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PALAEODIETARY AND PALAEOCLIMATIC INTERPRETATIONS FOR HERBIVORE FAUNA FROM LATE PLIOCENE TO EARLY PLEISTOCENE SIWALIKS OF PAKISTAN

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ABSTRACT

Stable isotopes analysis of carbon and oxygen have the potential to explore the diet and climate of past communities. The end of Miocene in the Siwaliks of Pakistan marks faunal turnover due to climatic change with higher rates of aridity and an expansion of C_4 grasslands. But after the Miocene, the studies regarding diet and climate of herbivore communities are still highly un-explored. We present here the analysis of $\delta^{13}C$ and $\delta^{18}O$ to estimate the diet and climate endeavored by herbivore communities from the Plio-Pleistocene Siwaliks of Pakistan. Our results indicate that the proportion of C_3 diet in the Pliocene fauna was diminished but not absent while Pleistocene fauna do not report any evidences of C_3 vegetation. The Pliocene and Pleistocene time span reports the flood plain environment with increased aridity which favored more C_4 grasses from 3.6 to 0.6 Ma. We found that Pliocene and Pleistocene Siwalik faunas have close affinities with African faunal communities with respect to their dietary and ecological niche.

Key words: Upper Siwaliks, Soan Formation, Palaeovegetation, Mammals.

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INTRODUCTION

The Stable isotope analysis of carbon and oxygen is a pivotal tool to explore the palaeodiet and palaeoecology of the past communities (Quade *et al*., 1992; Levin *et al*., 2008; Levin, 2015; Cerling *et al*., 2011, 2015; Wynn *et al*., 2013). The reconstruction of palaeovegetation on floodplains in sub-tropical regions can be done precisely by using stable isotopes of carbon (Quade *et al*., 1989, 1995; Barry *et al*., 2002). The SI analysis of carbon is a reliable tool to differentiate C_3 and C_4 cycles utilized by any regional flora for photosynthesis (Ehlinger and Cooper, 1988; Vogel, 1978). The particular carbon isotopes markers can subsequently be recorded in the body tissues of primary consumers as C_3 pathway mostly utilized by trees and most of the plants while C_4 pathway is utilized by some shrubs and most of the grasses (DeNiro and Epstein, 1978). Thus carbon isotopes can be used to infer the dietary preferences of animals living in a specific landscape and carbon & oxygen isotopes can be utilized to reconstruct palaeoclimatic picture endeavored by these animals (Bibi, 2007; Cerling *et al*., 2011, 2015; Sponheimer *et al*., 2013; Du *et al*., 2019). Thus, palaeo vegetation can be estimated from dietary signals being recorded in teeth of an animal, based on the fact that species dietary preferences are linked to physical as well as ecological attributes of its habitat (Cerling *et al*., 1997, 2015; Kingsten and Harris, 2007; Levin *et al*., 2015; Sponheimer *et al*., 2003, 2013; White *et al*., 2009). Such community based studies of carbon isotopes from enamel of herbivores are mostly used to infer the link between diet, vegetation and environment (Bibi, 2007; Levin, 2015).

Oxygen isotopes depict the water intake preferences of herbivores. $\delta^{18}O$ values of leaf are recorded to be higher than that of meteoric sources mainly due to evaporative enrichment factor (Yakir, 1997). Thus those mammals which take their water from plants tend to show a little higher $\delta^{18}O$ values than that are obligate drinkers (Spoonheimer and Lee Thorp, 1999, 2001). Thus, we think browser should represent a more negative values than that of grazers. But the interpretation of oxygen isotopes is not straightforward, the oxygen isotope values are also linked to canopy effect, open land, open water holes, flowing water as well as the drinking preferences of animal (Estes, 1991). In this paper we have utilized oxygen isotopes to infer water intake preferences of Plio-Pleistocene fauna of the Upper Siwaliks of Pakistan.

The Upper Siwaliks in Pakistan extends from 3.3-0.6 Ma, more conventionally, from late Pliocene to middle Pleistocene and allows us to investigate one of longest fluvial sequences (Dennell *et al*., 2006). Upper Siwaliks has been divided in three faunal stages viz. Tatrot, Pinjor and Boulder conglomerates (Pilgrim 1910, 1913). Tatrot/Pinjor boundary has been set at 2.58 Ma and latest Pinjor at <0.78 Ma. The Upper Siwaliks fauna has been explored scantily with reference to stable isotope analysis. Thus here we use stable isotopes of carbon and oxygen to explore the palaeodiet, palaeoclimate and palaeovegetation of mammalian communities of the Upper Siwaliks of Pakistan.

