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New Remains of Tragulids (Mammalia, Tragulidae) from the Dhok Pathan Formation of Hasnot (Late Miocene), Pakistan

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Abstract. – Tragulids, especially *Dorcatherium*, are the best represented ruminants in the Middle Siwaliks of Hasnot, northern Pakistan. New remains described here predominantly consist of isolated teeth, maxilla and mandible fragments. The material is assigned to two tragulid species *Dorcatherium minus* and *D. majus*. The extinction of the tragulid species at the end of Early Pliocene indicates the climatic conditions and landscapes experienced drastic change towards dryer and more open environments.

Keywords: Vertebrate, Artiodactyla, Ruminantia, Miocene, Pliocene, Siwaliks.

INTRODUCTION

The tragulids are the most primitive representatives of the extant ruminants (Janis, 1984; Scott and Janis, 1993; Hassanin and Douzery, 2003; Marcot, 2007; Agnarsson and May-Collado, 2008). The tragulids having small size in living pecorans are less advanced regarding their morphological and physiological features (Dubost, 1965; Kay, 1987; Métais *et al*., 2001; Rössner, 2007; Geraads, 2010; Sanchez *et al*., 2010). Six extant tragulid species are present in the Old World: *Tragulus* spp. in South-East Asia and Philippines (Meijaard and Groves, 2004), three or four in India and Sri Lanka (*Moschiola* spp.) (Groves and Meijaard, 2005) and one in tropical Africa (*Hyemoschus aquaticus*) (Meijaard *et al.*, 2010). The tragulid remains are common finds in the Lower and Middle Miocene deposits of Africa (Whitworth, 1958; Hamilton, 1973; Pickford, 2001, 2002; Quiralte *et al.*, 2008), Europe (Mein, 1989; Rössner, 2007; Gentry, 1999; Gentry *et al.*, 1999) and South Asia (Mein and Ginsburg, 1997; Ginsburg *et al.*, 2001; Sánchez *et al*., 2010; Khan *et al*., 2012; Khan and Akhtar, 2013).

Fossil Tragulidae are mainly represented by the extinct genus *Dorcatherium* Kaup & Scholl, 1834 with 22 recognized species during the Miocene–Pliocene (Rössner, 2007), exceeding by far the specific diversity of other genera such as *Siamotragulus* Thomas, Ginsburg, Hintong and Suteethorn, 1990, *Dorcabune* Pilgrim, 1910 and *Yunnanotherium* Han, 1986. *Dorcatherium* is amongst the five extinct genera of the family Tragulidae alongside *Dorcabune*, *Siamotragulus*, *Yunnanotherium* and *Archaeotragulus*, and it has a wide biogeographic distribution that includes Africa and Eurasia (Sánchez *et al*., 2010; Khan *et al*., 2012; Khan and Akhtar, 2013). The age range of this genus in Africa starts with the Early Miocene and probably extends onto the Early Pliocene (Arambourg, 1933; Whitworth, 1958; Janis, 1984; Fahlbusch, 1985; Gaur, 1992; Gentry *et al*., 1999; Pickford, 2001; Morales *et al*., 2003; Pickford *et al*., 2004; Rössner, 2007; Quiralte *et al*., 2008). *Dorcatherium* remains are known in south Asia, especially in Pakistan about 18 Ma (Welcomme *et al*., 2001; Khan and Akhtar, 2013).

The new recovered tragulid material comes from the outcrops nearby the Hasnot village (Lat. 32° 49′ N: Long. 73° 18′ E), northern Pakistan (Fig.1A). The Hasnot outcrops belong to the Late Miocene – Early Pliocene age (7 to 5 Ma) (Pilbeam *et al*., 1977; Barry *et al*., 2002; Khan *et al*., 2009, 2012). Numerous rich fossiliferous sites occur in the vicinity of the village (Fig. 1B). Lithostratigraphically, the Hasnot village belongs to the upper Dhok Pathan Formation (isochronous to the European Late Turolian age), and are characterized by the presence of sandstones with alternate clays and scattered conglomerates in the lower part and

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conglomerates with sandstones and clays in the upper part of the stratigraphical succession. The sediments composed of orange brown colored clay deposited around 7 to 5 Ma (Pilbeam *et al.*, 1977; Johnson *et al.*, 1982; Barry *et al.*, 1982; Barry, 1987; Khan *et al.*, 2009, 2012).

The material represents two tragulid species: *D. minus* and *D. majus* in the Hasnot, northern Pakistan. A strong attachment to wet forested habitats can be assumed for the tragulids, where the animals could hide from predators in vegetation or water. However, climatic and ecological conditions are different at present in Hasnot, northern Pakistan. This paper interprets the entire collection of tragulids recently recovered from the Hasnot outcrops of the Middle Siwaliks.

MATERIAL AND METHODS

Material

The ascribed tragulid material was recovered during 2010 to 2013 in the excavation at Hasnot conducted by the first author for the PhD research work (Fig. 1). The collected tragulid remains include isolated teeth, mandible and maxilla fragments. Different methods were used for the collection of the tragulid remains but surface collection remained the primary method of gathering tragulid fossils. Some excavations were conducted at a small number of sites, where dense concentrations of fossil bones occur in situ within sandstone deposits alternating with clay and conglomerate. Some fossils were found in the orange brown clay.

The embedded material was cautiously excavated with the help of instruments, such as chisels, geological hammers, fine needles, pen knifes, hand lances and brushes. The material was carefully washed and cleaned in the Palaeontology Laboratory of Wildlife and Fisheries Department, GC University Faisalabad, thus being prepared for the taxonomic and morphological determination. Each specimen was assigned a catalogue number that consists of series *i.e.*, yearly catalogue number and serial catalogue number, so figures on the specimen represent the collection year (nominator) and serial number of that year (denominator) (*e.g.* PC-GCUF 12/15, the upper figure denotes the collection year and the lower one represent the serial number of the respective year; PC-GCUF is an institutional abbreviation employed for the Palaeontological Collection of Government College University Faisalabad, Punjab, Pakistan). The metric and morphological characteristics of the tragulid remains are determined and systematic determination is discussed. The studied material is housed in the Zoology Department of GC University, Faisalabad, Pakistan.

