Pakistan J. Zool., vol. 45(4), pp. 981-988, 2013

Gazella lydekkeri (Cetartiodactyla: Ruminantia: Bovidae) from the Middle Siwaliks of Hasnot (Late Miocene), Pakistan

Muhammad Akbar Khan,[1]* Arifa Batool,[2] Abdul Qayyum Nayyer[3] and Muhammad Akhtar[1]
[1]*Palaeontology Laboratory, Department of Zoology, University of the Punjab, Quid-e-Azam Campus, Lahore*
[2]*Department of Wildlife and Fisheries, GC University, Faisalabad*
[3]*Department of Zoology, University of Azad Jammu & Kashmir, Muzaffrabad*

Abstract.– Newly discovered Late Miocene gazelle remains from the Middle Siwaliks of Hasnot (7-5 Ma), Northern Pakistan are described and discussed here. The samples presented herein include an opisthocranium with horn-cores, maxillar and mandibular fragments, and isolated upper and lower dentitions. The opisthocranium with horn cores referred to *Gazella lydekkeri* is the second best preserved specimen after the holotype which allows examining some additional skull morphological features of *G. lydekkeri*. This finding suggests the presence of abundant herbaceous vegetation with closed conditions during the Late Miocene in the Siwalik area.

Keywords: Vertebrate, Bovid, Antelope, Siwaliks, Dhok Pathan Formation, Potwar Plateau.

INTRODUCTION

Gazella (Bovidae, Gazellinae) is the most widespread and ancient genus of Antilopini. The genus ranges throughout Middle Miocene - Early Pliocene, and has been found across Eurasia from China to Spain, in the Siwaliks, and to the far south of South Africa (Pilgrim, 1937, 1939; Moya-Sola, 1983; Thomas, 1984; Chen, 1997; Bibi *et al*., 2009; Khan, 2008; Khan *et al*., 2010, 2012a). The first occurrences of *Gazella* have been recorded in the Neogene of Europe, Africa and Asia. Gazelles were very rare during the Early Pliocene of northern Europe due to unsuitable cooler climatic conditions but they survived in Africa and Middle East (Gentry, 1999; Kostopoulos, 2009). The earliest members of the group from Algeria and Turkey are represented by small forms with conical horns (Pilgrim, 1937; Kostopoulos, 2005, 2006, 2009). Early gazelles have small and slightly-compressed horn cores without keels and curved backwards. They have brachydont teeth with long premolar rows and m3s without an enlarged posterior lobe (Gentry, 1990).

The Hasnot village (Lat. 32 49 N: Long. 73 18 E) is placed on the east bank of the river Bunha, at about 70 km west of the Jhelum city in the Potwar Plateau of the Northern Pakistan (Fig. 1). The Hasnot outcrops consist of sandstones with alternate orange brown clays and scattered conglomerates in the lower part, and conglomerates with sandstones and clays in the upper part. The sediments are the products of a fluvial system which led to the formation of a complex landscape exhibiting waters, reedy marshes, meadows of herbs and shrubs, woodlands and forests. The time of deposition ranges from 7 to 5 Ma, isochronous to the European Late Turolian age and to the European MN 14 Mammal Zone (Pilbeam *et al.*, 1977; Johnson *et al.*, 1982; Barry, 1987; Barry *et al*., 1982, 2002; Khan *et al.*, 2009, 2012b).

In the present study, the new collection of gazelle fossil remains from Hasnot is described in detail. To date, a thorough study of the Late Miocene Siwalik gazelle had not been made yet and a few findings included only isolated dentition (Akhtar, 1992; Khan, 2007). Since the beginning of the last century, no new comprehensive gazelle material had been recovered in this area. It took nearly 75 years before another skull was assigned to this species. Therefore, the Late Miocene gazelles of Hasnot are considered here.

* Corresponding author: email: akbaar111@yahoo.ca
0030-9923/2013/0004-0981 $ 8.00/0

Abbreviations: PC-GCUF, Palaeontological Collection of Government College University Faisalabad; PUPC, Punjab University Paleontological Collection; AMNH, American Museum of Natural History; Ma, million years; MN, European Neogene Mammalian Zone; P, premolar; M, molar; DT, transverse diameter; DAP, antero-posterior diameter; L, largest length; W, width; l, left; r, right; mm, millimeters.