Geological Settings: Rendell, (2004**)** assigned two biostratigraphic intervals in the Upper Siwaliks on the basis of mammalian fauna and magnetostratigraphic controls. First is the *Elephas planifrons* interval spanning 3.6-2.6 Ma and second is *Equus sivalensis* interval spanning 2.6 to 0.6 Ma. These faunal intervals are based upon mammalian fauna and magnetostratigraphy. The taxa that are reported from *Elephas planifron* interval include Equids, Elephantids, Cervids, Bovids, Suids and Giraffes (Barry *et al*., 1982, 2002; Nanda, 2002). While *Equus sivalensis* interval also documents Equids, Cervids, Hippos, Giraffids, Suids, Bovids and Rhinos (Ghaffar *et al*., 2017).

The village of Tatrot (Fig. 1a) is situated in Upper Siwaliks, 70 km west of Jhelum city (32°22`N, 72°47`E). The composition of Tatrot Formation includes clays, siltstone and shales while the color varies from reddish orange to brown. The medium to fine sized sandstones along with interbedded dark gray conglomerates are part of Tatrot Fm. The average thickness is accounted to be 300 m (Shah, 1980).

The Pinjor Fm. is exposed at Sar Dhok and Pabbi Hills area (included in this study). The Sar Dhok (Fig. 1b) is characterized by greyish brown medium to fine grained sandstones with intermingling pebbles and large scaled cross stratification. Brown mudstones are also visible with pedogenic horizons while conglomerates are well imbricated in between. The type locality of Pinjor in India has been dated magneto-stratigraphically and has been assigned an age of 2.48-0.63 Ma. While Pabbi Hills also represent a large fluvial sequence with many fossiliferous sites (Fig. 1c) and the average thickness has been calculated as 1000 m. A comprehensive work of Dennell (2008) and Dennell *et al*., (2006) on Pabbi Hills reports the age of these foothills as upper Pliocene to middle Pleistocene (2.2-0.9 Ma). Our study includes the samples from Choawala Kas which contain the Sandstone 12 (Dennell *et al*., 2006) hence can be assigned an age of 1.2-1.4 Ma. So on the basis of above mentioned stratigraphic controls, we assign Tatrot as late Pliocene having an age of 3.4-2.6 Ma. While the samples which are recovered from Sar Dhok has been assigned an age of 2.5-0.6 Ma and samples collected from Pabbi Hills Sandstone, an age of 1.4-1.2 Ma (Hussain *et al*., 1992; Barry *et al*., 2002, Nanda, 2008; Dennell *et al*., 2006).

The collection for this study has been carried out from Tatrot, district Jhelum; Sar Dhok, district Gujrat and Pabbi Hills, northern Punjab, Pakistan (Fig. 1a,b,c).

The stable isotope analysis of carbon and oxygen from Tatrot and Pinjor stage along with above mentioned stratigraphic controls, allow us to investigate the palaeodiet, palaeovegetation and palaeoclimate of late Pliocene to early Pleistocene mammalian fauna of the Upper Siwaliks, Pakistan.

