TRUE UNGULATES FROM THE NAGRI TYPE LOCALITY (LATE MIOCENE), NORTHERN PAKISTAN

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ABSTRACT

The early Late Miocene type locality of the Nagri Formation from the Indo-Siwaliks has yielded remains of the true ungulates that are today extinct to the south Asian biogeographic realm. Thirteen species including *Brachypotherium*, *Hipparion*, *Listriodon* and the bovids of the true ungulates from the village Sethi Nagri, district Chakwal, Punjab, Pakistan, are recognized, described and discussed in details. The tooth positions of all thirteen species are documented. Quantitatively, the taxa of the bovids are the most predominant. But *Brachypotherium*, *Hipparion*, *Listriodon*, tragulid and giraffid fossils are approximately as common as each other at the type locality. *Pachyportax*, *Dorcabune*, *Miotragocerus* and *Gazella* seem to be uniformly rare at Sethi Nagri. The new findings from the type locality are the *Giraffokeryx*'s hemimandible and the deciduous premolar of *Dorcatherium minus*. The newly recovered hemimandible and deciduous premolar enlarge our knowledge on the anatomic features of the Nagri true ungulates. The Nagri type locality mammalian local fauna has similarities to late Miocene Eurasian faunas. The investigation comprises extensive taxonomic descriptions of all species represented and an interpretation of the palaeoecology based on an analysis of the community structure. It seems that the abundance of *Hipparion*, giraffids, rhinocerotids and bovids suggests a woodland to savannah environment at or near the type locality during the early Late Miocene. There is little evidence to suggest that there was a humid closed canopy forest interspersed with temporary and perennial waters and accompanying open areas forest in the vicinity at the time of deposition.

Key words: *Listriodon*, Bovidae, Giraffidae, Tragulidae, *Hipparion, Brachypotherium,* Siwaliks.

INTRODUCTION

Ungulate refers to any animal with hooves however, the "True Ungulates" are considered the members of Artiodactyla and Perissodactyla. Subungulates (Paenungulates) comprise Sirenia, Proboscidea and Hyracoidea. In addition to hooves, most Ungulates have developed reduced canine teeth, bunodont molars due to herbivorous condition. Ungulates diversified rapidly in the Eocene, but are thought to date back as far as the late Cretaceous (Gentry and Hooker, 1988). Most Ungulates are herbivores and some commonly known examples of Ungulates living today are the goat, sheep, giraffe, deer, antelope, gazelle, camel, hippopotamus, horse, zebra, donkey, cow and rhinoceros. The Nagri type area of the Nagri Formation, Middle Siwaliks has yielded very rich assemblage of the true ungulates mainly recorded by Pilgrim (1913, 1926, 1937, 1939), Anderson (1927), Colbert (1935), Lewis (1937), Pascoe (1964), Thomas (1977, 1984), Akhtar (1992), Barry *et al*. (2002), Farooq (2006) and Khan A. M. (2010). The fauna mainly consists of crocodiles, chelonins, proboscidians, rhinocerotides, artiodactyls, carnivores and primates (Table 1).

The main aim of this study has been to provide the first complete documentation of true ungulates found in the vicinity of the type locality of the Nagri Formation by tackling tooth morphology, taxonomy, and palaeontology of the Siwaliks of Pakistan. An ecologically important group, the ungulates, was selected for the study as the collected ungulate material presented notable diversity and thus could provide significant taxonomic and palaeoenvironmental information.

Table 1: Mammalian faunas of Nagri. Many species are under taxonomic revision.

Bovidae		
	Tragoportax browni T. salmontanus	
	T. perimense	*T. punjabicus*
	Miotragocerus gluten	*Elaschistoceros khauristanensis*
	Selenoportax vexillarius	*S. lydekkeri*
	Pachyportax latidens	*P. nagrii*
	Gazella lydekkeri	
Giraffidae		
	Giraffokeryx punjabiensis	*Giraffa priscilla*
	Giraffa punjabiensis	
Anthracotheriidae		
	Merrycopolumus nanus	*M. dissimilis*
Tragulidae		
	Dorcabune anthracotherioides	*Db. nagrii*
	Dorcatherium majus	*Dt. minus*
Anthracotheriidae		
	Chocromeryx silistrense	*Merycopotamus dissimilis*
Suidae		
	Propotamochoerus uliginosus	*P. hysudricus*
Equidae		
	Hipparion theobaldi	*H. nagriensis*
	H. perimense	
Rhinocerotidae		
	Chilotherium intermedium	*C. blanfordi*
	Subchilotherium intermedium	*Alicornops* sp.
	Brachypotherium perimense	
Chalicotheriidae		
	Chalicotherium salinum	
Proboscidea		
	Gomphotherium angustidens	
	Pentalophodon falconeri	*Dinotherium indicum*
Cercopithecidae		
	Sivapithecus sivalensis	*S. indicus*
	Ramapithecus punjabicus	
Rodentia		
	Rhizomys sivalensis	*Rhizomys* sp.
Carnivora		
	Progenella sp.	*Pathyaena sivalense*
	Percurocuta carnitex	*Sivaelurus chinjiensis*

Siwaliks

The Siwalik deposits are one of the most comprehensively studied fluvial sequences in the world (Lydekker, 1876, 1878; Matthew, 1929; Colbert, 1935; Pilgrim, 1937, 1939; Hooijer, 1958; Pilbeam *et al*., 1977, 1979; Shah, 1980; Thomas, 1984; Hussain *et al*., 1992; Flynn *et al*., 1995; Barry *et al*., 2002, 2005; Dennell *et al*., 2006, 2008; Nanda, 2002, 2008; Khan, 2008; Sheikh *et al*., 2008; Khan *et al*., 2009a, b, 2010a, b, c, 2011a, b, c; Khan and Akhtar, 2011a, b). The Siwalik Hills are located in the political boundaries of Pakistan, India, Nepal, and Bhutan (Fig. 1), and range between 6 to 90 km in width (Acharyya, 1994). They gradually become steeper and narrower in relief and width respectively, from northern Pakistan to Bhutan (over 2000 km in length) (Fig. 1).

The term Siwaliks denotes the Neogene terrestrial sediments which are found in widely separated areas all along the foot hills of Himalayas. The Himalaya rose, and the sedimentary rocks of the Siwaliks were deposited, because of the collision between the Indian and Asian plates 40 to 50 Ma (Kumaravel *et al*., 2009). These sedimentary deposits are over 6000 meters in thickness and provides an amazing opportunity to palaeontologists, geologists and natural history researchers to study fluvial dynamics, palaeomagnetic dating, palaeoclimatology, stratigraphic correlation, isotope geochemistry, and vertebrate biochronology across the last 20 Ma (Andrews and Cronin, 1982; Pilbeam, 1982).

On the basis of lithology, Medlicott (1864) divided the Siwaliks into Lower, Middle and Upper subgroups and used the term “Siwalik Series” for the first time. Oldham (1893) and Holland (1926) also used the term Siwalik Series. Pilgrim (1910) showed that such a division was also possible on the basis of fauna. On palaeontological basis Pilgrim (1913) further differentiated the six zones, with lithological characteristics in the three divisions. He (Pilgrim, 1913) described these rock units as Pinjor, Tatrot, Dhok Pathan, Nagri, Chinji and Kamlial faunal zones. He also applied the lithostratigraphic classification of Upper, Middle and Lower Siwaliks. Later, Anderson (1927) and Cotter (1933) applied the names in the sense of lithostratigraphic units but referred them as stages. Lewis (1937) modified this term as Chinji Formation, Nagri Formation and Dhok Pathan Formation, while Kravtchenko (1964) used Soan Formation for Pinjor and Tatrot zones. The Siwalik Group is a thick sequence of fluvial clastic rocks shed southward as the Himalaya was uplifted, beginning in the late Oligocene. The Neogene sedimentary deposits extend from western Pakistan to eastern India. At both extremities the mountains turn southward around the edges of the Indian plate and form the prominent Himalayan syntaxes.

The deposits are composed of mudstones, sandstones and coarsely bedded conglomerates deposited at times when the region was a colossal basin during Middle Miocene to Upper Pleistocene times. Rivers flowing southwards from the Greater Himalayas, resulting in extensive multi-ordered drainage systems, deposited the sediments. After this deposition, the sediments were uplifted through intense tectonic regimes commencing in Upper Miocene times, subsequently resulting in a unique topographical entity – the Siwaliks (Chauhan, 2003). The Siwalik Group rocks extend along the base of the broadest outcrop, occurring in the Potwar Plateau of Pakistan (West *et al.*, 2010).

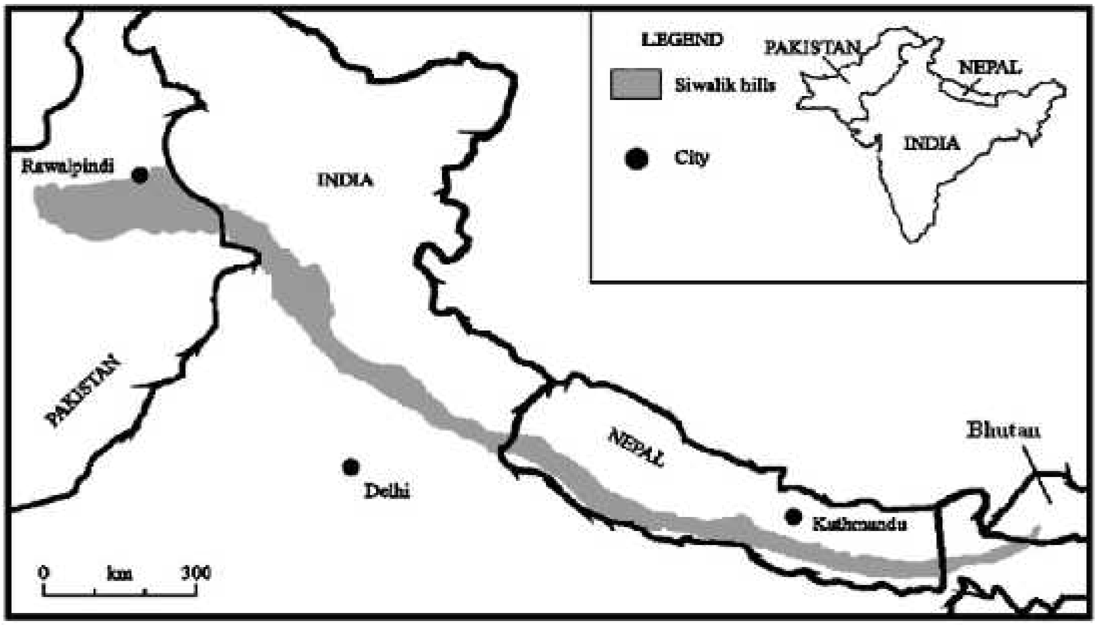


Fig. 1. Distribution of the Siwalik sediments along the foot hills of Himalayas.

Potwar Plateau of northern Pakistan

The Potwar Plateau (Lat. 33° 00´ N; Long. 72° 30´ E) is situated in the northern Pakistan (Fig. 2). It is an elevated area comprising some 30,000 km^2 bounded in the north by the Kala Chita and the Margala Hills, in the south by the Salt Range, in the east by the Jhelum River and in the west by the Indus River (Badgley *et al*., 2008) (Fig. 2). The Neogene's strata of the northern Pakistan have been divided into the Kamlial, Chinji, Nagri, Dhok Pathan and Soan formations. All these formations typically consist of gently tilted strata that form shallow strike-valleys and laterally extensive channel sandstones form higher ridges as the surface expression of the large structural synclinorium underlying the Potwar Plateau. Fossils come out of these strata due to erosion and accumulate on the outcrop surfaces between the ridges, providing best conditions for sampling within well-defined stratigraphic intervals (Pilbeam *et al*., 1977, 1997).

The Neogene Siwalik sequence from the Potwar Plateau, northern Pakistan, is a particularly good example of a long record of land mammals. This long faunal sequence records numerous vertebrate taxa and biotic events in the South Asian biogeographic realm (Pilbeam *et al*., 1997). The most extensive of the Neogene sediments, the Siwalik formations are widely distributed through Pakistan (Figs. 1-2) (Keller *et al*., 1977; Opdyke *et al*., 1979; Johnson N. *et al*., 1985; Barry *et al*., 2002). Within Pakistan they are best exposed in the Potwar Plateau (Fig. 2). The Potwar Plateau biostratigraphic and paleomagnetic framework continues to build on work published since the late 1970's. Many key stratigraphic sections measured and sampled (Opdyke *et al*., 1979; Pilbeam *et al*., 1979; Tauxe, 1979; Barry *et al*., 1980; Johnson N. *et al*., 1982, 1985; Tauxe and Opdyke, 1982) have been supplemented by radiometric dates and microstratigraphic studies in the Potwar Plateau (Johnson G. *et al*., 1982; Badgley, 1986; Behrensmeyer, 1987; Tauxe and Badgley, 1988; Badgley and Tauxe, 1990; Flynn *et al*., 1995). Consequently, the Potwar Plateau biostratigraphy is refined which represents almost the entire Neogene from about Middle Miocene to Pleistocene (Flynn *et al*., 1990; Jacobs *et al*., 1989, 1990; Barry *et al.,* 1982, 1990, 1991, 1995, 2002).

Geology and stratigraphy of Nagri

The described specimens in this article are recovered from the outcrops nearby the Sethi Nagri village (Lat. 32° 25' N: Long. 72° 14' E), a type locality of the Nagri Formation of the Middle Siwaliks. The type locality is designated nearby the Sethi Nagri village of the Chakwal district, Punjab, Pakistan which is situated at about 20 km south of Talagang, Chakwal district, Punjab, Pakistan (Fig. 3). The deposits consist mainly of thick, massive sandstone with occasional shale beds. At few places fine and coarse-grained beds may be encountered. In general the sandstone is immature and poor to moderately sort. The sandstone bodies are mainly composed of different storeys stacked both vertically and laterally (Shah, 1980).

The cross-bed thickness varies from a few centimeters to one meter in the lower part of the Formation. The basal surface of these cross-beds is usually erosional. The colour of sandstone varies from greenish gray to light gray and dark gray very rarely off white or gleaming white colours may be seen. Occasional interclast pebbles are also present within sandstone bodies. The conglomerates with varying thickness are present along different horizons (Pilbeam *et al*., 1997). Some limonitic staining is also present. It mainly shows a salt and pepper texture. The shales are reddish, brown, pale orange and sometimes chocolate coloured. The palaeochannels are very common within the outcrops (Barry *et al*., 2002).

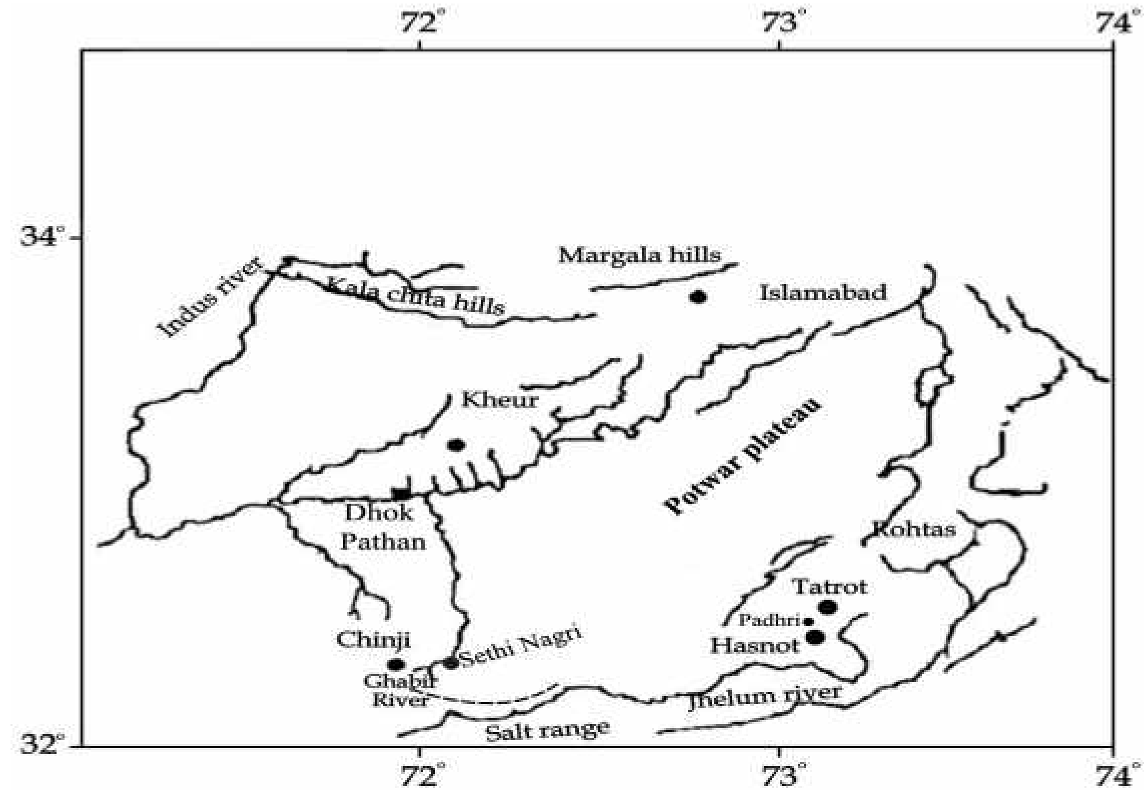


Fig. 2. Map of the Potwar Plateau showing main fossil localities in the Punjab, northern Pakistan.

The fossiliferous area is situated in the south of the Sethi Nagri village (Fig. 3). The average thickness of the deposits is about 650 m (Barry *et al*., 2002). Regionally the area is situated in the north of the Ghabir River (Fig. 3). The section from which the remains were excavated represents a typical sequence of fluvial sedimentation and consists of of bluish grey, massive and coarse sandstone with purple and orange clay and thick brown sandstone. Sites surrounding the Ghabir River present an abundance of vertebrate fossils that represent almost large size mammals.

The areas are thoroughly excavated and the discovered sites are indicated by 'SN' (abbreviation for the Sethi Nagri outcroping). During excavations fifteen sites (SN1-15) are found that are mostly situated the north of the Ghabir River (Fig. 3B). The three sites only are excavated from the south of the Ghabir River. The sites towards the east are more fertile than those of towards the west. The recovered specimens from these sites are characterized by large size mammals and a few sites represent small size mammals. The assemblage displays the regional characteristics of the Nagri Formation of the Middle Siwaliks. The fossils are mostly fragmentary in nature and the postcranial fossils are more abundant than the cranial ones. The weathering cracks, abrasion marks and byte marks are noted frequently while observing the specimens. Some sites (SN5-6) are highly fossiliferous and seems to expose for the long time. The fauna mainly consists of artiodactyls and perissodactyls. Lithofacies suggest a fluvial depositional environment of the type locality.

Barry *et al*. (1982) indicated an age for the Sethi Nagri type locality between 7.4 to 9.5 Ma. Johnson N. *et al.* (1985) date 10.8 Ma for the type locality, based on the fission-track dating of the volcanic ash near the type locality. Pilbeam *et al*. (1997) calculated the age 10.7 Ma for the '*Hipparion*' Datum, which is the oldest occurrence of *Hipparion* in the Siwaliks. This date is estimated for the localities on the top of the Ghabir kas long normal interval.

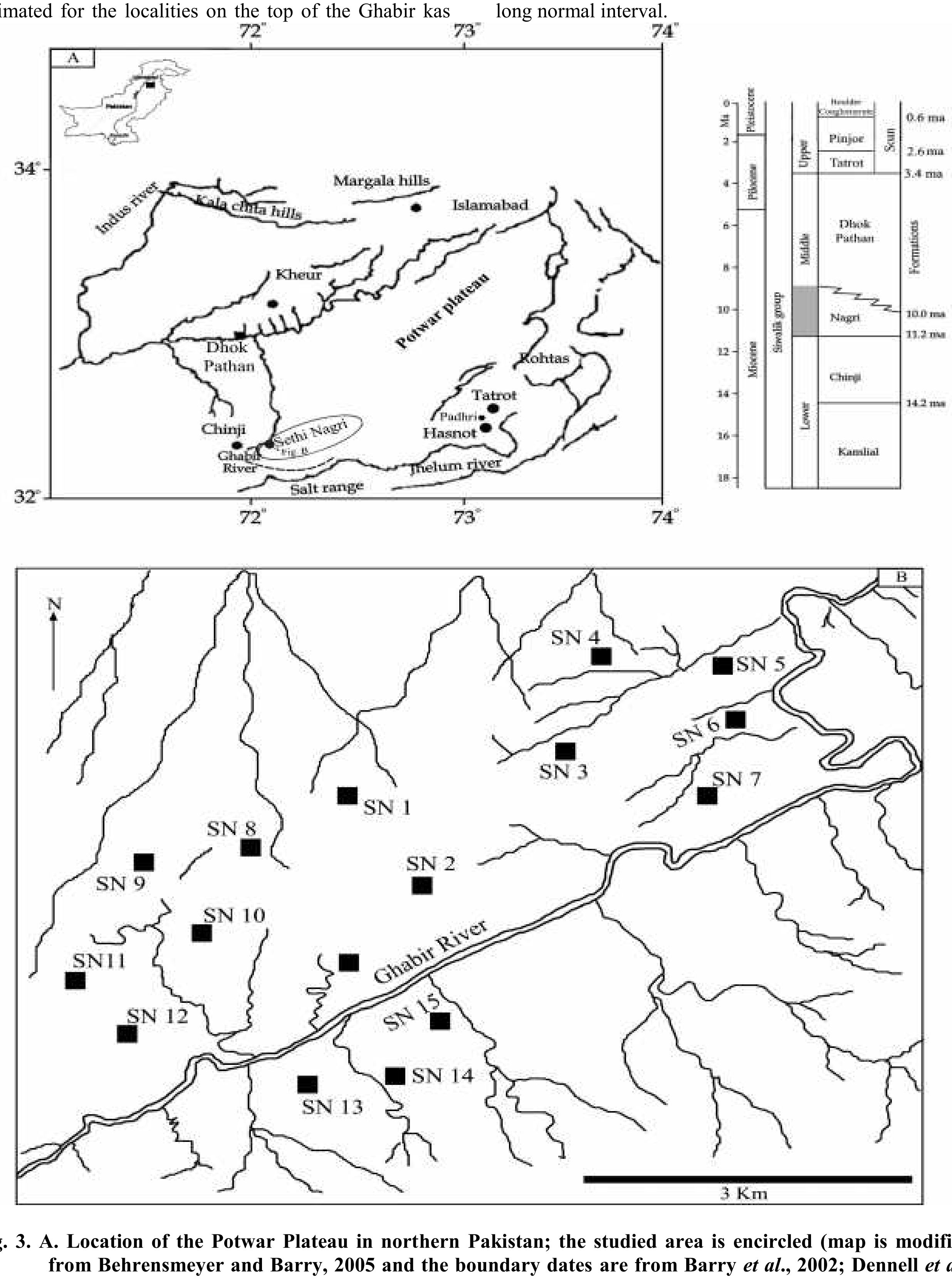


Fig. 3. A. Location of the Potwar Plateau in northern Pakistan; the studied area is encircled (map is modified from Behrensmeyer and Barry, 2005 and the boundary dates are from Barry *et al*., 2002; Dennell *et al*., 2008 and Nanda, 2008). B. Simplified geology map of the Nagri area indicating the fossiliferous sites along the Ghabir River (SN – abbreviation for Sethi Nagri) from where the studied material is recovered.

The Nagri type area belongs to the Middle Siwalk subgroup of the Siwaliks. Lewis (1937) introduced the name "Nagri Formation" which was later accepted by Stratigraphic Committee of Pakistan. Johnson N. *et al*. (1982) established six magnetic polarity sections over the Potwar Plateau region of Pakistan. In all the six sections the dominant feature of the magnetic polarity stratigraphy was a long normal polarity zone, which was contained within the Nagri Formation. This conspicuous normal polarity zone had been radiometrically dated as 9.5 ± 0.6 million years.

The Nagri Formation (11.2-10.1 Ma) consists mainly of massive sandstones; usually 15 m in thickness, with mudstone inter beds and occasional shale beds. Sandstone is of greenish grey, grey, or brownish grey in color, medium to coarse grained in size, highly thick and cross-bedded. It has a salt and pepper pattern produced by magnetite and ilmenite. Claystone is brown, reddish grey and orange and is sandy or silty. The thickness is about 500-900 m (Sheikh *et al*., 2008). The shales are reddish, brown, pale orange and sometimes chocolate colored. Conglomerates of varying thicknesses are present along different horizons. These are represented by some rounded pebbles of igneous and metamorphic rocks, in the upper part of the Formation. Palaeosols vary from place to place in central salt range and are red in color containing calcium carbonate. The lower contact of the Nagri Formation with underlying the Chinji Formation is gradational and with that of the overlying Dhok Pathan Formation is conformable.

Abbreviations: Ca, Circa; Myr, Million years; Ma, Million years ago; MN, Mein Zones; GPTS, Geomagnetic Polarity Time Scale; GRTS, Geomagnetic Reversal Time Scale; SN1-SN15, Fossilized sites of Sethi Nagri from numbers1 to 15; AMNH, American Museum of Natural History; BMNH, British Museum of Natural History; PMNH, Pakistan Museum of Natural History; PUPC, Punjab University Palaeontological Collection, Lahore, Pakistan; PC-GCUF, Palaeontological Collection of Government College University, Faisalabad, Punjab, Pakistan; I, Incisor; C, Canine; P, Premolar; M, Molar; GSI, Geological survey of India; GSP, Geological Survey of Pakistan; DP, Deciduous Premolar; W/L, Width/Length ratio; Fms/Fm, Formations/Formation; r, Right; l, Left; mm, Millimeters.

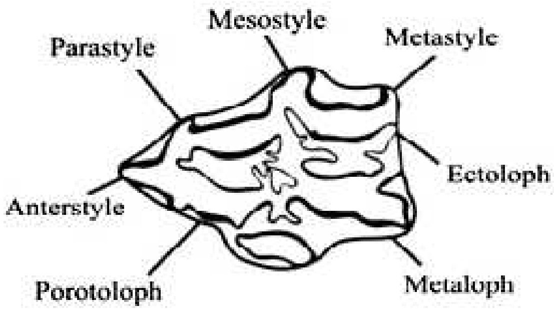
METHODOLOGY

The fossil remains of the true Ungulates include isolated dentition, mandible and maxilla fragments. The specimens are recovered from the Sethi Nagri type area of the Nagri Formation (Fig. 3). Surface collection was the primary method to recover the fossils from the type locality. Some fossils were exposed and easily available for the collection. Piercing instruments like chisels and geological hammers were employed for the excavation of partially embedded fossils. In due course numbers of field trips are carried out to the various fossilized sites of the Sethi Nagri village and the buried specimens were dug out with the help of the light hammers, chisels and fine needles. Careful measures were taken so as to prevent the fossils from disintegrating during excavation. Each specimen was wrapped with a cotton piece to avoid the shocks of transportation. Eventually the collected specimens were brought in the laboratory for taxonomic and morphological analysis.

In order to remove dust particles and prepare the specimens for clear observation, the specimens were carefully washed and cleaned in the Palaeontology laboratory of the Zoology Department of the Punjab University, Lahore, Punjab, Pakistan (institutional abbreviation – PUPC). Some specimens present in the Palaeontology laboratory of Zoology Department, GC University, Faisalabad (institutional abbreviation – PC-GCUF) are included in this study. Clay and other hardly adjoined sedimentary particles were removed with the help of fine needles and brushes. Accidentally broken fragments of the specimens were rejoined by using gums and resins such as Magic Stone, Elfy, and Fixings etc. A hand lens was used for keen observation of very small and ambiguous morphological characters.

The measurements of the specimens were taken in millimeters (mm) with the help of metric Vernier Caliper. The morphological and metrical characters of the specimens are described and their systematic determination is discussed. The catalogue number of the specimens consists of series i.e., yearly catalogue number and serial catalogue number, so figures of the specimen represent the collection year (numerator) and serial number (denominator) of that year (e.g. 09/12). Uppercase letter with superscript number stands for upper dentition (e.g. M^1) and with subscript number stands for lower dentition (e.g. M_1). In the discussion comparisons are made with fossils 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) and the specimens of Palaeontology laboratory of the Zoology department of the Punjab University (PUPC). The studied material is the property of the Palaeontology laboratory of the Zoology Department of the Punjab University, Lahore, Pakistan.

Tooth Morphology: Tooth cusp nomenclature in this article follows that of Heissig (1972), Janis and Scott (1987a, b), Pickford (1988), Akhtar (1992), Gentry (1994), and Cerdeno (1995) as shown in the figures 4-7. An entostyle can be found on the center of the lingual side of the upper molar and ectostylid is found on the buccal side of the lower molar, completely or partly separate from the rest of the occlusal surface. Tooth length and breadth 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 the lower premolar.