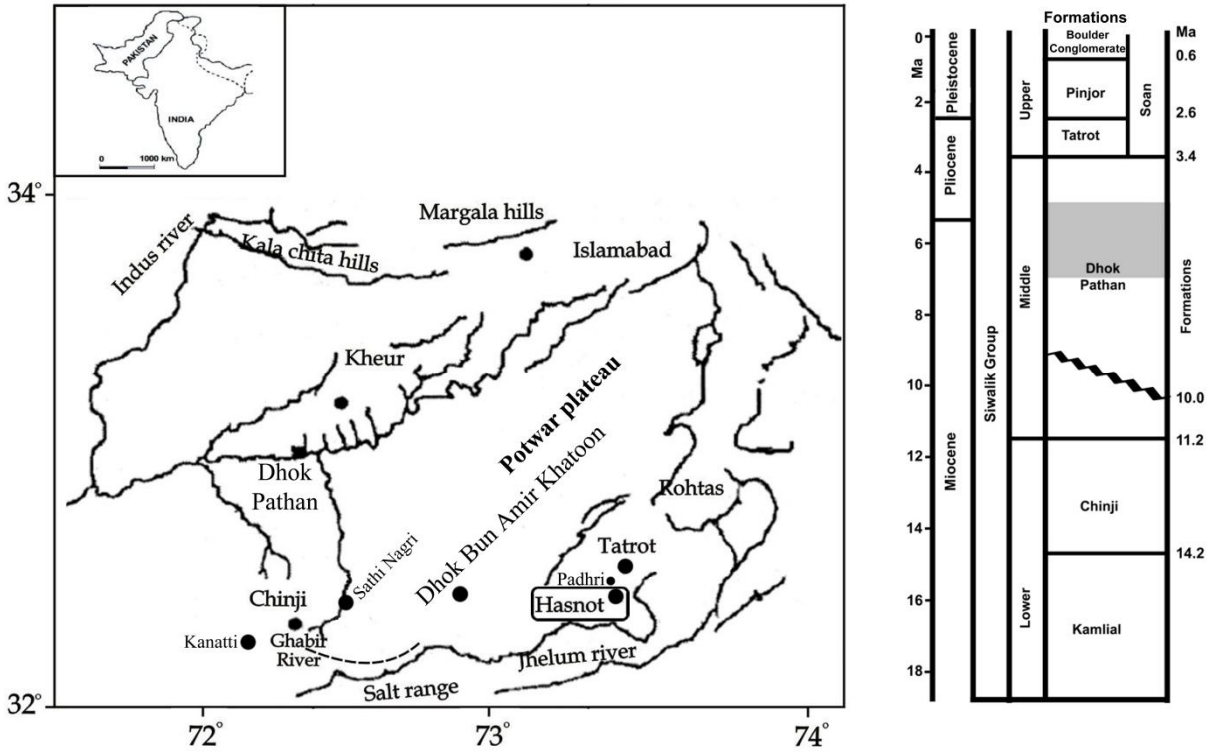

Fig. 1. Map of the Potwar Plateau in Northern Pakistan; reference locality of the Siwaliks encircled. Chronostratigraphic context is modified from Johnson *et al.* (1982), Behrensmeyer and Barry (2005), Dennell (2008), Nanda (2008), and Cohen and Gibbard (2008).

MATERIAL AND METHODS

Material

The studied material comes from the Late Miocene - Early Pliocene sediments at Hasnot, Jhelum district, Punjab province, Pakistan (Fig. 1). Frequent visits were made since 2010 to collect the material from fossiliferous sites in the vicinity of the Hasnot. The total sample number is 12: 1 opisthocranium with horn-cores, 2 horn-core fragments, 4 isolated upper molars, 1 isolated lower premolar, 3 isolated lower molars, and 1 mandible fragment. The collected material consists of exposed surface finds. The studied material is compared with other *G. lydekkeri* samples from the Siwaliks stored in the collections of the American Museum of Natural History in New York and in the Punjab University Palaeontological Collection in Lahore. The presented measurements were taken with calipers to the nearest 0.1 mm.

The studied material is housed in the Zoology Department, GC University, Faisalabad, Punjab, Pakistan and it is the part of the PhD research work of the 2nd author. The catalogue number of the specimens consists of a yearly catalogue number and a serial catalogue number, so figures on the specimens represent the collection year (numerator) and serial number (denominator) of that year (e.g. PC-GCUF 10/53). The institutional abbreviation 'PC-GCUF' is used for the Palaeontological Collection of Government College University Faisalabad. Uppercase letters stand for the upper dentition (*e.g.,* M) and lower case for the lower dentition (*e.g.*, m).

