Pakistan J. Zool., vol. 44 (3), pp. 799-808, 2012.

Hydaspitherium (Artiodactyla: Giraffidae) from the Dhok Pathan Formation of the Middle Siwaliks, Pakistan: New Collection

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Abstract.– A few dental remains from the late Miocene localities of the Dhok Pathan Formation have been identified as belonging to *Hydaspitherium* cf. *megacephalum*. The collection comprises an upper premolar, several upper molars, part of a maxilla and part of a mandible. The analysis of the dental characters shows individual variations and contributes to the knowledge of the Siwalik late Miocene giraffids. The systematic status of the Siwalik species of *Hydaspitherium* has been reviewed.

Key Words: Siwalik giraffids, *Hydaspitherium*, late Miocene, Dhok Pathan Formation, Mammalia.

INTRODUCTION

The Late Miocene Siwalik giraffids, despite their richness, are still rather poorly known and their systematics outdated, with unreliable identifications (Matthew, 1929; Gentry, 1997; Geraads and Gulec, 1999). They are mainly represented in the Siwaliks by the large-sized Sivatheriinae namely, *Bramatherium*, *Hydaspitherium*, *Helladotherium*, and *Sivatherium* (Matthew, 1929; Colbert, 1935; Gentry, 1997; Geraads and Gulec, 1999; Bhatti, 2005; Kostopoulos and Sarac, 2005). Recently, a few well preserved large giraffid specimens were collected from the village Dhok Pathan (Lat. 33°07'N: Long. 72°14'E) and the village Hasnot (Lat. 32°49′N: Long. 73°18′E) of the Dhok Pathan Formation, the Middle Siwaliks, Pakistan (Fig. 1). The giraffid sample yields a set of characters, morphologically similar to the late Miocene Siwalik giraffid, *Hydaspitherium* (Matthew, 1929; Colbert, 1935; Khan, 2007). The comparison of the specimens with the known species of *Hydaspitherium* has shown clearly that the specimens belong to species *Hydaspitherium* cf. *megacephalum*. The giraffid *Hydaspitherium megacephalum* is restricted to the Dhok Pathan Formation of the Middle Siwalik Subgroub in the northern Pakistan (Sehgal and Nanda, 2002; Barry *et al*., 2002; Badgley *et al*., 2005). The detailed stratigraphy and biochronolgy of the sites are given in Barry *et al*. (2002) and Khan *et al*. (2009).

The recovered giraffid material is associated with remains of *Tragoportax punjabicus*, *T. salmontanus*, *Selenoportax vexillarius*, *Pachyportax latidens*, *Gazella lydekkeri*, *Kobus porrecticornis*, *Caprotragoides potwaricus*, *Dorcatherium majus*, *Dorcabune anthracotherioides*, *Propotamochoerus hysudricus*, *Hippopotamodon sivalensis*, *Sivalhippus theobaldi*, *Sivalhippus perimense*, *Hipparion* sp., *Aceratherium perimense*, *Chilotherium intermedium*, *Stegolophodon latidens* and *Crocuta carnifex* (Pilgrim, 1937, 1939; Heissig, 1972; Bernor and Hussain, 1985; Akhtar, 1992; Bibi, 2007; Khan *et al*., 2009). The assemblage fits well with the Siwalik late Miocene fauna, indicating a late Miocene age (Barry *et al*., 2002; Khan *et al*., 2009). Four biostratigraphic interval-zones are proposed in the Potwar Plateau of the northern Pakistan in which the biostratigraphic studies are clubbed with magnetostratigraphic ages (Barry *et al*., 1982). These zones are *Hipparion* sl. Interval-Zone; *Selenoportax lydekkeri* Interval-Zone; *Hexaprotodon sivalensis* Interval-Zone and *Elephas planifrons* Interval-Zone. It is noticed that *Hydaspitherium megacephalum* occurs in the *Selenoportax lydekkeri* Interval-Zone (7.4 to 5.3 Ma) of the Middle Siwalik Subgroup (Barry *et al*., 1982).