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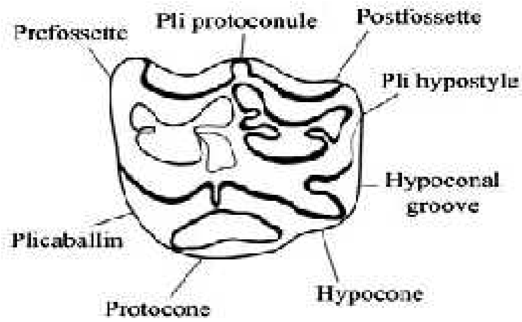

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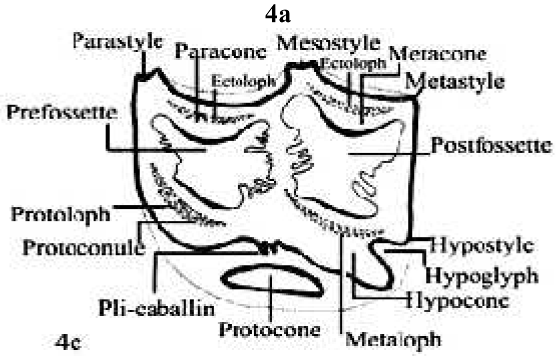

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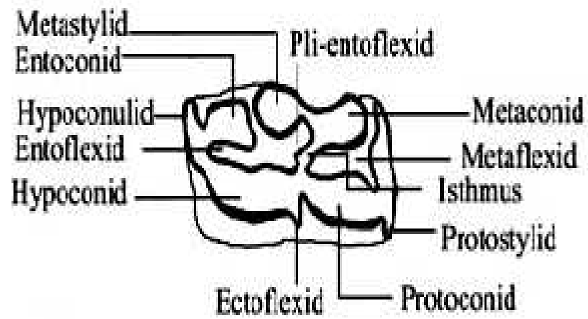

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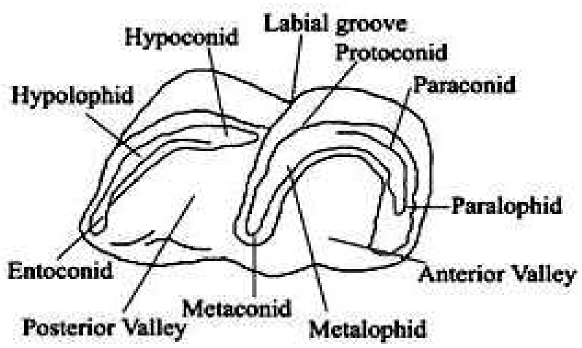

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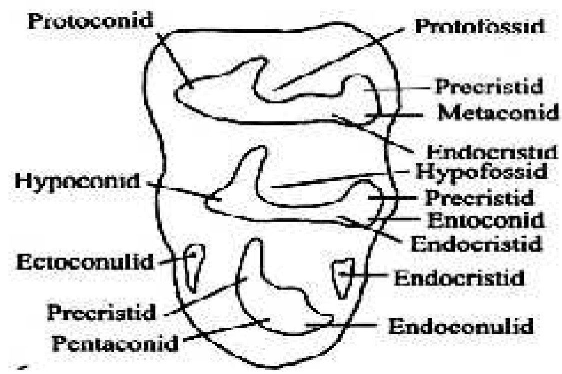

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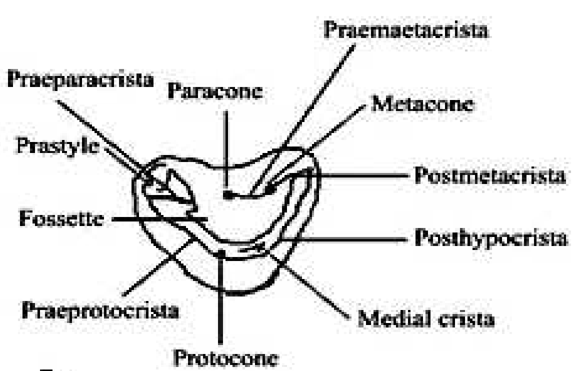

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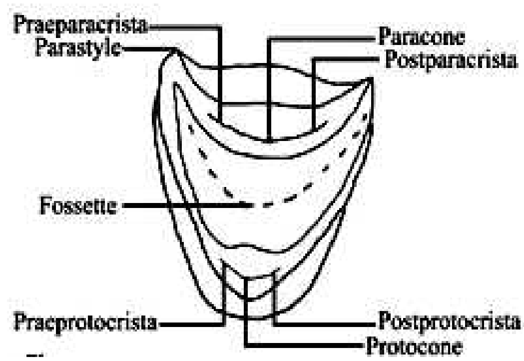

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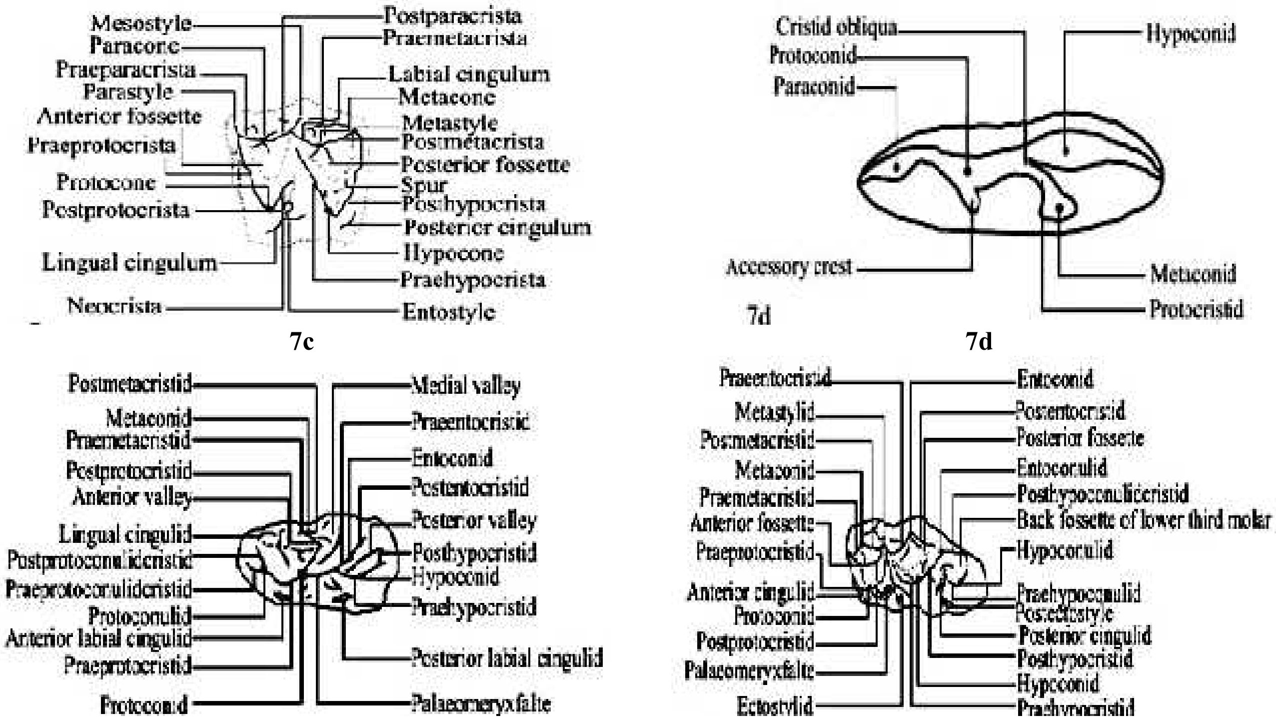


Figs. 4-7: 4a. *Hipparion* LP^2 (anterior to left, buccal up). 4b. *Hipparion* LP^4 (anterior to left, buccal up). 4c. *Hipparion* LM^2 (anterior to left, buccal up). 4d. *Hipparion* RP_4 (anterior to right, buccal down). 5. Rhinoceros LM_2 (anterior to right, buccal up). 6. Suinae LM_3 (buccal to right, anterior up). 7a. Topography of LP^3 in Artiodactyla (anterior to right, buccal up). 7b. Topography of LP^4 in Artiodactyla (anterior to right, buccal up). 7c. Topography of LM^2 in Artiodactyla (anterior to right, buccal up). 7d. Topography of RP_3 in Artiodactyla (anterior to right, buccal up). 7e. Topography of LP_4 in Artiodactyla (anterior to right, buccal down). 7f. Topography of LM_3 in Artiodactyla (anterior to right, buccal down).

SYSTEMATIC PALAEONTOLOGY

Order Artiodactyla Owen, 1848
Family Suidae Gray, 1821
Subfamily Listriodontinae Gervais, 1859

Genus *Listriodon* Von Meyer, 1846

Type Species: *Listriodon splendens* von Meyer, 1846.

Generic Diagnosis: Molars are lophodont. Tooth crests are perfect and have sharp cutting edges. Teeth are smaller in size than other genera of the family Suidae. Talon in M_3 present and varies in size in different species of the genus and symphysis also present (Colbert, 1935). The listriodonts are middle Miocene suids possessing features such as primitive basicranium, unflared zygoma, parietal lines not widely separated, no canine flanges, rounded snout and low glenoids. They possess a very elongated mandible, achieved both by elongation of the symphysis as well as by retiring the ascending ramus. In side view, the whole of M_3 is visible as well as gap behind M_3. The symphysis is splayed outwards, so that the lower canines emerge almost horizontally. The incisive margin is evenly curved and projects substantially in front of the canines. There is long diastema between the canines and anterior premolar (P_2). The borders of diastema lie well below the occlusal surface of the cheek teeth. P_1 is reduced or lost in most species. In Listriodontinae the I^1 is spatulate and occludes with $I_{1\text{-}2}$. In *Listriodon* females, upper canines are usually two rooted if they are not hypsodont although the lower canines seem to be more nearly single rooted. I^2 is a robust triangular tooth set vertically in the premaxillae. The tip is triangular in lingual view, with a lingual cingulum and a central rib. The crown is slightly offset from the root. There are two wear facets along the occlusal edge of the tooth; there are two wear facets along the occlusal edge of the tooth, the mesial facet corresponds to the outer portion of the scoop-shaped distal edge of I_2, while the distal one is caused by wear with the root ward half of the scoop in I_2. In I_2 the facet caused by I^2 is very prominent along the distal edge and in the body of the scoop, while I^1 occludes only at the tip. Unworn I^2 has bifurcate tip. M^1 is a square tooth with four main cusps disposed in two lophs, with anterior and posterior cingula. The anterior, median and posterior accessory cusps although present in all suids are very small in *Listriodon,* and soon disappear with wear (Pickford, 1988; Van der Made, 1996).

Known Distribution: The genus *Listriodon* is known from Europe, Africa as well as from the Lower Siwaliks and lower portion of the Middle Siwaliks (Pickford, 1988). In Europe (MN4 – MN7) it is known in the basal Middle Miocene deposits, in Africa it is known from Ngorora Formation and from the Siwaliks known from the Chinji Formation and the lower part of the Middle Siwaliks (Pilgrim, 1926; Pickford, 1988, 2001; Pickford and Morales, 2003; literature therein).

Listriodon pentapotamiae Falconer, 1868

Type Specimen: GSI B107, a complete right M^2 and fragment of right M^3; also right and left P^4.

Type Locality: Khushalghar, Pakistan (Pickford, 1988).

Stratigraphic Range: Lower Siwaliks and lower portion of the Middle Siwaliks (Colbert, 1935; Pickford, 1988, Pickford and Morales, 2003; Khan *et al*., 2005b).

Diagnosis: A species of *Listriodon* similar in size to *L. splendens* of Europe, but in which the upper central incisors are shorter mesiodistally and smaller; the upper canine shorter and narrower; P_1 usually present, but rudimentary; a large talon on the third molar, a strong cingulum in the fourth premolar, the shortness and more slenderness of symphysis (Pickford, 1988; Van der Made, 1996).

Studied Specimens: Upper dentition: PC-GCUF 10/04, left first upper incisor (I^1); PUPC 07/73, a maxillary ramus with M^{1-2}. Lower dentition: PC-GCUF 10/05, isolated left P_4; PUPC 07/72, almost complete mandible with the partial canines, the right hemimandible with M_{1-3} and the left hemimandible with M_{2-3}.

Description

Upper Dentition: The upper incisor PC-GCUF 10/04 (Fig. 8(1)) is in early wear on its lingual aspect. A cutting edge is present mesially which forms due to occlude with I1-2. The tooth is wide mesiodistally and its apical edge is divided into three lobes, the central one being the narrowest. The first incisor is a spatulate tooth with complete lingual cingulum. The occlusal tip has a deep sulcus near its mesial edge. The root is narrower than the crown.

PUPC 07/73 have lophodont upper first and second molars in late wear (Fig. 8(2)). A small part of the palatine is associated with the maxillary ramus. Cingulum is strong anteriorly and somewhat weak posteriorly. An evidence of cingulum is also present on the buccal as well as on the lingual sides. The buccal margin of the molars possesses relatively a well developed cingulum. The large dentinal islets indicate the late age of the animal. The posterior dentinal islet is more prominent than the anterior one. The buccal cones are vertically higher than the lingual ones. The enamel is thick. The molars are square shaped with four main cusps disposed in two lophs. The anterior, median and posterior accessory cusps are disappeared due to the late wear. These are very small in *Listrodon* and soon disappear with wear (Pickford, 1988). The upper first and second molars are so worn that little occlusal morphology is preserved. The M^1 and M^2 have almost same size and appearance.

Mandible: PUPC 07/72 is a complete mandible bearing partial canines with the M_{1-3} in the right hemimandible and the M_{2-3} in the left hemimandible (Fig. 8(4)). The mandible has long diastema and flat symphysis. The ascent begins well behind M_3, so there is a gap between the M_3 and the ascending ramus. The mandible is deep and broken fromwhere the ascending ramii retiring upwards. The symphysis is splayed outwards, so that the lower canines emerge horizontally. The lower border of the jaw below the third molar terminates in a prominent flange and lingual tubercle which is separated from the slightly descending angle by a low crest of bone. The internal and external surfaces of the jaw distal to the third molar are marked by well developed rugosities representing muscle attachments. The length of the molar series is 64 mm. The length of the mandible from anterior to posterior (PUPC 07/72) is 128 mm and the depth of the mandible at m3 is 44 mm.

Lower Dentition: The canines are broken at the apex in PUPC 07/72 (Fig. 8(4)). Both canines have triangular cross section. They emerge almost horizontally and sweep outwards. The tooth appears to have grown during all individual's life span. The male lower canines are permanently growing teeth of triangular section. In females the tooth is oval in section, and has closed roots (Pickford, 1988). The incisors and premolars are missing in the recovered mandible (PUPC 07/72). Nevertheless, the alveoli of the premolars are preserved ((Fig. 8(4)).

The lower fouth premolar, PC-GCUF 10/05 is an isolated excellently preserved molar (Fig. 8(3)). The P_4 is rectangular in occlusal outline with a very prominent innenhugel which is large and far offset from the main cusp. The cingula are large and the posterior accessory cusp is very prominent, placed closer to the buccal side of the tooth. The prominent talonid cusp joined lingually and buccally by a swollen cingulum.

The lower studied molars are early in wear ((Fig. 8(4)). The molars reflect lophodonty. The transverse valleys are wide. The fact that the lophids appear higher is possibly caused by a decrease of the antera-posterior diameter at the base of the lophid, resulting in wider transverse valleys with steeper slopes and by an increase of the transverse diameter at the top of the lophid. The M_1 is a four conids tooth but fragile. The conids are being disposed in two pairs forming lophs as in the upper molars. However, the lower molar is narrower than the upper and has less lingual and buccal flare. The posterior accessory cusplet is prominent and centrally placed ((Fig. 8(4)). The M_2 is a larger version of M_1. The second molar is a four conid tooth with anterior, median, and posterior accessory cusplets in the midline of the crown ((Fig. 8(4)). The posterior accessory cusplet is prominent and centrally placed. The molar is bunodont with the usual suid layout of four main cusps arranged in two lophs. The ectostylid is absent in the transverse valley. The M_3 differs from the M_2 by the presence of talonid and wide anterior lophid. The talonid of the M_3 is simple. It is really an enlarged cingulum, surrounding the posterior accessory cusplet. The comparative dental measurements are provided in table 2.

Comparison and Discussion

The sharp chisel shaped crest is a feature seen in the molar teeth of deinotheriid proboscideans, lophodonts pigs and some metatheres. The tooth under discussion is too small to be referred to any of the proboscideans. In lophodont metatheres the crest is imperfect while in lophodont pigs i.e. listriodonts, the tooth crests are perfect with very sharp cutting edges. All lophodont pigs are placed in a single genus, *Listriodon* that consists of three species, of these, the species *Listriodon pentapotamiae* is the smallest and is known from the middle Miocene of the Siwaliks (Pickford, 1988). Structurally, it is the most primitive species.

The specimens examined here belong to species *L. pentapotamiae* and are comparable to the specimens studied by Colbert (1935), Pickford (1988) and Van der Made (1996) (Table 2; Fig. 9). The most striking feature of *L. pentapotamiae*'s mandible is its very long diastema and flat symphysis which can be seen in the studied sample PUPC 07/72. In *Listriodon pentapotamiae* the male lower canine has triangular cross section which is observed in the sample. The lower molars are characterized by bilophids, possess elongated crown, development of post talonid which is well raised and tuberculated, and have a chisel shaped cutting edge. All the features correspond to species *Listriodon pentapotamiae* and consequently the recovered sample is assigned to the Siwalik suid *Listriodon pentapotamiae* which is very common in the Siwalik middle Miocene. But the rare findings are found in the lower part of the middle Siwaliks (Pickford, 1988). The new sample is also found from the lower part of the Middle Siwaliks, confirms its stratigraphic range in the earliest late Miocene of the Siwaliks.

The genus *Listriodon* was founded by Meyer H. von (1846) on dentition discovered from molasses of Switzerland, which he described under the name *L. splendens*. Falconer (1868) described the second molar of maxilla under the name *Tapirus pentapotamiae*. In the year 1876, Lydekker studied two isolated molars from the Salt Range area of the Punjab, and referred it to the genus *Listriodon*, one of which Falconer had named *Tapirus pentapotamiae.* In 1884, he refigured and described these, together with certain additional isolated molars, upper and lower, from the same area. He assigned his material to two species, the original *L. pentapotamiae* and *L. theobaldi* Stehlin. Lydekker (1879) pointed out that the two upper molars from the Laki Hills of Sind, figured by Lydekker under the names (?) *Hyotherium* sp. and (?) *Hyotherium sindiense,* belong in reality to the genus *Listriodon.* Colbert (1935) described and referred some maxillary and mandibular fragments to the genus *Listriodon*. Lydekker (1876) distinguished *Listriodon theobaldi* from *Listriodon pentapotamiae* on the basis of size. He documented that structurally no constant distinction could be drawn between smaller teeth of *L. theobaldi* and the larger teeth of *L. pentapotamiae*.

Table 2: Comparative measurements of the cheek teeth of the *L. pentapotamiae* in mm (millimeters).* The studied specimens. Referred data are taken from Colbert (1935), Pickford (1988), Van der Made (1996) and Khan *et al*. (2005b).

Taxon	Number	Nature/ Position	Length	Width
L. pentapotamiae	PC-GCUF 10/04*	I^1	17.0	9.70
	PUPC 07/73*	M^1	19.5	20.0
		M^2	20.0	20.0
	PC-GCUF 10/05*	P_4	13.0	11.5
	PUPC 07/72*	M_1	17.0	12.0
		M_2	19.0	14.0
		M_3	28.0	17.0
	PC-GCUF 08/22	I^1	21.7	9.90
	GSP 1424	I^1	22.7	11.3
	GSP 1378	I^1	21.7	10.5
	K 15/777	I^1	21.7	9.80
	K 13/772	I^1	19.2	10.5
	K 13/770	I^1	19.6	11.0

K 13/767	I^1	21.5	10.6
K 15/535	I^1	20.0	10.3
K 13/774	I^1	20.0	10.7
K 15/813	M^1	15.5	17.0
M 13586	M^1	17.3	16.3
M 13590	M^1	15.7	13.8
AMNH 19644	M^2	18.0	18.0
M 13257	M^2	18.3	18.3
M 13586	M^2	19.7	19.5
M 13590	M^2	17.9	16.0
M 31869	M^2	20.1	19.7
K 15/813	M^2	19.6	20.0
K 15/813	M^3	23.0	21.0
K 22/435	M^3	26.7	24.0
K 13/808	M^3	23.0	19.0
K 13/803	M^3	22.9	20.0
M 13257	M^3	21.0	20.4
M 31869	M^3	23.5	20.3
GSP 1606	M^3	21.7	20.5
AMNH 29836	M^3	23.0	20.0
K 13/808	P_4	15.3	12.3
K 13/436	P_4	17.4	11.3
K 23/721	P_4	16.1	12.5
K 14/492	P_4	16.5	11.8
K 15/520	M_1	19.0	14.2
GSP 4412	M_1	16.8	13.0
GSP 4527	M_1	15.7	14.0
GSP 4413	M_1	17.3	14.0
GSP 949	M_1	15.3	10.8
M 31867	M_1	16.5	13.2
M 13587	M_1	17.8	13.7
K 15/520	M_2	22.0	17.4
GSP 4527	M_2	22.0	17.0
GSP 4413	M_2	22.0	16.9
GSP 4412	M_2	21.0	16.6
GSP 4423	M_2	23.0	17.0
GSP 4478	M_2	23.4	18.3
M 31873	M_2	20.5	14.7
M 13592	M_2	21.5	16.7
AMNH 19519	M_2	19.0	16.0
PUPC 99/18	M_2	13.0	13.5
AMNH 19432	M_2	19.0	16.0
K 41/858	M_3	29.5	16.0
K 41/862	M_3	29.5	18.0
K 41/870	M_3	30.7	26.7
K 41/841	M_3	25.0	16.4
K 19/138	M_3	33.0	19.0
K 13/206	M_3	29.4	17.7
K 13/806	M_3	30.7	17.2
K 23/512	M_3	33.7	19.7
GSP 4527	M_3	36.5	20.0
GSP 4413	M_3	35.3	18.7
GSP 4412	M_3	32.5	18.8
GSP 1360	M_3	31.7	18.2
M 31873	M_3	29.5	16.8
M 13592	M_3	30.6	19.0
AMNH 19424	M_3	31.0	19.0
AMNH 19519	M_3	28.0	16.0

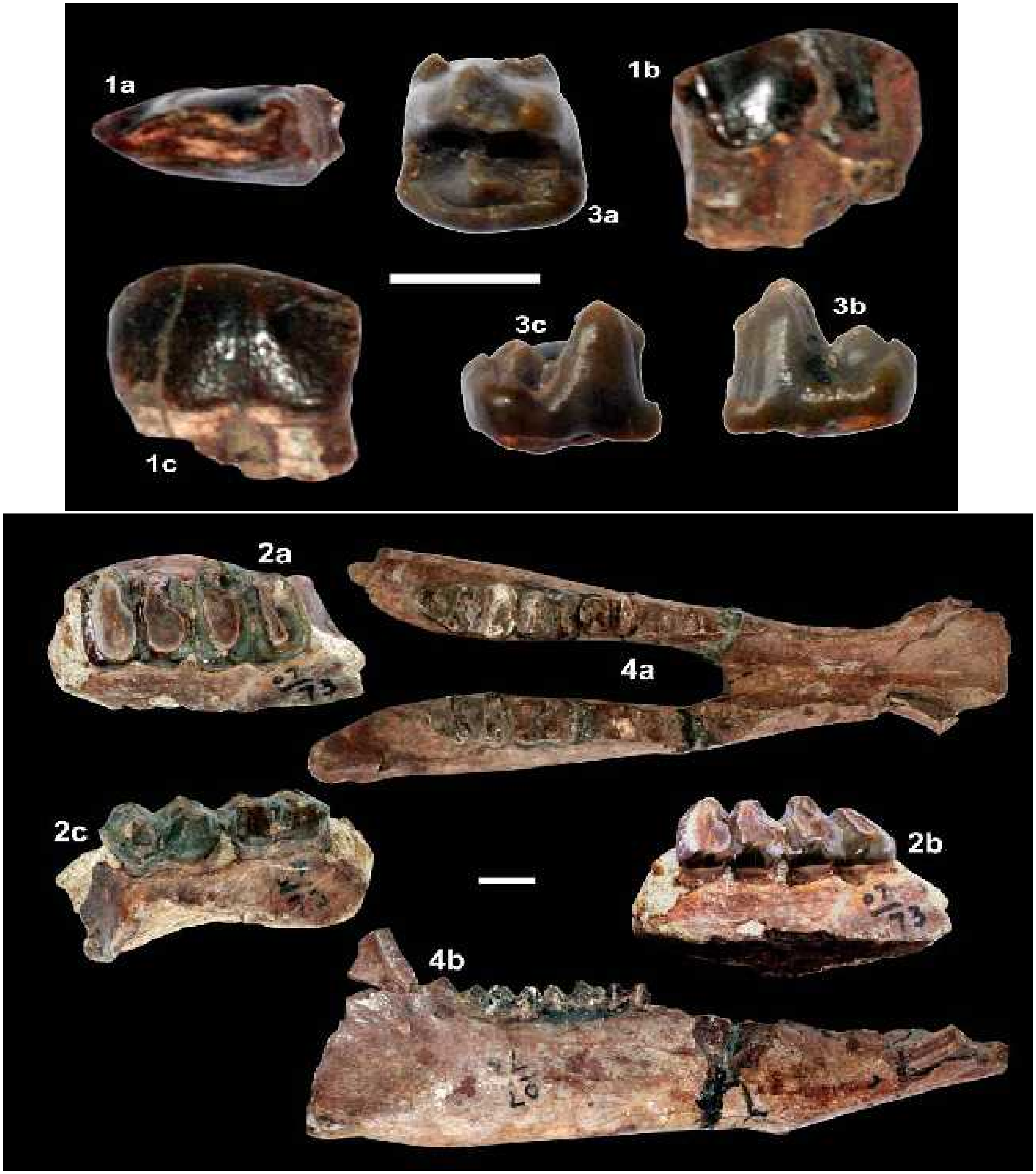


Fig. 8. ***Listriodon pentapotamiae*. 1. PC-GCUF 10/04, lI^{1}. 2. PUPC 07/73, right maxillary ramus with M$^{1-2}$. 3. PC-GCUF 10/05, lP$_{4}$. a = occlusal view, b = lingual view, c = buccal view. 4. PUPC 07/72, almost complete mandible with the partial canines, the right hemimandible with M$_{1-3}$ and the left hemimandible with M$_{2-3}$: a = occlusal view, b = buccal view, c = lingual view. Scale bar equals 10 mm.**

From the Siwaliks the genus *Listriodon* is known by three species *L. pentapotamiae, L. theobaldi* and *L. guptai* (Pilgrim, 1926; Colbert, 1935). *Listriodon theobaldi* is much smaller than the *L. pentapotamiae*. Pickford (1988) placed all the middle Miocene Siwalik lophodont pigs in *L. pentapotamiae* which is considered the smallest and primitive species of the genus *Listriodon* (Van der Made, 1996).

Pilgrim (1926) has referred to the existence of bunodont species of *Listriodon* in the lower Siwalik horizon of Sind, the Kamlial zone; this may be compared with *L. lockharti* and *L. latidens* of the Burdigalian and Vindobonian of Europe. *Listriodon pentapotamiae* is stratigraphically fairly long ranging species, extending from the base of the Lower Siwaliks to the lower portions of the Middle Siwalik beds (Pickford, 1988; Khan *et al*., 2005b; present study). *Listriodon pentapotamiae* is a fairly long ranging species, extending from the base of the Lower Siwaliks well up into the Middle Siwalik beds. Several specimens in the American Museum collection from the lower portion of the Middle Siwaliks should definitely establish the persistence of this genus beyond its typical Chinji development, a fact that was of some doubt to Matthew (1929).

Listriodon pentapotamiae is very close to *L. splendens,* from the Miocene of southeastern Europe, a fact that was pointed out in detail by many earlier researchers (e.g. see Pilgrim 1926; Colbert, 1935; Pickford, 1988; Van der Made, 1996). It is evident that the species *L. pentapotamiae* is allied to *L. splendens* and has reached the same stage of development as regards the formation of the molar crests, but in those features in which it differs from that species it seems to show a more primitive structure, which approximates to that of the bunodont forms *L. lockharti* and *L. latidens* (Van der Made, 1996).

