Pakistan J. Zool., vol. 46(4), pp. 897-908, 2014.

Proamphibos (Bovini: Bovidae: Ruminantia) from Sardhok Pleistocene of Pakistan

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Abstract. – Some new *Proamphibos* fossils have been reported from Quaternary basin near Sardhok village in Gujrat, northern Pakistan. The Sardhok *Proamphibos* sample includes an opisthocranium, maxillar and mandibular fragments, and isolated dentition. The bovine is well known in the Pakistani Siwaliks during Pleistocene. *Proamphibos* was represented by a reasonable number of specimens suggesting that the niche probably was filled by the large bovines. The new specimens suggest wooded grassland habitat and faunal turnover after 2.5 Ma. The paper represents one of the best *Proamphibos* records ever found from the subcontinent Siwaliks.

Keywords: Bovidae, Pleistocene of Pakistan, Pakistani Siwaliks.

INTRODUCTION

The Siwalik deposits represent a rich Neogene fossil records in the world, ranging in age from Early Miocene to Middle Pleistocene (Matthew, 1929; Colbert, 1935; Pilgrim, 1910, 1913, 1937, 1939; Pilbeam *et al.*, 1977, 1979; Opdyke *et al.*, 1979; Azzaroli and Napoleone, 1982; Johnson *et al.*, 1982, 1985; Cande and Kent, 1995; Barry *et al.*, 1980, 1982, 1985, 2002; Flynn *et al.*, 1995, Flynn, 2003; Flynn and Morgan, 2005; Khan *et al.*, 2009a, b, 2010, 2011, 2012a, b). The Upper Siwaliks (ca. 3.4 – 0.6 Ma) traditionally subdivided into three lithological and faunal stages: Tatrot, Pinjor and Boulder Conglomerates, and it is better exposed in the Pabbi Hills Pinjor Stage (2.58 – 0.6 Ma) of Gujrat in northern Pakistan (Sarwar, 1977; Hussain *et al.*, 1992; Dennell *et al.*, 2006, 2008; Dennell, 2008; Ghaffar *et al.*, 2012). The Pabbi Hills fluvial deposits of Sardhok comprise the Pinjor Formation of the Upper Siwaliks (Shah, 1977; Keller *et al.*, 1977; Ranga Rao *et al.*, 1988).

The Pinjor Formation of the type area in the Chandigarh region has been dated from 2.48 – 0.63 Ma by magnetostratigraphy (Kumaravel *et al.*, 2005; Nanda, 2008). The Pinjor mammalian fauna, ranging in age from 2.48 to 0.63 Ma, is the youngest fauna of the Siwalik Group. The principal feature of this community is continuing into the modern South Asian wildlife assemblages (Arif and Raza, 1991; Arif and Shah, 1991; Nanda, 2002), characterized by dominance of herbivore community of woodland habitat with a few adapted for riverine galley forests.

The studied outcrops of the Sardhok village (Lat. 32° 49' 39" N: Long. 73° 43' 51" E), Gujrat district, the Punjab province, Pakistan is situated at 25 km SW of Jhelum city, in the east of the Jhelum River and south of the Lahore – Islamabad GT (Grand Trunk) road (Fig. 1). It is situated in the low altitude Pabbi Hills of the Upper Siwaliks, yielding a very important mammalian fauna of Late Pliocene – Early Pleistocene age. The study area is characterized by brown to grayish-brown, fine, medium to coarse-grained sandstones with pebbles and large-scale cross stratifications, brown mudstones, pedogenic horizons, and well-imbricated stratified conglomerates.

The Sardhok outcrops have not been explored by pioneer researchers (*e.g.*, Falconer and Cautley, 1849; Lydekker, 1876, 1880, 1884; Pilgrim, 1910, 1913**,** 1937, 1939; Matthew, 1929; Colbert, 1935). A few specimens collected by Dr. Sarwar in the early 70ies and 80ies are mostly remained

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0030-9923/2014/0004-0897 $ 8.00/0

Abbreviations: PUPC, Punjab University Paleontological Collection, Zoology Department, University of the Punjab, Lahore, Pakistan; AMNH, American Museum of Natural History, New York, USA; 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.

