Indian Peninsula and represent a vast geographical distribution (Thomas, 1984). Pilgrim (1937, 1939) reported six species of boselaphines in the Lower Siwaliks and fourteen species in the Middle Siwaliks. He stressed the high density of boselaphines in the Siwalik group, where they constitute 95% of the bovid species. Thomas (1984) mentioned the same high diversity and density of boselaphines in the pre-hipparion Siwalik sediments but reported five species of boselaphines from the Chinji formation of the Siwaliks, contrary to Pilgrim (1937, 1939) and Gentry (1970) who mentioned six and four species, respectively.

Boselaphines are sporadically known from the Middle Miocene and abundantly from the Late Miocene of the Siwaliks. They can be split into two generic or suprageneric groups (Moya-Sola, 1983: 198, figs. 59, 60). The first group includes the medium-sized Siwalik boselaphines genera *Miotragocerus* Stromer, 1928 and *Tragoportax* Pilgrim, 1937. Thomas (1984) referred to this group all the specimens that came from the Nagri and the Dhok Pathan formations, and allotted the name Tragocerina. They appeared for the first time in the Middle Miocene but they are best known from the Turolian wherein, alongside *Gazella*, they are considered as the most widespread bovids. *Tragoportax* sp. is present in the Turolian of the Graeco-Irano-Afganian province as well as in the Hasnot (Solounias, 1981; Bernor, 1986; Kohler, 1987; Gentry and Heizmann, 1996). *T. cyrenaicus* at its type locality (France) is a morphologically advanced species of the very Late Miocene (Geraads, 1989: 790). Allied species to *T. cyrenaicus* are found in the presumed Early Pliocene locality of Langebaanweg, South Africa (*Tragoportax acrae*) and in the Hasnot localities (*Tragoportax salmontanus*; Gentry, 1999). *T. salmontanus* resembles closely to the Late Miocene Siwaliks species *Prostrepsiceros vinayaki* for which Thomas (1984: 42) accepts a date of 7.0–7.5 Ma.

The second group consists of the large-sized Siwalik boselaphines and includes the genera *Selenoportax* and *Pachyportax*, as well as allied forms such as *Austroportax latifrons* from the Middle Miocene of Europe. *Selenoportax* is a moderate to large-sized boselaphine, whereas *Pachyportax* is considered a gigantic-sized form (Lydekker, 1876; Gentry, 1999). Thomas (1984: fig. 18) highlighted the *Helicoportax*-*Selenoportax* relationships and recommended the name Helicoportacina for them. According to Heissig (1972), *Selenoportax* is a progressive form of *Helicoportax tragelaphoides* reported from the Chinji Formation of the Siwaliks (Thomas, 1984). *Selenoportax* and *Pachyportax* have been recovered from Middle (Lydekker, 1876, 1884; Pilgrim, 1937, 1939, 1947; Akhtar, 1992, 1995, 1996; Khan, 2008) and Upper Siwaliks deposits of Pakistan (Akhtar, 1992; *S. tatrotensis*, synonymized in this study).

According to our findings, although boselaphines have been continuously present from the Lower to Upper Siwaliks sequence, *Selenoportax* and *Pachyportax* are more abundant in the Hasnot succession (7–5 Ma). *Eotragus* has been recovered from the Lower Siwaliks (Solounias et al., 1995; Khan et al., 2008a) and from the Middle Siwaliks deposits (this paper). Barry et al. (2002) provide an age ranging from 18.3–3.3 Ma for the Kamlial to the Tatrot Formations (Lower to Upper Siwaliks), which have allowed us to assign a precise boselaphine faunal interval. The majority of the boselaphine specimens have been recovered from the Dhok Pathan Formation (10.1–*ca*. 3.5 Ma; dated by Barry et al., 2002) whereas boselaphine findings in low numbers were recovered from the other Siwalik formations (Kamlial, Chinji, Nagri and Tatrot).

In this study, *Eotragus*, *Selenoportax* and *Pachyportax* are recovered from Middle Siwaliks' localities in the Hasnot. *Miotragocerus* and the *Tragocerus*–*Tragoportax* complex are excluded from this study.

Besides the boselaphines and the other bovids, the fossiliferous layers of the Hasnot have exposed a rich and diverse fauna. The Hasnot fauna mainly consists of Artiodactyla (Cervidae, Tragulidae, Giraffidae, Suidae), Perissodactyla (Equidae, Rhinocerotidae), Proboscidea and Primates (Cercopithecoidea). Among carnivores members of the families Canidae, Ursidae, Hyaenidae and Felidae are present. The Hasnot mammalian fauna is given in Table 1.

3. Geology and stratigraphy

The recovered boselaphine material comes from localities around the Hasnot village (Lat. 32° 49′ N: Long. 73° 18′ E), which is situated at about 70 km west of Jhelum city in the Potwar Plateau of northern Pakistan (Fig. 1). The village is located on the east bank of the river Bunha, surrounded by a number of highly fossiliferous localities at an altitude of around 326 m (Fig. 2). It is surrounded by extensive Neogene freshwater sedimentary rocks. The region of the Hasnot

Table 1
Mammalian Fauna of Hasnot.

Cercopithecidae	
Cercopithecus hasnoti	*Macaca sivalensis*
Rodentia	
Rhizomys sivalensis	*Rhizomys* sp.
Hystrix sivalensis	
Carnivora	
Amphicyon lydekkeri	*Indarctos punjabiensis*
Promellivora punjabiensis	*Enhydriodon falconeri*
Sivaonyx bathygnathus	*Vishnuictis salmontanus*
Ictitherium sivalense	*Hyaenictitherium indicum*
Lycyaena macrostoma	*L. macrostoma-vinayaki*
Percrocuta carnifex	*Percrocuta gigantea*
Percrocuta gigantea-latro	*Adcrocuta eximia*
Mellivorodon palaeindicus	*Aeluropsis annectans*
Paramachairodus orientalis	*Felis* sp.
Proboscidea	
Deinotherium indicum	
Paratetralophodon hasnotensis	*Tetralophodon falconeri*
Tetralophodon punjabiensis	*Zygolophodon chinjiensis*
Choerolophodon corrugatus	*Anancus perimensis*
Stegolophodon latidens	*Stegolophodon cautleyi*
Stegodon bombifrons	*Stegodon clifti*
Stegodon elephantoides	
Equidae	
Cremohipparion antelopinum	*Cormohipparion theobaldi*
Sivalhippus perimense	
Rhinocerotidae	
Chilotherium blanfordi	*Subchilotherium intermedium*
Alicornops sp.	*Brachypotherium perimense*
Suidae	
Tetraconodon magnus	*Propotamochoerus ingens* (?)
Listriodon pentapotamiae	
Propotamochoerus hysudricus	
Hippopotamodon sivalense	
Hippopotamodon vagus	
Sivahyus punjabiensis	
	Hippohyus lydekkeri
Anthracotheriidae	
Microbunodon silistrensis	*Merycopotamus dissimilis*
Tragulidae	
Dorcabune anthracotherioides	*Dorcabune nagrii*
Dorcatherium majus	*Dorcatherium minus*
Dorcatherium minimus	
Cervidae	
Cervus simplicidens	*Cervus triplidens* (?)
Cervus sivalensis (?)	*Cervus punjabiensis*
Cervus rewati	
Giraffidae	
Bramatherium megacephalum	*Bramatherium perimense*
Giraffa punjabiensis	
Bovidae	
Taurotragus latidens	*Selenoportax vexillarius*
Tragoportax rugosifrons	*Pachyportax latidens*
Proleptobos birmanicus	*Eotragus* sp.
Selenoportax lydekkeri	
Pachyportax giganteus	
Gazella lydekkeri	
?Tragoportax curvicornis	
Tragoportax salmontanus	*Elaschistoceras khauristanensis*

exposes the most complete sequence of the Siwalik Group and yields a diversified sequence of the Middle Siwalik Formation. The average thickness of the sequence around this area is about 180 m. Sites surrounding the village present an abundance of vertebrate fossils from almost all major Eutherian groups.

Lithostratigraphically, the sediments belong to the Upper Dhok Pathan Formation (Middle Siwaliks; isochronous to the European Late Turolian age), which is characterized by sandstones with alternate clays and scattered conglomerates in the lower part and conglomerates with sandstones and clays in the upper part. The clays are orange brown in colour and the time of deposition ranges from 7 to 5 Ma (Fig. 3; Pilbeam et al., 1977; Johnson et al., 1982; Barry et al., 1982; Barry, 1987).

