Rivista Italiana di Paleontologia e Stratigrafia	volume 118	no. 2	pp. 325-341	July 2012

TRAGULIDS (ARTIODACTYLA, RUMINANTIA, TRAGULIDAE) FROM THE MIDDLE SIWALIKS OF HASNOT (LATE MIOCENE), PAKISTAN

MUHAMMAD AKBAR KHAN* [1], MUHAMMAD AKHTAR [2], GEORGE ILIOPOULOS [3] & HINA [4]

Received: October 4, 2010; accepted: February 1st, 2012

Key words: *Dorcatherium, Dorcabune*, Vertebrate fossils, Late Miocene, Siwaliks.

Abstract. Tragulids are the best represented ruminants in the Hasnot outcrops of the Pakistani Middle Siwaliks (Late Miocene). The remains described in this paper comprise predominantly isolated teeth, maxilla and mandible fragments. The specimens can be referred to three taxa, namely *Dorcatherium minus*, *Dorcatherium majus* and *Dorcabune anthracotherioides*. The collection of *Dorcatherium* fossils from Hasnot is the most extensive record of this genus in the Siwaliks. The tragulids suggest a humid habitat with abundant cover.

Riassunto. I tragulidi sono i ruminanti meglio rappresentati negli affioramenti di Hasnot riferibili al Siwaliks medio del Pakistan (Miocene Superiore). I resti descritti in questo articolo sono in prevalenza denti isolati, oppure frammenti di mascella e di mandibola. Gli esemplari sono riferibili a tre taxa, e precisamente *Dorcatherium minus*, *Dorcatherium majus* e *Dorcabune anthracotherioides*. La collezione di fossili di *Dorcatherium* da Hasnot rappresenta la documentazione più estesa di questo genere nei Siwaliks. Gli esemplari di tragulidi suggeriscono la presenza di un habitat umido con abbondante copertura vegetale.

Introduction

The small nonpecorans ruminants named the clade Tragulidae comprise the smallest living cetartiodactyls (Janis 1984; Scott & Janis 1992; Hassanin & Douzery 2003; Marcot 2007; Agnarsson & May-Collado 2008). Tragulids are concordantly considered as the most primitive still living ruminants (Janis & Scott 1987) with roots back to Eocene (Métais et al. 2001), and survived as tropical relicts: the water chevrotains (*Hyemoschus*) of Central Africa (Dubost 1965) and the mouse deer or Asiatic chevrotain (*Tragulus, Moschiola*) of South-East Asia (Meijaard & Groves 2004; Groves & Meijaard 2005). The earliest tragulids (*Archaeotragulus*), dependent on stable warm forests, are known in Pakistan, by 18.0 My (Rössner 2007; Farooq et al. 2007a-d, 2008).

The tragulid fauna from Hasnot (Fig. 1) is represented by four species *Dorcatherium minus*, *Dorcatherium majus*, *Dorcabune anthracotherioides* and *Dorcabune nagrii* (Farooq 2006; Farooq et al. 2007a-d, 2008 and literature therein). Previous reports on tragulids in the Late Miocene to the Early Pliocene of the Hasnot locality are sketchy (Farooq et al. 2007a-d, 2008) and the tragulid material was never described thoroughly after Colbert (1935). Furthermore, the taxonomy of the Siwalik tragulids is still unresolved and need to be reworked (Barry et al. 2005). The available material of tragulids from Hasnot is only dentition. Determination at species level can be attempted based on extensive and reliably determined dentition material from further Siwalik localities.

We describe here new material representing three (*Dorcatherium minus*, *Dorcatherium majus*, *Dorcabune anthracotherioides*) among the four species of the Siwalik tragulids in the Hasnot locality (Fig. 1) that provide a glimpse into the palaeoenvironment of the area during the Late Miocene and the Early Pliocene. This paper discusses and interprets the entire collection of tra-

1 *Corresponding author. Palaeontology laboratory, Department of Zoology, Quaid-e-Azam Campus, Punjab University, Lahore, Pakistan. E-mail: akbaar111@yahoo.ca
2 Palaeontology laboratory, Department of Zoology, Quaid-e-Azam Campus, Punjab University, Lahore, Pakistan. E-mail: drakhtarfdrc@hotmail.com. Phone- 003225605657; Fax- 0092-429231246
3 Natural History Museum of Crete, University of Crete, 71409 Heraklion, Greece. E-mail: gi6@nhmc.uoc.gr
4 Department of Zoology, Government College University, Faisalabad, Pakistan. E-mail: akm146@hotmail.com

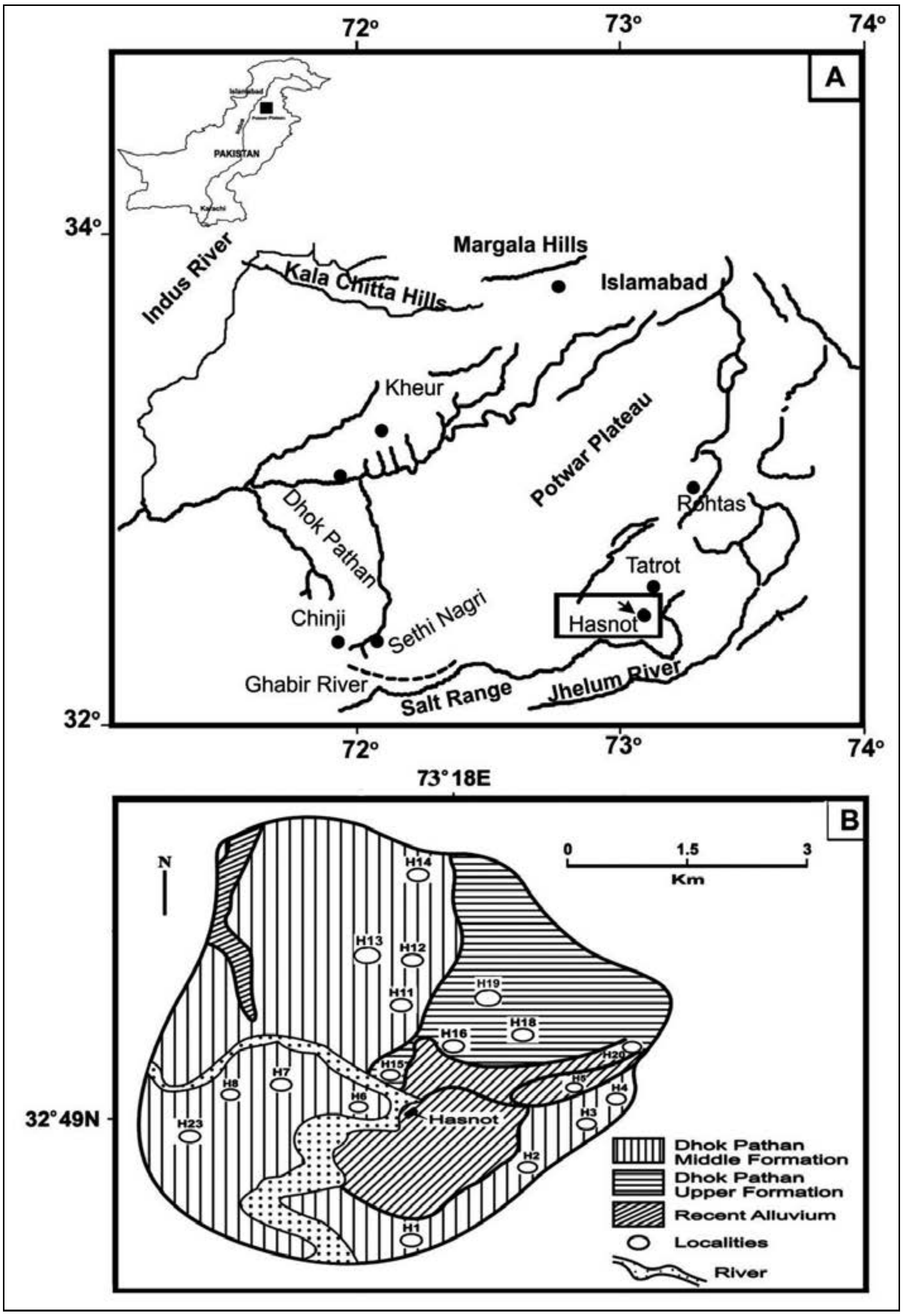

Fig. 1 - A – Simplified map of the Potwar Plateau in northern Pakistan; reference locality of the Siwaliks encircled. B – Simplified geologic map of Hasnot area with indicated localities around the village Hasnot (H = Hasnot) from where the studied material is recovered (map is modified from Colbert 1935).

gulids from the Hasnot outcrops of the Middle Siwaliks, northern Pakistan.

Definitions

Dorcatherium fold refers to the fold occurring on the postmetacristid on the lower molars of some primitive ruminants and extant tragulids and the entoconidian groove refers to the two parallel folds (thus forming a groove) occurring on the mesial side of the entoconid. *Tragulus* fold refers to the fold situated on the postprotocristid and basally linked to the prehypocristid. M-structure is formed by the bifurcation of the post-metacristid and post-protocristid (Métais et al. 2001).

Siwalik tragulids

The Siwalik tragulids are known to be represented by two genera *Dorcatherium* (*Dt.*) and *Dorcabune* (*Db.*) (Lydekker 1876; Pilgrim 1915; Colbert 1935; Farooq et al. 2007a-d, 2008) (Fig. 2). The extinct genus *Dorcatherium* is known from Asia (Lydekker 1876; Matthew 1929; Corbert & Hill 1980; Raza & Meyer 1984; Farooq et al. 2007a-b; Khan & Akhtar 2011), Europe (Rössner 2010) and Africa (Pickford 1986, 2001; Pickford et al. 2004). *Dorcatherium* are represented by four Siwalik species *Dt. minimus*, *Dt. nagrii*, *Dt. minus* and *Dt. majus* (Lydekker 1876; Colbert 1935; West 1980; Gaur et al. 1983; Farooq 2006; Farooq et al. 2007a-d, 2008; Khan & Akhtar 2011). *Dorcatherium minimus* is reported as the

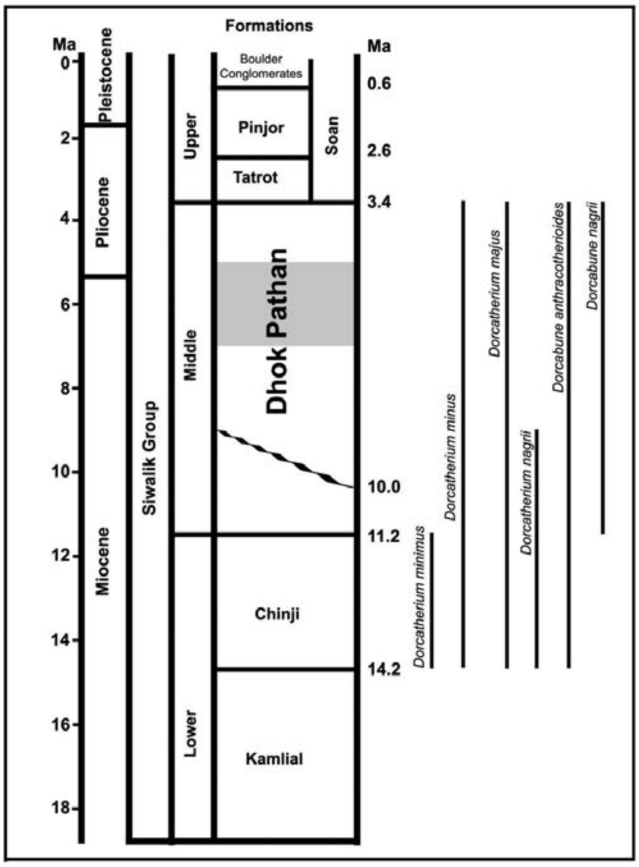

Fig. 2 - Chronological distribution of the Siwalik tragulids (modified from Behrensmeyer & Barry (2005) and the boundary dates are from Dennell (2008) and Nanda (2008)). Black bars represent distribution; the studied area is shaded.

smallest and rarest species of *Dorcatherium* from the Siwaliks (West 1980) (Fig. 2).