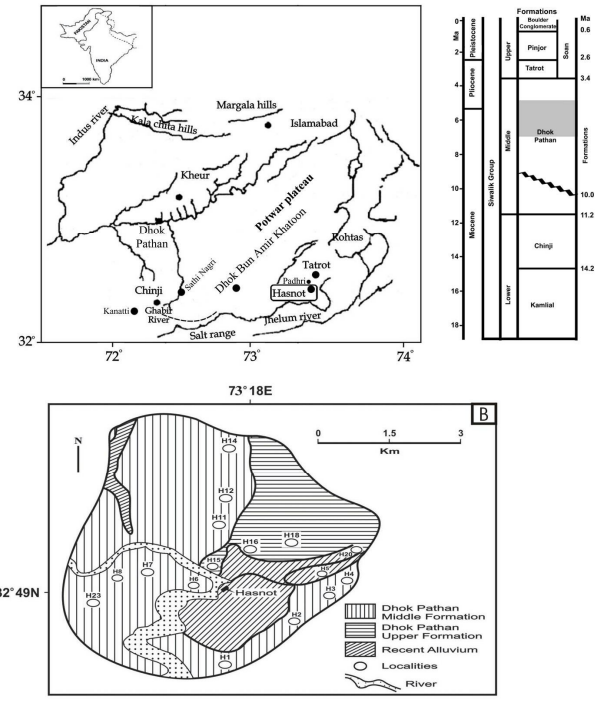

Fig. 1. A map of the Potwar Plateau in northern Pakistan; reference locality of the Siwaliks encircled. Chronological text modified from Behrensmeyer and Barry (2005), Dennell (2008) and Nanda (2008). B – Simplified geologic map of the Hasnot area with indicated localities around the village Hasnot (H = Hasnot), where the studied material is recovered from (modified from Colbert, 1935).

The metric and morphological characteristics of the tragulid are determined and systematic determination is discussed.

Photography

Well-preserved specimens were selected for photography and are illustrated in the respective

figures. Measurements of the specimens were taken with the help of a metric vernier caliper. The measurements were taken occlusally at maximum level (meso-distal = length, labio-lingual = width) and are expressed in millimeters.

Source of the comparative material

Comparison is made to fossils housed in the British Natural History Museum, London (BMNH), the American Museum of Natural History (AMNH), the Geological Survey of Pakistan (GSP), Islamabad and Quetta, the Geological Survey of India (GSI), Calcutta and the specimens of the Palaeontology Laboratory of the Zoology Department of the Punjab University, Lahore, Pakistan (PUPC). Dental measurements of the Siwalik *Dorcatherium* for comparison were also taken from literature (Khan *et al*., 2012; Khan and Akhtar, 2013).

Nomenclature

Tooth terminology generally follows Gentry *et al*. (1999), Khan *et al*. (2011, 2012), with some exceptions, substituting the terms anterior/posterior median ribs by paraconus/metaconus rib (following Bärmann and Rössner, 2011). Uppercase letters represent upper dentition (*e.g*. M1) and lowercase for lower dentition (*e.g*. m1).

SYSTEMATIC PALAEONTOLOGY

Suborder Ruminantia Scopoli, 1777
Family Tragulidae Milne-Edwards, 1864

Genus *DORCATHERIUM* Kaup and Scholl, 1834

Type species

Dorcatherium naui Kaup and Scholl, 1834.

Generic diagnosis

As in Kaup and Scholl (1834) and Rössner (2010: 128).

Occurrences

Europe, East Africa, South Asia.

Time range

Early Miocene – Early Pliocene.

Dorcatherium minus Lydekker, 1876

Type specimen

GSI B195, right upper first and second molars, figured in Lydekker (1876, p. 46, pl. VII, figs. 3, 7).

Specific diagnosis

As in Colbert (1935).

Type locality

Kushalgar, Attock district and Hasnot, Jhelum district, the Punjab province, Pakistan (Colbert, 1935).

Stratigraphic range

Middle Miocene – Early Pliocene (Lower – Middle Siwaliks).

Locality

Hasnot, Jhelum district, the Punjab province, Pakistan.

New material

PC-GCUF 11/178, left M1; PC-GCUF 12/39, probably a partially broken M1; PC-GCUF 11/184, right M3; PC-GCUF 12/40, right m1; PC-GCUF 12/41, left m1; PC-GCUF 10/21, left m2; PC-GCUF 10/54, right mandibular fragment with partial m2-3; PC-GCUF 12/12, left mandibular fragment of a juvenile animal with posterior lobe of m1 and complete m2.

Description

Upper dentition

The upper molars demonstrate greater width than length (Figs. 2A–C; Table I). The molar shows semi buno-selenodonty. The molars have broad and low cusps with strongly developed mesostyle and labial ribs. The paraconus rib is strong, whereas the metaconus one is weak. The pre-protocrista is longer than post-proto-crista which is isolated destolingually. The pre-and post-hypocristae are almost equal in length; however, the pre-hypocrista is isolated mesiolingually and the post-hypocrista is fused distally with the post-meta-crista. The cingulum is present mesiolingually and it is especially well-developed on the base of the protocone. There is no entostyle.

Table I.– Comparative measurements (mm) of the cheek teeth of *Dorcatherium minus* and *Dorcatherium majus*. *the studied specimens. Comparative measurements are taken from Colbert (1935), Farooq *et al.* (2007a, 2008), Iqbal *et al.* (2011), Khan *et al.* (2012) and Khan and Akhtar (2013).

Taxa	Number	Nature/Position	Length	Width	W/L
D. minus	PC-GCUF 11/178*	lM1	09.7	10.5	1.08
	PC-GCUF 12/39*	M1	11.0	06.2	0.54
	PC-GCUF 11/184*	rM3	12.8	12.8	1.00
	PC-GCUF 12/40*	rm1	10.0	05.1	0.51
	PC-GCUF 12/41*	lm1	09.3	05.4	0.58
	PC-GCUF 12/12*	lm1	-	-	-
		lm2	08.2	05.5	0.67
	PC-GCUF 10/21	lm2	11.0	07.0	0.63
	PC-GCUF 12/01*	lm2	11.0	06.9	062
	PC-GCUF 10/54*	rm2	-	07.0	-
		rm3	-	07.0	-
	PUPC 68/210	lm3	18.0	08.0	0.44
	PUPC 87/84	M1	09.3	10.0	1.07
	PUPC 87/40	M1	10.0	11.7	1.17
	GSI 09/01	M1	08.2	10.2	1.25
	GSI 09/02	M3	12.5	13.7	1.09
	PUPC 68/355	M3	11.7	13.0	1.11
	PUPC 02/158	m1	10.6	06.7	0.63
	PUPC 68/313	m1	08.9	05.6	0.62
	PUPC 68/312	m1	09.1	05.3	0.58
	PUPC 68/311	m2	10.0	06.6	0.66
	PUPC 68/312	m2	10.0	06.2	0.62
	PUPC 85/59	m2	09.5	07.0	0.73
	PUPC 02/158	m2	12.7	08.2	0.64
	AMNH 19365	m2	13.0	12.0	0.92
D. majus	PUPC 86/46*	rM3	20.0	21.6	1.08
	PC-GCUF 10/49*	lp3	13.8	05.8	0.42
		lp4	14.2	07.2	0.50
		lm1	15.5	10.2	0.65
		lm2	17.2	11.2	0.65
		lm3	23.3	12.0	0.51
	PC-GCUF 12/18*	lm1	16.6	09.6	0.57
		m2	20.0	10.3	0.51
	PC-GCUF 12/31*	lm2	19.0	11.0	0.57
	PC-GCUF 10/52*	rm3	27.1	12.1	0.44
	PC-GCUF 11/153*	rm3	19.4	-	-
	PC-GCUF 12/29*	m3	-	11.2	-
	AMNH 19354	M3	20.5	23.5	1.14
	GSI B198	M3	20.1	19.2	0.95
	PUPC 67/191	M3	13.6	15.2	1.11
	PUPC 87/197	M3	20.5	22.0	1.07
	PUPC 86/02	p4	13.3	06.0	0.45
	PUPC 86/05	p4	13.1	05.7	0.38
	AMNH19524	P4	14.5	05.0	0.34
	GSI B593	P4	17.3	06.2	0.35
	GSI B593	m1	15.7	09.5	0.60
	PUPC 01/21	rm1	17.5	09.0	0.51
	PUPC 86/05	m1	13.0	09.3	0.71
	AMNH 19524	m1	13.5	09.0	0.66