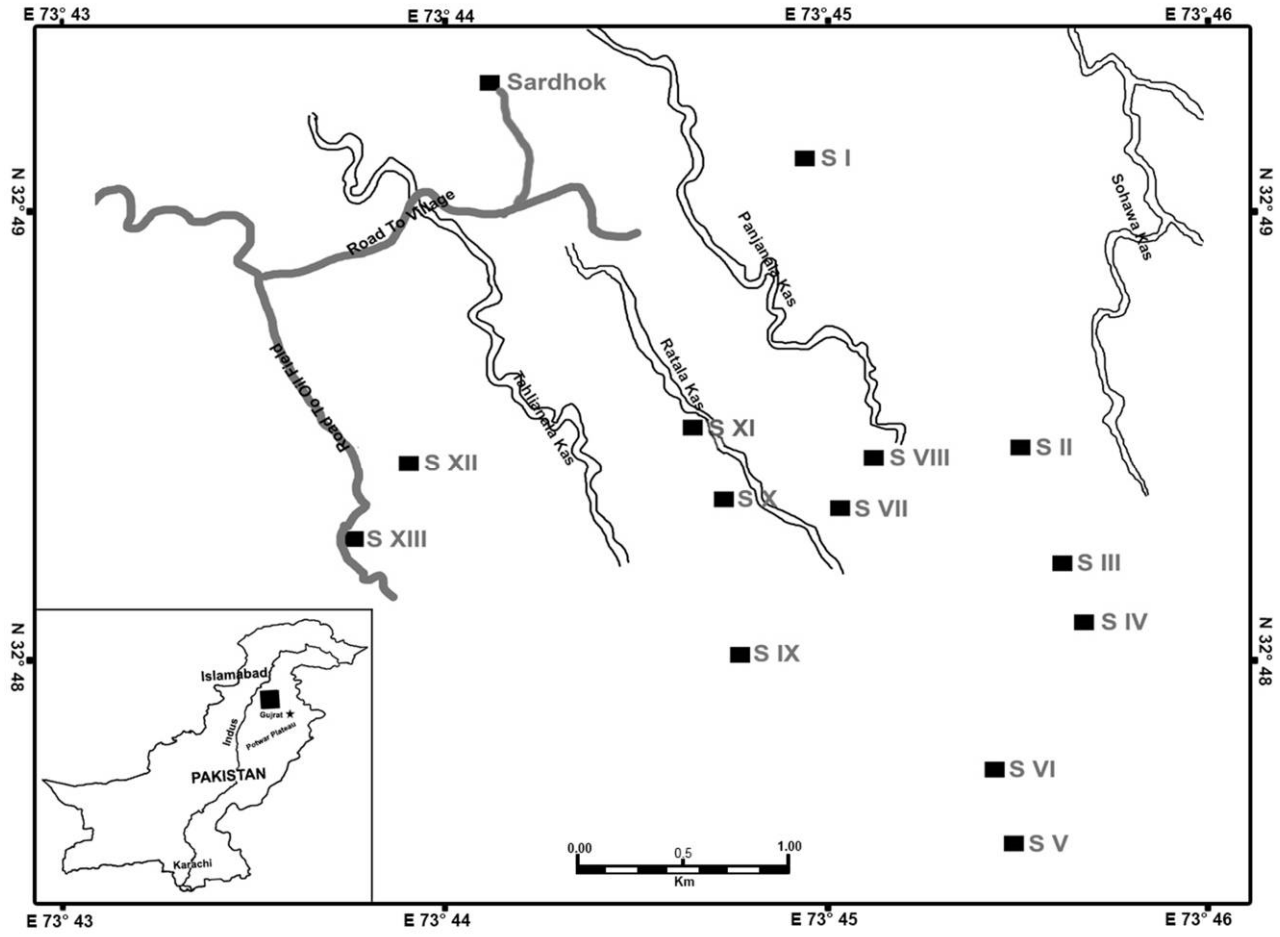

Fig. 1. Map of Pakistan (inset) with an enlargement of study area (Sardhok) with fossil localities from Gujrat district, Punjab, Pakistan (modified after Dennell *et al.*, 2006).

unpublished. The locality represents proboscideans, perissodactyls and artiodactyls (Sarwar, 1977; Dennell *et al.*, 2006; unpublished data). At present, the area in the vicinity of Sardhok has been thoroughly surveyed (Fig. 1). The specimens are comparatively scarce in these sites (numbered as SI, SIX, SXII, SXIII, S = Sardhok).

