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Research Article

Systematic Study of Boselaphine Remains from the Late Miocene of Hasnot, Pakistan

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MTW, AMK and SK perceived the study. AI and MA helped in taxonomic identification. MTW and RMA wrote the manuscript. SK wrote the description of specimen.

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Bovids, Palaeoenvironment, Boselaphini, Mammals, Siwaliks

Abstract | Current study deals with the systematic investigations of Boselaphine specimens belonging to genera *Pachyportax* and *Selenoportax*. The available information on both taxa is scanty and only few specimens are known for both genera especially *Pachyportax*. The members of both genera have medium to large sized body with strong hypsodonty of teeth representing grazing on coarse grasses and shrubs in the Late Miocene Siwalik habitats of Potwar Plateau. At the apex of molar, crown is narrow and represents selenodonty in *Selenoportax,* while a broader crown in *Pachyportax* which indicates strong hypsodonty. The present sample add valuable information on systematics, dental morphology and dietary habits of the Late Miocene (7-5 Ma) boselaphines which are represented today by their living kin *Boselaphus tragocamelus* and *Tetracerus quadricornis*.

Novelty Statement | This study adds new samples belonging to two extinct Bovini genera viz. Pachyportax and Selenoportax. *P. nagri* has been scarcely reported from the late Miocene of the Siwaliks.

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Introduction

The outcrops of Siwaliks (Figure 1) produced an exclusive and diversified fauna of vertebrates. These fossiliferous ranges (Middle Miocene to Early Pleistocene) extend from the Salt Range in the south to the Margalla Hills in the north, and from the Jhelum River in the east to the Indus on the west (Barry *et al*., 2002).

Late Miocene of the Siwaliks has been marked by many environmental changes and consequent faunal turnovers which resulted in the niche expansion of ruminants as compared to Middle Miocene hence yielded the increased diversity of the ruminants (Colbert, 1935; Pilgrim, 1937, 1939; Gentry, 1970; Gentry and Heizmann, 1996; Barry *et al*., 2002). Colbert (1935) reported 26 bovid species while Pilgrim (1937, 1939) reported 75 bovid species from the late Neogene. Some of the species were erected due to slight variations like styles/stylids, crests and median ribs (Akhtar, 1992; Pilgrim, 1937). In the Late Miocene, new forms of bovids like boselaphines were noted along with other related fauna (Bibi *et al*., 2009).

The diversified faunal elements of Boselaphine are mostly present in the Late Miocene of Pakistan which

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includes the Dhok Pathan Formation (Fm.) and some of Tatrot Fm (Figure 1) as well. A high diversity of Bovids has been reported from Dhok Pathan Formation (Pilgrim, 1937, 1939; Akhtar, 1992; Dennell, 2008). The definite existence of this family is reported around 18.5 Ma in Pakistan (Behrensmeyer and Barry, 2005). Tribe boselaphini is one of the significant and highly reported bovid recovered from Middle Siwaliks (Gentry, 1970; Khan *et al.*, 2009). Only two relatives of this family are living; *Tetracerus quadricornis* and *Boselaphus tragocamelus* (Khan *et al.*, 2008).

Boselaphines can further be categorized into two groups, the first are the medium sized genera, *Miotragocerus* (Stromer, 1928; Gentry, 1978) and *Tragoportax* (Pilgrim, 1937) while the second includes the large bodied genera *Selenoportax* (Pilgrim, 1937) and *Pachyportax* (Pilgrim, 1937, 1939; Barry *et al.*, 1982, 1991, 2002; Bibi, 2007, 2009). The former is well known from the Turolian faunas of the Irano-Greco as well as from the Hasnot (Figure S1) and have been considered as wide spread genera along with *Gazella* (Moya-Sola, 1983; Thomas, 1984; Bernor, 1986; Gentry and Heizmann, 1996; Khan *et al.*, 2009).