Continued

Taxa	Number	Nature/Position	Length	Width	W/L
	GSI B593	m2	17.5	10.0	0.57
	PUPC 01/26	lm2	17.0	09.0	0.52
	PUPC 07/09	lm2	18.0	12.0	0.66
	PUPC 63243	m2	17.0	10.1	0.59
	PUPC 84/115	m2	16.0	12.0	0.75
	PUPC 86/02	m2	15.6	09.8	0.62
	PUPC 86/05	m2	15.0	11.1	0.74
	PUPC 86/152	m2	16.2	12.0	0.74
	PUPC 98/61	m2	17.0	10.5	0.61
	AMNH 19520	m2	17.0	10.5	0.61
	AMNH 19524	m2	16.0	11.0	0.68

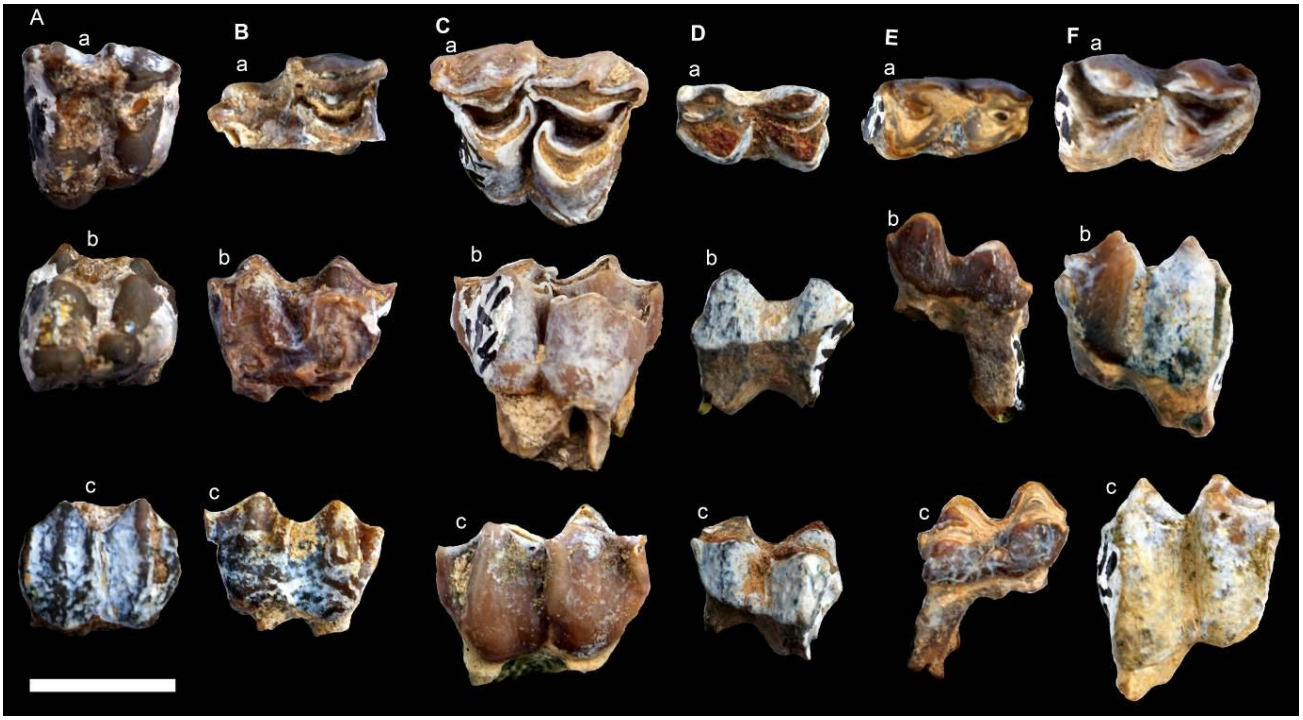

Fig. 2. *Dorcatherium minus*: **A**, PC-GCUF 11/178, lM1; **B**, PC-GCUF 12/39, partially broken probably ?M1; **C**, PC-GCUF 11/184 rM3; **D**, PC-GCUF 12/40 rm1; **E**, PC-GCUF 12/41 lm1; **F,** PC-GCUF 10/21 lm2. Views; a, occlusal; b, lingual; c, labial. Scale bar 10 mm.

Lower dentition

The lower dentition specimens described here include first and second molars, and two fragile mandibular fragments (Figs. 2D-F, 3A-B; Table I). The teeth are subhypsodont and narrow crowned. The major conids are well preserved. The lingual conids are pointed and slightly higher than the labial ones. The pre-metacristid is longer than the post-metacristid. The pre- and postfossettes are crescent. A rudimentary ectostylid is present at the base of the transverse valley. A well-developed cingulid is present labiolingually. The post-metacristid (in some sample post-protocristid) is bifurcated indicating *Dorcatherium* fold, a characteristic feature of the genus *Dorcatherium*. The *Dorcatherium* fold is directed posteriorly. The metaconid rib and stylid are weakly developed. A prominent entoconid rib is present but the entostylid is weak. The prefossette is less deep than the postfossette. The postfossette is not fused lingually

Fig. 3. *Dorcatherium minus*: **A**, PC-GCUF 10/54, right mandible fragment with posterior lobe of m2 and m3 with missing hypoconulid; **B**, PC-GCUF 12/12, left mandibular fragment of a juvenile animal with posterior lobe of m1 and complete m2. Views; a, occlusal; b, lingual; c, labial. Scale bar 10 mm.