The new *Proamphibos* material originates from seven fossil sites: SII, SIII, SIV, SV, SVI, SVIII and SX (Fig. 1). The systematic description of the new *Proamphibos* material is the focus of the article. The remains have been used to provide an indication of the probable age and paleoenvironment of these deposits.

MATERIALS AND METHODS

The present paper is a compilation of the *Proamphibos* fossil data newly recovered from the Sardhok Pleistocene of the Upper Siwaliks. The material is discovered by frequently visiting to macrofossil-yielding sites and part of the PhD thesis of the first author. The location of the excavated area in the Sardhok village is shown in figure 1. During the surveys a large area is covered, over which fossils were present, but at low densities, and probably derived from more than one sedimentary unit. The collecting method is general. Some specimens were collected in gullies and a few in find-spots. The specimens excavated from these

localities were generally in excellent condition, with very little surface damage, often complete, and sometimes in articulation or anatomically adjacent to other specimens. The specimens found on the erosional surfaces were also well preserved, particularly those that had not been exposed for long, as on steep, actively eroding slopes. The level surface specimens (fully exposed to sun and rain) are relatively poorly preserved. Almost all fossil specimens were found weathering out from or *in situ* within fine-grained yellow-buff sands and silts.

The spatial distribution of the fossil material was non-random and distributed in pockets, a typical pattern of the Siwaliks (Raza *et al.*, 2002; Barry *et al*., 2002). Many specimens were undiagnostic and few could be identified to cranial element and taxon at the generic or specific level. Measurements are expressed in millimeters. Morpho-metric features of the specimens are described and their systematic determination is discussed. The catalogue number on the specimen represents the collection year (numerator) and serial number (denominator) of that year (*e.g.*, PUPC 11/19. Uppercase letters are used for upper dentition (*e.g.*, M) and lower case for lower dentition (*e.g.*, m). The crown terminology and measurement manners follow Pilgrim (1937, 1939), Gentry *et al*. (1999), and Bärmann and Rössner (2011). The skull measurement manners follow Lei Zhu (2012).

SYSTEMATIC PALAEONTOLOGY

Mammalia Linnaeus, 1758
Cetartiodactyla Montgelard, Catzeflis and Douzery, 1997
Pecora Linnaeus, 1758 sensu Webb and Taylor, 1980
Family Bovidae Gray, 1821
Tribe *Bubalina* Pilgrim, 1939
Genus *PROAMPHIBOS* Pilgrim, 1939

Type species

Proamphibos lachrymans Pilgrim, 1939.

Geographic distribution

Proamphibos is recorded from the Upper Siwaliks of Pakistan, India and Nepal (Pilgrim, 1939; Khan *et al.*, 2009a; Khan and Akhtar, 2011).

Proamphibos kashmiricus Pilgrim, 1939

Type specimen

A skull, Geol. Surv. Ind. No. B 556.

Type locality

South east of Parmandal, Samba tehsil, Jammu State, India.

Diagnosis

Original diagnosis (Pilgrim, 1939: 278).

Stratigraphic range

Upper Siwaliks.