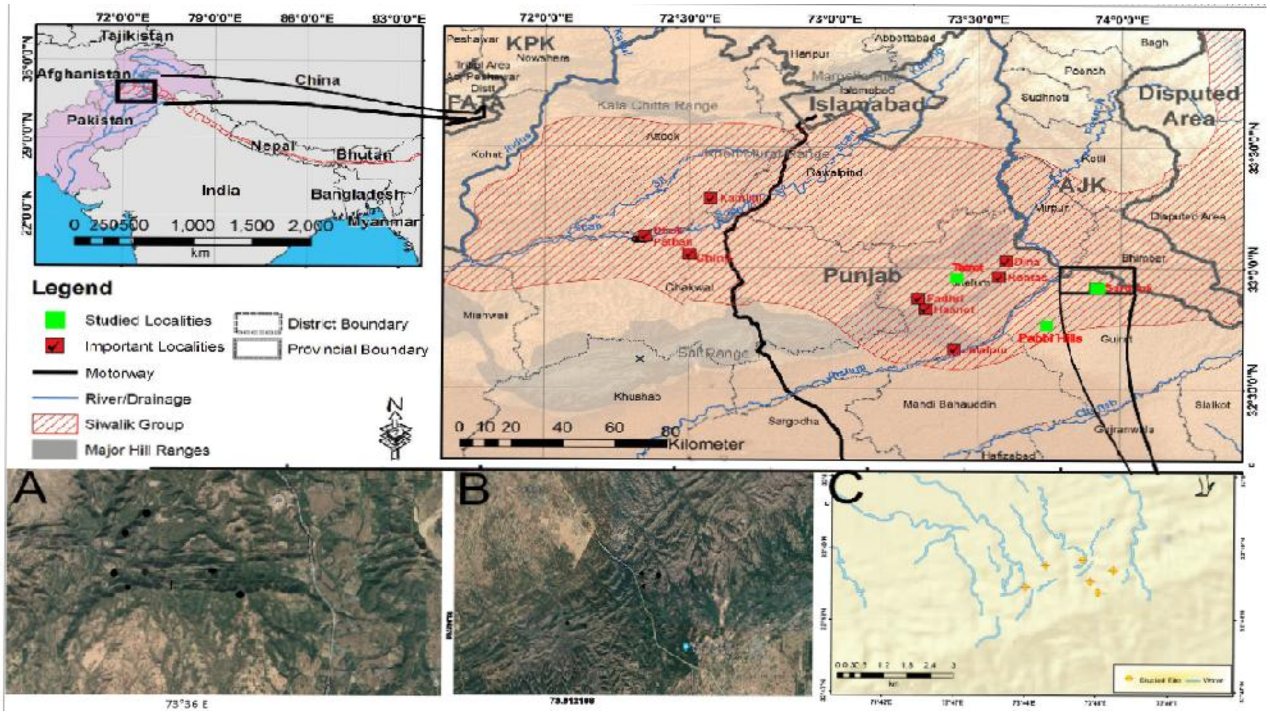

Fig. 1. The sample collection sites along the Upper Siwaliks of Pakistan. A = Tatrot localities, B = Sar Dhok , C = Pabbi Hills localities.

MATERIALS AND METHODS

A sum of 40 fossil specimens were selected on the basis of their morphologic and morphometric characteristics and their stratigraphic provenance. The specimens were cleaned by using detergents and water while dust was separated by using low speed drills. Specimens were then identified up to the species level. Twenty specimens from the Tatrot Fm. and twenty specimens from the Pinjor Fm. (5 from each studied family from Tatrot and Pinjor, respectively) were sampled for stable isotope analysis to check our hypothesis that there are significant differences in palaeodiet and palaeoclimate among the Pliocene and Pleistocene mammalian communities. The studied families included Rhinocerotidae, Bovidae, Suidae, Elephantidae and Equidae.

For the extraction of enamel, Foredom Rotary Dental Drill with carbide burrs was used. 15-20 mg of enamel was extracted from each tooth (only molars and pre-molars were included). Enamel was extracted along one single transect from root to crown (longitudinal) from buccal surface of upper and lingual surface of lower molars. Enamel was selected for the analysis due to its high resistance against diagenesis and large crystal size which make it the best tissue for isotope analysis (Koch *et al.*, 1997).

The powdered enamel was further pre-treated with 10 ml of 2% NaOCl for one hour and the solution was decanted and rinsed with distilled water for 3 times. The samples were than treated with 10 ml of 0.1% Acetic Acid for 1 hour and then samples were oven dried for further isotope analysis (Basics from Koch *et al.*, 1997).

For the Isotopic Ratio Mass Spectrometry, samples were shipped to PINSTECH, Islamabad, where further analysis was done. Carbon and oxygen isotope values were reported to isotope standards such that:

$\delta^{13}C$ or $\delta^{18}O = (R_{\text{sample}}/R_{\text{standard}} - 1)/1000$

The values were reported in V-PDB for both carbon and oxygen isotopes. As isotopic values were calculated from enamel samples of large herbivore species, thus a fractionation factor of 14 ‰ for elephants, bovids, equids, rhinos and 13‰ for suids was selected according to the Cerling and Harris (1999) and Sponheimer *et al.*, (2003). For the Statistical analysis between Pinjor and Tatrot fauna, student t-test along with Wilcoxon test was used assuming un-equal variances. For the analysis of families within each stage, one-way ANOVA was applied along with post-hoc test. All the analysis and graphs were made using SPSS, version 16.

RESULTS

Carbon Isotopes Values: In carbon isotopes ratios, a range of values across Tatrot and Pinjor Fm. was found to be in between -9.38 ‰ to 3.29 ‰ and the difference of 12.67 ‰ was calculated for all the forty samples and across all the five families. The mean of all the analyzed samples is -3.55 ‰. The t-test along with the Wilcoxon test revealed significant differences ($p<0.05$; $p=0.023$) among late Pliocene (average $\delta^{13}C = -5.7‰$) and Pleistocene (average $\delta^{13}C = 1.17‰$) samples. When one-way ANOVA was applied, to check out the differences among Tatrot families (Pliocene), a significant difference was recorded ($p=0.004$). While Pleistocene families did not show any significant differences ($p=0.138$) among each other. The Pinjor (Pleistocene) fauna represented more enriched values of carbon stable isotopes as compared to the Tatrot fauna (late Pliocene) (Table 1).