Dorcabune is known from the Middle Miocene to the Early Pliocene of the Siwaliks (Pilgrim 1915; Colbert 1935; Métais et al. 2001; Geraads et al. 2005; Farooq et al. 2007c-d) and the Late Miocene of Crete (Van der Made 1996). *Dorcabune* was a large tragulid, which had very bunodont molars and could have weighed close to 100 kg (Janis 1984). Pilgrim (1915) suggested that *Dorcabune* is morphologically close to anthracotheres and more primitive than *Dorcatherium*. Gentry (1978) claimed that *Dorcabune* might be a primitive anthracothere. With the exception of the M structure and the presence of a weak entoconidian groove, *Dorcabune* does not display other apomorphies with *Archaeotragulus*. Nevertheless, this genus is a primitive representative of the group but has interesting derived characters shared with other genera such as the M-structure, a marked "tragulid" character (Sánchez, pers. communication 2011).

Dorcatherium and *Dorcabune* are reported from the Chinji Formation of the Lower Siwaliks in the northern Pakistan (Fig. 2). *Dorcatherium* is represented by four species: *Dt. minimus*, *Dt. nagrii, Dt. minus* and *Dt. majus* and *Dorcabune* is known by the single species *Db. anthracotherioides* from the Chinji Formation (Colbert 1935; West 1980; Farooq 2006; Khan & Akhtar 2011). The Nagri Formation represents three *Dorcatherium* species (*Db. nagrii, Dt. minus* and *Dt. majus*), and one *Dorcabune* species (*Db. nagrii*; Colbert 1935; Prasad 1968; Farooq 2006). The Dhok Pathan Formation represents all the known Siwalik species of the tragulids except *Dt. minimus* and *Db. nagrii* (Fig. 2) (West 1980; Gaur et al. 1983; Farooq et al. 2007a-d, 2008). Tragulids are not recorded from the Upper Siwaliks of Pakistan (Farooq 2006).

Six species of tragulids from the Siwaliks, namely *Dt. minimus* West, 1980, *Dt. nagrii* Gaur et al., 1983, *Dt. minus* Lydekker, 1876, *Dt. majus* Lydekker, 1876, as well as *Db. anthracotherioides* Pilgrim, 1910 and *Db. nagrii* Pilgrim, 1915 which are considered valid (West 1980; Gaur et al. 1983; Farooq 2006; Farooq et al. 2007a-d, 2008; Khan & Akhtar 2011) (Fig. 2). *Dorcabune hyaemoschoides* Pilgrim, 1915, *Db. sindiense* Pilgrim, 1915, and *Db. latidens* Pilgrim, 1915 have been rejected owing to the dubiety of the diagnostic material (Colbert 1935; Farooq 2006).

Geological and Stratigraphical Setting

The ascribed tragulid material comes from the outcrops nearby the village Hasnot (Lat. 32 49 N: Long. 73 18 E), which is situated at about 70 km west of Jhelum city in the Potwar Plateau of northern Pakistan (Fig. 1). The village is located on the east bank of the river Bunha, surrounded by a number of highly fossiliferous localities at an altitude of around 326 meters (Fig. 1). It is surrounded by extensive Neogene freshwater sedimentary rocks from the Late Miocene to the Early Pliocene (Pilbeam et al. 1977, 1979; Barry et al. 2002; Khan et al. 2009). Sixteen fossil mammal localities are known in this area (Fig. 1). The fossil sites of Hasnot are among the richest Late Miocene localities of the Siwaliks and contain a diverse and abundant ruminant fauna, including *Eotragus*, *Selenoportax*, *Pachyportax*, *Tragoportax*, *Gazella*, *Bramatherium*, *Propotamochoerus, Dorcatherium, Dorcabune* and cervids (Tab. 1). These faunas have yielded the age of the Late Miocene to the Early Pliocene (Akhtar 1992; Pickford 1988; Farooq et al. 2007a-d, 2008; Khan 2007a, 2008; Khan et al. 2009; Ghaffar et al. 2010).

The generalized stratigraphic section of Hasnot (Fig. 1) is modified after Colbert (1935). The tragulid specimens were found the following sites of Hasnot: H 6, H 7, H 8, H 11, H 12, H 14, H 16, H 18, H 23 (H – abbreviation for Hasnot locality). These are the same sites from where cervid, bovid and giraffid specimens were recovered (Khan 2007b; Khan et al. 2009; Ghaffar

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

Tab. 1 - Mammalian Fauna from Hasnot area (referred data are taken from Colbert 1935; Pilgrim 1937, 1939; Hussain 1971; Sarwar 1977; Bernor & Hussain 1985; Akhtar 1992; Farooq et al. 2007a-d; Khan et al. 2009; Khan A. M. 2010; Ghaffar et al. 2010).

et al. 2010). The lithology of Hasnot consists of the upper Dhok Pathan Formation (Middle Siwaliks) (isochronous to the European late Turolian age), which is characterized by sandstones with alternate clays and scattered conglomerates in the lower part and conglomerates with sandstones and clays in the upper part. The clays are orange brown in color and the time of deposition ranges from 7 to 5 Ma (Fig. 2) (Pilbeam et al. 1977; Johnson et al. 1982; Barry 1987; Barry et al. 1982, 2002; Khan et al. 2009).

Taphonomy

The Hasnot localities are characterized by the occurrence of scattered vertebrate bones and teeth found in a restricted stratigraphic interval and areal distribution. The fossils are mostly fragmentary in nature, no complete skeletons have been found yet, and articulated remains are rare. The weathering cracks, abrasion marks and byte marks are noted frequently on the specimens. The scale for most localities is between 0.5 to several meters thick and a few of them cover an area of tens of square meters (Badgley 1986). The taphonomic study of the exposed and collected material showed that a variety of pre-burial and post-burial processes affected the bones and teeth of the localities. Significant modifications were observed in the vast majority of the examined specimens. Extensive weathering cracks indicate that some of the collected specimens were exposed on the surface of the ground for a significant period of time. Partly articulated, partly associated and mostly dispersed skeletal parts indicate the long transportation and the significant dispersal of the occurred skeletal elements (Badgley & Behrensmeyer 1980).

Four main types of fossil occurrences were noted during the excavation/survey. The first one consists of fossils that were found in large accumulations over a small area. The second one consists of fossils scattered or in patches. The third one consists of survey collections and, finally, the fourth one is represented by fossils embedded in crevasses. The sites are enriched in isolated teeth, skull fragments, mandibles, horn cores, limb elements and are slightly depleted in vertebrae and phalanges. Fossil assemblages from lag facies (deposits) exhibit many features indicative of fluvial transport, including abraded bones, bones dispersed through the sediment matrix, lack of single-individual skeletal association, and under-representation of the more transportable elements such as vertebrae and ribs (Behrensmeyer 1988). The bovids (artiodactyla) are the most common group found in the localities.

Materials and methods

The material described in this paper is largely part of the PhD study of the senior author, for what collecting was carried out during field trips from 2003 to 2006. Surface collection was the primary method. In addition some specimens considered, already belonged to the collections of the Palaeontology Laboratory, University of the Punjab, Lahore, Pakistan (PUPC), have been collected at the localities around Hasnot village. Further material was collected by the staff of Palaeontological Collection of the Government College University, Faisalabad (PC-GCUF) during an excavation in 2009.

In total, fifteen teeth, six mandible fragments and three maxilla fragments are included in this study. The specimens were catalogued and given a number composed of the year collection and a serial catalogue number (e.g. 09/11). The indication of tooth positions refers with uppercase numbers to upper teeth, with lowercase numbers to lower teeth. All measurements are given in millimeters (mm) and taken with the help of metric vernier caliper. Tooth length and width were measured at occlusal level. Measurements given for teeth are occlusal length and occlusal width. The terminology and measurement of the teeth follow Gentry & Hooker (1988) and Gentry et al. (1999).

Comparisons were made with specimens from the Natural History Museum, London (BMNH), the American Museum of Natural History (AMNH), the Geological Survey of Pakistan (GSP), the Geological Survey of India (GSI), the Palaeontological collection of Government College University, Faisalabad, Pakistan (PC-GCUF) and the specimens from the Palaeontology laboratory of the Zoology Department of University of the Punjab, Lahore, Pakistan (PUPC). The studied material is stored in the Palaeontology laboratory of the Zoology Department of University of the Punjab, in Lahore, Pakistan (PUPC) and the Zoology Department of the GC University, in Faisalabad, Pakistan (PC-GCUF).

Systematic Palaeontology

Artiodactyla Owen, 1848

Ruminantia Scopoli, 1777

Tragulidae Milne-Edwards, 1864

Dorcatherium Kaup & Scholl, 1834

Type species: *Dorcatherium naui* Kaup & Scholl, 1834

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 M1 to M3. 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 'M' shape. The premolars are comparatively long and consist mainly of the buccal conids and crests. Lingual crown elements are underrepresented. At the p4 the entoconid fuses with the postprotocristid. The p3 has only a short lingual entocristid originating at the hypoconid. An exception is the P4, which is shorter and does not have an anteroposterior longish shape" (Rössner 2010: 128). The cheek teeth are high crowned. The upper molars bear strongly developed buccal styles. The lower molars are characterized, either by well-developed ectostylid or by a vestigial ectostylid (Kaup & Scholl 1834).

Geographic distribution. *Dorcatherium* is described from the lower Miocene of Europe by Kaup (1833), Arambourg & Piveteau (1929), Hillenbrand et al. (2009) and Rössner (2007, 2010). It is reported from the Miocene deposits of East Africa by Arambourg (1933), Whitworth (1958), Hamilton (1973), Pickford (2002), Pickford et al. (2004), Quiralte et al. (2008), Sánchez et al. (2010) and Geraads (2010). It is recorded from middle Miocene to early Pliocene of south Asia by Lydekker (1876), Colbert (1935), Prasad (1968), Sahni et al. (1980), West (1980), Farooq (2006) and Farooq et al. (2007a-b, 2008).

Dorcatherium minus Lydekker, 1876

Figs 3A-N, 4A-I, 5J-Q; Tab. 2-3

Type specimen: Right M1-2 (GSI B195), figured in Lydekker (1876, p. 46, pl. VII, figs. 3, 7).

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

Stratigraphic range: Lower to Middle Siwaliks (Colbert 1935; Farooq et al. 2007a).

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

Studied specimens: Upper dentition: left P4 (PC-GCUF 09/22), a fragment of right maxilla with DP4 and M1-3 (PUPC 04/30), a fragment of left maxilla with P4 and M1-2 (PUPC 01/13), left M1 (PUPC 04/3), left M2s (PC-GCUF 09/21, PUPC 86/200, PUPC 04/13), right M2s (PUPC 03/15, PUPC 06/06), right M3 (PUPC 06/4), a fragment of left maxilla with M1-3 (PUPC 04/60). Lower dentition: a fragment of right mandible with p4 and m1 (PUPC 04/33), right and left mandible fragments with m1-m3 and semi erupted p4 (PC-GCUF 09/18, PC-GCUF 09/19), right m1 (PUPC 05/3), right m2 (PUPC 04/2), a fragment of right mandible with broken m1 and complete m2-3 (PUPC 87/25), a fragment of right mandible with broken m2 and complete m3 (PUPC 04/6).

Localities: Hasnot (H 6, H 7-8, H 11, H 14-15, H 16, H 18, H 23), Jhelum district, the Punjab province, Pakistan.

Description

Upper dentition. *P4*. The P4 is triangular, selenodont and rugose with strong anterior and posterior folds (Fig. 3A-N). The labial cusp has anterior, central and posterior styles (Fig. 3A-C). The pre-paracrista is smaller and less curved than the post-paracrista. Lingually, the P4 of PUPC 01/13 has a crest that descends into the central valley posteriorly. The lingual cusp is lower than the main one, and it has wide crests anteriorly and posteriorly which join the ends of the main cusp at the base of the styles, thereby closing off the central fovea anteriorly and posteriorly (Fig. 3I-K).

