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Tragulidae (Artiodactyla, Ruminantia) from the Middle Miocene Chinji Formation of Pakistan

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Abstract: The fossil record of the Siwalik tragulids remains poorly documented. The study of the tragulid material from the Chinji Formation allows the identification of 3 species: *Dorcatherium minus*, *Dorcatherium majus* and *Dorcabune anthracotherioides*. The tragulid assemblage is quite rich and *Dorcatherium* is the predominant taxon in the Chinji Formation of Pakistan. The fossils from the Chinji Formation of the Chakwal district, northern Pakistan, may document the first appearance of the 3 tragulid species in the Lower Siwaliks. The selenodonty and palaeoecology of the Siwalik tragulids are also discussed.

Key Words: Vertebrates, Mammalia, *Dorcatherium*, *Dorcabune*, Siwaliks, Miocene

1. Introduction

Tragulidae is an ancient family of ungulates with a history dating back to the early Miocene, and it is considered to be the sister group of the remaining living Ruminantia (Groves & Grubb 1982; Groves & Meijaards 2005). As noted by many researchers, the Tragulidae are the most primitive representatives of the extant Ruminantia; they are less advanced than living pecorans in many of their morphological and physiological features (Dubost 1965; Kay 1987; Métais *et al.* 2001; Rössner 2007). Six species of tragulids survive today: *Tragulus* spp. in South-East Asia (Meijaard & Groves 2004), 3 or 4 in India and Sri Lanka (*Moschiola* spp.) (Groves & Meijaard 2005) and 1 in tropical Africa (*Hyemoschus aquaticus*) (Meijaard *et al.* 2010); they became extinct in Europe in the late Miocene. In Africa they first appeared in the Miocene and have lived there ever since (Gentry 1999; Pickford 2001, 2002; Sánchez *et al.* 2010). At present, they are restricted to some humid environments of the Old World tropical zone (Geraads 2010).

In Pakistan, tragulids are found in fossil assemblages dated at 18 Ma (Welcomme *et al.* 2001), although they reached their highest diversity during the deposition of the Chinji Formation of the Siwaliks at about 11.5 Myr (Barry *et al.* 1991 and literature therein). They appear to have been more species-rich during the Miocene than now, with, for example, at least 5 different tragulid species (*Dorcatherium minimus*, *Dt. nagrii*, *Dt. minus*, *Dt. majus* and *Dorcabune anthracotherioides*) coexisting in the Chinji Formation of the Lower Siwaliks (Pilgrim 1915; Colbert 1935; West 1980; Gaur 1992; Farooq *et al.* 2007a, 2007b, 2007c, 2007d, 2008; Khan & Akhtar 2011) and several other Miocene species in Africa and Europe (Pickford 2001, 2002; Rössner 2007, 2010; Sánchez *et al.* 2010). After 7 Myr ago, the tragulid family declined significantly in diversity in southern Asia (Barry *et al.* 1991), because of the evolution of more open vegetation types (Meijaard & Groves 2004). They are now virtually extinct in Pakistan.

We describe here the late middle Miocene tragulids from the outcrops exposed south of Chinji and Kanatti villages and west of Dhok Bun Amir Khatoon village, Chakwal, Punjab, Pakistan (Figure 1). The outcrops belong to the Chinji Formation of the Lower Siwalik subgroup and contain a diverse and abundant fauna (Table 1). The balanced mammal assemblage of the Formation indicates a late middle Miocene age (Raza 1983; Khan *et al.* 2008, 2009). The lithostratigraphy of the Formation was described in detail by Barry *et al.* (2002) and is characterised by bright red clay, interbedded with grey, soft sandstone (Badgley *et al.* 2005, 2008; Khan *et al.* 2009).

The material from the Chinji Formation has been described and figured, as the Siwalik tragulid species were first described on the basis of limited material. The scarce ascribed fossil material thus enlarges our knowledge of the species.

2. Materials and methods

The material was collected during fieldwork by palaeontologists of Government College University Faisalabad and University of the Punjab during the past 5

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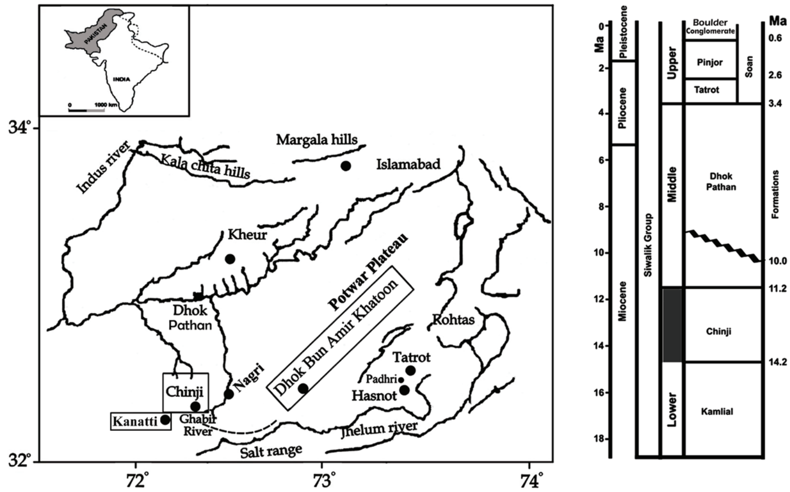

Figure 1. The location of Chinji, Kanatti and Dhok Bun Amir Khatoon in the Chakwal district, northern Pakistan, where the described material was collected, and the chronostratigraphic context of the Siwaliks Neogene-Quaternary deposits (data from Johnson *et al.* 1982; Hussain *et al.* 1992; Barry *et al.* 2002; Nanda 2002, 2008; Kumaravel *et al.* 2005; Dennell *et al.* 2006).

decades, and in most cases represents dentitions that were previously poorly known. The fossils represent at least 3 species belonging to 2 genera. Almost all fossil specimens were found weathering out from, or in situ within, the bright reddish clay and shale. Fossils were generally very well preserved. The material came from 3 localities (Figure 1), at which the fossils excavated were generally in excellent condition with little surface damage. Most specimens found on erosional surfaces were also well preserved, particularly those that had not been exposed for long, as on steep, actively eroding slopes.