Nomenclature

In the descriptions of the studied cranial material we use the terminology of Pilgrim (1937, 1939), Gentry and Hooker (1988), Gentry *et al.* (1999), and Bärmann and Rössner (2011).

Source of the comparative material
Pilgrim (1937, 1939) and Akhtar (1992).

SYSTEMATIC PALAEONTOLOGY

Mammalia Linnaeus, 1758
Cetartiodactyla Montgelard, Catzeflis and Douzery, 1997
Pecora Linnaeus, 1758 sensu Webb and Taylor, 1980
Family Bovidae Gray, 1821
Genus *GAZELLA* Blainville, 1816
Type species: Gazella dorcas Linnaeus, 1758.
Gazella lydekkeri Pilgrim, 1937

Type specimen
AMNH 19663, a skull and conjoined mandible (Pilgrim, 1937).

Type locality
Dhok Pathan (Middle Siwaliks), Chakwal district, the Punjab Province, Pakistan (Pilgrim, 1937).

Stratigraphic range
Middle Siwaliks (Late Miocene to Pliocene).

Diagnosis
Upper molars moderately hypsodont, styles narrow and strong with entostyles very small or absent, enamel moderately thick and rugose, fossettes narrow and deep, paraconus rib stronger than metaconus one, premolar series rather long. Lower molars high crowned approaching quadrate shape, with small ectostylids, prominent goat folds, fossettes fairly simple in outline, stylids and ribs moderately developed. Horn cores moderately long, spaced, slightly curved backward, broadly elliptical in cross-section, fine ribs becoming rudimentary near the tips, one deep furrow posteriorly (Pilgrim, 1937, 1939).

New material
PC-GCUF 10/50, opisthocranium with horn-cores; PC-GCUF 10/86, piece of horn-core; PC-GCUF 11/150, piece of horn-core; PC-GCUF 11/175, lM1; PC-GCUF 11/165, lM2; PC-GCUF 12/35, partially broken rM2; PC-GCUF 10/82, rM3; PC-GCUF 12/43, rp2; PUPC 96/6, rm1; PC-GCUF 10/53, left mandible fragment with partial m3; PC-GCUF 11/180, right partial m3; PC-GCUF 12/36, right partial m3.

Table I.- Comparative measurements (mm) of the skull of *Gazellla lydekkeri*.

Description	PC-GCUF 10/50*	AMNH 19663
Preserved length of right horn core	117	100
Preserved length of left horn core	118	-
DAP of horn core at the base	35.0	26
DT of horn core at the base	27.0	21
DAP of pedicle	31	-
DT of pedicle	25	-
DT of foramen magnum	23.0	20.3
Bi mastoid breadth	75.0	60
Skull width at the coronal suture	63.0	58
Length of nuchal line	15.0	-
Skull width at orbit	ca. 71.0	79
Height of orbit	38.0	28
DT of orbit	32	34
Length of interfrontal suture	47.0	-
Distance between bregma and lambda	44.0	-
Distance between fronto-parietal suture to summit of occipital crest	61.0	53
Length of inter parietal suture	18.0	17
Length of coronal suture	43.0	
Height of supraoccipital	26.0	-
Length of exoccipital area	24.0	-
Length of temporal bone	49.0	-
Width over lateral boarders of pedicles	77.0	-
Length from supraorbital foramen to top of occipital	104	-
Length from middle of orbit to summit of occipital crest	87	78
Distance between supraorbital pits	36	27
Minimum distance apart from the horn-cores just above the frontal swelling	25	18

*the studied specimen. Referred data are taken from Pilgrim (1937).

Description

Skull

The skull is partially preserved having part of the cranial roof and supraoccipital area (Fig. 2; Table I). In dorsal profile the braincase is convex. The interparietal is large, and the frontals form two shallow depressions at the postero-medial side of the pedicles. The frontoparietal suture is open while the interfrontal suture is narrow and appears slightly constricted between the horn-cores. The pedicles of

