Stable isotope analysis of middle Miocene mammals from the Siwalik sub-Group of Pakistan

MUHAMMAD TAHIR WASEEM, ABDUL MAJID KHAN, JAY QUADE, ANTHONY KRUPA, DAVID L. DETTMAN, AMTUR RAFEH, and RANA MANZOOR AHMAD

Stable isotope analysis is pivotal for investigating the paleodiet and paleoecology of past mammals. In this paper, we analyzed thirty fossil enamel samples belonging to the families Suidae, Rhinocerotidae, and Deinotheriidae for $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ composition to investigate paleodiet and paleoecology of middle Miocene mammals of the Siwalik sub-Group of Pakistan. The three mammalian groups, when combined together, yielded an average $\delta^{13}C_{enamel}$ value of -12.2 ± 2‰, indicating a pure to nearly pure C_3 diet. Suids show slightly higher $\delta^{13}C_{enamel}$ values of -11.2 ± 1.4‰ when compared to rhinocerotids and deinotheres (-12.3 ± 0.8‰ and -12.5 ± 1.3‰, respectively), which could be explained by selective foraging on new leaf shoots or feeding from open spaces. Alternatively, the differences in $\delta^{13}C_{enamel}$ could be due to different digestive physiologies and different enamel-diet enrichment factors. Members of all three families showed significant differences in $\delta^{18}O_{enamel}$ values, where suids yielded higher $\delta^{18}O$ values of -8.2 ± 1.2‰ compared to rhinocerotids and deinotheres (-11.4 ± 1.8‰ and -10.4 ± 1.7‰, respectively). Based upon these results, we assume that these mammals inhabited subtropical forests similar that of mid-Miocene of the Siwalik Group, India and Nepal. The modern analogues of such vegetation system are present in East and South of Myanmar, Nepal, and Malaya where precipitation is enough to support evergreen C_3 forests. By contrast, today's floodplain environments in Pakistan are dominated by C_4 grasses, and C_3 vegetation is only present in non-floodplain settings.

Key words: Mammalia, paleoclimate, paleodiet, Miocene, Chinji Formation, Pakistan.

Muhammad Tahir Waseem [tahirmuhammad1213@gmail.com], Abdul Majid Khan [majid.zool@pu.edu.pk] (corresponding author), and Amtur Rafeh [amturrafeh@gmail.com], Department of Zoology, University of the Punjab, Lahore 54590, Pakistan.
Jay Quade [quadej@email.arizona.edu], Anthony Krupa [akrupa@email.arizona.edu], and David L. Dettman ([dettman @email.arizona.edu], Department of Geosciences, University of Arizona, Tucson AZ 85721, USA.
Rana Manzoor Ahmad [manzoor.zoology@uo.edu.pk], Department of Zoology, University of Okara, Punjab 56300, Pakistan.

