Fossil Bovidae from Late Miocene Dhok Pathan Formation of Siwaliks, Northern Pakistan

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ABSTRACT

New bovid remains are recovered from Dhok Pathan type locality of Northern Pakistan. The assemblage presents seven bovid species *Pachyportax latidens*, *P. cf. nagrii, Selenoportax cf. vexillarius, Tragoportax punjabicus, T. cf. salmontanus, Elachistoceras khauristanensis* and *Gazella lydekkeri*. The boselaphines are predominant at the type locality. The taxa are consistent with a Late Miocene-Early Pliocene age of the deposits. The findings expand our knowledge on the dental anatomic features of the described species that existed in the Middle Siwalik Subgroup during the Late Miocene-Early Pliocene.

INTRODUCTION

Siwalik Group bears a very good record of fossil bovids in comparison of other parts of the world (Colbert, 1935; Akhtar, 1992; Khan, 2008; Khan et al., 2014, 2015), spanning from Early Miocene to Pleistocene (Pilgrim, 1913; Colbert, 1935; Barry et al., 2002, 2013; Khan et al., 2015; Siddig et al., 2016). The Dhok Pathan Formation has yielded richest fossil records of bovid fauna in South Asia (Khan et al., 2010a). The Dhok Pathan type locality (Lat. 33° 07' N: Long. 72° 14' E) is situated about 18 km on the Talagang Rawalpindi road at Soan River in district Chakwal, Punjab, Pakistan (Fig. 1). The outcrops are composed of gray sandstone and red-brown mudstone with a few thin conglomerate interbeds. The sandstones and superposed red mudstones often form fining-upward couplets where the lower contact is erosional and lined with ripped-up clasts of the underlying mottled and brown clay stone. The measured thickness of the Formation is about 500-825 m and has a conformable contact with the underlying Nagri Formation and overlying Soan Formation. The Formation represents the typical Middle Siwalik fauna of age 10.2-3.4 Ma (Khan et al., 2010a; Barry et al., 2002, 2013).

This paper deals with a taxonomic investigation



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Authors' Contribution MAK, AG and MA provided the concept and design of the study. SGA did acquisition of data. MAB and SGA analysised and interpreted the data. AR, KA and MAB drafted the manuscript.

Key words Mammalia, Artiodactyla, Bovidae, Boselaphini, Taxonomy, Paleontology.

of the Late Miocene bovid fauna in the Chakwal district, Punjab, Pakistan (Fig. 1). The aim of this work is to expose as brief as possible the richness and diversity of the bovids from the Dhok Pathan type locality by taxonomy updating of the fossil sites.

MATERIAL AND METHODS

The bovid remains were collected from the outcrops nearby the Dhok Pathan type locality, Chakwal district, Punjab, Pakistan. The material excavated from ten fossilized sites of type locality (Fig. 1). During excavation, careful measures were taken to prevent fossil fragments from disintegration. The dental specimens comprise upper and lower dentition, maxillary and mandible fragments. The measurements of the specimens were expressed in millimeters and rounded to one decimal.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; BMNH, British Museum of Natural History, London, UK; GSI, Geological survey of India, Calcutta, India; GSP, Geological Survey of Pakistan, Islamabad, Pakistan; PC-GCUF, Palaeontological Collection of Government College University, Faisalabad, Punjab, Pakistan; PUPC, Punjab University Palaeontological Collection, Lahore, Pakistan.

Anatomical abbreviations

I/i, Incisor; C/c, Canine; P/p, Premolar; M/m, Molar; dm, deciduous molar; W/L, Width/Length ratio; r, Right; l, Left.

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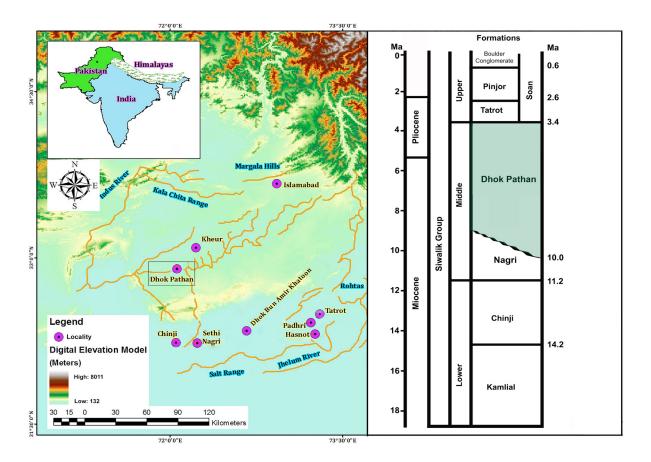


Fig. 1. Location map of Potwar Plateau in Northern Pakistan showing the type locality of the Dhok Pathan Formation in Chakwal district, northern Pakistan (data from Johnson *et al.*, 1982; Barry *et al.*, 2002; Dennell *et al.*, 2008; Nanda, 2008).