The primary goal of this paper is to present a new collection of *Hydaspitherium* from Dhok Pathan and Hasnot in the northern Pakistan (Fig. 1). The unpublished collection could greatly improve our knowledge of the Late Miocene giraffid, *Hydaspitherium*. Geraads and Güleç (1999) suggest

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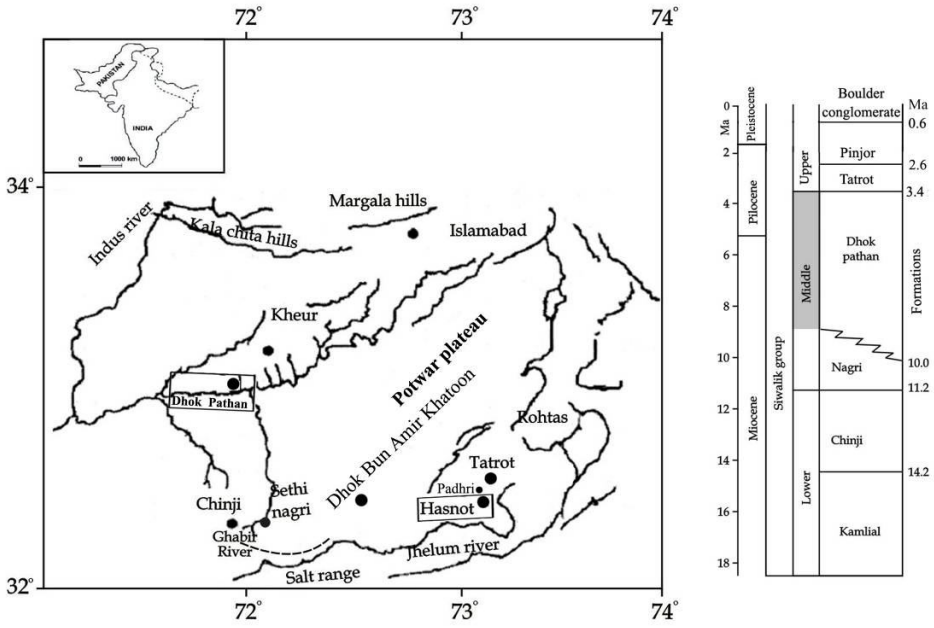

Fig. 1. The location of Dhok Pathan and Hasnot in the northern Pakistan where the described material has been found. Boundary dates are from Barry *et al.* (2002) and Nanda (2002, 2008).

a provisional synonymy of *Hydaspitherium* Lydekker, 1876 with *Bramatherium* Falconer, 1845 in the Greco-Iranian province. Although quite possible, this synonymy is not yet formally founded and, following Matthew (1929) and Colbert (1935), we shall continue to use *Hydaspitherium* as a valid taxon in the Siwaliks.

Almost all specimens were found weathering out from or in situ within the matrix. Some specimens were exposed on surface and but some are entrenched partially. Piercing instruments (Chisels and Geological hammers) were used for mining of partially entrenched fossils. The specimens were catalogued and given a number which consists of a yearly and a serial catalogue number, so figures on the specimen represent the collection year and the serial number of that year (e.g. 67/155). Uppercase letters with superscript stand for upper dentition (*e.g.* M^1) and with subscript number stand for lower dentition (*e.g.* M_1). Various measurements of the studied specimens in millimeters were taken with the help of a metric vernier caliper. Tooth length and width were measured at occlusal level. Heights were measured on the mesostyle of the upper molar, the metastylid of the lower molar and the protoconid of the lower premolar. All the described fossils are housed in the Palaeontological Collection of the Punjab University, Lahore, Punjab, Pakistan (PUPC-institutional abbreviation).

*Abbreviations***:** PUPC, Punjab University Paleontological Collection; AMNH, American Museum of Natural History; Ma, million years; MN, European Neogene Mammalian Zone; d, deciduous; M, molar; P, premolar; L, largest length; W, width; H, height; l, left; r, right.

SYSTEMATIC PALAEONTOLOGY

Order Artiodactyla Owen, 1848
Suborder Ruminantia Scopoli, 1777
Family Giraffidae Gray, 1821
Subfamily Sivatheriinae Zittel, 1893

Genus *HYDASPITHERIUM* Lydekker, 1876

Type species

Hydaspitherium megacephalum Lydekker, 1876.

Abbreviated generic diagnosis

Teeth large, quadrate, with rugose enamel. Lower teeth broader and somewhat longer. The parastyle of *Hydaspitherium megacephalum* is stronger than the mesostyle and the metastyle. The anterior fossette is transversely compressed (Matthew, 1929; Colbert, 1935; Bhatti, 2005).

Stratigraphic range

Middle Siwaliks (Colbert, 1935; Sehgal and Nanda, 2002; Bhatti, 2005; Khan, 2007).

Geographic distribution

South Asia (Subcontinent). The occurrence of the genus is recorded from the various localities of the Potwar Plateau (Middle Siwaliks) of Pakistan, Dhok Pathan, Hasnot as well as from Azad Kashmir, Bhimber (Lydekker, 1876; Pilgrim, 1910; Bhatti, 2005; Khan, 2007). It is reported from the late Miocene and Pliocene sediments of India (Matthew, 1929; Colbert, 1935; Sehgal and Nanda, 2002).