New material

Opisthocranium: PUPC 10/87, female partial skull; Upper dentition: PUPC 66/80, rP4; PUPC 66/141, lP4; PUPC 68/54, rM1; PUPC 66/22, rM2; PUPC 67/295, rM2; Lower dentition: PUPC 10/4, rp3; PUPC 68/55, rp4; PUPC 69/475, lm1; PUPC 67/268, rm2; PUPC 67/116, a right mandible fragment with m2-3; PUPC 68/50, left mandible fragment with m2-3; PUPC 66/72, rm3; PUPC 67/283, rm3; PUPC 67/412, rm3; PUPC 68/196, rm3; PUPC 67/36, partial rm3; PUPC 67/302, partial rm3; PUPC 67/406, partial rm3; PUPC 68/59, partial rm3; PUPC 68/204, partial rm3; PUPC 66/144, lm3.

Locality

Sardhok, Gujrat district, Punjab, Pakistan.

Description

Opisthocranium

The skull is lacking the occipital condyles, auditory bullae, basioccipital area, temporal fossa and most of the brain case (Fig. 2). The skull is not compressed dorso-ventrally. The frontal, maxillary and premaxillary portion is preserved. The nasals are present. The frontals are perfect and narrow comparatively. It is slightly arched. The skull is hornless and therefore it is confirmed a female. The dentition is present but it is not clear for the morphological study (Fig. 2). The molars are lost their crown completely. The orbits are trapezoidal-shaped and partial damaged along the edges. The sutures separating the various bones are clearly

Fig. 2. *Proamphibos kashmiricus*. Opisthocranium: PUPC 10/87, female opisthocranium (a, dorsal; b, lateral; c, ventral view). Scale bar 30 mm.

