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

MUHAMMAD AKBAR KHAN†, MUHAMMAD AKHTAR 2, GEORGE ILOPOULOS3 & HINA4

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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 Dorcatatherium minus, Dorcatatherium majus and Dorcabune antbrachoferoidei. The collection of Dorcatatherium fossils from Hasnot is the most extensive record of this genus in the Siwaliks. The tragulids suggest a humid habitat with abundant cover.


Introduction

The small nonpecoran ruminants named the clade Tragulidae comprise the smallest living cetartiodactyls (Janis 1984; Scott & Janis 1992; Hassanin & Douzery 2003; Marten 2007; Aigrinsson & May-Collado 2008). Tragulids are concordantly considered as the most primitive still living ruminants (Janis & Scott 1987) with roots back to Eocene (Métas 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 Dorcatatherium minus, Dorcatatherium majus, Dorcabune antbracoferoidei and Dorcabune nagri (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 (Dorcatatherium minus, Dorcatatherium majus, Dorcabune antbracoferoidei) 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-
gulids from the Hasnot outcrops of the Middle Siwaliks, northern Pakistan.

Definitions

*Dorcatheirium* fold refers to the fold occurring on the postmetacrictid on the lower molars of some primitive ruminants and extant tragulids and the entocnidian 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-metacrictid and post-protocristid (Métais et al. 2001).

Siwalik tragulids

The Siwalik tragulids are known to be represented by two genera *Dorcatheirium* (*Dt.*) and *Dorcabune* (*Db.*) (Lydekker 1876; Pilgrim 1915; Colbert 1935; Farooq et al. 2007a-d, 2008) (Fig. 2). The extinct genus *Dorcatheirium* is known from Asia (Lydekker 1876; Matthew 1929; Corbet & 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). *Dorcatheirium* are represented by four Siwalik species *Dt. minimus*, *Dt. nagris*, *Dt. minus* and *Dt. magus* (Lydekker 1876; Colbert 1935; West 1980; Gaur et al. 1983; Farooq 2006; Farooq et al. 2007a-d, 2008; Khan & Akhtar 2011). *Dorcatheirium minimus* is reported as the
Smallest and rarest species of *Dorcatheirium* from the Siwaliks (West 1980) (Fig. 2).

*Dorcasbume* is known from the Middle Miocene to the Early Pliocene of the Siwaliks (Pilgrim 1915; Colbert 1935; Météis et al. 2001; Geraads et al. 2005; Farooq et al. 2007c-d) and the Late Miocene of Crete (Van der Made 1996). *Dorcasbume* was a large tragulid, which had very bunodont molars and could have weighed close to 100 kg (Janis 1984). Pilgrim (1915) suggested that *Dorcasbume* is morphologically close to anthracotheres and more primitive than *Dorcatheirium*. Gentry (1978) claimed that *Dorcasbume* might be a primitive anthracothere. With the exception of the M structure and the presence of a weak entocoidian groove, *Dorcasbume* 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).

*Dorcatheirium* and *Dorcasbume* are reported from the Chini Formation of the Lower Siwaliks in the northern Pakistan (Fig. 2). *Dorcatheirium* is represented by four species: *D. minus*, *D. nagni*, *D. minus* and *D. majus* and *Dorcasbume* is known by the single species *Dh. Anthracotherioides* from the Chini Formation (Colbert 1935; West 1980; Farooq 2006; Khan & Akhtar 2011). The Nagri Formation represents three *Dorcatheirium* species (*Dh. nagni*, *Dh. minus* and *Dh. majus*), and one *Dorcasbume* species (*Dh. nagni*; Colbert 1935; Prasad 1968; Farooq 2006). The Dhok Pathan Formation represents all the known Siwalik species of the tragulids except *Dh. minus* and *Dh. nagni* (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 *Dh. minus* West, 1980, *Dh. nagni* Gaur et al., 1983, *Dh. minus* Lydekker, 1876, *Dh. majus* Lydekker, 1876, as well as *Dh. Anthracotherioides* Pilgrim, 1910 and *Dh. nagni* 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). *Dorcasbume hayemosboides* Pilgrim, 1915, *Dh. sindense* Pilgrim, 1915, and *Dh. tattens* 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, Selenopontos, Pachyportax, Tragopontax, Gazella, Brahmathherium, Propotamochoerus, Dorcatheirium, Dorcasbume* 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 hansi
Macacus sivalensis

Rodentia
Rhizomys sivalensis
Rhizomys sp.