In 1935, Colbert (p. 46, fig. 22) mentioned 27 fossiliferous localities in the Hasnot area. After him, no one else worked there until recently, when the area surrounding the Hasnot was thoroughly surveyed and 23 fossiliferous localities were recorded (H 1 to H 23; Fig. 2). Colbert's localities have been revised and two new localities, not mentioned in Colbert's original report (1935), have been excavated for the first time (localities H 14 and H 23). East of Bhandar locality H 5 was traced, which probably coincides with the localities 15, 16, 119, and 154 that Colbert mentioned (1935) in this area. The localities 140 and 162 (Colbert, 1935) near the Dheri, north of the Hasnot are represented here by H 15 on the basis of the new excavated site (Fig. 2) and the localities 116 and 117 (Colbert, 1935) are also revised to H 7. The fossils are comparatively abundant in all localities; however, (Fig. 2) in the localities H 22 and H 9 no determinable specimens were found.

4. Materials and methods

The boselaphine material used in this study has been collected from 15 of the localities around the Hasnot village, and these are H 1–8, 11, 12, 14–16, 18, and 23 (Fig. 3). The collections were carried out during field trips that took place from 2003 to 2006. Surface collection was the primary method of collecting exposed remains of boselaphines. In addition, some of the specimens used in this study already belonged to the collections of the Palaeontology Laboratory, University of the Punjab, Lahore, Pakistan, and had been collected in the past from the above-mentioned localities around the Hasnot. Most of the specimens were found partly exposed, thus, excavation methods had to be employed, while a few others were found lying completely exposed on the surface. The embedded material was carefully excavated with the help of chisels, geological hammers, fine needles, pen knifes, hand lances and brushes. In the laboratory, the material was carefully prepared, washed, and broken parts were reassembled with the use of various types of resins such as Araldite, Peligom, Magic stone, Elfy, Elite and Fixin. The specimens were catalogued and given a number which consists of a collection year and a serial catalogue number (e.g., 2004/23). Various measurements of the studied specimens in millimeters were taken with the help of metric vernier calipers. Tooth length and width were measured at occlusal level. Heights were measured on the mesostyle of the upper molar, the metastylid of the lower molar and the protoconid of

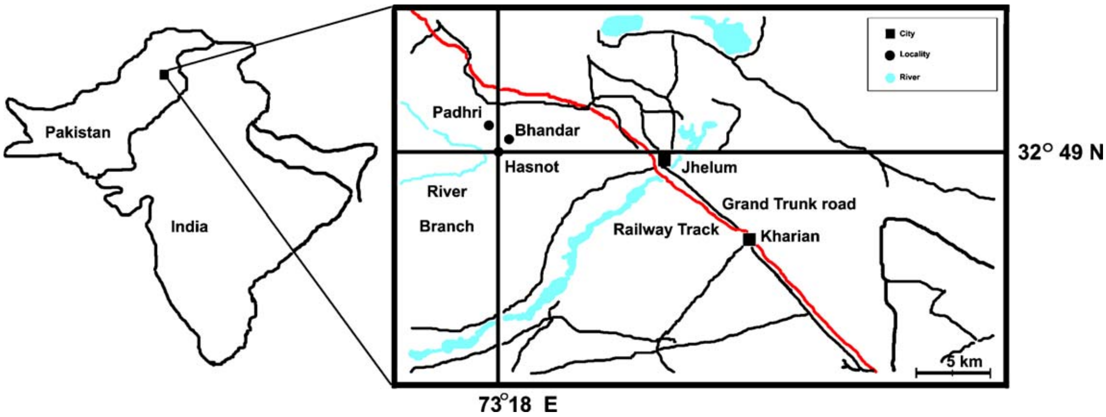

Fig. 1. Location of the Hasnot area in the Potwar Plateau, northern Pakistan.

the lower premolar. Measurements given for teeth are occlusal length and width.

Tooth cusp terminology in this paper follows the nomenclature of Gentry (1994). Comparisons were made with specimens from the Natural History Museum, London (BMNH), the American Museum of Natural History (AMNH), the Geological Survey of Pakistan (GSP), the Geological Survey of India (GSI), the Natural History Museum of the United Emirates of Abu Dhabi (AUH), the Palaeontological collection of Government College University, Faisalabad, Pakistan (PC-GCUF) and the specimens from the Palaeontology laboratory of the Zoology department of the Punjab University, Lahore, Pakistan (PUPC). The studied material is stored in the Palaeontology Laboratory of the Zoology Department of the Punjab University, in Lahore, Pakistan.

5. Systematic paleontology

Superfamily BOVOIDEA Simpson, 1931
Family BOVIDAE Gray, 1821
Subfamily BOVINAE Gray, 1821
Tribe BOSELAPHINI Knottnerus-Meyer, 1907
Genus ***Selenoportax*** Pilgrim, 1937

Selenoportax vexillarius Pilgrim, 1937

Stratigraphic Range: Middle and Upper Siwaliks.

Localities: Hasnot (H 1, 8, 11, 12, 5), Jhelum district, the Punjab, Pakistan.

Material examined: Right M^2 (PUPC 00/53, PUPC 96/39), left M^2 (PUPC 01/23), left M^3 (PUPC 87/199), a fragment of left mandible with P_4 and M_{2-3} (PUPC 04/1), a fragment of left mandible with M_{2-3} (PUPC 98/78), left M_1 (PUPC 85/40), left M_2 (PUPC 04/12), left M_3 (PUPC 87/90).

Diagnosis (Pilgrim, 1937; Akhtar, 1992)**:** Moderate- to large-sized Siwalik bovid with hypsodont to extremely hypsodont teeth, upper molars quadrate with strong divergent styles, median ribs well developed, entostyle strongly developed and ectostylid moderately developed, enamel very rugose.

Description: The second upper molars are in an excellent state of preservation (Fig. 4) and in an early stage of wear. The

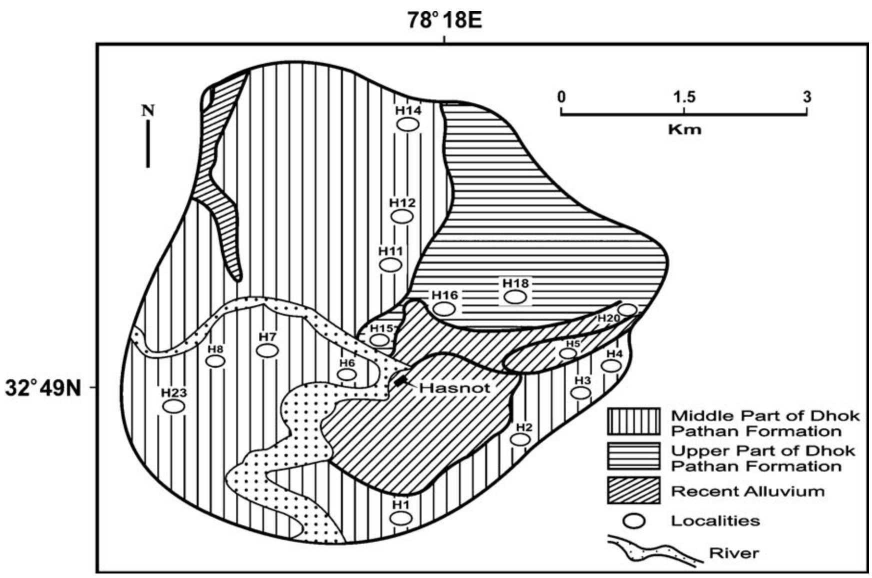

Fig. 2. Simplified geological map of the Hasnot area indicating the studied fossiliferous localities around the village of the Hasnot (H, abbreviation for Hasnot).