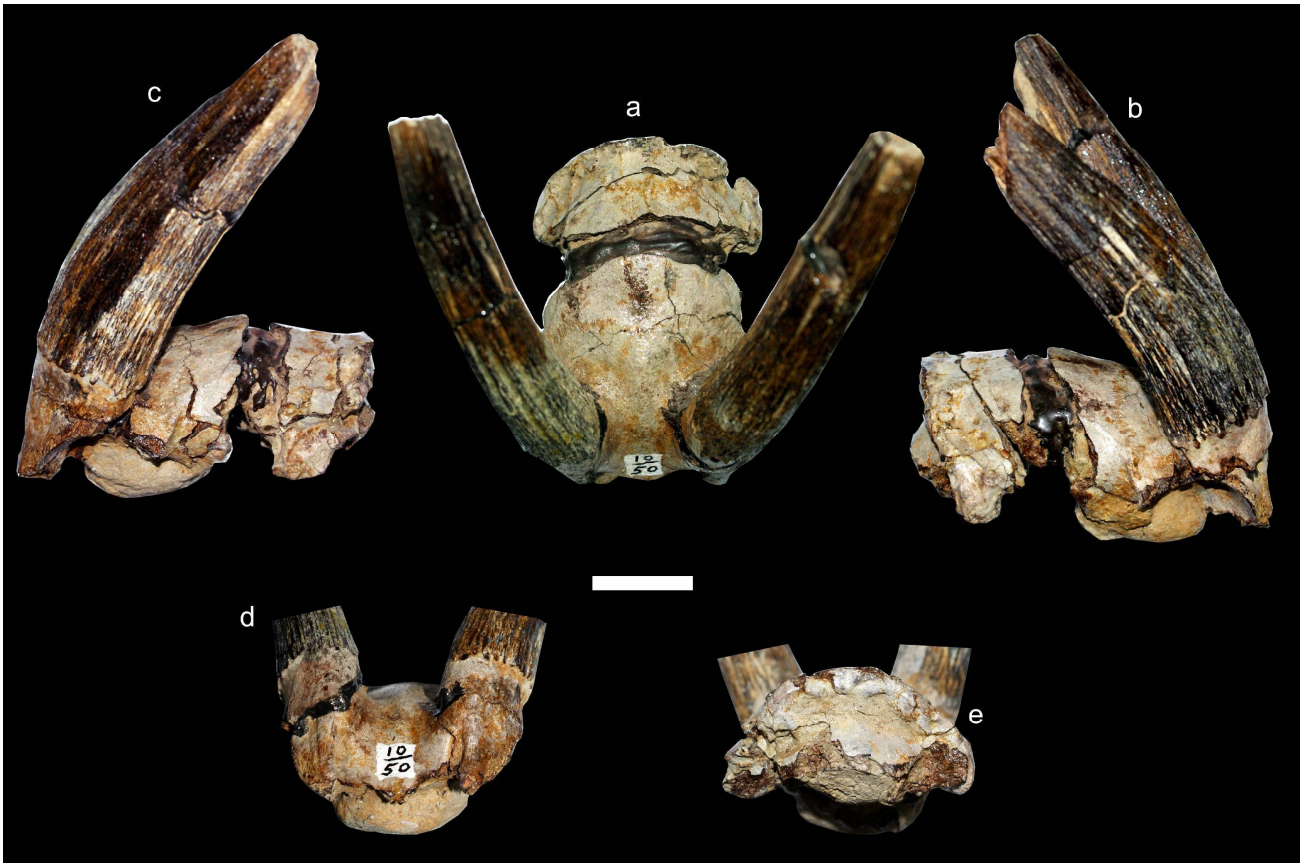

Fig. 2. *Gazella lydekkeri*: PC-GCUF 10/50, opisthocranium with horn-cores (a, dorsal view; b, right lateral view; c, left lateral view; d, frontal view; e, occipital view. Scale bar 30 mm.

the horn cores are relatively high. Supraorbital foramina set in large triangular pits beneath the pedicles of the horn cores, opening anteriorly with flattened frontal region in between. The postcornual groove is elongated and shallow. The orbit is not completely preserved but it looks large and rounded (Fig. 2).

Horn-cores

Horn-cores are relatively short, robust, inserted just above the orbits, smoothly curving backwards and weakly divergent with slight medio-lateral compression. The basal cross-section is sub-circular with a flattened lateral face (Fig. 2; Table I). They are inserted far apart with deep longitudinal grooves along surfaces: the anterior surface bears three longitudinal grooves and the posterior one with one longitudinal groove, placed in a posterocentral position, seems to be the most stable. They are moderately inclined against parietal. The lateral face of the horn-cores is flat and the internal one slightly convex. The mean index DT×100/DAP (26×100/36) is 72.22 at the base and 84.61 (22×100/26) at 7 cm from the base, indicating a reduction of the medio-lateral compression from the base to the top.