Hystrix sivalensis

Carnivora
Amphicyon lydekkeri
Indarctos punjabiensis
Promellivora punjabiensis
Enhydridodon falconeri
Sivamachairos anthracotherium
Vishnuictis indicum
Preocretacuta carnifex
Preocretacuta gigantea
Preocretacuta gigantea-latro
Adrocuta eximia
Melivorodon palaeicum
Achropius annicetus
Paramachairos orientalis
Felis sp.

Protopomsilus sivalensis

Probosidea
Dinotherium indicum
Paratetralophodon haustenii
Tetralophodon falconeri
Tetralophodon punjabiensis
Zygorhopodon chinjiensis
Chororhopodon coragutus
Anancus perimensis
Stegolophodon latidens
Stegolophodon cautleyi
Stegodon orbilform
Stegodon cliftii
Stegodon clinti
Stegodon elephantoides

Equidae
Cormohipparion antelpinum
Cormohipparion theobaldi
Sivalhippus perimensis
Hippopotamodon vagus
Cormohipparion antelpinum
Cormohipparion theobaldi
Sivalhippus sivalensis
Hippopotamodon vagus
Sivalhippus punjabiensis
Hippolebas lydekkeri

Artiodactyla
Microbuson sivalensis
Merycopotamus dissimilis

Tragulidae
Dorcabane anthracotherioides
Dorcabana nagi
Dorcatherium majus
Dorcatherium minus
Dorcatherium minimus

Cervidae
Rucervus simplicidens
Cervus tridens
Cervus sivalensis
Cervus punjabiensis
Cervus revalt

Giraffidae
Brachyatherium megacephalum
Brachyatherium perimense
Giraffa punjabiensis

Bovidae
Taurotragus latidens
Tragoparctus sylvanus
Tragoportax punjabiacus
Tragoparctus browni
Prolleporus bicornatus
Selenoparctus vezzilarius
Selenoparctus lydekkeri
Pachyportax latidens
Pachyportax giganteus
Gazella lyderkei
Gazella panderi
Elasmochoerana pharoustanensis
Eotragus sp.

Tab. 1 - Mammalian Fauna from Hasnot area (referred data are taken from Colbert 1955; Pilgrim 1937, 1939; Husain 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).

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 bite 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. Particulate, 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 (PUPL), have been collected at the localities around Hasnot village. Further material was collected by the staff of Palaeon-
Tragulids (Artiodactyla, Ruminantia) from the Late Miocene of Pakistan

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Artiodactyla Owen, 1848
Ruminantia Scopoli, 1777
Tragulidae Milne-Edwards, 1864

Dorcattherium Kaup & Scholl, 1834

Type species: Dorcattherium nanum Kaup & Scholl, 1834

Generic diagnosis: 'Bunoseleodont to selodont teeth with more or less cingula and cingulideae and mostly strong stylus and stylidiae at the molars. The upper molars increase in size from M1 to M3. The lower molars show a special crest complex called the 'Dorcattherium 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 p3 the entoconid fuses with the postprotocristid. The p3 has only a short lingual entoconid originating at the hypoconid. An exception is the p4, which is shorter and does not have an antero-protocristid longish shape' (Rösner 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 ectostyloid or by a vestigial ectostyloid (Kaup & Scholl 1834).

Geographic distribution. Dorcattherium is described from the lower Miocene of Europe by Kaup (1833), Arambourg & Piveteau (1929), Hillenbrand et al. (2009) and Rösner (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).

Dorcattherium minus Lydekker, 1876
Fig 3A-N, 4A-I, 5J-Q; Tab. 2-3

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

Type locality: Kushgal near Attock and Hasnott, Punjab, Pakistan (Colbert 1935).

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

Diagnosis: "A small species of the genus Dorcattherium with selodont 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 M2r (PC-GCUF 09/21, PUPC 86/202, PUPC 04/13), right M2s (PUPC 03/15, PUPC 06/56), right M3 (PUPC 06/4), a fragment of left maxilla with M1-3 (PUPC 04/60). Lower dentition: a fragment of right mandible with p3 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 08/3), 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: Hasnott (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, selodont 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 fossa anteriorly and posteriorly (Fig. 31-K).

DP4. The only available DP4 is in late wear and low crowned (Fig. 31-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. 31-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
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 lingual 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 parastyle 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 entoconid 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 cusp, which is joined lingually by an accessory cusp. The latter is separated from the lingual ridge of the main cusp by a deep groove. The anterior cusp 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 entoconid is weaker than the metaconid. The Dorcatherium-fold is present and directed posteriorly. It is formed by the bifurcation of the post-metaconid 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. nagrus* (Tabs 2, 4), the presence of mesio-lingual

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

cingula, the strong styles/stylids and the presence of *Dorcatitherium*-fold in lower molars (Lydekker 1876; Collbrant 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 *Dorcatitherium*-fold (Collbrant 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 (Collbrant 1935; Farooq 2006; Farooq et al. 2007a).