Hydaspitherium cf. *megacephalum* Lydekker, 1876

Type specimen

A skull: GSI D150.

Abbreviated diagnosis

The parastyle of *Hydaspitherium megacephalum* is prominent as compared to the mesostyle and the metastyle. The anterior median rib is moderately developed, whereas the posterior median rib is weakly developed. The enamel is rugose. The stylids are present and the anterior fossette is transversely compressed. *Hydaspitherium megacephalum* generally is smaller than those of *H. grande* and *H. magnum* (Colbert, 1935; Khan, 2007).

Studied material

Upper dentition: PUPC 97/20, rP^4 (Dhok Pathan); PUPC 91/23, rM^1 (Hasnot); PUPC 67/155, lM^2 (Dhok Pathan); PUPC 97/16, right maxillary fragment with M^{1-2} (Dhok Pathan). Lower dentition: PUPC 95/24, ldM (Dhok Pathan); PUPC 97/17, right mandibular fragment with partially P_{3-4} and complete M_{1-3} (Dhok Pathan).

Source of the comparative material

Matthew (1929), Colbert (1935), Bhatti (2005).

DESCRIPTION

Upper dentition

The upper dentition comprises one premolar, two isolated molars and one maxillary fragment with first and second molars (Fig. 2). The molars are moderately hypsodont and they have simple occlusal pattern.

P^4: PUPC 97/20 is partially preserved and in an early wear (Fig. 2A). The premolar is greater in length than in width, and the tooth is characterized by a strong parastyle, and an internal posterior swelling (Fig. 2A). The tooth is damaged on the labial side. The three rooted premolar have thick and rugose enamel. The cingulum is not developed. The fossette is well developed. The internal side of the buccal crescent is weakly divided into paracone and metacone. The premolars look subquadrangular with an antero-lingual protuberance of the lingual wall (Fig. 2A).

M^1: PUPC 91/23 is in an early wear (Fig. 2B, D). The enamel surface is highly rugose. The cingulum is poorly developed. It is slightly developed on the anterior side of the protocone. The entostyle is weak, placing in the transverse valley between the protocone and the hypocone. The major cusps are well developed. The buccal cusps are higher than the lingual ones. The protocone is crescentic in shape, but it is less crescentic than the hypocone. The prae-and postprotocrista run parallel to the longitudinal axis of the molar. The paracone is pointed in the middle with the two cristae sloping antero-posteriorly. The postparacrista is broader than the praeparacrista, which is somewhat narrow. The praeparacrista is united with the parastyle whereas the postparacrista is touching with the praehypocrista. The metacone is slightly higher vertically than the paracone. It is pointed in the middle with two sharp running prae-and postmetacristae. The hypocone is present posterior to the protocone. The praehypocrista contacts with the postparacrista and the posthypocrista contacts with the metastyle. The styles are strongly developed. The mesostyle present at the anterior