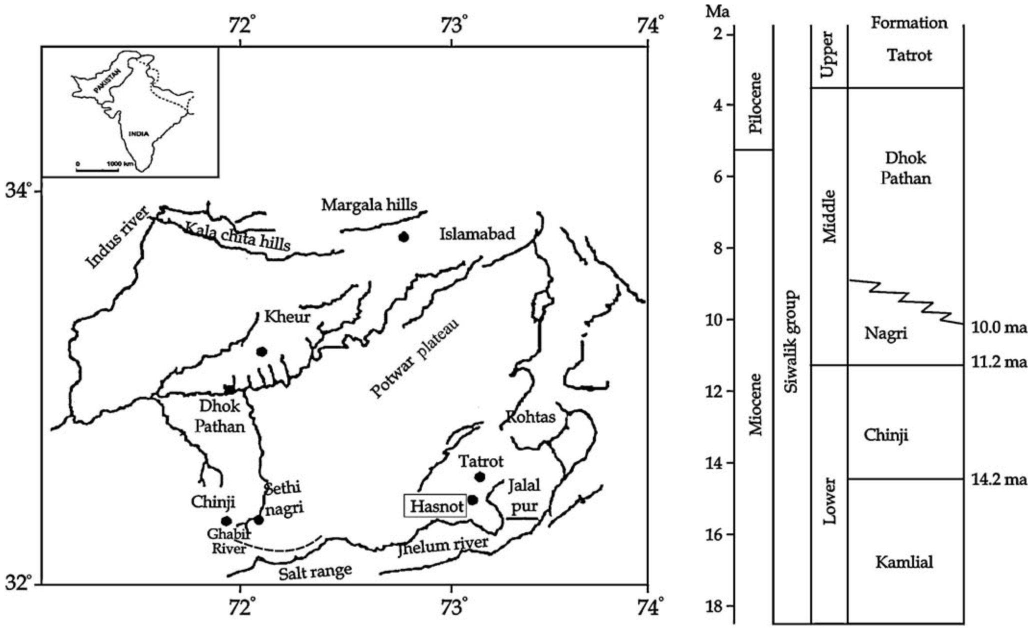

Fig. 3. Map of the Potwar Plateau (northern Pakistan) surrounding the study place and a generalized stratigraphic section of the major Siwalik formations showing succession and ages (modified from Behrensmeyer and Barry, 2005).

enamel is finely rugose and the rugosity is more evident on the lingual side than the buccal side. The entostyles are strongly developed in all the molars but a large part of its anterior end is missing in PUPC 01/23 (Fig. 4(2)). The principal cones are well developed and the buccal cusps are higher than the lingual ones, which at this stage of wear are not attached to each other at the transverse valley. The styles and median ribs are well developed. The fossettes are wide and no enamel spur seems to project into these fossettes. The right M^2 (PUPC 00/53; Fig. 4(3)) is a rather well preserved molar with the exception of its missing protocone, and its broken metacone at the apex. The paracone is well developed and pointed in the middle with two running cristae. The enamel is moderately thick and rugose. The rugosity is more distinct on the buccal side than on the lingual side of the tooth. The entostyle is missing in the transverse valley between the protocone and the hypocone, whereas the other styles are generally well developed (Fig. 4(3)). The parastyle is very strong and prominent. The mesostyle and the metastyle are moderately developed and the anterior median rib is more prominent than the posterior rib. The left M^3 (PUPC 87/199; Fig. 4(1)) is generally a well-preserved molar, presenting an early stage of wear. The posterior median rib is more prominent than the anterior median rib while the fossettes are broad. The lower dentition specimens present well developed fourth premolars, and second and third molars (Fig. 5(1, 2)). The protoconulid is well preserved in the premolars, whereas the molars have fully developed conids. The conids are narrower than the cones and the anterior transverse flange is moderately developed in the lower molars. The molars present various stages of wear and have prominent ectostylids. In the third molars the hypoconulid is well developed, long and narrow, with a wide and inflated central area having two sloping cristids (Fig. 5(1, 2)). The dimensions of the studied cheek teeth of *S. vexillarius* are presented in Table 2.

Discussion: The general contour of the studied specimens, the rugosity of the enamel, the strong entostyles and ectostylids, the prominent median ribs and the strong and divergent styles exclude the specimens from the genus *Pachyportax* and favor their inclusion in the genus *Selenoportax*. The dimensions and the morphology of the studied material reveal all the features of the species *S. vexillarius* as described by Pilgrim in 1937. Specimens PUPC 00/53, PUPC 96/39, and PUPC 01/23 (Fig. 4) present the same morphological features of the type specimen AMNH 19844 (Pilgrim, 1937). Notably, the M^3 (PUPC 87/199, Fig. 4(1)) of *S. vexillarius* is being described here for the first time. As indicated by its measurements, the specimen is an extremely hypsodont and narrow crowned tooth. The molar shows fine enamel plications, which are relatively more prominent on the lingual than on the buccal side. Specimen PUPC 00/53 shows the same basic features of the species such as the increased antero-posterior diameter near the summit of the crown and the strong development of styles and ribs. The structure of specimen PUPC 04/1 resembles with the specimens AMNH 29946 and AMNH 29917 (Pilgrim, 1937) in its antero-posterior length and transverse width. The paraconid, the parastylid, the protoconid, the entoconid, and the development of the stylids are fairly similar. The M_2 in specimen PUPC 98/78 is narrow crowned, as indicated by its width and length ratio. Specimen PUPC 98/78 resembles with the specimens AMNH 19844, AMNH 19514 and AMNH 29917 as discussed by Pilgrim in 1937. In M_3, the enamel layer is finely plicated (Fig. 5(1, 2)) and it compares very well with AMNH 19514 (Pilgrim, 1937). The shape of the cristids and the roughness of the enamel in left M_1 (PUPC 85/40), left M_2 (PUPC 04/12), and left M_3 (PUPC 87/90), are very evident and have similar

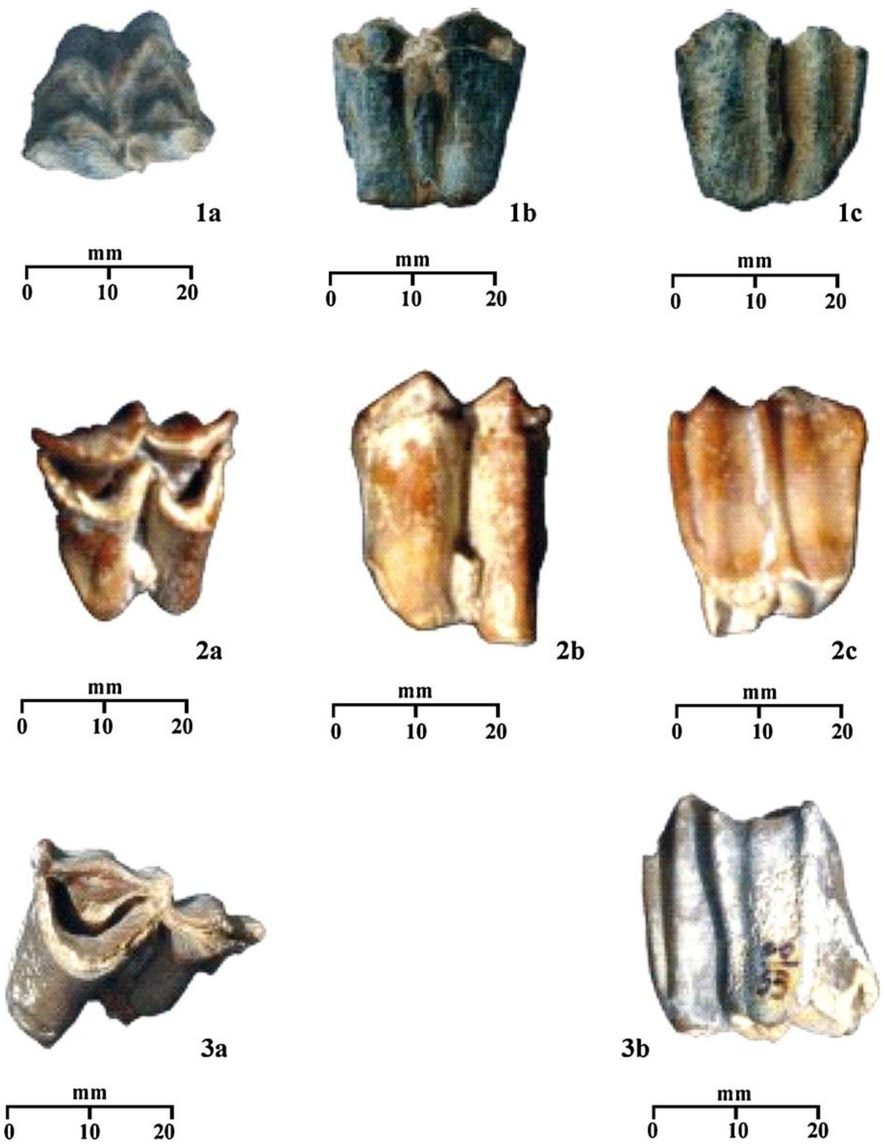

Fig. 4. Isolated upper *S. vexillarius* cheek teeth. **1**. Left third upper molar (PUPC 87/199): a, occlusal view; b, lingual view; c, buccal view. **2.** Right second upper molar (PUPC 01/23): a, occlusal view; b, lingual view; c, buccal view. **3.** Right second upper molar (PUPC 00/53): a, occlusal view; b, buccal view.

morphology with specimens AMNH 19514, AMNH 29917, AMNH 19844 (Pilgrim, 1937).

Selenoportax lydekkeri (Pilgrim, 1910)

Type specimen: A left maxilla with DP^{2-4} and M^{1-2} (GSI B213).