**Dorcatitherium 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: Hsann, Jhelum, Punjab, Pakistan (Collbrant 1935).

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

Diagnosis: "*Dorcatitherium majus* is a tragiulid species larger than *Dt. minus* and is equal in size to *Dh. anthracotheriodes*. It is characterized by strong parasyle and mesostyle, well-developed cingulum in upper molars and stoutly developed ectostylid" (Collbrant 1935).

Studied specimens: Left M2 (PUPC 05/2), a fragment of left mandible with m2-3 (PUPC 05/1).
*Dorcatheirium minus*, lower dentition: A-C, fragment of right mandible with p4 and m1, P UPC 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, D), labial (B, E, H) and lingual (A, D, G). Scale bar equals 10 mm.

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

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

**Description**

*Upper dentition.* The tooth P UPC 05/2 is quadratate 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 preprotocrista 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). P UPC 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 *Dorcatheirium*-fold directly posteriorly is present in the last molar (Fig. 6F).

**Comparison.** The specimens show trigulid features: the bunoselenodonty, isolated strong styles, basal cingula/cingulids, prominent anterior median ribs and the presence of M-structure (Métai & Vislobokova 2007; Rossner 2010). The features full corroborate the
tragulid status of the Hsnot fossils (Fig. 6A-F). *Siamotragulus* and *Yunnanotherium* differ from those of the studied specimens in displaying a derived morphology: their molars are more selenedont and hypsodont, their premetacristid is well developed and closes the anterior side of the trigonid, and they display a strong ectostyloid (Thomas et al. 1995; Vislobokova 2001). The absence of flat cusps in the studied lower molars associate them to *Dorcadon*, *Hyemoschus* and *Dorcatotherium* in distinction to *Afrotragulus*, *Siamotragulus*, *Yunnanotherium*, *Moschiolae*, 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).

*Dorcadon* 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 *Dorcadon* 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 Hsnot molars differ from those of *Hyemoschus* species in its semiselenedont (= bunoselenedont) cusps/conids and the orientation of the posterior crest of the protocone. In *Dorcatotherium*, this crest is oriented directly distally.
(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 *Dorcatatherium* (Morales et al. 2003). Thus, the Hasnot molars are much closer morphologically to *Dorcatatherium* 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 *Dorcatatherium* are characterized by submesodonty, strong cingulum and bunoseolenodonty with an isolated pillar like parastyle. The metastyle is always found weakly formed in *Dorcatatherium* (Lydekker 1876; Pilgrim 1915; Colbert 1935; Farooq et al. 2007b, 2008; Rössner 2010). The lower teeth are typically *Dorcatatherium* i.e., *Dorcatatherium*-folds, vestigial ectostylic, weak stylids, submesodont, narrowly crowned and well pronounced metaconus ribs. The features full corroborate the tragulid *Dorcatatherium* status of the Hasnot fossils (Fig. 6A-F). The teeth of *Dt. majus* are larger than those of *Dt. minimus, Dt. minus* and *Dt. nagni* (Tab. 2, 4) and morphologically they differentiate from *Dt. minus* and *Dt. nagni* 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

Fig. 6 - *Dorcatatherium 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.
and proportions to that of the holotype of *D. major* (Colbert 1935).

**Dorabune** Pilgrim, 1910

*Type species:* *Dorabune anthracotherioides* Pilgrim, 1910

**Generic diagnosis:** Very large tragulids having bunodont teeth. Isolated parastyle and mesostyle, prominent cingulum and enamel rugosities 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 *Doracatherium* teeth are semiluselodonts and parastyle is not isolated pillar. Upper molars of *Dorabune* are characterized by their brachydonty and bunodonty whereas in *Doracatherium* the molars are semiluselodonts and subhypsidonts to hypsidonts. The lingual cusps of upper molars in *Dorabune* are bucco-semicolonodont, whereas the labial ones are quite bugodont and absolutely conical in their general appearance. In *Dorabune* the protoconid, instead of being a simple crescent like *Doracatherium*, 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 *Dorabune*, 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 *Doracatherium* it is weak. In *Dorabune*, the conids are bunodont and conical. The cingulum 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-metaconid while the other one is attached to the pre-hypocristid producing 'M' structure. While in *Doracatherium* the lower molars show a special crest complex called the *Doracatherium-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).

**Dorabune anthracotherioides** Pilgrim, 1910

Figs 7A-L; Tab. 5

1915 *Dorabune hysaenochrois* Pilgrim, p. 231, pl. 21, fig. 6, pl. 22, figs 2, 3.