Selenoportax is a large sized boselaphine while *Pachyportax* is considered as of gigantic sized form (Gentry *et al.*, 1999). Heissig (1972) reported the *Selenoportax* as more diverse and advanced form reported from the Chinji formation of the Siwaliks by Thomas (1984). *Selenoportax* and *Pachyportax* have been reported from Middle and Upper Siwaliks of Pakistan (Pilgrim, 1937, 1939; Akhtar, 1992; Barry *et al.*, 2002; Nanda, 2008; Khan *et al.*, 2009). Both of these genera are more abundant in the Hasnot outcrops (7-5 Ma) (Age after Pilbeam *et al.*, 1977; Johnson *et al.*, 1982; Barry *et al.*, 1982; Barry, 1987).

Geological context

Hasnot (Lat. 32^0 49$^`$ N: Long. 73$^0$ 18$^`$ E) is situated in 70 kilometers west of the main city of Jhelum in northern areas of Pakistan around the Potwar Plateau representing highly divers faunal element of Dhok Pathan Fm (Figure S1). In the peripheries of Hasnot village, a wide range of Neogene freshwater sedimentary rocks are exposed. It represents one of the most complete sequences of the Siwaliks group and provide abundant records of vertebrate faunal elements. Lithologicaly, the sediments show characteristics (Orange brown sandstone, clay and conglomerates) of Upper Dhok Pathan Formation. The nature of fluvial deposits of Hasnot are characterized by waters channels, bogs, forests and backwoods (Barry *et al.*, 2002). Twenty-seven fossiliferous localities are reported around the Hasnot by Colbert (1935). The thickness of these sedimentary rocks is 180 m.

The outcrops of Hasnot mostly yield scattered bones and teeth of vertebrates. Most of the samples are found as broken or disarticulated and a single complete skeleton has to be recorded yet. Most of the fossils are being collected from the fossil pockets, mostly referred as localities by surface collection as well as partial excavation. Bovids are found to be abundant among all the Hasnot fauna including Rhinos, Hipparions, Suids, Cervids, etc. (detail has been given in the text).

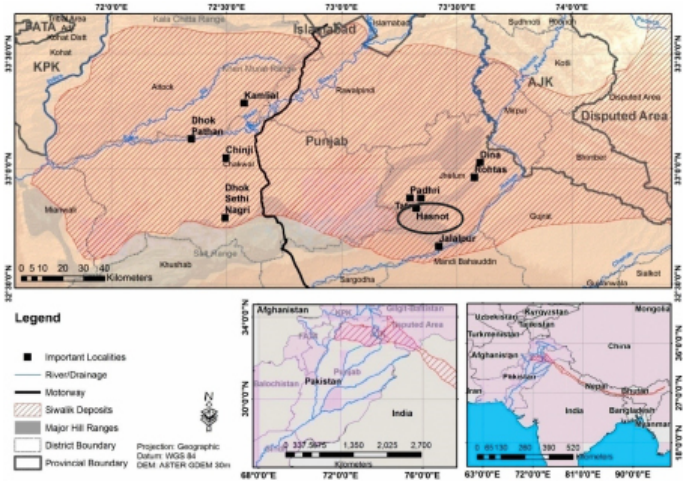

Figure 1: Map of Potwar Plateau of Pakistan with reported localities (modified after Behrensmeyer and Barry, 2005).

Abbreviations

PUPC, Punjab University Palaeontological Collection; AMNH, American Museum of Natural History; GSP, Geological Survey of Pakistan; GSI, Geological Survey of India; L, length; M^x, upper molar; M$_x$, lower molar; Fm. Formation; P$_x$, Lower Premolar; P^x, Upper Premolar.

Materials and Methods

New boselaphine specimens were recovered from various localities of Hasnot (Table S1). Most of the collection was done during the field trips and surface collection method was adopted for the exposed strata. Few of the embedded specimens were excavated by using hammers, chisels, knives and fine needles. Then all the samples were taken to laboratory for further processing where the samples were washed and cleaned by using micro-rotatory drill (Champion M-3) equipped with carbide burrs to clean the dirt attached to the samples. Broken parts were assembled carefully by using adhesives. The samples were catalogued and allotted a number which depicts the collection years and serial number (e.g. 15/381). Digital metric Vernier calipers was used to take the measurements in millimeters (mm). Length and width were taken. Heights were measured on the Metastylid/ Mesostyle. For the terminology of the dentition, Gentry *et al.* (1999) was used as standard. For the comparison, available data of AMNH, BMNH, GSP and PUPC used. All the studied specimens are housed in Palaeoclimate and Environmental Biology Laboratory, University of the Punjab, Lahore, Pakistan.