Localities: Hasnot (H 23, 6, 7) Jhelum district, the Punjab, Pakistan.

Material examined: Left M^2 (PUPC 95/1), right M_1 (PUPC 85/26, PUPC 87/144), a fragment of left mandible with M_2 (PUPC 86/6), left M_2 (PUPC 85/106), left M_3 (PUPC 95/21, PUPC 85/24), right M_3 (PUPC 96/8).

Description: The specimens are limited to eight isolated cheek teeth of which one is an upper molar and the rest belongs to lower dentition (Fig. 5). In the M^2, the paracone and the metacone are badly damaged buccally and all the styles are missing however; a very strong and slightly transversely extended entostyle is present in the median valley of the tooth. Lower first molars (PUPC 85/26 and PUPC 87/144; Fig. 5(3–5)) present an advanced stage of wear and have moderately developed and divergent stylids. Second molars (PUPC 86/6 and PUPC 85/106; Fig. 5(4)) are rooted in left mandibular ramii which are broken anteriorly as well as posteriorly and fairly eroded all along the ventral side revealing the roots of M_2. The anterior transverse flange and the ectostylid are strongly developed. In the third lower molars (Fig. 5(5)), the lingual conids are relatively higher than the buccal ones. The praeprotocristid is thicker than the postprotocristid; the greater part of the praeprotocristid projects more inwardly than the posthypocristid (Fig. 5(5)).

Discussion: Lydekker (1884) described for the first time under the genus name *Boselaphus* seven different specimens from the Punjab without mentioning their exact locality. These specimens are a maxilla, a mandible and some isolated teeth. Pilgrim (1910) established the species *B. lydekkeri* for this material. However, he (Pilgrim, 1937) later established the

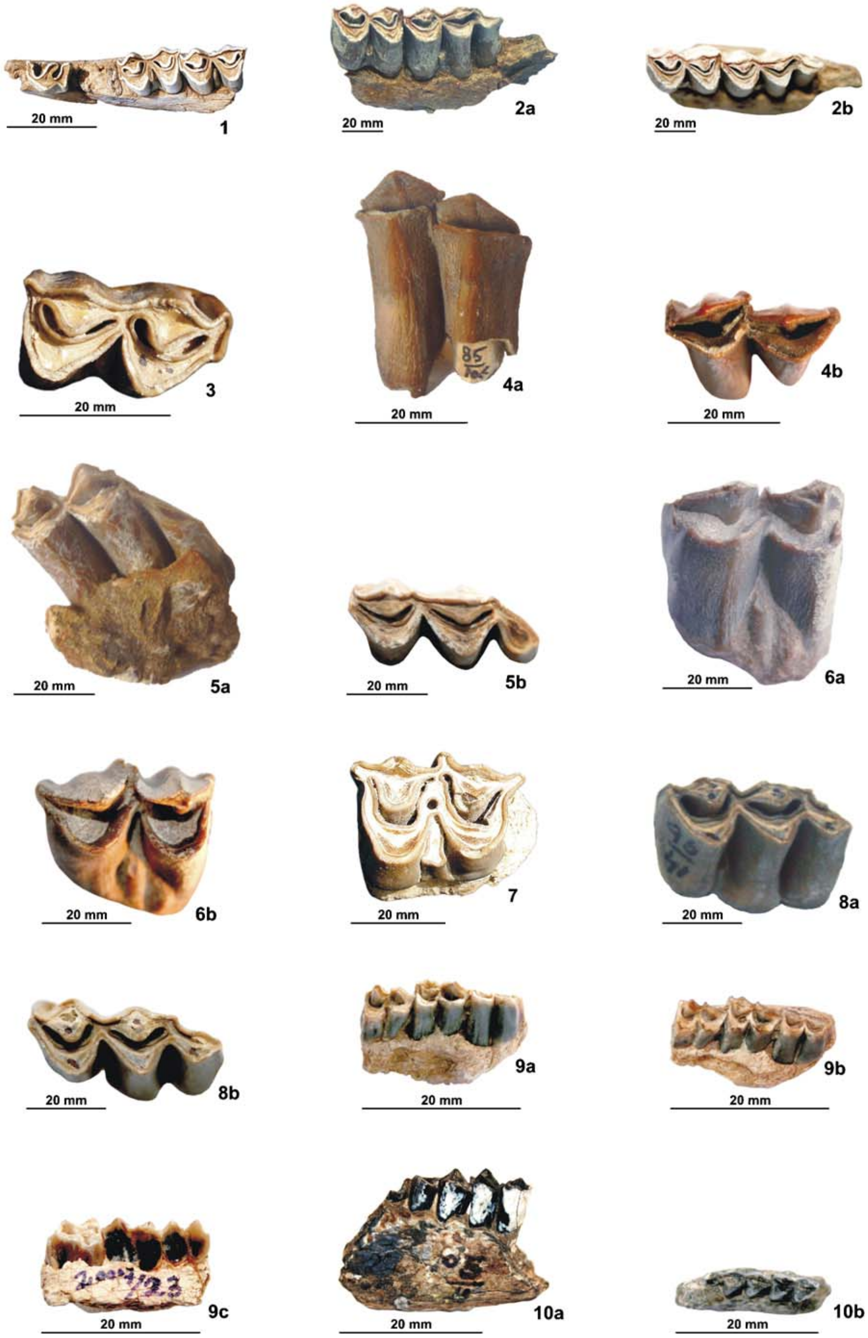

Fig. 5. Upper and lower boselaphine cheek teeth. **1**. *S. vexillarius*, a fragment of left mandible with a fourth premolar, and second and third molars (PUPC 04/1), occlusal view. **2.** *S. vexillarius*, a fragment of left mandible with second and third molars (PUPC 98/78): a, buccal view; b, occlusal view. **3.** *S. lydekkeri*, a right first lower molar (PUPC 87/144): occlusal view. **4.** *S. lydekkeri*, a left second lower molar (85/106): a, buccal view; b, occlusal view. **5**. *S. lydekkeri*, a left third lower molar (PUPC 95/21): a, buccal view; b, occlusal view. **6**. *P. latidens*, a right second upper molar (PUPC 83/744): a, lingual view; b, occlusal view. **7**. *P. latidens*, a left third upper molar (PUPC 01/24), occlusal view. **8**. *P. latidens*, a left third lower molar (PUPC 96/41): a, buccal view; b, occlusal view. **9**. *Eotragus* sp., a fragment of left maxilla with upper first, second and third molars (PUPC 04/23): a, lingual view; b, occlusal view; c, buccal view. **10**. *Eotragus* sp., a fragment of right mandible with lower second and third molars (PUPC 05/11): a, buccal view; b, occlusal view.

genus *Selenoportax* and thus renamed the species to *S. lydekkeri.*

The teeth of *S. lydekkeri* are much larger than those of *S. vexillarius* (Tables 2 and 3; Fig. 6), and morphologically they differentiate from *S. vexillarius* in terms of the strong and extended entostyle and the stronger, divergent and larger in size styles (Table 4; Fig. 6).

There is only one second upper molar out of the eight described specimens. It presents a late stage of wear but it clearly shows all the morphological features of the species *S. lydekkeri* as cited by Pilgrim (1937) and Akhtar (1992). Morphologically, specimen PUPC 95/1 resembles the type specimen GSI B123 in the structure of the lingual cusps and the antero-posterior length. All the molars show fine wrinkles,

Table 2
Comparative measurements (in mm) of the cheek teeth of *Selenoportax vexillarius* (data taken from Pilgrim, 1937, 1939; Akhtar, 1992 and Khan, 2008). In parenthesis: locality code from where the specimen was collected; *: studied specimens.