The catalogue number of the specimens consists of series *i.e.*, yearly catalogue number and serial catalogue number, so figures on the specimen represent the collection year (numerator) and serial number (denominator) of that year (*e.g.*, PC-GCUF 11/24). Uppercase letters stand for upper dentition (*e.g.*, M) and lower case for lower dentition (*e.g.*, m). The recovered dental material represents a good preservation to analyze the taxonomic characteristics of the specimens. The morphological and metrical characters of the specimens are described and their systematic determination is discussed. The terminology of the tooth crown elements and manners of measurements follow Gentry and Hooker (1988) and Gentry (1999).

SYSTEMATIC PALAEONTOLOGY Bovidae Gray, 1821

Boselaphini Knottnerus-Meyer, 1907 Genus Pachyportax Pilgrim, 1937 Pachyportax latidens Pilgrim, 1937

Studied material

PC-GCUF 11/132, isolated right P3; PC-GCUF

11/100, partially broken upper molar; PC-GCUF 11/138, isolated left M3; PC-GCUF 11/82, right mandible fragment with p4-m3; PC-GCUF 11/133, isolated right m2.

Locality

Dhok Pathan (Kundrali), Chakwal district, Punjab province, Pakistan.

Description

The third premolar is a triangular shaped tooth and in late wear. The enamel is shiny and wrinkled. The cingulum is present anteriorly. The paracone rib lies close to the parastyle. A strong entostyle is present in the upper molars (Fig. 2A). There are strong parastyle, mesostyle and metastyle. The prefossette is narrower and longer than the post one. The lower molars have prominent ectostylids (Fig. 2B). The postcingulid is present labially. The metaconid and entoconids have pointed apices while the protoconid and the hypoconid have rounded apices. The hypoconulid in lower third molar comprises prehypoconulideristid and posthypoconulideristid.

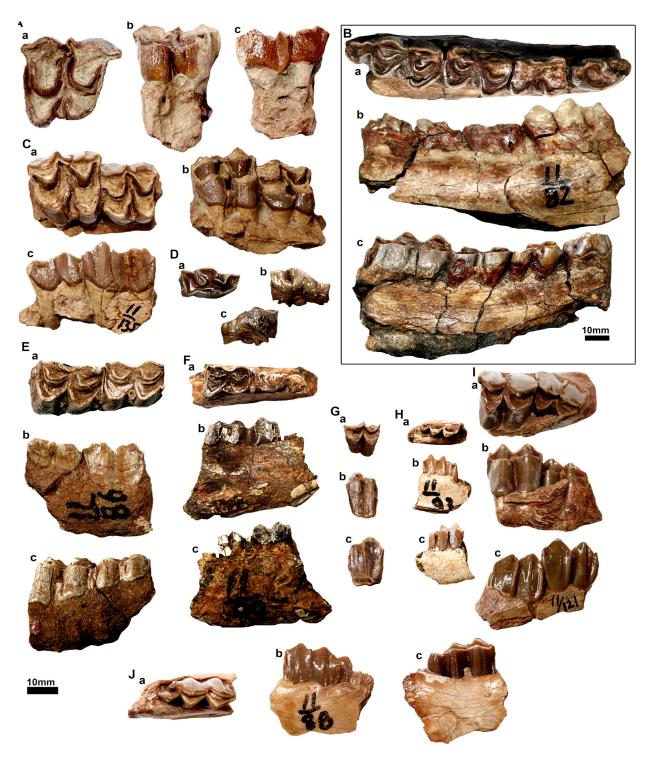


Fig. 2. *Pachyportax latidens*: **A**, PC-GCUF 11/138, left M3; **B**, PC-GCUF 11/82, right mandible fragment with p4-m3. *Tragoportax punjabicus*: **C**, PC-GCUF 11/135, right maxilla fragment with M1-2; **D**, PC-GCUF 11/137, right p4; **E**, PC-GCUF 11/86, right mandible fragment with m1-2. *Tragoportax* cf. *salmontanus*: **F**, PC-GCUF 11/90, right mandible fragment with p4-m1. *Elachistoceras khauristanensis*: **G**, PC-GCUF 11/126, right M2; **H**, PC-GCUF 11/93, right mandible fragment with m3. *Gazella lydekkeri*: **I**, PC-GCUF 11/121, left maxilla fragment with M2-3; **J**, PC-GCUF 11/88, right mandible fragment with m3. Views: **a**, occlusal; **b**, lingual; **c**, labial.