The species level identification was done on the premise of morphological determination and its correlation with detailed information of this species.

Associated fauna of hasnot

Fauna of Hasnot includes Carnivora, Rodentia, Cercopithecidae, Proboscidea, Suidae, Rhinocerotidae, Equidae, Anthracotheridae, Cervidae, Bovidae, Giraffidae and Tragulidae (Mathew, 1929; Pilgrim, 1937, 1939; Bernor and Hussain, 1985; Wolf *et al*., 2013).

Systematic palaeontlogy

Family: Bovidae Gray, 1821
Subfamily: Bovinae Gill, 1872
Tribe: Bovini Gray, 1821
Genus: Pachyportax Pilgrim, 1937
Pachyportax latidens (Lydekker) Pilgrim, 1937.
Plate I, Figures. 1a-4c, 8a-8c; Plate II, Figures. 10a-14c, 16a-16c

Holotype

A right upper M^3 (GSI No. B219)

Diagnosis

A large sized bovid with transversely extended strong entostyles and quadrate upper molar representing extreme hypsodonty. No constriction in crown at apex, ribs and styles strong, rugosity while thickness of enamel moderate with slight cementation. Crown is narrow at the base in *Selenoportax* while in *Pachyportax*, crown is not constricted. Basal pillar is strong. *Pachyportax* represents a flattened rib while in *Selenoportax*, it is strong (Khan *et al*., 2009). However, Bibi (2007) argues that *Selenoportax* and *Pachyportax* do not show considerable differences in dentition and can only be diagnosed by horn cores.

Generic distribution

The genus *Pachyportax* is present in Middle Siwaliks including the Nagri and Dhok Pathan formations (Lydekker, 1876; Pilgrim, 1937, 1939) and also distributed in Arabian Peninsula (Gentry *et al*., 1999).

Localities

Localities are mentioned in the Supplementary information (Table S1; Figure S1).

Description

All the second upper molars are partially preserved. Cingulum is absent in all the samples except PUPC 17/417 which shows precingulum. All the principal cones are present while the metacone is damaged in one molar. Strong and divergent basal pillars are present which extend transversely while mesostyles are well developed. All the upper molars show quadrate appearance. PUPC 17/419 and PUPC 17/417 represent an early stage of wear and more pointed cusps. Anterior median ribs are present except in PUPC 15/381. The wrinkling of enamel is equally present on lingual and labial sides. Lingual cusps are lower in comparison to labial cusps. Postprotocrista and praeprotocrista are present alongside the protocone. The posterior and anterior central cavities are present. The protocone in 3rd upper molar (PUPC 17/420) is damaged. The third molars represent middle to late stage of wear with uniform wrinkles. Hypoconulid in lower 3rd molar (15/383) is present but slightly damaged posteriorly. Median basal pillar is strongly developed and all the conids are intact representing wide cavities. Stylids are less prominent and tooth represent middle stage of wear.

Comparison and Discussion

Pilgrim (1937) erected the genus *Pachyportax* when he ascribed this name to all the specimen described by Lydekker (1876) under *Cervus latidens*. He further gave two species, *Pachyportax latidens* and *Pachyportax nagrii*. The genus incorporated large sized boselaphine species from the Siwalik group, which were considered as cladistically closer to Bovini (Bibi, 2007) as compared to *Tragoportax*. The type species *P. latidens* is from the Late Miocene and indicated an upper molar as type specimen. However, Pilgrim (1939), gave a better picture when he described a cranium associated to the species. *Parabos* is a genus which is considered very similar to *Pachyportax* and it is reported from the Early Pliocene of France (Bibi, 2007, 2009). *Parabos* may be a senior synonym of *Pachyportax* as argued by Gromolard (1980). Gentry *et al*. (1999) reported that boselaphine made the way for bovines or bovine like bovids at the end of Late Miocene. No complete skull of *P. latidens* has been recovered, and the present sample adds to the collection of *Pachyportax latidens* from the Siwalik group.