Introduction

The temporal and spatial records of climate archived in thick Neogene and Quaternary continental deposits in northern Pakistan provide an exceptional opportunity to explore the patterns of evolution and adaptation of mammals over the time span of million years (Badgley et al. 2008; Morgan et al. 2009; Patnaik et al. 2019). Stable isotope (SI) analysis of carbon and oxygen of enamel from mammals, both expressed in the familiar delta (δ) notation in per mil (‰) according to V-PDB (Vienna Pee Dee Belemnite) standards, allow us to reconstruct the past diets ($\delta^{13}C_{diets}$) and paleo-environmental meteoric water ($\delta^{18}O_{mw}$), which in turn reflect paleovegetation and paleoclimate during the Neogene and Quaternary (Quade et al. 1992, 1995a, b; Cerling et al. 1997a, 2015; White et al. 2009; Sanyal et al. 2005, 2010; Uno et al. 2011; Ben-David and Flaherty 2012; Khan et al. 2020; Waseem et al. 2020a). The Siwalik sub-Group of northern Pakistan contains a high-resolution fossil record spanning the Neogene time period (Quade et al. 1989; Barry et al. 2002, 2013; Dennell et al. 2006; Flynn et al. 2016; Fig. 1). Morgan et al. (1994), Uno et al. (2011), and Hynek et al. (2012) interpreted elevated $\delta^{13}C$ values in fossil herbivore enamel ($\delta^{13}C_{enamel}$) to reflect a component of C_4 vegetation in the mid-Miocene (~11–10 Ma) across several continents.
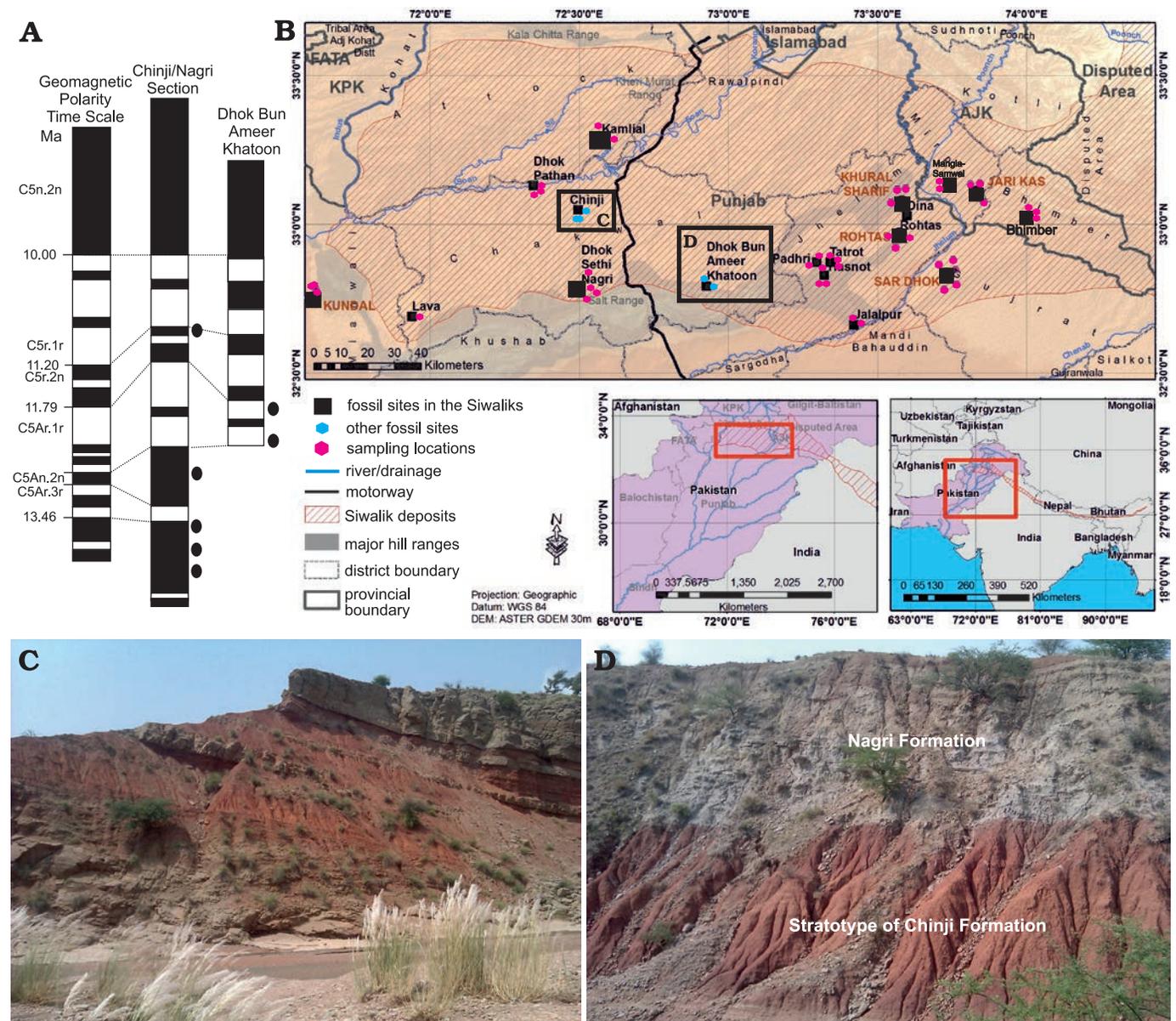
Fig. 1. Map of the Siwaliks indicating the middle Miocene localities from where fossil material for this study was recovered. **A**. Geomagnetic polarity time scale (Gradstein et al. 2012). **B**. Map of the Siwalik sub-Group of Pakistan along with the localities and studied area. **C**. Overview of Chinji-Nagri section. **D**. Overview of Dhok Bun Ameer Khatoon (DBAK) section.