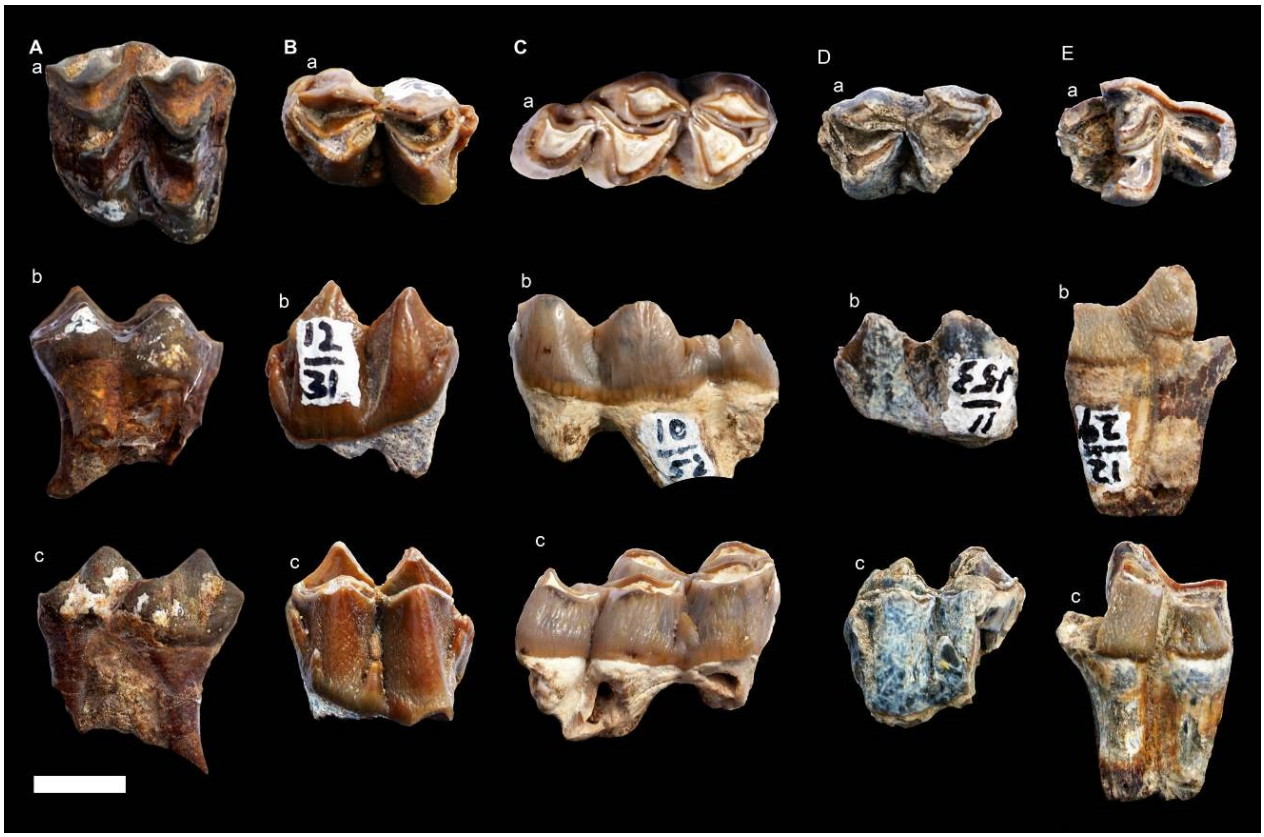

Fig. 4. *Dorcatherium majus*: **A**, rM3, PUPC 86/46; **B**, PC-GCUF 12/31, lm2; **C**, PC-GCUF 10/52, rm3; **D**, PC-GCUF 11/53 broken rm3; **E**, PC-GCUF 12/29, partially preserved left m3 with missing anterior lobe. Views; a, occlusal; b, lingual; c, labial. Scale bar 10 mm.

and consequently, the entoconid is completely separated from the hypoconid.

Comparison

The studied specimens prove their inclusion in the family Tragulidae, based on the selenobunodont to selenodont pattern with strong cingula and cingulidae, and mostly strong styli and stylidae (Rossner, 2007; Khan *et al*., 2012; Khan and Akhtar, 2013). Tragulidae in the Siwaliks are represented by two genera *Dorcatherium* and *Dorcabune* with many species. *Dorcabune* is a large extinct tragulid of the Siwaliks and close to anthracotherioides having bunodont molars. The paraconus rib is more conspicuous in *Dorcabune* than in *Dorcatherium* (Colbert, 1935; Farooq *et al*., 2007a, b; Khan and Akhtar, 2013).

The studied specimens differ from *Dorcabune* showing selenodont cusp/conid pattern (crescentic cusp/conids). The teeth are characterized by well-developed styli/stylidae, the basal cingulum in the upper molars, and the vestigial ectostylid and *Dorcatherium*-fold in the lower molars. These characteristics associate them to the genus *Dorcatherium*. In *Dorcatherium*, the lower molars show a special crest complex called '*Dorcatherium* fold'. The *Dorcatherium* fold represents a double fold protoconid. It is formed by the bifurcation of post-protocristid and post-metacristid resulting in a '∑' shape.

The Siwalik *Dorcatherium* is represented by four species *D. majus, D. minus, D. nagrii* and *D. minimus* (Colbert, 1935; West, 1980; Farooq *et al*., 2007a, b; Khan and Akhtar, 2011; Khan *et al*., 2012). *Dorcatherium majus* is the large Siwalik species of *Dorcatherium* (Farooq *et al*., 2008; Khan *et al*., 2012). *Dorcatherium minus* is more brachydont than *D. majus* (Khan and Akhtar, 2013).

Fig. 5. *Dorcatherium majus*: **A**, PC-GCUF 10/49, left hemimandible with broken p2 and complete tooth series p3-m3; **B**, PC-GCUF 12/18, left mandibular fragment with m1-2. Views; a, occlusal; b, lingual; c, labial. Scale bar 30 mm.

Dorcatherium nagrii and *D. minimus* are minute species of the Siwalik tragulids (Khan and Akhtar, 2011). *Dorcatherium* has semiselenodont teeth and its numerous species mainly differ by their size (West, 1980; Farooq *et al*., 2007a, b, 2008; Iqbal *et al*., 2011; Khan *et al*., 2012; Khan and Akhtar, 2013).

The sample matches well with *D. minus*, morphometrically (Table I; Figs. 2-3). The molars clearly overlap in size with the type material and earlier ascribed material of *D. minus*. However, the spectrum of intraspecific size variability in *Dorcatherium* is large and enables sexual dimorphism in body size to be hypothesized. However, in extant tragulids females are a little larger than males (Dubost, 1965; Terai *et al*., 1998), as is generally true for small ruminants (Loison *et al*., 1999). Therefore, the same dimorphism can be assumed for *D. minus*.

Dorcatherium majus Lydekker, 1876

Type specimen

GSI B197, right upper first and second molars, figured in Lydekker (1876, p. 44, pl. VII, figs. 4, 6, 9, 10, 11).

Specific diagnosis

As in Colbert (1935).

Type locality

Hasnot, Jhelum district, the Punjab province, Pakistan (Colbert, 1935).

Stratigraphic range

Middle Miocene – Early Pliocene (Lower – Middle Siwaliks).

Locality

Hasnot, Jhelum district, the Punjab province, Pakistan.