Taxa	Number	Nature / Position	Length	Width	W/L
P. latidens	PC-GCUF 11/132*	rP3	18	16 ca	0.88
	PC-GCUF 11/138*	1M3	27.5	31	1.13
	PC-GCUF 11/100*	М	22 ca	-	-
	PC-GCUF 11/82*	rp4	20	13	0.65
		rm1	21	15	0.65
		rm2	24	17	0.71
		rm3	36	18	0.71
	PC-GCUF 11/133*	rm2	24	16	0.67
P. cf. nagrii	PC-GCUF 11/139*	1M2	19	23	1.21
S. cf. vexillarius	PC-GCUF 11/131*	1P3	13	12	0.92
	PC-GCUF 11/134*	rP3	16	14	0.88
	PC-GCUF 11/130*	lp2	17	10	0.59
	PC-GCUF 11/129*	lm3	34	15	0.44
	PC-GCUF 11/84*	rm2	27	14	0.52
		rm3	35	13	0.37
T. punjabicus	PC-GCUF 11/109*	rM1	14	16	1.14
	PC-GCUF 11/94*	M1	20	16	0.83
	PC-GCUF 11/141*	1M2	17	19	1.12
	PC-GCUF 11/140*	1M2	18	19	1.05
	PC-GCUF 11/85*	rM1	20	20	1
		rM2	21	21.5	1.02
	PC-GCUF 11/135*	rM1	21.5	22	1.02
		rM2	17	19	1.12
	PC-GCUF 11/110*	rp3	12.5	7	0.56
	PC-GCUF 11/98*	rp3	12	7	0.63
	PC-GCUF 11/136*	lp4	14.5	7.5	0.52
	PC-GCUF 11/137*	rp4	18	9	0.5
	PC-GCUF 11/83*	rp4	16	9	0.56
		rm1	15.5	11	0.71
		rm2	18	12	0.67
		rm3	25	11	0.44
	PC-GCUF 11/86*	rm1	17.5	13	0.72
		rm2	20	15	0.75
	PC-GCUF 11/87*	lp4	-	-	-
		lm1	17	11	0.64
	PC-GCUF 11/124*	rp4	9	8	0.89
		rm1	16	6	0.38
	PC-GCUF 11/114*	lm1	17.5	12	0.69
	PC-GCUF 11/113*	rm2	18.5	11	0.59
	PC-GCUF 11/95*	rm3	24	11	0.46
	PC-GCUF 11/96*	rm3	25 ca	11	0.44
T. salmontanus	PC-GCUF 11/90*	rp4	11	7	0.64
1. Sumonulus		rm1	13	9	0.69
E. khauristanensis	PC-GCUF 11/126*	rM2	11	10	0.91
	PC-GCUF 11/91*	lm1	9	6	0.69
	PC-GCUF 11/92*	rm3	11	5.5	0.41
	PC-GCUF 11/93*	rm3	11	4.5	0.5

Table I.- Comparative measurements (mm) of cheek teeth of the Siwalik boselaphines. *The studied specimens.(Referred data are taken from Pilgrim, 1937, 1939; Akhtar, 1992; Khan et al., 2009, 2010a).

Dhok Pathan Bovids	3
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Taxa	Number	Nature / Position	Length	Width	W/L
Gazella lydekkeri	PC-GCUF 11/119*	rM1	8	9.5	1.19
	PC-GCUF 11/121*	1M2	17	18	1.06
		1M3	15	16	1.07
	PC-GCUF 11/128*	1M3	15	13.5	0.9
	PC-GCUF 11/123*	dm	17.5	8	0.45
	PC-GCUF 11/111*	1p3	12	7	0.58
	PC-GCUF 11/120*	lp3	12.5	6.5	0.52
	PC-GCUF 11/112*	rm1	9.5	7	0.73
	PC-GCUF 11/116*	lm1	14	10	0.71
	PC-GCUF 11/89*	rm1	12.5	9	0.72
	PC-GCUF 11/117*	rm1	13	9	0.69
	PC-GCUF 11/125*	rm2	9.5	7.5	0.79
	PC-GCUF 11/127*	rm2	10.5	8	0.76
	PC-GCUF 11/115*	rm2	16	10	0.65
	PC-GCUF 11/118*	rm3	19.9	10	0.50
	PC-GCUF 11/88*	rm3	21	9.5	0.45

Comparison

The teeth are characterized by a large size, entostyle/ ectostylid very extended transversely; relatively strong styles and ribs, median ribs broad and relatively prominent, enamel moderately thick and rugose with traces of cement. There is no constricted crown neck as in *Selenoportax*. The specimens show all the basic features of the genus *Pachyportax*. The Middle Siwalik subgroup is represented by two species of *Pachyportax*: large size *P. latidens* and small size *P. nagrii* (Pilgrim, 1937; Khan *et al.*, 2009, 2010a). The teeth are unambiguously referable to *Pachyportax latidens*, a large size Siwalik boselaphine (Pilgrim, 1937; Khan *et al.*, 2009, 2010a) (Figs. 2 and 4, Table I).