However, the major C_4 radiation in the Siwalik sub-Group has been documented to occur after ~10 Ma (Barry et al. 1982, 2002; Quade et al. 1995a, b; Morgan et al. 2009). In this study, we explore the isotopic composition of enamel from three families of large herbivores to reconstruct paleo-environments and check for evidence of C_4 dietary intake in the middle Miocene (14.2–11.2 Ma) of the Siwalik sub-Group of Pakistan. Enamel was selected for the analysis due to its high resistance to diagenesis and large crystal size and low porosity, which makes it the best material for paleodietary reconstruction in ancient ecosystems (Quade et al. 1992; Kohn et al. 1996, 2002; Kohn and Cerling 2002).

There are three metabolic pathways through which carbon is incorporated in the plants. Trees, nearly all shrubs, forbs, ferns, sedges, and most non-tropical or high altitude grasses utilize the C_3 pathway of photosynthesis in which $\delta^{13}C_{diet}$ ranges from -34 to -22‰ (Koch 1998; Pérez-Crespo et al. 2017), and average around -28.2 ± 6‰ under the present $\delta^{13}C_{CO2}$ = -8‰, or -6.7‰, pre-industrially (Kohn 2010). The C_4 pathway is found in most of the warm region-grasses and some sedges with a range of $\delta^{13}C_{diet}$ values from -14 to -10‰ (Cerling 1999). The abundance of C_3/C_4 vegetation in an ecosystem is governed by many factors, including the mean annual temperature (MAT), mean annual precipitation (MAP), and partial pressure of carbon dioxide in the atmosphere (pCO_2) (Kohn 2010; Waseem et al. 2020b). The comparatively cooler areas (MAT <25°C) with precipitation higher than 1–2 m/year show a dominance of C_3 vegetation while warmer areas (MAT >25°C) with drier conditions (MAP <1–2 m/year) show a dominance of C_4

grasses (Nelson 2007). Furthermore, the C_4 pathway can work efficiently under lower pCO_2 and lower humidity levels compared to C_3 pathway (Medrano and Flexas 2000; Bellasio et al. 2018) due to the fact that carbon is fixed twice in C_4 pathway as compared to C_3 pathway (Kohn and Cerling 2002). The $\delta^{13}C$ values of plants are governed by other factors such as low light intensity, saline soil, water availability, and local microhabitat conditions (Ehleringer et al. 1987; Codron et al. 2005; Bibi 2007).

These averages and ranges in $\delta^{13}C$ value for modern plants were ~1.3‰ higher during the middle Miocene in fossil C_3 and C_4 plants, due largely to the effect of fossil fuel burning in decreasing $\delta^{13}C_{CO2}$ of the atmosphere (see Tipple et al. 2010). Thus, we use the $\delta^{13}C_{CO2}$ (-5.2‰) as in Tipple et al. (2010) for pre-10 Ma time span. The third photosynthetic pathway, crassulacean acid metabolism (CAM), is found in succulent plants which are mostly present in deserts or epiphytic plants in closed forests (Passey et al. 2005; Andrade et al. 2007) and were probably negligible in the Siwaliks.