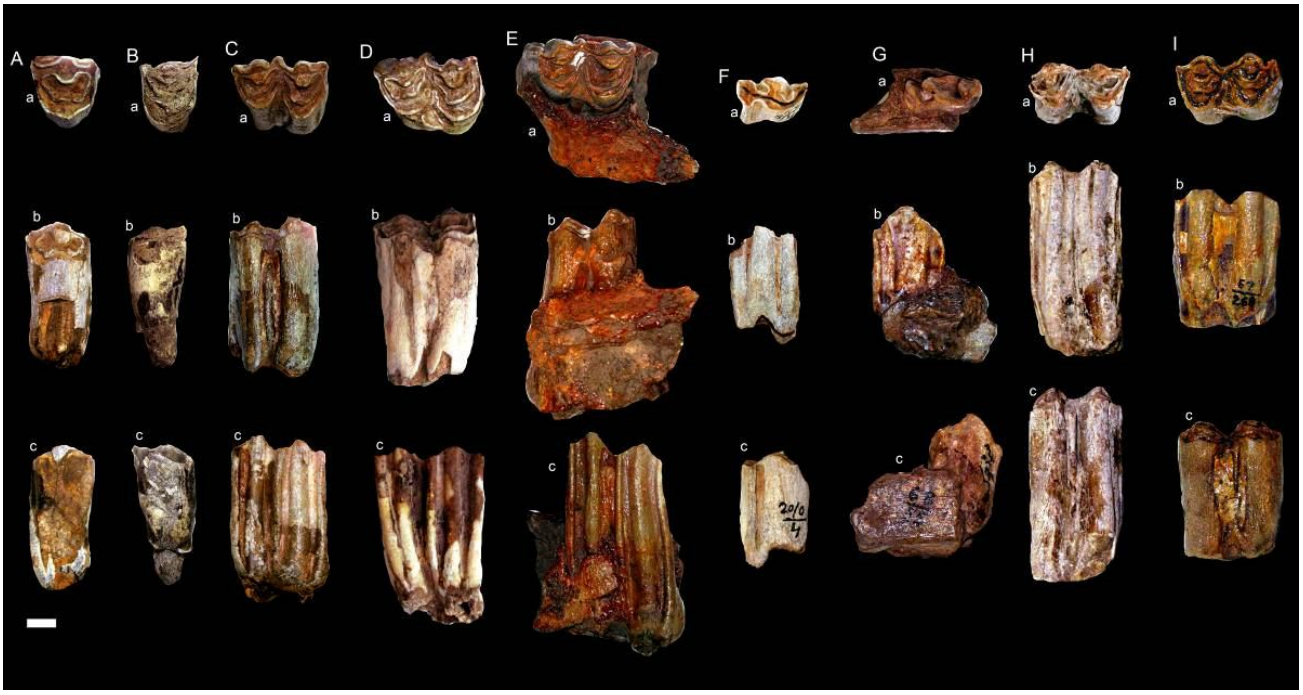

Fig. 3. *Proamphibos kashmiricus*. Upper dentition: **A**, PUPC 66/80, rP4; **B**, PUPC 66/141, lP4; **C**, PUPC 68/54, rM1; **D**, PUPC 66/22, rM2; **E**, PUPC 67/295, rM2. Lower dentition: **F**, PUPC 10/4, rp3; **G**, PUPC 68/55, rp4; **H**, PUPC 69/475, lm1; **I**, PUPC 67/268, rm2. Views: a, occlusal; b, lingual; c, labial. Scale bar 10 mm.

visible; the interfrontal suture is also visible. The frontoparietal suture is partially preserved. The skull is slenderical dorsally and somewhat elongated. The brain case is partially preserved. The bregma separating the frontal from the parietal behind the horn cores is well represented. The lambda between the parietal and the supraoccipital is missing. The frontals form two shallow depressions along the medial suture. The temporal ridges are absent. The orbit is laterally projected, large and semi round (Fig. 2).

Upper dentition

The fourth premolars have half moon like outline (Fig. 3A, B). The parastyle is moderately developed and the metastyle is strongly developed; between the two styles there is a prominent rib all along the crown height. The cementation is present labially. The cingulum is absent. The premolars are rugose and have three roots. The metastyle is slender, rugose and covered by cement. The fossette with spur is crescent shape. The upper molars have four roots (Fig. 3C-E). The labial border of the anterior lobe is V-shaped and the posterior lobe is U-shaped. The molars have strongly developed parastyle, mesostyle and metastyle. The paraconus and metaconus ribs are very strong. The vertical grooves are present between the mesostyle and the metaconus rib, and between the paraconus rib and the mesostyle labially. The praeprotocrista is longer than postparacrista. The praehypocrista is smaller than the posthypocrista. The prae- and postmetacristae are of almost equal size. The prae- and postfossette are wide and deep.

Lower dentition

The p3 is compressed transversely, with a deep and wide anterolingual valley all along the crown height. There is a deep narrow valley posterolingually. The paraconid and protoconid occupies two-thirds of the premolar length (Fig. 3F). The p4 has a triangular outline; it has a deep anterolingual valley present all along the crown height. The paraconid, bracketed by the anterolingual valley, has in its lingual side a small stylid. In the posterolingual side of the premolar there is a deep valley (Fig. 3G). The circular-shaped fossettid is present by the fusion of the metaconid