Oxygen Isotope Values: The $\delta^{18}O$ ratios between all samples range from -11.2 ‰ to +2.46 ‰ and the average is -6.52 ‰. The t-test along with Wilcoxon test among Pinjor and Tatrot samples revealed non-significant differences ($p=0.397$). When the inter family comparison was carried out by applying one-way ANOVA with post hoc test, non-significant differences were found for oxygen isotopic ratios ($p=0.072$ and 0.342 for Tatrot and Pinjor families respectively).

Table 1. Stable isotope analysis of carbon and oxygen of the mammalian communities of Upper Siwaliks (late Pliocene to early Pleistocene).

Sample Number	Family	Species	Epoch	Localities	Position	d13C (‰ V-PDB)	d18O$_C$ (‰ V-PDB)
EB-301	Equidae	*Equus sivalensis*	Pleistocene	Sar Dhok	m3	-0.1	-6.18
EB-302	Equidae	*Equus sivalensis*	Pleistocene	Pabbi Hills	m3	-2.42	-4.69
EB-303	Equidae	*Equus sivalensis*	Pleistocene	Sar Dhok	m2	-0.3	-5.77
EB-304	Equidae	*Equus sivalensis*	Pleistocene	Sar Dhok	m3	-0.06	-0.56
EB-305	Equidae	*Equus sivalensis*	Pleistocene	Sar Dhok	m3	-0.22	-3.04
EB-306	Rhinocerotidae	*Rhinoceros sondaicus*	Pleistocene	Sar Dhok	Tusk	-1.27	-9.24
EB-307	Rhinocerotidae	*Rhinoceros unicornis*	Pleistocene	Dhok Gall	M1	1.71	-4.45
EB-308	Rhinocerotidae	*R. unicornis*	Pleistocene	Sar Dhok	M2	0.85	-6.27
EB-309	Rhinocerotidae	*R. unicornis*	Pleistocene	Dhok Gall	M1	1.1	-3.34

EB-310	Rhinocerotidae	*Rhinoceros sondaicus*	Pleistocene	Dhok Gall	m3	-0.89	-5.67
EB-311	Bovidae	*Bison sivalensis*	Pleistocene	Sar Dhok	m3	-1.02	-7.29
EB-312	Bovidae	*Bison sivalensis*	Pleistocene	Sar Dhok	m1	1.2	-6.22
EB-313	Bovidae	*Bos*	Pleistocene	Sar Dhok	M1	-1.9	-6.77
EB-314	Bovidae	*Bos*	Pleistocene	Pabbi Hills	m2	-2.4	-5.9
EB-315	Bovidae	*Bos*	Pleistocene	Pabbi Hills	P2	-7.76	-5.83
EB-316	Suidae	*Sus*	Pleistocene	Pabbi Hills	M3	-2.3	-6.5
EB-317	Suidae	*Sus*	Pleistocene	Sar Dhok	M3	-3.4	-6.9
EB-318	Suidae	*Sus*	Pleistocene	Sar Dhok	M1	-1.2	-8.9
EB-319	Suidae	*Sus*	Pleistocene	Sar Dhok	M1	-1.4	-7.6
EB-320	Suidae	*Sus*	Pleistocene	Sar Dhok	P4	-1.7	-4.3
EB-321	Equidae	*Equus sivalensis*	Pliocene	Tatrot	m3	-2.37	-1.07
EB-322	Equidae	*Equus sivalensis*	Pliocene	Tatrot	M3	-1.56	-4.56
EB-323	Equidae	*Equus sivalensis*	Pliocene	Tatrot	m3	-7.7	-5.11
EB-324	Equidae	*Equus sivalensis*	Pliocene	Tatrot	m3	-1.77	2.46
EB-325	Equidae	*Equus sivalensis*	Pliocene	Tatrot	m2	-8.18	-9.82
EB-326	Bovidae	*Pachyportax nagrii*	Pliocene	Tatrot	P4	-1.44	-10.31
EB-327	Bovidae	*Pachyportax nagrii*	Pliocene	Tatrot	P4	3.29	-7.02
EB-328	Bovidae	*Bos*	Pliocene	Jarikas	M3	1.85	-7.70
EB-329	Bovidae	*Bos*	Pliocene	Tatrot	P2	-7.76	-5.83
EB-330	Bovidae	*Bos*	Pliocene	Kotal Kund	P2	-0.29	-7.39
EB-331	Elephantidae	*Elephas hysudricus*	Pliocene	Kotal Kund	M1	0.28	-5.68
EB-332	Elephantidae	*Elephas planifrons*	Pliocene	Tatrot	M3	-1.41	-6.99
EB-333	Elephantidae	*Elephas planifrons*	Pliocene	Tatrot	M2	-1.27	-4.80
EB-334	Elephantidae	*Elephas planifrons*	Pliocene	Tatrot	m1	0.63	-2.14
EB-335	Elephantidae	*Elephas planifrons*	Pliocene	Tatrot	M3	-3.40	-6.80
EB-336	Rhinocerotidae	*Rhinoceros sivalensis*	Pliocene	Tatrot	M3	-7.6	-8.36
EB-337	Rhinocerotidae	*Rhinoceros sivalensis*	Pliocene	Tatrot	M2	-8.46	-9.52
EB-338	Rhinocerotidae	*Rhinoceros sivalensis*	Pliocene	Tatrot	M1	-7.27	-9.61
EB-339	Rhinocerotidae	*Rhinoceros platirhinus*	Pliocene	Tatrot	M3	-9.38	-9.11
EB-340	Rhinocerotidae	*Rhinoceros sp.*	Pliocene	Tatrot	M1	-7.11	-11.12