The material is housed in the Zoology Department, University of the Punjab, Lahore, Pakistan and the Zoology Department of Government College University

Table 1. List of various species of the Chinji Formation in the Indo-Pakistan region (referred data are taken from Lydekker 1876, 1880, 1883a, 1883b, 1884; Pilgrim 1910, 1915, 1937, 1939; Colbert 1933, 1935; Raza 1983; Thomas 1984; Akhtar 1992; Badgley *et al.* 2008; Khan *et al.* 2008, 2009, 2010; Khan & Akhtar 2011).

Reptilia	Crocodylidae: *Crocodylus* sp.; Chelonidae: *Trionyx* sp.
Creodonta	Hyaenodontidae: *Dissopsalis carnifex*, *Dissopsalis rubber*
Carnivora	Canidae: *Amphicyon palaeindicus*, *A. pithecohilus*, *Vishnucyon chinjiensis*; Procyonidae: *Sivanasua palaeindica*; Mustelidae: *Martes lydekkeri*; Viverridae: *Viverra chinjiensis*
Proboscidea	Deinotheriidae: *Deinotherium pentapotamiae*, *D. indicum*; Gomphotheriidae: *Gomphotherium angustidens*, *G. macrognathus*, *G. chinjiensis*; *Tetralophodon falconeri*
Perissodactyla	Chalicotheriidae: *Nestoritherium (?) sindiense*, *Macrotherium salinum*; Rhinocerotidae: *Gaindatherium browni*, *Aceratherium perimense*, *A. blanfordi*, *Chilotherium intermedium*, *Brachypotherium fatehjangense*
Artiodactyla	Tayassuidae: *Pecarichoerus orientalis*; Suidae: *Palaeochoerus perimensis*, *Conohyus sindiense*, *C. chinjiensis*, *Listriodon pentapotamiae*; Anthracotheriidae: *Anthracotherium punjabiense*, *Hemimeryx blanfordi*, *H. pusillus*; Tragulidae: *Dorcabune anthracotherioides*, *Dorcatherium majus*, *D. minus*, *D. nagrii*, *D. minimus*; Giraffidae: *Giraffokeryx punjabiensis*, *Giraffa priscilla*; Bovidae: *Miotragocerus gluten*, *Kubanotragus sokolovi*, *Sivoreas eremita*, *Sivaceros gradiens*, *Caprotragoides potwaricus*, *Elachistoceras khauristanensis*, *Helicoportax tragelaphoides*, *H. praecox*, *Eotragus* sp., *Gazella* sp., *Palaeohypsodontus* sp.
Primates	*Sivapithecus sivalensis*, *S. indicus*, *Ramapithecus punjabicus*, *Dryopithecus punjabicus*, *D. pilgrimi*, *D. chinjiensis*
Rodentia	*Rhizomyoides punjabiensis*

Faisalabad, Pakistan. Each specimen is registered by the year and a serial catalogued number (e.g., 69/37). All measurements are expressed in millimetres. Uppercase letters are used for upper teeth and lowercase for lower teeth. The terminology and measurement of the teeth follow the methods of Gentry and Hooker (1988) and Gentry *et al.* (1999). Careful and extensive morphometric comparison led to the taxonomical identification of 3 tragulid species. The identified tragulid species are listed in systematic order with information on holotype, geographic distribution, type locality, stratigraphic range, diagnosis, description, comparison and discussion.

SYSTEMATIC PALAEONTOLOGY

Suborder RUMINANTIA Scopoli, 1777

Family TRAGULIDAE Milne-Edwards, 1864

Genus *Dorcatherium* Kaup, 1833

Type species. *Dorcatherium naui* Kaup, 1833

Distribution. *Dorcatherium* has been reported from the lower Miocene of Europe (Kaup 1833; Arambourg & Piveteau 1929; Rössner 2007, 2010; Hillenbrand *et al.* 2009), the Miocene of Africa (Arambourg 1933; Whitworth 1958; Hamilton 1973; Pickford 2002; Pickford *et al.* 2004; Quiralte *et al.* 2008; Geraads 2010; Sánchez *et al.* 2010) and the middle Miocene to early Pliocene of South Asia (Lydekker 1876; Colbert 1935; Prasad 1970; Sahni *et al.* 1980; West 1980; Farooq 2006; Farooq *et al.* 2007b, 2007c, 2008; Khan *et al.* 2011).

Dorcatherium minus Lydekker, 1876

Figure 2; Table 2

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

Type locality. Kushalgar near Attock, Punjab, Pakistan.

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

Diagnosis. A small species of the genus *Dorcatherium* with hypsodont, selenodont and broad crowned molars having well-developed cingulum, rugosity, styles, moderately developed ribs and vestigial ectostylids (Colbert 1935; Farooq 2006).

Studied specimens. PUPC 68/8 – right M2 (Dhok Bun Amir Khatoon), PUPC 69/31 – partial M2 (Dhok Bun Amir Khatoon), PUPC 69/259 – left M3 (Kanatti), PC-GCUF 10/92 – left dm (Chinji), PUPC 68/107 – right m1 (Chinji), PUPC 72/10 – left partial m2 (Chinji), PUPC 69/178 – right m1-2, PUPC 68/210 – left m3 (Chinji).