Pachyportax cf. nagrii Pilgrim, 1939

Studied material

PC-GCUF 11/139, isolated left M2.

Locality

Dhok Pathan (near Rest House), Chakwal district, the Punjab province, Pakistan.

Description and comparison

The molar is small with divergent styles. A prominent transversally extended entostyle is present. The molar indicates basic features of *Pachyportax* boselaphine: the entostyle is expanded transversely, the lingual lobes are less constricted and the fossettes are open. The crown neck of the tooth is not narrow as in *Selenoportax* (Khan *et al.*, 2009). The molar is smaller than *P. latidens* (Table I) and could be associated to *P. nagrii*. Lacking adequate material it is assigned to *P. cf. nagrii*.

Discussion

Pachyportax is found abundantly in the Middle Siwaliks (Lydekker, 1876; Pilgrim, 1937; Akhtar, 1992; Khan, 2008; Khan *et al.*, 2009, 2010a, 2014) and quite rare in Arabian Peninsula (Gentry, 1999). It is a typical Late Miocene taxon, which occurs in the Nagri and Dhok Pathan formations of the Siwaliks (Pilgrim, 1937; Khan *et al.*, 2009). Few specimens were also recovered from the Baynunah Formation of Abu Dhabi, United Arab Emirates (Gentry, 1999).

Pachyportax was restricted to the Middle Siwaliks because Himalayan Mountains acted as a barrier in its dispersal out of southern Asia prior to Late Miocene hence isolating the Siwalik faunas (Bernor, 1984). Pachyportax occurred in the Nagri and the Dhok Pathan zones of the Siwaliks, until large bovines (e.g., Proamphibos, Hemibos, Bison) replaced it soon after the start of the Tatrot Formation. The French boselaphine Parabos cordieri resembles Pachyportax and occurred in the European mammal zone MN 14 (Mein, 1989), which is equal to the Early Pliocene; hence, it is younger than Pachyportax species.

Selenoportax Pilgrim, 1937 Selenoportax cf. vexillarius Pilgrim, 1937

Studied material

PC-GCUF 11/131, isolated left P3; PC-GCUF 11/134, isolated right P3; PC-GCUF 11/130, isolated left p2; PC-GCUF 11/97, isolated m1; PC-GCUF 11/129, isolated left m3; PC-GCUF 11/84, right mandible fragment with m2-3.

Locality

Dhok Pathan (Kundrali), Chakwal district, Punjab province, Pakistan.

Description

The paracone is round and prominent among the cusps in premolars. The paracone rib is narrow, unfused anteriorly with well-distinguished parastyle. The metastyle is less prominent and thin. The protoconid rib is narrow and short in the lower molars. The transverse flange is present anteriorly. The paraconid is well distinguished and compressed laterally. The metaconid is short, broad at the base and less projected. The postprotocristid leads to the entoconid through a thin premetacristid. The postentocristid is directed towards the hypoconid. A lingual cingulid is placed adjacent to the entoconid. The m3 is similar to m2 with addition of hypoconulid. The back fossette of the m3 is oblique.

Comparison and discussion

The rugosity, prominence of median ribs, entostyles/ ectostylids, divergent styles/stylids and narrowing of the crown neck exclude the specimen from the genus *Pachyportax* and make their inclusion in the genus *Selenoportax* (Pilgrim, 1937; Akhtar, 1992; Khan *et al.*, 2009, 2010a). *Selenoportax* is represented by two species in the Siwaliks, *S. vexillarius* and *S. lydekkeri* (Pilgrim, 1937; Khan *et al.*, 2009). The cheek teeth of *S. vexillarius* are smaller than those of *S. lydekkeri* (Khan *et al.*, 2009). The sample shows the basic features of *S. vexillarius*, and moreover the material falls within the size range of *S. vexillarius* (Fig. 4, Table I). Accordingly, the specimens are referred to *S. cf. vexillarius*.