Their larger size and no constriction at the base of crown excludes them from *Tragoportax* and *Selenoportax* while favors their inclusion in *Pachyportax latidens*. The upper second and third molars are well in line with those described by Pilgrim (1939) in respect to their length and width. They depict the same structural details like the shape of cusps, extension of entostyles, and strong median ribs. However, minute differences in the length and width are noted which may be neglected because of different development stages in individuals as well as intra-specific differences (Table 1).

Occurrence

Middle Siwaliks, Dhok Pathan Formation.

Material studied

PUPC 15/384, an isolated second right molar of maxilla (rM^2); PUPC 15/381, an second right molar of maxilla (rM^2); PUPC 15/388 an isolated third right molar of maxilla (rM^3); PUPC 17/418, an isolated second maxillary right molar (rM^2); PUPC 15/382, an

isolated deciduous fourth upper left pre-molar (ldP^4); PUPC17/421, an isolated deciduous third upper right pre-molar (rdP^3) PUPC 17/417, an isolated third upper right molar(rM^3) ; PUPC17/419, an isolated second upper left molar (lM^2) ; PUPC 17/420, an isolated third upper left molar (lM^3) ; PUPC 17/418, an isolated second upper left molar (lM^2) and PUPC 15/383, an isolated third lower right molar (rM$_3$).

Table 1: Comparative measurements (mm) of *Pacyportax latidens* (Pilgrim, 1937, 1939; Khan *et al.*, 2009). *indicates the presently studied specimens.

Sample number	Position	Length	Width	W/L ratio
PUPC 15/384*	M^2	26.9	22.47	0.83
PUPC 15/381*	M^2	28.6	18	0.62
PUPC 15/388*	M^3	28	23.9	0.85
PUPC 17/418*	M^2	28.3	22.48	0.79
PUPC 15/382*	dP^4	20.79	22.8	1.09
PUPC 17/421*	dP^3	21.24	19.94	0.93
PUPC 17/417*	M^3	30.07	24.64	0.81
PUPC 17/419*	M^2	26.08	23.81	0.91
PUPC 17/420*	M^3	30.5	23.26	0.76
PUPC 17/416*	M^2	27.38	24.81	0.89
PUPC 15/383*	M$_3$	27.1	17.25	0.63
AMNH 19730	M^3	29.5	27	0.91
AMNH 29913	M^3	31	29	0.93
PUPC 96/38	M^3	34.4	29	0.84
PUPC 01/24	M^3	28.4	25	0.88
PUPC 96/42	M^3	30.2	22.5	0.74
PUPC 96/43	M$_3$	25.5	14	0.54
AMNH 29964	M^2	28	25	0.89
AMNH 19730	M^2	28.5	28.5	1
PUPC 97/103	M^2	26.4	17.9	0.68

Pachyportax nagrii Pilgrim, 1939

Plate I, Figures 5a-7c; Plate II, Figures. 15a-15c.

Locality

Mentioned in the Supplementary Information (Table S1, Figure S1)

Description

Both the upper molars (PUPC 17/423 and PUPC 15/386) represent early stage of wear and less rugosity. All the cones and styles are intact. The praehypocrista is joining with posthypocrista. The metacone as well as paracone shows sloping cristae. Fosettes are not clearly formed. However, cavities are well developed and quite apparent antero-posteriorly. Median basal pillar is not developed completely (PUPC 17/423) and broken in PUPC 15/386.

Right lower second molar is highly worn out and partially damaged however all the conids and stylids are intact and represent sharp characters. Basal pillars are present. In PUPC 15/387, hypoconid is broken but protoconid is well preserved. Bulky median ribs near the crown.