Listriodonts disappeared more or less simultaneously everywhere, around the arrival of *Hipparion*. In Europe, the last *L. splendens* is known in MN 9/10 transition. In Pakistan, *L. pentapotamiae* is known to co-occur with *Hipparion* (Hussain, 1971; present study). In Africa, *Lopholistriodon kidogosana* is found in Member D of the Ngorora Formation, which is dated between 9.7 and 9.8 Ma and which has locally the first *Hipparion*. In Europe, the density of data is greatest and indicate that *L. splendens* became extinct a considerable period after the entry of *Hipparion* (the whole of MN 9). At about this time, there was a marked drop in suoid diversity in Europe, but not in Pakistan (Van der Made, 1996).

The origin of the Listriodontinae is unknown. The oldest Suoidea known are the Tayassuidae from the Oligocene of North America (Pearson, 1932), the Palaeochoeridae from the Oligocene of Europe (Ginsburg, 1974; Van der Made, 1994) and the palaeochoerid *Odoichoerus* from the Eocene (?) of China (Tong *et al*., 1986). The first suids appear in Europe in MN 1 as immigrants. This indicates that Suidae probably originated in Asia. The first record of Listriodontinae is from Africa in Set I (Faunal Sets: Pickford, 1981) and in Bugti, Pakistan. They are absent in Meswa Bridge (Set 0) and in Pakistan, there is no earliest Miocene or Oligocene record of mammals. Later members of the subfamily are found in Europe and China, suggesting that the earliest listriodonts evolved somewhere south of the Himalayas (Van der Made, 1996).

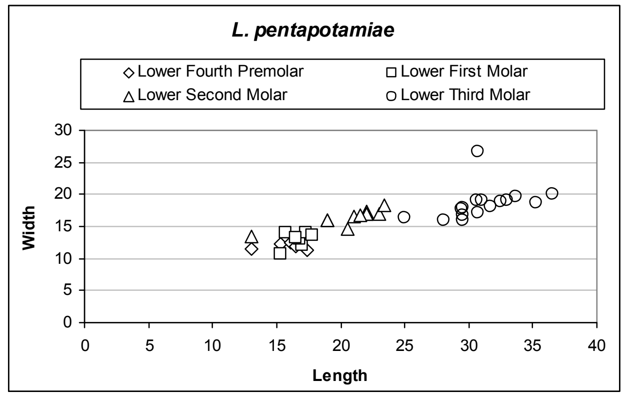


Fig. 9. Scatter diagram showing dental proportions of *L. pentapotamiae*'s studied sample. Referred data are taken from Colbert (1935), Pickford (1988), Van der Made (1996) and Khan *et al.* (2005b).

Family Bovidae Gray, 1821
Tribe Boselaphini Knottnerus-Meyer, 1907

Genus *Selenoportax* Pilgrim, 1937

Type Species: *Selenoportax vexillarius* Pilgrim, 1937.

Generic Diagnosis: Moderate to large sized Siwalik bovid; skull wide both at frontals and occipital, face slightly bent down on the cranial axis; frontals moderately depressed behind the horn-cores and form slightly elevated surface between the horn-cores; 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 (Pilgrim, 1937). 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 as anterior median rib (Pilgrim, 1937, 1939; Khan *et al.,* 2009a).

Known Distribution: The genus *Selenoportax* is well known from the Nagri and the Dhok Pathan formations of the Middle Siwaliks (Pilgrim, 1937; Akhtar, 1992; Khan *et al.,* 2009a).

Selenoportax cf. *vexillarius* Pilgrim, 1937

Type Specimen: AMNH 19748, a skull lacking maxilla and dentition and most of the basicranium.

Type Locality: Hasnot, Jhelum, Punjab, Pakistan (Pilgrim, 1937).

Stratigraphic Range: Middle and Upper Siwaliks (Pilgrim, 1937, 1939; Akhtar, 1992; Khan *et al.*, 2009a).

Diagnosis: Cheek teeth large and strongly hypsodont, enemal very rugose. Upper molars quadrate with strong and divergent styles near the neck of the crown, ribs quite large, entostyle and ectostylid strongly developed. Central cavities without indentations and simple in outlines, transverse anterior goat folds developed at front of lower molars (Pilgrim, 1937, 1939).

Studied Specimens: Upper dentition: PC-GCUF 10/07, isolated left M^1. Lower dentition: PC-GCUF 10/06, isolated left incisor (I_1); PUPC 09/117, isolated right M_1; PUPC 07/135, a fragment of right mandible having M_{1-3}.

Description

Upper Dentition: The first upper molar PC-GCUF 10/07 (Fig. 10(1)) is in an excellent state of preservation and in middle wear. The enamel is finely rugose and the rugosity is more evident on the lingual side than on the buccal one. The entostyle is strongly developed, exposing the dentine at the apex. 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 protocone is V-shaped. The styles and median ribs are well developed. The central cavities are wide and no spur of enamel seems to project into these central cavities.

Lower Dentition: The left lower incisor is in early wear (Fig. 10(2)). It has a simple outline. The incisor has a wide cutting edge with the outer angle pulled outwards. In buccal view the crown is slightly inclined upwards posteriorly.

PUPC 09/117 is a well preserved and in early wear (Fig. 10(3)). The appearance of the molar indicates a high crown and narrow tooth. The enamel is thick and shows fine plications all over the crown. These plications are more prominent and distinct on the buccal conids than on the lingual ones. The anterior transverse flange is developed on the anterior side of the lower molar. The ectostylid is strongly developed and looks as an isolated pillar in the transverse valley. As it is commonly observed the lingual conids are higher than the buccal ones. The protoconid is crescentic in shape. The praeprotocristid is larger than the postprotocristid. The metaconid is represented antero-lingually with two slightly worn sloping cristids. The entoconid is slightly higher than the metaconid and pointed in the middle. The wear is more distinct to the center of the entoconid than to the sloping cristids. The hypoconid is more V-shaped than the protoconid. The metastylid and the entostylid are strongly developed while the mesostylid is not distinct. The median ribs are developed but these are distinct to the base of the crown. The central cavities are moderately wide and deep, having no indentation (Fig. 10(3)).

The fragile mandible PUPC 07/135 has many vertical cracks and in a poor state of preservation (Fig. 11(4)). It is broken anteriorly and posteriorly. A small part of ascending ramus is present posteriorly behind the 3rd molar. The molars on the mandible are in an excellent state of preservation but the premolars are missing. The roots of the P_4 and the P_3 are preserved. The M_1 has a long and wide transverse valley between the anterior and posterior ribs. There is an ectostylid present in the transverse valley. The central cavities are wide and deep. The anterior central cavity is compressed at its centre. The M_2 is comparatively larger than the M_1. The ectostylid is not visible owing to the deposition of sand stone. The anterior transverse flange is large enough to look as a goat fold. The metastylid and the entostylid are strongly developed while the mesostylid is not distinct. The 3rd molar crown is high. The buccal side of the molar is covered with the matrix and consequently, the occlusal and lingual views are available for the morphological study. The major conids and hypoconulid are well developed. The hypoconulid is attached to the ascending ramus posteriorly. The M_3 also has strongly developed metastylid and the entostylid as in the M_1 and the M_2. The mesostylid is not prominent. The comparative dental measurements are provided in table 3.

Comparison and Discussion

The seleno-hypsodonty pattern of the studied material confirms its inclusion to Ruminantia. The specimen has hypsodonty, greater strength of external lobes and ribs, and fairly rapid increase in antero-posterior diameter from base to summit of crown. The specimen morphology differs from tragulids, cervids and giraffids (Colbert, 1935; Pilgrim, 1937; Bhatti, 2005; Farooq, 2006). The specimens, morphometrically clearly indicate a large sized Miocene bovid. To this group belong *Selenoportax* and *Pachyportax* of the Middle Siwaliks. Crown is narrow at the base and broad at the apex in *Selenoportax* whereas in *Pachyportax* the crown is not extended at the apex. The general contour of the studied specimens, the rugosity of the enamel, the srong entostyles/ectostylids, the prominent median ribs, the strong and divergent styles exclude the studied specimen from the genus *Pachyportax* and favour its inclusion in the genus *Selenoportax.* The recovered sample represents features of *Selenoportax* (Pilgrim, 1937, 1939; Akhtar, 1992; Khan *et al*., 2009a) and proves its inclusion to the

Siwalik genus *Selenoportax*. The Siwalik *Selenoportax* is recorded by two species: a small *S. vexillarius* and a large *S. lydekkeri* (Khan *et al*., 2009a). The studied specimens correspond to *S. vexillarius* morphometrically (Figs. 10-12; Table 3) and assign to *S.* cf. *vexillarius* because of the insufficient material.

Pilgrim (1937) erected the genus *Selenoportax*, based on a collection from the various Siwaliks localities of Pakistan and India. Akhtar (1992) added two species in it; one is *S. dhokpathanensis*, based on a damaged cranium. It differs from *S. vexillarius* by its gigantic size. The second is *S. tatrotensis*, based upon a maxillary ramus with right P^3-M^3 and left P^4-M^3. More recently, Khan *et al.* (2009a) reviewed the boselaphines from the Middle Siwaliks of the Hasnot, Punjab, Pakistan, and they considered that *S. vexillarious* and *S. lydekkeri* are valid species in the Middle Siwaliks of the subcontinent. Reviewing the Siwaliks *Selenoportax* species, they (Khan *et al.*, 2009a) synonymized *S. dhkopathanensis* Akhtar, 1992 with *S. lydekkeri* and *S. tatrotensis* Akhtar, 1992 with *S. vexillarius*.

Genus *Pachyportax* Pilgrim, 1937

Type Species: *Pachyportax latidens* (Lydekker) Pilgrim, 1937.

Generic Diagnosis: Boselaphinae of small to large or very large size; closely allied to *Strepsiportax* but differing from that genus by the much more massive skull, with horn-cores longer, stouter, more twisted and less curved inwardly; occipital condyles and foramen magnum larger; mastoid process and squamosal shelf more developed; supraoccipital exposed on the upper surface of the occiput as a narrowly elliptical area much extended transversely; basioccipital approaching a rectangular shape, with posterior tuberosities not greatly expanded; upper molars strongly hypsodont but less so than in *Selenoportax,* quaderate, with strong entostyle, external folds weaker and less divergent than in *Selenoportax,* external ribs weaker than in *Selenoportax,* in particular the median rib of the posterior lobe flattened, enamel rather thick, somewhat less rugose than in *Selenoportax,* with traces of cement (Pilgrim, 1937).

Known Distribution: The genus *Pachyportax* is present in the Nagri and the Dhok Pathan formations of the Middle Siwaliks (Lydekker, 1876; Pilgrim, 1937; Khan *et al*., 2009a). It is also present in the Tatrot zone of the Upper Siwaliks (Akhtar, 1992). The material under study comes from the type locality of the Nagri Formation of the Middle Siwaliks, Pakistan. Gentry (1999) describes the species from Abu Dhabi.

Pachyportax cf. *latidens* Pilgrim, 1937

Type Specimen: GSI B560, a skull fragment (Pilgrim, 1939).

Type Locality: Nagri, Middle Siwaliks, Punjab, Pakistan (Pilgrim, 1939).

Stratigraphic Range: Middle Siwaliks (Pilgrim, 1939; Akhtar, 1992).

Diagnosis: A large *Pachyportax*, with quadrate upper molars and strong entostyle 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. *Pachyportax* has strong entostyle extending transversely while in *Selenoportax* it is not much extended transversely. In *Pachyportax* posterior median rib is flattened whereas in *Selenoportax* it is strong like anterior median rib (Pilgrim, 1937, 1939).

Studied Specimens: Upper dentition: PUPC 09/46, isolated right P^3; PUPC 09/69, isolated left M^2.

Description

Upper Dentition: The recoverd material comprises only upper dentition. The P3, PUPC 09/46 is a triangular tooth (Fig. 13(1)). The anterior median rib is closed to the parastyle forming a narrow vertical groove on antero-buccal side of the premolar. The posterior groove is wide and shallow. The premolar is in middle wear. The paracone is round. The metastyle is prominent and narrow. The cingulum is absent on both the lingual as well as on the buccal side and a slight indication is present buccally at the base of the metacone. A wide cavity in the center of the tooth becomes extremely narrow anteriorly.

Table 3: Comparative measurements of the cheek teeth of *S. vexillarius* in mm (millimeters). * The studied specimens. Referred data are taken from Pilgrim (1937, 1939); Akhtar (1992), Khan (2008) and Khan *et al*. (2009a).

Number	Nature/Position	Length	Width
PC-GCUF 10/06*	I_1	21.0	13.0
PC-GCUF 10/07*	M^1	20.0	20.5
PUPC 09/117*	M_1	20.4	12.0
PUPC 07/135*	M_1	21.0	14.0
	M_2	26.6	15.0
	M_3	32.0	15.0
	M_2	27.9	16.1
	M_3	31.4	16.0
PUPC 98/78	M_2	25.0	16.0
	M_3	36.0	15.0
PUPC 85/40	M_1	19.7	12.5

PUPC 04/12	M_2	20.0	12.5
PUPC 87/90	M_3	38.0	16.5
AMNH 10514	M_3	33.0	15.0
AMNH 29917	M_1	18.0	13.0
AMNH 19844	M^2	25.7	24.0
AMNH 19844	M_2	25.9	16.5
AMNH 19514	M_2	22.0	15.5
AMNH 29917	M_2	21.0	15.0
AMNH 19514	M_3	33.0	21.5
PUPC 87/19	M^1	24.2	21.5

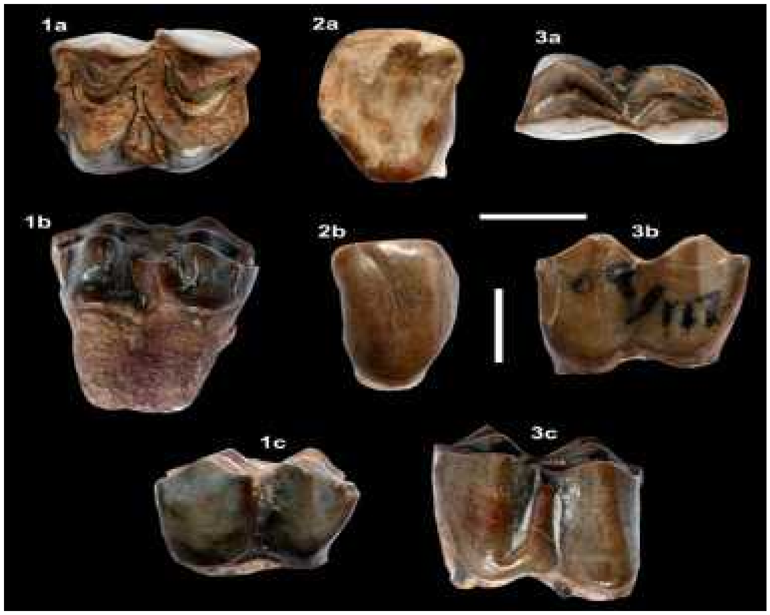


Fig. 10. *Selenoportax* cf. *vexillarius*. 1. PC-GCUF 10/07, lM^1. 2. PC-GCUF 10/06, lI_1. 3. PUPC 09/117, rM_1. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.

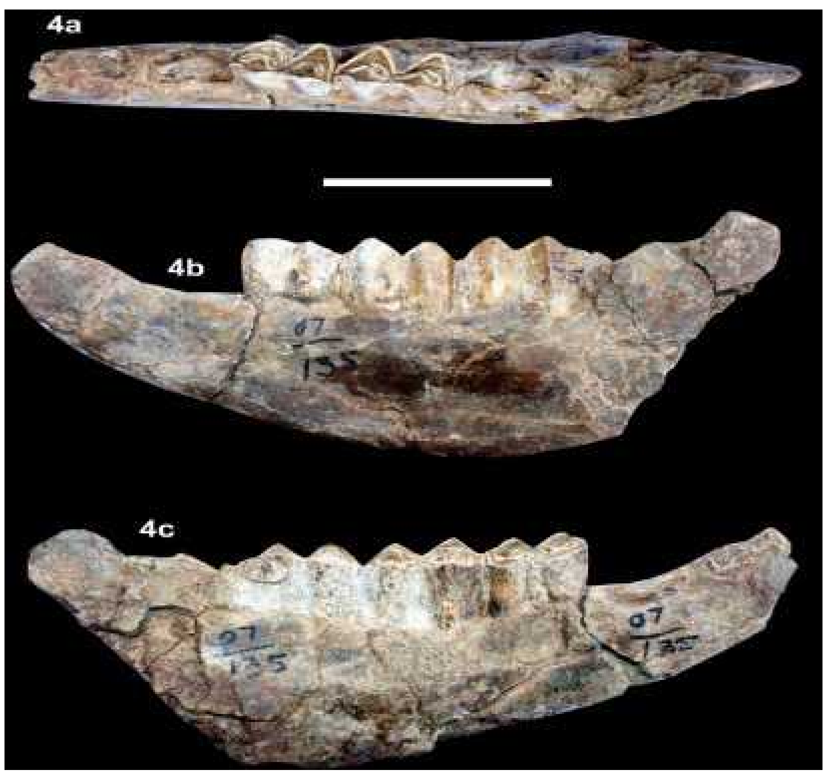


Fig. 11. 4. PUPC 07/135, a fragment of right mandible having M_{1-3}. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 50 mm.

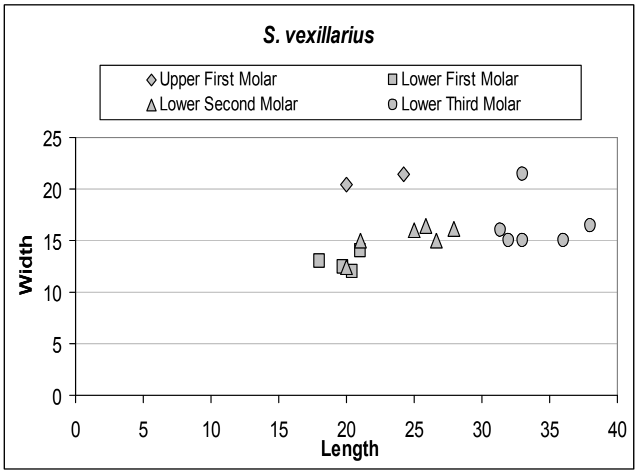


Fig. 12. Scatter diagram showing dental proportions of *S.* cf. *vexillarius*'s studied sample. Referred data are taken from Pilgrim (1937, 1939), Akhtar (1992), Khan (2008) and Khan *et al*. (2009a).

PUPC 09/69 is a well preserved second molar (Fig. 13(2)). It is in late early stage of wear. The contact facets present antero-posterior sides of the molar. The enamel is rugose. The molar has divergent styles. The entostyle is present in the transverse valley between the protocone and hypocone of the molar. The protocone is relatively narrower transversely than the hypocone with two running praeprotocrista and postprotocrista towards the parastyle and mesostyle. The hypocone is slightly higher and more crescentic than the protocone. The anterior and posterior central cavities are wide, isolated and deep. The anterior rib is strong whereas the posterior one is flattened. The comparative measurements are provided in table 4.

Table 4: Comparative measurements of the cheek teeth of *P. latidens* in mm (millimeters). * The studied specimens. Referred data are taken from Pilgrim (1937, 1939), Akhtar (1992), Khan *et al*. (2009a).

Number	Nature/Position	Length	Width
PUPC 09/46*	P^3	16.0	15.0
GSI B218	P^3	19.0	19.0
PUPC 09/69*	M^2	25.0	23.0
PUPC 98/59	M^2	22.0	17.3
PUPC 96/40	M^2	19.4	18.4
PUPC 96/3	M^2	27.0	22.0
PUPC 86/37	M^2	27.4	18.0
PUPC 86/36	M^2	30.0	23.0
PUPC 83/718	M^2	27.4	26.0
PUPC 83/646	M^2	30.0	18.0
PUPC 83/744	M^2	30.2	21.9
PUPC 86/210	M^2	26	17.1
PUPC 00/100	M^2	25.5	25.0
PUPC 04/14	M^2	29.3	20.6
PUPC 98/60	M^2	23.1	15.9
PUPC 97/103	M^2	24.5	17.7
PUPC 86/203	M^2	26.4	17.9
AMNH 29964	M^2	28.0	25.0
AMNH 19730	M^2	28.5	28.5
PUPC 96/42	M^3	30.2	22.5
PUPC 01/24	M^3	28.4	25.0
PUPC 96/38	M^3	34.4	29.0
GSI B219	M^3	34.5	28.0
AMNH 29914	M^3	36.0	34.0
AMNH 29913	M^3	31.0	29.0
AMNH 19730	M^3	29.5	27.0
PUPC 83/840	M^3	31.9	23.0
PUPC 87/88	M^3	27.2	16.6
PUPC 04/15	M^3	28.0	21.2
PUPC 00/87	M^3	25.9	17.6
AMNH 29913	M^3	31.0	29.0
AMNH 19730	M^3	29.5	27.0

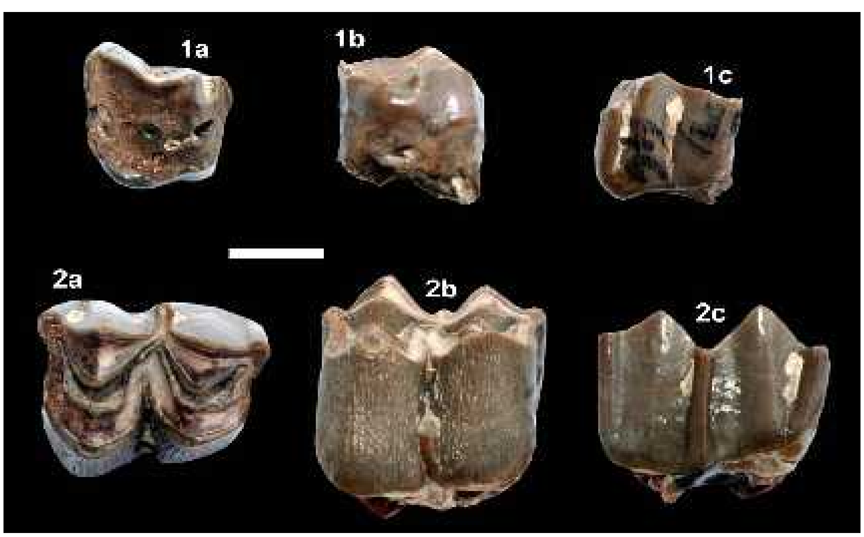


Fig. 13. *Pachyportax* cf. *latidens*.1. PUPC 09/46, rP^3. 2. PUPC 09/69, lM^2. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.

DISCUSSION

Lydekker (1876) described a right M^3 (GSI B219) under the name *Cervus latidens*. In the same paper he described a lower molar (GSI 23) also and referred it to this species. Later on, he (1884) realized that an upper and lower molar of a large ruminant from the Siwaliks of the Punjab which were described and figured under the name *Cervus latidens* do not belong to the family Cervidae. To the same species Lydekker referred a left maxilla with $P^2 – M^3$ (GSI B218a) and provisionally assigned these three specimens to the genus *Oreas* (?). Lydekker (1878) described and figured a horn-core under the name *Capra* sp.

Pilgrim (1937) applied the generic term *Pachyportax* to all these specimens which were described by Lydekker under the names *Cervus latidens* (1876), *Capra* sp. (1878) and *Oreas (?) latidens* (1884). He referred these specimens to *Pachyportax latidens* (Lydekker) Pilgrim, making the type specimen an isolated M^3 (GSI B219) which was described by Lydekker (1876) under the name *Cervus latidens.* Pilgrim (1939) reported the occurrence of *Pachyportax* from Nagri by describing a new species *Pachyportax nagrii.* The species is based upon a hornless female cranium. According to Gentry (1974), *Pachyportax nagrii* is a probably invalid species. Akhtar *et al.* (1997) ascribed *Pachyportax nagrii* from the Nagri Formation, based on the left maxilla PUPC 86/77. *Pachyportax nagrii* is of smaller size than those of *Pachyportax latidens* (Akhtar *et al*., 1997).

Pachyportax is a gigantic sized boselaphine (Lydekker, 1876, 1884; Gentry, 1999). *Pachyportax latidens* although have been continuously present from the Middle Siwaliks to Upper Siwaliks sequence but it is more abundant in the Hasnot succession (Khan *et al.,* 2009a). Bibi (2007) discussed the origin of the early bovines and grouped *Selenoportax* and *Pachyportax* with them*. Pachyportax* have been recovered from the late Miocene of the Middle Siwaliks (Lydekker 1876, 1884; Pilgrim, 1937, 1939; Akhtar, 1992, 1995, 1996; Khan, 2008; Khan *et al.,* 2009a) and from the early Pliocene of the Upper Siwaliks (Akhtar, 1992).

The faunas of Negeringerawa, Namurungulea and Nakali dated 10-8 Ma and the faunas from the Mpsida, dated 7-6 Ma in Africa do not have the genus *Pachyportax* (Hill *et al*., 1985; Nakaya, 1994; Kingston *et al.*, 2002). *Pachyportax* is also lacking from localities of the same age such as the Afghani locality of Tagar dated at 8.7-8 Ma (Sen *et al.*, 1997) and Iranian locality Marageh dated 9.5-7 Ma (Bernor, 1986). *Pachyportax* is a typical Late Miocene taxon, occurring in the Nagri and the Dhok Pathan formations of the Siwaliks (Akhtar *et al.* 1997). Recently, Khan *et al.* (2009a) ascribed *Pachyportax* from the Middle Siwaliks of Hasnot, Pakistan. *Pachyportax* was restricted to the Middle Siwaliks because Himalyan Mountains acted as a barrier in the dispersal of *Pachyportax* out of southerns Asia prior to the late Miocene, isolating the Siwalik faunas (Barry *et al.* 1982; Bernor, 1984).

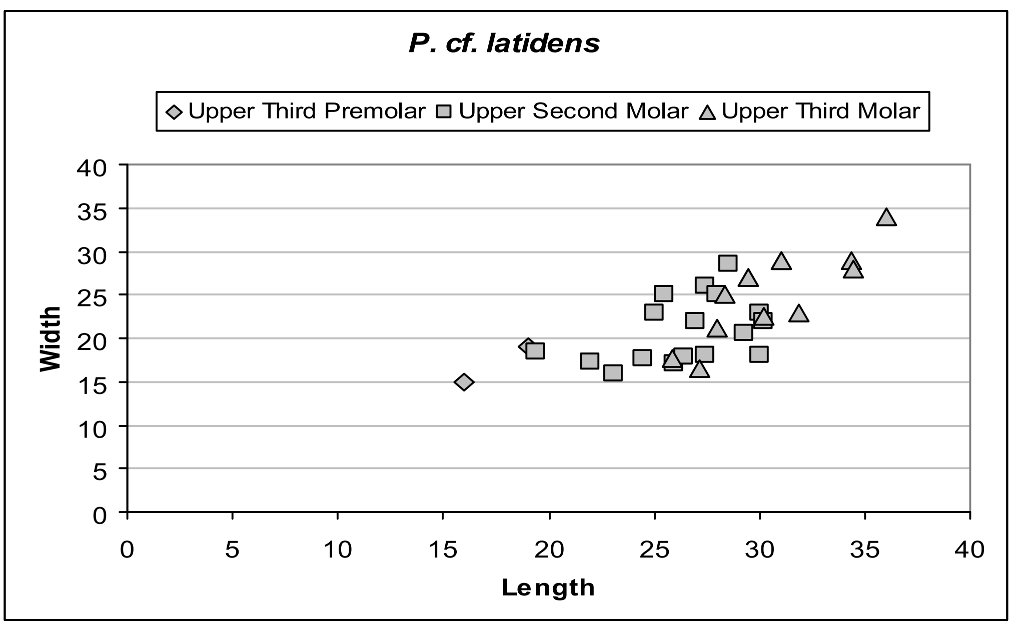


Fig. 14. Scatter diagram showing dental proportions of *P. latidens*'s studied sample. Referred data are taken from Pilgrim (1937, 1939), Akhtar (1992), Khan *et al*. (2009a).

Genus *Tragoportax* Pilgrim, 1937

Type Species: *Tragoportax salmontanus* Pilgrim, 1937.

Generic Diagnosis: Moderate to large sized Eurasian bovid. Skull long and slender, brain-case rather slender, temporal ridge very strong, occipital rather high and narrow, lambdoidal crest prominent, occipital condyles large, basiocoipital short, subtriangular, with a shallow median furrow, paraoccipital process elongate and narrow. Upper molars hypsodont, quadrate, with small entostyles, enamel rugose, moderately strong styles and ribs, central cavities connect at mid-wear, upper premolar series large and long, P^2 long with small parastyle; P^3 with large hypocone in relation to protocone. Retention of plesiomorphic dental features and is para-phyletic, large boselaphines from late Miocene assemblages, greater size, slightly more reduced premolar rows, and more inflated P_4 metaconids (Pilgrim, 1937; Spassov and Geraads, 2004).

Known Distribution: Eurasia, Africa and the Indian subcontinent (Pilgrim, 1937, 1939; Spassov and Geraads, 2004; Kostopoulos, 2009).