Upon feeding on plants, the carbon is incorporated in the herbivores tooth enamel during the period of tooth formation. When carbon isotopes are incorporated in the enamel of herbivores, $\delta^{13}C_{enamel}$ values are fractionated by an enrichment factor ($e_{enamel-diet}$):

$$e_{enamel-diet} = (a_{enamel-diet} - 1) \times 1000 \qquad (1)$$

where:

$$a_{enamel-diet} = (d_{enamel} + 1000)/(d_{diet} + 1000)$$

Thus, middle Miocene animals consuming C_3 vegetation outside of rainforests and deserts with $\delta^{13}C_{diet}$ values from -28.1 to -23.1‰ should show $\delta^{13}C_{enamel}$ values ranging from about -14 to -9‰, whereas middle Miocene animals feeding on C_4 vegetation should show $\delta^{13}C_{enamel}$ values ranging from ~-2 to ~+2‰. The values between ~-9 to ~-2‰ are considered to reflect mixed feeding on C_3/C_4 vegetation (MacFadden and Cerling 1996). In this study, we assume that $\delta^{13}C_{enamel}$ values ≤-16.1‰ denote browsing under closed-canopy forests, -16 to -14‰ for sub-canopy browsing, -14 to -12‰ for browsing in forests, and -12 to -8‰ for browsing in woodlands (Cerling and Harris 1999; Domingo et al. 2012). The $\delta^{13}C_{enamel}$ between -8 to -3‰ will be considered as mixed feeding on C_3/C_4 vegetation while values >-2‰ can be interpreted as grazing on dominantly C_4 grasses (Cerling et al. 1997a, b, 2004; Kohn 2010). However, $e_{enamel-diet}$ does not solely depend upon one factor. Tejada-Lara et al. (2018) argue that a single value of $e_{enamel-diet}$ of ~14.1‰ does not account for all the mammals from monkeys to elephants by overlooking the other metabolic and physiological effect on carbon fractionation. For example, different mammals show different $e_{enamel-diet}$ depending on body mass and digestive physiology (Tejada-Lara et al. 2018). Combining all factors, we assume an average $e_{enamel-diet}$ of ~+14.1‰ for large-bodied rhinocerotids and deinotheres and ~+13.1‰ for suids according to Codron et al. (2011) and Tejada-Lara et al. (2018).

Oxygen enters an animal's body in three main ways: (i) from drinking water, (ii) water derived from food, and (iii) inhalation, and leaves the body through sweat, exhalation, and urination (Sponheimer and Lee-Thorp 1999; Koch 2007; Sánchez 2005; Blumenthal et al. 2017, 2018). Of these sources, the majority of oxygen isotopes incorporated into enamel are from drinking water and diet, and $\delta^{18}O$ values of local meteoric water ($\delta^{18}O_{mw}$) are affected by environmental temperature, amount of precipitation, latitude, and altitude (Dansgaard 1964). The general trend of $\delta^{18}O_{enamel}$ values is set by the ecology as the animals living under closed habitat and in humid conditions (forests) tend to show lower $\delta^{18}O_{enamel}$ values compared to the animals living in open and arid (savannah or grasslands) areas (Feranec and MacFadden 2006). Levin et al. (2006) categorized the animals under two broad categories on the basis of their physiology and behavior. Evaporation sensitive (ES) taxa tend to obtain most of their water from their diet (leafy plants) and generally are ruminants ($\delta^{18}O$ values of their enamel is correlated to the evaporation of leaf water), whereas evaporation insensitive (EI) taxa are mostly non-ruminants that depend on surface water for their body water requirements ($\delta^{18}O_{enamel}$ is correlated to local drinking water sources). In this study, all the families sampled can be categorized as EI taxa on the basis of the physiology of the modern analogues, providing better insights into the $\delta^{18}O$ value of palaeo-precipitation (Levin et al. 2006; Blumenthal et al. 2017; Faith 2018).