Description. The upper molars of *Dt. minus* are broader than long (Figure 2(1-3)). The molars are selenobunodont with high tubercles. The third molar PUPC 69/259 is the best preserved known molar of *Dt. minus* (Figure 2(3)). They have broad and high cusps with strongly developed mesostyle and labial ribs. The paracone has a strong labial rib, whereas the metacone has only a faint rib. The pre-protocrista is longer than the post-protocrista, which is isolated disto-lingually. The pre- and post-hypocristae are almost equal in length, although the pre-hypocrista is isolated mesio-lingually and the post-hypocrista is fused distally with the post-metacrista. The cingulum is present on the anterior and lingual aspects of the molars; it is especially well developed at the base of the protocone. There is no entostyle.

The partial lower deciduous molar with 2 complete lobes and 1 broken lobe has a thin layer of enamel (Figure 2(4)). Labial and lingual sides show growth stripes and enamel spurs produced by longitudinal undulated irregularities of the tooth surface. The lower molars are brachyodont with rugose enamel, distinctly selenodont protoconid and hypoconid, and cuspidate metaconid and entoconid (Figure 2(5-7)). The trigonid is slightly narrower than the talonid, and the metaconid and entoconid are somewhat transversely compressed. The pre-metacristid extends parallel to the long axis of the tooth and contacts a curved pre-protocristid just above the anterior cingulid, leaving a forward-facing anterior fossette. The post-metacristid is a swollen crest with a lingual concavity expressing a *Dorcatherium* fold. The post-protocristid displays a deep incisure on its posterior part, characteristic of a variable *Tragulus* fold. A weak ectostylid is present in some molars. The third lobe of m3 is compressed with a crested hypoconulid. The mesial cristid of the hypoconulid connects with the post-hypocristid distally. The mesio-lingual cristid of the hypoconulid forms the disto-lingual edge of m3 and is not connected to the post-entocristid, leaving the post-fossette open distally.

Comparison. The specimens are attributed to *Dorcatherium* based on their selenodont upper molars with strong cingulum, styles and labial ribs, and the presence of an M-structure (*Dorcatherium* fold) in lower molars. These features show striking affinity with the genus *Dorcatherium* of the family Tragulidae. *Dorcatherium* has bunoselenodont teeth and its numerous species mainly differ in their size (West 1980; Farooq *et al.* 2007b, 2007c, 2008; Iqbal *et al.* 2011). *Dorcatherium minus* is more brachyodont than *Dt. majus*. The studied specimens clearly overlap in size with the type material and earlier ascribed material of *Dt. minus* (Tables 2 and 3; Figure 5); the mandible fragment PUPC 69/178 bearing 2 molars could have been referred to a large species, because of the dentary large size. However, the spectrum of intraspecific size variability in *Dorcatherium* is large and enables sexual dimorphism in body size to be hypothesised. 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 *Dt. minus*.