DISCUSSION

Palaeodiet: Generally, the carbon isotope ratios follow the inferences based upon the functional morphology of tooth structure (Bibi, 2007), but sometimes it leads to confusions. For example, while predicting the diet for elephants, there was a confusion raised when some of the researchers reported that the recent elephants graze while other reported a browsing behavior (Tangley, 1997; Laws *et al*., 1974; Dublin, 1995; Norten and Griffiths, 1979). Such confusions while estimating the dietary niche of species require a more accurate proxy such as stable isotopes of carbon (Cerling and Harris, 1999).

Here we try to reconstruct dietary and habitat preferences among 5 families across the Plio-Pleistocene Siwaliks of Pakistan. We present a comparative approach between 3 families from Pliocene and Pleistocene respectively, while elephantidae and suidae are reported only from Pliocene and Pleistocene respectively.

Family Equidae: Family Equidae has been considered as one of the early families who shifted their diets towards C_4 grasses (Uno *et al*., 2011). The samples analyzed in this study show an average value for $\delta^{13}C$ of -4.31‰ from Pliocene and -0.62‰ from Pleistocene indicating a clear shift towards C_4 grasses (Fig. 3,4). Our results for equid diet are in-line with Uno *et al*., (2011) who explored the African fauna and reported an average of -1.0 ‰ from Apak Formation dated early Pliocene (4.2 Ma).

The reported isotopic data complements the hypothesis based on morphological as well as mesowear analysis. The high HI index, sharp or blunt buccal apices of cusp and the increased complexity has indicated a grazing diet for Equid (Wolf *et al*., 2013; Fortelius and Solunieus, 2000). Such type of characters are also evident in recent horses which are grazers.

The higher values for $\delta^{18}O$ (-3.62 ‰ and -4.04 ‰ for Pliocene and Pleistocene Equids respectively) as compared to late Miocene horses (Nelson, 2005) indicate that open evaporating water holes were available for drinking to the horses in Pliocene and Pleistocene time spans while the riverine system was shrank as compared to late Miocene (Barry *et al*., 2002; Dennell, 2008).

Family Rhinocerotidae: The family Rhinocerotidae represents an interesting case across the Plio-Pleistocene Siwaliks of Pakistan. The Pliocene Rhinos (*R. sivalensis* and *R. platirhinus*) represent $\delta^{13}C$ average of -7.96‰ which is indicative of mixed C_3 and C_4 feeding with closer affinities towards C_3 type feeding. *R. sivalensis* show dental affinities towards C_3 type vegetation as its dental size is smaller and less complex but *R. platirhinus* has complex dental pattern with high crown (Khan *et al.*, 2014) indicative of C_4 feeding. While the Rhinos from Pleistocene (*R. sondicus* and *R. unicornis*) reveals highly enriched values with $\delta^{13}C$ averaging as 0.3 ‰ which is indicative of feeding purely on C_4 grasses. The picture in African faunal community is synchronous to Pleistocene of Siwaliks but not with Pliocene values. Uno *et al.*, (2011) report a $\delta^{13}C$ average of -2.4‰ and 0.3‰ from Apak (4.2Ma) and Kaymun Formation (3.2Ma) which represents that Rhinos shifted on C_4 type feeding at the end of late Miocene time span in Africa. We suggest that some species of Rhinos were still C_3 feeders in Pliocene while other shifted to C_4 feeding. This hypothesis needs further attestation with larger sample size across all the Plio-Pleistocene *Rhinoceros* species of the Siwaliks of Pakistan.