The fossil fauna of Chinji Formation includes Rhinocerotidae, Suidae, Tragulidae, Bovidae, Giraffidae, Deinotheriidae, Gomphotheriidae, and other taxa including Hominidae, Rodentia, and Carnivora (Pilgrim 1937; Khan et al. 2013; Barry et al. 2013; Flynn et al. 2016). We focus here on the paleodiets, paleoenvironments, and niche partitioning among Rhinocerotidae, Suidae, and Deinotheriidae from the middle Miocene of northern Pakistan. We selected these three EI taxa over non-EI taxa as $\delta^{18}O_{enamel}$ value of EI taxa is correlated to their water source (Faith 2011, 2018). Furthermore, we selected one specialized browser (deinotheres), one taxon (i.e., *Hyotherium pilgrimi*) which disappeared from the Siwalik record during the late Miocene, and one taxon (rhinocerotid, *Chilotherium intermedium*) which shifted towards a C_4 diet during the late Miocene (Badgley et al. 2008; Morgan et al. 2009) to evaluate whether these taxa ate C_3 or C_4 plants during the middle Miocene time span in the Siwalik sub-Group of Pakistan.

The rhinocerotid, *Chilotherium intermedium*, was widespread in the Siwalik sub-Group of India and Pakistan, and existed up to the late Miocene (~7 Ma) in China. This species is characterized by low-crowned cheek teeth (brachydonty) with thin enamel folding and less complexity, indicating a diet composed of soft and less-gritty vegetation, preferably leaves of plants and trees (Khan 2009). *C. intermedium* was comparatively smaller (height 1.5 m and weight 1–2 tons) than modern black rhinos (*Diceros bicornis*) (height up to 1.8 m and weight up to 2.2 tons) (Decher 1999; Deng 2005).

Deinotherium pentapotamiae and *D. indicum* (Deinotheriidae) (body weight up to 11 tons and height up to 5 m, Larramendi 2016) was widespread in the Siwalik Group

and contemporaneous African sites for most of the middle Miocene, and it persisted as late as ~9 Ma in the Indian sub-continental region (Sarwar 1977). Two hooked shaped lower tusks were present in the species of *Deinotherium* with a flat skull, unlike other proboscideans, along with low-crowned teeth, indicating a browsing diet (Sarwar 1977; Shoshani and Tassy 2005).

Hyotherium pilgrimi (Suidae) was a species with buno-dont (rounded cusps) and brachyodont cheek teeth which existed during the middle Miocene time span in the Siwaliks. It had a range of body weight from 150–200 kg and height up to 1.1 m (Sorkin 2008). The mesowear and morphological studies (low hypsodonty index of 1.1, simple bunodont dentition with thick enamel) show that this species browsed on leaves and fruits (Barry et al. 2002; Tariq 2010; Aslam 2018). In general, all the middle Miocene mammals of the Siwalik sub-Group of Pakistan show morphological characters indicating browsing diets in forests and woodland settings, like their Indian counterparts (Patnaik et al. 2019).

Institutional abbreviations.—EB, Environmental Biology Laboratory, Institute of Zoology, University of the Punjab, Lahore, Pakistan.

Other abbreviations.—CAM, crassulacean acid metabolism; EI, evaporation insensitive; ES, evaporation sensitive; MAP, mean annual precipitation; MAT, mean annual temperature; SI, stable isotopes; V-PDB, Vienna Pee Dee Belemnite.