Dorcatherium majus Lydekker, 1876

Figure 3; Table 3

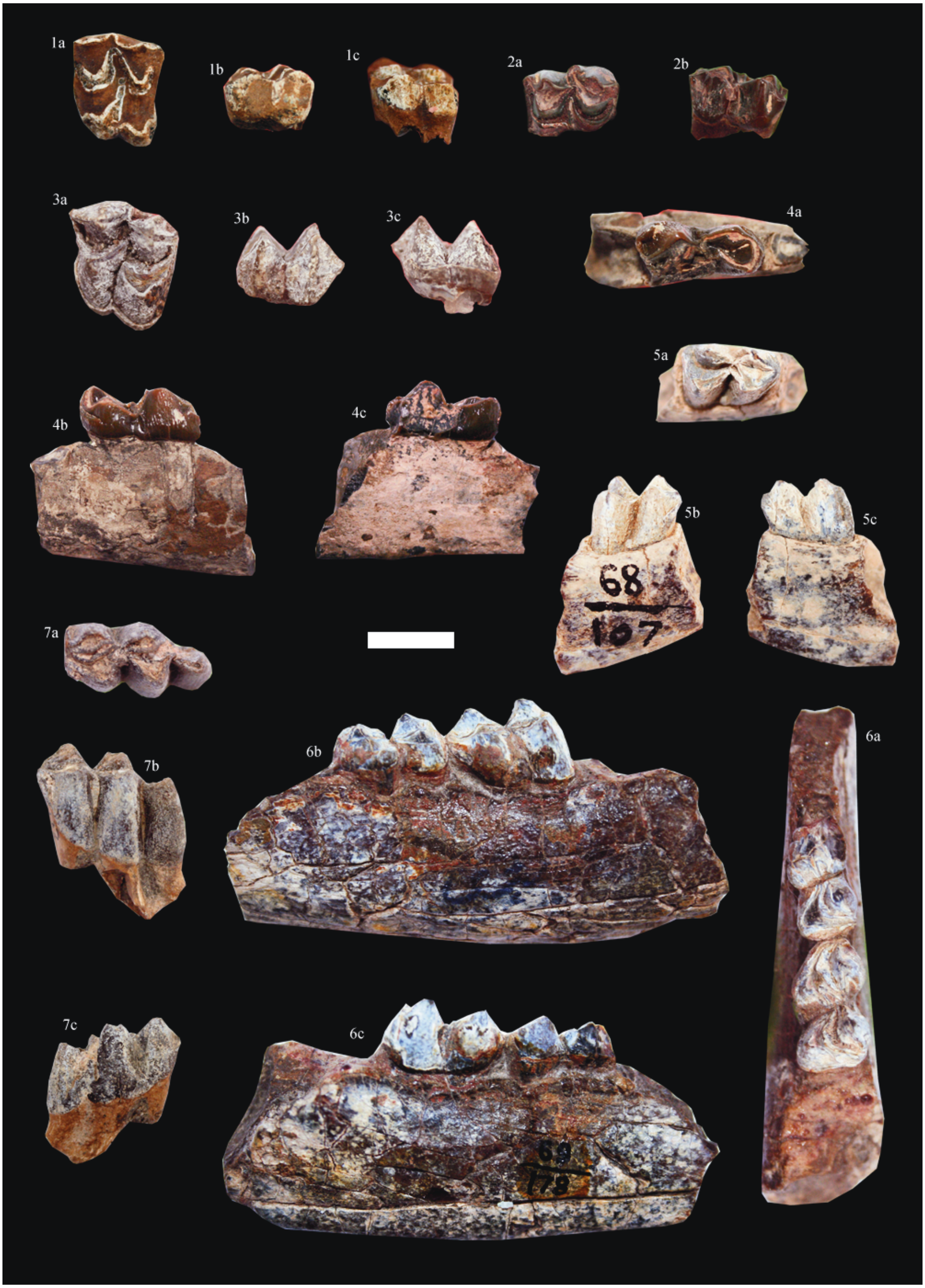

Figure 2. *Dorcatherium minus*: **1**, right M2, PUPC 68/8; **2**, ?M2, PUPC 69/31; **3**, left M3, PUPC 69/259; **4**, a left mandible fragment with partial deciduous molar, PC-GCUF 10/92; **5**, right m1, PUPC 68/107; **6**, a right mandible fragment with first and second molars, PUPC 69/178; **7**, left m3, PUPC 68/210. a = occlusal view, b = labial view, c = lingual view. Scale bar = 10 mm.

Table 2. Comparative measurements of the cheek teeth of the Siwalik small-sized *Dorcatherium* species in millimetres. *Studied specimens. Referred data are taken from Colbert (1935), Prasad (1970), West (1980), Vasishat *et al.* (1985), Farooq *et al.* (2007b) and Khan and Akhtar (2011).

Number	Description	Length	Width	W/L ratio
Dt. minus				
PUPC 68/8*	right M2	11.0	13.4 (1st lobe)	1.21
			12.6 (2nd lobe)	1.14
PUPC 69/31*	?M2	12.0	-	-
PUPC 69/259*	left M3	13.3	14.2 (1st lobe)	1.06
			14.0 (2nd lobe)	1.05
PUPC 68/107*	right m1	10.7	5.60 (1st lobe)	0.52
			6.50 (2nd lobe)	0.60
PUPC 69/178*	left m1	13.0	6.70 (1st lobe)	0.51
			7.00 (2nd lobe)	0.53
	left m2	13.6	8.00 (1st lobe)	0.58
			8.30 (2nd lobe)	0.61
PUPC 72/10*	left m2	11.2	7.00 (1st lobe)	0.62
			8.00 (2nd lobe)	0.71
PUPC 68/210*	left m3	18.0	8.00 (1st lobe)	0.44
			8.50 (2nd lobe)	0.47
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 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

Table 2. (continued).

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 18081	M3	7.10	7.00	0.98
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
PUA 89/76 RN	right m1	7.10	4.10	0.57
	right m2	8.30	4.90	0.59
	right m3	10.5	5.20	0.49
GSI K21.658	m1	7.00	4.00	0.57
	m2	7.50	4.50	0.60
GSI 18079	m1	6.50	3.60	0.55
	m2	6.60	4.00	0.60
	m3	10.0	4.50	0.45
GSI K21.744	m2	7.50	4.00	0.53
	m3	9.00	4.50	0.50
Dt. minimus				
H-GSP 1983	left M3	5.10	5.50	1.07
H-GSP 1983	right M3	4.80	5.10	1.06

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.* 2007c, 2008).

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

Studied specimens. PC-GCUF 10/93 – left M1 (Chinji), PUPC 69/60 – left M2 (Chinji), PC-GCUF 10/94 – left M2 (Chinji), PUPC 69/5 – right M2 (Kanatti), PUPC 69/268 – left M3 (Kanatti), PUPC 69/193 – right M3 (Kanatti), PUPC 69/189 – left m3 with broken hypoconulid (Chinji).

Description. Morphologically, the 6 specimens are typically tragulid, with the upper molars having strong labial styles and lingual cingulum, bunoselenodonty and the lower molar with a *Dorcatherium* fold (Rössner 2010). These are characterised by a very strong cingulum surrounding the protocone and the hypocone. The lingual cusps have a complete cingulum, which fades out on the labial face of the molar. Parastyle, mesostyle, and paracone ribs are very strong (Figure 3(1-6)). The post-paracrista and pre-metacrista are connected in a low position on the crown but are not directly attached to the mesostyle. There is a lingual cingulum at the base of the protocone and thick cingular shelves extending mesio-lingually and disto-lingually. The fossettes are deep and open in the transverse valley in the third molars. The lingual lobes are more crescent-shaped 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 in the third molars (Figure 3(5-6)). The post-hypocrista terminates in the midline of the crown at the distal cingulum.