1915 *Dorabune sindiene* Pilgrim, p. 234, pl. 21, figs 3, 4.

**Type specimen:** A maxilla with M1-3 (GSI B582), figured in Pilgrim (1910, p. 68).

**Type locality:** Chini, Chakwal, Punjab, Pakistan.

**Stratigraphic range:** Lower to Middle Siwaliks (Pilgrim 1910, 1915; Colbert 1935; Farooq 2004; Farooq et al. 2007c).

**Diagnosis:** *Dorabune anthracotherioides* is a large species of the genus, almost equal to that of *D. crassum* (Roëssner 2010). Upper molars are bunodont and have a prominent paracone. Lower margin of ramus is deep in *D. anthracotherioiides*. Mandible bears a fairly deep groove starting beneath p4 and propagating towards posterior side behind the teeth. This groove exists in *D. major* and *D. minor* but it is absent in *D. nigrus*. 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-GCUP 10/22) (Fig. 7, Tab. 5).

**Localities:** Hamot (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-protocristid is larger than the post-protocristid 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-meta cristata. The post-hypocrista slopes downwards larger than the pre-hypocrista and fuses with the posterior cingulum. The pillar like labiöa paracone rib is separated from para style by a vertical groove. The post-meta cristata is connected with the post-parameta and the post-meta cristata is linked with the post-hypocrista through a small ridge. The strong para style 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
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 semiselenodonty with bunodont pattern and can be associated with tragulids. The bunodont conical cusp pattern of the studied samples makes its inclusion to genus *Dorabune* (Fig. 7). Two valid species of *Dorabune*, *D. nagrii* and *D. anthracotherioides* are recorded from the Siwaliks (Farooq et al. 2007c-d). The described upper and lower dentitions reflect morphometric characteristics of *D. anthracotherioides*. The studied molars are comparable with the holotype as well as the earlier described specimens of *D. anthracotherioides* (Tab. 5). Therefore, *D. anthracotherioides* can be reasonably assigned for the dentitions, based on the mor-
Tragulids (Artiodactyla, Ruminantia) from the Late Miocene of Pakistan

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Tab. 5 - Comparative measurements of the cheek teeth of *Dorcacum* 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 Hasnát 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 Hasnát corresponds to the Late Miocene of Eurasia and Africa (Harris 1987; Solounias 1981; Bernor 1986; Köhler 1987; Gerads 1989; Gentry & Heizmann 1996; Gentry 1978, 1999, 2005; Gentry et al. 1999; Solounias et al. 1999; Illopolulos 2003; Khan et al. 2009), based on the co-occurrence of *Pachypax*, *Tragopax*, *Eotragus*, *Gazella*, *Hydaspatherium*, *Hipparion*, *Dorcapax* and *Dorcatatherium* (Khan 2007b; Farooq et al. 2007a-d, 2008; Khan et al. 2009; Ghaffar et al. 2010).

The Hasnát 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 Hasnát area to the Middle Dhok Pathan Formation having yielded the taxa *Dt. minus* and *Dh. anthracotherioides* which are unknown from the upper Dhok Pathan Formation towards Bhandar deposits (H 16, H 18). The Bhandar deposits, east of the Hasnát 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 Tattroc (Upper Siwaliks) fauna (Brown 1926; Colbert 1935).

*Dorcapax anthracotherioides*, *Dh. majus* and *Dt. minus* are known from the stratigraphical context of the Siwaliks from the Middle Miocene onwards (Pilgrím 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 Hasnát 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 habitat and mode of life in more or less dense forests (Köhler 1993; Rössner 2006) can be reconstructed. *Pachypax* and *Selenopax* are long legged boseaphines 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 *Dorcatatherium* with *Dorcapax*, *Eotragus*, *Tragopax*, *Miotragocerus*, *Pachypax*, *Selenopax*, and *Hydaspatherium* 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; Pilgrím 1937, 1939; Farooq et al. 2007a-d, 2008; Khan et al. 2009, 2010). Bouvain (1994) suggested that *Tragopax* 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). Merceran et al. (2006) suggest that *Tragopax* were engaged in both browsing and grazing. The abundance of *Dorcatatherium* 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

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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 Hasnôt outcrops are represented by the four tragulid species *D. majus*, *D. minus*, *Db. Anthracotherioides*, and *Db. magni* (Farooq et al. 2007d; present study). *Dorcatatherium* is much better represented. *Dorcatatherium 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 Hasnôt 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 Hasnôt 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 Hasnôt indicates wetland highly probable.

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