Geological setting

The middle Miocene is represented by the Chinji Formation in the Siwalik sub-Group of Pakistan (Fig. 1), which spans 14.2–11.2 Ma (Barry et al. 2002). The thickness and near-continuous deposition of the strata have permitted the development of a robust chronostratigraphic framework for the Chinji Formation on the basis of paleomagnetic dating. The samples for this study were collected from the Chinji-Nagri and Dhok Bun Ameer Khatoon sections (Fig. 1). The Chinji-Nagri section (Fig. 1B, C) is present in Chakwal District, Punjab (32°39′N, 72°22′E), whereas the Dhok Bun Ameer Khatoon section (DBAK) (Fig. 1B, D) is located 50 km north of Chinji Village (32°47′N, 72°55′E). The boundary between Chinji and Nagri formations can be placed at 11.2 Ma (Fig. 1A), between magnetic zones C5r.3r and C5n.3n (Johnson et al. 1982, calibrated according to Gradstein et al. 2012). The lower boundary of the Chinji Formation with the underlying Kamlial Formation (Fig. 1A) can be placed between C5ACr and C5ADn at 14.2 Ma (Channell et al. 2013). Siltstone and sandstone deposited in an overall fluvial environment dominate the general lithology of the Siwalik sub-Group sediments. Most of the samples come from reddish to gray mudstone (Fig. 1C, D) marginal to large-river paleochannels. The ages are assigned as the mid points following Barry et al. (2002).

Material and methods

For SI analysis, thirty samples from three mammalian families were selected across the middle Miocene of the Siwalik sub-Group of Pakistan. The samples were identified to the species level and further processed for SI analysis. Statistical analysis was conducted using Statistical Package for Social Studies (SPSS) version 20.0.

For the extraction of enamel, a rotary dental drill with carbide burrs was used. Around 15–20 mg of enamel was extracted from each tooth (only molars and premolars were included). Enamel was extracted along one single transect from cervix to crown apex (longitudinal) from buccal surface of upper teeth and lingual surface of lower teeth.

Powdered enamel was further pre-treated with 10 ml of 2% NaOCl for one hour to remove organic matter and the solution was decanted and rinsed with distilled water three times. The samples were than treated with 10 ml of 0.1% acetic acid for 1 hour to remove exogenous carbonates and rinsed with water (Nelson 2007). Samples were then oven dried before isotope analysis (Koch et al. 1997).

$\delta^{18}O_{enamel}$ and $\delta^{13}C_{enamel}$ values were measured at the University of Arizona, USA, using an automated carbonate preparation device (KIEL-III) coupled to a gas-ratio mass spectrometer (Finnigan MAT 252). Powdered samples were reacted with dehydrated phosphoric acid under vacuum at 70°C. The isotope ratio measurement is calibrated based on repeated measurements of NBS-19 and NBS-18, and precision is 0.11‰ for $\delta^{18}O$ (V-PDB) and 0.08‰ for $\delta^{13}C$ (V-PDB).

Results

Stable Carbon Isotopes.—The average $\delta^{13}C_{enamel}$ across all the families was found to be -12.2 ± 2.2‰. The Suidae, Rhinocerotidae, and Deinotheriidae returned average values of $\delta^{13}C_{enamel}$ of -11.2 ± 1.4‰ (n = 10), -12.3 ± 0.8‰ (n = 10), and -12.5 ± 1.3‰ (n = 10), respectively (Table 1). Normality tests indicate that data were normally distributed. One-way ANOVA along with the post-hoc (Tukey's HSD) test show no significant differences in $\delta^{13}C$ values between Rhinocerotidae and Deinotheriidae (p = 0.061), whereas Suidae showed significant differences compared to Deinotheriidae (p = 0.039) and Rhinocerotidae (p = 0.041).