Number	Position	Length	Width	W/L
PUPC 00/53 (H1)*	M^2 (dext)	27.5	18.5	0.67
PUPC 96/39 (H8)*	M^2 (dext)	26.0	19.0	0.73
PUPC 01/23 (H11)*	M^2 (sin)	23.5	19.5	0.82
PUPC 87/199 (H8)*	M^3 (sin)	25.0	21.2	0.84
PUPC 04/1 (H12)*	P_4 (sin)	20.0	12.4	0.62
	M_2 (sin)	27.9	16.1	0.57
	M_3 (sin)	31.4	16.0	0.50
PUPC 98/78 (H12)*	M_2 (sin)	25.0	16.0	0.64
	M_3 (sin)	36.0	15.0	0.41
PUPC 85/40 (H8)*	M_1 (sin)	19.7	12.5	0.63
PUPC 04/12 (H5)*	M_2 (sin)	20.0	12.5	0.62
PUPC 87/90 (H5)*	M_3 (sin)	38.0	16.5	0.43
AMNH 10514	M_3 (sin)	33.0	15.0	0.45
AMNH 29917	M_1 (sin)	18	13	0.72
AMNH 19844	M^2 (dext)	25.7	24.0	0.93
AMNH 29946	P_4 (sin)	21.0	11.0	0.52
AMNH 29917	P_4 (sin)	21.7	10.0	0.46
AMNH 19844	M_2 (sin)	25.9	16.5	0.63
AMNH 19514	M_2 (sin)	22.0	15.5	0.70
AMNH 29917	M_2 (sin)	21.0	15.0	0.71
AMNH 19514	M_3 (sin)	33.0	21.5	0.65
PUPC 87/19*	P^3 (dext)	19.5	16.5	0.84
	P^4 (dext)	19	17	0.89
	M^1 (dext)	24.2	21.5	0.88
	M^2 (dext)	29	21	0.72
	M^3 (dext)	28.7	18	0.62

which are more prominent on the lingual side of the tooth. A common character of these molars, as mentioned by Pilgrim (1937), is the presence of well-developed entostyles. The first lower molars (PUPC 85/26, PUPC 87/144) are narrow crowned and morphologically they resemble the specimens from the American Natural History Museum collection and the Indian Museum collection as discussed by Pilgrim (1937). These specimens are similar to AMNH 19957 in the shape of the ectostylid, the metastylid, the entostylid and particularly the mesostylid, which is prominent only near the summit of the crown of the M_2. The M_2 compares very well with AMNH 19981. A common feature among these specimens is that the protoconid is not V shaped, but crescentic in its general appearance. The specimens PUPC 95/21 and PUPC 85/24 are narrow crowned and the observed metrical difference in their measurements is quite insignificant and can be regarded within the range of intraspecific variation. The referred specimens (AMNH 19908, AMNH 29916, GSI B211) and the studied specimens show about the same width/length index values.

Genus ***Pachyportax*** Pilgrim, 1937

Pachyportax latidens (Lydekker) Pilgrim, 1937

Stratigraphic Range: Middle Siwaliks.

Localities: Hasnot (H 23, 8, 14, 2, 7, 4, 3, 6, 15, 20, 11), Jhelum district, the Punjab province, Pakistan.

Material examined: Right M^2 (PUPC 98/59, PUPC 83/744, PUPC 86/210, PUPC 00/100), left M^3 (PUPC 96/42, PUPC 01/24), right M^3 (PUPC 83/840, PUPC 87/88, PUPC 04/15), left M_2 (PUPC 99/21), right M_2 (PUPC 86/24), right M_3 (PUPC 04/16), left M_3 (PUPC 86/7, PUPC 96/41, PUPC 96/43).

Table 3
Comparative measurements (in mm) of the cheek teeth of *Selenoportax lydekkeri* (data taken from Pilgrim, 1937, 1939; Akhtar, 1992 and Khan, 2008). In parenthesis: locality code from where the specimen was collected; *: studied specimens.

Number	Position	Length	Width	W/L
PUPC 86/6 (H7)*	M_2 (sin)	27.0	16.0	0.59
PUPC 95/21 (H7)*	M_3 (sin)	36.0	15.0	0.41
PUPC 85/24 (H23)*	M_3 (sin)	30.0	14.0	0.46
PUPC 85/106 (H7)*	M_2 (sin)	33.3	15.0	0.45
PUPC 96/8 (H7)*	M_3 (dext)	39.0	15.0	0.38
PUPC 95/1 (H23)*	M^2 (sin)	28.0	27.0	0.96
PUPC 85/26 (H6)*	M_1 (dext)	25.5	12.0	0.47
PUPC 87/144 (H7)*	M_1 (dext)	27.0	16.0	0.59
AMNH 19981	M_2 (sin)	32.5	19.0	0.58
AMNH 19908	M_3 (sin)	37.5	19.5	0.52
AMNH 29916	M_3 (sin)	37.5	20.5	0.52
AMNH 29966	M_3 (dext)	39.0	18.0	0.46
AMNH 19933	M^2 (sin)	30.0	30.0	1.0
AMNH 29846	M^2 (sin)	28.0	28.5	1.01
AMNH 19986	M^2 (sin)	29.0	27.0	0.93
GSI B213	M^2 (sin)	29.0	27.0	0.93
AMNH 19957	M_1 (dext)	28.5	18.5	0.64
GSI B211	M_1 (dext)	25.0	17.0	0.68

Diagnosis: A very large-sized *Pachyportax*, with quadrate upper molars and strong entostyle much extended transversely; the crown is not constricted at the apex, relatively strong styles and ribs, enamel moderately thick and rugose with traces of cement. Crown is narrow at the base and broad at the apex in *Selenoportax* whereas in *Pachyportax* the crown is not constricted at the apex. Entostyle is strong and much extending transversely in *Pachyportax* while in Selenoportax it is not much extending transversely. In *Pachyportax*, posterior median rib is flattened whereas in *Selenoportax* it is strong like anterior median rib.

Description: The second upper molars are finely preserved lingually (Fig. 5(6)). The cingulum is absent and all principal cusps (protocone, paracone, metacone and hypocone) are present. On the buccal side of the paracone, the parastyle is present, whereas the anterior median rib and the mesostyle are also well developed. The inner portion of the cusp is well preserved and pointed in the middle, with two sloping cristae running anteroposteriorly (e.g., Fig. 5(6)). Third upper molars are quadrangular in shape (Fig. 5(7)); their lingual cones are not connected with each other, showing an early stage of wear. The entostyles are strongly developed and extend transversely. The dentine of the lingual cusps is separated from that of the buccal ones and is only connected with the praeparacristae. The molars are subhypsodont and narrow crowned. The styles are well developed and the mesostyle is more developed than the parastyle and the metastyle (Fig. 5(7)). The second lower molars are extremely hypsodont and narrow crowned. The metaconid and the entoconid are slightly damaged at the apex while all ribs and stylids are well developed. The third molars are lower and well preserved (Fig. 5(8)). The height of the

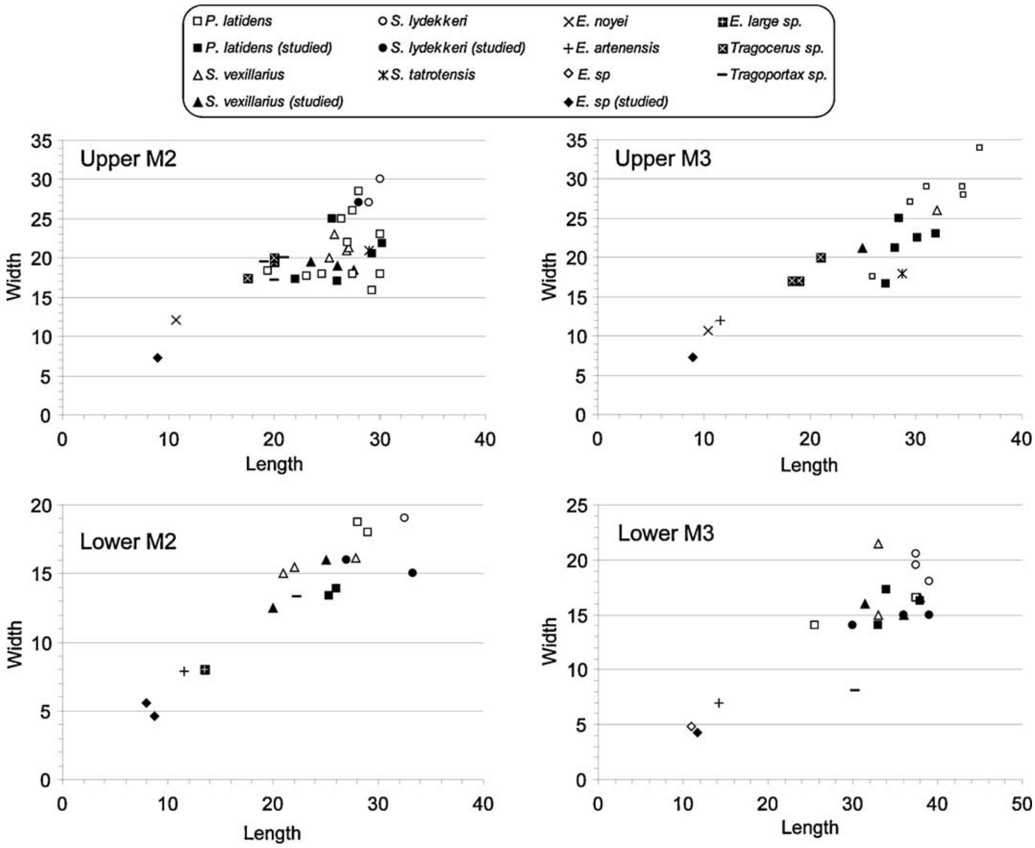

Fig. 6. Size variation in the described species of Hasnot boselaphines.

molars is comparatively greater than its transverse width. The cement layer is absolutely absent, whereas the principal conids and the ectostylid are well developed. The metaconid is spindle shaped with an inflated median part, which produces the moderately strong anterior median rib of the metaconid (Fig. 5(8)). The roughness of the enamel is also variable, owing to weathering.