Tragoportax punjabicus (Pilgrim, 1910)

Type Specimen: GSI B486, skull.

Type Locality: Dhok Pathan, Middle Siwaliks, Punjab, Pakistan (Pilgrim, 1910, 1939).

Stratigraphic Range: Middle Siwaliks (Pilgrim, 1939; Akhtar, 1992).

Diagnosis: A species slightly smaller than *Tragoportax browni*, with relatively short upper premolar series; P^2 rather longer than P^3; upper molars with small entostyle; moderately developed styles and ribs; central cavities connect at mid wear and enamel moderately rugose (Pilgrim, 1937).

Studied Specimens: Upper dentition: PC-GCUF 10/08, isolated left P^3; PUPC 09/66, isolated right M^1; PC-GCUF 10/09, partial tooth probably M^1. Lower dentition: PC-GCUF 10/11, isolated right P_3; PUPC 09/70, isolated left P_4; PUPC 07/77, isolated left M_1; PUPC 07/86, isolated left M_1; PUPC 07/138, a mandibular ramus with P_4-M_2.

Description

Upper Dentition: PC-GCUF 10/08 is in early wear and triangular tooth showing all the morphological characteristics (Fig. 15(1)). The enamel is somewhat wrinkled and rugose. A prominent central cavity is present. A small, very thin, transverse enamel layer connects the posterior end of the protocone with the hypocone. The paracone is comparatively higher than the protocone. The anterior median rib is very prominent and closer to the parastyle. A furrow of moderate depth is present between the parastyle and the anterior median rib. The posterior groove is wider than the anterior one. The hypocone is inflated lingually.

PUPC 09/66 is in an early wear and an excellent state of preservation (Fig. 15(2)). The crown is quadrate. The crown height and width shows that it is a subhypsodont tooth. A faint cingulum is present on the antero internal and postero-internal surface of the molar. The entostyle near to hypocone is present. The cones are very well developed and broad. The protocone and the hypocone are similar in their general appearance. They are crescentric in shape. The metacone is higher than the paracone vertically. Both these cones are spindle shaped, broad in the center and narrowing at the sides. The styles are well developed and divergent. The metastyle is stronger than the parastyle. The mesostyle is also well developed. The posterior rib of the molar is stronger than the anterior one. The anterior cavity is deep and narrow while the posterior cavity is broader than the anterior one. PC-GCUF 10/09 is a partial tooth and most of the crown portion is missing. The occlusal view is somewhat available for the morphological study. The cavities and the posterior median rib can be seen in the tooth. The cones are crescentic and the rib is prominent in the molar. The styles, some parts of the protocone, the metacone and the hypocone are missing.

Lower Dentition: PC-GCUF 10/11 is an isolated dainty premolar (Fig. 15(3)). The metaconid of the premolar is backwardly directed. The entoconid of the premolar is stronger than the metaconid. The paraconid of the tooth is stronger than parastylid and placed antero-posterior axis of the premolar. The buccal surface appears flat and the lingul one presents two vertical grooves. The anterior one is open.

The P_4 PUPC 09/70 is in middle wear and has a postprotoconulidcristid, a metaconid, and a postmetacristid (Fig. 15(4)). The P_4 has a strong paraconid, metaconid and entoconid. The entoconid is fused with the endostylid. The prominence of the hypoconid is noteworthy and has a deep and narrow valley in front of it. The P_4 is extended antero-posteriorly. The metaconid of the premolar is larger than the P_3. It is splayed lingually forming T-shaped on the P_4, with an open anterior valley (Fig. 15(4)).

PUPC 07/77 and PUPC 07/86 are the first molars of the left lower molar series (Figs. 15(5-6)). The protocone of PUPC 07/77 is missing and the other parts are available for the crown study (Fig. 15(5)). PUPC 07/86 is broken anteriorly and posteriorly. The metastylid and the parastylid are prominent whereas the mesostylid is absent. The ectostylid is present but weak. The anterior transverse flange is present.

PUPC 07/133 with P_4-M_2 is well preserved and in an early wear (Fig. 16(7)). In the P_4 the enamel is finely wrinkled and it is thick on the lingual side. The P_4 has a strong paraconid, metaconid and entoconid and the metaconid of the P_4 is splayed lingually forming T-shaped with an open anterior valley (Fig. 16(7)). The M_1 ectostylid is strong and almost circular in cross section. The principlal conids are well developed and crescentic. The metaconid and the entoconid are spindle shaped with narrowing borders. The metastylid and the entostylid are prominent. The anterior and the posteriro median ribs are present. The anterior and the posterior central cavities are narrow. The M_2 is somewhat worn out on the lingual side. The overall contour indicates that it is subhypsodont and narrow crowned tooth. A very small ectostylid is located in the transverse valley between the protoconid and the hypoconid. The entoconid is highest vertically than the other conids. The central cavities are narrow and with simple outlines without any indentation. The metastylid and the mesostylid are more prominent than the entostylid. The comparative measurements are provided in table 5.

Comparison and Discussion

Being a squared and tetratuberculated sample it can be referred to some herbivorous mammalian group. Crescentic cusps of selenodont nature represents that it can safely be included in the order Artiodactyla (Zittel, 1925; Romer, 1974). The compressed outer cusps favour its inclusion in the family Bovidae. The teeth are small size and selenodont. The teeth may be distinguished at a glance from teeth of *Pachyportax* and *Selenoportax* by their smaller size and the weaker basal pillar (Gaudry, 1865; Arambourg and Piveteau, 1929; Pilgrim, 1937).

The studied P^3 indicates inflated hypocone which is the feature of the genus *Tragoportax*. The P_4s display a T-shaped feature of *Tragoportax* (Spassov and Geraads, 2004). The described character somewhat corresponds to numerous medium-sized boselaphine *Tragoportax* from the Siwaliks to which this specimen could be attributed. The teeth are same in size and general morphology to *T. punjabicus* (Fig. 17; Table 5) and consequently, the sample can be assigned to *T. punjabicus*.

Tragoportax are known in the Siwaliks by five species namely *T. perimensis, T. islami, T. salmontanus, T. browni* and *T. punjabicus* (Pilgrim, 1937, 1939). The species is distinguished based on the horn-cores. *Tragoportax perimensis* and *T. islami* are represented by the poor fossil record. Kostopoulos (2009) contributed in an extensive systematic revision of the Samos bovids and synonymised *T. curvicornis* and *T. browni* with *T. punjubicus*. Kostopoulos (2009) adapted Moya-Sola's recommendations to synonymies *T. browni* with *T. punjabicus* because both of them are indistinguishable and have common stratigraphic origin from the Dhok Pathan Formation of the Middle Siwaliks. However, a more findings are required from the Middle Siwaliks for the exact specific determination of the Siwalik *Tragoportax*.

Table 5: Comparative measurements of the cheek teeth of *T. punjabicus* in mm (millimeters). * The studied specimens. Referred data are taken from Pilgrim (1939) and Akhtar (1992).

Number	Nature/ Position	Length	Width
PC-GCUF 10/08*	P^3	14.0	11.5
PUPC 09/66*	M^1	18.4	18.5
PC-GCUF 10/11*	P_3	14.0	7.00
PUPC 09/70*	P_4	15.5	8.20
PUPC 07/77*	M_1	18.0	12.3
PUPC 07/86*	M_1	17.4	11.5
PUPC 07/138*	P_4	14.6	9.00
	M_1	17.3	12.0
	M_2	19.7	12.0
GSI B486	P^3	14.5	12.0
	P^4	11.0	15.5
	M^1	18.0	18.0
GSI B574	M^1	18.0	19.0
GSI B563	M_1	19.0	12.5
	M_2	21.0	13.0
GSI B564	P_3	16.0	8.50
	P_4	17.5	10.0
	M_1	17.5	12.0
	M_2	20.5	14.0

Fig. 15. ***Tragoportax punjabicus*****. 1. PC-GCUF 10/08, lP^3. 2. PUPC 09/66, rM^1. 3. PC-GCUF 10/11, rP_3. 4. PUPC 09/70, lP_4. 5. PUPC 07/77, lM_1. 6. PUPC 07/86, lM_1. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.**

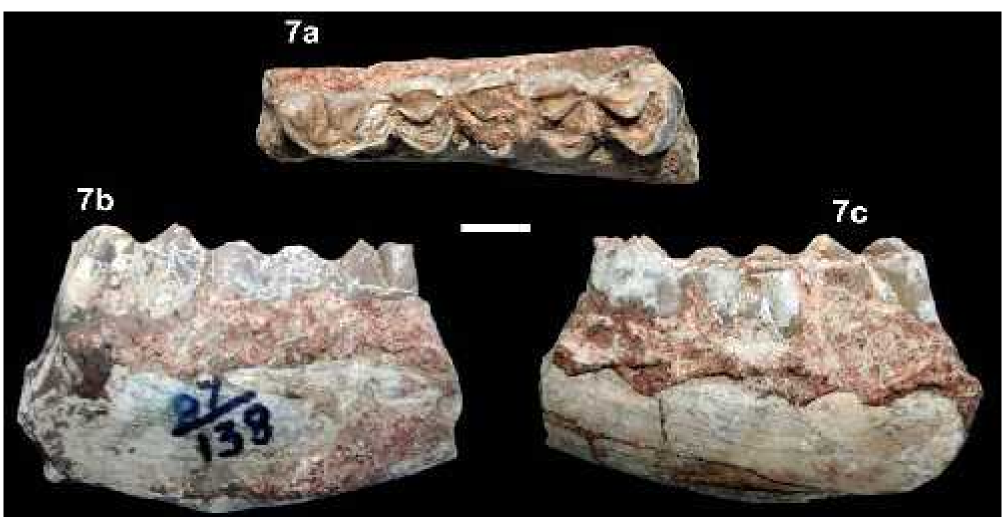


Fig. 16. ***Tragoportax punjabicus*****. 7. PUPC 07/138, a mandibular ramus with P_4-M_2. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.**

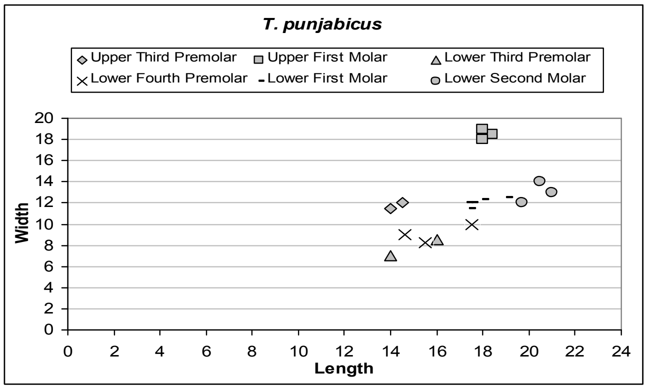


Fig. 17. Scatter diagram showing dental proportions of *T. punjabicus*'s studied sample. Referred data are taken from Pilgrim (1939) and Akhtar (1992).

Genus *Miotragocerus* Stromer, 1928

Type Species: *Miotragocerus monacensis* Stromer, 1928.

Generic Diagnosis: Horn-cores triangular in cross section; above the orbits; not particularly compressed; converging anteriorly and forming a pronounced frontal buttress; not particularly twisted but with twist restricted to tips; gently diverging with tips neither turned in nor out; posterior grooves; anterior keel blunt, stopping about two-thirds from base forming at least one characteristic anterior demarcation (bump); horn-core thinner and rounder in cross section from point at which keel stops to tip; horn-core axis more vertical and bases broader anteroposteriorly, pedicals more poorly formed than in *Tragoportax*. Anterior keel blunter, often with several distinct growth bumps in males; less blunt, with a single bump in females. No postcornual pits; frontals strongly depressed behind horns; basicranium not particularly angled in relation to palate; preorbital fossa deep; supraorbital pits small, variable in number and position. Premolars longer in relation to the molars than in *Tragoportax*; P^2 long; P^3 with small hypocone in relation to protocone; upper molar central cavities connect at mid-wear; entostyle small on upper molars. P_4 cavity between paraconid and metaconid open; P_4 paraconid tends to be larger than parastylid. Differs from *Mesembriportax* in having less sinused frontals; differs from *Protragocerus* in having longer, more compressed horn-cores with an anterior keel (Solounias, 1981).

Known Distribution: Europe and south Asia (Pilgrim, 1937; Spassov and Geraads, 2004).

***Miotragocerus* cf. *gluten* (Pilgrim, 1937)**

Type Specimen: AMNH 19746, Skull laking face and most of the dentition.

Type Locality: West of Hasnot, upper boundary of the Chinji, Lower Siwaliks, Punjab, Pakistan.

Stratigraphic Range: Lower and Middle Siwaliks (Pilgrim, 1937; Thomas, 1984).

Abbreviated Diagnosis: Low crowned teeth with strongly folded walls. The upper molar central cavities connect at mid-wear and the entostyles are smaller than in *Tragoportax*. The lower dentition is more primitive than *Tragoportax*. The P_4 cavity between the paraconid and the metaconid is open and therefore P_4 is similar to P_3. The metaconids of $P_{3\text{-}4}$ are weak. The lower molars have transversely situated protoconids and hypoconids (Pilgrim, 1937, 1939; Solounias, 1981; Spassov and Geraads, 2004).

Studied Material: Upper dentition: PUPC 07/138, isolated left M^1. Lower dentition: PC-GCUF 10/12, isolated right P_3.

Description

Upper Dentition: The upper dentition only includes one molar. The molar PUPC 07/138 is brachydont (Fig. 18(1)). It is in early wear. The enamel is rugose. The molar has smart entostyle. The buccal styles and ribs are well developed and strongly projected in the molar (Fig. 18(1c)). The anterior median rib is well projected than the posterior one. The mesostyle is robust pillar like structure. The styles are divergent. The upper molar is with strong folded walls.

Lower Dentition: PC-GCUF 10/12 has a weak groove between the paraconid and the parastylid. The P_3 is unworn and well preserved (Fig. 18(2)). The preprotoconulidcristid distinguishes from the postprotoconulidcristid. The metaconid is located behind the protoconid. It has flat lingual wall and enlarges from the tip to the base, tending to close the medial valley. The anterior lingual valley is much wider than the posterior ones. The protoconid is the highest among the conids. The postprotocristid leads to the entoconid through a thin praemetacristid. The postentocristid is directed towards the hypoconid. The posterior lingual valley is narrow relative to the anterior one. A short and moderately developed entostylid is present adjacent to the entoconid. The anterior half of the tooth is elevated relative to the posterior one. The cingulid is absent and enamel is rugose. The hypoconid is separated from the protoconid through a buccal groove. The comparative measurements are provided in table 6.

Comparison and Discussion

The recovered sample indicates the medium size bovid. Morphometrically, these specimens are typical of Miocene boselaphines in appearance; the divergent styles of the teeth make their inclusion in boselaphines. There are many differences among the boselaphines from the Dhok Pathan (Pilgrim, 1937, 1939; Thomas, 1984; Khan *et al*., 2009a). *Selenoportax* and *Pachyportax* are large size boselaphines found in the Dhok Pathan Formation (Khan *et al*. 2009a). The *Helicoportax, Elachistocerus* and *Eotragus* are comparatively small size boselaphines (Pilgrim, 1937, 1939; Akhtar, 1992; Khan *et al*., 2009a). The medium size boselaphines include *Tragoportax* and *Miotragocerus*.

The studied molar and premolar are well accentuated distinguished than those of *Tragoportax* (Spassov and Geraads, 2004). The morphology of the teeth show that the samples reflects the diagnostic features of *Miotragocerus* and differentiate them to *Tragoportax*, other Siwalik medium size boselaphine of the common stratigraphic range, and should be assigned to *Miotragocerus* (Figs. 18-19; Table 6). In the Siwalik, *Miotragocerus gluten* represents from the Chinji and the Nagri formations. The material resembles *Miotragocerus gluten* and it can be assigned to *M. gluten.* However, the material is insufficient for the specific determination and designates *M.* cf. *gluten* for the recovered sample.

Table 6: Comparative measurements of the cheek teeth of *Miotragocerus* (Pilgrim, 1937) in mm (millimeters). * The studied specimens. Referred data are taken from Pilgrim (1937).

Taxa	Number	Nature/ Position	Length	Width
M. cf. *gluten*	PUPC 07/138*	M^1	17.0	17.0
	PC-GCUF 10/12*	P_3	12.0	6.20
M. gluten	AMNH 29862	P^4	9.50	13.0
		M^1	13.0	15.0
		M^2	16.0	18.0
		M^3	16.0	16.0
	AMNH 19993	M_1	14.5	9.00
		M_2	16.5	11.0

Fig. 18. *Miotragocerus* cf. *gluten*. 1. PUPC 07/138, lM^1. 2. PC-GCUF 10/12, rP_3. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.

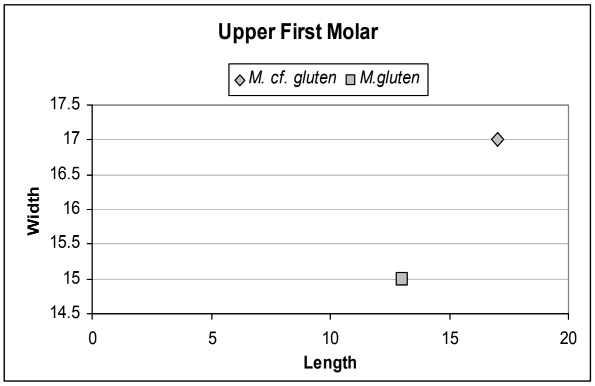


Fig. 19. Scatter diagram showing dental proportions of *M.* cf. *gluten*'s studied sample. Referred data are taken from Pilgrim (1937).

Tribe Antilopini

Genus *Gazella* Blainville, 1816

Type Species: *Gazella dorcas* Linneaus, 1758.
Generic Diagnosis: A *Gazella* of the size and type of the living *G. bennetti* but females hornless; skull long and slender; face bent down on cranial axis at about 35°; occipital rather high. Upper molars moderately hypsodont, styles narrow and strong with entostyles very small or absent, enamel moderately thick and rugose, central cavities narrow and deep, anterior median rib stronger than posterior one, premolar series rather long. Lower molars extremely hypsodont approaching quadrate shape, with small ectostylids, prominent goat folds, central cavities fairly simple in outline, stylids and ribs moderately developed. Horn cores moderately long, spaced, slightly curved backward, broadly elliptical in cross-section, fine ribs becoming rudimentary near the tips, one deep furrow posteriorly (Pilgrim, 1937).

Known Distribution: The occurrence of *Gazella* is recorded from the Lower Pliocene of Eurasia and several Pleistocene localities of Africa. It is abundantly found in the Lower Pliocene fauna of Asia and the southern parts of Europe. It is also recorded from the Siwaliks of the Subcontinent (Pilgrim, 1937, 1939; Thomas, 1984). *Gazella* is reported from the late Miocene of Sivas, Turkey (Bibi and Gulec, 2008) and Greece (Kostopoulos, 2009).

***Gazella* cf. *lydekkeri* Pilgrim, 1937**

Type Specimen: AMNH 19663, a skull and conjoined mandible (Pilgrim, 1937).

Type Locality: Dhok Pathan (the Middle Siwaliks), Punjab, Pakistan (Pilgrim, 1937).

Stratigraphic Range: The Lower and the Middle Siwaliks (Pilgrim, 1937; Khan, 2008).

Diagnosis: Hypsodont upper molars, strong styles, entostyles very small or absent, enamel moderately thick and rugose, central cavities narrow and deep, anterior median rib stronger than posterior one, premolar series rather long. Lower molars extremely hypsodont approaching quadrate shape, with small ectostylids, prominent goat folds, central cavities fairly simple in outline, stylids and ribs moderately developed (Pilgrim, 1937).

Studied Specimens: Lower dentition: PC-GCUF 09/02, a right mandibular ramus with M_{1-3}; PUPC 07/71, isolated left M_3.

Description

Lower dentition: The studied material comprises only lower dentition. A complete lower molar series is preserved in PC-GCUF 09/02 but the hypoconulid in the M_3 (Fig. 20(1)).

The ramus is poorly preserved and the molars are in early wear. The ectostylid size gradually decreases towards posterior of the molar series and consequently, the large ectostylid is in the M_1 and the small one is in the M_3 (Fig. 20(1c)). A goat fold is present anteriorly in the molars. The stylids are moderately developed and the mesostylid is the weakest. The anterior median rib is broad. The lingual conids are higher than the buccal ones. The hypoconulid is broken distally in the M_3.

PUPC 07/71 is in an early wear. The protoconid and the talonid are damaged slightly (Fig. 20(2)). The enamel is moderately thin on the lingual side while it is thick and shining on the buccal sides. The conids are well developed. The hypoconid appears to be more cresentric in shape than the protoconid. The apex of the entoconid is damaged. The metastylid is more developed than entostylid. The hypoconulid is well developed, high with a wide and inflated area. It is some what damaged posteriorly. The central cavities are narrow. The anterior central cavity is wider than the posterior one. The comparative measurements are provided in table 7.

Comparison and Discussion

The studied specimens present the typical structure of the molars for the genus *Gazella* and these are the prominent median ribs, the narrow styles and the appearance of the ectostylids in the lower molar. The presence of these characteristics in the studied specimens clearly confirms their inclusion to *Gazella.* The morphometrical characters of the described specimens resemble with the holotype of *G. lydekkeri* in the structure of the conids, the development of the stylids and ribs, and the presence of the ectostylids (Figs. 20-21; Table 7). However, the material is not enough to the specific identification. Therefore, *G.* cf. *lydekkeri* is assigned for the sample.

Table 7: Comparative measurements (mm) of the cheek teeth of *G. lydekkeri*. * The studied specimens. Referred data are taken from Pilgrim (1937, 1939); Akhtar (1992) and Khan (2008).

Number	Nature/Position	Length	Width
PC-GCUF 09/02*	M_1	15.0	10.0
	M_2	16.0	10.5
PUPC 07/71*	M_3	23.0	11.0
PUPC 04/08	M_3	20.0	9.00
AMNH 19663	M_1	10.0	12.0
PUPC 84/133	M_1	12.0	6.00
PUPC 84/67	M_1	14.5	9.00
PUPC 86/04	M_2	15.0	10.0
PUPC 87/ 162	M_3	22.0	10.5
PUPC 67/42	M_3	20.0	9.00
PUPC 84/67	M_1	15.0	9.00
	M_2	16.6	10.0
PUPC 87/160	M_1	12.2	8.00
	M_2	14.0	9.00
PUPC 04/02	M_1	11.0	8.20
	M_2	14.0	8.70
	M_3	19.0	8.60

The genus *Gazella* was erected by Blainville (1816) and was recorded for the first time as fossil horn-cores of *G. stehlini* in the European upper Vindobonian (Gentry, 1966). Most species of *Gazella* from Europe are founded on fragmentary material such as isolated teeth and horn-cores. All these species are small. Pilgrim and Hopwood (1928) simply summarized all the nomenclature of fossil gazelles propagating the existence of a large number of species. In their opinion the curvature, degree of divergence, and size of horn-cores should be the main criteria for species identification. They did not consider age, sexual variation and specimen deformation. Akhtar (1992) has noticed that these characters change with the age of the individual of a species in the living forms. Solounias (1981) has suggested that the type and degree of longitudinal grooving as well as the shape of the cross-section might be better species features although their variability is not known.

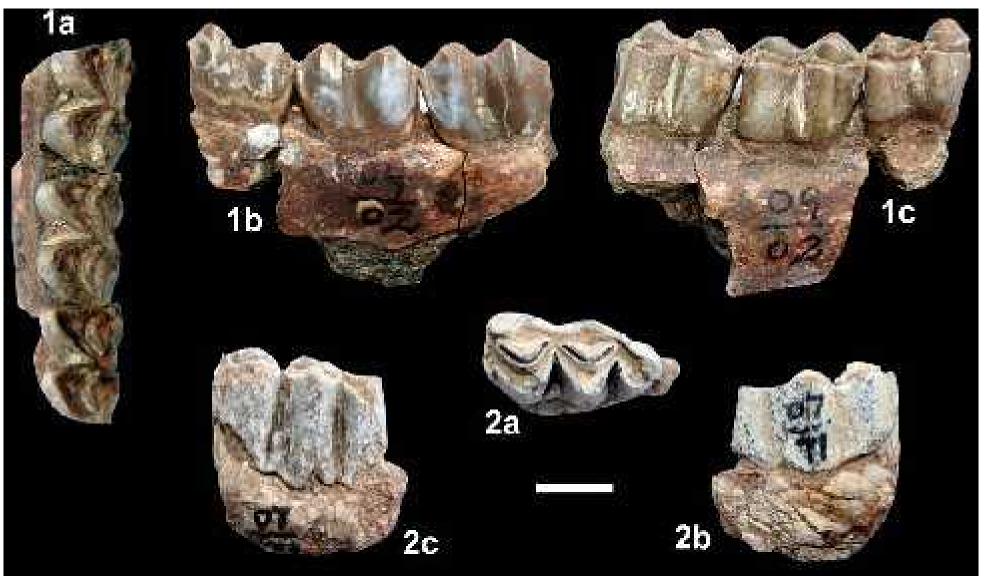


Fig. 20. *Gazella* cf. *lydekkeri.* 1. PC-GCUF 09/02, right mandibular ramus with $M_{1\text{-}3}$. 2. PUPC 07/71, lM_3. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.

Pilgrim (1937) erected a new species *G. lydekkeri* from the Siwaliks of Pakistan. The holotype is almost complete and comprising a skull and conjoined mandible (AMNH 19663). It is much more like the living forms of *Gazella* in having its longer and more slender skull, the higher occipital and the shape and direction of its horn-cores. *Gazella capricornis*, the best known of the European Pontian species is represented by more material than *G. deperdita.* It differs from *G. lydekkeri* in having large size of the skull, and less hypsodonty. In this respect, *G. lydekkeri* is more primitive than *Gazella capricornis*, the most progressive feature of *G. lydekkeri* is its hypsodonty.

The Chinese Pontian gazelles are more progressive especially the species *G. dorcadoides.* In all the Chinese species the skull seems to be less slender than in *G. lydekkeri* although the width at the orbits is greater. The horn-cores seem to be identical in their morphology with *G. lydekkeri* and the nasals are somewhat shorter. In *G. dorcadoides* and *G. altidens* the teeth are still more hypsodont than in *G. lydekkeri.* Gentry (1970) and Solounias (1981) considered *G. lydekkeri* as an invalid species. Recently, Khan and Farooq (2006) described ruminant fauna from the Neogene of the Siwaliks of Pakistan. They discussed the appearance of the ruminant species in the Siwalik Hills of Pakistan. According to their report, *G. lydekkeri* and *G. padriensis* Akhtar, 1992 appeared in the Middle Siwaliks of the Siwalik Hills of Pakistan.

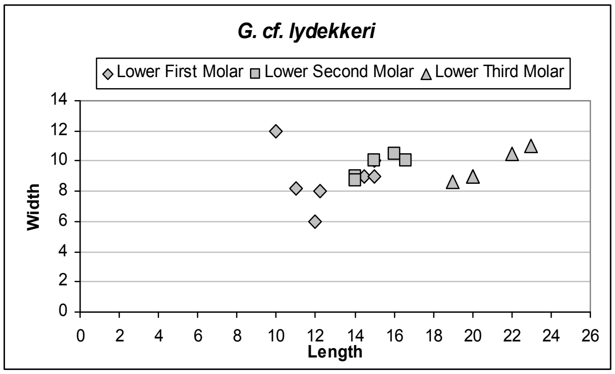


Fig. 21. Scatter diagram showing dental proportions of *G.* cf. *lydekkeri*'s studied sample. Referred data are taken from Pilgrim (1937, 1939); Akhtar (1992) and Khan (2008).

Family Giraffidae Gray, 1821
Subfamily Palaeotraginae Pilgrim, 1911

Genus *Giraffokeryx* Pilgrim, 1910

Type Species: *Giraffokeryx punjabiensis* Pilgrim, 1910.

Generic Diagnosis: Medium size giraffid with four horns, two at the anterior extremities of the frontal and two on the fronto-parietal region. Posterior horn overhanging the temporal fossa. Limbs and feet presumably of medium length. Teeth are brachydont with rugose enamel as in the other genera of the Giraffidae. *Giraffokeryx* was a medium sized member of the Giraffidae distinguished by two pairs of horn cores (ossicones) (Matthew, 1929; Colbert, 1935).

Known Distribution: Indian subcontinent and Eurasia (Pilgrim, 1910; Colbert, 1935; Geraads, 1986; Janis and Scott, 1987a; Gerntry and Hooker, 1988; Bhatti, 2005; Bhatti *et al*., 2007; Khan *et al*., 2010b).

Giraffokeryx punjabiensis Pilgrim, 1910

Lectotype: GSI B502, a third molar of the right maxilla.
Type Locality: Chinji, Lower Siwaliks, Punjab, Pakistan (Colbert, 1935).