DP4. The only available DP4 is in late wear and low crowned (Fig. 3I-K). It is a molariform tooth with a low nonsymmetrical crown that is strongly expanded labially. The milk molar has small hypocone and metacone. The parastyle is stronger than the other styles. A cingulum is present lingually and labially. The fossettes look to be absent owing to the late wear. The protoconule is lower in height and broader than the other major cusps (Fig. 3I-K).

M1-3. The molars are almost quadrate in shape and rugose (Fig. 3D-N, Tab. 2). The molars become larger from M1 to M3 within a tooth row. Lingually at the base of the crown, a cingulum extends from the anterior side of the protoconus to the posterior side of the hypoconus. The entostyle is either absent or weakly present in some molars. The anterior and the posterior fossettes are wide and deep. The principal cusps are inclined towards the median longitudinal line of the

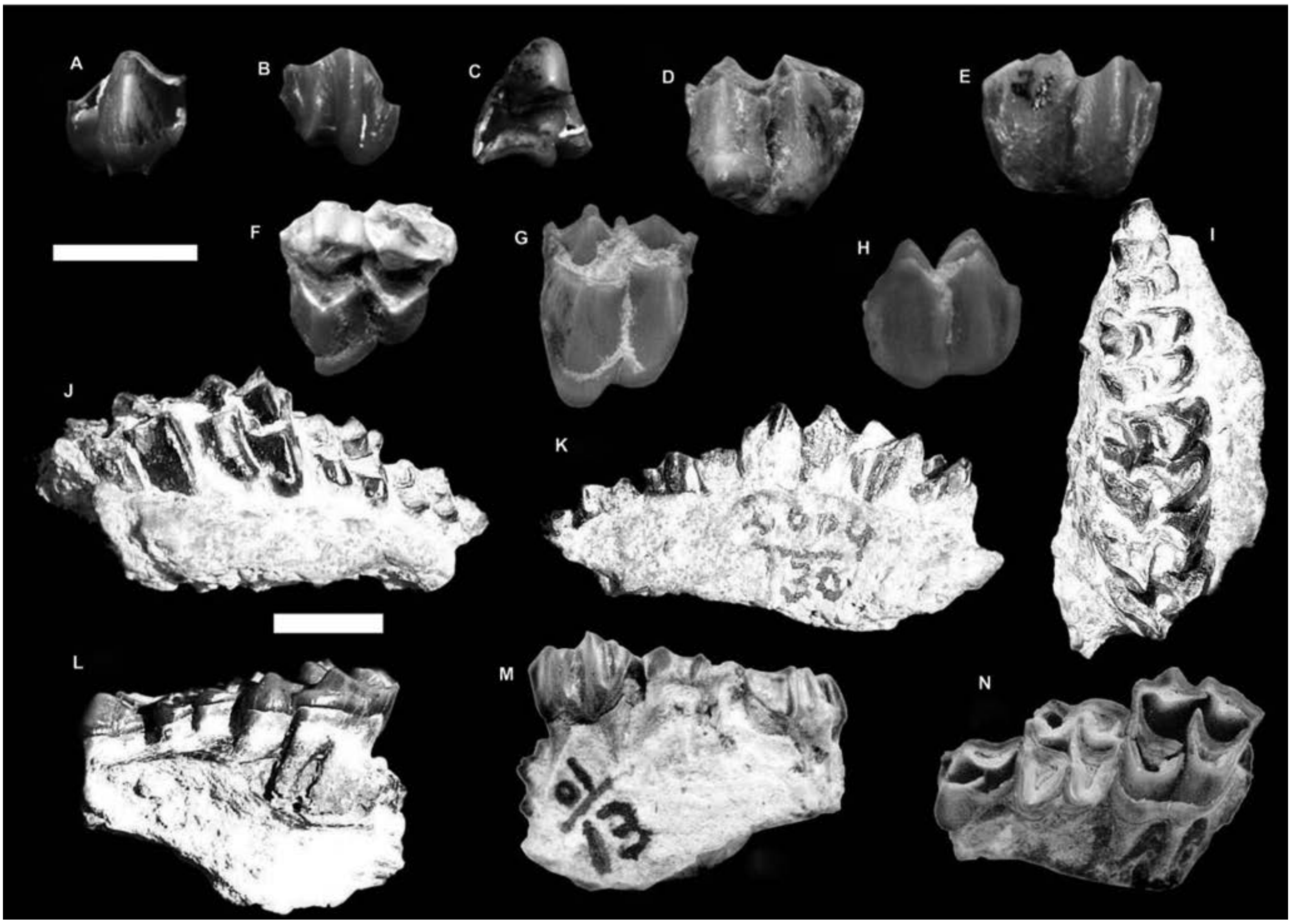

Fig. 3 - *Dorcatherium minus,* upper dentition; A-C, left P4, PC-GCUF 09/22. D-F, left M2, PC-GCUF 09/21. G-H, left M2, PUPC 04/13. I-K, a fragment of right maxilla with DP4 and M1-3, PUPC 04/30. L-N, a fragment of left maxilla with P4 and M1-2, PUPC 01/13. Views are occlusal (C, F, I, N), labial (B, E, H, K, M) and lingual (A, D, G, J, L). Scale bar equals 10 mm. Upper scale bar is for figures A-H; Lower scale bar is for figures I-N.

molar and this inclination is more conspicuous in the lingual cusps than those of the labial ones. The anterolabial cusp has a strong anterior groove descending from its apex to the base of the crown, which separates the anterior style from the main cusp. The parastyle is very well developed and connected to the base of the paraconus rib. The paraconus rib is more prominent than the metaconus rib. On labial view, the styles and the columns are strong (Fig. 3 B, E, H, K, M).

Mandible. The antero-posterior parts of the ramii are damaged having some cracks vertically. The mandible fragments are shallow and slim, there is no part of the symphysis preserved (Fig. 4D-I, Tab. 3).

Lower dentition. *p4*. The p4 in PUPC 04/33 appears to be more complicated than generally in *Dorcatherium* (Fig. 4A-C). The parastylid and paraconid are separated by a shallow furrow. The elongated metaconid takes almost antero-posterior position directed to the rear and leaving a wide open anterior valley. The entostylid is well developed and distinct from the entoconid. Labially, wide anterior and narrow posterior grooves are present. The ridge on the anterior valley is well developed. The latter ridge on the posterior valley terminates posteriorly in a swelling that forms a posterior cusplet, which is joined lingually by an accessory cusplet. The latter is separated from the lingual ridge of the main cusp by a deep groove. The anterior cusplet is low and more lingually positioned.

m1-3. The molars are submesodont and narrow crowned (Figs. 4D-I, 5J-Q). The m2 is larger than the m1; the m3 is characterized by tiny hypoconulid in the midline. The pre-protocristid is less curved in m1 and most curved in m3. The rudimentary ectostylid is present and its size varies. The posterior fossette is crescent shaped and opens linguo-distally. An anterior cingulid is present. The entostylid is weaker than the metastylid. The *Dorcatherium*-fold is present and directed posteriorly. It is formed by the bifurcation of the post-metacristid and post-protocristid and resulting formed a 'M' shape, a diagnostic feature of tragulids.

Comparison. The studied upper and lower dentitions show all the morphological features of the species *Dt. minus*: smaller molars than *Dt. majus* and larger than *Dt. nagrii* (Tabs 2, 4), the presence of mesio-lingual

Number	Description	Width	Length	W/L ratio
Dt. minus				
PC-GCUF 09/22 (H14)*	left P4	8.50	9.00	1.05
PUPC 04/30 (H16)*	right DP4	9.60	5.00	0.52
	right M1	8.00	7.10	0.88
	right M2	9.20	7.80	0.84
	right M3	9.40	8.40	0.89
PUPC 01/13 (H23)*	left P4	9.50	8.00	0.84
	left M1	8.00	9.00	1.10
	left M2	9.00	11.2	1.20
PUPC 04/3 (H7)*	left M1	9.60	6.10	0.63
PC-GCUF 09/21 (H14)*	left M2	12.3	12.0	0.97
PUPC 86/200 (H18)*	left M2	11.0	11.9	1.08
PUPC 04/13 (H8)*	left M2	11.2	9.50	0.84
PUPC 03/15 (H15)*	right M2	11.0	13.0	1.10
PUPC 06/06 (H11)*	right M2	10.6	9.00	0.84
PUPC 06/4 (H11)*	right M3	9.10	9.10	1.00
PUPC 04/60 (H18)*	left M1	9.00	9.00	1.00
	left M2	10.0	10.0	1.00
	left M3	10.0	8.00	0.80
PUPC 68/355	left M1	9.20	10.2	1.10
PUPC 87/40	left M1	10.0	11.7	1.10
PUPC 87/84	left M1	9.30	10.0	1.00
PUPC 95/01	right M1	9.30	9.00	0.96
PUPC 02/01	right M1	8.00	10.0	1.20
AMNH 19517	left M1	12.0	11.0	0.91
AMNH 29856	left M1	9.80	10.0	1.00
GSI B195	left M1	10.0	10.0	1.00
PUPC 68/41	right M2	11.0	13.0	1.10
PUPC 68/355	left M2	10.5	11.8	1.10
PUPC 86/81	right M2	10.5	12.2	1.10
PUPC 95/01	right M2	10.0	11.0	1.10
PUPC 02/01	right M2	10.5	11.6	1.10
AMNH 29856	left M2	11.3	12.0	1.00
GSI B195	left M2	11.0	12.0	1.00
PUPC 68/355	left M3	11.7	13.0	1.10
PUPC 02/01	right M3	11.7	12.3	1.00
AMNH 29856	left M3	11.5	13.0	1.10
PUPC 04/33 (H16)*	right p4	9.00	4.00	0.44
	right m1	9.30	5.60	0.60
PC-GCUF 09/18 (H 14)*	right m1	9.30	6.00	0.64
	right m2	10.0	7.00	0.70
	right m3	12.2	7.80	0.63
PC-GCUF 09/19 (H 14)*	left m2	10.4	7.40	0.71
	left m3	11.5	7.40	0.64
PUPC 05/3 (H8)*	right m2	9.60	6.10	0.63
PUPC 04/2 (H6)*	right m2	11.0	6.00	0.54
PUPC 87/25 (H8)*	right m2	13.0	8.50	0.65
	right m3	19.0	8.60	0.45
PUPC 04/6 (H16)*	right m3	15.0	5.20	0.34
PUPC 02/158	right p4	10.9	4.60	0.42
PUPC 68/312	right m1	9.10	5.30	0.58
PUPC 68/313	right m1	8.90	5.60	0.62
PUPC 02/158	right m1	10.6	6.70	0.63
GSI B594	right m1	10.8	6.80	0.62
PUPC 68/294	right m2	11.0	6.40	0.58
PUPC 68/311	right m2	10.0	6.60	0.6
PUPC 68/312	left m2	10.0	6.20	0.62
PUPC 68/313	right m2	10.2	6.70	0.65
PUPC 85/59	right m2	9.50	7.00	0.73
PUPC 02/158	right m2	12.7	8.20	0.64
AMNH 19365	right m2	13.0	7.50	0.57
AMNH 19366	right m2	12.0	7.50	0.62
GSI B594	right m2	12.5	7.50	0.60
PUPC 68/294	right m3	16.1	6.80	0.42
PUPC 68/311	right m3	14.8	7.80	0.53
PUPC 68/313	left m3	15.6	7.40	0.47
PUPC 83/610	left m3	18.5	8.50	0.45
PUPC 83/626	left m3	12.5	8.00	0.64
PUPC 84/82	right m3	18.4	8.30	0.45
PUPC 85/35	left m3	15.0	7.00	0.64
PUPC 85/59	left m3	14.2	7.00	0.49
PUPC 86/266	right m3	14.5	6.40	0.44
PUPC 96/66	left m3	13.0	6.30	0.48
PUPC 02/158	right m3	18.5	8.70	0.46
AMNH 19365	right m3	18.0	8.00	0.44
AMNH 19366	right m3	16.0	8.00	0.50
GSI B594	right m3	16.7	8.30	0.49
Dt. nagrii				
AMNH 19306	right M1	8.00	9.00	1.12
	right M2	8.50	8.50	1.00
	right M3	9.50	9.00	0.94
	right m2	8.00	5.00	0.62
	right m3	11.5	5.00	0.43
GSI 18079	m1	6.50	3.00	0.46
	m2	6.60	3.00	0.45
PC-GCUF 10/23	right m1	8.00	4.80	0.60
	right m2	8.40	5.00	0.59
	right m3	12.6	5.00	0.39