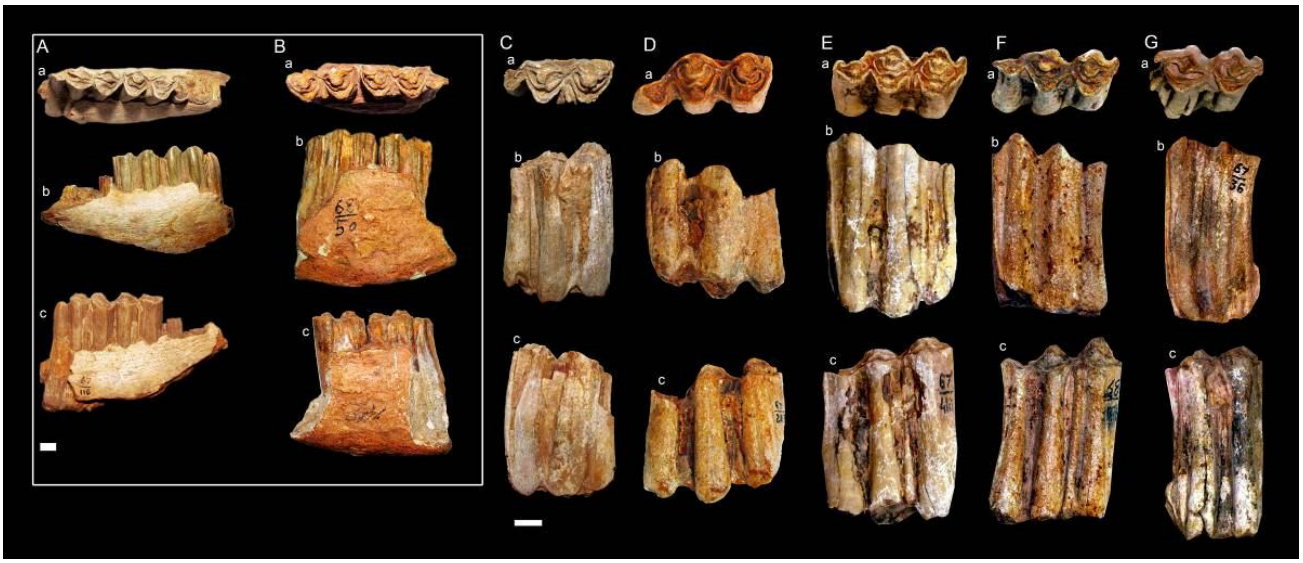

Fig. 4. *Proamphibos kashmiricus*. Lower dentition: **A**, PUPC 67/116, a right mandible fragment with m2-3; **B**, PUPC 68/50, left mandible fragment with m2-3; **C**, PUPC 66/72, rm3; **D**, PUPC 67/283, rm3; **E**, PUPC 67/412, rm3; **F**, PUPC 68/196, rm3; **G**, PUPC 67/36, partial rm3. Views; a = occlusal, b = lingual, c = labial. Scale bar 10 mm.

and the entoconid. A shallow vertical groove is present posterolabially. The cementation is present and the cingulum is absent.

The lower molars are finely preserved with rugose enamel (Figs. 3H, I; 4A-G). The protoconid, hypoconid, paraconid, metaconid and entoconid are excellently preserved. The shallow vertical groove separating the protoconid from the protostylid is present antero-labially. The metastylid is heavy and looks like slender. The fossettids with spurs are crescent shape. There is a basal expansion of the metastylid. The ectostylid is heavy and more close to the protoconid than the hypoconid. The prae-entocristid is smaller than the postentocristid. The deep vertical groove narrow at the base and broad towards the top is present between entostylid and entoconid. The m3 is a three-lobed tooth with a strongly developed parastylid. The talonid of m3 is present posteriorly (Fig. 4). The measurements of the teeth are given in Table I.

Comparison

The absence of temporal lines is an indication of the absence of horn cores. The studied skull differs from the respective ones of *Bison*, *Bubalus*, *Bos*, *Leptobos* and male *Proamphibos* in the absence of strong temporal lines (Martinez-Navarro *et al*., 2007). The weak or absent temporal lines of the skull are the features found in *Bucapra*, *Hemibos* and female *Proamphibos*. *Bucapra* differs from the studied skull in having a narrow and high skull. The small mastoid width of the skull associates it to *Proamphibos* in distinction to *Hemibos* (Pilgrim, 1937, 1939). Two species of *Proamphibos, P. lachrymans* and *P. kashmiricus* are present in the Siwaliks. The skull surface is not rugose, the rugosity is normally absent in female *P. kashmiricus* (Pilgrim, 1939). Morphometrically, the studied skull resembles with that of a female *P. kashmiricus* (Table I; Fig. 2). The absence of the temporal lines indicates that the specimen belongs to a hornless female of *P. kashmiricus*. The features width of the skull at the mastoid process and the narrowness of the skull fit pretty well with the previously described female skull of *P. kashmiricus* (Table II with comparative measures).

The teeth differ from Alcelaphini in having anterior transverse flange and ectostylid which are absent in alcelaphines (Gentry, 1978). The teeth differ from Boselaphini in having cement, disappearance of enamel wrinkling and enlargement of entostyle. The teeth associate with Bovini in having large size, anterior transverse flange, hypsodonty, strong entostyle/ectostylid, strong

Table I.- Comparison of the cheek teeth (mm) of *Proamphibos*. * the studied specimens. Referred data are taken from Pilgrim (1939), Akhtar (1992) and Khan *et al.* (2009a).