The lower molar shows early wear, with irregular lingual wall and strong anterior cingulid (Figure 3(7)). The tiny ectostylid is present. The anterior lobe is wider than the posterior one in this molar. There are well-developed *Dorcatherium* and *Tragulus* folds on the post-metacristid and the post-protocristid, respectively. The post-metacristid extends distally to join a pre-entocristid, which also joins the post-protocristid in the midline. The hypoconid is more selenodont than the other cusps, with the pre-hypocristid ending in the midline of the crown, whilst the post-hypocristid extends across the midline to end behind the post-entocristid. The post-entocristid descends from the apex of the conid to the bottom of the valley that separates it from the post-hypocristid. This valley opens lingually. The broken hypoconulid looks small, is placed in the midline and is connected to the cingulum spur labially.

Comparison. Metrically the molars fall within the range of variation of the species *Dt. majus* from the Siwaliks (Colbert 1935; Farooq 2006; Farooq *et al.* 2007b, 2007c, 2008; Khan *et al.* 2010). They are appreciably larger than the material assigned to *Dt. minus*, *Dt. nagrii* and *Dt. minimus*, which are common at Chakwal during the late middle Miocene (Colbert 1935; West 1980; Farooq *et al.* 2007b, 2007c, 2008; Khan *et al.* 2010; Iqbal *et al.* 2011).

Dorcabune Pilgrim, 1910

Type species. *Dorcabune anthracotherioides* Pilgrim, 1910.

*Distribution***.** The genus is found in the Lower Manchar of Bhagothoro, Pakistan, Siwaliks, China and Greece (Pilgrim 1910, 1915; Colbert 1935; Han 1974; Made 1996; Farooq *et al.* 2007a, 2007d).

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 the lower molars are characterised by their broadness, a wide talonid in the third molar and a pyramidal protoconid with 2 posteriorly directed folds (Pilgrim 1910, 1915; Colbert 1935). In *Dorcatherium*, teeth are semiselenodonts and the parastyle is not an isolated pillar. Upper molars of *Dorcabune* are characterised 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 3 equally strong folds, the first 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 is attached to the pre-hypocristid, producing an M-structure. In *Dorcatherium* the lower molars show a special crest complex called the '*Dorcatherium* fold', formed by the bifurcation of the post-protocristid and the metaconid, resulting in an Σ-shape.

Dorcabune anthracotherioides Pilgrim, 1910

Figure 4; Table 4

1915 *Dorcabune hyaemoschoides* Pilgrim, p. 231, pl. XXI, fig. 6, pl. XXII, figs 2, 3.