New material

PUPC 86/46, right M3; PC-GCUF 10/49, left hemimandible with broken p2 and complete tooth series p3-m3; PC-GCUF 12/31, left m2; PC-GCUF 12/18, left mandibular fragment with m1-2; PC-GCUF 10/52, right m3; PC-GCUF 11/153, broken right m3; PC-GCUF 12/29, partially preserved left m3 with missing anterior lobe.

Description

Upper dentition

The newly discovered upper dentition includes the third molar PUPC 86/46 (Fig. 4A). The molar is quadrate in its general appearance, rugose and subhypsodont. The molar represents strong labial styles, lingual cingulum and semiselenodonty. The cingulum is surrounded by the protocone and the hypocone. There is a lingual cingulum at the base of the protocone, and thick cingular shelves extending mesiolingually and distolingually. The parastyle, mesostyle, metastyle and paraconus ribs are very strong. The post-paracrista and pre-metacrista are connected in a low position on the crown but they are not directly attached to the mesostyle. The fossettes are deep and open in the transverse valley. The lingual lobes are more crescent-shape than the labial ones. The paracone has a strong anterior groove descending from its apex to the base of the crown, which separates the parastyle from the labial pillar. The post-hypocrista terminates in the midline of the crown at the distal cingulum.

Mandible

The mandible fragment is broken vertically during the excavation which is assembled. The anterior and posterior parts of the fragment are damaged. There are no preserved parts of the symphysis and angular process. The jaw is shallow and slim, with a mental foramen below the anterior root of the p2. The body of the mandible descends anteriorly and is markedly higher under the m3 than under the p2. The ventral border of the body of the mandible is weakly curved downward. Apart from the relatively long mandible (ML = 154 mm), the mandible fragment is shallow and slim as is typical in tragulids (Fig. 5A; Table I). The jaw deepens rapidly distally being 20 mm deep below the p3 and 37 mm below the m3. The ascending ramus begins right at the posterior end of the hypoconulid, so there is no gap between the m3 and the ascending ramus. The lingual surface of the jaw is marked by a

groove distolaterally. The labial side of the hemimandible is clearly convex anteriorly and the lingual side is slightly concave below the m1. The molar series length is 55 mm and the premolar series is 40 mm long.

Lower dentition

The p1 is absent. The p2 is broken anteriorly (Fig. 5). The posterior lobe of the p2 representing a short lingual entocristid originating at the hypoconid. The p3 is longish - a tragulid feature, with three labial conids (protoconulid, protoconid, hypoconid). The p2 has two conids (protoconulid, protoconid). The p4 is shorter than p3: the p3 is slightly more elongated than the p4. In the p3, a strong protoconid linked by a straight longitudinal crest to a small mesio-lingually situated paraconid. The latter crest is slightly curved lingually, and joins the more lingually situated paraconid. The conical hypoconid is weaker and lower than the protoconid, located behind a strong protoconid at the posterior of the premolar. The hypoconid forms a well-marked transverse spur posteriorly on the p3 where it delimits a small lingually open vertical basin.

The p4 is the widest of the premolars owing to a lingually located post-protocristid. In the p4, the pre-protocristid is curved anterolingually with paraconid which is more lingually situated. The pre-protoconulidcristid runs straight mesiolingually. The pre-protocristid joins the paraconid and two parallel crests extend from the apex of the strong protoconid to the distal border of the premolar, forming a triangular and narrow basined talonid. The anterior valley is opened lingually. The entoconid complex is absent – a tragulid feature. A short distolabial crista at the hypoconid is absent. The p1, p2 and p3 are two-rooted.

The trigonid is narrower than the talonid in the m1. The lingual conids are transversely compressed owing to the large size of the hypoconid. The labial conids are crescent shape. The anterior cingulum is slightly extending on the labial side of the protoconid. The post-protocristid is bifurcated into *Dorcatherium* fold, connected with the outer flank of the well-marked *Dorcatherium* fold at the rear of the metaconid and open at the lingual base of the metaconid on worn tooth. The fusion of both crests into a single edge joining the pre-entocristid, involving an '∑' shape on the posterior side of the trigonid. The entoconid is rounded posteriorly and situated forward with respect to the hypoconid displaying a deep groove opens lingually on the unworn m3.

The post-hypocristid extends disto-lingually reaching the post-hypoconulidcristid lingually. The hypoconulid of m3 labially twisted and transversely compressed with one crest extending forward from the apex of the hypoconulid to reach the post-hypocristid labially of the second lobe without any accessory small tubercle. The lingual crest of the hypoconulid units with lingual cingulid is extending between the hypoconid and hypoconulid lingually. The weak ectostylid like labial cingulid is present in the transverse valley. The pre-fossette is not crescent shape but it is somewhat compressed and straight whereas the post-fossette is crescentic and opens distolingually.

Comparison

The studied material presents semi-selenodonty, isolated strong style, basal cingula/cingulid, prominent paraconus rib and the presence of ∑-structure (*Dorcatherium* fold) in the lower molars. The material characterized by these features can be associated with tragulids (Métais and Vislobokova, 2007; Rössner, 2010; Khan *et al*., 2012; Khan and Akhtar, 2013). *Siamotragulus* and *Yunnanotherium* differ from those of the studied samples in: more selenodont and hypsodont aspect, premetacristid is well developed and closes the anterior side of the trigonid, and a strong ectostylid (Thomas *et al*., 1990; Vislobokova, 2001). *Afrotragulus*, *Siamotragulus*, *Yunnanotherium*, *Moschiola*, and *Tragulus* teeth differ from the studied specimens in having flat cusps. They are characterized by the presence of flat main cusps with cristids that are elongated and vertically developed (Sánchez *et al.*, 2010).

Nevertheless, the features reflected by the studied specimens associate them to *Dorcabune*, *Hyemoschus* and *Dorcatherium*. *Dorcabune* differs from that of the studied material in: very bunodont conical molars, thick and rugosed enamel, 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