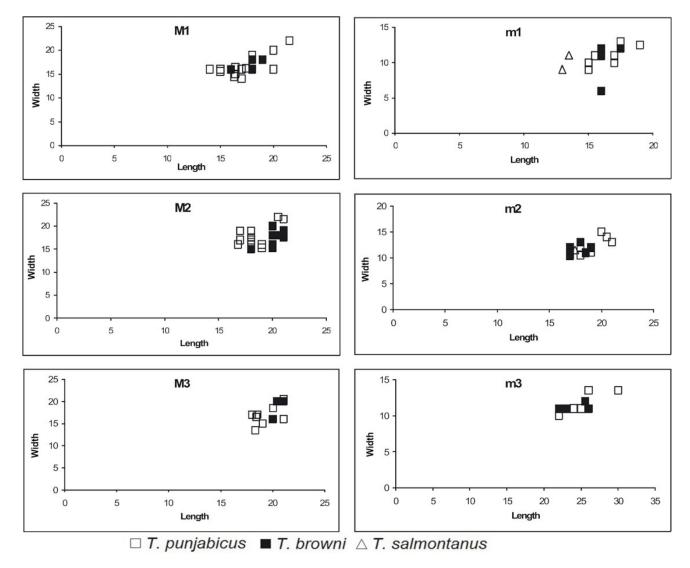
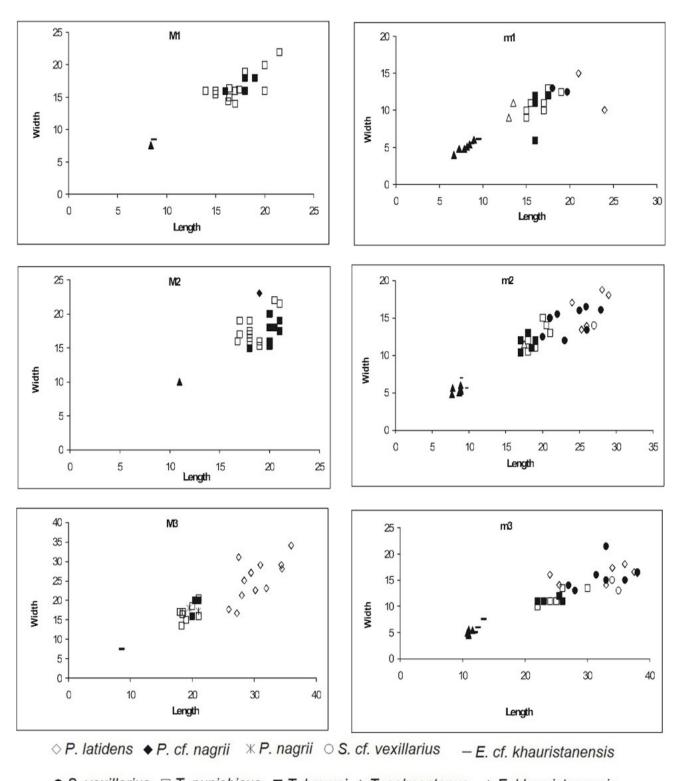


Fig. 3. Bivariate plot (in mm) of the Siwalik *Tragoportax*. Note the overlapping position of *T. punjabicus* (Pilgrim, 1910) and *T. browni* (Pilgrim, 1937) in the Late Miocene Dhok Pathan Formation in Northern Pakistan.



● S. vexillarius □ T. punjabicus ■ T. browni △ T. salmontanus ▲ E. khauristanensis

Fig. 4. Bivariate plot (in mm) of the Siwalik boselaphines. Note the three morphs (small, medium and large) of the Siwalik boselaphines.

The *Selenoportax* remains are known from the Late Miocene of the Siwaliks (Pilgrim, 1937; Akhtar, 1992; Khan *et al.*, 2009, 2010a). The *Selenoportax* record indicates that it was present in the Siwaliks from the Late Miocene to Pliocene (Akhtar, 1992; Barry *et al.*, 2002; Khan *et al.*, 2009, 2010a). A few specimens collected from the Tatrot Formation (Akhtar, 1992) extend the range of *Selenoportax* from 10.3 to 2 Ma, contrary to the previous findings from 10.3 to 7.9 Ma (Barry *et al.*, 2002).

Nevertheless, some uncertain occurrences are mentioned out of the Siwaliks. Solounias (1981) referred a *Selenoportax* horn core from Pikermi; according to him the material is not diagnostic enough for a more specific determination. This supposed occurrence of a single horn core cannot be taken as indicative for the presence of *Selenoportax* in Europe. Qiu and Qiu (1995) list *Selenoportax* sp. from the Lufeng fauna (Miocene of China), age of 11.1–8.0 Ma (Flynn and Qi, 1982). These specimens represent the sole record of *Selenoportax* from Miocene of Northern and Central Asia (Qiu and Qiu, 1995).