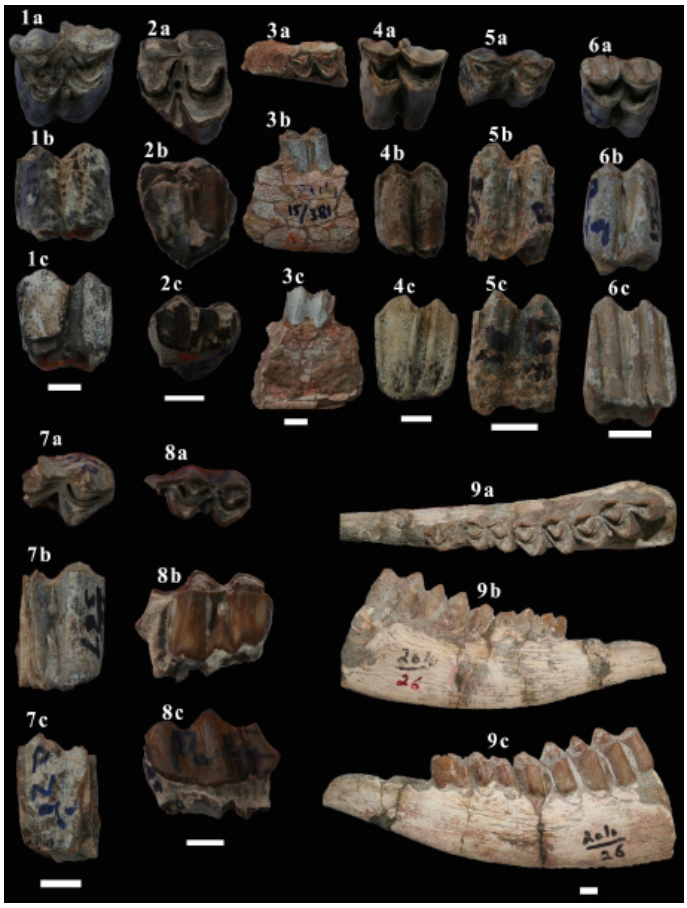

Plate I: Boselaphine dental specimens representing a= Occlusal view, b= Lingual view, c= Buccal view (*Pachyportax latidens*: 1a-4c, 8a-8c; *Pachyportax nagrii*: 5a-7c and *Selenoporatx vexillarious*: 9a-9c. Scale bar measures 10mm).

Comparison and discussion Table 2

In addition to *P. latidens*, Pilgrim (1939) also reported another species under the same genus, *Pachyportx nagrii*, which has the older occurrence in the Siwaliks. The reports regarding *P. nagrii* are too scanty while lower dentition is rarely known (reported in our data). A hornless female cranium is considered as the holotype for the species, which represents much similarities with *S. vexillarious*. *P. nagrii* is smaller compared to *P. latidens* (Pilgrim, 1939). The main difference between *P. latidens* and *P. nagrii* is the absence of constriction at the base of crown in in latter. It can be assumed that in the Siwaliks, *P. nagrii* was not as abundant as *P. latidens* and was confined to small pockets which were isolated towards the end of Late Miocene (Barry, 2002). The appearance of *P. nagrii* from Hasnot (7-5 Ma) adds the authenticity of range expansion of this species from Nagri to Dhok Pathan Fm (from 11.2-10.2 Ma and 10.2-5.0 Ma) (Khan *et al.*, 2009).

Table 2: Comparative measurements (mm) of *Pachyportax nagrii* (Pilgrim, 1937, 1939; Khan *et al.*, 2009). * indicates the presently studied specimens.

Sample number	Position	Length	Width	W/L ratio
PUPC 15/389*	M_2	19.08	12.29	0.64
PUPC 15/385*	M_3	22.51	13.5	0.59
PUPC 15/387*	M_2	18.7	14.54	0.77
PUPC 17/423*	M^1	21.5	18	0.83
PUPC 15/386*	M^1	20.17	17.8	0.88
GSI B808	M^3	21	17.02	0.82
PUPC 04/4	M^1	22	20	0.91

Studied material

PUPC 15/389, an isolated second left lower molar (lM_2); PUPC 15/385, an isolated third right lower molar (rM_3); PUPC 15/386, an isolated first left upper molar (lM^1); PUPC 17/423, an isolated first left upper molar (lM^1); PUPC 15/387, an isolated second lower right molar (rM_2).

Selenoportax vexillarius Pilgrim, 1937

Plate I, Figures 9a-9c; Plate II, Figures. 17a-17c

Holotype

A skull without dentition and most of the basicranium (Amer. Mus. No. 19748) (Pilgrim, 1937)

Diagnosis

A Siwalik bovid with large body size and hypsodont tooth morphology. Rugose enamel and ectostylid moderately developed. Lower more constricted at the base of crown.