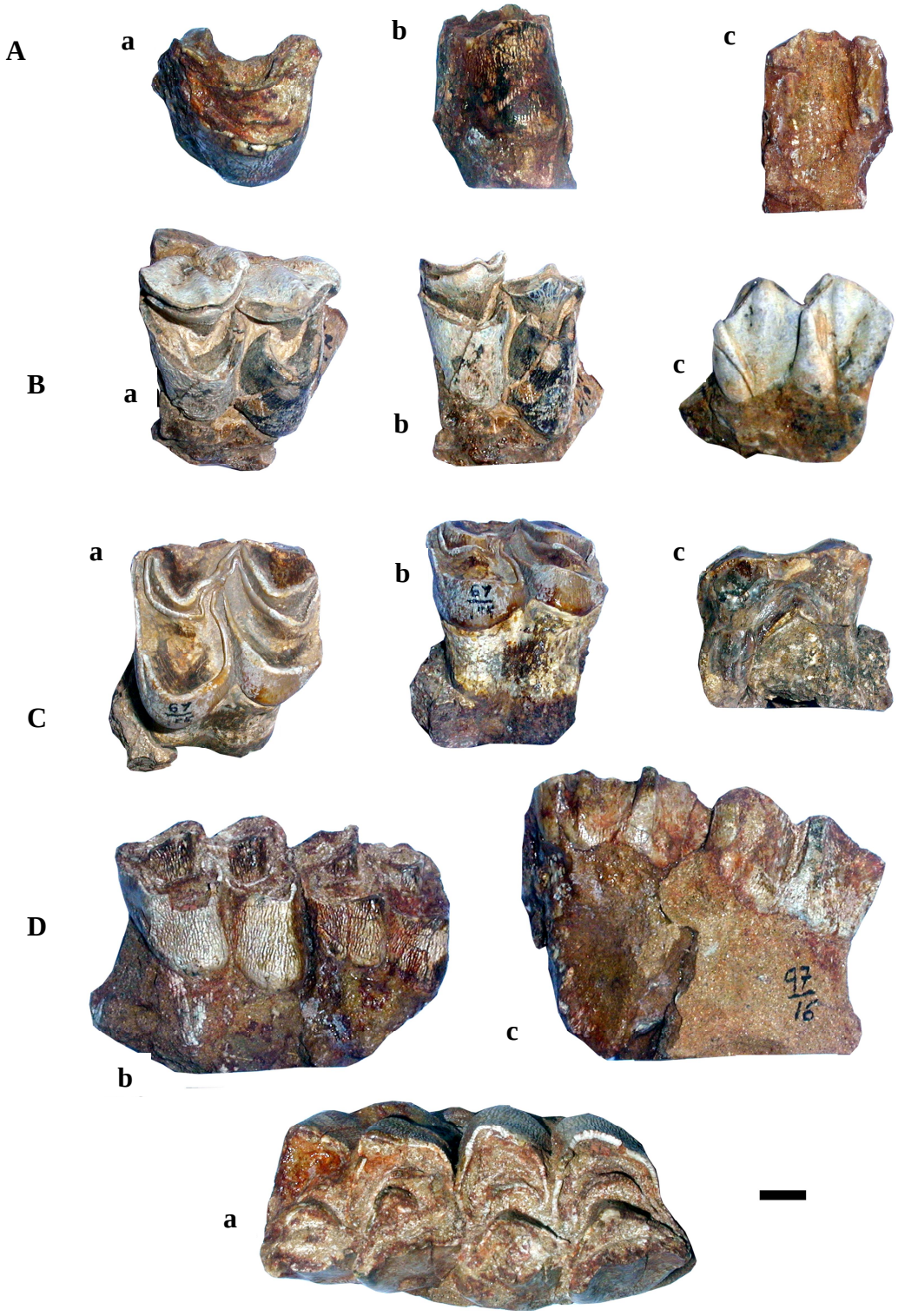

Fig. 2. *Hydaspitherium* cf. *megacephalum*, upper dentition. A, PUPC 97/20 – rP^4; B, PUPC 91/23 – rM^1; C, PUPC 67/155 – lM^2; D, PUPC 97/16, right maxillary fragment with M^{1-2}. Views are occlusal (a) lingual (b) and labial (c). Scale bar equals 10 mm.

side of the metaconal lobe is nearly as high as the parastyle but it is comparatively weak and inflected. The metastyle is weaker than the parastyle and the mesostyle. The median ribs are fairly developed. The anterior rib is stronger than the posterior one. The anterior rib is broad at the tip and narrow at the base (Fig. 2B, D).

M^2: The molars are nearly quadrate and rugose (Fig. 2C-D). The cingulum is poorly developed on the anterior side of the protocone as well as on the posterior side of the hypocone. The fossettes seem to be wide and crescent. The para- and metacones are higher vertically than the proto- and hypocones. The paracone median rib is stronger than the metacone median rib. The styles are well preserved and prominent. The parastyle is comparatively broad and heavily build. The paracone is higher than all the other cones. The protocone is more pointed than the hypocone. Between the para and metacones the enamel is much folded producing a strongly developed mesostyle. The metacone is oblique anteroposteriorly whereas the paracone is straight than being oblique. The hypocone is connected with the metacone through a narrow ridge posteriorly (Fig. 2C-D).

Lower dentition

The lower dentition includes one deciduous molar and a mandibular fragment with two premolars and complete series of molars (Fig. 3).

dM: The deciduous molar consists of three lobes of almost similar shape but they have variation in width and length (Fig. 3E). The anterior lobe is much longer than the posterior one, a primitive character found in all Sivatheriinae (Geraads and Aslan, 2003). The crown height is moderate. The labial halves of the three lobes are crescent, whereas the lingual halves are spindle-shaped. The anterior most part of the crown is relatively more worn. The enamel is moderately thick and rugose. The deciduous molar is crescentic-shaped with widely divergent arms labially. The lingual part of the anterior most part is strongly A-shaped with two anterior and posterior cristae. The median part of the tooth is quite similar except that the posterior end of its lingual part is produced into a well formed style. The posterior lobe of the crown is least worn. The posterior crista of the labial half bears a deep vertical groove. There are small entostyles on the tooth (Fig. 3E).