Stratigraphic Range: Lower Siwaliks and the lower portion of the Middle Siwaliks (Colbert, 1935; Bhatti, 2005).

Diagnosis: Larger than the other species of the genus. Upper molars are comparatively large and subhypsodont. Parastyles and mesostyles are well pronounced. Accessory column present blocking the transverse valley (Colbert, 1935).

Studied Material: Upper dentition: PUPC 07/88, isolated left P^3; PUPC 09/67, partially preserved isolated right P^3; PUPC 07/133, isolated right M^2. Lower dentition: PUPC 09/43, left hemimandible with M_{2-3}, broken canine and alveoli of P_3-M_1; PUPC 07/90, isolated right M_3.

Description

Upper dentition: PUPC 07/88 and PUPC 09/67 are in middle wear. PUPC 07/88 is well preserved (Fig. 22(1)) whereas PUPC 09/67 is broken lingually and buccally (Fig. 22(2)). The premolars are greater in length than in width, and each tooth is characterized by a strong parastyle, and an internal posterior swelling (Fig. 22(1-2)). A well developed paracone rib is present close to the parastyle forming two vertical grooves. The anterior groove is narrow and the posterior groove is broad. The three rooted premolars have thick and rugose. The cingulum is not developed. The central cavity is well developed. The internal side of the buccal crescent is weakly divided into paracone and metacone. The premolars look subquadrangular with an antero-lingual protuberance of the lingual wall (Fig. 22(1)).

The second molar is approximately quadrate, with the protocone and the metaconule of about equal size and with strong parastyle and mesostyle (Fig. 22(3)). The molar is in middle wear. The enamel is thick and rugose. All the major cusps are well developed and prominent. The buccal cusps are slightly higher than the lingual ones. The entostyle is absent. The cingulum is present anteriorly, posteriorly and lingually. The praeprotocrista is narrow and touches to the parastyle. The general contour of the paracone is like spindle with maximum width in the middle. The metacone resembles the paracone in general shape and it is pyramidal with two sloping cristae. The hypocone is crecentic in shape and it is connected with the metacone through a narrow ridge posteriorly. The anterior central cavity is shallower than the posterior one. The styles are well developed. The mesostyle is strongly developed and the parastyle is more prominent than the metastyle. The anterior median rib is absent but the posterior one is very prominent and broad at the tip of crown.

Mandible: PUPC 09/43 hemimandible is an incomplete specimen retaining only broken canine, two last molars and the base of the ascending ramus (Fig. 23(4)). The anterior part of the symphysis is broken. The symphysis is flat. The length of the hemimandible is 263 mm. The body of the mandible is typical of giraffid species; it is bucco-lingually narrow. The depth of the mandible below P_2 is 47 mm and it is 61 mm below M_3. The diastema between the canine and the P_2 is excellenty preserved having length of about 46 mm. It is hitherto recovered for the first time for the species *Giraffokeryx punjabiensis* from the Nagri type locality. Colbert (1933) restored diastema based on comparison with *Palaeotragus*. The length of the lower molar series is 79 mm and the premolar series is 56 mm. The ventral edge of the horizontal ramus is thick. The posterior edge of the angle of the mandible is thin and the masseteric fossa is deep (Fig. 23(4)). The lower molars in the hemimandible are in the latest wear but they consist of the familiar ruminant crescents, and in the third molar there is a talonid.

Lower dentition: PUPC 07/90 is a high crowned tooth with hypoconulid and rugose enamel (Fig. 24(5)). Its length is much more than the transverse width. The cigulum is well developed anteriorly. The protoconid is well developed and V-shaped. The metaconid is slightly worn out and it is spindle shaped. It is slightly wider in the middle with the narrow sloping cristids. The postmetacristid is overlaping with the praeentocristid. The praehypocristid and posthypocristid are simple. A well developed ovate central cavity is present in the hypoconulid. The mesostylid is well developed whereas the metastylid and the entosylid are weakly developed. The ectostylid is present on the buccal side in front of the hypoconid and a supplementary one is present between the hypoconid and the talonid. The comparative measurements are provided in table 8.

Table 8: Comparative dental measurements of the cheek teeth of the Siwalik *Giraffokeryx* and *Giraffa* in mm (millimeters). * The studied specimens. Referred data are taken from Matthew (1929), Colbert (1935) and Bhatti (2005).

Taxa	Number	Nature/Position	Length	Width
Giraffokeryx	PUPC 07/88*	P^3	24.0	21.3
punjabiensis	PUPC 09/67*	P^3	25.0	?22
	PUPC 07/133*	M^2	25.6	27.0
	PUPC 09/43*	M_2	23.0	17.0
		M_3	38.0	20.0
	PUPC 07/90*	M_3	39.0	13.0
	AMNH 19475	P^3	20.5	20.0
		M^1	22.0	24.0
		M^2	25.0	27.0
	AMNH 19334	M^1	25.5	25.0
	AMNH 19311	M^1	23.0	22.0
	AMNH 19930	P^3	22.0	20.0
	AMNH 19472	M^2	27.0	25.5
	AMNH 19587	M_2	25.0	17.0
		M_3	37.0	17.0
Giraffa priscilla	PUPC 07/131*	M^1	25.0	25.0
	PUPC 07/89*	M^1	27.0	27.0
	PUPC 02/99	M^1	24.0	24.0
Giraffa punjabiensis	GSI K 13/349	M^1	30.0	24.0
	PUPC 86/84	M^1	31.0	28.0
	PUPC 95/23	M^1	31.0	27.0

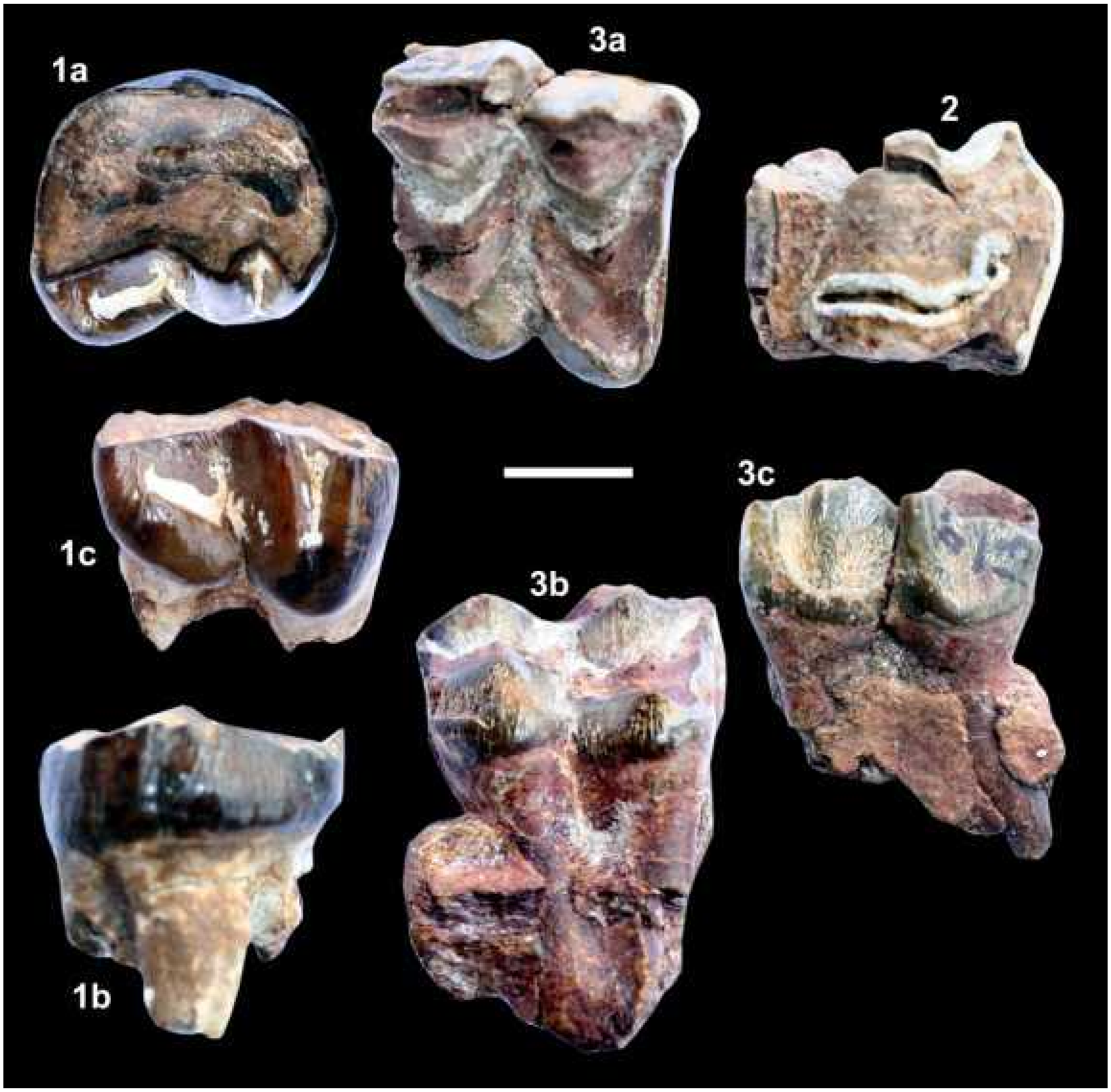


Fig. 22. ***Giraffokeryx punjabiensis*****. 1. PUPC 07/88, lP^3. 2. PUPC 09/67, rP^3: occlusal view. 3. PUPC 07/133, rM^2. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.**

Fig. 23. ***Giraffokeryx punjabiensis*****. 4. PUPC 09/43, left hemimandible with $M_{2\text{-}3}$, broken canine and alveoli of P_3-M_1. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 50 mm.**

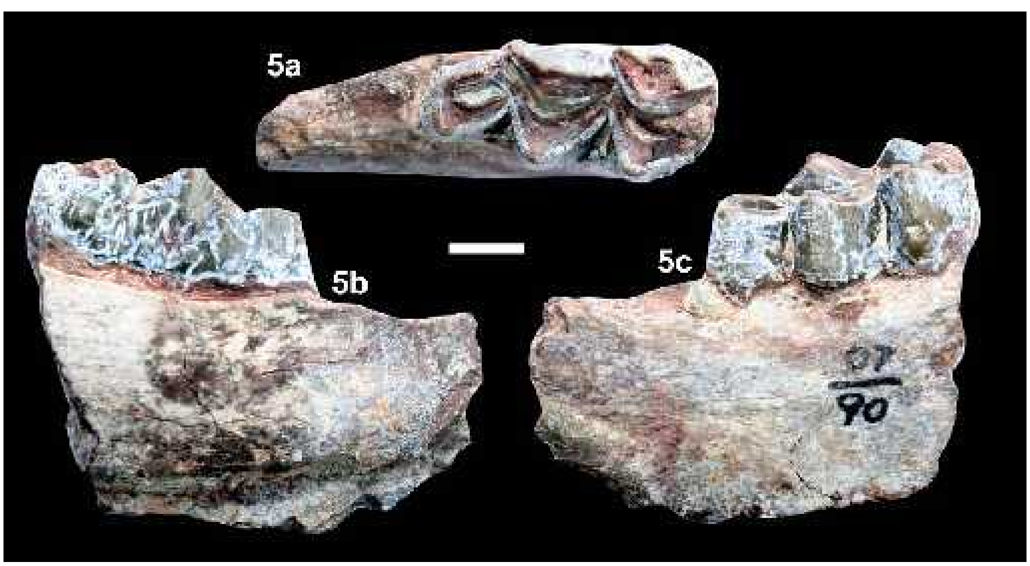


Fig. 24. ***Giraffokeryx punjabiensis*****. 5. PUPC 07/90, rM_3. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.**

Comparison and Discussion

The studied specimens include selenodont teeth and these may be referred to some tylopods or ruminants. Since the specimens under study have very rugose enamel and this fine rugosity is not seen in any tylopods so they can be referred to ruminants. In ruminants, such a heavy rugosity is the characteristic of the giraffids (Pilgrim, 1911). The Siwalik giraffids may be divided into two groups, one consisting of the large forms and other small forms (Sarwar and Akhtar, 1987). The small forms include the genera *Giraffokeryx* and *Giraffa,* while the large forms include the genera *Bramatherium*, *Hydaspitherium*, *Sivatherium*, and *Vishnutherium*.

The teeth are small in size and can be included *Giraffokeryx* and *Giraffa*. *Giraffokeryx punjabiensis* is very close to *Giraffa priscilla* in size (Colbert, 1935). The external folds (parastyles) are comparatively more developed in the premolars of the *Giraffa punjabiensis* which can be observed in the studied premolar. Moreover, the anteroposterior length and transverse width of the premolars are same to the already known material of the species *Giraffokeryx punjabiensis* (Table 8). The second molar shows the typical morphology of the species *Giraffokeryx punjabiensis.* The stylids and median ribs are less pronounced in the studied specimens, the feature of *Giraffokeryx punjabiensis.* Morphometrically, the specimens resemble to the already described samples of *Giraffokeryx punjabiensis* (Fig. 25) and should be assigned to *Giraffokeryx punjabiensis.* The hemimandible with diastema is new to science from Nagri, Middle Siwaliks of Pakistan and reports for the first time in this article.

Giraffokeryx was founded by Pilgrim (1910) on the genotype *Giraffokeryx punjabiensis.* The genus and species has been found from the Siwaliks of Pakistan and India, and is known from Turkey (Geraads *et al*., 1995). Pilgrim (1910) based *Giraffokeryx* upon a collection from various Lower Siwalik localities of Pakistan and India. The collection consisted of a skull, cranial fragments, mandibular fragments and many isolated teeth from the Nagri Formation of the Middle Siwaliks and the Chinji Formation of the Lower Siwaliks, which are described and figured by Pilgrim (1910, 1911) and Colbert (1935). *Giraffokeryx* attributes of a giraffe ancestor and occupies the right evolutionary position. Its features straddle its Palaeomerycine antecedents on the one hand and the Palaeotraginae assemblage that seems to have arisen from them. Colbert (1935) concluded from his analysis of its fossils that it had an elongated neck and drew it as a small giraffe (e.g. see p. 331). The reconstruction by Savage and Long (1986) shows it looking more like an okapi. According to Mitchell and Skinner (2003) is that *Giraffokeryx* is a primitive palaeotragine and an ancestral species to *Giraffa*.

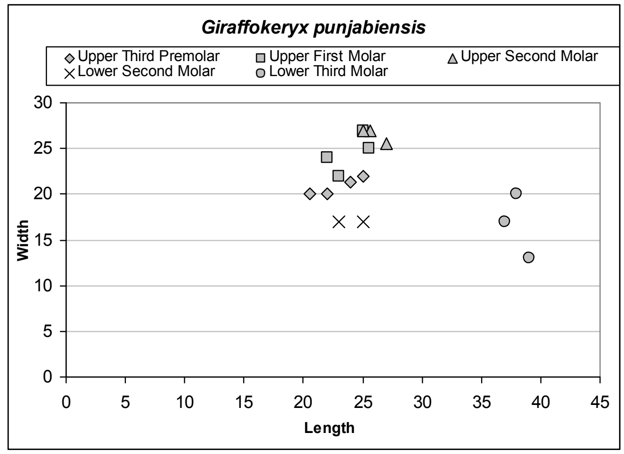


Fig. 25. Scatter diagram showing dental proportions of *G. punjabiensis*'s studied sample. Referred data are taken from Matthew (1929), Colbert (1935) and Bhatti (2005).

Subfamily Giraffinae Zittel, 1893

Genus *Giraffa* Brunnich, 1771

Type Species: *Giraffa giraffe* Brunnich, 1771.

Generic Diagnosis: Medium sized giraffids with extremely elongated neck and limbs, skull with a moderately large post-orbital development; basicranial and basifacial axes inclined at a small angle. Paired parieto-frontal bony processes of small size and a median naso-frontal protuberance in both sexes; in some species paired occipital processes. A pre-lachrymal vacuity is present (Colbert, 1935). Dentition very brachydont, enamel very rugose, enamel folds penetrating deeply into the crown and enamel islands not formed until a late period of dentition, lobes very oblique to the axis. External ribs of upper teeth very strongly marked, outgrowths of enamel from the crescents into the central cavity. Length not in excess of breadth, tubercles variable, but generally rudimentary, cingulum absent. Lower molars not elongated, tubercles in the external valleys variables but a large one always present in M_1 and generally in M_3 (Matthew, 1929; Colbert, 1935).

Known Distribution: Indian subcontinent, Greeco-Iranian province and Africa (Pilgrim, 1910, 1911; Matthew, 1929; Colbert, 1935; Gentry, 1997).

Giraffa cf. *priscilla* Matthew, 1929

Type: GSI B511, a left M^3.

Type Locality: Upper portion of Chinji, Lower Siwaliks, Punjab, Pakistan (Matthew, 1929).

Stratigraphic Range: Lower Siwaliks and lower portion of the Middle Siwaliks (Matthew, 1929; Colbert, 1935; present study).

Diagnosis: The broad and more brachydont teeth than those of *Giraffokeryx*. The metastyle and anterior rib are heavy; in M_3 the more oblique-set inner crescents, broad third lobe with strong accessory basal cusp in front of it, as well as shorter crown (Matthew, 1929).

Studied Specimens: Upper dentition: PUPC 07/131, isolated left M^1; PUPC 07/89, isolated right M^1.

Description

Upper dentition: The recovered material includes only upper dentition; one complete tooth and one partial tooth (Fig. 26(1-2)). The molars are brachydont and square shaped. The enamel sculpture is present. The buccal cones are higher than the lingual ones. The cusps are oblique to the axis of the tooth. The praepotocrista and the praehypocrista are larger than the postprotocrista and the posthypocrista Entotyle is present in the transverse valley. The median ribs are prominent. The styles are heavy; para-, meso- and metastyles are prominent in the buccal side. The anterior cingulum is present. The central cavity between protocane and paracone is closed at its front, and a spur is present in it posteriorly. The central cavity between hypocone and metacone is closed at its rear, and a spur in the cavity is triangular shaped closing the posterior ridge of the cavity at its center (Fig. 26(1-2)).

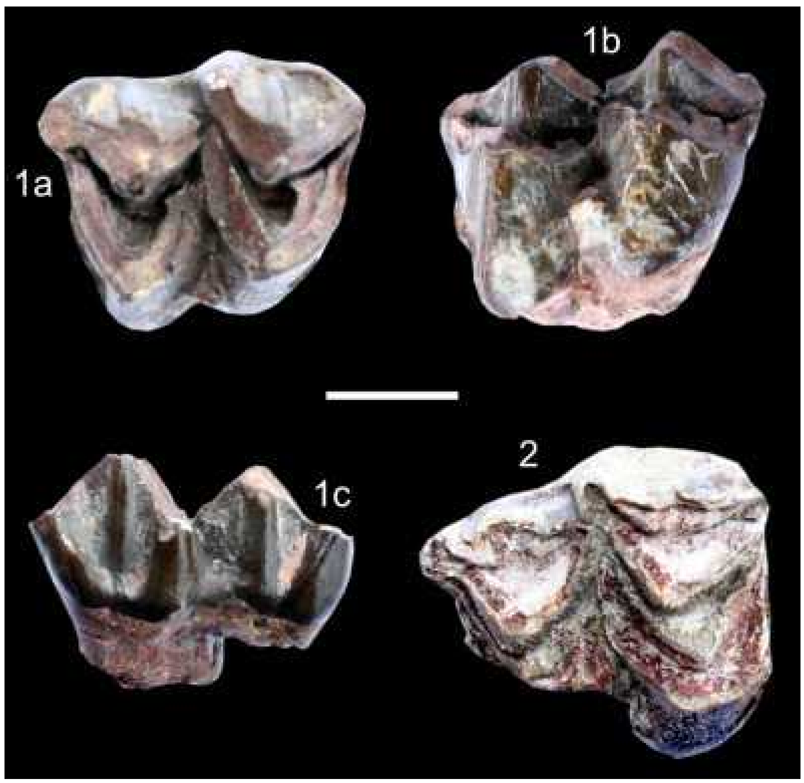


Fig. 26. *Giraffa* cf. *priscilla.* 1. PUPC 07/131, lM^1. 2. PUPC 07/89, rM^1: occlusal view. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.

Comparison and Discussion

The molars are about the same size as in *Giraffa priscilla* (Table 8) and the size is in practice the only distinguishing criterion in *Giraffa* (Gentry, 1997). The small size brachydont Siwalik giraffids include *Giraffokeryx* and *Giraffa* (Colbert, 1935; Bhatti, 2005; Khan *et al.*, 2010b). The styles are very weak in *Giraffokeryx* whereas these are strong in *Giraffa*. Median ribs are absent or very weak in *Giraffokeryx* and these are well pronounced in *Giraffa* (Matthew, 1929; Colbert, 1935). Furthermore, the crown is narrow in *Giraffokeryx* and it is broad in *Giraffa*. The cusps are not straight line in the studied molars. The recovered sample exhibits all the features present in *Giraffa* and the sample can be assigned to *Giraffa*.

The Siwalik *Giraffa* is represented by three species *G. sivalensis*, *G. punjabiensis* and *G. priscilla* (Colbert, 1935). The posterior half is reduced in *G. sivalensis* and *G. punjabiensis,* however, it is much reduced in *G. sivalensis*. The metastyle is strong in *G. priscilla* and weak in *G. sivalensis*, *G. punjabiensis*. *Giraffa sivalensis* and *G. punjabiensis* are somewhat large species and *G. priscilla* is small species of the Siwalik *Giraffa*. The recovered sample is pretty fit to *G. priscilla* in morphometrically (Fig. 27; Table 8). Nevertheless the sample is insufficient for the exact specific determination and assigns to *G.* cf. *priscilla*.

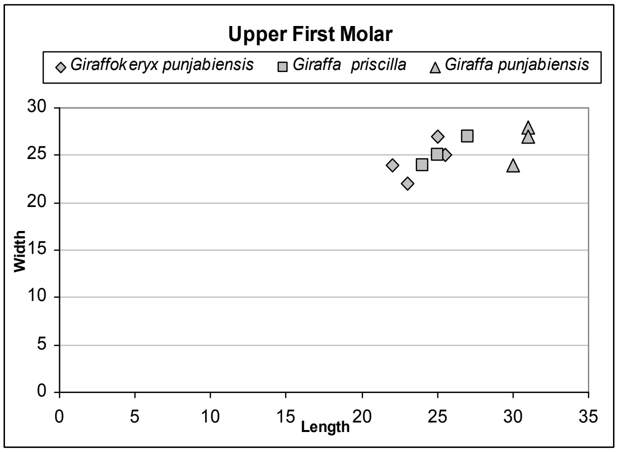


Fig. 27. Scatter diagram showing dental proportions of *G.* cf. *priscilla*'s studied sample. Referred data are taken from Matthew (1929), Colbert (1935) and Bhatti (2005).

Family Tragulidae Milne-Edwards, 1864

Genus *Dorcatherium* Kaup 1833

Type Species: *Dorcatherium naui* Kaup, 1833.

Generic Diagnosis: Bunoselenodont to selenodont teeth with more or less strong cingula and cingulidae and mostly strong styli and stylidae at the molars. The upper molars increase in size from M^1 to M^3. The lower molars show a special crest complex called the '*Dorcatherium*-fold'. It is formed by the bifurcation of the posterior slopes of the protoconid and the metaconid resulting in a 'Σ' shape. The premolars are comparatively long and consist mainly of the buccal conids and crests. Lingual crown elements are underrepresented. At the P_4 the entoconid fuses with the postprotocristid. The P_3 has only a short lingual entocristid originating at the hypoconid. An exception is the P^4, which is shorter and does not have an anteroposterior longish shape. The cheek teeth are high crown. The upper molars bear strongly developed buccal styles. The lower molars are characterized, either by well-developed ectostylid or by a vestigial ectostylid (Kaup, 1833; Rössner, 2010).

Known Distribution: *Dorcatherium* is known from the Lower Miocene of Europe by Kaup (1833) and Arambourg & Piveteau (1929). It is also reported from the Miocene deposits of East Africa by Arambourg (1933), Whitworth (1958) and Hamilton (1973). It is distributed from middle Miocene to early Pliocene in Asia, and late early Miocene to early Pliocene in Africa (Pickford *et al.,* 2004). *Dorcatherium* is recorded from the Siwaliks by Lydekker (1876), Colbert (1935), Prasad (1968), Sahni *et al.* (1980), West (1980), Farooq (2006) and Farooq *et al*. (2008).

***Dorcatherium* cf. *minus* Lydekker 1876**

Type Specimen: GSI B195, right $M^{1\text{-}2}$.

Type Locality: Kushalgar near Attock and Hasnot, Punjab, Pakistan (Colbert, 1935).

Stratigraphic Range: Lower to Middle Siwaliks.

Diagnosis: A small species of the genus *Dorcatherium* with sub-hypsodont molar and broad crowned molars having well developed cingulum, rugosity, styles, moderately developed ribs and vestigial ectostylids (Colbert, 1935).

Studied Specimens: Upper dentition: PC-GCUF 10/10, isolated left dP^4. Lower dentition: PUPC 07/69, a right mandibular ramus with partial M_1 and complete M_2.

Description

Upper Dentition: The recovered upper dentition comprises only one deciduous premolar (Fig. 28(1)). The tooth is in early wear and extremely brachydont. The central cavities are filled with matrix. The front and back walls of the tooth are convergent. The anterior rib is strong enough to form two vertical grooves: one between the parastyle and the anterior median rib and the second is between the anterior median rib and the mesostyle. The occlusal length of 15.5 mm buccally and it is 6.4 mm lingually. It has a notably large parastyle and a cingulum on its lingual lobes (Fig. 28(1b)). The strong parastyle and the convergent front and back walls of the tooth suggest it is a dP^4 and not a molar.

Lower Dentition: PUPC 07/69 is a fragile mandibular fragment having a posterior half of the first molar and the complete second molar (Fig. 28(2)). The second molar is hypsodont and narrow crowned tooth. It is almost unworn tooth. The metaconid is pointed and higher than the protoconid and the hypoconid. The entoconid is more pointed and higher than the hypoconid. The rudimentary ectostylid is present. The posterior cavity is crescentic in shape and opening out of the tooth at the lingual side. An anterior cingulid is present. The anterior rib and stylid are well developed. A prominent and narrow posterior rib is present but posterior stylid is weak. The *Dorcatherium* fold is present and directed posteriorly. It is formed by the bifurcation of the posterior slopes of the protoconid resulting formed a 'Σ' shape, a diagnostic feature of

Dorcatherium. The comparative measurements are provided in table 9.

Comparison and Discussion

The upper and lower molars show all the morphological features of the species *D. minus* as described by Lydekker (1876) and Colbert (1935) e.g., the small sized upper and lower molars. The upper molars are specifically characterized by their finely rugose enamel, a comparatively weak mesostyle and well-developed lingual cingulum, whereas the lower molars are characterized by the slight rugosity and the vestigial ectostylid (Colbert, 1935; Farooq, 2006). The described specimens are found to closely resemble to the type specimens regarding the measurements (Table 9). Consequently, the material assigns to *D.* cf. *minus*, based on the morphometric features (Fig. 30). The above said discussion confirms that the specimens belong to the species *Dorcatherium* cf. *minus* undoubtedly.

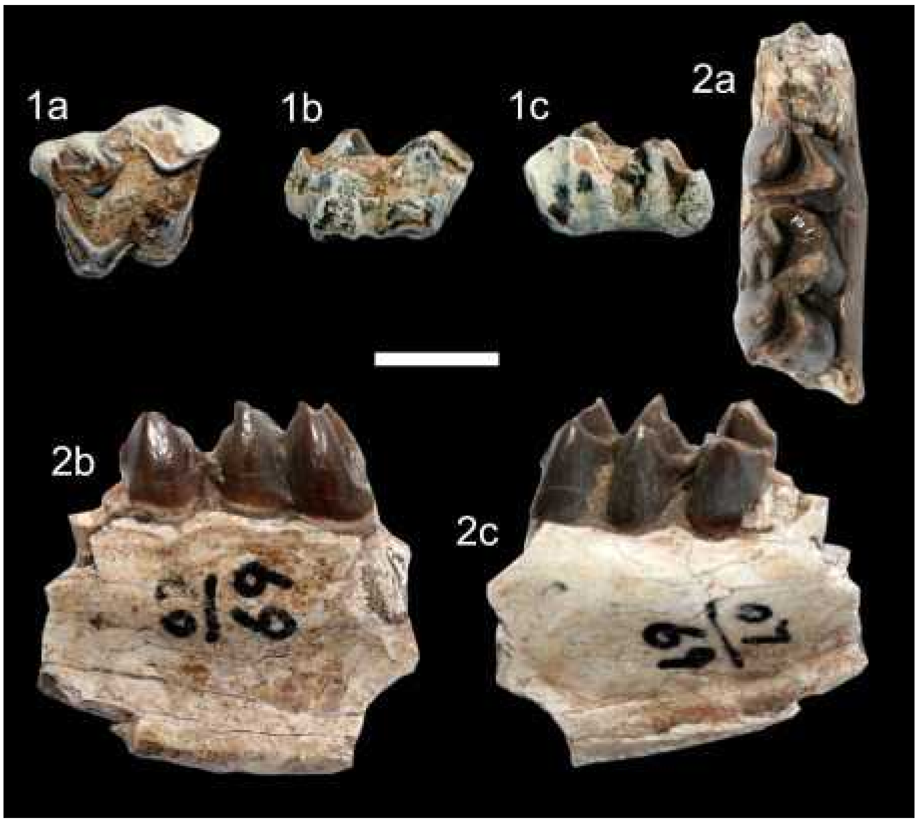


Fig. 28. *Dorcatherium* cf. *minus*. 1. PC-GCUF 10/10, ldP^4. 2. PUPC 07/69, a right mandibular ramus with partial M_1 and complete M_2. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.