Genus *Tragoportax* Pilgrim, 1937 *Tragoportax punjabicus* (Pilgrim, 1910)

Studied material

PC-GCUF 11/109, isolated right M1; PC-GCUF 11/94, partially broken M1; PC-GCUF 11/141, isolated left M2; PC-GCUF 11/140, isolated left M2; PC-GCUF 11/185, right maxilla fragment with M1-2; PC-GCUF 11/135, right maxilla fragment with M1-2; PC-GCUF 11/110, isolated right p3; PC-GCUF 11/98, isolated left p3; PC-GCUF 11/136, isolated left p4; PC-GCUF 11/137, isolated right p4; PC-GCUF 11/124, right mandible fragment with p4-m3; PC-GCUF 11/124, right mandible fragment with m1-2; PC-GCUF 11/86, right mandible fragment with m1-2; PC-GCUF 11/86, right mandible fragment with m1-2; PC-GCUF 11/87, left mandible fragment with m1-2; PC-GCUF 11/87, isolated right m3; PC-GCUF 11/14, isolated left m1; PC-GCUF 11/113, isolated right m2; PC-GCUF 11/95, isolated right m3; PC-GCUF 11/96, right broken m3.

Locality

Dhok Pathan (Kundrali, Police Chowki, Dhindhar), Chakwal district, Punjab province, Pakistan.

Description

In upper molars, the prefossette is wider than postfossette and both narrow anteriorly (Fig. 2C). The parastyle and mesostyle are weaker than metastyle. The enamel is rugose with white and brown tinges. The M2 is a large version of M1 (Fig. 2C). The metaconid of p3 is backwardly directed. The entoconid is stronger than the metaconid and the paraconid of p3 is stronger than the parastylid and placed antero-posterior axis of the premolar. The p4 is extended antero-posteriorly and similar to the p3. The p4 has a strong paraconid and T shaped metaconid (Fig. 2D). The entoconid is fused with the endostylid. The anterior valley of the p4 is open. The ectostylid is well developed in m1. A cingulum is present postero-labially in m2. The third molar has pre- and postfossettes as well as the back fossette of the hypoconulid (Fig. 2E). The molar is represented by the metastylid, the mesostylid, the entostylid as well as the hypoconulid stylid.

Comparison

The teeth may be distinguished from the teeth of *Pachyportax* and *Selenoportax* in having small size and weak ectostylid (Pilgrim, 1937). The described characters somewhat correspond to a medium size boselaphine *Tragoportax* from the Siwaliks to which these specimens could be attributed. The p3 and p4 indicate "T" shaped metaconids (Fig. 2D), a feature of the genus *Tragoportax* (Spassov and Geraads, 2004). Morphological and metric features of the studied teeth coincide with *T. punjabicus* (Fig. 3, Table I) and consequently the specimens are related to *T. punjabicus* (Pilgrim, 1937; Khan *et al.*, 2010a).

Tragoportax cf. salmontanus Pilgrim, 1937

Studied material

PC-GCUF 11/90, right mandible fragment with p4-m1.

Locality

Dhok Pathan (near Rest House), Chakwal district, Punjab province, Pakistan.

Description

The p4 is represented by the typical morphology of the bovid premolar (Fig. 2F). The anterior valley is broader than the posterior one. The p4 is extended anteroposteriorly. The p4 has a strong paraconid, metaconid and entoconid. The entoconid is fused with the endostylid. The m1 is complete representing major conids (Fig. 2F). The metastylid and entostylid are not prominent. The prefossette is narrower than the postfossette. A strong ectostylid is present.

Comparison

The p4 is characterized by metaconid "T" structure (Fig. 2F). The 'T' structure of the p4 and the morphology of the m1 associate them to *Tragoportax* (Spassov and Geraads, 2004). *Tragoportax* is represented by three Siwalik species *T. browni, T. punjabicus* and *T. salmontanus,* distinguishing on the basis of the size

(Pilgrim, 1937; Khan *et al.*, 2010a). *Tragoportax browni* and *T. punjabicus* are of the large sized species (almost same size) while *T. salmontanus* is the small one (Fig. 3, Table I). The sample size with morphological evidence can be attributed to the small species of the Siwalik *Tragoportax* and either corresponds to *T.* cf. *salmontanus* as it is often the case.

Discussion

Previously, the different species of the Siwalik tragoportacines are distinguished on the basis of horncores namely, T. salmontanus, T. perimensis, T. islami, T. punjabicus and T. browni (Pilgrim, 1937; Khan et al., 2010a). The horn-cores of the poorly known T. perimensis from the Middle Siwaliks (Pilgrim, 1939) are much shorter than other Eurasian species. Another poorly known species from the Siwaliks is T. islami. Tragoportax islami and T. perimensis are a possible synonym of T. salmontanus. The difference in horn-core curvature and in size of these poorly known species may be due to individual variability (Kostopoulos, 2009). The two large Siwalik species T. punjabicus and T. browni shows overlapping in size. Tragoportax browni might be synonym of T. punjabicus as proposed by Kostopoulos (2009) but it needs a more reliable material (e.g., skull, horn-cores) to confirm this hypothesis.