Discussion: The genus *Pachyportax* was erected by Pilgrim in 1937 when he applied the generic name *Pachyportax* to all the specimens which were described and figured by Lydekker in 1876 under the name *C. latidens.* He determined two species, *P. latidens* (Lydekker) and *P. nagrii*, one subspecies *P. latidens dhokpathanensis* and one variety *P. latidens* var. *dhokpathanensis*. Akhtar (1995) synonymized the subspecies *P. latidens dhokpathanensis* with the species *P. latidens* (Lydekker) and added the new species *P. giganteus* to the genus. The genus was originally founded to incorporate the large boselaphines of the Siwaliks, which probably have a closer ancestry to the Bovini than *Tragoportax*. The type species originated in the Late Miocene, possibly extending its range into the Pliocene. The type specimen of *P. latidens* is an upper molar, but it is best represented by a cranium described by Pilgrim (1939) and stored in the Calcutta Museum (India), a cast of which is found in London (BMNH M26573). A second species, *P. nagrii* Pilgrim, 1939, occurred earlier in the Siwalik layers. The holotype is a hornless female cranium, which is not adequately differentiated from *S. vexillarius*. A very similar boselaphine to *Pachyportax* is *Parabos* Arambourg and Piveteau of which the type and only species, *Pachyportax* or *Parabos cordieri,* comes from the Lower Pliocene of Montpellier, southern France. According to Gromolard's (1980) revision of *Parabos*, it may be assumed that this generic name is a senior synonym for *Pachyportax*. Around the end of the Late Miocene, boselaphines gave way to bovini or bovine-like bovids (Gentry, 1999).

Table 4
Comparison study of the entostyles, styles, median ribs, and enamels of *Selenoportax tatrotensis* and *Selenoportax vexillarius* (*: taken from Akhtar, 1992).

Species	Position	Entostyle	Style	Median ribs	Enamels
*S. tatrotensis** (PUPC 87/19)	M^2	Strong	Slightly weak	Weak	Less rugose
*S. tatrotensis** (PUPC 87/19)	M^3	Strong	Slightly weak	Weak	Less rugose
S. vexillarius (PUPC 00/53)	M^2	Strong	Strong	Strong	Rugose
S. vexillarius (PUPC 96/39)	M^2	Strong	Slightly weak	Weak	Less rugose
S. vexillarius (PUPC 01/23)	M^2	Strong	Slightly weak	Strong	Less rugose
S. vexillarius (PUPC 87/199)	M^3	Strong	Strong	Weak	Rugose

To date, a complete skull of *P. latidens* has not been recovered yet.

The cheek teeth of the studied material are clearly different from a giraffid in that the teeth are too hypsodont, their entostyles and ectostylids are too large, and the central fossettes on the occlusal surface are isolated from the exterior, even in the middle wear of the molars. The studied specimens definitely belong to a boselaphine bovid, and they are too large to be accommodated in *Tragoportax cyrenaicus*. They show all the basic features of the genus *Pachyportax*: the strongly hypsodont and quadrate upper molars, having extended transversely entostyles, with relatively strong styles and ribs. The studied specimens are of appropriate size to match that of *P. latidens*. The most important recognized feature of the upper molars of *P. latidens* is the transverse extension of the entostyle as mentioned by Pilgrim (1937). It varies to some extent in its longitudinal dimension towards the lingual side; in some it is slightly broader. The studied specimens present all the distinguished features of the species. These specimens also provide additional information about the M^2 and M^3 of the genus. The M^2 and M^3 compare well with the referred specimens present in AMNH, and described by Pilgrim (1937). They resemble in all the structural details like cusps, entostyle, styles, and median ribs. The only difference between the molars is found in their dental measurements, but this difference is too low to be considered of taxonomic importance. Hence, on the basis of the above-mentioned similarities the studied specimens are being referred to *P. latidens*. To date, the M_3 of *P. latidens* had been unknown, and they are described here for the first time (Table 5; Fig. 6).

Table 5
Comparative measurements (in mm) of the cheek teeth of *Pachyportax latidens* (data taken from Pilgrim, 1937, 1939, and Gentry, 1999). In parenthesis: locality code from where the specimen was collected; *: studied specimens.

Number	Position	Length	Width	W/L
PUPC 96/42 (H2)*	M^3 (sin)	30.2	22.5	0.74
PUPC 01/24 (H7)*	M^3 (sin)	28.4	25.0	0.88
PUPC 96/38	M^3 (sin)	34.4	29.0	0.84
GSI B219	M^3 (sin)	34.5	28	0.81
AMNH 29914	M^3 (sin)	36.0	34.0	0.94
AMNH 29913	M^3 (sin)	31.0	29.0	0.93
AMNH 19730	M^3 (sin)	29.5	27.0	0.91
PUPC 83/840 (H4)*	M^3 (dext)	31.9	23.0	0.72
PUPC 87/88 (H4)*	M^3 (dext)	27.2	16.6	0.61
PUPC 04/15 (H3)*	M^3 (dext)	28.0	21.2	0.75
PUPC 00/87	M^3 (dext)	25.9	17.6	0.67
AMNH 29913	M^3 (dext)	31.0	29.0	0.93
AMNH 19730	M^3 (dext)	29.5	27.0	0.91
PUPC 98/59 (H23)*	M^2 (dext)	22.0	17.3	0.78
PUPC 96/40	M^2 (dext)	19.4	18.4	0.94
PUPC 96/3	M^2 (dext)	27.0	22.0	0.81
PUPC 86/37	M^2 (dext)	27.4	18.0	0.65
PUPC 86/36	M^2 (dext)	30.0	23.0	0.76
PUPC 83/718	M^2 (dext)	27.4	26.0	0.94
PUPC 83/646	M^2 (dext)	30.0	18.0	0.6
PUPC 83/744 (H8)*	M^2 (dext)	30.2	21.9	0.72
PUPC 86/210 (H8)*	M^2 (dext)	26	17.1	0.65
PUPC 00/100 (H14)*	M^2 (dext)	25.5	25.0	0.98
PUPC 04/14	M^2 (dext)	29.3	20.6	0.70
PUPC 98/60	M^2 (dext)	23.1	15.9	0.68
PUPC 97/103	M^2 (dext)	24.5	17.7	0.72
PUPC 86/203	M^2 (dext)	26.4	17.9	0.67
AMNH 29964	M^2 (dext)	28.0	25.0	0.89
AMNH 19730	M^2 (dext)	28.5	28.5	1.0
PUPC 99/21 (H23)*	M_2 (sin)	26.0	13.9	0.53
PUPC 86/24 (H6)*	M_2 (dext)	25.3	13.4	0.52
GSI B268	M_2 (dext)	29.0	18.0	0.62
PUPC 04/16 (H15)*	M_3 (dext)	34.0	17.3	0.50
PUPC 86/7 (H20)*	M_3 (sin)	33.0	14.0	0.42
PUPC 96/41 (H11)*	M_3 (sin)	38.0	16.3	0.42
PUPC 96/43*	M_3 (sin)	25.5	14.0	0.54
AUH 266	M_2 (dext)	28.1	18.7	0.66
	M_3 (dext)	37.5	16.5	0.44

Genus ***Eotragus*** Pilgrim, 1939

Eotragus sp.

Stratigraphic Range: Lower and Middle Siwaliks.

Localities: Hasnot (H 16, 18; Fig. 2), Jhelum district, the Punjab province, Pakistan.

Material examined: A fragment of left maxilla having $M^{1\text{-}3}$ (PUPC 04/23), a fragment of left mandible having $M_{1\text{-}2}$ and a broken anterior part of M_3 (PUPC 04/24), a fragment of right mandible having $M_{2\text{-}3}$ (PUPC 05/11).

Description: A small-sized boselaphine with a small ectostylid, no diagonal fold on the rear wall of the protoconid, a weak metastylid and a weak anterior rib on its lingual wall. The buccal walls of the upper molars, especially the metacone areas, are more inclined. Because of this metaconal inclination, the metastyle is rotated in relation to the anteroposterior tooth axis, and thus it is situated more lingually.