Tab. 2 - Comparative measurements of the cheek teeth of *Dorcatherium minus* and *D. nagrii* in mm. * Studied specimens. In parenthesis the locality code, from where the specimen was collected. Referred data are taken from Colbert (1935), Farooq et al. (2007a), and Khan and Akhtar (2011).

cingula, the strong styles/stylids and the presence of *Dorcatherium*-fold in lower molars (Lydekker 1876; Colbert 1935; Farooq et al. 2007a). The upper molars are specifically characterized by their finely rugose enamel, a comparatively weak mesostyle and well-developed lingual cingula, whereas the lower molars are characterized by the slight rugosity, the vestigial ectostylid and the *Dorcatherium*-fold (Colbert 1935; Farooq 2006; Farooq et al. 2007a). Morphometrically, the described sample is similar to the type specimens of *Dt. minus* (Tab. 2). Consequently, the material is assigned to *Dt. minus*, based on the morphometric features (Figs. 3-5, Table 2-3). The P4 of PUPC 01/13 shows somewhat morphological variation (Fig. 3L-N). It might be a pathological tooth. The P4s of *Dt. minus* are barely described, which hampers morphological comparisons. However, morphology and size of PUPC 01/13 correspond to the general morphology of *Dt. minus* from the Siwaliks (Colbert 1935; Farooq 2006; Farooq et al. 2007a).

Dorcatherium majus Lydekker, 1876

Figs 6A-F; Tab. 4

Type specimen: Right M1-2 (GSI B197), figured in Lydekker (1876, p. 44, pl. VII, figs. 4, 6, 9, 10, 11).

Type locality: Hasnot, Jhelum, Punjab, Pakistan (Colbert 1935).

Stratigraphic range: Lower to Middle Siwaliks (Colbert 1935; Farooq 2006; Farooq et al. 2007b, 2008).

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

Studied specimens: Left M2 (PUPC 05/2), a fragment of left mandible with m2-3 (PUPC 05/1).

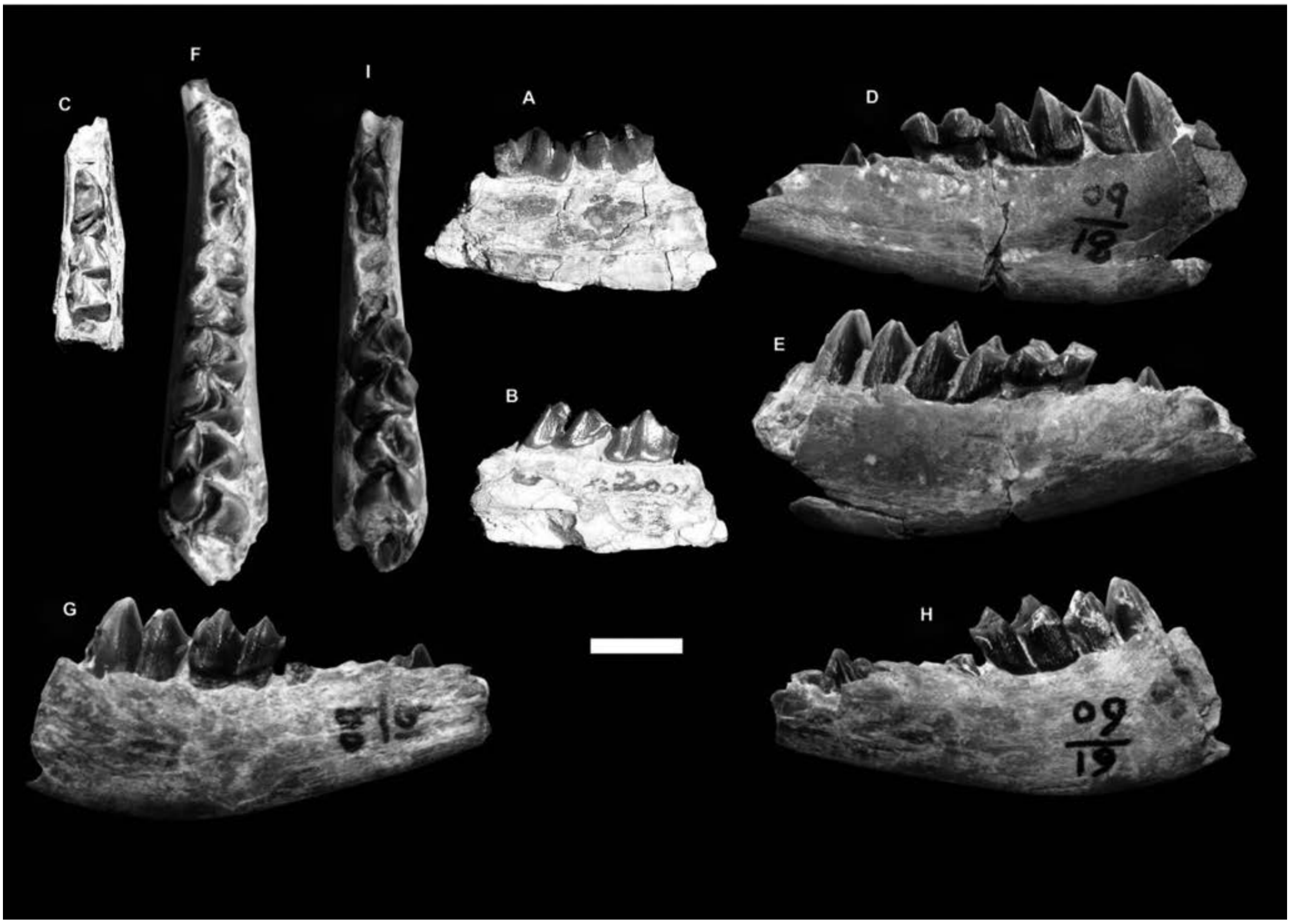

Fig. 4 - *Dorcatherium minus,* lower dentition; A-C, fragment of right mandible with p4 and m1, PUPC 04/33. D-F, right mandible fragments with m1-m3 and semi erupted p4, PC-GCUF 09/18. G-I, left mandible fragments with m1-m3 and semi erupted p4, PC-GCUF 09/19. Views are occlusal (C, F, I), labial (B, E, H) and lingual (A, D, G). Scale bar equals 10 mm.

Specimen	Description	mm
PC-GCUF 09/18	Length of the right mandible fragment	56.0
	Height of the right mandible fragment below the first molar	14.4
	Height of the right mandible fragment below the last molar	16.3
	Length of the molar series	32.0
PC-GCUF 09/19	Length of the left mandible fragment	53.0
	Height of the left mandible fragment below the first molar	14.3
	Height of the left mandible fragment below the last molar	18.0
	Length of the molar series	33.0

Tab. 3 - Measurements of the studied mandible fragments of *Dt. minus*.

Localities: Hasnot (H 7, H 12) Jhelum district, the Punjab province, Pakistan.

Description

Upper dentition. The tooth PUPC 05/2 is quadrate in its general appearance, rugose and submesodont (Fig. 6A-C, Tab. 4). Transversely, it is wider anteriorly than posteriorly. The cingulum is thick lingually especially at the entrance of the transverse valley, weak antero-posteriorly and it is entirely absent labially. The pre-protocrista contacts with the parastyle through a thin crista of the enamel and the post-protocrista on the other hand is free. The metaconus rib is weaker than the paraconus rib. The pre-hypocrista does not reach the post-protocrista.

Lower dentition. The lower molars are in late middle wear nevertheless, the most of the morphological features are visible (Fig. 6D-F). PUPC 05/1 is a fragile mandibular fragment with a posterior half of the second molar and the complete third molar (Fig. 6D-F). The molars are narrowly crowned. The metaconid lobe is pointed and higher than the protoconid and the hypoconid in the third molar. The hypoconulid in the third molar is lower in height than those of the associated conids. The *Dorcatherium*-fold directly posteriorly is present in the last molar (Fig. 6F).

Comparison. The specimens show tragulid features: the bunoselenodonty, isolated strong styles, basal cingula/cingulids, prominent anterior median ribs and the presence of M-structure (Métais & Vislobokova 2007; Rössner 2010). The features full corroborate the

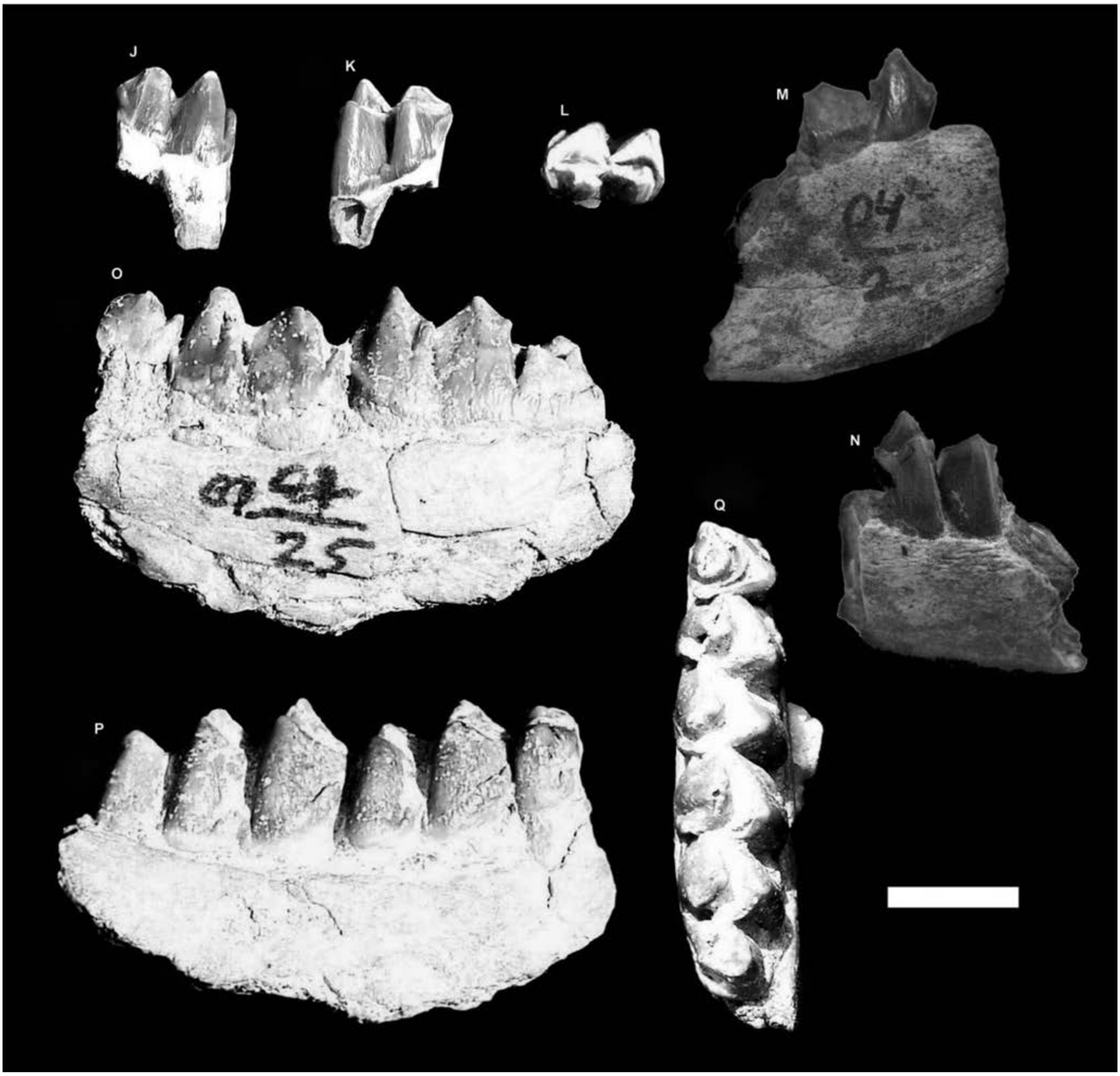

Fig. 5 - *Dorcatherium minus,* lower dentition; J-L, right m1, PUPC 05/3. M-N, right m2, PUPC 04/2. O-Q, fragment of right mandible with broken m1 and complete m2-3, PUPC 87/25. Views are occlusal (L, Q), labial (K, N, P) and lingual (J, M, O). Scale bar equals 10 mm.

tragulid status of the Hasnot fossils (Fig. 6A-F). *Siamotragulus* and *Yunnanotherium* differ from those of the studied specimens in displaying a derived morphology: their molars are more selenodont and hypsodont, their premetacristid is well developed and closes the anterior side of the trigonid, and they display a strong ectostylid (Thomas et al. 1990; Vislobokova 2001). The absence of flat cusps in the studied lower molars associate them to *Dorcabune, Hyemoschus* and *Dorcatherium* in distinction to *Afrotragulus*, *Siamotragulus*, *Yunnanotherium*, *Moschiola*, and *Tragulus* that are characterized by the presence of flat main cusps with cristids that are not only elongated but also very vertically developed (Sánchez et al. 2010).