The genus Tragoportax characteristics are intermediate between Selenoportax and Miotragocerus. Tragoportax horn-cores are much similar to Miotragocerus in cross-section while different from the isosceles triangle of Selenoportax. Tragoportax differs from Miotragocerus in horn-cores position, which are more widely spaced in Miotragocerus (Pilgrim, 1937). It was noted that Tragoportax were found in woody area as well as in less community areas. This habitat type shows that their range more widespread in Oriental as well as in denser areas of Western Europe. Tragoportax show that they were living in open areas and not had any ability to penetrate into thick forest areas (Spassov and Geraads, 2004).

Elachistoceras Thomas, 1977 Elachistoceras khauristanensis Thomas, 1977

Studied material

PC-GCUF 11/126, isolated right M2; PC-GCUF 11/91, left mandible fragment with m1-2; PC-GCUF 11/92, right mandible fragment with m3; PC-GCUF 11/93, right mandible fragment with m3.

Locality

Dhok Pathan (near Rest House), Chakwal district, Punjab province, Pakistan.

Description

The teeth are tiny (Fig. 2G, H). The parastyle, mesostyle and metastyle are well differentiated. The m2 is completely preserved (Fig. 2G). The protoconid is present obliquely. The m3 is complete and in early wear with hypoconulid (Fig. 2H). The morphological features of the molar are well reflected and have been observed in detail.

Comparison and discussion

Brachydont, definitely convex non-smooth lingual wall, rugose enamel, small size and presence of weak caprine fold are distinct features of *Elachistoceras*. Morphometrically, the teeth can be compared very likely with the paratype and hypodigm of the species *Elachistoceras khauristanensis* (Fig. 4, Table I). Based on their general characters and size, the specific determination of the teeth could only be assigned to *E. khauristanensis*. The species is only known from the Lower and Middle Siwalik subgroups (Thomas, 1977; Akhtar, 1992; Khan *et al.*, 2009).

During the Late Miocene, the Dhok Pathan Formation of Chakwal district was represented by three morphotypes of boselaphines (Fig. 4). The morphotype 1 is the largesized boselaphines representing *Pachyportax latidens*, *Selenoportax vexillarius* and *S. lydekkeri*. The morphotype 2 is the medium-sized boselaphines including *Pachyportax nagrii*, *Tragoportax punjabicus* and *T. salmontanus*. The morphotype 3 represents the small-sized boselaphines (Fig. 4) including *Elachistoceras khauristanensis* and *Eotragus* sp. (Thomas, 1977; Akhtar, 1992; Khan *et al.*, 2009, 2010a). The specific richness of the boselaphines in the Middle Siwalik sediments is remarkable, where apparently endemic advanced high crowned forms (*Selenoportax*, *Pachyportax*) existed along with mesodonts (*Tragoportax*) and primitive brachydonts (*Elachistoceras*).

Tribe Antilopini Gray, 1821 Genus *Gazella* Blainville, 1816 *Gazella lydekkeri* Pilgrim, 1939

Studied material

PC-GCUF 11/119, isolated right upper M1; PC-GCUF 11/121, left maxilla fragment with M2-3; PC-GCUF 11/128, isolated left M3; PC-GCUF 11/123, right mandible fragment with deciduous molar; PC-GCUF 11/111, isolated left p3; PC-GCUF 11/120, isolated left p3; PC-GCUF 11/120, isolated left p3; PC-GCUF 11/112, isolated right m1; PC-GCUF 11/116, isolated left m1; PC-GCUF 11/189, right mandible fragment with m1; PC-GCUF 11/117, isolated right m1; PC-GCUF 11/125, isolated right m2; PC-GCUF 11/115, isolated right m2; PC-GCUF 11/125, right mandible fragment with m3; PC-GCUF 11/188, right mandible fragment with m3; PC-GCUF 11/189, right mandible fragment with m3; PC-GCUF 11/115, right mandible fragment with m3; PC-GCUF 11/1120, right mandible fragment with m3; PC-GCUF 11/120, right mandible fragment with m3; PC-GCUF 11/120,

GCUF 11/118, isolated right m3.

Locality

Dhok Pathan (Parrayala, Kundrali, Dhindhar), Chakwal district, Punjab province, Pakistan.

Description

The enamel is shiny and smooth. The mesostyle is thick and prominent. The parastyle and mesostyle are heavier than the metastyle in M2. The M3 is smaller than M2 and looks like M2 (Fig. 21). The deciduous molar is a trilobed tooth. The cingulids are present labially in the valleys between the first and second lobes as well as in the second and third lobes. The p3 is bilobed and asymmetrical. The paraconid and the parastylid are independent in the upper part of the p3. The paraconid is well distinguished from the parastylid and compressed laterally. The metaconid directs backwards but not fused with the entoconid. It is short, broad at the base and less projected.