Upper dentition

The upper molars (PC-GCUF 11/175, PC-GCUF 11/165) are quadrate shaped teeth (Fig. 3A-D; Table II). The major cones are pointed. The lingual cones are low and crescent. The posthypocrista is longer than the praehypocrista as in the protocone. The fossettes are narrow and crescent. The paraconus rib is strong at the base while the metaconus is weak. The mesostyle is

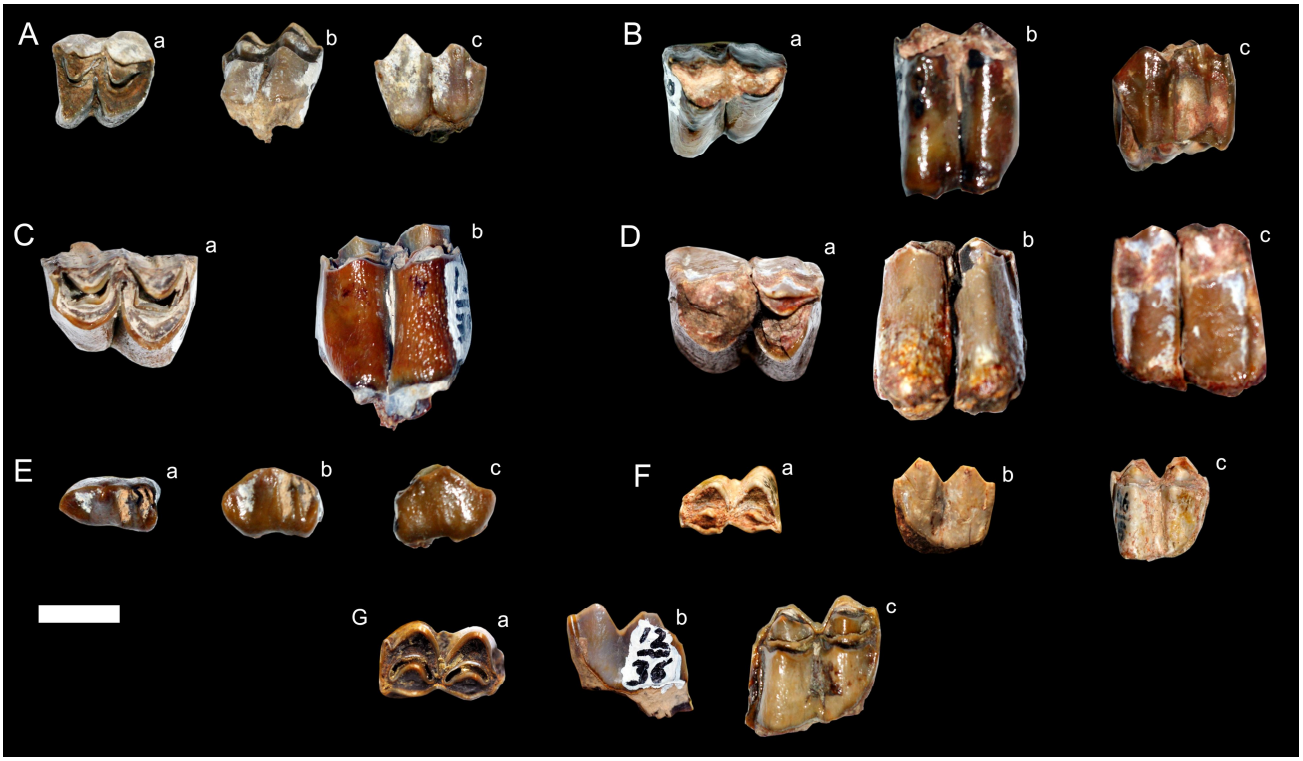

Fig. 3. *Gazella lydekkeri*; A, PC-GCUF 11/175 - left M1; B, PC-GCUF 11/165 - left M2; C, PC-GCUF 12/35 - partially broken right M2; D, PC-GCUF 10/82 - right M3; E, PC-GCUF 12/43- right p2; F, PUPC 96/6 – right m1; G, PC-GCUF 12/36 - right partial m3. a, occlusal view; b, lingual view; c, labial view. Scale bar 10 mm.

prominent, and the transverse valley on the lingual side is occupied by a small tubercle.