Dorcabune is also different from the studied material in having very bunodont molars with thick and wrinkled enamel, a well developed cingulum, the presence of the 'double fold' on the protocone of the upper molars and a well-pronounced M structure with a double fold on the posterior side of the protoconid on the lower molars (Pilgrim 1915). The molars of *Dorcabune* are less compressed and display the primitive state in having the pointed principal cusps and lack crescents, as in ancient eutherians (Sánchez et al. 2010). The Hasnot molars differ from those of *Hyemoschus* species in its semiselenodont (= bunoselenodont) cusps/conids and the orientation of the posterior crest of the protocone. In *Dorcatherium,* this crest is oriented directly distally

Fig. 6 - *Dorcatherium majus,* upper dentition; A-C, left M2, PUPC 05/2. Lower dentition; D-F, fragment of left mandible with m2-3, PUPC 05/1. Views are occlusal (C, F), labial (B, E) and lingual (A, D). Scale bar equals 10 mm.

(Pickford 2002), whereas in *Hyemoschus* it is directed disto-buccally (Pickford et al. 2004). The cingulum usually weak or absent in upper molars of *Hyemoschus* which is prominent in *Dorcatherium* (Morales et al. 2003). Thus, the Hasnot molars are much closer morphologically to *Dorcatherium* than to *Hyemoschus* or other Miocene tragulids such as *Dorcabune* (Farooq et al. 2007c) and *Siamotragulus* (Thomas et al. 1990) or extant ones such as *Tragulus*.

The upper molars of *Dorcatherium* are characterized by submesodonty, strong cingulum and bunoselenodonty with an isolated pillar like parastyle. The metastyle is always found weakly formed in *Dorcatherium* (Lydekker 1876; Pilgrim 1915; Colbert 1935; Farooq et al. 2007b, 2008; Rössner 2010). The lower teeth are typically *Dorcatherium* i.e., *Dorcatherium*-folds, vestigial ectostylids, weak stylids, submesodont, narrowly crowned and well pronounced metaconus ribs. The features full corroborate the tragulid *Dorcatherium* status of the Hasnot fossils (Fig. 6A-F). The teeth of *Dt. majus* are larger than those of *Dt. minimus*, *Dt. minus* and *Dt. nagrii* (Tab. 2, 4) and morphologically they differentiate from *Dt. minus* and *Dt. nagrii* in terms of the strong basal cingula and the stronger and larger styles (Fig. 5) (Lydekker 1876; Pilgrim 1915; Colbert 1935; Farooq et al. 2007b, 2008). The upper molar is comparable in size

Number	Description	Length	Width	W/L ratio
PUPC 05/2 (H12)*	left M2	19.0	22.8	1.20
PUPC 67/191	left M2	13.3	14.5	1.00
PUPC 68/33	left M2	13.3	14.5	1.00
PUPC 68/250	left M2	15.7	16.4	1.00
PUPC 85/15	left M2	19.0	20.0	1.00
PUPC 85/21	left M2	18.0	22.0	1.20
PUPC 87/328	left M2	17.7	19.0	1.00
AMNH 19302	left M2	18.5	21.5	1.10
GSI B197	left M2	19.6	19.6	1.00
PUPC 05/1 (H7)*	left m3	26.6	13.0	0.48
PUPC 84/115	left m3	24.0	11.0	0.45
PUPC 86/2	left m3	25.1	11.0	0.43
PUPC 86/3	left m3	25.0	11.4	0.45
PUPC 86/152	left m3	23.0	11.0	0.47
PUPC 96/64	left m3	22.0	11.0	0.50
PUPC 98/61	left m3	16.0	11.0	0.68
AMNH 19939	left m3	25.5	12.0	0.47
GSI B593	left m3	25.0	11.4	0.45

Tab. 4 - Comparative measurements of the cheek teeth of *Dt. majus* in mm. * Studied specimens. In parenthesis the locality code, from where the specimen was collected. Referred data are taken from Colbert (1935) and Farooq et a l. (2007b, 2008).

and proportions to that of the holotype of *Dt. majus* (Colbert 1935).

Dorcabune Pilgrim, 1910

Type species: *Dorcabune anthracotherioides* Pilgrim, 1910

Generic diagnosis: Very 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). In *Dorcatherium* teeth are semiselenodonts and parastyle is not isolated pillar. Upper molars of *Dorcabune* are characterized by their brachyodonty and bunodonty whereas in *Dorcatherium* the molars are semiselenodonts and subhypsodonts to hypsodonts. The lingual cusps of upper molars in *Dorcabune* are buno-semiselenodont, whereas the labial ones are quite bunodont and absolutely conical in their general appearance. In *Dorcabune* the protocone, instead of being a simple crescent like Dorcatherium, 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. In *Dorcabune,* the median rib on the labial face of the paracone and metacone is so broad and prominent that it occupies almost all the space between the styles whereas in *Dorcatherium* it is weak. In *Dorcabune,* the conids are bunodont and conical. The cingulid is present anteriorly and posteriorly. The pre-protocristid terminates in a broad shelf, almost parallel to the anterior margin of the tooth. The post-protocristid is bifurcated and one cristid of the bifurcation is attached to the post-metacristid while the other one is attached to the pre-hypocristid producing 'M' structure. While in *Dorcatherium* the lower molars show a special crest complex called the '*Dorcatherium*-fold'. It is formed by the bifurcation of the post-protocristid and the metaconid resulting in a 'M' shape.

Geographic distribution: The genus is found in the Lower Manchar of Bhagothoro, Pakistan, Siwaliks, China and Greece (Pilgrim 1910, 1915; Colbert 1935; Han De-Fen 1974; Van der Made 1996; Farooq et al. 2007c-d).

Dorcabune anthracotherioides Pilgrim, 1910

Figs 7A-L; Tab. 5

1915 *Dorcabune hyaemoschoides* Pilgrim, p. 231, pl. 21, fig. 6, pl. 22, figs 2, 3.

1915 *Dorcabune sindiense* Pilgrim, p. 234, pl. 21, figs 3, 4.

Type specimen: A maxilla with M1-3 (GSI B580), figured in Pilgrim (1910, p. 68).

Type locality: Chinji, Chakwal, Punjab, Pakistan.

Stratigraphic range: Lower to Middle Siwaliks (Pilgrim 1910, 1915; Colbert 1935; Farooq 2006; Farooq et al. 2007c).

Diagnosis: *Dorcabune anthracotherioides* is a large size species of the genus, almost equal to that of *Dt. crassum* (Rössner 2010). Upper molars are bunodont and have a prominent parastyle. Lower margin of ramus is deep in *Db. anthracotherioides*. Mandible bears a fairly deep groove starting beneath p4 and propagating towards posterior side behind the teeth. This groove exists in *Dt. majus* and *Dt. minus* but it is absent in *Db. nagrii*. p4 is slightly shorter in length than p3. p4 is broad with three lobes, of which middle one is the highest, whereas the first and the last lobes are equal in length (Pilgrim 1910, 1915).

Studied specimens: Right M2 (PUPC 04/21), left m1 (PUPC 86/40), two partial left m3 (PUPC 84/66, PC-GCUF 10/22) (Fig. 7, Tab. 5).

Localities: Hasnot (H 12, H 23) Jhelum district, the Punjab province, Pakistan.

Description

Upper dentition. The molar PUPC 04/21 is in an early middle wear, bunodont, rugose and broad crowned (Fig. 7A-C). The major cones are inclined towards the median longitudinal line of the molar. The protocone is semi-crescentic in shape and displays three equally strong folds, one proceeding forwards and outwards, the second backwards and a third backwards with an inwards tendency. The pre-protocrista is larger than the post-protocrista and it is continuous with the parastyle of the paracone. The hypocone is smaller in antero-posterior length than the protocone (Fig. 7A-C). The pre-hypocrista is very small, not fused with the post-protocrista and the pre-metacrista. The post-hypocrista slopes downwards larger than the pre-hypocrista and fuses with the posterior cingulum. The pillar like labiaö paracone rib is separated to parastyle by a vertical groove. The pre-metacrista is connected with the post-paracrista and the post-metacrista is linked with the post-hypocrista through a small ridge. The strong parastyle is connected to the base of the labial paracone rib. The mesostyle seems to be more associated with the metacone than that of the paracone. It is thin towards its apex and thick at the base. The central fossettes are continuous with one another. The fossettes are deep; anterior one isolates mesially and the posterior