Mandible: PUPC 97/17 is a fragile mandibular fragment broken anteriorly and posteriorly (Fig. 3F). Posteriorly, the mandible is broken posterior to the talonid of the third molar and it is broken anterior to the third premolar anteriorly. The premolars are semierupted and there morphological features are visible only on the lingual and on the occlusal sides. The P_3 is more erupted than the P_4. The semierupted P_4 can be observed lingually in the mandibular ramus.

P_3: The paraconid is well separated from the parastylid but they are closed lingually (Fig. 3F). The metaconid extends forwards, meeting the base of the paraconid and the crest joining the protoconid to the metaconid oblique backwards. The elongated metaconid is independent from the endoconid. The talonid is comparatively shortened. The reduced endostylid is obliquely settled. Labially, a well developed furrow separates the bulgy hypoconid from the strong protoconid.

P_4: It is molariform (Fig. 3F). Its metaconid is long and the parastylid thinner than in P_3. The crest joins to the metaconid and incorporates the entoconid. The entoconid is independent from the metaconid. A well developed furrow separates the hypoconid from the strong protoconid on the buccal side. The enamel is thick and rugose. The entoconid is well distinct and oblique.

M_1: The molar is in middle wear. The major conids are interconnected with each other at the grinding surface due to the middle wear (Fig. 3F). The ectostylid is weakly developed. The longitudinal valleys are not much deep. The valley between the anterior cones is shallower than the posterior cones. The cristids of the protoconid are quite simple. The metaconid is fairly developed. It is spindle-shaped. It is slightly wider in the middle with two narrow sloping cristids. The entoconid is relatively lower vertically than the metaconid. The hypoconid is V-shaped. The mesostylid is well developed as compared to the meta- and entostylids. The metaconid rib is moderately developed and the entoconid rib is weakly developed.

M_2: The second molar is moderately high. The length of the tooth is more than the transverse width (Table I). The cingulum is present. The