PUPC 04/23 is a left maxilla fragment with a length of 27.0 mm and a width of 14.0 mm (Fig. 5(9)). The vertical height of the maxilla beneath the M^2 is 8.2 mm. A small piece of the palate is also attached to the preserved maxillary bone. The teeth are situated obliquely so that their buccal walls do not line up (Fig. 5(9)). In M^1, all the major cones are finely preserved. The molar presents a middle stage of wear and along the fossettes dentine is visible. The protocone is more projected lingually, having a long postprotocrista. The median ribs and styles are weakly developed and the entostyle is absent. The molar is brachydont and narrow crowned; it shows the confluence of the postparacrista, the praemetacrista, the postmetaconule crista and postmetacrista. The metacone is inclined relatively to the paracone, with the metastyle being situated more lingually. The buccal face of the metacone is inclined medially at a moderate angle, while the buccal faces of the fossettes are slightly steeper. The enamel is finely rugose and the cingulum is absent. The M^2 and M^3 are approximately equal in size (Fig. 5(9)). The M^2 is well preserved except from the paracone, which is damaged at the apex. The anterior rib is stronger than the posterior one. The parastyle, the mesostyle and the metastyle are medium-sized. The M^3 is damaged buccally; the paracrista and metacrista are absent (Fig. 5(9)).

PUPC 05/11 is a practically unworn specimen and seems to belong to a young individual (Fig. 5(10)). The mandibular height beneath the M_2 crown is 12.6 mm. The M_2 and M_3 are smaller than specimen PUPC 04/24. All the crown features are preserved and the teeth show the confluence of the metacristid, the protocristid and the postmetacristid (Fig. 5(10)). In M_3, a well-developed hypoconulid is present and its height is comparatively lower than the other major conids. The fossettes are extremely narrow and their buccal faces are slightly steeper than their lingual ones (Fig. 5(10)). PUPC 04/24 is a left mandible fragment having M_{1-2} and a broken M_3. The length of the mandibular ramus is 30.0 mm and its width is 16.0 mm. The height of the mandible beneath the M_1 is 15.7 mm. The teeth present a number of fractures owing to seasonal weathering. M_1 presents a middle stage of wear and a small ectostylid is attached posteriorly to the base of the protoconid. The M_2 is damaged posteriorly and the cristids of the hypoconid and the entoconid are not differentiated. A crack is also present along the transverse valley.

Discussion: By their physical aspect, PUPC 04/23 and PUPC 04/24 specimens probably belong to the same individual. The increased selenodonty with conical cusps, ectostylids, and anterior transverse flange clearly indicate a Middle Miocene representative of a small-sized Boselaphini. Several morphological features, such as the crests of the cusps join up earlier in wear; styles, stylids and ribs are less bulky; obliquely situated hypoconulid and weaker cingula are characters corresponding to the genus *Eotragus* (Gentry, 1999; Rössner, 2006). The morphological features of the studied specimens, such as the obliquely situated teeth without lined up buccal walls and the confluence of the metacristid, protocristid and postmetacristid allow us to include them in to *Eotragus,* but more material is needed for precise species identification.

The dentitions of *E. artenensis*, *E. sansaniensis*, and *Eotragus* sp. from Bunyol have less inclined buccal walls, larger lingual cingula, larger entostyles, and larger molar metaconules than *E. noyei* recovered by Solounias et al. (1995) from the Lower Siwaliks. *E. artenensis* from Artenay, France, is similar to *E. noyei* and approximately of the same age (Solounias et al., 1995). *E. cristatus* from Velheim is approximately 15.5 Ma old, whereas *E. haplodon*, which is probably conspecific with *E. sansaniensis,* is known from the Austrian locality of Goriach (15 Ma, MN6, Mein, 1989; Steininger et al., 1989). Hamilton (1973: pl. 13, fig. 1) described *Eotragus* sp. from Gebel Zelten, Libya, which was reported to have an age of 16.5 Ma (Mein, 1989). Tchernov et al. (1987: fig. 2G, H) reported the occurrence of *E.* cf. *sansaniensis* in the Negev of Israel. Also, *E. halamagaiensis* was reported by Ye (1989) from the middle Miocene of China. Moya-Sola (1983: pl. 1, figs. 1, 2) reported *Eotragus* sp. from Can Canals and Bunyol (Valencia), and *Eotragus* cf. *artenensis*, from Corcoles, Spain. The latter is probably of Middle Miocene age. Sansan (France) is a 14.5 Ma old locality and is the type locality of *Eotragus* (*E. sansaniensis*; Lartet, 1851; Filhol, 1891; Ginsburg, 1963; Heissig, 2006). Thomas (1984) reported *Eotragus* sp. from the Gaj formation of Sind, which is equivalent to the Chinji formation of the Siwaliks. Recently, Khan et al. (2008a) reported the presence of *Eotragus* sp. from the Early Miocene sediments of the Dhok Bin Mir Khatoon, Pakistan. This finding has approximately the same age (16.5 Ma; Mein, 1989) as the *Eotragus* sp. reported by Hamilton (1973) from Gebel Zelten, Libya, but the presence of this taxon in the Hasnot (7 Ma; Pilbeam et al., 1977) considerably extends its geographical distribution.

Table 6
Comparative measurements (in mm) of the cheek teeth of *Eotragus* sp. (data taken from Alfarez et al., 1980; Solounias et al., 1995; Khan et al., 2008a). In parenthesis: locality code from where the specimen was collected; *: studied specimens.

Number	Position	Length	Width	W/L
PUPC 04/23 (H16)*	M^1 (sin)	8.0	7.0	0.87
	M^2 (sin)	9.0	7.3	0.81
	M^3 (sin)	9.0	7.3	0.81
PUPC 04/24 (H16)*	M_1 (sin)	8.0	5.0	0.62
	M_2 (sin)	8.0	5.6	0.7
PUPC 05/11 (H18)*	M_2 (dext)	8.7	4.6	0.52
	M_3 (dext)	11.7	4.3	0.36
PC-GCUF 08/01	M_3 (dext)	11.0	4.84	0.43
PUPC 69/272	M_1	13.5	8.0	0.59
	M_2	13.5	8.0	0.59
GSP-Y 41459	M^2 (sin)	10.7	12.1	1.13
GSP-Y 41459	M^3 (sin)	10.4	10.7	1.02
CO-483	M^1	10.1	11.3	1.11
CO-484	M^1	10.1	10.5	1.03
CO-485	M^1	10.7	11.3	1.05
CO-487	M^3	11.5	11.9	1.03
CO-488	M^3	11.6	12.0	1.03
CO-489	M_1	9.4	6.2	0.65
CO-490	M_2	11.6	7.9	0.69
CO-491	M_3	14.2	7.0	0.49

E. noyei was erected by Solounias et al. (1995) on the basis of a cranial specimen, a horn core (type specimen) and five postcranial specimens recovered from the Lower Siwaliks, with an estimated age between 18.0 and 18.3 Ma (Barry and Flynn, 1989). To date, it is considered as the oldest and smallest species of the genus (Solounias et al., 1995). Morphologically and metrically, the studied specimens are clearly comparable with specimen GSP-Y 41459 recovered by Solounias et al. (1995), and with specimens PC-GCUF 08/01 and PUPC 69/272 recovered by Khan et al. (2008b) from the Lower Siwaliks (Table 6; Fig. 6). The size of the animal found in the Middle Siwaliks is smaller than the animal found in the Lower Siwaliks (Solounias et al., 1995; Khan et al., 2008b), and therefore, probably it can be considered as the smallest boselaphine in the world (Fig. 6; Table 6).

6. Synonymisation of *Selenoportax* species

In 1937, Pilgrim raised the genus *Selenoportax* based on a collection from various Middle Siwalik localities in Pakistan and India and added two species in it, *S. vexillarius* and *S. lydekkeri*. According to Gentry (1974), the systematic position of *S. lydekkeri* is uncertain. Contrary to this point of view, Akhtar (1992) included not only *S. vexillarius* and *S. lydekkeri* from the Middle and Upper Siwaliks in the genus *Selenoportax*, but added two new species: *S. dhokpathanensis* and *S. tatrotensis*, the former being based on a damaged cranium (PUPC 86/248) and the later upon a maxillary portion bearing right P^3-M^3 and left P^4-M^3 (PUPC 87/19).