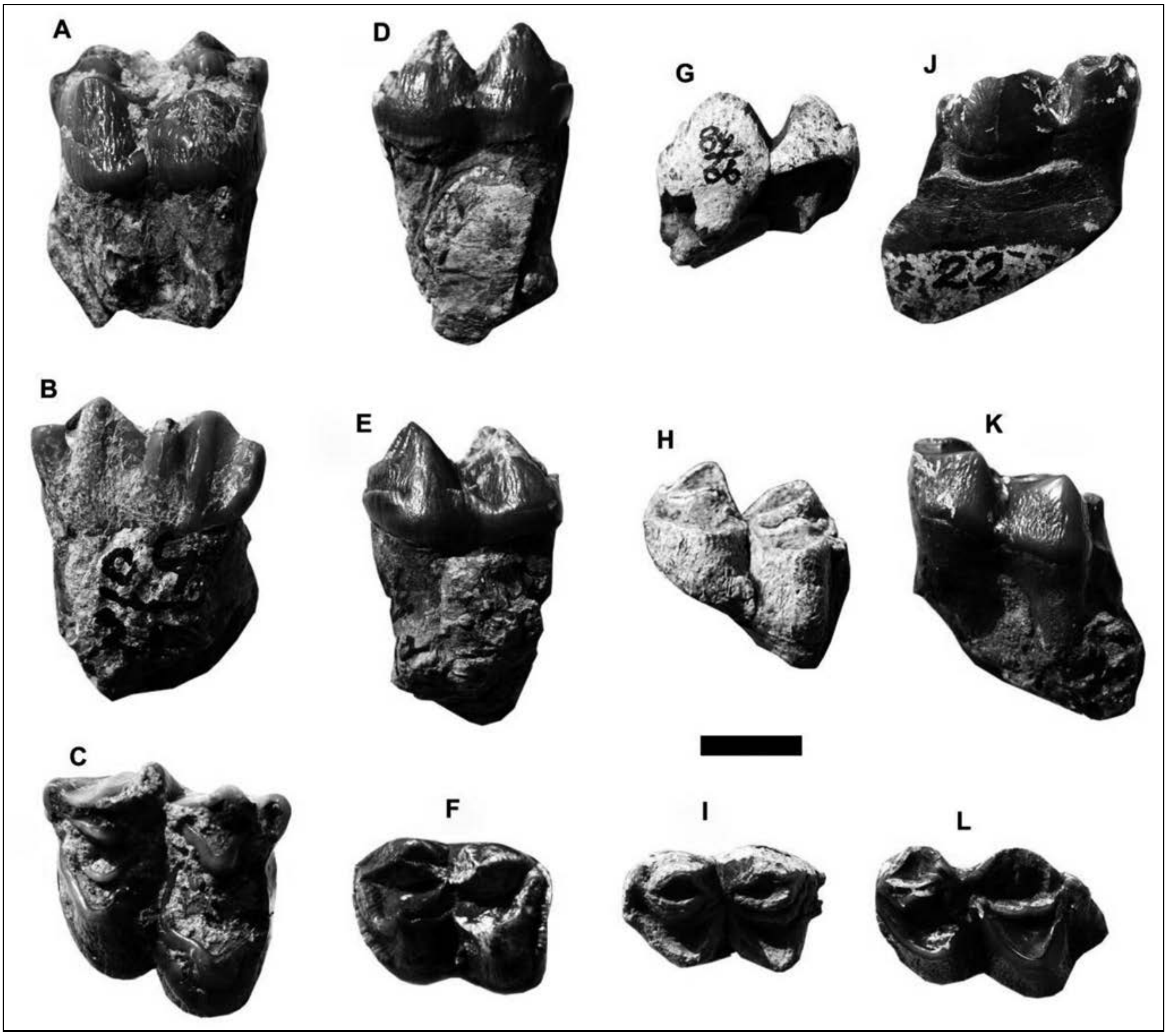

Fig. 7 - *Dorcabune anthracotherioides,* upper dentition; A-C, right M2, PUPC 04/21. Lower dentition; D-F, left m1, PUPC 86/40. G-I, partial left m3, PUPC 84/66. J-L, partial left m3, PC-GCUF-10/22. Views are occlusal (C, F, I, L), labial (B, E, H, K) and lingual (A, D, G, J). Scale bar equals 10 mm.

one isolates distally. The transverse valley is deep and narrow (Fig. 7A-C).

Lower dentition. The bunodont second lower molar PUPC 86/40 with shiny, rugose enamel is one of the best preserved unworn tooth (Fig. 7D-F). The conids are bunodont and conical. The cingulid is present anteriorly and posteriorly. The pre-protocristid terminates in a broad shelf, almost parallel to the anterior margin of the tooth. The post-protocristid is bifurcated and one crestid of the bifurcation is attached to the post-metacristid while the other one is attached to the pre-hypocristid producing 'M' structure (Fig. 7F). The pre-hypocristid touches the post-protocristid, whereas the post-hypocristid runs inwards and completely encircles the posterior base of the entoconid. The third lower molars (PUPC 84/66 and PC-GCUF 10/22) are in late wear and broken posteriorly (Fig. 7G-L). The cingulid is well developed anteriorly and it is absent labially, lingually and posteriorly.

Comparison. The studied sample reflects semi-selenodonty with bunodont pattern and can be associated with tragulids. The bunodont conical cusp pattern of the studied samples makes its inclusion to genus *Dorcabune* (Fig. 7). Two valid species of *Dorcabune*, *Db. nagrii* and *Db. anthracotherioides* are recorded from the Siwaliks (Farooq et al. 2007c-d). The described upper and lower dentitions reflect morphometric characteristics of *Db. anthracotherioides*. The studied molars are comparable with the holotype as well as the earlier described specimens of *Db. anthracotherioides* (Tab. 5). Therefore, *Db. anthracotherioides* can be reasonably assigned for the dentitions, based on the mor-

Number	Description	Length	Width	W/L ratio
Db. anthracotherioides				
PUPC 04/21 (H12)*	M2	21.0	21.0	1.00
PUPC 86/40 (H23)*	m1	19.3	14.0	0.72
PUPC 84/66 (H23)*	m3	-	11.6	-
PC-GCUF 10/22 (H23)*	m3	-	11.6	-
PUPC 87/37	M2	17.5	17.7	1.01
AMNH 19652	M2	18.0	22.5	1.25
GSI B580	M2	21.7	26.7	1.23
AMNH 19355	m1	17.0	12.0	0.72
PUPC 85/28	m3	26.00	13.00	0.50
AMNH 19353	m3	28.00	14.00	0.50
GSI B682/683	m3	30.90	16.00	0.51
Db. nagrii				
PUPC 70/13	m3	22.6	10.4	0.46
GSI B591	m3	21.7	11.4	0.52

Tab. 5 - Comparative measurements of the cheek teeth of *Dorcabune* in mm. * Studied specimens. The locality codes, from where the specimens were collected are given in parentheses. Referred data are taken from Colbert (1935) and Farooq et al. (2007c-d).

phometric characteristics (Colbert 1935; Farooq et al. 2007c).

Discussion

Biochronology

The mammalian fauna from Hasnot is represented by various Late Miocene groups: rodents, carnivores, proboscideans, cercopithecids, rhinoceroses, equids, suids, tragulids, giraffids, cervids and bovids (Tab. 1). This faunal association contains enough significant elements to allow comparison with some other Late Miocene faunas from Europe, Africa and Greco-Iranian Province. The macrofauna from Hasnot corresponds to the Late Miocene of Eurasia and Africa (Harris 1987; Solounias 1981; Bernor 1986; Köhler 1987; Geraads 1989; Gentry & Heizmann 1996; Gentry 1978, 1999, 2005; Gentry et al. 1999; Solounias et al. 1999; Iliopoulos 2003; Khan et al. 2009), based on the co-occurrence of *Pachyportax*, *Tragoportax*, *Eotragus, Gazella, Hydaspitherium*, *Hipparion*, *Dorcabune* and *Dorcatherium* (Khan 2007b; Farooq et al. 2007a-d, 2008; Khan et al. 2009; Ghaffar et al. 2010).

The Hasnot tragulid fauna is clearly of Late Miocene to Early Pliocene age, being associated with above mentioned taxa of the Late Miocene and the Early Pliocene (Pilbeam et al. 1977; Barry et al. 2002; Khan et al. 2009). In detail, there are differences between the stratigraphic levels of the Hasnot area to the Middle Dhok Pathan Formation having yielded the taxa *Dt. minus* and *Db. antheracotherioides* which are unknown from the upper Dhok Pathan Formation towards Bhandar deposits (H 16, H 18). The Bhandar deposits, east of the Hasnot area yielded cervids, *Eotragus* and *Dt. majus* (Khan 2007b; Khan et al. 2009). From this, we infer that the deposits in the vicinity of Bhandar (H 16, H 18) are closer in age to Early Pliocene and an age of about 5 Ma would accord with the available evidence (Khan 2007b). This is in agreement with the former authors who stated the Bhandar bed fauna more close to the Tatrot (Upper Siwaliks) fauna (Brown 1926; Colbert 1935).

Dorcabune antheracotherioides, *Db. nagrii, Dt. majus* and *Dt. minus* are known from the stratigraphical context of the Siwaliks from the Middle Miocene onwards (Pilgrim 1915; Colbert 1935; Farooq et al. 2007a-d, 2008). Their total occurrence spans are restricted in the Siwaliks from the Middle Miocene to the Early Pliocene. In a whole, the biochronological age indicated by the tragulid fossils from the Hasnot area is restricted from the Late Miocene to the Early Pliocene, dated approximately between 7-5 Ma.

Palaeoecology

Regarding palaeoecological interpretation, *Eotragus* is a typical representative for terrestrial faunas from the Middle Miocene of the Siwaliks (Solounias et al. 1995). For *Eotragus* a Duiker-like habitus and mode of life in more or less dense forests (Köhler 1993; Rössner 2006) can be reconstructed. *Pachyportax* and *Selenoportax* are long legged boselaphines with relatively long metapodials, what is typical for bovids living in open country (Scott 1985; Khan et al. 2009). The tragulids indicate strongly moist ground conditions in a habitat with lots of small open standing water bodies (Köhler 1993; Rössner 1997, 2004, 2010) as observed in extant tragulids (Meijaard et al. 2010).

The association of *Dorcatherium* with *Dorcabune*, *Eotragus, Tragoportax, Miotragocerus, Pachyportax, Selenoportax,* and *Hydaspitherium* is common in the Siwaliks, implying that that there was a mosaic of different environments and these species had different resource use preferences (different feeding niches), so they could exist at the same time (Colbert 1935; Pilgrim 1937, 1939; Farooq et al. 2007a-d, 2008; Khan et al. 2009, 2010). Bouvrain (1994) suggested that '*Tragoportax*' lived in a more wooded environment, because it is more often associated with cervids and tragulids (Farooq 2006; Khan 2007b; Khan et al. 2010; Ghaffar et al. 2010). Merceron et al. (2006) suggest that *Tragoportax* were engaged in both browsing and grazing. The abundance of *Dorcatherium* sympatric with bovids reflects humid/wooded landscape, more like the one known in the Late Miocene of Africa (Pickford 2001, 2002).

As noted by Barry et al. (2002), the carbon isotope record of the Siwaliks demonstrates that after 8.1 Ma significant amounts of C4 grasses began to appear and that by 6.8 Ma floodplain habitats included extensive C4 grasslands. The transition between C3- and C4 dominated communities was rapid. Plant communities having predominantly C3 plants were greatly diminished after 7.0 Ma (Quade et al. 1989; Quade & Cerling 1995). The predominantly C4 plants with open woodlands or grassy woodlands would have been appeared as early as 7.4 Ma (Badgley et al. 2005, 2008). The transitional plant communities were spatial and temporal mosaics with forest, woodland, brush, and grassland.

Diverse paleosols superimposed on sandy and silty sediments suggest a mosaic of vegetation patches across the landscape (Behrensmeyer et al. 1995). The consequence was an increase in the duration of dry phase and spatial spread of dryness. This result drying, small rivers, marshes and tree stands. Significant differences in species composition among the Siwalik faunas of the Late Pliocene were demonstrated by Akhtar (1992), Khan (2007b), Nanda (2008) and Khan et al. (2009). These led to the conclusion of changes from a humid to a more dry climate in the Siwaliks.

Conclusions

The Hasnot outcrops are represented by the four tragulid species *Dt. majus, Dt. minus, Db. Anthracotherioides,* and *Db. nagrii* (Farooq et al. 2007d; present study). *Dorcatherium* is much better represented. *Dorcatherium majus* is a typical Late Miocene species that featured more or less closed and humid habitats (Farooq et al. 2007b, 2008). Tragulids probably avoided the less suitable habitat in the more proximal and marginal part of the wetland basin and favored swampy habitats (Rössner 2007). This supports the assumption of the Late Miocene Hasnot humid habitat with abundant cover. This strongly indicates the dominance of forested landscapes along the riverine lake shores during the Dhok Pathan Formation of the Upper Middle Siwaliks. The discovery of tragulids in the Late Miocene to the Early Pliocene of Hasnot confirms that swamp was present in the Siwaliks from about 7-5 Ma, while forest and dense woodland has been inferred even earlier in the Dhok Pathan Formation. The tragulid preference for Hasnot indicates wetland highly probable.

Acknowledgements. We wish to thank Gertrud E. Rössner for giving so much time and providing us with fruitful comments on this manuscript. The first author is grateful to Adeeb Babar for technical assistance, to Maskeen Ali for efficient help during fieldwork and to Qazi Saeed and Annar Khan for their help in the field and hospitality. Israel M. Sánchez and Lorenzo Rook are deeply thanked for their fruitful reviews and comments on the manuscript.

REFERENCES

Agnarsson I. & May-Collado L.J. (2008) - The phylogeny of Cetartiodactyla: the importance of dense taxon sampling, missing data, and the remarkable promise of cytochrome b to provide reliable species level phylogenies. *Mol. Phylogenet. Evol.,* 48: 964-985.