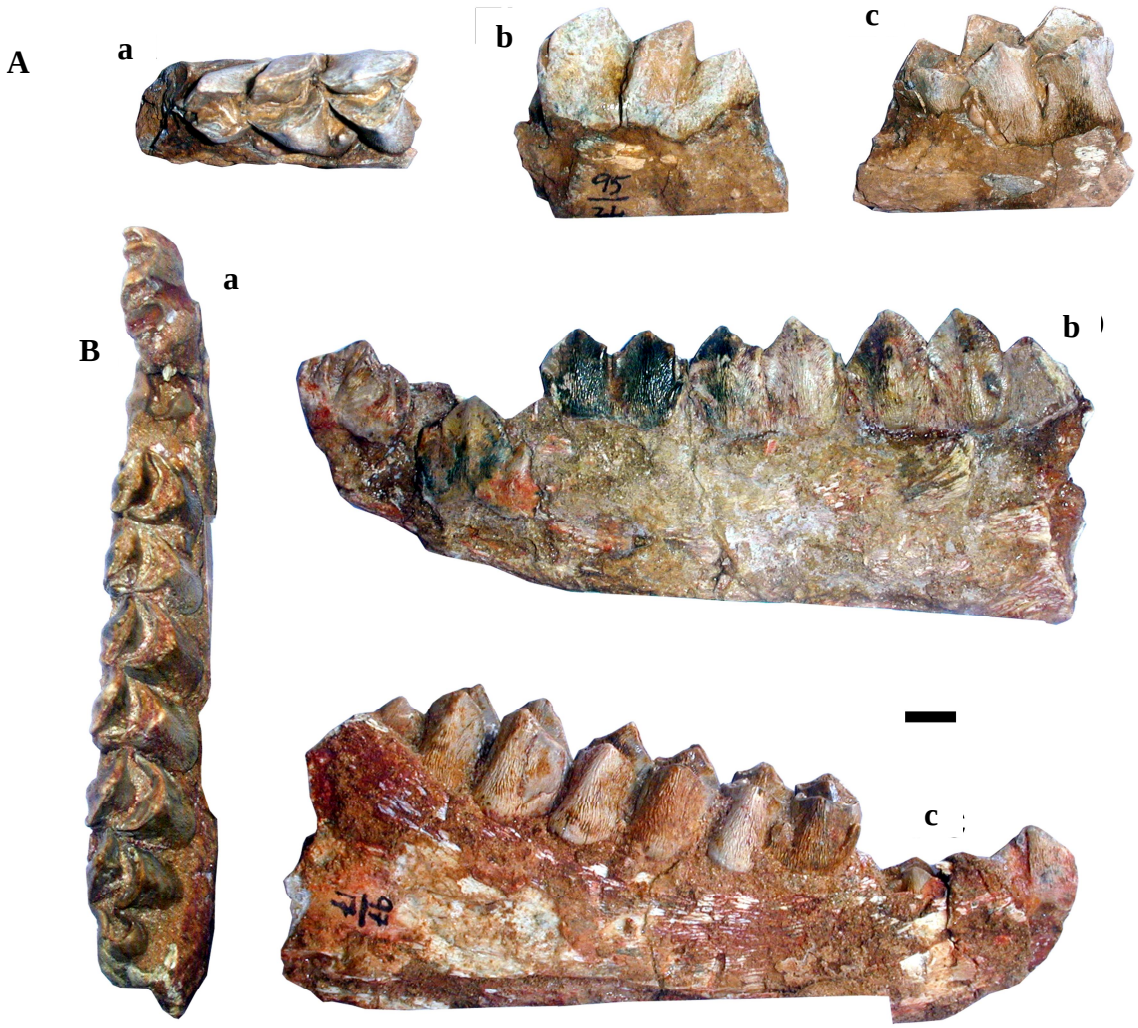

Fig. 3. *Hydaspitherium* cf. *megacephalum*, lower dentition. A, PUPC 95/24 – ldM, B, PUPC 97/17, right mandibular fragment with partially P_{3-4} and complete M_{1-3}. Views are occlusal (a), lingual (b) and labial (c). Scale bar equals 10 mm.

postmetacristid is overlapping with praentocristid. The entoconid is well developed and spindle-shaped. It is pointed in the middle with two sloping cristids. The hypoconid is perfectly V-shaped. The mesostylid is well developed as compared to the meta- and entostylids (Fig. 3F).

M_3: The third molar well preserved with the hypoconulid (Fig. 3F). The cingulum is well developed on the anterior side of the tooth. The protoconid is well developed and V-shaped. The apex of the 'V' is broad at the base becoming pointed and narrower towards the distal end due to the middle stage of wear. The praeprotocristid is narrower than the postprotocristid. The valley enclosed by the posterior conids is compressed transversely. The praehypocristid and the posthypocristid are simple. The comparative measurements are provided in Table I.

COMPARISON

Being squared and tetra tuberculated teeth, it

Table I.- Comparative measurements of the cheek teeth of the Siwalik *Hydaspitherium*. *The studied specimens. Referred data are taken from Matthew (1929) and Colbert (1935).

Taxa	Number	Nature/Position	Length	Width	W/L ratio
H. cf. *megacephalum*	PUPC 97/20*	rP^4	29.0	35.0	1.20
	PUPC 91/23*	rM^1	36.0	35.0	0.97
	PUPC 97/16*	rM^1	36.0	35.0	0.97
		rM^2	38.0	39.0	1.02
	PUPC 67/155*	lM^2	38.0	39.5	1.03
	PUPC 97/17*	rM_1	31.0	19.0	0.61
		rM_2	32.5	19.0	0.58
		rM_3	44.0	19.0	0.28
	PUPC 95/24*	ldM	44.0	20.0	0.45
H. megacephalum	AMNH 19488	P^4	29.0	35.0	1.20
		M^1	36.0	35.0	0.97
		M^2	37.5	40.0	1.06
	BW 9	dM_4	44.0	19.0	0.43
	AMNH 19669	lM_1	38.0	27.0	0.71
		lM_2	38.0	28.0	0.73
		lM_3	50.0	28.5	0.57
	PUPC 95/24	lM_3	44.0	20.0	0.45
H. grande	Ind. Mus. B135	M^1	60.0	56.0	0.93
		M^2	68.0	56.0	0.82
	Ind. Mus. B135	M^3	64.0	55.0	0.85
H. magnum	GSI B514	M^2	56.0	56.0	1.00
		M^3	56.0	57.0	1.02
	PUPC 67/195	rM_2	50.0	34.0	0.68
		rM_3	68.0	32.0	0.47

can be referred to some herbivorous mammalian group. Since the cones/conids are crescentic in outline, it can safely be included in Ruminantia and Tylopoda (Romer, 1974; Zittel, 1925). Tylopoda includes Camelidae having teeth with finely rugose enamel. In addition, the Camelidae is not reported from the Siwalik late Miocene (Matthew, 1929; Colbert, 1935). Ruminantia comprises four families namely, Tragulidae, Cervidae, Bovidae and Giraffidae. The tragulids and cervids are small and medium size ruminants (Gentry *et al*., 1999). The bovids are commonly medium size ruminants however some forms are large but without rippled enamels (Pilgrim, 1937, 1939; Thomas, 1984). The giraffids are large-sized ruminants having teeth with rippled enamel. The studied premolars and molars with rippled enamel are large enough to include in giraffids. They have typical giraffid's features, including large size and finely rippled enamel (Matthew, 1929; Colbert, 1935; Geraads and Aslan, 2003; Kostopoulos and Sarac, 2005).