Generic distribution

It is described from the Dhok Pathan and Nagri formations of the Middle Siwaliks (Pilgrim, 1937). The first reported specimen was a horn core reported by Solounias (1981) which was attributed to *Selenoportax*.

Localities

Localities are mentioned in SI (Table S1; Figure S1).

Description

PUPC 10/26 is a well preserved mandibulary ramus of *Selenoportax vexillarius* with crescentic pattern of cusps. P_4 is fully intact and highly preserved. It has a slight cementation around it. All the conids are well preserved. M_1 is in a good shape but protoconid and hypoconid are little broken. Median basal pillar is present and slightly fused with metaconid. It represents middle stage of wearing. M_2 of this mandible is little worn out and protoconid is slightly damaged at the crown. Median basal pillar is present. All the remaining conids are intact. M_3 is also in middle stage of wearing and highly preserved with a strong median basal pillar. There is a little bit cementation present around the talonid. The appearance is robust and all the stylids are intact. However, a slight mark is present on the posterior side of protoconid. The PUPC 17/422 has intact conids, anterior transverse flange is slightly developed. Ectostylid is apparent and molar is in middle to late stage of wear.

Comparison and discussion

Large dental size, strong ectostylids, divergent stylids, constriction at the base of the crown of the studied specimens favors their inclusion in the Siwaliks Boselaphines, *Selenoportax*, which has moderate to large body size (Pilgrim, 1937; 1939). *Selenoportax* is represented by two species viz. *Selenoporatx lydekkeri* and *Selenoportax vexillarous* (Pilgrim, 1939). The smaller size of molars favored their inclusion in *Selenoportax vexillarious*. The size and dimensions of the studied specimens indicate that these are moderate to large sized boselaphines of the Siwaliks. The specimens are highly narrow crowned and extremely hypsodont in their appearance. Enamel plications are apparent on the lingual side pronouncedly. The measurements are in line with those reported by Pilgrim, (1939) (Table 3).

Occurrence

Middle and Upper Siwaliks.

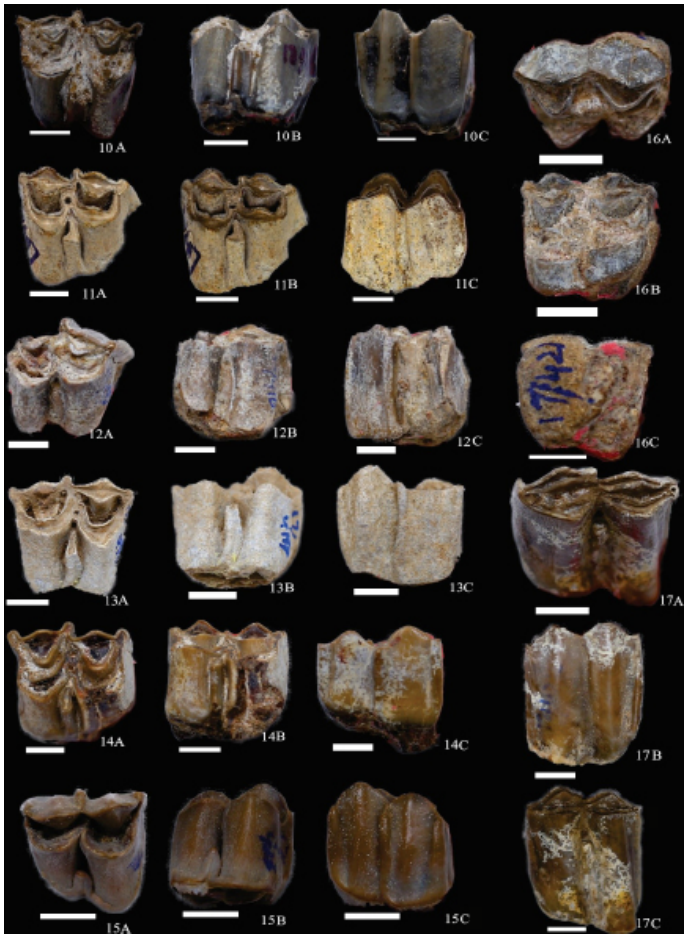

Plate II. Boselaphine dental specimens representing a= Occlusal view, b= Lingual view, c= Buccal view (*Pachyportax latidens*: 10a-14c, 16a-16c; *Pachyportax nagrii*: 15a-15c and *Selenoporatx vexillarious*: 17a-17c. Scale bar measures 10mm).