Akhtar M. (1992) - Taxonomy and Distribution of the Siwalik Bovids. PhD Thesis (unpublished), University of the Punjab, Lahore, Pakistan, 475 pp.

Arambourg C. (1933) - Mammiferes Miocenes du Turkana (Afrique Orientale). *Ann. Paleontol.,* 22: 121-148.

Arambourg C. & Piveteau J. (1929) - Les Vertebres du Pontien de Salonique. *Ann. Paleontol.,* 18: 57-140.

Badgley C. (1986) - Taphonomy of mammalian fossil remains from Siwalik rocks of Pakistan. *Paleobiology,* 12: 119-142.

Badgley C. & Behrensmeyer A.K. (1980) - Paleoecology of Middle Siwalik sediments and faunas. *Palaeogeogr., Palaeoclim., Palaeoecol.*, 30: 133-155.

Badgley C., Nelson S., Barry J., Behrensmeyer A.K. & Cerling T. (2005) - Testing Models of Faunal Turnover with Neogene Mammals from Pakistan. In: Lieberman D.E., Smith R.J. & Kelley J. (Eds) - Interpreting the Past: Essays on Human, Primate, and Mammal Evolution in Honor of David Pilbeam: 29-46, Brill Academic Publishers, Boston.

Badgley C., Will D. & Lawrence F. (2008) - Taphonomy of small-mammal fossil assemblages from the Middle Miocene Chinji Formation, Siwalik Group, Pakistan. *National Science Museum monographs,* 14: 145-166.

Barry J.C. (1987) - The history and chronology of Siwalik cercopithecoids. *Human Evolution,* 2: 47-58.

Barry J.C., Cote S., Maclatchy L., Lindsay E.H., Kityo R. & Rajpar A.R. (2005) - Oligocene and Early Miocene Ruminants (Mammalia, Artiodactyla) from Pakistan and Uganda, *Palaeontologia Electronica,* 8(1): 1-29.

Barry J.C., Lindsay E.H. & Jacobs L.L. (1982) - A biostratigraphic zonation of the middle and upper Siwaliks of the Potwar Plateau of northern Pakistan. *Palaeogeogr., Palaeoclim., Palaeoecol.*, 37: 95-130.

Barry J., Morgan M., Flynn L., Pilbeam D., Behrensmeyer A.K., Raza S., Khan I., Badgely C., Hicks J. & Kelley J. (2002) - Faunal and Environmental change in the Late Miocene Siwaliks of Northern Pakistan. *Paleobiology,* 28: 1-72.

Behrensmeyer A.K. (1988) - Vertebrate preservation in fluvial channels. *Palaeogeogr., Palaeoclim., Palaeoecol.*, 63: 183-199.

Behrensmeyer A.K. & Barry J. (2005) - Biostratigraphic Surveys in the Siwaliks of Pakistan. A Method for Standardized Surface Sampling of the Vertebrate Fossil Record. *Palaeontologia Electronica,* 8(1): 1-24.

Behrensmeyer A.K., Willis B.J. & Quade J. (1995) - Floodplains and paleosols of Pakistan Neogene and Wyoming Paleogene deposits: a comparative study. *Palaeogeogr., Palaeoclim., Palaeoecol.*, 115: 37-60.

Bernor R.L. (1986) - Mammalian biostratigraphy, geochronology, and zoogeographic relationships of the Late Miocene Maragheh fauna, Iran. *J. Vert. Palaeontol.,* 6: 76-95.

Bernor R.L. & Hussain S.T. (1985) - An assessment of the systematics phylogenetic and biogeographic relationships of Siwalik Hipparionine Horses. *J. Vert. Palaeontol.,* 5(1): 32-87.

Bouvrain G. (1994) - Un bovidé du Turolien inférieur d'Europe orientale: *Tragoportax rugosifrons*. *Ann. Paleontol.,* 80(1): 61-87.

Brown B. (1926) - A new deer from the Siwalik. *Am. Mus. Novitates*, 242: 1-6.

Colbert E.H. (1935) - Siwalik mammals in the American Museum of Natural History. *Trans. Am. Phil. Soc., New Series*, 26: 1-401.

Corbet G.B. & Hill J.E. (1980) - A World List of Mammalian species. *British Mus. Nat. Hist., Comstock Pub. Ass., Ithaca,* 6 pp.

Dennell R. (2008) - The Taphonomic Record of Upper Siwalik (Pinjor stage) Landscapes in the Pabbi Hills, Northern Pakistan, with consideration regarding the preservation of Hominin remains. *Quatern. Int.,* 192: 62-77.

Dubost G. (1965) - Quelques traits remarquables du comportement de *Hyaemoschus aquaticus* (Tragulidae, Ruminantia, Artiodactyla). *Biologia gabonica,* 1: 282-287.

Farooq U. (2006) - Studies of evolutionary trends in dentition of the Siwalik tragulids. PhD Thesis (unpublished), University of the Punjab, Lahore, Pakistan, 266 pp.

Farooq U., Khan M.A., Akhtar M. & Khan A.M. (2007a) - *Dorcatherium minus* from the Siwaliks, Pakistan. *J. Animal Plant Sci.*, 17(3-4): 86-89.

Farooq U., Khan M.A., Akhtar M. & Khan A.M. (2007b) - *Dorcatherium majus*, a study of upper dentition from the Lower and Middle Siwaliks of Pakistan. *J. Applied Sci.*, 7(9): 1299-1303.

Farooq U., Khan M.A., Akhtar M. & Khan A.M. (2007c) - *Dorcabune anthracotherioides* (Artiodactyla, Ruminantia, Tragulidae) from Hasnot, the Middle Siwaliks, Pakistan. *Pakistan J. Zool.*, 39(6): 353-360.

Farooq U., Khan M.A. & Akhtar M. (2007d) - *Dorcabune nagrii* (Ruminantia, Tragulidae) from the Upper Part of the Middle Siwaliks. *J. Applied Sci.*, 7(10): 1428-1431.

Farooq U., Khan M.A., Akhtar M. & Khan A.M. (2008) - Lower Dentition of *Dorcatherium majus* (Tragulidae, Mammalia) in the Lower and Middle Siwaliks (Miocene) of Pakistan. *Turkish J. Zool.*, 32: 91-98.

Flower W.H. (1883) - On the arrangement of the orders and families of existing Mammalia. *Proc. Zool. Soc. London*, 1883: 178-186.

Gaur R., Vasishat R.N., Suneja I.J. & Chopra S.R.K. (1983) - Fossil mammals (tragulids, giraffids and bovids) from the Neogene Siwalik deposits exposed in Nurpur-Ranital terrains. Western Himachal Pradesh, India. *Pub. Contr. Adv. Stud. Geol., Punjab Univ.,* 13: 180-187.

Gentry A.W. (1978) - Bovidae. In: Maglio V.J. & Cooke H.B.S. (Eds) - Evolution of African Mammals: 540-572, Harvard University Press, Cambridge, Massachusetts.

Gentry A.W. (1999) - Fossil Pecorans from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In: Whybrow P.J. & Hill A. (Eds) - Fossil Vertebrates of Arabia: 290-316. Yale University Press, New Haven.

Gentry A.W. (2005) - Ruminants of Rudabanya. *Palaeontographia Italica*, 90: 283-302.

Gentry A. & Heinzmann E.P.J. (1996) - Miocene ruminants of the Central and Eastern Tethys and Paratethys. In: Bernor R.L., Fahlbusch V. & Mittmann H.W. (Eds) - The evolution of Western Eurasian Neogene mammal faunas: 378-391, New York, Columbia University Press.

Gentry A.W. & Hooker J.J. (1988) - The phylogeny of Artiodactyla. In: Benton M.J. (Ed.) - The Phylogeny and Classification of the Tetrapods, Vol. 2: Mammals: 235-272, Syst. Ass. Spec. Vol., No. 35B Clarendon, Oxford.

Gentry A.W., Rössner G.E. & Heizmann E.P.S. (1999) - Suborder Ruminantia. In: Rössner G.E. & Heissig K. (Eds) - The Miocene land mammals of Europe: 225-258, Verlag Dr. Friedrich Pfeil, Munchen.

Geraads D. (1989) - Vertebres fossils du Miocene superieur du Djebel Krechem el Artsouma (Tunisie centrale): comparisons biostratigraphiques. *Géobios*, 22: 777-801.

Geraads D. (2010) - Tragulidae. In: Werdelin L. & Sanders W.J. (Eds) - Cenozoic mammals of Africa: 723-729, University of California Press, Berkeley.

Geraads D., Kaya T. & Mayda S. (2005) - Late Miocene large mammals from Yulafli, Thrace region, Turkey, and their biogeographic implications. *Acta Palaeontol. Pol.,* 50(3): 523-544.

Ghaffar A., Khan M.A. & Akhtar M. (2010) - Early Pliocene Cervids (Artiodactyla-Mammalia) from the Siwaliks of Pakistan. *Yerbilimleri (Earth Sciences)*, 31(3): 217-231.

Groves P. & Meijaard E. (2005) - Interspecific variation in *Moschiola*, the Indian chevrotain. *The Raffles Bull. Zool., Suppl.*, 12: 413-421.

Hamilton W.R. (1973) - The lower Miocene ruminants of Gebel Zelten, Libya. *Bull. British Mus. (Nat. Hist.) London, Geol.,* 21(3): 75-150.

Han De-fen (1974) - First discovery of *Dorcabune* in China. *Vertebrata Palasiatica,* 12(3): 217-221.

Harris J.M. (1987) - Fossil Giraffidae from Sahabi, Libya. In: Boaz N.T., El-Arnauti A., Gaziry A.W., de Heinzelin J. & Boaz D.D. (Eds) - Neogene Paleontology and Geology of Sahabi: 317-321, Alan R. Liss, New York.

Hassanin A. & Douzery E.J.P. (2003) - Molecular and morphological phylogenies of Ruminantia and the alternative position of the Moschidae. *Syst. Biol.,* 52: 206-228.

Hillenbrand V., Gohlich U.B. & Rössner G. (2009) - The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria). *Ann. Naturhist. Mus. Wien,* 111A: 519-556.

Hussain S.T. (1971) - Revision of *Hipparion* (Equidae, Mammals) from the Siwalik Hills of Pakistan and India. *Bayer Akad. Wiss., Abh.,* 147: 1-68.

Iliopoulos G. (2003) - The Giraffidae (Mammalia, Artiodactyla) and the Study of the Histology and Chemistry of Fossil Mammal Bone from the Late Miocene of Kerassia (Euboea Island, Greece). PhD Thesis, University of Leicester, Leicester, United Kingdom, 130 pp.

Janis C.M. (1984) - Tragulids as living fossils. In: Eldredge N. & Stanley S.M. (Eds) - Living Fossils: 87-94, Casebooks in Earth Sciences, New York.

Janis C.M. & Scott K.M. (1987) - The interrelationships of higher ruminant families with special emphasis on the members of the Cervoidea. *Am. Mus. Novitates,* 2893: 1-85.

Johnson G.D., Zeitler P., Naeser C.W., Johnson N.M., Summers D.M., Frost C.D., Opdyke N.D. & Tahirkheli R.A.K. (1982) - The occurrence and fission-track ages of Late Neogene and Quaternary volcanic sediments, Siwalik group, northern Pakistan. *Palaeogeogr., Palaeoclim., Palaeoecol.,* 37: 63-93.

Kaup J.J. (1833) - Vier urweltliche Hirsche des Darmstadter Museum. *Archeology Mineralogy, Geography, Bergbau und Huttenkunde*, 6: 217-228.

Kaup J.J. & Scholl J.B. (1834) - Verzeichniss der Gypsabgusse von den ausgezeichnetsten urweltlichen Thierresten des Grossherzoglichen Museums zu Darmstadt (2. Ausgabe): 6-28, Diehl, Darmstadt.