The Siwalik giraffids may be divided into two groups, the Middle Miocene Palaeotraginae and the Late Miocene Sivatheriinae (Colbert, 1935; Sarwar and Akhtar, 1987). The Siwalik middle Miocene small forms include the genera *Giraffokeryx* and *Giraffa,* while the late Miocene large forms include the genera *Bramatherium*, *Hydaspitherium* and *Sivatherium* (Bhatti, 2005). The recovered teeth are large-sized as in *Bramatherium*, *Hydaspitherium* and *Sivatherium* (Colbert, 1935; Geraads and Gulec, 1999). In addition, characters as the flat entoconid wall and brachydonty present in Eurasian palaeotragines, are absent in the studied sample. According to Falconer and Cautley (1861) *Sivatherium* differs from *Hydaspitherium* having less pointed lobes and weak parastyle. *Bramatherium* differs from *Hydaspitherium* having L-shaped protocone (Khan and Sarwar, 2002). In the described specimen the anterior fossette is

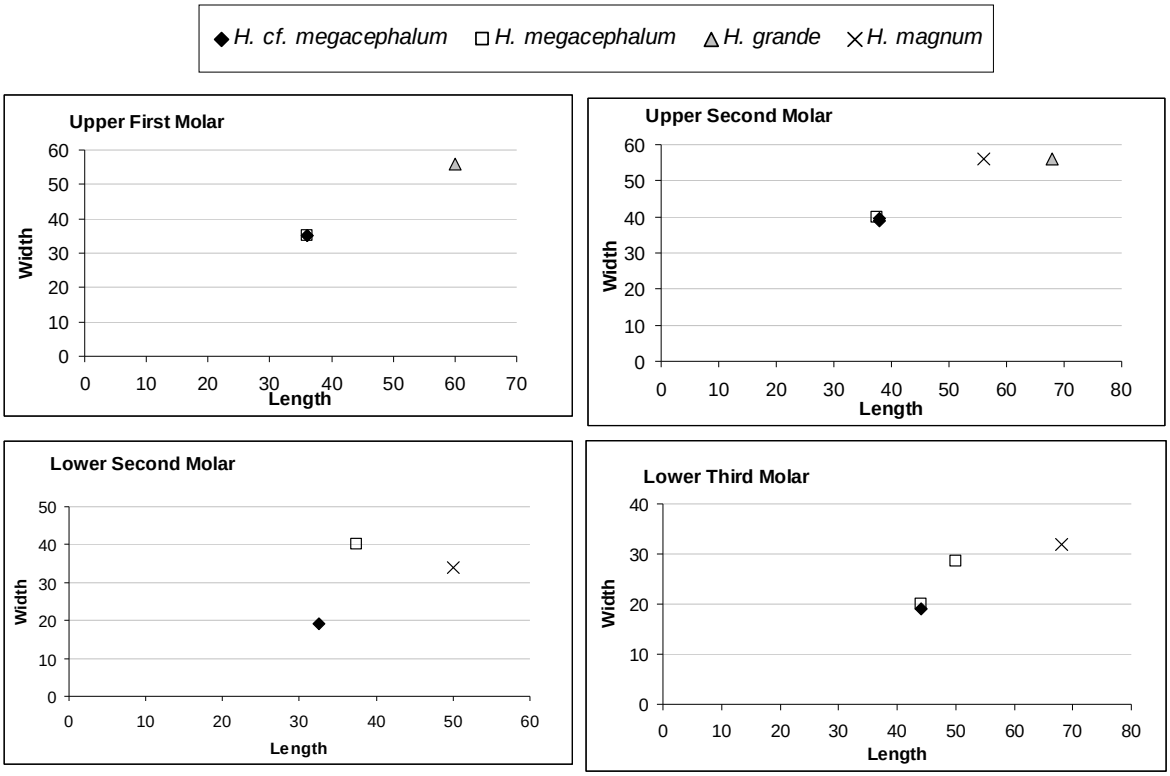

Fig. 4. Bivariate plots showing dental proportions of the Siwalik *Hydaspitherium*. Referred data are taken from Matthew (1929) and Colbert (1935).