Oxygen isotope analysis of family Rhinocerotidae shows $\delta^{18}O$ average of -9.54‰ and -5.79‰ for Pliocene and Pleistocene Rhinos respectively. These values indicate that the water intake behavior of Pliocene Rhinos was different from Pleistocene Rhinos with former drinking under shaded ecosystem while later drinking on open water bodies with higher rates of evaporation. Alternatively, there was a shift in rainfall seasons or amount rainfall from Pliocene to Pleistocene due to further uplift of Himalaya which caused more pronounced seasonality (Nelson, 2007).

Family Bovidae: Family Bovidae has been reported to be adapted towards more C_4 feeding at the end of late Miocene (Barry *et al.*, 2002; Uno *et al.*, 2011) and shifted completely on C_4 feeding in Plio-Pleistocene as our results show $\delta^{13}C$ average value of 0.87‰ and -2.37‰ (Figure 2,3) from Pliocene and Pleistocene respectively. Contemporary African bovids shows a range of -6.6‰ to -2.2‰ at 3.2 Ma (Uno *et al.*, 2011) indicating a slow shift towards C_4 vegetation. However, our results show no significant difference between Pliocene to Pleistocene bovids ($p>0.05$) thus, we assume that bovids were consistently grazers throughout the Upper Siwaliks. Our results agree with the findings of Wynn *et al.*, (2013); Cerling *et al.*, (2015) and White *et al.*, (2009) who reported that bovids fed on C_4 grasses at the start of Pliocene.

The $\delta^{18}O$ values of -7.65‰ and -6.40 ‰ across Plio-Pleistocene respectively indicate that former utilized plant water (based on the bovids physiology) from shaded areas while later utilized foliage from more open environment with higher rates of evapotranspiration (Bibi, 2007, 2009). We suppose that the environment of Pleistocene has more pronounced seasonality which effected the pattern of rainfall, plant cover and overall environment.

Family Elephantidae and Suidae: Stable isotope values of carbon and oxygen for Elephants and Suids are reported from Pliocene and Pleistocene respectively. Our analysis of Elephants (*E. planifrons* and *E. hysudricus*) indicate a pure C_4 grazing behavior for Pliocene elephants with $\delta^{13}C$ average of -1.3 ‰. In the late Miocene, the elephants were more browsers but they shifted their dietary niche towards grazing in Pliocene having enriched carbon isotope value (Cerling and Harris, 1999; Sukumar and Ramesh, 1995 and Uno *et al.*, 2011).

The average $\delta^{13}C$ value for suids in Pleistocene is -2.0‰ which supports that suids fed on grasses in Pleistocene. The results are in-line with African picture with suids feeding on C_4 vegetation in Pleistocene. Extant suids also feed on C_4 grasses (Cerling *et al.*, 2015).

The $\delta^{18}O$ values for Elephants from Pliocene and Suids from Pleistocene are -5.28‰ and -6.84‰ (Figure 2,3) respectively indicating that these animals preferred a mosaic of shady and open environment. The role of seasonality should be evaluated in order to understand amount of annual rainfall. We suppose that the rainfall was seasonal where few months of summers have more rainfall as compared to other months of dry winters (Unpublished data).

Comments on Palaeoecology: The carbon isotope composition is a reliable tool to reconstruct the palaeoecology of the extinct animals (DeNiro and Epstein, 1978; ven der Merwe and Medina, 1991; Quade *et al.*, 1995; Nelson, 2007; Cerling *et al.*, 2011; Uno *et al.*, 2011). The rates of assimilation for C_3 and C_4 vegetation are different and these are preferred in different environments. The C_3 pathway is mostly adopted by the trees and plants in average temperature regimes, mostly in 20-30°C. While C_4 type vegetation is supported by extreme temperature and sometime referred as cool season grasses. Thus carbon isotope data can reveal the environment in which an animal fed (*Kohn et al.*, 2002; Barry *et al.*, 2002; Sanyal *et al.*, 2005a,b; Badgely *et al.*, 2008).

The carbon isotope data reports that Pliocene herbivore community in the Tatrot Formation of the Siwaliks endeavored a C_4 dominated environment with mostly grasslands and few shrub-lands. However, the possibility of C_3 vegetation cannot be ruled out (as Rhino samples showed depleted values indicating tendencies towards C_3 feeding). But the possibility of closed canopy forest is minimum and almost ruled out. The carbon isotope record indicate that a significant environmental change occurred at the end of Miocene where C_3 forests replaced by C_4 grasses and mammalian communities shifted to open lands (Cerling *et al.*, 1997; Quade *et al.*, 1995 and Barry *et al.*, 1982, 2002, 2013).