Taxa	Specimen inventory No.	Nature	Length	Width	W/L
P. kashmiricus	PUPC 66/80*	rP4	21.25	21.10	0.98
	PUPC 66/141*	lP4	19.85	21.70	1.09
	PUPC 68/54*	rM1	30.35	19.10	0.62
	PUPC 66/22*	rM2	35.60	26.05	0.73
	PUPC 67/295*	rM2	30.25	19.25	0.63
	PUPC 68/55*	rp4	23.7	9.250	0.39
	PUPC 69/475*	lm1	30.75	14.10	0.45
	PUPC 67/116*	rm2	27.70	13.30	0.48
		rm3	36.00	13.65	0.37
	PUPC 67/268*	rm2	32.75	18.25	0.55
	PUPC 68/50*	lm2	32.30	16.05	0.49
		lm3	42.10	16.05	0.38
	PUPC 66/72*	rm3	37.80	14.85	0.39
	PUPC 67/36*	rm3	35.30	14.90	0.42
	PUPC 67/283*	rm3	44.35	17.25	0.38
	PUPC 67/302*	rm3	35.80	16.15	0.45
	PUPC 67/406*	rm3	37.70	16.80	0.44
	PUPC 67/412*	rm3	44.50	16.25	0.36
	PUPC 68/59*	rm3	41.50	13.70	0.33
	PUPC 68/196*	rm3	42.20	15.90	0.37
	PUPC 68/204*	rm3	35.05	13.20	0.37
	PUPC 66/144*	lm3	31.75	15.05	0.47
	GSI B561	P4	19.00	25.00	1.31
		M1	26.00	26.00	1.00
		M2	31.00	27.00	0.87
	PUPC 84/27	P4	18	19.5	1.08
		M1	27	25	0.92
		M2	32	23	0.71
	PUPC 72/57	P4	20	23	1.15
	GSI B561	m3	31	24	0.77
P. sp.	PUPC 69/641	P4	21	24	1.14
		M1	24	26	1.08
		M2	30	27	0.90
P. lachrymans	PUPC 68/79	m1	25	16	0.64
		m2	28	16	0.57
		m3	42	16	0.38
	B810	m1	22.5	18	0.80
		m2	24.5	18	0.73
		m3	34.5	18	0.52
	B811	m1	21	16	0.76
P. dhokawanensis	PUPC 69/351	m1	29	14	0.48
		m2	35	15	0.38
		m3	39	15	0.38

Table II.- Comparison of the cranial measurements (mm) of female *Proamphibos*.

Description	*P. kashmiricus* female (PUPC 71/57) Khan and Akhtar (2011)	*P. kashmiricus* female (GSI B817) Pilgrim (1939)	*Bucapra daviesii* (BMNH 36677, Rutimeyer, 1878) Pilgrim, 1939	*P. kashmiricus* female (PUPC 10/87*) studied sample
Breadth of skull at mastoid	200	?164	160	138
Skull length	-	-	-	156.5
Cranial length	-	-	-	102
Width of the braincase	114	112	105	96
Basal length	-	-	-	333
Distance from fronto-nasal suture to fronto-parietal suture	-	126	-	104
Premolare-prosthion	-	-	-	62
Short skull length	-	-	-	263.6
Oral palatal length	-	-	-	174.4
Basion-palatinoorale	-	-	-	155.5
Lateral length of the premaxilla	-	-	-	72.4
Lateral facial length	-	-	-	135.8
Length of the braincase	-	-	-	112
Greatest inner length of the orbit	-	-	-	62
Greatest inner height of the orbit	-	-	-	62
Height of nuchal crest	-	-	-	48.7
Distance between orbital ridge and frontal suture	-	-	-	66
Length of frontal suture	-	-	-	117.8
Distance between supra-orbital pit and orbital ridge	-	-	-	28.3
Distance between supra-orbital pits	-	82	-	68
Distance between supra-orbital pit and frontal suture	-	-	-	38
Length of upper premolar series	-	62	63	48.6
Length of upper molar series	-	87	85	78.5