Khan A.M. (2010) - Taxonomy and Distribution of Rhinoceroses from the Siwalik Hills of Pakistan. PhD Thesis (unpublished), University of the Punjab, Lahore, Pakistan, pp. 310.

Khan M.A. (2007a) - Description of *Selenoportax vexillarius* Molars from Dhok Pathan Village (Middle Siwaliks), Pakistan. *Pakistan J. Biol. Sci.,* 10(18): 3166-3169.

Khan M.A. (2007b) - Taxonomic Studies on Fossil Remains of Ruminants from Tertiary Hills of Hasnot, Pakistan. PhD Thesis (unpublished), University of the Punjab, Lahore, Pakistan, 372 pp.

Khan M.A. (2008) - Fossil bovids from the late Miocene of Padri, Jhelum, Pakistan. *Pakistan J. Zool.*, 40(1): 25-29.

Khan M.A. & Akhtar M. (2011) - *Dorcatherium* cf. *nagrii* from the Chinji Type Locality (Chakwal, northern Pakistan) of the Chinji Formation, Lower Siwaliks, Pakistan. *Pakistan J. Zool.*, 43(6): 1101-1109.

Khan M.A., Akhtar M. & Iqbal M. (2010) - The Late Miocene Artiodactyls in the Dhok Pathan Type Locality of the Dhok Pathan Formation, the Middle Siwaliks, Pakistan. *Pakistan J. Zool.*, Suppl. Ser., 10: 1-90.

Khan M.A., Iliopoulos G. & Akhtar M. (2009) - Boselaphines (Artiodactyla, Ruminantia, Bovidae) from the Middle Siwaliks of Hasnot. Pakistan. *Géobios,* 42: 739-753.

Köhler M. (1987) - Boviden des turkischen Miozans (Kanozoikum und Braunkohlen der Turkei, 28). *Paleontologia i Evolució*, 21: 133-246.

Köhler M. (1993) - Skeleton and habitat of recent and fossil ruminants. *Münchner Geowissen. Abh. (A),* 25: 1-88.

Lydekker R. (1876) - Molar teeth and other remains of Mammalia from the India Tertiaries. *Palaeontologia Indica,* 10(2): 19-87.

Made J. van der (1996) - Pre-Pleistocene Land Mammals from Crete. In: Reese D.S. (Ed.) - Pleistocene and Holocene Fauna of Crete and Its First Settlers: 69-79, Prehistory Press, Madison.

Marcot J.D. (2007) - Molecular Phylogeny of Terrestrial Artiodactyls. Conflicts and Resolution. In: Prothero D.R. & Foss S.E. (Eds) - The Evolution of Artiodactyls: 4-18, The Johns Hopkins University Press, Baltimore.

Matthew W.D. (1929) - Critical observations upon Siwalik mammals (exclusive of Proboscidea). *Am. Mus. Nat. Hist. Bull.,* 56: 437-560.

Meijaard E. & Groves C.P. (2004) - A taxonomic revision of the *Tragulus* mouse deer (Artiodactyla). *Zool. J. Linnaean Soc.*, 140: 63-102.

Meijaard E., Umilaela U. & Wijeyeratne G. (2010) - Aquatic escape behaviour in mouse deer provides insight into tragulid evolution. *Mammalian Biol.,* 75: 471-473.

Merceron G., Zazzo A., Spassov N., Geraads D. & Kovachev D. (2006) - Bovid Palaeoecology and Palaeoenvironments from the Late Miocene of Bulgaria: evidence from dental microwear and stable isotopes. *Palaeogeogr., Palaeoclim., Palaeoecol.*, 241(3-4): 637-654.

Métais G. & Vislobokova I. (2007) - Basal Ruminants. In: Prothero D.R. & Foss S.E. (Eds) - The Evolution of Artiodactyls: 189-212. The Johns Hopkins University Press, Baltimore.

Métais G., Chaimanee Y., Jaeger J.J. & Ducrocq S. (2001) - New remains of primitive ruminants from Thailand: evidence of the early evolution of the Ruminantia in Asia. *Zool. Scr.,* 30: 231-248.

Milne-Edwards A. (1864) - Recherches anatomiques, zoologiques et paléontologiques sur la famille des Chevrotains: 132 pp. Martinet, Paris.

Morales J., Soria D., Sánchez, I.M., Quiralte V. & Pickford M. (2003) - Tragulidae from Arrisdrift, Basal Middle Miocene, Southern Namibia. *Mem. Geol. Surv. Namibia,* 19: 359-370.

Nanda A.C. (2008) - Comments on the Pinjor Mammalian Fauna of the Siwalik Group in relation to the Post-Siwalik Faunas of Peninsular India and Indo-Gangetic Plain. *Quatern. Int.*, 192: 6-13.

Owen R. (1848) - Contributions to the History of British Fossil Mammals. V. of 71 pp., Taylor, London.

Pickford M. (1986) - Cainozoic palaeontological sites of Western Kenya. *Münchner Geowiss. Abh.(A),* 8: 1151.

Pickford M. (1988) - Revision of the Miocene Suidae of the Indian Subcontinent. *Münchner Geowiss. Abh. (A),*12: 1-91.

Pickford M. (2001) - Africa's smallest ruminant: a new tragulid from the Miocene of Kenya and the biostratigraphy of East African Tragulidae. *Géobios,* 34: 437-47.

Pickford M. (2002) - Ruminants from the Early Miocene of Napak, Uganda. *Ann. Paléontol.,* 88: 85-113.

Pickford M., Senut B. & Mourer-Chauviré C. (2004) - Early Pliocene Tragulidae and Peafowls in the Rift Valley, Kenya: evidence for rainforest in East Africa. *CR Palévol,* 3: 179-189.

Pilbeam D.R., Behrensmeyer A.K., Barry J.C. & Shah S.M.I. (1979) - Miocene sediments and faunas of Pakistan. *Postilla,* 179: 1-45.

Pilbeam D., Barry J., Meyer G.E., Shah S.M.I., Pickford M.H.L., Bishop W.W., Thomas H. & Jacobs L.L. (1977) - Geology and palaeontology of Neogene strata of Pakistan. *Nature*, 270: 684-689.

Pilgrim G.E. (1910) - Notices of new Mammalian genera and species from the Tertiaries of India-Calcutta. *Records Geol. Surv. India*, 40: 63-71.

Pilgrim G.E. (1915) - The dentition of the Tragulid genus *Dorcabune*. *Records Geol. Surv. India*, 45: 226-238.

Pilgrim G.E. (1937) - Siwalik antelopes and oxen in the American Museum of Natural History. *Bull. Am. Mus. Nat. Hist.,* 72: 729-874.

Pilgrim G.E. (1939) - The fossil Bovidae of India. *Palaeontologia Indica, New Series*, 26(1): 1-356.

Prasad K.N. (1968) - The vertebrate fauna from the Siwalik beds of Haritalyangar, Himachal Pradesh, India. *Palaeontologia Indica, New Series,* 39: 1-55.

Quade J. & Cerling T.E. (1995) - Expansion of C4 grasses in the Late Miocene of northern Pakistan: Evidence from stable isotopes in paleosols. *Palaeogeogr., Palaeoclim., Palaeoecol.,* 115: 91-116.

Quade J., Cerling T.E. & Bowman J.R. (1989) - Dramatic ecologic shift in the latest Miocene of northern Pakistan, and its significance to the development of the Asian Monsoon. *Nature,* 342: 163-166.

Quiralte V., Sanchez, I.M., Morales. J. & Pickford M. (2008) - Tragulidae (Artiodactyla, Ruminantia) from the Lower Miocene of the Sperrgebiet, Southern Namibia. *Mem. Geol. Surv. Namibia,* 20: 387-396.

Raza S.M. & Meyer G.E. (1984) - Early Miocene geology and paleontology of the Bugti Hills. *Geol. Surv. Pakistan,* 11: 43-63.

Rössner G.E. (1997) - Biochronology of Ruminant Assemblages in the Lower Miocene of Southern Germany. In: Aguilar J.P., Legendre S. & Michaux J. (Eds) - Actes du Congrés BiochroM'97. Memoires et Travaux E.P.H.E., 21: 609-618, Montpellier.

Rössner G.E. (2004) - Community structure and regional patterns in late Early to Middle Miocene Ruminantia of Central Europe. *Courier Forsch.-Inst. Senckenberg*, 249: 91-100.

Rössner G.E. (2006) - A Community of Middle Miocene Ruminantia (Mammalia, Artiodactyla) from the German Molasse Basin. *Palaeontographica, A,* 277: 103-112.

Rössner G.E. (2007) - Family Tragulidae. In: Prothero D.R. & Foss S.E. (Eds) - The Evolution of Artiodactyls: 213-220, The John Hopkins University Press, Baltimore.

Rössner G.E. (2010) - Systematics and palaeoecology of Ruminantia (Artiodactyla, Mammalia) from the Miocene of Sandelzhausen (southern Germany, Northern Alpine Foreland Basin). *Paläontol. Zeit.,* 84: 123-162.

Sahni A., Tiwari B.N. & Kumar K. (1980) - An Additional Lower Siwalik Vertebrate Fauna from the Kalagarh Area, District Pauri Garhwal, Uttar Pradesh. *Proceedings of 3rd Indian Geological Congress,* Poona: 81-90.

Sanchez I.M., Quiralte V., Morales J. & Pickford M. (2010) - A new genus of tragulid ruminant from the early Miocene of Kenya. *Acta Palaeontol. Pol.,* 55(2): 177-187.

Sarwar M. (1977) - Taxonomy and distribution of the Siwalik Proboscidea. *Bull. Dep. Zool. Univ. Punjab, New Series,* 10: 1-172.

Scopoli G.A. (1777) - Introductio ad historiam naturalem, sistens genera Lapidum, Plantarum et Animalium hactenus detecta, caracteribus essentialibus donata subinde ad leges Naturae. Gerle: in tribus divisa: 547 pp., W. Gerle, Prague.

Scott K.M. (1985) - Allometric trends and locomotor adaptations in the Bovidae. *Bull. Am. Mus. Nat. Hist.*, 179(2): 197-288.

Scott K.M. & Janis C.M. (1992) - Relationships of the Ruminantia (Artiodactyla) and an analysis of the characters used in Ruminant taxonomy. In: Szalay F.S., Novacek M.J. & McKenna M.C. (Eds) - Mammal Phylogeny, Placentals: 282-302, Springer-Verlag, New York.

Solounias N. (1981) - The Turolian fauna from the Island of Samos, Greece. *Contr. Vert. Evol.,* 6: 99-232.

Solounias N., Barry J.C., Bernor R.L., Lindsay, E.H. & Raza S.M. (1995) - The oldest bovid from the Siwaliks, Pakistan. *J. Vert. Palaeontol.*, 15(4): 806-814.

Solounias N., Plavcan J.M., Quade J. & Witmer L. (1999) - The Paleoecology of the Pikermian Biome and the savanna myth. In: Agustí J., Andrews P. & Rook L. (Eds) - Hominoid evolution and climatic change in Europe I: the evolution of Neogene terrestrial ecosystems in Europe: 436-453, Cambridge University Press, Edimburgh.

Thomas H., Ginsburg L., Hintong C. & Suteethorn V. (1990) - A new tragulid, *Siamotragulus sanyathanai* n. g., n. sp. (Artiodactyla, Mammalia) from the Miocene of Thailand (Amphoe Pong, Phayao Province). *CR Acad. Sci., Paris, Ser. II, 310*, 989-995.

Vislobokova I.A. (2001) - Evolution and Classification of Tragulina (Ruminantia, Artiodactyla). *Paleontol. J.,* Suppl., 35(2): 69-145.

West R.M. (1980) - A minute new species of *Dorcatherium* (Tragulidae, Mammalia) from the Chinji Formation near Daud Khel, Mianwali district, Pakistan. *MILW. Contr. Biol. Geol., Mus. publ.,* 3(33): 1-6.

Whitworth T. (1958) - Miocene ruminants of East Africa. *British Mus. (Nat. Hist.), Fossil Mammals of Africa*, 15: 1-50.