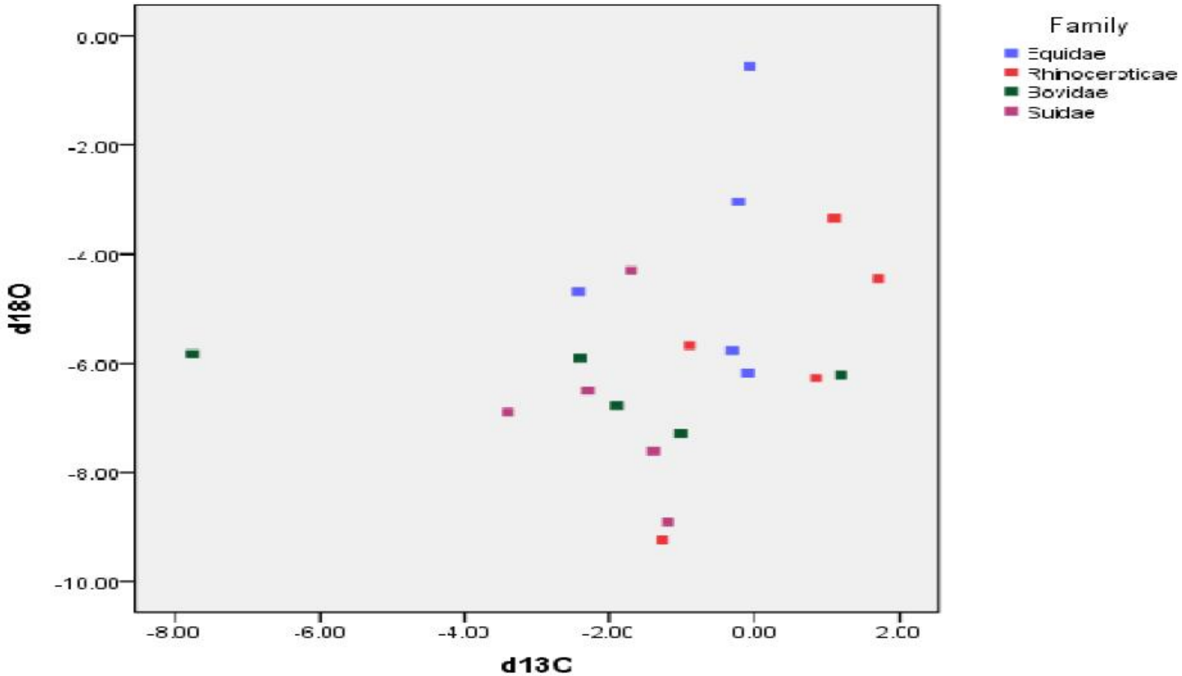

Figure 2. Comparison of $\delta^{13}C$ and $\delta^{18}O$ between families of Pinjor (early Pleistocene) fauna.