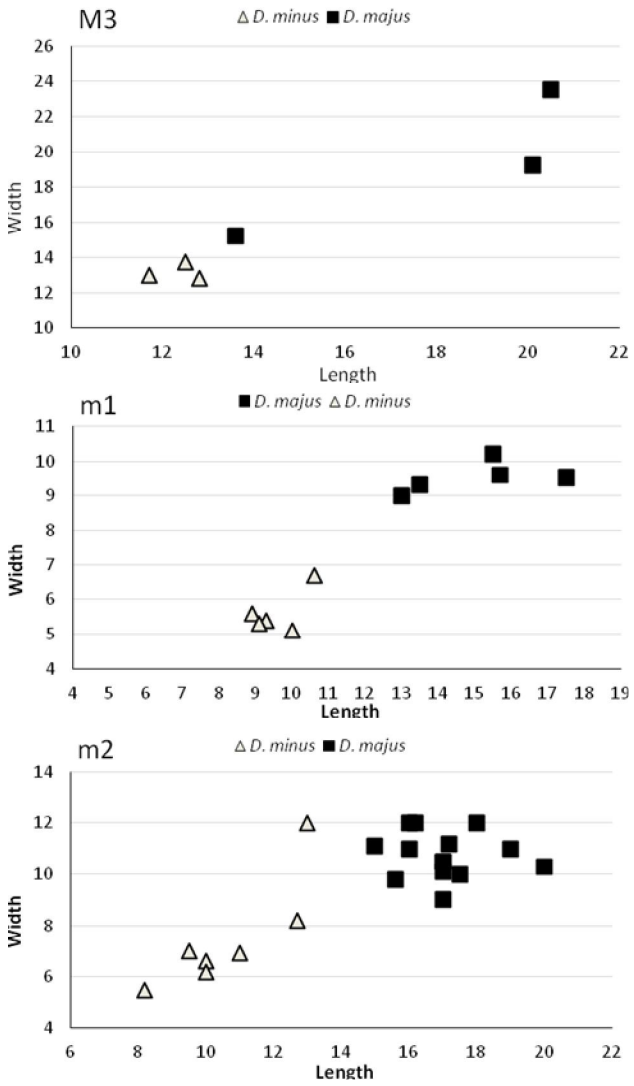

Fig. 6. Scatter diagram showing dental proportions (in mm) of the Hasnot *Dorcatherium minus and D. majus*. Referred data are taken from Colbert (1935), Farooq *et al*. (2007a, b, 2008), Iqbal *et al*. (2011), Khan *et al*. (2012) and Khan and Akhtar (2013).

the posterior side of the protoconid on the lower molars (Pilgrim, 1915; Khan *et al*., 2012). The studied molars differ from those of *Hyemoschus* in: weak cingulum, semiselenodont (= bunoselenodont) cusps/conids pattern and the orientation of the post-protocristid (Pickford, 2002; Morales *et al*., 2003; Pickford *et al*., 2004). On the basis of the selenodont upper molars with strong cingulum, styles and labial ribs, and the presence of the ∑ structure (*Dorcatherium* fold) in the lower molars, the specimens are attributed to *Dorcatherium* rather than to *Hyemoschus* or other Miocene tragulids such as *Dorcabune* (Khan *et al*., 2012) and *Siamotragulus* (Thomas *et al*., 1990), or extant ones such as *Tragulus*.

The teeth are much closer morphometrically to the Siwalik *Dorcatherium majus* (Table I; Fig. 4-6). The teeth of *D. majus* are larger than those of *D. minimus*, *D. minus* and *D. nagrii* (Table 1) and morphologically they differ from *D. minus* and *D. nagrii* in terms of the strong basal cingula and the stronger and larger styles (Fig. 4-5) (Lydekker, 1876; Pilgrim, 1915; Colbert, 1935; Farooq *et al*., 2007b, 2008; Khan *et al*., 2012).

DISCUSSION

Tragulids, representing the best-described ruminant family of the Late Miocene (Vislobokova, 2001; Pickford, 2002; Khan *et al*., 2012), have been found in the Hasnot outcrops (Farooq *et al*., 2007c, 2008; Khan *et al*., 2012). The presence of Tragulids (*Dorcatherium*) suggests highly humid ecological conditions with habitats of small swamps and patches of dense forests (Meijaard *et al*., 2010; Khan *et al*., 2012). Living chevrotains favor dense habitats of the rain forests (Dubost, 1978; Meijaard *et al*., 2010), which serve as shady shelters from predators. Their dry-land dietary habits include fruits and leaves, whereas the species apparently can enter water for the purpose of safety (Dubost, 1978). The presence of the tragulid fossils in the Late Miocene of the Siwaliks indicates the presence of dense pockets of rain forest.

Dorcatherium majus and *D. minus* are typical representatives of the browsing guild, such as *Dorcabune, Eotragus, Elachistoceros, Tragoportax, Miotragocerus, Selenoportax* and *Pachyportax* (Thomas, 1977, 1984; Solounias *et al*., 1995; Barry *et al*., 2005; Bibi, 2007; Khan *et al*., 2010, 2012; Khan and Akhtar, 2013). These species fed on a broad array of leaves, shoots, and buds with high protein content, as well as on limited amounts of vegetation with abrasive particles (Bouvrain, 1994; Khan *et al*., 2009, 2010, 2012) and found their food in lowland forests and ecotones to open areas (Stuart and Stuart, 1997; Geist, 1998).

Dorcatherium majus and *D. minus* are indicated to have had a browsing diet with a wide spectrum including water plants and occasional fruit and grass intake. The difference between feeding strategies of *Hyemoschus* and *Dorcatherium* suggests the use of different ecological niches. Nevertheless, both the genera must have overlapped in wet forested habitats (Dubost, 1978; Stuart and Stuart, 1997). Closed low canopy forest with minimal ground cover would have been suitable for *Dorcatherium,* on a limited home range.

CONCLUSIONS

The Hasnot tragulids are placed in Late Miocene to Pliocene age based on its associated fauna of the Late Miocene to Pliocene taxa such as *Selenoportax*, *Pachyportax*, *Tragoportax* and *Hipparion*. The tragulid-associated fauna shows abundant vegetation with significant food supply for the diversified, mostly brachydont, large mammalian fauna. An association of tragulids with other artiodactyls indicates the existence of habitats with humid conditions along with open drier areas. The Hasnot area is suggestive for such a mosaic of both more open and forested landscapes with an enormous wetland environment, strongly subjected to alternating dry and flood seasons.

REFERENCES

AGNARSSON, I. AND 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. Phylog. Evol.*, **48**: 964-985.

ARAMBOURG, C., 1933. Mammifères Miocènes du Turkana (Afrique Orientale). *Annl. Paléontol.*, **22**: 121-148.

BARRY, J. C., 1987. The history and chronology of Siwalik cercopithecoids. *Hum. Evol.*, **2**: 47-58.

BARRY, J.C., LINDSAY, E.H. AND JACOBS, L.L., 1982. A biostratigraphic zonation of the middle and upper Siwaliks of the Potwar Plateau of northern Pakistan. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, **37**: 95-130.

BARRY, J.C., MORGAN, M.E., FLYNN, L.J., PILBEAM, D., BEHRENSMEYER, A.K., RAZA, S.M. AND KELLEY, J., 2002. Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. *Paleobiology*, **28**, 1-71.

BARRY, J.C., COTE, S.L., MACLATCHY, E., LINDSAY, H., KITYO, R. AND RAJPAR, A. R., 2005. Oligocene and early Miocene ruminants (Mammalia, Artiodactyla) from Pakistan and Uganda. *Palaeontol. Electron.*, **8**: 1-29.

BEHRENSMEYER, A. AND BARRY, J., 2005. Biostratigraphic surveys in the Siwaliks of Pakistan. A method for standardized surface sampling of the vertebrate fossil record. *Palaeontol. Electron.*, **8**: 1-24.