The protoconid is the highest among the conids. The protoconid rib is narrow and short. The postparacristid is broad as compared to the extremely thin preparacristid. The postprotocristid leads to the entoconid through a thin premetacristid. The postentocristid is directed towards the hypoconid. A short and moderately developed entostylid is located adjacent to the entoconid. The hypoconid is the lowest one among the conids. The anterior lingual valley is much wider than the posterior one. The anterior half of the tooth is elevated relative to the posterior one.

The conids are conical in the lower molars. A prominent goat fold is present anteriorly (Fig. 2J). The ribs are broader at the base and gradually narrow toward the tips. The mesostylid on the lingual side is very weak, visible only on the upper half of the tooth crown. The ectostylid is moderately developed. The m2 is slightly greater in size than m1. The entostylid is sharp and prominent. The preentocristid and the postentocristid are sloped downwardly. The fossettes are narrow, crescentic and not very deep. The hypoconulid is prominent, oval shaped with a furrow on the lingual side and it is inclined towards the labial side (Fig. 2J). In some molars it is compressed and in some specimens it is almost rounded.

Comparison

The studied dental material affords no justification for separating them generically from *Gazella*: prominent narrow styles, absence/vestigial entostyles, small ectostylids and prominent goat folds on the lower molars are the characters that support their inclusion to the genus *Gazella* (Table I). The presence of rudimentary entostyles in some molars, the prominence of paracone rib as compared to the metacone rib and the open p4 anterior valley as opposed to the partially closed posterior one, are the characters that strongly suggest their inclusion to an extinct Siwalik species *G. lydekkeri* (Pilgrim, 1937).

Discussion

Pilgrim (1937) and (1939) described two species of *Gazella* from the sediments of the Middle Siwaliks, *G. lydekkeri* and *G. superba* on the basis of the horn-core size variation and the curvature. Akhtar (1992) erected another species of *Gazella*, *G. padriensis*. *Gazella superba* was recorded only by frontlet and not even one single molar has been described for the species *G. superba* yet. More recently, few specimens of *G. superba* are recovered from Hasnot (Dhok Pathan Formation) and *Gazella padriensis* (Akhtar, 1992) was synonymized with *G. lydekkeri* (Khan *et al.*, 2015). Nevertheless, there is size variability in *Gazella* species as variation within single samples may be very large (Kostopoulos, 2009).

GENERAL DISCUSSION

The major bovid groups present in the Dhok Pathan Formation are Tragoportacina, *Pachyportax, Selenoportax* and *Gazella*, as in other Eurasian Late Miocene sites (Vrba and Haile-Selassie, 2006; Bibi *et al.*, 2009; Khan *et al.*, 2009, 2010a, 2011, 2012, 2014; Gentry *et al.* 2014). As noted by the earlier researchers, the bovid fauna suggests a much higher diversity during the Late Miocene-Early Pliocene of the Siwaliks (Lydekker, 1878; Colbert, 1935; Pilgrim, 1937, 1939; Akhtar, 1992; Khan *et al.*, 2010a, 2014). The boselaphines in the Dhok Pathan Formation may have been more diverse than boselaphines from the earlier Siwalik formations (*e.g.*, Chinji, Nagri) and intermediate habitats are more likely to have been available to boselaphines.

The Late Miocene – Early Pliocene was a time of increasing habitat diversity and fragmentation, or that boselaphines radiated to fill open niches. Forests may have declined or fragmented and open plains developed (Pilgrim, 1937, 1939; Thomas, 1984; Akhtar, 1992; Bibi *et al.*, 2009; Khan *et al.*, 2009, 2010a). The general body mass and habitat relationship is noted that the largest bovids (*Pachyportax, Selenoportax*) are preferably found in open country while the smallest bovids (*Elachistoceras*) are known to inhabit closed environment (Kappelman *et al.*, 1997).

The taxonomic composition of the Dhok Pathan Formation fauna indicates that during the Late Miocene an arid palaeoclimate had been established in the Siwaliks, which supported pockets of forested areas. This is in agreement with previous studies as indicated by stable isotopes for the development of C4 grasslands between 10

and 3.4Ma (Barry *et al.*, 2002, 2013). This shift to a drier and more seasonal climate in the Siwaliks might cause the extinction of a number of medium-sized boselaphine species, and induced the establishment of high crowned large boselaphines such as *Selenoportax* and *Pachyportax*. The abundance of large bovids from Chakwal suggests that light cover to open country was a major component in Chakwal during Late Miocene-Early Pliocene.

CONCLUSIONS

There is evidence of at least seven bovid species at the Dhok Pathan type locality of Northern Pakistan. The boselaphine bovids are highly diversified around the Late Miocene-Early Pliocene of Chakwal. The abundance of boselaphines with reduncines and antilopines indicates a mixture of woodland and grassland biomes.

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Statement of conflict of interest

Authors have declared no conflict of interest.

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