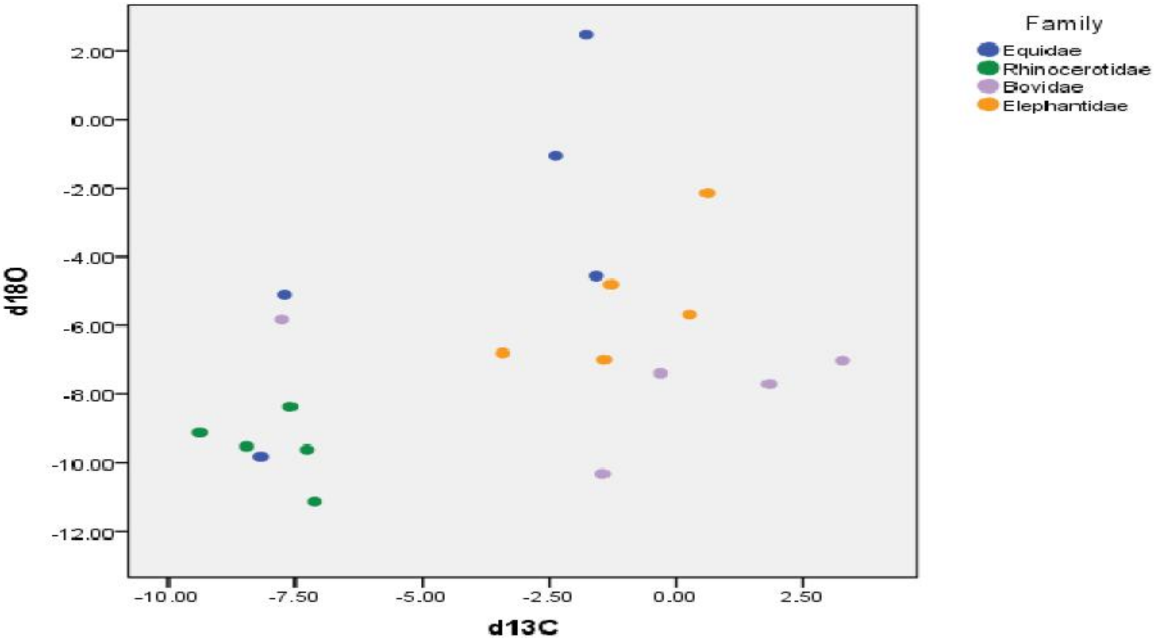

Figure 3. Comparative picture of Tatrot (late Pliocene) fauna of Upper Siwaliks Pakistan.

While the environment became harsher gradually in the Pleistocene time span which documents more arid environments as compared to the Pliocene environment ($\delta^{18}O$ = -5.6‰ and -6.5‰ respectively). Currently the Upper Siwaliks region in Pakistan represents a semi-arid ecosystem with seasonal monsoon. We assume that although C_3 environment started to be replaced with C_4 at the end of late Miocene but some amount of C_3 vegetation were still present in Pliocene of the Siwaliks of Pakistan. Such harsh environment of Plio-Pleistocene timespan forced mammalian species to evolve more advanced characters like increased hypsodonty and tooth crown complexity to cope up with the changing environment.

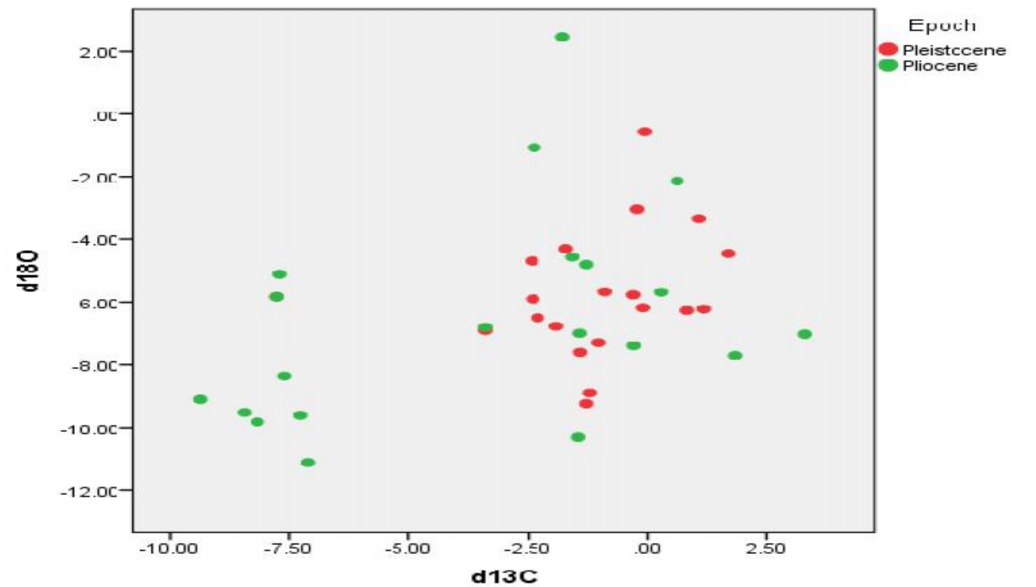

Fig. 4: $\delta^{13}C$ and $\delta^{18}O$ values across late Pliocene to early Pleistocene mammalian communities from the Upper Siwaliks of Pakistan.

Conclusion: The analysis of carbon and oxygen stable isotopes revealed that Plio-Pleistocene environment supported C_4 grasslands at the expense of C_3 vegetation and most of the mammalian species fed on grasses which is also evident from morphological and mesowear analysis. The environment was arid and the aridity increased towards Pleistocene times while most of the animals relied on evaporative water holes or on the foliage cover of open areas for their water intake. The higher oxygen isotope values in Pleistocene indicate that the riverine system was shrunk as compared to late Miocene and Pliocene.

We suggest a detailed study of seasonality with large samples size across the Upper Siwaliks which can answer our question more precisely and will allow us to reconstruct the role of seasonal extremes in the Upper Siwalik mammalian communities.

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