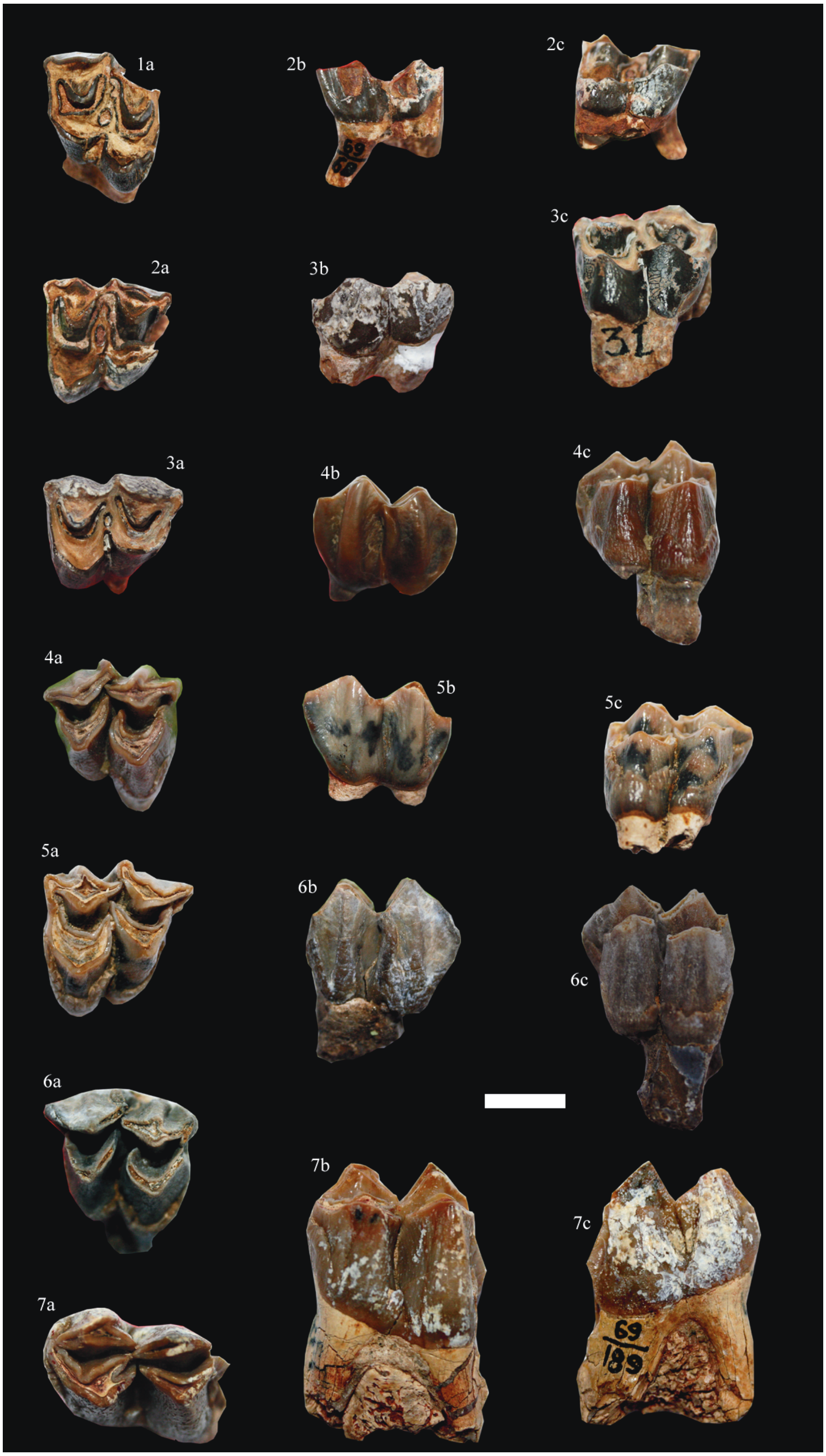

Figure 3. *Dorcatherium majus*: **1**, left M1, PC-GCUF 10/93; **2**, left M2, PUPC 69/60; **3**, left M2, PC-GCUF 10/94; **4**, right M2, PUPC 69/5; **5**, left M3, PUPC 69/268; **6**, right M3, PUPC 69/193; **7**, left m3, PUPC 69/189. a = occlusal view, b = labial view, c = lingual view. Scale bar = 10 mm.

Table 3. Comparative measurements of the cheek teeth of *Dorcatherium majus* in millimetres. *Studied specimens. Referred data are taken from Colbert (1935) and Farooq *et al.* (2007c, 2008).

Number	Description	Length	Width	W/L ratio
PC-GCUF 10/93*	left M1	15.0	15.4 (1st lobe)	1.02
			14.0 (2nd lobe)	0.93
PC-GCUF 10/94*	left M2	18.5	15.4 (1st lobe)	0.86
			13.6 (2nd lobe)	0.73
PUPC 69/60*	left M2	16.5	16.0 (1st lobe)	1.00
			14.0 (2nd lobe)	0.87
PUPC 69/5*	right M2	18.5	17.3 (1st lobe)	0.93
			14.0 (2nd lobe)	0.75
PUPC 69/268*	left M3	19.4	18.6 (1st lobe)	0.95
			17.0 (2nd lobe)	0.87
PUPC 69/193*	right M3	20.0	18.5 (1st lobe)	0.92
			17.4 (2nd lobe)	0.87
PUPC 69/189*	left m3	ca 24	11.3 (1st lobe)	0.47
			12.0 (2nd lobe)	0.50
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 B198	left M2	19.6	19.6	1.00
PUPC 67/191	left M3	13.6	15.2	1.11
PUPC 87/197	left M3	20.5	22.0	1.07
PUPC 87/328	right M3	19.1	18.2	0.95
AMNH 19354	M3	20.5	23.5	1.14
GSI B198	M3	20.1	19.2	0.95
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

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

Holotype. 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.* 2007d).

Diagnosis. *Dorcabune anthracotherioides* is a large-sized species of the genus, almost equal in size to *Dt. crassum* (see Rössner 2010). Upper molars are bunodont and have a prominent parastyle. The lower margin of the ramus is deep. The mandible bears a fairly deep groove starting beneath p4 and propagating towards the posterior side behind the teeth. This groove exists in *Dt. majus* and *Dt. minus* but is absent from *Db. nagrii*. p4 is slightly shorter than p3. p4 is broad with 3 lobes, of which the middle lobe is the highest, whereas the first and the last lobes are equal in length (Pilgrim 1910, 1915). The other valid species, *Db. Nagrii*, is smaller than *Db. anthracotherioides* (Farooq *et al.* 2007a).

Studied specimens. PUPC 68/444 – left m1 (Chinji), PC-GCUF 10/95 – left partial m3 (Chinji).

*Description***.** The lower molars have very bunodont conids with a heavy mesio-distal cingulid and rugose enamel (Figure 4). The distal cingulid is thick medially and becomes thinner labially in the first molar. The anterior fossette is open, due to a forward orientation of the pre-protocristid, and the post-protocristid is oblique. The metaconid and the entoconid are pyramidal. The protoconid and the metaconid display a weak *Tragulus* fold and a deep incisure distally (M-structure), respectively. The trigonid and talonid are lingually open, with a trigonid more tapered than the talonid. The talonid is broader than the trigonid.

The post-metacristid and the post-protocristid join to form a deep V that connects with the pre-entocristid in m1 (Figure 4(1)). In m1, the entoconid is anterior to the hypoconid and its posterior side is rounded (without cristid). There is a marked entoconidian groove mesially, of which the labial flank is formed by the longitudinal pre-entocristid that connects the post-metacristid–post-protocristid contact. The lingual flank of the entoconidian groove is formed by a *Zhailimeryx* fold (Guo *et al.* 2000), leaving the mesial extremity of the groove open lingually (Figure 4(1)). The post-hypocristid extends transversely in m3, but it does not reach the posterior and rounded side of the entoconid on m1. In m3 the entoconid is well rounded on its posterior part, without a post-entocristid, and the anterior part of the entoconid is tapered, with a relatively striking pre-entocristid that joins the post-metacristid and forms a keel (Figure 4(2)).

Comparison. The molars display a bunoselenodonty pattern. This kind of tooth pattern is represented by the tragulid genus *Dorcabune* (Colbert 1935; Farooq *et al.* 2007b, 2007c). In the Siwaliks, 2 tragulid genera occur: *Dorcabune* and *Dorcatherium*. *Dorcabune* reflects a bunoselenodonty (Figure 4) pattern and *Dorcatherium* is selenodonty (Figures 2 and 3). The bunodont conical cusp pattern of the studied samples with an M-structure confirms its inclusion in *Dorcabune* (Métais & Vislobokova 2007). The m3 molar has the same size as the already recovered sample of *D. anthracotherioides* (Pilgrim 1915; Colbert 1935; Farooq *et al.* 2007a, 2007d; Khan *et al.* 2010) and is comparable with the holotype and the previously described specimens (Figure 5; Table 4). The m1 is a new find, representing all the characteristics of this species. Therefore, the molars are assigned to *Db. anthracotherioides*.