Akhtar (1992) in his PhD thesis compared *S. dhokpathanensis* (PUPC 86/248) with *S. vexillarius* but not with *S. lydekkeri* and considered that its gigantic size clearly made it different from *S. vexillarius*. *S. dhokpathanensis* has the same characteristics as *S. lydekkeri*, and both of them are larger in size than *S. vexillarius*. Moreover, a large number of *S. vexillarius* and *S. lydekkeri* cheek teeth have been described until now, though not even one single molar has been described for the species *S. dhokpathanensis* yet. Although, a complete or part of a *S. lydekkeri* skull with dentition has not been found yet, the size of specimen PUPC 86/248 is comparable with the potential size of a *S. lydekkeri* skull. The characters such as crown flare and enamel folding are insufficiently diagnostic, as such features are highly variable even within a single individual (Bibi, 2007). Thus, *S. dhokpathanensis* is considered a junior synonym of *S. lydekkeri*.

The description of *S. tatrotensis* was based on the upper premolars and molars: strong and extended transversely entostyles and ectostylids, styles that are slightly weaker and less divergent, weaker median ribs and less rugose enamel with traces of cement. All these variations can be observed in *S. vexillarius* and metrically the specimen PUPC 87/19 falls within the range of this species, which evidently supports its inclusion within *S. vexillarius* (Tables 2 and 3; Fig. 6). Therefore, we consider that the genus *Selenoportax* consists only of two valid species in the Siwaliks: *S. vexillarius* and *S. lydekkeri*, the former being the smaller one (Fig. 6).

7. Paleoecology

7.1. Vegetation record

The boselaphine remains in this study document the occurrence of *Selenoportax*, *Pachyportax* and *Eotragus*, which testify a change in the composition of the Siwalik boselaphine community. The taxonomic composition of the Hasnot indicates an arid palaeoclimate that nevertheless supported pockets of forested areas. The oxygen isotopic record of the Late Miocene indicates significant changes in the patterns of precipitation beginning at 9.2 Ma toward a drier and more seasonal climate (Barry et al., 2002), and thus resulting into the extinction of various species of medium-sized boselaphines in the Siwaliks. The carbon isotope record demonstrates that after 8.1 Ma significant amounts of C_4 grasses began to appear and by 6.8 Ma floodplain habitats included extensive C_4 grasslands. Plant communities with predominantly C_3 plants were greatly diminished after 7 Ma and those with predominantly C_4 plants, which would have been open or grassy woodlands, appeared as early as 7.4 Ma (Cerling et al., 1997; Barry et al., 2002). All the collected specimens come from sediments spanning from 7 to 5 Ma (Pilbeam et al., 1977; Barry et al., 1982, 2002) and show an increase in size, hypsodonty and degree of molarization, suggesting a move towards more fibrous C_4 diets and more open habitats. It is considered that, while dietary overlap among savanna grazers can be quite high during the wet growing season, niche differentiation among such species is mainly marked during, or even restricted to the dry season (Bell, 1969; Dekker et al., 1996; Schuette et al., 1998; Traill, 2004).

7.2. Paleoclimate and diet adaptations

The larger-sized savanna species are able to differentiate their diets, incorporating greater quantities of the taller, more fibrous, and less protein rich grasses that remain in greater abundances during the dry season (Bell, 1969). This can be largely attributed to the fact that larger animals have relatively lower protein metabolic requirements than smaller ones (Hungate et al., 1959; Bell, 1969). Studies demonstrating a strong negative relationship between hypsodonty and mean annual precipitation (Damuth et al., 2002; Fortelius et al., 2002, 2006), suggest that the high-crowned teeth are indicative of lessened rainfall.

The fauna of the Hasnot is indicative of such lessened rainfall and local environmental aridification which seemed to be the favorable habitat for the boselaphines, especially *Selenoportax* and *Pachyportax* (high crowned herbivores). The functional morphology of *Selenoportax* and *Pachyportax* teeth had been adjusted to the exploitation of more open habitats as their teeth became more complex than other contemporaneous large herbivores with the development of folds and pillars, and round wearing cusps (see Bibi, 2007).

7.3. Biostratigraphy and paleobiogeography

The specific richness of boselaphines in the Hasnot sediments is remarkable. *Eotragus* is known from the Late Early Miocene of Europe (15 Ma, MN6; Mein, 1989; Steininger et al., 1989; Gentry et al., 1999), Pakistan (18–5 Ma; Solounias et al., 1995; Khan et al., 2008a; this paper) and from the Middle Miocene of China (16 Ma; Ye, 1989). Nevertheless, the genus is reported here for the first time from the Middle Siwaliks of Pakistan (7–5 Ma). The age of the Hasnot has been reported to be between 7 to 5 Ma (Pilbeam et al., 1977; Barry et al., 2002). The new findings of *Eotragus* extend the stratigraphic range of the genus from the Lower Siwaliks to the Middle Siwaliks (18.3 Ma to 5.0 Ma) and document the occurrence of the smallest *Eotragus* in the Middle Siwaliks of Pakistan (Fig. 6).

The *Selenoportax* record indicates that it was present in the Siwaliks from the Late Middle Miocene to the Pliocene (Akhtar, 1992; Barry et al., 2002). The specimen collected from the Tatrot formation (Akhtar, 1992) extends the range of *Selenoportax* from 10.3 to 2 Ma, contrary to the findings of Barry et al. (2002) who recognised a maximum range of 10.3 to 7.9 Ma for this taxon. Nevertheless, some uncertain occurrences are mentioned out of the Siwaliks. Solounias (1981) referred a *Selenoportax* horn core from Pikermi; according to him the material is not diagnostic enough for a more specific determination. So, this supposed occurrence of a single horn core cannot be taken as indicative for the presence of *Selenoportax* in Europe. Qiu and Qiu (1995) list *Selenoportax* sp. from the Lufeng fauna (Chinese Miocene), age of 11.1–8.0 Ma (Steininger, 1999; Flynn and Qi, 1982). These specimens represent the sole record of *Selenoportax* from the Miocene of Northern and Central Asia (Tedford et al., 1991; Nakaya, 1994; Qiu and Qiu, 1995).

Pachyportax, on the other hand, is considered as a typical Late Miocene taxon. *Pachyportax* occurs in the Nagri and the Dhok Pathan zones of the Siwaliks, until *Proamphibos* replaces it soon after the start of the Tatrot. Hence, a Latest Miocene date around 7.0 Ma (Barry et al., 1991) would be considered as a possible date for a fauna containing *P. latidens*. The French boselaphine *Parabos cordieri* resembles *Pachyportax* and occurs in the European mammal zone MN 14 (Mein, 1989), which is equal to the Early Pliocene; hence, it is younger than most *Pachyportax* species. Gentry (1999) recovered six boselaphine specimens from the Baynunah Formation of the United Arab Emirates and assigned them to *P. latidens* and *Tragoportax cyrenaicus*. Biochronological estimates for this formation range from 8 to 6 Ma (Whybrow and Hill, 1999), which is about the same age as the Hasnot.

In Africa, the faunas of Ngeringerowa, Namurungule, and Nakali, dated to 10–8 Ma and the faunas from the Mpesida, dated to 7–6 Ma lack *Pachyportax* and *Selenoportax* (Hill et al., 1985; Nakaya, 1994; Kingston et al., 2002). Also, these taxa are absent from nearby localities of the same age, such as the Afghani localities of Tagar and Marageh (Iran), dated at 8.7–8 Ma (Sen et al., 1997) and 9.5–7 Ma (Bernor, 1986), respectively.

8. Conclusion

During the Late Miocene, the Middle Siwaliks were mainly characterized by the presence of several boselaphine taxa which remained restricted to Southern Asia, south of the Himalayas. Large-sized boselaphines such as *S. vexillarius*, *S. lydekkeri*, *P. latidens*, and the small boselaphine *Eotragus* sp. were identified from the area of the Hasnot. The presence of *Selenoportax* and *Pachyportax* in the Middle Siwaliks of the Subcontinent implies that at this time, the Himalayan Mountains acted as a barrier in the dispersal of the fauna out of Southern Asia prior to this time, isolating the Siwalik faunas (Barry et al., 1982; Bernor, 1984; Brunet et al., 1984) from the nearby Greco-Irano-Afganian province. The range contraction of these genera suggests that they remained confined in this southern area and should be ascribed to a separate faunal province.

The taxonomic composition of the Hasnot fauna indicates that during the Late Miocene (middle Middle Siwaliks, Middle Turolian for Europe) an arid palaeoclimate had been established in the Siwaliks area which nevertheless supported pockets of forested areas. This is in agreement with previous works on stable isotopes. This shift to a drier and more seasonal climate in the Siwaliks caused the extinction of a number of medium-sized boselaphine species, and induced the establishment of high crowned large boselaphines such as *Selenoportax* and *Pachyportax*.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.geobios.2009.04.003.

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