BIBI, F., 2007. Origin, paleoecology, and paleobiogeography of early Bovini. *Palaeogeogr., Palaeoclimat. Palaeoecol.*, **248**: 60-72.

BOUVRAIN, G., 1994. Un bovidé du Turolien inférieur d'Europe orientale: *Tragoportax rugosifrons*. *Ann. Paléontol.*, **80**: 61-87.

BÄRMANN, E.V. AND RÖSSNER, G., 2011. Dental nomenclature in Ruminantia: Towards a standard terminological framework. *Mammal. Biol.*, **76**: 762–768.

COLBERT, E.H., 1935. Siwalik mammals in the American Museum of Natural History. *Trans. Am. phil. Soc. N. S.*, **26**: 1-401.

DENNELL, R. W., 2008. The taphonomic record of Upper Siwalik (Pinjor stage) landscapes in the Pabbi Hills, northern Pakistan, with consideration regarding the preservation of hominin remains. *Quat. Int.*, **192**: 62-77.

DUBOST, G., 1965. Quelques traits remarquables du comportement de *Hyaemoschus aquaticus*. *Biol. Gabon.*, **1**: 282-287.

DUBOST, G., 1978. Un aperçu sur l'écologie du chevrotain africain *Hyemoschus aquaticus* Ogilby, Artiodactyle Tragulide. *Mammalia,* **42**: 1-62.

FAHLBUSCH, V., 1985. Säugetierrestre (*Dorcatherium, Steneofiber*) aus der Miozanen Braunkhole von Wackersdorf/Oberpfalz. *Mitteil. Bayer. Staatssamml. Paläontol. Histor. Geol.*, **25**: 81-94.

FAROOQ, U., KHAN, M.A., AKHTAR, M. AND KHAN, A.M., 2007a. *Dorcatherium minus* from the Siwaliks, Pakistan. *J. Anim. Pl. Sci.*, **17**: 86-89.

FAROOQ, U., KHAN, M. A., AKHTAR, M. AND KHAN, A. M., 2007b. *Dorcatherium majus*, a study of upper dentition from the lower and middle Siwaliks of Pakistan. *J. appl. Sci.*, **7**: 1299-1303.

FAROOQ, U., KHAN, M. A., AKHTAR, M. AND KHAN, A. M., 2007c. *Dorcabune anthracotherioides* (Artiodactyla, Ruminantia, Tragulidae) from Hasnot, the Middle Siwaliks, Pakistan. *Pakistan J. Zool.*, **39**: 353-360.

FAROOQ, U., KHAN, M.A., AKHTAR, M. AND KHAN, A.M., 2008. Lower Dentition of *Dorcatherium majus* (Tragulidae, Mammalia) in the Lower and Middle Siwaliks (Miocene) of Pakistan. *Turk. J. Zool.*, **32**: 91-98.

GAUR, R., 1992. On *Dorcatherium nagrii* (Tragulidae, Mammalia) with a review of Siwalik tragulids. *Riv. Ital. Paleontol. Stratigr.*, **98**: 353-370.

GEIST, V., 1998. *Deer of the world. Their evolution, behaviour and ecology*. Pennsylvania; Stackpole Books, 421 pp. 415.

GENTRY, A.W., 1999. Fossil Pecorans from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In: *Abu Dhabi Pecorans*. chap. 22 (ed. E.S. Vrba and G.B. Schaller). Yale University Press, New Haven, pp. 290-316.

GENTRY, A.W., ROSSNER, G.E. AND HEIZMANN, E.P.S., 1999. Suborder Ruminantia. In: *The Miocene land mammals of Europe* (eds. G. E. Rossner and K. Heissig). Verlag Dr. Friedrich Pfeil, München, pp. 225-258.

GERAADS, D., 2010. Tragulidae. In: *Cenozoic mammals of Africa* (eds. L. Werdelin and W.J. Sanders). University of California Press, Berkeley, pp. 723-729.

GINSBURG, L., MORALES, J. AND SORIA, D., 2001. Les Ruminantia (Artiodactyla, Mammalia) du Miocène des Bugti (Balouchistan, Pakistan). *Estud. Geol.*, **57**: 155-170.

GROVES, P. AND 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. Brit. Mus. Lond. Geol*, **21**: 75-150.

HASSANIN, A. AND DOUZERY, E.J.P., 2003. Molecular and morphological phylogenies of Ruminantia and the alternative position of the Moschidae. *Sys. Biol.*, **52**: 206-228.

IQBAL, M., KHAN, M.A., ATIQ, M., IKRAM, T. AND AKHTAR, M., 2011. *Dorcatherium minus* from the Nagri type area of the Nagri Formation, Middle Siwaliks, northern Pakistan: new collection. *Yerbilimleri (Earth Sci.)*, **32**: 59-68.

JANIS, C.M., 1984. Tragulids as living fossils. In: *Living fossils* (eds. N. Eldredge and S.M. Stanley), Casebooks in Earth Sciences, New York, pp. 87-94.

JOHNSON, N. M., OPDYKE, N. D., JOHNSON, G. D., LINDSAY, E. H. AND TAHIRKHELI, R.A.K., 1982. Magnetic polarity, stratigraphy and ages of Siwalik group rocks of the Potwar Plateau, Pakistan. *Palaeogeogr., Palaeoclimat., Palaeoecol.*, **37**: 17-42.

KAUP, J.J. AND SCHOLL, J.B., 1834. *Verzeichniss der Gypsabgüsse von den ausgezeichnetsten urweltlichen Thierresten des Grossherzoglichen Museum zu Darmstadt* (2.Ausgabe), Diehl, Darmstadt, pp. 6-28.

KAY, R.N.B., 1987. The comparative anatomy and physiology of digestion in tragulids and cervids, and its relation to food intake. In: *Biology and management of the Cervidae, Research symposia of the National Zoological Park* (ed. C.M. Wemmer). Smithsonian Institution Press, Washington, pp. 214-222.

KHAN, M.A. AND 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:** 1101-1109.

KHAN, M. A., ILIOPOULOS, G. AND AKHTAR, M., 2009. Boselaphines (Artiodactyla, Ruminantia, Bovidae) from the middle Siwaliks of Hasnot. Pakistan. *Geobios*, **42**: 739-753.

KHAN, M. A., KHAN, M. A., AKHTAR, M. AND 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., AKHTAR, M., ILIOPOULOS, G. AND HINA, 2012. Tragulids (Artiodactyla, Ruminantia, Tragulidae) from the middle Siwaliks of Hasnot (late Miocene), Pakistan. *Riv. Ital. Paleontol. Stratigr.*, **118**: 325-341.

KHAN, M.A. AND AKHTAR, M., 2013. Tragulidae (Artiodactyla; Ruminantia) from the middle Miocene Chinji Formation of Pakistan. *Turk. J. Earth Sci.*, **22**: 339-353.