Lower dentition

The p2 PC-GCUF 12/43 is a single lobed tooth (Figs. 3E-G; Table II). The protoconid is pointed. A slight paraconid rib is present labially and a rib like structure is present lingually. The metaconid and the entoconid are fused. The lower first molar conids are conical in form (Fig. 3F), whereas a goat fold is present anteriorly. The ribs are broader at the base and gradually narrow toward the tips. The mesostylid on the lingual side is very weak, visible only on the upper half of the tooth crown. The labial transverse valley is occupied at the base by a short and robust ectostylid. The lingual cusps are higher than the labial ones. The fossettes are moderately wide and simple. The third lower molars are partially broken. The hypoconulid is missing. The praeentocristid and postentocristid are sloped downwardly. The fossettes are narrow, crescentic and not very deep. A well preserved goat fold is present at the anterior side of the molars.

DISCUSSION

The horn-cores are indicative of *Gazella* in exhibiting an oval cross-section with mediolateral compression, a flattened lateral surface and deep longitudinal grooves. Such fossil horn-cores from the Late Miocene of Europe have been reported principally as *G. capricornis*, *G. deperdita*, and *G. pilgrimi*, from the Late Miocene of China as *G. gaudryi* and from the Late Miocene of the Siwaliks as *G. lydekkeri* (Pilgrim, 1937, 1939; Akhtar, 1992, Kostopoulos, 2009). Pilgrim (1937, 1939) identified two species of *Gazella* from the sediments of the Middle Siwaliks, *G. lydekkeri* Pilgrim, 1937 and ?*G. superba* Pilgrim, 1939, on the basis of the horn-core curvature and size variation. The described gazelle sample corresponds to that of *G. lydekkeri* Pilgrim, 1937 from the Middle Siwaliks. Morphometrically

the studied sample matches with the holotype AMNH 19663 of *G. lydekkeri* Pilgrim, 1937 ascribed from the Late Miocene of the Siwaliks (Table I-II; Figs. 2-3). The styles and the median ribs of the molars are observed equally strong in the holotype as well as in the studied specimens (Pilgrim, 1937, 1939; Akhtar, 1992; Khan, 2007).

The Hasnot sample of *Gazella* exhibits some minor variations that can be considered merely the individual variations (Tables I-II; Figs. 2-3). This type of variation in size, cross section, curvature, inclination and divergence of horn-cores is also common to living and many Miocene species of *Gazella* (Bibi and Güleç, 2008). Nevertheless, over a dozen species of *Gazella* have been erected from the Miocene alone and many of these might be synonymous (Bibi and Güleç, 2008). Even the best studied Miocene gazelle species namely *G. pilgrimi*, *G. deperdita*, and *G. capricornis* reflect minor variation and the validity of the species is yet problematic. The studied specimens display similar differences. The poor studied species ?*G. superba* from the Middle Siwaliks differs in having large size from *G. lydekkeri* could probably be considered by the range of variation within *G. lydekkeri,* deserves a comprehensive study, because, researchers are still unclear as to the extent of the range of interspecific variation (Chen, 1997).

Gazella lydekkeri is the most abundant taxon after the boselaphines, collected among the large mammals in the Hasnot outcrops and is present in all the stratigraphic sequences of the Middle Siwaliks (Pilgrim, 1937, 1939; Akhtar, 1992; Barry *et al.*, 2002; Khan, 2007, 2008, Khan *et al*., 2009, 2010, unpublished data). The commonly collected mammalian taxa from the same sediments from the Hasnot where the *Gazella* specimens were recovered are: *Dorcatherium, Dorcabune, Tragoportax, Selenoportax, Pachyportax, Elachistoceras, Cervus, Bramatherium* (*Hydaspitherium*), *Giraffa, Stegodon, Stegolophodon, Merycopotamus, Propotamochoerus, Hippohyus, Hippopotamodon, Sivalhippus, Chilotherium, Percrocuta* and *Indarctos* (Colbert, 1935; Pilgrim, 1937, 1939; Akhtar, 1992; Barry *et al.*, 2002; Khan, 2007, 2008, Khan *et al*., 2009, 2010, 2012b; Ghaffar *et al*., 2011; Bhatti *et al*., 2012a, b; unpublished data).

Table II.- Comparative measurements (mm) of the cheek teeth of *G. lydekkeri*.