compressed transversely, the styles/stylids are present, the anterior median rib is prominent and the enamel sculpture is coarse (Figs. 2-3). These characteristics are found in the genus *Hydaspitherium* (Pilgrim, 1911; Matthew, 1929; Colbert, 1935; Bhatti, 2005). The studied sample shows the maximum resemblance with *Hydaspitherium* among the known Siwalik Sivatheriinae. The studied material's dimensions close to species *H. megacephalum* (Fig. 4). The described molars are clearly smaller than those of *H. magnum* (Table I; fig. 4). The described specimen and the referred specimens of *H. megacephalum* appear same in size (Fig. 4) and crown structure (Pilgrim, 1911; Colbert, 1935; Bhatti, 2005). Dimensions of the teeth are very similar to those of the *H. megacephalum* holotype and also to those of the already recovered specimens from the Siwaliks (Matthew, 1929; Colbert 1935). The small difference in size may be considered as intraspecific variability. Consequently, the material is assigned to *H.* cf. *megacephalum* as the material is insufficient for a definitive specific determination.

DISCUSSION AND CONCLUSIONS

Lydekker (1876) described the genus *Hydaspitherium*, based on a collection from the different localities of the Siwaliks. Further collection of *Hydaspitherium* had been made by Pilgrim (1910), Bohlin (1926) and Matthew (1929). These collections comprise cranial and postcranial elements. Four species of *Hydaspitherium* were described in the Siwaliks: *H. megacephalum* Lydekker, 1876, *H. grande* Lydekker (1878), *H. magnum* Pilgrim, 1910 and *H. birmanicum* Pilgrim, 1910 (Lydekker, 1876; Pilgrim, 1910; Bohlin, 1926; Matthew, 1929; Colbert, 1935). The number of these determined species has already been considered as exaggerated, nevertheless the taxonomy and the validity of the giraffid species in the Siwaliks has not been fully resolved yet

(Matthew, 1929; Gentry, 1997; Geraads and Gulec, 1999).

The description of *H. birmanicum* Pilgrim, 1910 was simply based on a single specimen, GSI B517, a right upper molar (Matthew, 1929; Colbert, 1935). *Hydaspitherium grande* Lydekker (1878) and *H. magnum* Pilgrim, 1910 were only erected to display minor variations in size (Matthew, 1929; Colbert, 1935). In our opinion the systematic position of *H. birmanicum* Pilgrim, 1910 is doubtful and it may be an invalid species. Similarly, *H. grande* Lydekker (1878) has the same characteristics as *H. magnum* Pilgrim, 1910 and both of them are larger in size (Fig. 4) than *H. megacephalum* Lydekker, 1876 (*e.g.*, see Matthew, 1929, p. 543). Morphological and metrical dental characters (Table I) of *H. grande* Lydekker (1878) and *H. magnum* Pilgrim, 1910 indicate that the differences among the specimens do occur, but do not exceed ordinary intraspecific variability (Matthew, 1929; Colbert, 1935). The difference probably reflects sexual dimorphism, subject to intraspecific variability in the late Miocene Siwalik Sivatheriinae. This is especially true if one considers the range of variation observed within species of extinct Eurasian sivatheriines (e.g., see Geraads and Gulec, 1999; Gentry *et al*., 1999).

Earlier authors (Matthew, 1929, p. 243; Colbert, 1935) already proposed close affinities among *H. grande* Lydekker (1878), *H. magnum* Pilgrim, 1910 and *H. birmanicum* Pilgrim, 1910. Moreover, there is no apparent reason to keep them separate; the common stratigraphic origin of three species from the Dhok Pathan Formation, strengthens such a decision. At present, it is convincing to say that there are two species of *Hydaspitherium* in the Siwalik late Miocene: a small species *H. megacephalum* and a large species *H. grande*. Following nomenclature rules, it is obvious that *H. grande* Lydekker (1878) has priority over both *H. magnum* Pilgrim, 1910 and *H. birmanicum* Pilgrim, 1910. In our view, the generic attribution of *Hydaspitherium* is open. However, further work is needed, pending the recovery of more diagnostic material of *Hydaspitherium* from the subcontinental Siwaliks.

Hydaspitherium is the most common giraffid at Dhok Pathan and Hasnot, and the equivalent sites dated between the late Miocene and early Pliocene (e.g. for biochronology see, Barry *et al*., 1982, 2002; Badgley *et al*., 2005). The late Miocene sample provides a new evidence of the normal variability of giraffid teeth which seems to confirm the previous hypothesis of teeth variability in the late Miocene sivatheriines (Geraads, 1989; Geraads and Aslan, 2003; Khan, 2007).

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(Received 24 September 2010, revised 2 August 2011, accepted 16 March 2012)