style/stylid and prominent ribs (Pilgrim, 1939; Khan *et al*., 2009a). The excessive antero-posterior compression confirms the specimens of Bovini (Figs. 3, 4). The excessive antero-posterior compression of Bovini molars has produced median ribs of extraordinary strength. The quadrate shape of the upper molars is a feature of the bovine kinds *Proleptobos* and *Proamphibos* and equally some elongation has taken place in *Leptobos*, *Hemibos* and in a much less degree in *Bubalus*. The morphometery of the dental remains fit with *Proamphibos kashmiricus* (Pilgrim, 1939; Khan and Akhtar, 2011) and the material is referred to *Proamphibos kashmiricus.*

DISCUSSION

The fossil occurrence of *Proamphibos* along with *Equus, Cervus, Bubalus* and *Elephas* were recorded from the Sardhok outcrops. The genus *Equus* appeared in south Asia ca. 2.5 Ma (Lindsay *et al.*, 1980). *Equus sivalensis* Interval-Zone or the

Pinjor Stage is still treated as a single unit that lasts without internal subdivisions from 2.6–0.6 Ma. *Elephas planifrons* Interval-Zone is little later ca. 2.9 Ma. *Equus* and cervids with antlers entered arrived in the Subcontinent around the Gauss–Matuyama boundary ca. 2.58 Ma (Barry *et al*., 1995). The stratigraphic range of the assemblage suggests the age dated between 2.6 and 0.6 Ma.

The hypsodont teeth are actual an adaptation for more fibrous or abrasive plants in more open and arid habitat (Van Valen, 1960; Fortelius, 1985; Janis and Fortelius, 1988; Solounias *et al*., 1994; Fortelius and Solounias, 2000). Damuth and Fortelius (2001) noted that hypsodonty might be result of overall dry environment or a regularly occurring dry season with other factors (Fortelius, 1985; Janis and Fortelius, 1988). The large body size, hypsodonty and robust dentition in bovines indicate dry-season grasslands during Early Pleistocene. *Proamphibos* implies grassy woodlands penetrating open forests formed under drier conditions and opened vegetation. The bovines would live here together with proboscideans, cervids and antilopes (Dennell *et al*., 2006, 2008; Khan *et al.*, 2011).

The present study suggests a major turnover in land mammals which occurred after 2.5 Ma, indicating a change towards a cooler, drier and more variable climate. *Proamphibos* is the grazer and inhabitant more-open areas near water. Many other species that were bound to forest and wet habitats (*e.g., Tragoportax, Selenoportax, Pachyportax, Dorcatherium, Dorcabune*) disappeared during the time interval (Khan *et al*., 2009b, 2012b). The associated change has been observed in the Northern Hemisphere and Africa at about this time (2.5 Ma) (Montgelard *et al*., 1997; Behrensmeyer *et al*., 1997; Williams *et al*., 1999).

The faunal change has been observed in the outcrops nearby the Sardhok village in the Pleistocene. The macro-fauna is indicatives of climatic change in the Pleistocene, leading to increase aridity, cooling and variable seasonality. The large mammals might have adapted wooded grassland, semiarid sandy plains, and seasonal pool, pond bank. The significant findings of the large hypsodont mammals may be related to the intensification of wooded grassland (Fortelius *et al*., 2002).

CONCLUSIONS

The large mammals have been noticed in the outcrops of Sardhok. The Sardhok outcrops were mainly characterized by the presence *Proamphibos kashmiricus* with other mammalian taxa like *Equus*, *Elephas*, *Hemibos*, *Hexaprotodon* and *Rhinoceros* during the Pleistocene. These taxa indicate the open wooded grasslands ecosystem in the Pabbi Hills of Sardhok, northern Pakistan. *Proamphibos* indicates open country forms (Graze or Browse) and support aridity in the Pleistocene. The habitat spectrum indicates grazing forms dominated over browsers and browsing-grazing forms.

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(Received 27 November 2013, revised 26 May 2014)