LOISON, A., GAILLARD, J.M., PELABON, C. AND YOCCOZ, N.G., 1999. What factors shape sexual size dimorphism in ungulates? *Evolut. Ecol. Res.*, **1**: 611-633.

LYDEKKER, R., 1876. Molar teeth and other remains of Mammalia from the India Tertiaries. *Palaeontol. Ind.*, **10**: 19-87.

MARCOT, J.D., 2007. Molecular phylogeny of terrestrial artiodactyls. Conflicts and resolution. In: *The evolution of artiodactyls* (eds. D.R. Prothero and S.E. Foss). The Johns Hopkins University Press, Baltimore, pp. 4-18.

MEIJAARD, E. AND GROVES, C.P., 2004. A taxonomic revision of the *Tragulus* mouse deer (Artiodactyla). *Zool. J. Linn. Soc.*, **140**: 63-102.

MEIJAARD, E., UMILAELA AND WIJEYERATNE, G., 2010. Aquatic escape behaviour in mouse deer provides insight into tragulid evolution. *Mammal. Biol.*, **75**: 471-473.

MEIN, P. AND GINSBURG, L., 1997. Les mammifères du gisement miocène inférieur de Li Mae Long, Thailand: systematique, biostratigraphie et palaéoenvironnement. *Geodiversitas*, **19**: 783-844.

MEIN, P., 1989. Updating of MN zones. In: *European neogene mammal chronology* (eds. E.H. Lindsay, V. Fahlbusch, and P. Mein). NATOASI Series 180, New York, London, pp. 73-90.

METAIS, G. AND VISLOBOKOVA, I., 2007. Basal ruminants. In: *The evolution of artiodactyls* (eds. D.R. Prothero and S.C. Foss). The Johns Hopkins University Press, Baltimore, pp. 189-212.

MÉTAIS, G., CHAIMANEE, Y., JAEGER, J.J. AND DUCROCQ, S., 2001. New remains of primitive ruminants from Thailand: evidence of the early evolution of the Ruminantia in Asia. *Zool. Scripta*, **30**: 231-248.

MORALES, J., SORIA, D., SÁNCHEZ, I.M., QUIRALTE, V.

AND PICKFORD, M., 2003. Tragulidae from Arrisdrift, Basal Middle Miocene, Southern Namibia. *Mem. Geolog. Sur. 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. *Quat. Int.*, **192**: 6-13.

PICKFORD, M., 2001. Africa's smallest ruminant: A new tragulid from the Miocene of Kenya and the biostratigraphy of East African Tragulidae. *Geobios*, **34**: 437-447.

PICKFORD, M., 2002. Ruminants from the early Miocene of Napak, Uganda. *Annl. Paléontol.*, **88**: 85-113.

PICKFORD, M., SENUT, B. AND MOURER-CHAUVIRE, C., 2004. Early pliocene Tragulidae and peafowls in the Rift Valley, Kenya: Evidence for rainforest in East Africa. *C. R. Palevol*, **3**: 179-189.

PILBEAM, D., BARRY, J., MEYER, G. E., SHAH, S.M.I., PICKFORD, M.H.L., BISHOP, W.W., THOMAS H. AND JACOBS, L.L., 1977. Geology and palaeontology of Neogene strata of Pakistan. *Nature*, London, **270**: 684-689.

PILGRIM, G. E., 1915. The dentition of the tragulid genus *Dorcabune*. *Rec. geolog. Surv. India*, **45**: 226-238.

QUIRALTE, V., SÁNCHEZ, I.M., MORALES, J. AND PICKFORD, M., 2008. Tragulidae (Artiodactyla, Ruminantia) from the lower Miocene of the Sperrgebiet, Southern Namibia. *Mem. geolog. Surv. Namibia*, **20**: 387-396.

RÖSSNER, G.E., 2007. Family Tragulidae. In: *The evolution of artiodactyls* (eds. D.R. Prothero and S.E. Foss). The Johns Hopkins University Press, Baltimore, pp. 213-220.

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

SANCHEZ, I.M., QUIRALTE, V., MORALES, J. AND PICKFORD, M., 2010. A new genus of tragulid ruminant from the early Miocene of Kenya. *Acta Palaeont. Pol.*, **55**: 177-187.

SCOTT, K.M. AND JANIS, C.M., 1993. Relationships of the Ruminantia (Artiodactyla) and an analysis of the characters used in ruminant taxonomy. In: *Mammal phylogeny: Placentals* (eds. F.S. Szalay, M.J. Novacek and M.C. McKenna), Springer Verlag, New York, pp. 282-302.

SOLOUNIAS, N., BARRY, J.C., BERNOR, R.L., LINDSAY, E.H. AND RAZA, S.M., 1995. The oldest Bovid from the Siwaliks, Pakistan. *J. Verteb. Paleontol.*, **15**: 806-814.

STUART, C. AND STUART, T., 1997. *Field guide to the larger mammals of Africa*. Cape Town, Struik Publishers, pp. 260.

TERAI, S., ENDO, H., RERKAMNUAYCHOKE, W., HONDO, E., AGUNGPRIYONO, S., KITAMURA, N., KUROHMARU, M., KIMURA, J., HAYASHI, Y., NISHIDA, T. AND YAMADA, J., 1998. An osteometrical study of the cranium and mandible of the mouse deer (Chevrotain), *Tragulus javanicus*. *J. Vet. Med. Sci.*, **60**: 1097-1105.

THOMAS, H., 1977. Un nouveau Bovidé dans les couches à Hominoidea du Nagri (Siwaliks moyens), Plateau du Potwar, Pakistan: *Elachistoceras khauristanensis* gen. et sp. nov. (Bovidae, Artiodactyla, Mammalia). *Bull. Soc. géologique de France*, **19**: 375-383.

THOMAS, H., 1984. Les bovidés anté-hipparions des Siwaliks inférieurs (Plateau du Potwar), Pakistan. *Mém. Soc. Géol.* de *France, Paris*, **145**:1-68.

THOMAS, H., GINSBURG, L., HINTONG, C. AND SUTEETHORN, V., 1990. A new tragulid, *Siamotragulus sanyathanai* n.g., n.sp. (Artiodactyla, Mammalia) from the Miocene of Thailand (Amphoe Pong, Phayao Province). *C.R. Acad. Sci., Paris, Ser, II*, **310**: 989-995.

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

WELCOMME, J.L., BENAMMI, M., CROCHET, J.Y., MARIVAUX, L., METAIS, G., ANTOINE, P.O. AND BALOCH, I.S., 2001. Himalayan Forelands: palaeontological evidence for Oligocene detrital deposits in the Bugti Hills (Balochistan, Pakistan). *Geol. Mag.*, **138**: 397-405.

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

WHITWORTH, T., 1958. Miocene ruminants of East Africa. Fossil mammals of Africa. *Bull. Brit. Mus. Nat. Hist.*, **15**: 1-50.

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