Number	Nature/Position	Length	Width	W/L ratio
PC-GCUF 11/175*	lM1	13.0	14.0	1.07
PC-GCUF 11/165*	lM2	16.0	14.0	0.87
PC-GCUF 12/35*	rM2	20.0	-	-
PC-GCUF 10/82*	rM3	20.0	15.0	0.75
PC-GCUF 12/43*	rp2	13.0	7.00	0.53
PUPC 96/6*	rm1	13.0	8.00	0.61
PC-GCUF 10/53*	lm3	-	8.00	-
PC-GCUF 11/180*	rm3	-	10.0	-
PC-GCUF 12/36*	rm3	-	10.0	-
PUPC 97/22	lM2	13.5	13.0	0.96
PUPC 84/65	lM2	18.0	17.3	0.96
PUPC 97/21	lM2	12.0	12.0	1.00
AMNH 19663	lM2	13.5	11.5	0.85
PUPC 84/133	rM2	15.5	10.0	0.64
PUPC 02/37	rM2	14.5	9.00	0.62
AMNH 19663	rM2	13.0	7.50	0.57
PUPC 02/16	rM3	22.0	10.0	0.45
PUPC 94/21	rM3	21.5	8.50	0.39
PUPC 86/39	rM3	21.0	10.0	0.47
PUPC 84/133	rM3	20.0	9.00	0.45
AMNH 19663	rM3	17.5	7.00	0.40
PUPC 83/617	rM1	13.8	14.0	1.01
PUPC 86/49	rM1	12.0	12.0	1.00
PUPC 97/21	rM1	10.0	12.0	1.20
AMNH 19663	rM1	11.0	11.0	1.00
AMNH 19663	rm1	10.0	12.0	1.20
PUPC 84/133	rm1	12.0	6.00	0.50
PUPC 04/08	lm3	20.0	9.00	0.45

* the studied specimens. Measurements are taken from Pilgrim (1937, 1939), Akhtar (1992) and Khan (2008).

Microwear analysis shows that *Gazella* species were mostly browsers and generalist mixed feeders (Merceron *et al.*, 2006). The mixed feeders suggest the presence of abundant herbaceous vegetation, which excluded a dense tree cover. This suggests herbaceous, grassy and bushy vegetation in the Hasnot surroundings. However, the above-mentioned Late Miocene - Early Pliocene faunal association of the Hasnot suggests closed wet to open grassland habitats. The results tentatively suggest the presence of a mosaic habitat representing dense humid dominated forest to open conditions.

CONCLUSIONS

The study provides evidences of variation in the *Gazella lydekkeri* fossil record from the Late Miocene - Early Pliocene of the Hasnot in northern Pakistan. It is concluded that a range of open to

closed wet habitats existed during the Late Miocene - Early Pliocene of northern Pakistan. We infer that forested habitats predominated at the Hasnot surroundings of northern Pakistan but that some less densely covered areas may also have been present.

REFERENCES

AKHTAR, M., 1992. *Taxonomy and distribution of the Siwalik bovids.* Ph.D. Diss. (unpublished), University of the Punjab, Lahore, Pakistan, pp. 475.

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

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., MORGAN, M., FLYNN, L., PILBEAM, D., BEHRENSMEYER, A. K., RAZA, S., KHAN, I., BADGELY, C., HICKS, J. AND KELLEY, J., 2002. Faunal and Environmental change in the Late Miocene Siwaliks of Northern Pakistan. *Paleobiology*, **28**: 1-72.

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.

BHATTI, Z. H., KHAN, M.A. AND AKHTAR, M., 2012a. *Hydaspitherium* (Artiodactyla, Giraffidae) from the Dhok Pathan Formation of the Middle Siwaliks, Pakistan: New Collection. *Pakistan J. Zool.*, **44**: 799-808.

BHATTI, Z. H., KHAN, M. A., AKHTAR, M., KHAN, A. M., GHAFFAR, A., IQBAL, M. AND SIDDIQ, M.K., 2012b. *Giraffa punjabiensis* (Giraffidae: Mammalia) from Middle Siwaliks of Pakistan. *Pakistan J. Zool.*, **44**: 1689-1695.

BIBI, F. AND GÜLEÇ, E. S., 2008. Bovidae (Mammalia: Artiodactyla) from the Late Miocene of Sivas, Turkey. *J. Verteb. Palaeontol.*, **28**: 501-519.

BIBI, F., BUKHSIANIDZE, M., GENTRY, A.W., GERAADS, D., KOSTOPOULOS, D.S. AND VRBA, E.S., 2009. The fossil record and evolution of Bovidae: State of the field. *Palaeontol. Electron.*, **12**: 1-11.

BLAINVILLE, H. M., 1816. Sur plusieurs espèces d animaux mammifères de 1′ order des Ruminants. *Bull. Soc. Phil.* Paris, 73-82.