***Dorcatherium* cf. *majus* Lydekker, 1876**

Type Specimen: GSI B197, two upper molars (right M^{1-2}).
Type Locality: Hasnot, Jhelum, Punjab, Pakistan.

Stratigraphic Range: Lower to Middle Siwaliks (Colbert, 1935; Farooq, 2006; Farooq *et al*., 2008).

Diagnosis: *Dorcatherium majus* is a species larger than *Dorcatherium minus* and is equal in size to *Dorcabune anthracotherioides*. It is characterized by strong parastyle and mesostyle, well-developed cingulum in upper molars and stoutly developed ectostylid (Colbert, 1935).

Studied Specimens: Upper dentition: PC-GCUF 09/46, isolated right M^2.

Description

Upper Dentition: PC-GCUF 09/46 (Fig. 29(1)) is a well preserved specimen, in early wear. The tooth is quadrate in its general appearance. Transversely, it is more wide anteriorly than posteriorly. The specimen under study is brachydont and broad crown. The enamel is uniformly thick and rugose. The cingulum is thick and well developed on the lingual side, especially at the entrance of the transverse valley, whereas on the anterior and posterior sides of the tooth the cingulum becomes thin and high. It is entirely absent around the buccal cones. The anterior and posterior cavities are deep and wide. All four major cusps are inclined towards the median longitudinal axis of the molar, although the degree of inclination is greater in the lingual cusps than the buccal ones. The protocone is more worn than the other cusps. It exhibits semi-crescentic shape, as its praeprotocrista is longer than the postprotocrista. The praeprotocrista is linked with the parastyle through a thin crista of the enamel and the postprotocrista on the other hand is free. The paracone is higher than the protocone. The praeparacrista and the postparacrista seem to be equally worn. The parastyle and the anterior median rib are well developed and linked together at their base. The metacone is the highest cone among all cones. It is also equally worn anteriorly and posteriorly. The posterior median rib is weaker than the anterior one. The mesostyle is well developed, whereas the metastyle is comparatively weak. The hypocone is more crescentic than the protocone, because the praehypocrista and the posthypocrista are almost equal in length, exhibiting V-shaped structure. The praehypocrista is not linked with the postprotocrista. The comparative measurements are provided in table 9.

Fig. 29. *Dorcatherium* cf. *majus.* 1. PC-GCUF 09/46, isolated right M^2. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.

Comparison and Discussion

The studied specimens prove their inclusion in the family Tragulidae, based on the selenobunodont to selenodont pattern with strong cingula (Rössner, 2010). There are two genera *Dorcatherium* and *Dorcabune* of family Tragulidae present in the Siwaliks (Colbert, 1935). The *Dorcabune* is a large extinct tragulid of the Siwaliks and close to the anthracotherioides having the most bunodont molars. The anterior median rib is also heavier in *Dorcabune* than *Dorcatherium* (Colbert, 1935; Farooq *et al*., 2007a, b). The presence of the selenobunodonty cusp pattern, cingula and strong styles in the sample proves that the material belongs to the genus *Dorcatherium*. The Siwalik *Dorcatherium* is represented by three species *Dt. majus, Dt. minus* and *Dt. minimus* (Colbert, 1935; West, 1980) and show variation in size (Fig. 30). *Dorcatherium minimus* is erected by West (1980), based on the single upper third molar and it is probably considered invalid species (see Farooq, 2006). *Dorcatherium minus* is a small Siwalik tragulid and *Dorcatherium majus* is the large Siwalik species of *Dorcatherium* (Farooq *et al*., 2008). The studied specimen morphometrically pretty fit with *D. majus* (Table 9; Fig. 30) and should assign to *D. majus*. Nevertheless, the material is insufficient and assigns to *D.* cf. *majus*.

Genus *Dorcabune* Pilgrim, 1910

Type Species: *Dorcabune anthracotherioides* Pilgrim, 1910.

Generic Diagnosis: Primitive large tragulids having bunodont teeth. Isolated parastyle and mesostyle, prominent cingulum and enamel rugosity are the diagnostic characteristics of the upper molars, whereas lower molars are characterized by their broadness, a wide talonid in the third molar, and a pyramidal protoconid with two posteriorly directed folds (Pilgrim, 1910, 1915; Colbert, 1935). The upper molars of *Dorcabune anthracotherioides* are characterized by their brachydonty and bunodonty. The inner cusps of upper molars are truly selenodont, whereas the outer ones are quite bunodont and absolutely conical in their general appearance. The median rib on the buccal face of the paracone and metacone is so broad and prominent that it occupies almost all the space between the styles. This feature is very much pronounced in the paracone, the buccal surface of which is in fact entirely rib. The parastyle and mesostyle are strong, massive and isolated, whereas the metastyle is very weakly developed. With wear, the mesostyle clearly displays its closer association with the metacone instead of fusing equally to both paracone and metacone. The protocone, instead of being a simple crescent, is more pyramidal in shape and displays three equally strong folds, one proceeding forwards and outwards, the second backwards and a third backwards with a tendency sometimes inwards and sometimes outwards. A strong cingulum runs antero-posteriorly, but is very much pronounced round the protocone. It often rises into a small tubercle at the entrance of the transverse valley between the protocone and hypocone. The enamel is heavy and has moderately fine rugosity (Pilgrim, 1915; Colbert, 1935). The lower molars are also characterized by well pronounced brachydonty, bunodonty and presence of a typical tragulid M structure at the rear of the tragonid. The anterior arm of protoconid terminates on a broad shelf almost parallel to the anterior margin of the tooth. Entoconid is conical, producing out anteriorly a short process in the direction of the mid line between the two anterior cusps. The hypoconid is crescentic; its anterior arm touches to the external process of the protoconid, while its posterior arm runs inward and completely encircles the posterior base of the entoconid (Pilgrim, 1915; Colbert, 1935).

Known Distribution: The genus is found in the Lower Manchar of Bhagothoro, Pakistan, and the Lower and the Middle Siwaliks, and China (Pilgrim, 1910, 1915; Colbert, 1935; Han De-Fen, 1974; Farooq *et al*., 2007c).

Dorcabune cf. *anthracotherioides* Pilgrim, 1910

Type Specimen: GSI B580, a maxilla with molars.

Type Locality: Near Chinji, Chakwal, Punjab, Pakistan (Colbert, 1935).

Stratigraphic Range: Lower to Middle Siwaliks (Pilgrim, 1910, 1915; Colbert, 1935; Farooq *et al*., 2007c).

Table 9: Comparative measurements of the cheek teeth of *Dt. majus* and *Dt. minus* in mm (millimeters). * The studied specimens. Referred data are taken from Colbert (1935) and Farooq *et al*. (2007a, b, 2008).

Taxa	Number	Nature/Position	Length	Width
Dt. majus	PUPC 09/46*	M^2	19.4	19.0
	AMNH 19302	M^2	18.5	21.5
	GSI B198	M^2	19.6	19.6
	PUPC 85/15	M^2	19.0	20.0
	PUPC 85/21	M^2	18.0	22.0
	PUPC 87/328	M^2	17.7	19.0
	PUPC 67/191	M^2	13.3	14.5
	PUPC 68/33	M^2	13.3	14.5
	PUPC 68/250	M^2	15.7	16.4
	AMNH 19524	M_2	16.0	11.0
	GSI B593	M_2	17.5	10.0
	PUPC 63/243	M_2	17.0	10.1
	PUPC 84/115	M_2	16.0	12.0
	PUPC 86/02	M_2	15.6	9.80
	PUPC 86/05	M_2	15.0	11.1
	PUPC 86/152	M_2	16.2	12.0
	PUPC 98/61	M_2	17.0	10.5
	AMNH 19520	M_2	17.0	10.5
Dt. minus	PC-GCUF10/10*	dP^4	15.5	13.4
	PUPC 07/69*	M_2	13.0	8.00
	PUPC 68/41	M^2	11.0	13.0
	PUPC 68/355	M^2	10.5	11.8
	PUPC 86/81	M^2	10.0	12.2
	PUPC 95/01	M^2	10.0	11.0
	PUPC 02/01	M^2	10.5	11.6
	AMNH 29856	M^2	11.3	12.0
	GSI B195	M^2	11.0	12.0
	PUPC 68/294	M_2	11.0	6.40
	PUPC 68/311	M_2	10.0	6.60
	PUPC 68/312	M_2	10.0	6.20
	PUPC 68/313	M_2	10.2	6.70
	PUPC 85/59	M_2	9.50	7.00
	PUPC 02/158	M_2	12.7	8.20
	AMNH 19365	M_2	13.0	12.0

Diagnosis: *Dorcabune anthracotherioides* is larger than *Dorcabune hyaemoschoides* and almost equal to that of *Dorcatherium crassum* (Pilgrim, 1915; Colbert, 1935). The mandible bears a fairly deep groove starting beneath the P_4 and propagating towards the posterior side behind the teeth. This groove exists also in *Dorcatherium majus* and *minus* and in *Dorcabune latidens* but is absent in *Dorcabune nagrii* (Pilgrim, 1915). The upper molars of *Dorcabune anthracotherioides* are very similar to that of *Dorcabune hyaemoschoides* and differ only by the possession of prominent parastyle. The lower fourth premolar (P_4) is slightly shorter in length than the lower third premolar (P_3). P_4 is broad and consisting of three lobes, of which middle one is the highest and longest, whereas first and the last lobes are equal in length, though the third lobe is higher in unworn condition. Third lobe is massive and crescent-shaped facing towards the inner and the anterior sides. The posterior arm of the crescent is running out to a level with the internal margin of the tooth. A small notch separates this arm from a long wing which runs backward from the summit of the principal cusp and forms the inner wall of the tooth. This wing is separated by a deep elongated cavity from the crest, which connects the principal cusp to the hinder lobe (Pilgrim, 1915). *Dorcabune anthracotherioides* differentiates *Dorcabune latidens* by characterizing a less deep mandible bearing moderately broader molars and possessing much smaller size (Pilgrim, 1915).

Studied Specimens: Lower dentition: PUPC 07/87, isolated left M_2.

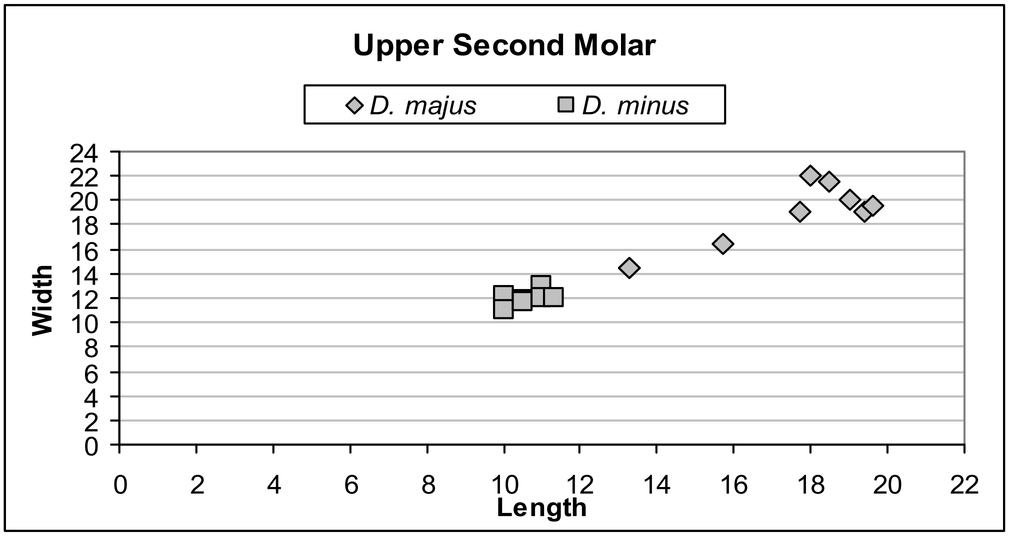
Description

Lower Dentition: The bunodont second lower molar is in a good state of preservation (Fig. 31(1)). It is in an early wear. It is hypsodont and narrow crown. The enamel is heavy, thick and very rugose. The cingulid is well developed on anterior and posterior sides but it is absent buccally and lingually. A small singular tubercle is also present between the hypoconid and the protoconid on the buccal side. The praeprotocristid terminates in a broad shelf, almost parallel to the anterior margin of the tooth. The postprotocristid is bifurcated and one limb of the bifurcation is attached to the postmetacristid while the other one is attached to the praehypocristid producing M structure (Fig. 31(1a)). The hypoconid is somewhat crescentic in shape; the praehypocristed touches the postprotocristid, whereas the posthypocristid runs inwards and completely encircles the posterior base of the entoconid. The metaconid is conical and bunodont. The entoconid is conical with a short anterior process proceeding between the two anterior conids. There is a vertical groove between the metaconid and the entoconid lingually. The comparative measurements are provided in table 10.

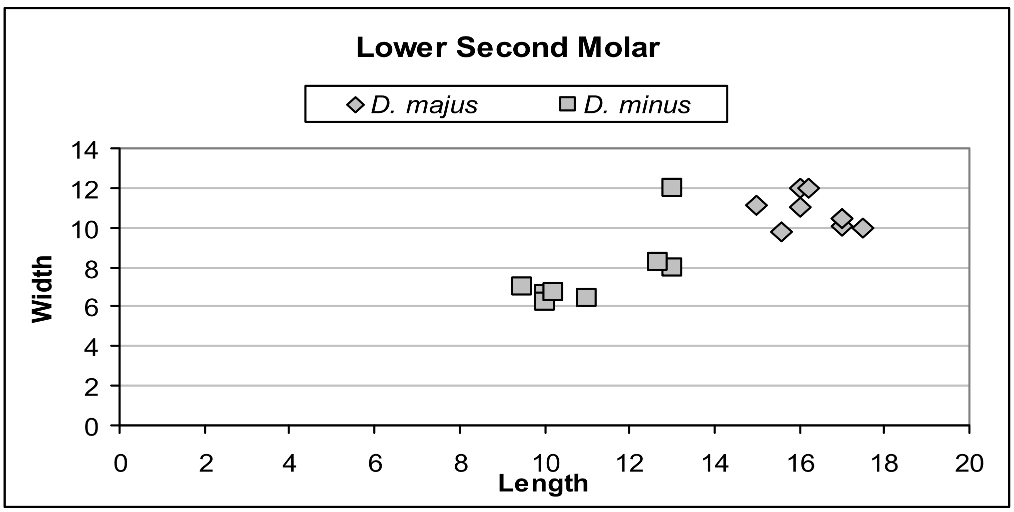
Comparison and Discussion

The recovered molar from the Nagri type area exhibits buno-selenodonty pattern. The selenodonty are found in families of Bovidae, Cervidae, Giraffidae and Camelidae and the semi-selenodonty with bunodont pattern is found in family Tragulidae (Colbert, 1935). The studied specimens reflect semi-selenodonty with bunodont pattern and belong to family Tragulidae. The Siwaliks are represented by two tragulid genera *Dorcatherium* and *Dorcabune* (Colbert, 1935; Farooq *et al*., 2007a-d). *Dorcabune* reflects bunodonty pattern and *Dorcatherium* is somewhat selenodont (Fig. 31). The bunodont conical cusp pattern of the studied samples confirms its inclusion to *Dorcabune* (Fig. 32). The molar has the same size of the already recovered sample of *D. anthracotherioides*. The molar is comparable with the holotype and the earlier described specimens (Table 10). Therefore, the molar assigns to *D.* cf. *anthracotherioides* (Colbert, 1935; Farooq *et al*., 2007c).

Dorcabune from the Siwaliks of Pakistan were erected by Pilgrim (1915), named three species: *Dorcabune anthracotherioides*, *Dorcabune hyaemoschoides*, *Dorcabune nagrii*, and *Dorcabune latidens*. *Dorcabune anthracotherioides* and *Db. nagrii* are considered as valid species where as *Db. hyaemoschoides* and *Db. latidens* are known by very poor record (Colbert, 1935; Farooq, 2006). According to Gentry (1978) *Dorcabune* is most probably an anthracotheriid, however a number of collected dental specimens from the Middle Siwaliks after Pilgrim (1910) evidently prove its inclusion in Tragulina.



A.



B.

Fig. 30. Scatter diagram showing dental proportions of *Dorcatherium*'s studied sample. Referred data are taken from Colbert (1935) and Farooq *et al*. (2007a, b, 2008).

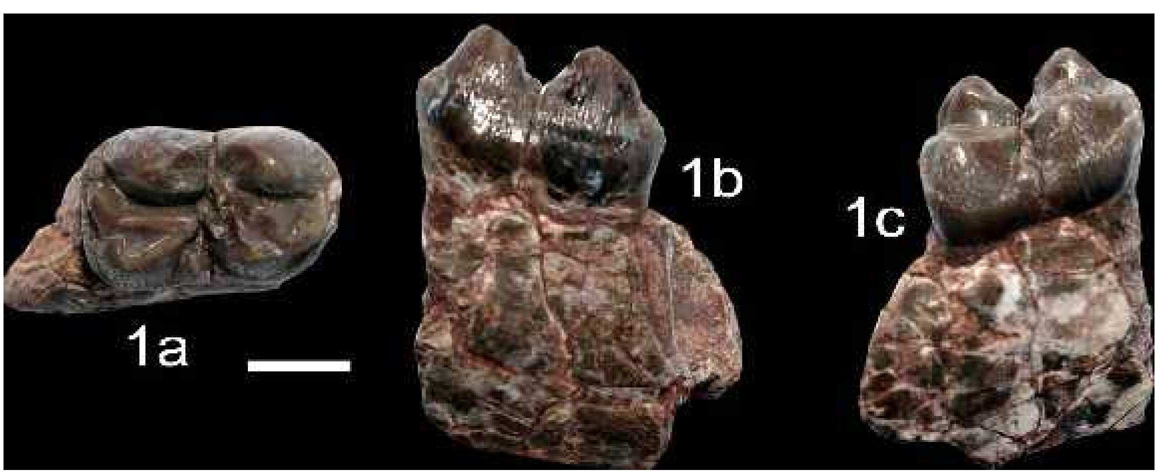


Fig. 31. *Dorcabune* cf. *anthracotherioides*. 1. PUPC 07/87, lM_2. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.

Table 10: Comparative measurements of the cheek teeth of *Dorcabune* cf. *anthracotherioides* in millimeters (mm). * The studied specimens. Referred data are taken from Colbert (1935) and Farooq *et al*. (2007c).

Number	Nature/Position	Length	Width
PUPC 07/87*	M_2	22.4	16.0
PUPC 96/65	M_2	20.30	13.30
PUPC 96/66	M_2	19.00	12.00
PUPC 99/89	M_2	19.60	11.55
AMNH 19355	M_2	17.50	13.00
GSI B.682/683	M_2	19.50	14.70
PUPC 85/28	M_3	26.00	13.00
AMNH 19353	M_3	28.00	14.00
GSI B682/683	M_3	30.90	16.00

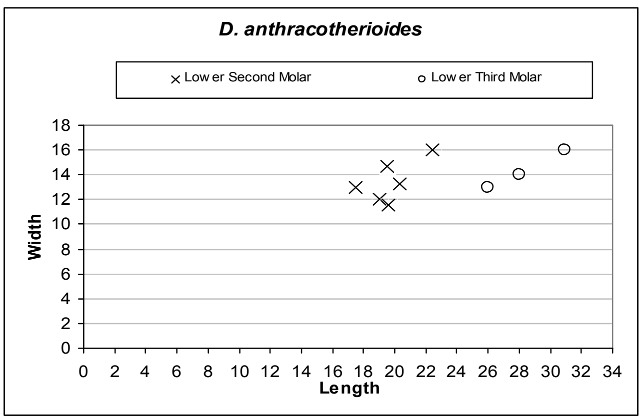


Fig. 32. Scatter diagram showing dental proportions of *Db.* cf. *anthracotherioides*'s studied sample. Comparative data are taken from Colbert (1935) and Farooq *et al*. (2007c).

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Subfamily Equinae Steinmann and Doderlein, 1890

Genus *Hipparion* de Chirstol, 1832

Type species: *Hipparion prostylum* Gervias, 1849.

Generic Diagnosis: Isolated and usually oval-elongated protocones in upper molars during early to late stage of wear. Tridactyl feet with elongate slender third metapodials. Prominent nasomaxillary fossa with a relatively well developed anterior rim. Hipparionine horses with markded reduction of preorbital fossa in length, dorsoventral height, medial depth and posterior pocketing. Maxillary cheek teeth show a tendency towards simplification of prefossette and postfossette ornamentation with thinner enamel bands. Plicaballins become simplified to a single morphology. Hypoglyph usually, moderately to shallowly incised in middle adult wear (Colbert, 1935).

Known Distribution: North America, Asia, Africa (Colbert, 1935; Pilbeam *et al*., 1997).

***"Hipparion theobaldi"* (*Sivalhippus* Complex)**

Type Specimen: GSI C153, a left maxilla with milk molars.

Type Locality: Keypar, Middle Siwaliks (Colbert, 1935).

Stratigraphic Range: Middle Siwaliks (Ghaffar, 2005; Naseem *et al*., 2009).

Diagnosis: A large *Hipparion* with tridactyl feet and deep preorbital facial fossa separated from the orbit by a relatively wide preorbital bar, fossa deeply pocketed posteriorly, medially deep and with a well defined continuous peripheral border including the anterior rim, cheek teeth complexly ornamented with thickly banded fossette plication and bifid to trifid plicaballins, protocones distinctly flattened lingually and rounded buccally, hypoglyphs deeply incised, P^2 anterostyle elongate (Colbert 1935).

Studied Material: Upper dentition**:** PUPC 07/61, isolated left P^2; PUPC 07/65, isolated left M^1; PUPC 07/66, isolated right M^1; PUPC 07/57, isolated left M^2; PUPC 07/58, isolated left M^3. Lower dentition: PUPC 07/60, isolated right P_2; PUPC 07/59, isolated right P_3; PUPC 07/78, isolated left P_4; PUPC 07/124, isolated right M_3.

Description

Upper Dentition: PUPC 07/61 is a well preserved tooth and it is in early wear. The premolar is almost triangular with characteristically well developed anterostyle. It is strongly elongated and pillar like (Fig. 33(1)). All the major cusps are well developed and preserved. The protocone is an isolated compressed pillar and elongated in shape. It is covered by a moderately thick layer of cement. The hypoconal groove is well developed and placed posteriorly. The styles are well preserved, strongly developed and prominent. The mesostyle is pillar like structure and is similar to the parastyle in general appearance. Both the styles are broad at the base and narrow at the apex. The metastyle is moderately developed and straight in shape. The hypostyle is weak and not prominent like the other styles. The protoloph, the metaloph, and the ectoloph are distinguished. The crown is highly plicated (Fig. 33(1)). The prefossette and postfossette are plicated with maximum enamel foldings. The plicaballin consists of bifurcated folds.

PUPC 07/65 and PUPC 07/66 (Figs. 33(2-3)) are the first upper molars of maxillary series. The molars are hypsodont and well preserved. The enamel is moderately thick and wrinkled. The layer of matrix is present all over the crown. The protocone, paracone, metacone and hypocone are preserved. The protoloph, ectoloph and metaloph reflect the loph pattern clearly. The protocone is not pillar like but sub-ovate and isolated. The paracone and the hypocone are not broad while the metacone is angulatory. The styles are well preserved. The mesostyle is strongly developed while metastyle is weakly developed. The pre-fossette and post-fosesstte are richly plicated with maximum enamel foldings at the posterior border of prefossette and at the anterior border of postfossette. The pliprotoloph, plihypostyle of postfossette are well preserved. The hypoconal groove is prominent and the fossettes are clear.

PUPC 07/57 is the well preserved second hypsodont molar (Fig. 33(4)). The enamel is rugose, moderately thick and wrinkled. The protocone is pillar like, sub-ovate and isolated which is the diagnostic character of *Hipparion* molar. The styles are well preserved on the buccal side. The mesostyle is strongly developed and more prominent than the parastyle and the metastyle. The parastyle is weak comparatively than the mesostyle and the metastyle. The ectoloph, protoloph and metaloph are well preserved. The thick layer of the cement is present lingually. The pliprotoloph, pre-fossttes and plipost-fossettes are clearly visible. The hypoconal groove is well developed, prominent and present posteriorly of the molars.

The M^3 is somewhat narrow posteriorly (Fig. 33(5)). The plicabillins are bifid and the hypoglaph is deeply incised. The protocone is rounded lingually and buccally. The tooth is in early wear. The pre- and postfossettes are moderately complex.

Lower Dentition: PUPC 07/60 comprises right isolated second premolar (Fig. 34(6)). The enamel is moderately thick. The principal conids are well developed. The protoconid is completely isolated from rest of the premolar and it is an oval shape. The buccal conids are spindle or cresentric in shape i.e. both are broad in the middle and narrow anteroposteriorly. The entoconid are triangular in shape and join with the metastylid through an isthamus, giving the appearance of double knot. The hypoconid is broad. The stylids are well developed and prominent like the conids. The ptycostylid is a fold like structure present at the mesial border of the hypoconid. The mesostylid is triangular in its outline. It is joined with metaconid by a narrow isthamus giving the appearance of double knot like structure. There is no demarcation of the ptycostylid and the anterior end of the hypoconid.

Table 11: Comparative measurements of the cheek teeth of *H. theobaldi* in mm (millimeters). * The studied specimens. Referred materials are taken from Colbert (1935) and Ghaffar (2005).