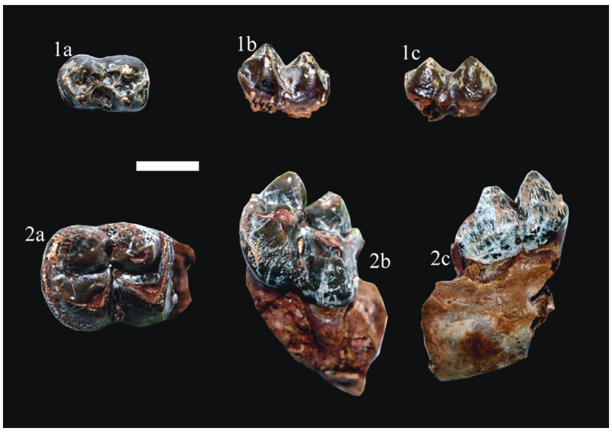

Figure 4. *Dorcabune anthracotherioides*: **1**, left m1, PUPC 68/444; **2**, partial left m3, PC-GCUF 10/95. a = occlusal view, b = labial view, c = lingual view. Scale bar = 10 mm.

3. Discussion

3.1. Selenodonty and hypsodonty

The Siwalik tragulids in the Chinji Formation appear to have 2 radiations; apparently an advanced selenodont form (*Dorcatherium*) existed alongside a primitive endemic bunoselenodont form (*Dorcabune*), which remained more or less isolated since its early Miocene first appearance (Ginsburg *et al.* 2001). The fossil record indicates that the species diversity of the Tragulidae increased in the late middle Miocene of the Chinji Formation (West 1980; Farooq *et al.* 2007a, 2007b, 2007c, 2007d, 2008; Khan & Akhtar 2011), as in Eurasia (Rössner 2010) and in Africa (Pickford 2001, 2002; Geraads 2010). Specifically, the lower molars of *Dorcatherium* show a variable amount of selenodonty (i.e. extension of the cristids, as in *Dt. majus*) but do not show the characters of fully selenodont forms, as in Pecora. The general lower molar plan of *Dorcatherium* persists in all the Siwalik species through a wide range of body sizes, from large species (*Dt. majus*, *Dt. minus*) to small species (*Dt. minimus*, *Dt. nagrii*), although the Σ-structure is better developed in *Dt. nagrii* (Khan & Akhtar 2011).

The conids are clearly bunoid in *Dorcabune*, displaying an M-structure with deep incisures on the trigonid distally. The function of the M-structure is not still clear, but it may increase chewing efficiency (Métais *et al.* 2001). *Dorcabune* is a more primitive Asian genus than *Dorcatherium* (Ginsburg *et al.* 2001; Sánchez *et al.* 2010). *Dorcatherium* is considered the "African" branch of Tragulidae, since it is first recorded in the African early Miocene (Whitworth 1958; Pickford 2001, 2002; Quiralte *et al.* 2008), whereas *Dorcabune* is considered the "Asian" branch, first recorded in Asia almost coevally in the early Miocene (Ginsburg *et al.* 2001; Khan *et al.* 2010) and restricted to the Siwaliks (Pilgrim 1915; Colbert 1935; Métais *et al.* 2001; Geraads *et al.* 2005; Farooq *et al.* 2007a, 2007d), China (Han 1974) and Greece (Made 1996).

Table 4. Comparative measurements of the cheek teeth of *Dorcabune* in millimetres. *Studied specimens. Referred data are taken from Colbert (1935) and Farooq *et al.* (2007a, 2007d).

Number	Description	Length	Width	W/L ratio
Db. anthracotherioides				
PUPC 68/444*	left m1	15.4	9.00 (1st lobe)	0.58
			9.40 (2nd lobe)	0.61
PC-GCUF 10/95*	left m3	ca 28.4	14.0 (1st lobe)	0.49
			14.7 (2nd lobe)	0.51
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

Dorcabune is generally larger and more bunodont and brachyodont than *Dorcatherium* (Métais *et al.* 2007). *Dorcatherium* shows a tendency to develop high crowned cheek teeth. The hypsodonty trend expressed by the dental morphology of *Dorcatherium* may indicate a fibrous diet based on abrasive food in more or less closed and humid habitats (e.g., Köhler 1993; Eronen & Rössner 2007). As noted by earlier researchers, there are many other factors favouring hypsodonty, such as increasing aridity and openness of the landscape (Fortelius, 1985; Janis, 1988; Janis & Fortelius, 1988; Fortelius & Solounias, 2000). Overall, the hypsodonty trend in *Dorcatherium* reflects water stress and tends to reinforce the idea of mixed feeders in the Chinji Formation.

3.2. Palaeoecology

The living chevrotain (Dubost 1978; Meijaard *et al.* 2010) prefers rain forest with dense shelter, which provides shade and safety from predators. It feeds on fruits and leaves and lives on dry ground, entering water only for refuge (Dubost 1978). The extant chevrotain genera have a population density of about 10 individuals per square kilometre. The abundance of fossils found in the late middle Miocene and the late Miocene of the Siwaliks indicates dense pockets of rain forest. The tragulids are absent in the open environment of the Upper Siwaliks, northern Pakistan (Farooq 2006; Khan *et al.* 2011). Their complete disappearance in the Upper Siwaliks is certainly linked with the expansion of grasslands and this seems to be the main reason why they are not found in the Upper Siwaliks of northern Pakistan.