CHEN, G., 1997. The genus *Gazella* Blainville, 1816 (Bovidae, Artiodactyla) from the Late Neogene of Yushe Basin, Shanxi, Province, China. *Verteb. PalAsiat.*, **35**: 233–249.

COHEN, K.M. AND GIBBARD, P.L., 2008. Global chronostratigraphical correlation table for the last 2.7 million years. *Episodes*, **31**: 243-247.

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.

GENTRY, A. W. AND HOOKER, J. J., 1988. The phylogeny of Artiodactyla. In: *The phylogeny and classification of the tetrapods, Vol. 2: Mammals* (ed. M.J. Benton), Systematics Association Special Volume No. 35B Clarendon, Oxford, pp. 235-272.

GENTRY, A.W., 1990. Ruminant artiodactyls of Pasalar, Turkey. *J. Human Evol.*, **19**: 529-550.

GENTRY, A.W., 1999. Fossil Pecorans from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In: *Chap. 22, Abu Dhabi pecorans*, 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, Munchen, pp. 225-258.

GHAFFAR, A., AKHTAR, M., KHAN, M. A., BUTT, M. J. AND KHAN, A. M., 2011. *Cervus* cf. *rewati* (Cervidae, Mammalia) from the Dhok Pathan Formation (Middle Siwaliks), Pakistan. *Aust. J. Earth Sci.*, **104**: 107-113.

GRAY, J.E., 1821. On the natural arrangement of vertebrose animals. *Lond. Med. Reposit.*, **15**: 296-310.

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.

KHAN, M. A., 2007. *Taxonomic studies on fossil remains of ruminants from tertiary hills of Hasnot, Pakistan*. Ph.D. Diss., Punjab University, Lahore, Pakistan, pp. 269.

KHAN, M.A., 2008. Fossil bovids from the Late Miocene of Padri, Jhelum, Pakistan. *Pakistan J. Zool.*, **40**: 25-29.

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

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. Sr.*, **10**: 1-90.

KHAN, M. A., AKHTAR, M. AND IKRAM, T., 2012a. True ungulates from the Nagri type locality (Late Miocene), Northern Pakistan. *J. Anim. Pl. Sci., Suppl. Ser.*, **1**: 1-59.

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

KOSTOPOULOS, D.S., 2005. The Bovidae (Mammalia, Artiodactyla) from the Late Miocene of Akkasdagı, Turkey. *Geodiversity*, **27**: 747-791.

KOSTOPOULOS, D.S., 2006. Late Miocene Vertebrate Locality of Perivolaki, Thessaly, Greece. *Palaeontograph. Abt*., **276**: 151-183.

KOSTOPOULOS, D.S., 2009. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 14. Bovidae. *Beitr. Paläontol*., **31**: 339–383.

LINNAEUS, C., 1758. *Systema Naturae, Ed. X (Systema naturae per regna tria naturae, secundumclasses, ordines, genera, species, cum characteribus, diferentiis, synonymis, locis.* Tomus I. Editio decima reformata). Holmiae, Laurentii Salvii, Stockholm, pp. 824.

MERCERON, G., ZAZZO, A., SPASSOV, N., GERAADS, D. AND KOVACHEV, D., 2006. Bovid paleoecology and paleoenvironments from the Late Miocene of Bulgaria: Evidence from dental microwear and stable isotopes. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, **241**: 637–654

MONTGELARD, C., CATZEFLIS, F. AND DOUZERY, E., 1997. Phylogenetic relationships of artiodactyls and cetaceans as deduced from the comparison of cytochrome b and 12S rRNA mitochondrial sequences. *Mol. Biol. Evol.*, **14**: 550-559.

MOYA-SOLA, S., 1983. Los Boselaphini (Bovidae, Mammalia) del Neogeno de la Peninsula Iberica. Dissertation, Universidad Autonoma de Barcelona, *Public. Geol.*, **18**: 1-236.

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.

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, Lond.*, **270**: 684-689.

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

PILGRIM, G. E., 1939. The fossil Bovidae of India. *Pal. Ind., N. S.*, **26**: 1-356.

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

WEBB, S. D. AND TAYLOR, B. E., 1980. The phylogeny of hornless ruminants and a description of the cranium of *Archaeomeryx*. *Bull. Am. Mus. nat. Hist.,* **167**:117–158.

(Received 12 February 2013, revised 12 June 2013)