Taxon	Number	Nature/Position	Length	Width
H. theobaldi	PUPC 07/61*	P^2	37.0	26.0
	PUPC 07/65*	M^1	26.0	27.0
	PUPC 07/66*	M^1	26.5	25.5
	PUPC 07/57*	M^2	27.5	27.5
	PUPC 07/58*	M^3	28.0	20.7
	PUPC 07/60*	P_2	33.0	15.6
	PUPC 07/59 *	P_3	30.5	20.0
	PUPC 07/78*	P_4	25.3	20.0
	PUPC 07/124*	M_3	33.0	13.0
	AMNH 19857	P^2	32.0	26.5
	PUPC 83/284	P^2	39.5	21.5
	GSI C153	P^2	38.5	26.0
	PUPC 83/498	P^2	40.0	22.0
	AMNH 19466	M^1	26.0	26.0
	AMNH 19857	M^1	25.0	21.0
	AMNH 19836	M^2	22.0	21.0
	AMNH 19492	M^2	20.0	22.0
	AMNH 19711	M^2	28.0	29.0
	AMNH 19466	M^2	26.0	26.0
	AMNH 19466	M^3	24.0	22.0
	AMNH 19857	M^3	25.0	23.0
	PUPC 83/498	P_2	31.0	12.0
	PUPC 83/285	P_2	31.0	15.0
	PUPC 83/290	P_2	30.0	12.0
	PUPC 83/786	P_2	32.5	13.5
	PUPC 83/787	P_2	33.0	13.0
	PUPC 86/183	P_2	30.5	14.0
	PUPC 00/94	P_2	31.0	18.5
	PUPC 00/94	P_3	25.0	18.0
	PUPC 83/498	P_3	26.5	13.0
	PUPC 00/94	P_4	25.0	18.0
	PUPC 83/498	P_4	25.0	24.0
	PUPC 87/309	P_4	26.0	15.5
	PUPC 83/498	M_3	28.0	11.5
	PUPC 87/255	M_3	26.5	13.0
	PUPC 96/23	M_3	28.5	13.5
	PUPC 00/94	M_3	30.0	13.5

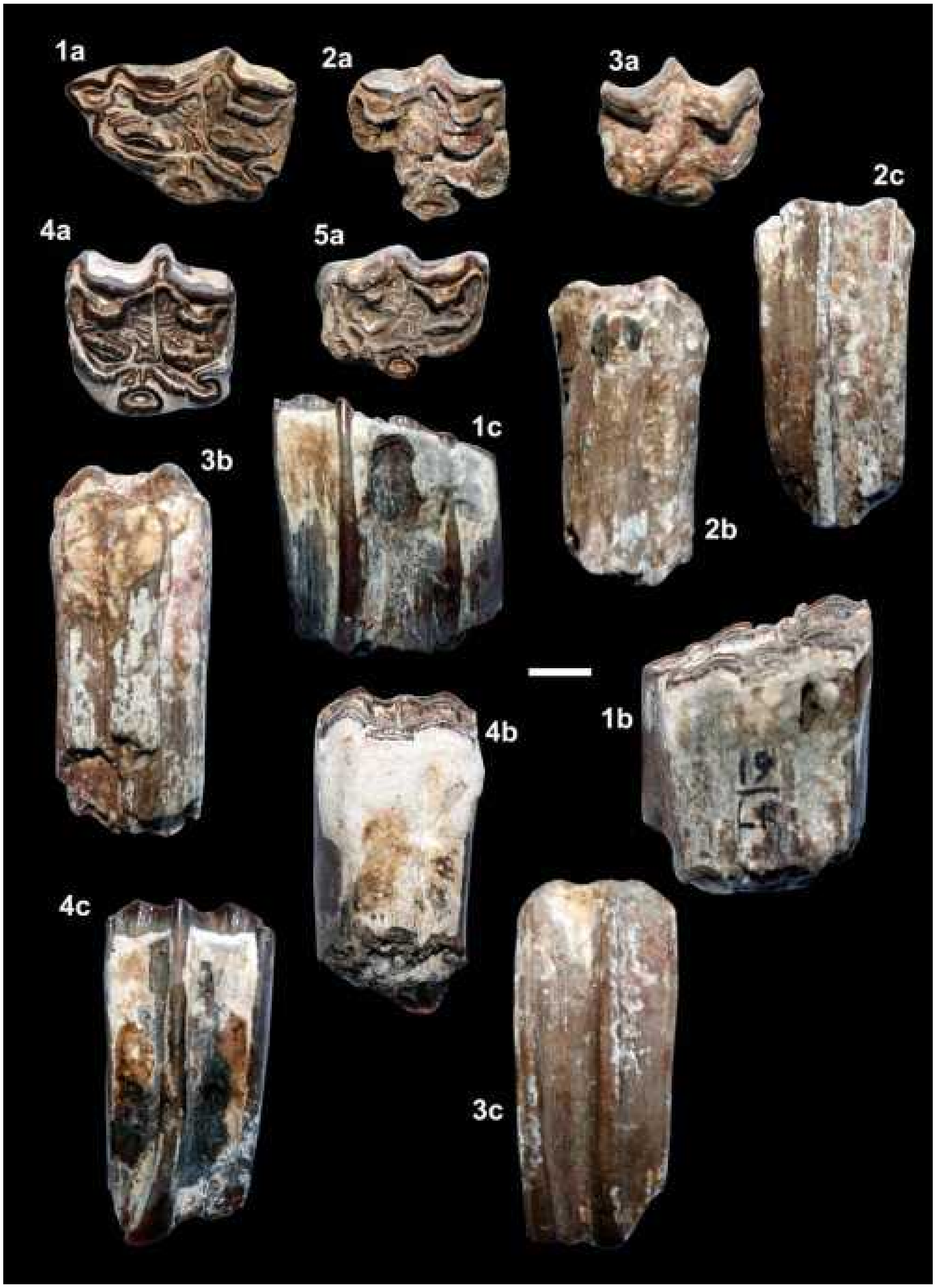


Fig. 33. ***Hipparion theobaldi*****. 1. PUPC 07/61, lP^2. 2. PUPC 07/65, lM^1. 3. PUPC 07/66, rM^1. 4. PUPC 07/57, lM^2. 5. PUPC 07/58, lM^3. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.**

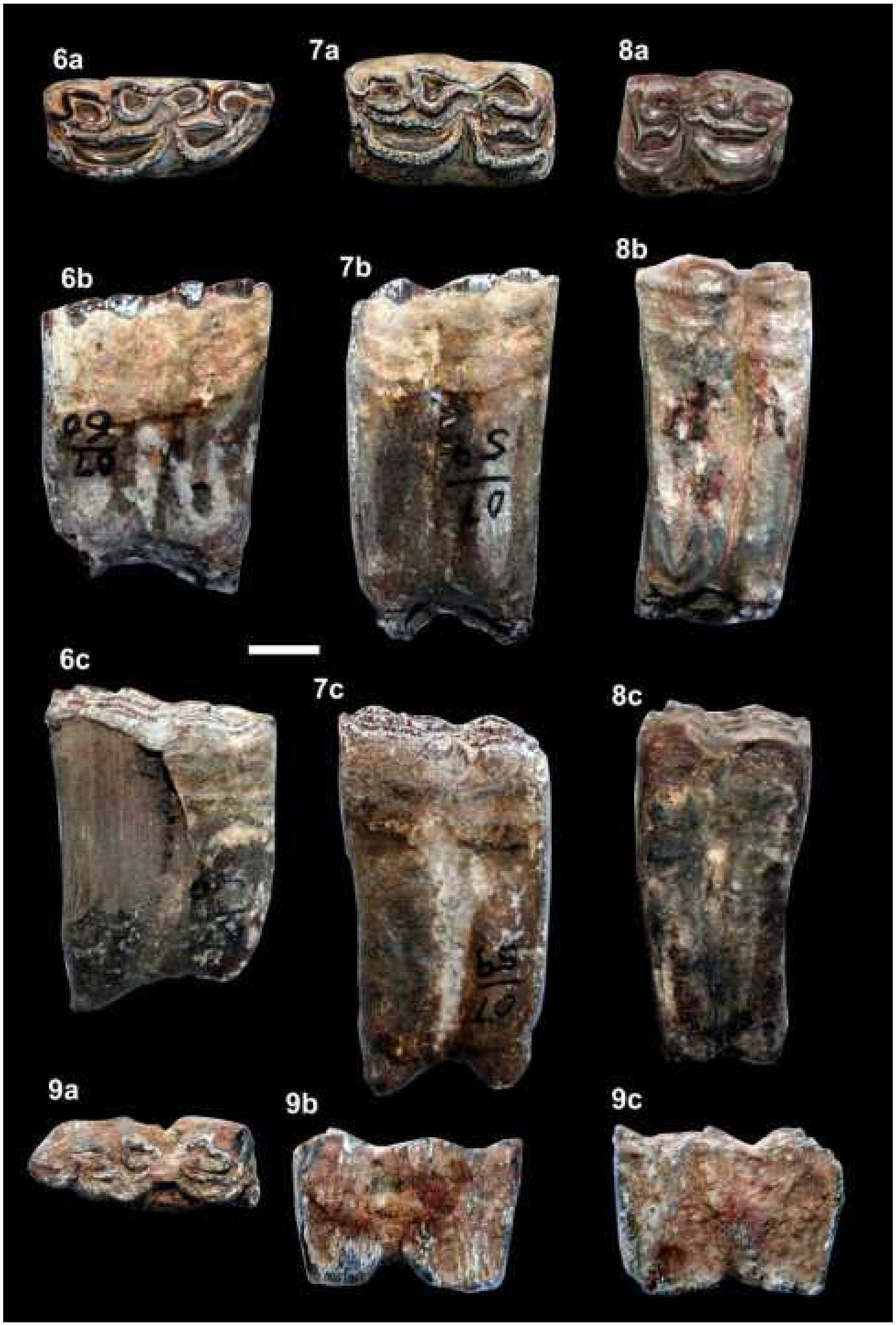


Fig. 34. ***Hipparion theobaldi*****. 6. PUPC 07/60, rP_2. 7. PUPC 07/59, rP_3. 8. PUPC 07/78, lP_4. 9. PUPC 07/124, rM_3. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 10 mm.**

PUPC 07/59 includes the P_3 of the right mandible (Fig. 34(7)). It is in excellent state of preservation and in an early stage of wear. The metaconid and metasylid are joined by a narrow isthamus giving the appearance of double knot. The lingual side of the tooth is vertically higher than the buccal one. The ectostylid and mesostylid are well preserved and prominent. The ectosylid is prominent pillar like structure. The protostylid is absent. There is a deep plication formed by the union of the posterior side of the parastylid and the anterior side of the protoconid. There are two prominent invaginations lingually, named the metaflexid anteriorly and the entoflexid posteriorly. The metaflexid is narrow in the middle, while broad anteroposteriorly. The entoflexid is elongated, curved anteriorly, while broad posteriorly. The wall of the entoflexid is wrinkled.

The lower fourh premolar PUPC 07/78 is in early wear (Fig. 34(8)). The protoconid and the hypoconid are comparatively broad. The metaconid is broad and triangular and united with narrow isthmus. The protostylid is bulky and narrow, while the mesostylid and the entostylid are weak. The metaflexid is narrow while the entoflexid is triangular in shape and narrow. The hypoconulid is absent but the mesostylid is present on the lingual side.

Lingualflexids are shallow on all premolars. Entoflexids are elongate and have complex anteriormost borders where they separate metaconid/metastylid. The premolars have ectoflexids which do not separate the metaconids/metastylids. Metaconid is rounded on the P_2, having angular posterior borders on the $P_{3\text{-}4}$. Metastylids have marked angular posterior borders on all premolars. Protostylids are present on $P_{3\text{-}4}$.

The ectoflexid in the lower third molar PUPC 07/124 (Fig. 34(9)) does not separate metaconid and metaflexid. The molar has angular facing borders of metaconid and metastylid. There are no plicaballinids. Lingualflexid is deeply incised and elongate. Entoflexid is elongate and has a complex border. Metaflexid is square and has complex border. The protostylid is present in the molar. The hypoconulid is present which is concave buccally. The comparative dental measurements are provided in table 11.

Comparison and Discussion

The general appearance of the studied specimens and strong pillar like isolated protocone exclude the specimens from the genus *Equus* and favor their inclusion in the genus *Hipparion*. The Middle Siwalik is represented by four *Hipparion* species *H. nagriensis*, *H. perimense*, *H. theobaldi* and *H. antiopinum* (Colbert, 1935). Two of them are found abundant in the Middle Siwaliks (Iqbal *et al*., 2009). *Hipparion nagriensis* is comparatively small species (Mac Fadden and Woodburne, 1982; Naseem *et al*., 2009). The protocone of *H. perimense* is flattened lingually and rounded buccally (Ghaffar, 2005). *Hipparion antilopinum* is large with complicated plications and oval shape protocone. *Hipparion theobaldi* are large, having less complicated plications. *Hipparion theobaldi* differs from *H. antilopinum* of having compressed protocone, as compared to round oval shape protocone in *H. antilopinum*. Furthermore, the enamel borders of cavities relatively simple in *H. theobaldi* and complicated in *H. antilopinum* (Lydekker, 1882; Colbert, 1935).

The morphometric study of the specimens reveal all the features of species *H. theobaldi* (Figs. 33-35) as described by Lydekker (1882), Colbert (1935) and Ghaffar (2005) and the specimens are assigned to *H. theobaldi*. This species is characterized by the isolated, compressed and pillar like protocone, the molar size is greater than *H. antilopinum* and *H. nagriensis,* and smaller than *H. perimense*. The enamel bordering of the cavities are relatively simple. The specimens are extremely hypsodont and show less complicated plications. The studied specimens show the same basic features of the species such as an anterostyle in premolars and isolated protocone in cheek teeth, simple enamel bordering of central cavities with large size. According to Colbert (1935), it is heavy and larger species as compared to *H. antilopinum* and *H. nagriensis*. All the studied premolars reflect hipparionine features i.e., they are longer than broad with longitudinally elongated protocones and hypocones (Figs. 33-34). The enamel plications are moderately complicated. These features are also mentioned by Lydekker (1882) with type specimen.

The genus *Hipparion* was erected by Christol de (1832) on the basis of fossil material collected from the Turolian age locality of Mt-Luberon in the province of Vaucluse in France. Christol de (1832) characterized this Mt-Luberon horse with isolated protocones in the upper molars and tridactyl feet. Christol did not designate a type species of the genus. This was done by Gervais (1849) when he described a syntypic series from Mt-Luberon, including *H. prostylum, H. mesostylum* and *H. diplostylum.*

The name *Sivalhippus theobaldi* was introduced by Lydekker (1877a). Shortly thereafter Lydekker (1877b) synonymized *Sivalhippus* with *Hippotherium* retaining the name *Hippotherium*. Lydekker used the combination *Hippotherium theobaldi* in two subsequent publications (1882, 1883) until finally synonymizing the genus with *Hipparion* as *H. theobaldi* (Lydekker, 1885, 1886). Later on, the name *H. theobaldi* was followed by Pilgrim (1913), Matthew (1929), Colbert (1935), Gromova (1952), Hussain (1971) as referring smaller specimens to *H. antilopinum* and large to *H. theobaldi.* Forsten (1968) however choose not to recognize *H. antelopinum* arguing that all Siwalik hipparions belong to one polytypic species *H. primigenium* Skinner and Mac Fadden (1977) recognize the distinctiveness of both these species but referred them *Cormohipparion.* Mac Fadden (1984) similarly recognizing the species *Cormohipparion theobaldi.* Phylogenetically *Cormohipparion theobaldi* appears to lie close to primitive Eurasian *Hipparion* as morphologically idealized by *H. primigenium*. The specimen in AMNH and yale-GSP collection referred to *Cormohipparion theobaldi* are more robust then any of the metapodial material for Eurasian primitive hipparionines.

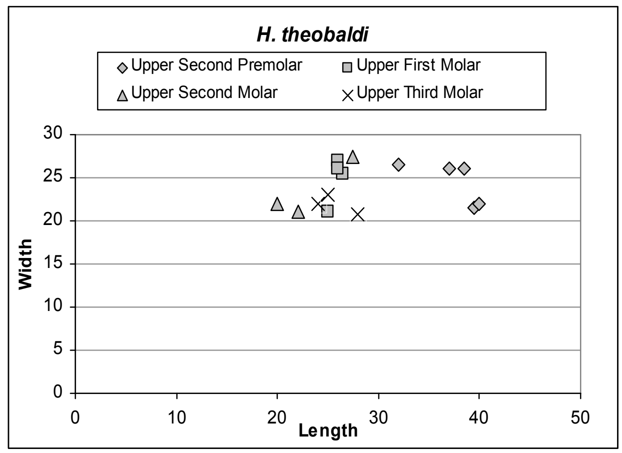
Skinner and Mac Fadden (1977) created new genus *Cormohipparion* and stated that all the hipparionine should be included in this new genus. But later on Bernor and Hussain (1985) stated that there is no need to erect new genus. Moreover, Mac Fadden and Skinner (1977) have also suggested that it is highly probable that all the Siwalik hipparionines should be included in the genus *Cormohipparion* with specific differences based on dentition size and feet which are characteristics, classically employed in hipparion taxonomy. Forsten (1968) was the most extreme in jumping all the Siwalik *Hipparion* specimens into single highly variable population of *H. primigenium.* According to him, the Siwalik *Hipparion* group is evolutionary conservative, and compares closely with *H. primigenium* and other primitive horses in complex cheek teeth fossette ornamentation, double or complex plicaballins, deeply incised hypoglyph and elongate P2 anterostyle. He further argued that *C. gracile* and *C. moldavicum* are also best derived from Eurasian horses similar to *H. primigenium.* The presence of an anterior rim on facial fossa is also a primitive character shared by several Holarctic hipparionines.

Hipparion antilopium and *H. theobaldi* are significantly different in facial, dental and possibly posteranial features from species of North American cormohipparions (Ghaffar, 2005). The North American cormohipparions and Eurasian hipparionines obscure the plylogentic relationship of Holarctic cormohipparion. Subsequently, a long series of investigations on old world hipparions, have incorporated these original morphological characters in referring a vast array of species to this one genus. Consequently, a strong central dogma has arisen in the systematics of *Hipparion.* Most palaeontologists believed that hipparion evolved in the New World from an unidentified species of *Merychippus*. But some recent investigators have argued that several distinct lineages may be present in the Old World and the Old World morphology evolutionary pattern may not be accurate. As a result, the genus *Hipparion* has become more circumscribed in its morphological characterization and the number of species included within the genus.

Hipparion first appeared in the Siwaliks by a single migration record in lithologic boundary of the Nagri Formation (Hussain, 1971). The Nagri, type locality of the Nagri Formation has yielded the richest record of the Siwalik hipparions. *Hipparion* species are important markers in faunal correlations known as fossil record from middle Miocene to Pleistocene. The oldest occurrence of the Siwalik hipparion is from the Nagri Formation, ca 9.5 Ma (Hussain, 1971), while the old world occurrence of *Equus* is from Hasnot, ca 2.48 Ma (Barry *et al.,* 1982) that is the oldest occurrence of *Equus* in Southern Asia. Hussain (1971) made the first contemporary revision of the Siwalik hipparions. He suggested that *Hipparion* first appeared in the Siwaliks by a single migration record in lithologic boundary of the Nagri Formation and subsequently underwent autochthonous evolution. He recognized three species of the Siwalik *Hipparion*: (1) *H. nagriensis*, (2) *H. theobaldi*, and (3) *H. antilopium*. More recently, Ghaffar *et al.* (2003) considered the validity of the genus *Hipparion* with its four species *H. antilopinum*, *H. sivalensis*, *H. theobaldi* and *H. nagriensis*.

Recently, Bernor *et al*. (1996) again grouped the Siwalik hipparion into two genera: *Sivalhippus* and *Hipparion*. *Sivalhippus* is a large size genus with two species, *S. theobaldi* and *S. perimense,* and a small size genus *Hipparion* with one species *H.* sp. (Bernor *et al*., 1996).

A.



B.

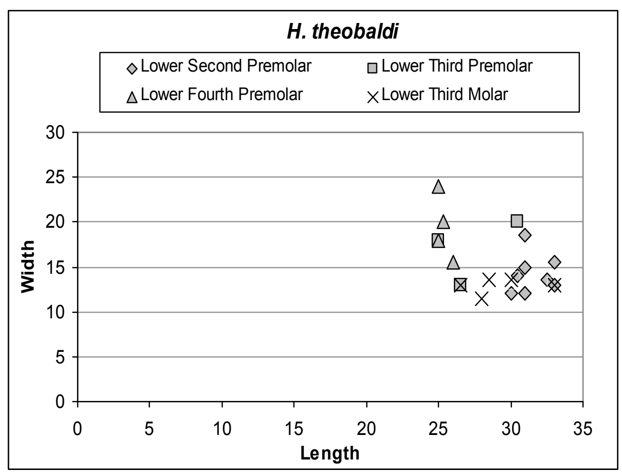


Fig. 35. Scatter diagram showing dental proportions of *H. theobaldi*'s studied sample. The referred materials are taken from Colbert (1935) and Ghaffar (2005).

Family Rhinocerotidae Owen, 1848
Subfamily Rhinocerotinae Owen, 1845
Tribe Teleoceratini Hay, 1885

Genus *Brachypotherium* Roger, 1904

Type Species: *Aceratherium perimense* Falconer and Cautley, 1847.

Generic Diagnosis: A rhinoceros of gigantic size with hypsodont teeth. Skull rather short and deep, with retracted nasals; zygomatic arch heavy; postglenoid separate from posttympanie. Upper incisor present and well developed. Molars with moderately developed crochet, weaker antecrochet and rudimentary crista. Protocone somewhat pinehed off. Lower molars narrow and compressed. Mandibular symphysis narrow (Heissig, 1972).

Known Distribution: Southern Asia, South-Eastern Asia and Western Asia (Heissig, 1972).

Brachypotherium perimense **Falconer and Cautley, 1847**

Cotypes: The specimens figured by Falconer and Cautley, (1847: pl. LXXV, figs. 13-16, and LXXVI, figs. 14-17).

Type locality: Peram Island**,** India (Colbert, 1935).

Stratigraphic Range: Lower to Middle Siwaliks (Khan A. M., 2010).

Diagnosis: Very large species of the genus *Brachypotherium* with relatively high cheek teeth. All generic features are extremely developed. Nasals are shortened and hornless. The upper molars have weak constrictions of the inner cusp; reduced antecrochet usually present. Upper Premolars are molariform, usually with highly convex exterior. Lower molars are almost without buccal fold; cingula usually reduced and short (Heissig, 1972).

Studied Specimens: Lower dentition: PUPC 07/52, a right mandibular ramus having $P_3 – M_3$. PUPC 07/53, a left mandibular ramus having $P_{3 -} M_2$.

Description

Mandible: PUPC 07/52 and PUPC 07/53 is a well preserved right and left mandibular ramii respectively (Figs. 36-37). The hemimandible PUPC 07/52 is moderately long having 390 mm length. PUPC 07/52 mandible depth at the P_3 is 62 mm, at the P_4 is 67 mm, at the M_1 is 82 mm, at the M_2 is 84 mm and at the M_3 is 86 mm (Fig. 36). The horizontal ramii are thick and their lower margins are slightly curved. The sagittal lingual groove is wide posteriorly and absent anteriorly.

Lower Dentition: The molars are large and wide. All the cheek teeth are in early wear and show the distinct morphology of rhinoceros; the valleys are open lingually (Figs. 36(1a), 37(1a)). The enamel is fairly thick, uniform in thickness and rugose. The buccal and the lingual cingula are absent. In P_3 the paraconid has an anterior extension. The protoconid is round and has a buccal extension. The hypoconid is large and the entoconid is round. The paralophid is long and the protolophid and the metalophid are broad. The hypolophid is long. The anterior valley is not well developed. The posterior valley is U-shaped.

The paraconid is round in the P_4. The metalophid is not distinct from the hypolophid at the point of wear. The anterior valley is not well developed and V- shaped. The posterior valley is deep and U-shaped. In M_1 the paraconid is long and narrow but shorter than that of the protoconid. The hypolophid is long and prominent but not distinct from the metalophid at their junction due to wear. The paralophid is long and narrow than the protolophid. The anterior and the posterior valleys are V – shaped. The damaged paraconid is slightly round in the M_2. The protoconid is long and broad. The metaconid is short. The hypoconid is broad. The entoconid is long, little worn and have lingual extension. The paralophid is short. The protolophid and the hypolophid are broad and long. The anterior valley is slightly U-shaped. The posterior valley is deep and U-shaped. The M_3 hypolophid is long. The valleys are U-shaped.

PUPC 07/53 is a well-preserved left mandibular ramus with P_3-M_2 (Fig. 37). It is 280 mm in length. All the cheek teeth are well preserved and show the distinct morphology. The mandible is moderately long. The vertical height below P_3 is 62 mm, below P_4 is 66 mm, below M_1 is 82 mm, and below M_2 is 85 mm. The P_3 has anterior extension in the paraconid. The protoconid is broad. The metaconid and the entoconid are round. The hypoconid is wide. The metalophid and the protolophid are joined. The anterior valley is not well developed. The posterior valley is V – shaped. The buccal and lingual cingula are absent.

P_4 has slightly broad paraconid. The entoconid, protoconid and metaconid are round but the metaconid is not distinct from protoconid due to wear. The hypoconid is long while the paralophid is short. The metaconid and the entoconid have lingual extension. The protolophid is long. The metalophid is broad. The hypolophid is long and wide. The protolophid and the hypolophid seem to be joining each other due to wear. The anterior valley is not well developed while the posterior valley is U – shaped. There is V – shaped trigonid.

The paraconid is short in M_1. The protoconid is broad. The metaconid is not distinct due to wear. The hypoconid is indistinct but long. The entoconid is pointed and has lingual extension. The paralophid is narrow. The protolophid is long and broad. The hypolophid is long and wide. The metalophid is broad. The posterior valley is U-shaped. The paraconid is constricted in M_2. The protoconid is broken but broad. The metaconid is round. The hypoconid is pointed and the entoconid is round. The parolophid is short and narrow. The protolophid is worn. The hypolophid is prominent and long. The anterior valley is slightly V – shaped. The posterior valley is wide, deep, long and U – shaped. The measurements are provided in table 12.

Comparison and Discussion

The studied lower dentition from the Nagri type area is identical to *Brachypotherium perimense* in morphology to that described by Heissig (1972) from the Nagri Formation of the Middle Siwaliks. PUPC 07/52 and PUPC 07/53 are comparable to AMNH 19454, as identified of *Aceratherium perimense* (Colbert, 1935). PUPC 07/652 and PUPC 07/53 (Table 12; Fig. 38) are comparable to the sample described by Cerdeno and Hussain (1997). The dental measurements of PUPC 07/52 and PUPC 07/53 show that both specimens probably belong to the same animal.

Colbert (1935) recognized *Aceratherium perimense* from the Lower and the Middle Siwalik sediments while Heissig (1972) placed the species in *Brachypotherium*. Heissig (1972) reported *Brachypotherium* in the Kamlial Formation of the Lower Siwaliks. Cerdeno and Hussain (1997) described fossil remains of *Brachypotherium perimense* from the Miocene Manchar Formation, Sind, Pakistan, whose morphology is similar to those described by Heissig (1972) from the Siwlaiks of Pakistan; the P^1 being wider, the M^2 narrower, and the lower teeth having closer dimensions. Other postcranial remains from the Sind are smaller than those described by Heissig (1972), but this difference in size may be due to older age of the Manchar Formation (Lower Chinji) with respect to the latter specimens that belongs to the middle and upper Chinji, Nagri or Dhok Pathan formations (Cerdeno and Hussain, 1997). The difference of the dental remains size may also be attributed to the age differences of animals.

Gentry (1987) while describing the *Brachypotherium* sp. from Miocene of Saudi Arabia considered the large size and flatness of the buccal wall of upper molars and the small size of the paracone rib in comparison with the large flat area, persistent internal cingula on its upper cheek teeth and external cingula on its upper and lower molars as important characteristics for its generic identity. Antoine *et al.* (2000) considered the European *Brachypotherium brachypus* as an Asiatic migrant because closely related species have previous occurrence in Pakistan and the surrounding areas. They (Antoine *et al*. 2000) suggested that *Aprotodon fatehjangense* (Pilgrim, 1910) described from Asia has a very close resemblance with *Brachypotherium brachypus* and must be regarded as recent synonym of *Brachypotherium* Roger, 1904. *Brachypotherium fatehjangense* is senior synonym of *Aprotodon fatehjangense* (Antoine and Welcomme, 2000).

Brachypotherium is supposed to have a preference for soft diet and a more forested environment (Andrew *et al*., 1996, 1997), which is comparable to the middle Miocene Dhok Pathan Formation in the Siwlaiks. *Brachypotherium perimense* (Colbert 1935) is a large species; lower teeth are charactersized by the smooth external groove, hardly marked, as it is in other teleocertines (Cerdeno and Hussain, 1997). Heissig (2003) indicated that *Brachypotherium perimense* is the most frequent species in times of transition and rare during most humid and most arid times and this species point out in the Nagri Formation the beginnings of less humid conditions. *Brachypotherium* has often been compared to hippos, and was certainly a marsh or lake dweller (Geraads and Sarac, 2003).

Table 12: Comparative dental measurements of the cheek teeth of *Brachypotherium* in mm (millimeters). * The studied specimens. Referred data are taken from Colbert (1935), Heissig (1972), and Cerdino and Hussain (1997).