Table 3: Comparative measurements (mm) of *Selenoportax vexillarious* (Pilgrim, 1937, 1939; Khan *et al.*, 2009). * indicates the presently studied specimens.

Sample number	Position	Length	Width	W/L ratio
PUPC 10/26*	M_3	36.44	16.33	0.44
	M_2	25.7	17.66	0.68
	M_1	20.01	15.5	0.77
	P_4	19.25	11.86	0.61
PUPC 17/422*	M_2	25	16.02	0.64
AMNH 10514	M_3	33	15	0.45
AMNH 29917	M_1	18	13	0.72
AMNH 29946	P_4	21	11	0.52
AMNH 29917	P_4	21.7	10	0.46
AMNH 19514	M_2	22	15.5	0.7
AMNH 19844	M_2	25.9	16.5	0.63
AMNH 19514	M_3	33	21.5	0.65
AMNH 29917	M_2	21	15	0.71

Material studied

PUPC 10/26, A left mandibulary ramus having M_3-P_4; PUPC 17/422, an isolated left second lower molar (lM_2).

Conclusion

In the current study, two extinct genera of family Bovidae viz. *Pachyportax* and *Selenoportax* are described on the basis of comparative dental characters of new collection of fossils from Late Miocene of Hasnot, Pakistan. The samples include two species of *Pachyportax* and one species of *Selenoportax*. The faunal composition of Hasnot is strongly evident of broad vegetation which indicates the Bovid evolution in the time span of the Late Miocene (Behrensmeyer and Barry, 2005). The evolution towards large and heavy bodied Boselaphine was, in-fact, a consequence of natural variations, as the harsh environmental (increased aridity, C^3/C^4 transition and less water bodies. Quade and Cerling, 1995; Cerling *et al.*, 1997) conditions were augmented in southern part of Asia in the Late Miocene time span (6 Ma). We suggest that *Pachyportax latidens* is comparatively a larger species than *P. nagrii*. The age of *P. latidens* is from the Late Miocene-Early Pliocene of the Dhok Pathan Formation whereas *P. nagrii* from the early Late Miocene middle Late Miocene (Figure 2) of both Nagri and Dhok Pathan Formations, in contrast to the past suggestions that place this species in the Nagri Formation (early Late Miocene) (Ikram *et al.*, 2016). Thus we may assume, that both these species coexisted for some time span and later *P. latidens* outcompeted *P. nagrii* towards the end of Late Miocene. According to Khan *et al.* (2008) *Selenoportax* ranges in age from Middle Siwaliks to Upper Siwaliks but it was more dominantly present in the Late Miocene and only one species has been reported from the Upper Siwaliks. However, Barry *et al.* (2002) reported the presence of this taxon from the Late Miocene inhibiting a mixture of grass land and wood land.

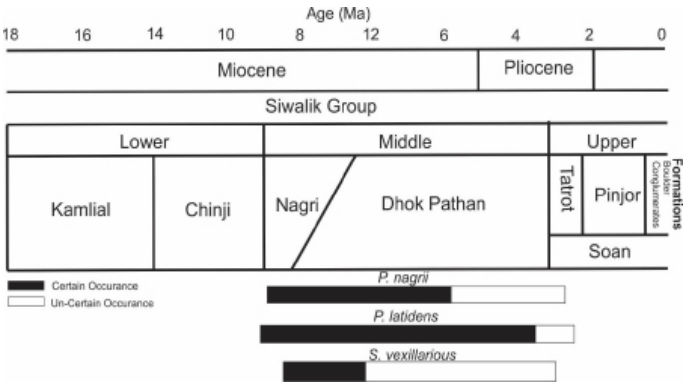

Figure 2: Chronology of the Siwaliks and occurance of the reported species (Barry *et al.*, 2002; Behrensmeyer and Barry, 2005; Nanda, 2008, Dennell, 2008).

Supplementary material

There is supplementary material associated with this article. Access the material online at: https://dx.doi.org/10.17582/journal.pujz/2020.....

Conflict of interest

The authors have declared no conflict of interest.

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