There is increasing evidence for inferring the palaeoenvironment in which *Dorcatherium* and *Dorcabune* lived. The tragulid-associated fauna would rather indicate a lush vegetation with substantial food supply for the diversified, mostly brachyodont large mammal fauna (Table 1). The vertebrate remains (Table 1) suggest a lightly forested environment with the existence of numerous wetlands near which the tragulids might have lived (Khan & Akhtar 2011). The fauna (Table 1) associated with the tragulids suggests a mosaic of both more open and forested landscapes with a vast wetland environment strongly influenced by alternating dry and flood seasons.

4. Conclusions

Tragulids are very common at Chinji, Kannati and Dhok Bun Amir Khatoon villages, northern Pakistan, and there is evidence for at least 5 tragulid species (West 1980; Farooq *et al.* 2007a, 2007b, 2007c, 2007d, 2008; Khan & Akhtar 2011; literature therein). *Dorcabune* is represented by 1 species, *Db. Anthracotherioides*, from the Chinji Formation and by 2 species, *Db. anthracotherioides* and *Db. Nagrii*, from the Nagri and Dhok Pathan formations (Farooq *et al.* 2007a, 2007d). *Dorcatherium* is represented by 4 species, *Dt. minimus*, *Dt. nagrii*, *Dt. minus* and *Dt. majus*, in the late middle Miocene of the Chinji Formation. It is also present in the late Miocene of the Nagri Formation and the late Miocene–early Pliocene of the Dhok Pathan Formation of the Siwaliks. The tragulids are absent from the Soan Formation of the Siwaliks.

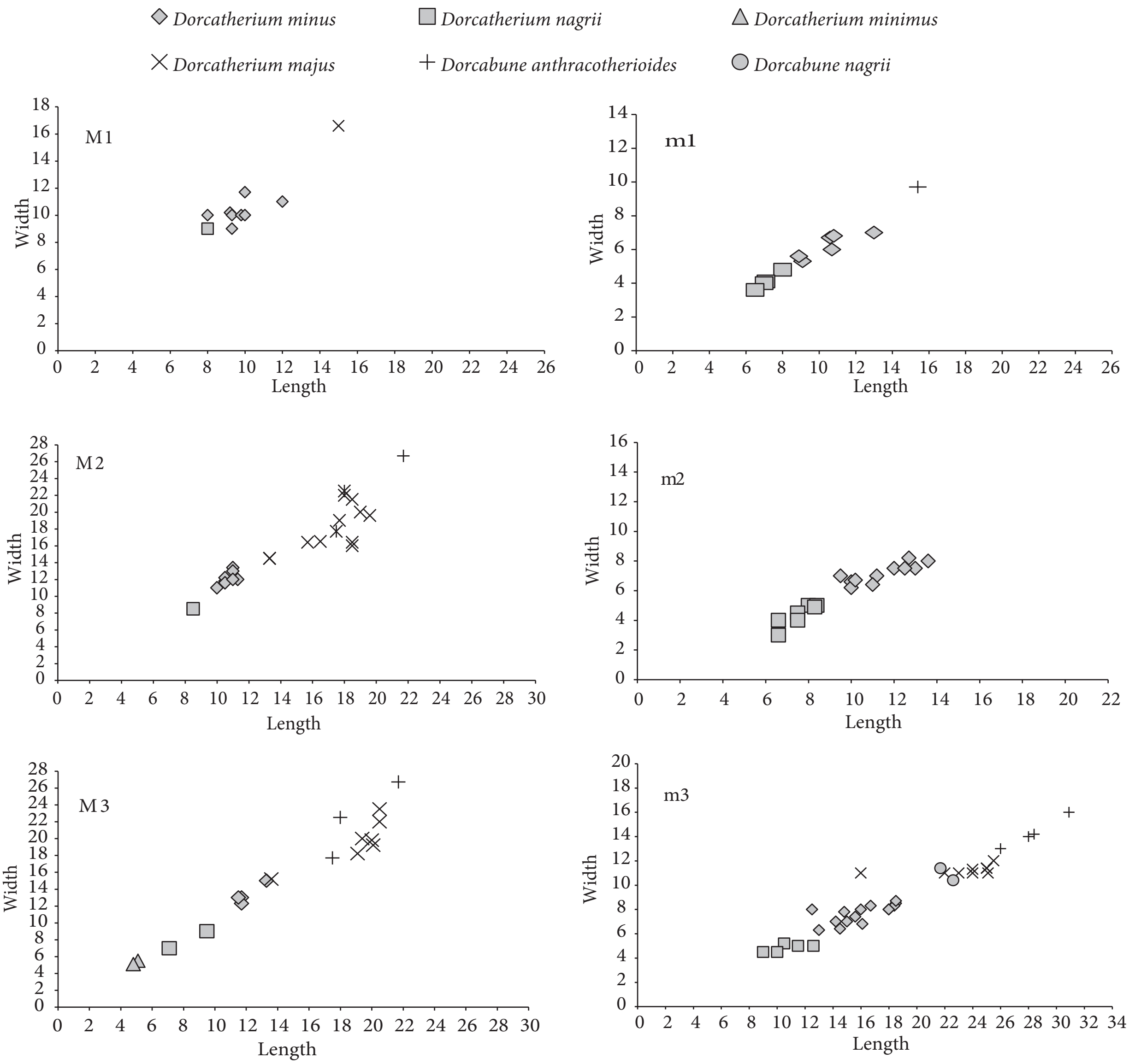

Figure 5. Size variation in the described species of Chinji tragulids.

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