Taxon	Number	Nature/ Position	Length	Width
B. perimense	PUPC 07/52*	P_3	41	31
		P_4	48	33
		M_1	56	32
		M_2	62	35
		M_3	55	35
	PUPC 07/53*	P_3	40	31
		P_4	47	34
		M_1	56	33
		M_2	62	36
	AMNH 19454	P_3	40	26
		P_4	49	37
		M_1	53	36
		M_2	64	40
		M_3	72	35
		M_2	-	33
		M_2	55	30
		M_3	67	33

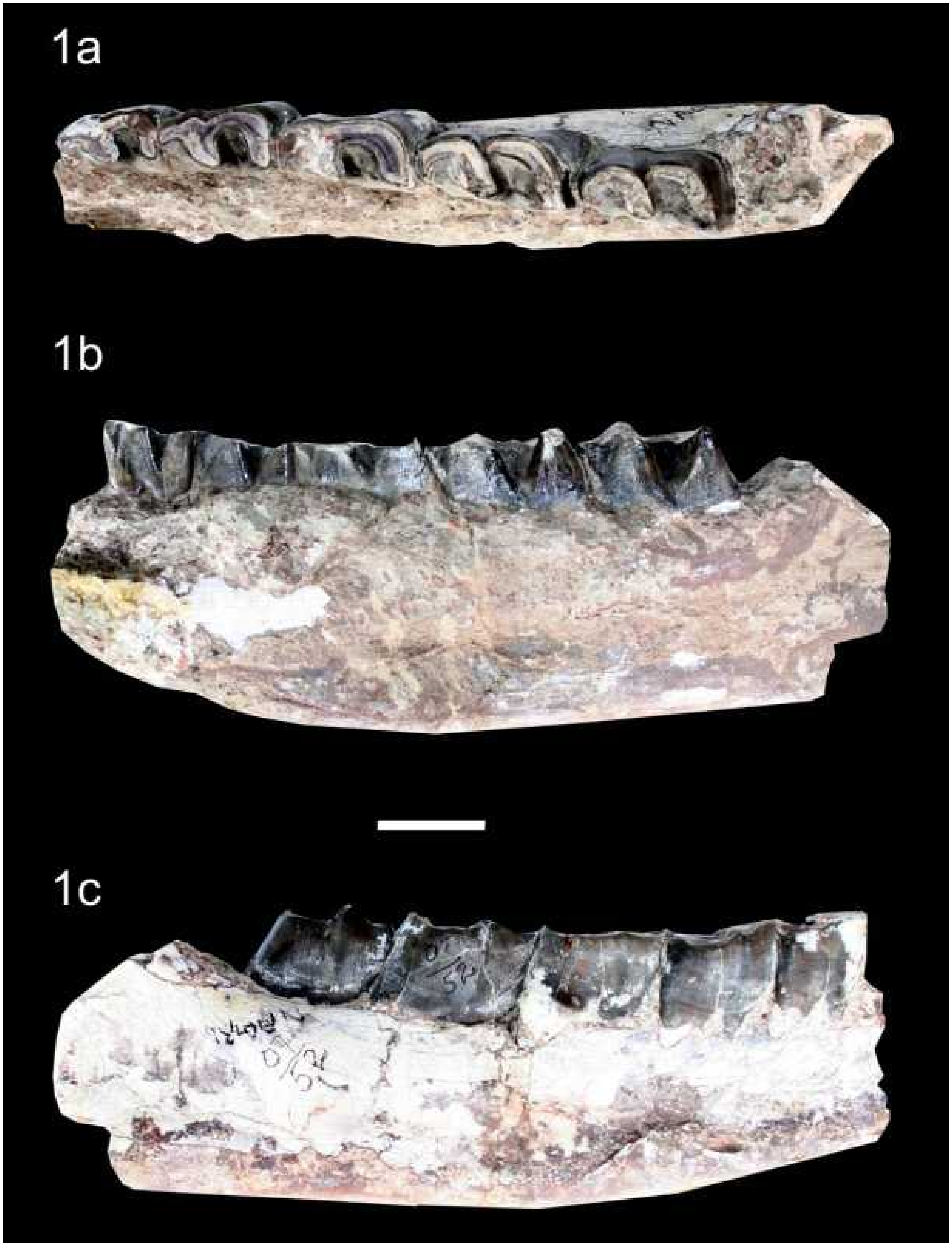


Fig. 36. ***Brachypotherium perimense*. 1. PUPC 07/52, a right mandibular ramus having $P_3 – M_3$. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 50 mm.**

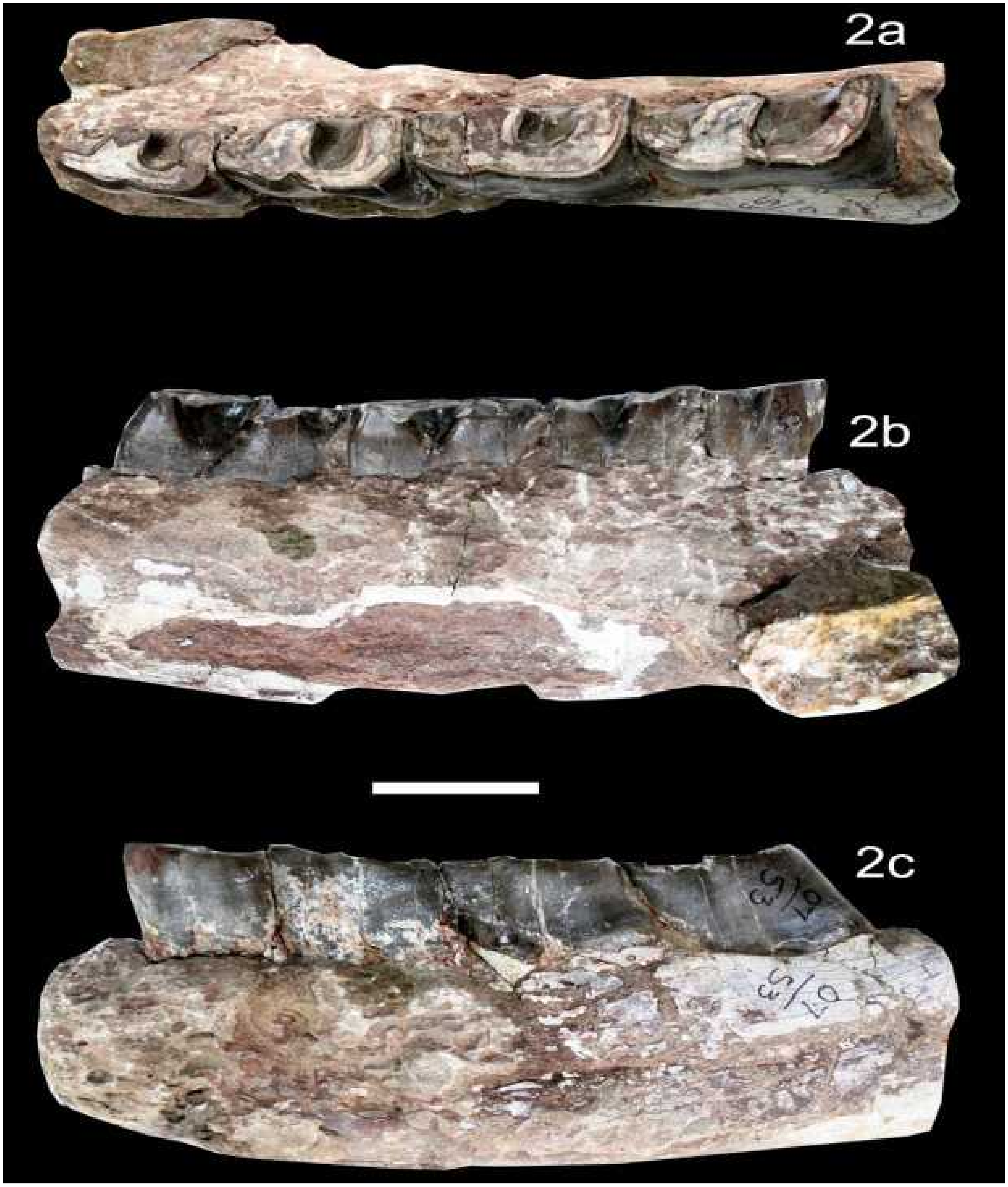


Fig. 37. ***Brachypotherium perimense*****. 2. PUPC 07/53, a left mandibular ramus having P_3 – M_2. a = occlusal view, b = lingual view, c = buccal view. Scale bar equals 50 mm.**

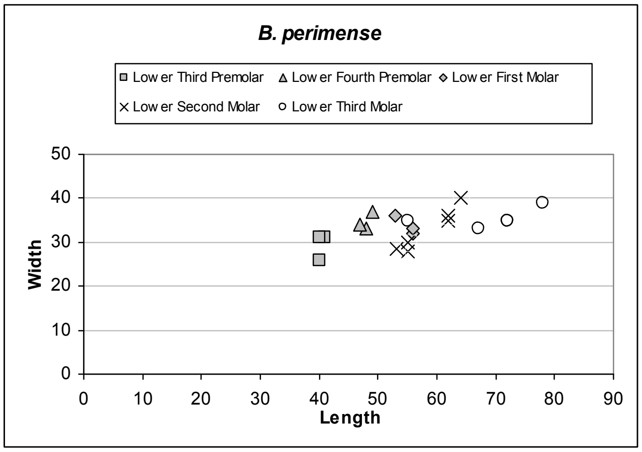


Fig. 38. Scatter diagram showing dental proportions of *B. perimense*'s studied sample. Referred data are taken from Colbert (1935), Heissig (1972), and Cerdeno and Hussain (1997).

DISCUSSION

Faunal Correlation: The fauna from the Nagri includes at present the following species: *Listriodon pentapotamiae, Selenoportax* cf. *vexillarius, Pachyportax* cf. *latidens, Tragoportax punjabicus, Miotragocerus* cf. *gluten, Gazella* cf. *lydekkeri, Giraffokeryx punjabiensis, Giraffa* cf. *priscilla, Dorcatherium* cf. *minus, Dorcatherium* cf. *majus, Dorcabune* cf. *anthracotherioides, Hipparion theobaldi, Brachypotherium perimense*. The thirteen taxa of the true ungulates have been recognized from the late Miocene deposits exposed in the Nagri type locality of the Nagri Formation, northern Pakistan. This faunal list may be compared with that of other late Miocene Siwalik localities, Dhok Pathan and Hasnot and the middle Miocene Siwalik locality, Chinji. This list obviously indicates a faunal spectrum of only orders Artiodactyla and Perissodactyla and several orders such as Proboscidea, Carnivora are not included in this study. However, well documented late Miocene mammalian faunal successions are known from the Siwaliks (Lydekker, 1876, 1878; Pilgrim, 1937, 1939; Matthew, 1929; Colbert, 1935; Thomas, 1984; Akhtar, 1992, 1996; Bhatti, 2005; Farooq, 2006; Khan, 2007, 2008; Khan A. M., 2010). Among the common taxa, the Nagri *Dorcatherium* seems more primitive than the Dhok Pathan one because of its heavy styles and more bunodont teeth. The Nagri *Hipparion* also shows a simplification in plicaballins. The Nagri stratigraphically is situated below the Dhok Pathan Formation and the list is characteristic of the early Late Miocene in the chronologic successions of faunas in the Siwaliks (Barry *et al*., 2002).

This faunal list is biased towards large mammals, because many fossils were recovered during quarry work, and excavations have been of very limited extent. Still, this faunal association contains enough significant elements to allow comparison with some other upper Miocene faunas from Europe and the Near Siwaliks. Although the latest Miocene (7.5 – 5.3 Ma) faunas of the Siwaliks are well known (Pilgrim, 1937, 1939; Akhtar, 1992; Khan, 2007, 2008; Bibi, 2007; Khan *et al*., 2009a; Khan, A. M., 2010), the early Late Miocene (11 – 10 Ma) fauna are poorly known in the Siwaliks. However, the Nagri fauna is one of the best representatives for this age.

The Nagri fauna indicates strong resemblance to the late Miocene fauna of Dhok Pathan and Hasnot (Akhtar, 1992; Khan, 2007) and the early Late Miocene faunas of East Africa (Pickford, 1981). However, the Nagri fauna indicates weak resemblance to the late middle Miocene of the Chinji Formation (Thomas, 1984). The Nagri fauna is similar to the faunas from Samos and Pikermi of Greece, Maragheh of Iran, and Dhok Pathan Formation of the Siwaliks (Solounias, 1981; Thomas, 1984; Akhtar, 1992; Khan, 2007; Kostopoulos, 2009). This fauna is particularly significant in providing evidence regarding the late Miocene faunal interchange between African and Eurasia (Pickford, 1981; Thomas, 1984; Pilbeam *et al*., 1997; Barry *et al*., 2002; Bibi and Gulec, 2008; Kostopoulos, 2009). The occurrence of several bovids (*Selenoportax vexillarius, Pachyportax latidens, Tragoportax punjabicus, Miotragocerus gluten, Gazella lydekkeri*), tragulids (*Dorcatherium minus, Dorcatherium majus, Dorcatherium nagrii, Dorcabune anthracotherioides*), hipparionines ("*Hipparion theobaldi" Sivalhippus Complex, Hipparion* sp.) and rhinos (*Brachypotherium perimense*) was also mentioned in the late Miocene of the Siwalik, Greco-Iranian province and Eurasia (Sen *et al*., 1997; Bibi *et al*., 2009; Kostopoulos, 2009). The Nagri fauna is different from that of Dhok Pathan and Hasnot by not having cervids, *Bramatherium*, and large suids.

Gazella is abundantly recorded from Samos, Pikermi, Maragheh, Dhok Pathan and Hasnot (Pilgrim, 1939; Akhtar, 1992; Khan, 2007; Bibi and Gulec, 2008; Kostopoulos, 2009). The Siwalik *Gazella lydekkeri* most closely approximates the morphology and perhaps the evolutionary stage of the Eurasian *Gazella capricornis* based on primarily on the degree of premolar row reduction (Bibi and Gulec, 2008). *Gazella lydekkeri* is known primarily from the Nagri Formation and the known age range of *Gazella lydekkeri* upto the Mio-Pliocene boundary or beyond (Thomas, 1984). *Selenoportax vexillarius* and *Pachyportax latidens* are recorded from the late Miocene and Pliocene faunas at the Siwaliks, the main bone beds of Dhok Pathan and Hasnot (Khan *et al*., 2009a). The Dhok Pathan and the Hasnot faunas are contemporaneous (10.1-3.4 Ma) but the Nagri faunas are older (ca 11.2-10.1 Ma). An age range for these species that includes all these localities would be quite broad, potentially as old as the base of the Nagri up until 3.4 Ma, the upper limit to the Dhok Pathan Formation (Barry *et al*., 2002). *Tragoportax* is present in the Nagri Formation and also in the Dhok Pathan Formation (Pilgrim, 1937, 1939; Bibi *et al*., 2009). *Tragoportax* is recorded also from the late Miocene of Pikermi, Molayan, Samos and Mytilini (Bibi and Gulec, 2008; Bibi *et al*., 2009).

Listriodon pentapotamiae have been found in the Siwalik localities ranging in age from Middle Miocene to early Late Miocene (Pickford, 1988; Van der Made, 1996; present study). In Europe a few specimens have been found in sites which have also yielded the equid *Hipparion* as in the Nagri type section but by the end of MN9 listriodonts were extinct everywhere. It is noted that listriodonts became extinct in Europe, China, India and Africa over a short period at the end of the Middle Miocene and the beginning of the Late Miocene. Thus, the available evidence about the broad tendencies of listriodont evolution in the Indian subcontinent accords with that from Europe and China, which supports the view that for much of the middle Miocene and the early Late Miocene, Europe, Asia and the Indian subcontinent were all part of a single biogeographic region (Pickford and Morales, 2003).

In summary then, the Nagri faunas are similar to those from Dhok Pathan, Pikermi, Samos, Maragheh and Sivas, though also some elements to older site like Chinji (Pickford, 1981; Thomas, 1984; Akhtar, 1992; Pilbeam *et al*., 1997; Sen *et al*., 1997; Barry *et al*., 2002; Bibi and Gulec, 2008; Bibi *et al*., 2009; Kostopoulos, 2009).

Biostratigraphy: The stratigraphical ranges of the bovids of Nagri are restricted to Late Miocene (Bibi, 2007; Khan, 2007; Khan *et al*., 2009a). The suid *Listriodon pentapotamiae* is restricted to the earliest Late Miocene of the Siwaliks (Pickford, 1988; Van der Made, 1996). More recently, the cervids have been recorded in the latest Late Miocene of the Siwaliks: Dhok Pathan and Hasnot (Ghaffar, 2005; Ghaffar *et al*., 2010). Prior to it the first appearance of the cervids are recorded from the late Pliocene of the Siwaliks (Barry *et al*., 2002). The cervids are absent in the earliest Late Miocene of the Siwaliks. The presence of *Tragoportax* confirms Late Miocene age but allows no further refinement. Nevertheless, *Miotragocerus* indicates a more primitive bovid assemblage.

Listriodon pentapotamiae is recorded in the Siwaliks from as early as the middle Miocene until the earliest Late Miocene (Welcomme *et al.*, 2001). In the Chinji strata *Listriodon pentapotamiae* is the most common suid (Pickford, 1988). Several Middle Siwalik localities of the Nagri Formation exhibit the presence of *Listriodon pentapotamiae* and however, the species is widely distributed in the Middle Miocene (Pickford, 1988; Pickford and Morales, 2003). *Brachyopotherium perimense* is a common species of the Siwalik late Miocene (Heissig, 1972) and its stratigraphic range is the earliest Late Miocene to the latest Late Miocene (Heissig, 1972).

Palaeotraginae is documented sporadically in the Chinji Formation of the Lower Siwaliks (Colbert, 1933; Bhatti *et al*., 2007). *Giraffokeryx punjabiensis* has already been mentioned several localities of the late Middle Miocene age (Bhatti, 2005), occupying a wide territory from Western Europe to India (Bohlin, 1926; Gentry *et al.,* 1999; NOW database, 2003). A rare occurrence of the species is found in the early Late Miocene and now from the Nagri type section confirms its presence in the early Late Miocene. The persistence of *Giraffokeryx punjabiensis* and *Listriodon pentapotamiae* in the Nagri type section seems to contradict their time range in the Siwaliks, where they are considered to be typical Lower Siwalik elements. *Giraffokeryx punjabiensis* and *Listriodon pentapotamiae* are here rather in favour of an early Late Miocene age. The Nagri specimens attributed to *Dorcatherium* and *Dorcobune* lack any stratigraphic indication. The specimens have the typical fossilization status seen in specimens from the Nagri ravine, suggesting an early Late Miocene age.

Accordingly, an estimated age of early Late Miocene age is reasonable for the Nagri fauna, equating to somewhere between about 11 to 10.1 Ma. This estimate, based solely on the true ungulates, is in agreement with previous estimates of 11.2-10.1 Ma for the Nagri Formation sites of the Siwaliks using radiometric dating data (Pilbeam *et al*., 1997; Barry *et al.*, 1980, 1982, 2002). Pilbeam *et al*. (1997) gave the chronology of the top Ghabir sites of the type section and suggested 10.75 and 10.84 Ma for this section. Barry *et al*. (2002) suggested early Late Miocene age for the type section. Their arguments were mainly magnetostratigraphic (using ages from the Berggren *et al*., 1985, and Cande and Kent, 1995 time scale) and also palaeontological (to get possible ages for the Siwalik hipparionines). The fossiliferous level of the Nagri type section was radiometrically bracketed between 10.1 and 11.2 Ma (Pilbeam *et al*., 1997; Barry *et al*., 2002) and should consequently be correlated to the earliest Vallesian, MN9 (Bernor *et al*., 1996).

In general, the Nagri true ungulates are strongly indicative of the Middle Siwaliks, which have a combined absolute range of 10.1-11.2 Ma (Barry *et al*., 2002) and relate well to other late Miocene Eurasian faunas. On the whole, the faunas suggest that the Nagri is older than Dhok Pathan and Hasnot. The biostratigraphical position of the Nagri locality relative to Dhok Pathan and the differences in appearance and disappearance of fauna suggest that the Nagri fauna is of early Late Miocene age.

Palaeoecology and Palaeoenvironment: Recent work on the geology of Nagri (Barry *et al*., 2002) has documented that the deposits were formed as part of a large river system by coexisting emergent and interfan river system, with the larger emergent Nagri system beginning at 10.1 Ma (Willis and Behrensmeyer, 1995). Mammal fossils at the Nagri are recovered from fluvial channel deposits. The interpretation of the Nagri palaeoenvironment based on geological information is supported by palaeontological evidence. The Nagri fauna has an aquatic component that includes a mix of freshwater animals that can tolerate slow-moving water with a high sediment contents (e.g. crocodiles, turtles). The land mammal fauna is dominated by a number of artiodactyl and perissodactyl species that were likely preferred an aquatic-margin habitat, as they are found most commonly in fluviatile deposits (Barry *et al*., 2002). Recovery of a fair number of well preserved terrestrial vertebrates supports previous interpretations of the Nagri palaeoenvironment, they appear to be preferentially preserved in swampy and fluviatile settings. As for palaeoenvironmental indications, the Nagri faunas are consistently found in deposits that accumulated in or near swamps and shallow lakes (Badgley and Behrensmeyer, 1980; Badgley, 1986; Badgley and Tauxe, 1990; Barry *et al*., 1980, 1982, 2002) and suggest the presence of forest in the Nagri region at the time of deposition.

The presence of the tragulids and the giraffids, which were certainly browsers, definitely speaks in favour of wet forested environments. *Hipparion* fauna suggests a sclerophyllous evergreen woodland environment, similar to today's mixed monsoon forest and grassland glades of north central India (Solounias, 1999). Fortelius *et al*. (1996) studied the body mass diversity of the West Eurasian suoids in relationship to environmental conditions, and suggested that the loss of species of small size was correlated to a progressive development of increasingly open and seasonal habitats. During the late Miocene, suid diversity in western Eurasia was very low, and suids in MN12 and MN13 are only recorded in the largest size class (201-1000 kg). *Microstonyx major* has been recorded from the type section (Van der Made and Hussain, 1989). The presence of *Microstonyx major* and *Listriodon pentapotamiae* in the type area of the Nagri Formation confirm that the environment appears to have been more humid than the latest late Miocene (Pickford, 1988; Van der Made and Hussain, 1989; Pickford *et al*., 2004). It should be noted that the Nagri has some hypsodont members (Thomas, 1977; Akhtar, 1992). This provides evidence for an open environment.

Palaeoenvironmental interpretations using vertebrate fossils are often based largely on palaeodietary reconstructions using dento-gnathic and postcranial functional analyses in conjunction with the relative abundances of ecologically differentiated taxa (Bibi and Gulec, 2008). *Tragoportax* from the sites of Pikermi and Samos (Solounias and Hayek, 1993) as well as Molayan (Merceron *et al*., 2004) concluded that *Tragoportax* species were variable mixed feeders with strong grazing habits. An analysis of maxillary and zygomatic morphology among living and fossil bovids indicated that *Tragoportax* were mixed feeders while *Gazella* was a mixed feeder or browser (Solounias *et al*., 1995). More balanced mixed-feeding was interpreted for microwear of *Gazella* (Merceron *et al*., 2004). A comprehensive study of the postcranial morphology of extant and extinct bovids by Köhler (1993) found similarities between the build and proportions of *Tragoportax amalthea* and certain deer (*Cervus*) and found a leafy diet and light woodland habitat as most likely for this species. Köhler also reconstructed *Gazella* as a browser inhabiting more open country. *Miotragocerus* was interpreted as a leaf and herb-eater inhabiting shrubland to light woodland.

In terms of number of specimens, the Nagri true ungulate assemblage is dominated by bovids, giraffids and tragulids with *Hipparion* and *Listriodon*, *Brachypotherium* constituting much smaller percentages (Appendix 1). The high proportion of boselaphines may be representative of the presence of drier and more open habitats than would be expected for the remaining bovids, particularly if the fossil gazelle resembled the living species in their ability to inhabit semi-arid to arid environments. The specific richness of the boselaphins in the Nagri type section suggests open areas biomass (Thomas, 1984) as the living boselaphins (*Boselaphus tragocamelus* and *Tetracerus quadricornis*) prefer open areas.

Dorcatherium and *Miotragocerus* are familiar for more or less closed and humid habitats (Köhler, 1993; Gentry, 2005; Eronen and Rössner, 2007). This supports the assumption of an earliest Late Miocene Siwalik humid habitat with abundant cover. The taxonomic faunal composition suggests a humid habitat pocket with abundant cover indicating the dominance of forested landscapes during the early Late Miocene times of the Siwaliks. The presence of *Dorcatherium* in the type section can be assumed a strong attachment to wet, forested habitats with dense understory, where the animals could hide in vegetation or water from predators (Rössner, 2010).

In summary, the dominance of boselaphins in the Nagri reflects an environment of mainly open forest. A significant representation of tragulids with adaptations to ecotonal wet and swampy habitats indicates humid conditions. The alternation of dry and flood seasons would have caused a highly differentiated mosaic ecotone environment, which would have offered an outstanding number of habitats and niches and consequently an exceptionally large number of species. Because of alternation of ground conditions seasonal migration events might have occurred. Finally, the Nagri fauna suggest the existence of a vast wetland environment with alternating dry and flood seasons which forced a mosaic of ecotonal habitats with many niches and corresponding adaptations.

CONCLUSIONS

The study of the new true ungulate material collected from the Nagri type area, the Middle Siwaliks, Pakistan, allows recognizing 13 species from fifteen fossil sites, SN1-15. This includes a species of *Listriodon,* a species of *Hipparion*, a species of *Selenoportax,* a species of *Pachyportax,* a great abundance of the bovid *Tragoportax*, a *Gazella*, a *Miotragocerus*, a species of *Giraffokeryx*, and only rare representation of *Dorcatherium*, *Dorcabune* and *Giraffa*. The early Late Miocene fossil ungulates from the Nagri constitute an assemblage that is fairly typical of the Siwalik region during this time.

From biochronological point of view, the co-existence of *Listriodon pentapotamiae*, *Hipparion theolbaldi*, *Brachypotherium perimense*, *Selenoportax* and *Pachyportax* indicate close relationships to the early Late Miocene of the Siwaliks. The true ungulate fauna allows a biochronological estimate of early Late Miocene for the Nagri assemblage based on similarities with faunas from Dhok Pathan, Hasnot, Maragheh, Pikermi and Samos, corresponding well to previous estimates (Thomas, 1984; Barry *et al*., 2002; Bibi and Gulec, 2008; Kostopoulos, 2009; Khan *et al*., 2009a). In conclusion, the true ungulate assemblage of the Nagri type section rather indicates an early Late Miocene age (earliest Vallesian, MN 9) which is in agreement with the radiometric dating data provided by Barry *et al.* (2002).

The fossil ungulates indicate the ancient environment at Nagri comprised woodland to shrubland. The type area may have comprised relatively more humid, closed habitats based on the ecomorphology of their taxa, particularly *Miotragocerus* and *Dorcatherium*, which may have been an inhabitant of wetlands (Köhler, 1993). The Nagri occurrence increases again the similarities between Indo-Siwalik faunas and those of the Greco-Iranian province, the early Late Miocene ungulates common to both realms.

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APPENDIX 1

Studied Material

Listriodon pentapotamiae: Upper dentition: PC-GCUF 10/04, left first upper incisor (I^1); PUPC 07/73, right maxillary ramus with M^{1-2}. Lower dentition: PC-GCUF 10/05, isolated left P_4; PUPC 07/72, almost complete mandible with the partial canines, the right hemimandible with M_{1-3} and the left hemimandible with M_{2-3}.

Selenoportax* cf. *vexillarius: Upper dentition: PC-GCUF 10/07, isolated left M^1. Lower dentition: PC-GCUF 10/06, isolated left incisor (I_1); PUPC 09/117, isolated right M_1; PUPC 07/135, a fragment of right mandible having M_{1-3}.

Pachyportax* cf. *latidens: Upper dentition: PUPC 09/46, isolated right P^3; PUPC 09/69, isolated left M^2.

Tragoportax punjabicus: Upper dentition: PC-GCUF 10/08, isolated left P^3; PUPC 09/66, isolated right M^1; PC-GCUF 10/09, partial tooth probably M^1. Lower dentition: PC-GCUF 10/11, isolated right P_3; PUPC 09/70, isolated left P_4; PUPC 07/77, isolated left M_1; PUPC 07/86, isolated left M_1; PUPC 07/138, a mandibular ramus with P_4-M_2.

Miotragocerus* cf. *gluten: Upper dentition: PUPC 07/138, isolated left M^1. Lower dentition: PC-GCUF 10/12, isolated right P_3.

Gazella* cf. *lydekkeri: Lower dentition: PC-GCUF 09/02, a right mandibular ramus with M_{1-3}; PUPC 07/71, isolated left M_3.

Giraffokeryx punjabiensis: Upper dentition: PUPC 07/88, isolated left P^3; PUPC 09/67, partially preserved isolated right P^3; PUPC 07/133, isolated right M^2. Lower dentition: PUPC 09/43, left hemimandible with M_{2-3}, broken canine and alveoli of P_3-M_1; PUPC 07/90, isolated right M_3.

Giraffa* cf. *Priscilla: Upper dentition: PUPC 07/131, isolated left M^1; PUPC 07/89, isolated right M^1.
Dorcatherium* cf. *minus: Upper dentition: PC-GCUF 10/10, isolated left dP^4. Lower dentition: PUPC 07/69, a right mandibular ramus with partial M_1 and complete M_2.

Dorcatherium* cf. *majus: Upper dentition: PC-GCUF 09/46, isolated right M^2.

***Dorcabune* cf. *anthracotherioides*:** Lower dentition: PUPC 07/87, isolated left M_2.

***Hipparion theobaldi*:** Upper dentition: PUPC 07/61, isolated left P^2; PUPC 07/65, isolated left M^1; PUPC 07/66, isolated right M^1; PUPC 07/57, isolated left M^2; PUPC 07/58, isolated left M^3. Lower dentition: PUPC 07/60, isolated right P_2; PUPC 07/59, isolated right P_3; PUPC 07/78, isolated left P_4; PUPC 07/124, isolated right M_3.

Brachypotherium perimense: Lower dentition: PUPC 07/52, a right mandibular ramus having P_3 – M_3. PUPC 07/53, a left mandibular ramus having P_3 – M_2.