Stable Oxygen Isotopes.—The average $\delta^{18}O_{enamel}$ (V-PDB) across all the families was -9.9 ± 3‰, wherein Suidae, Rhinocerotidae, and Deinotheriidae yielded average values for $\delta^{18}O_{enamel}$ of -8.2 ± 1.2‰ (n = 10), -11.4 ± 1.8‰ (n = 10), and -10.4 ± 1.7‰ (n = 10), respectively (Table 1). The data were normally distributed. One-way ANOVA along with post-hoc test indicated that the $\delta^{18}O_{enamel}$ of suids is significantly different from the $\delta^{18}O_{enamel}$ of rhinos and deinotheres (p = 0.041) (Table 1, Fig. 2).
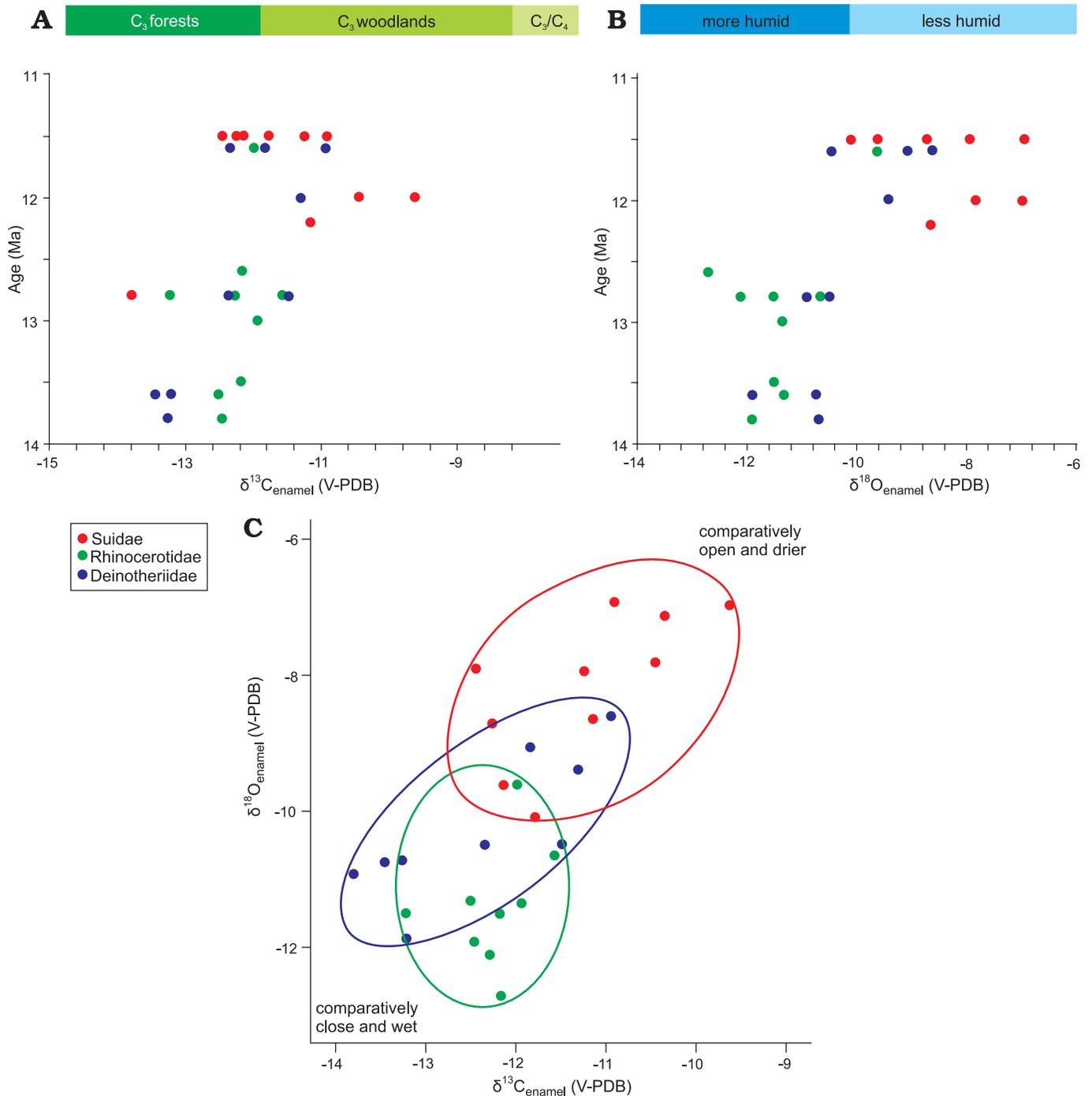
Fig. 2. $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ of all results on three herbivore families from the Chinji Formation. **A**. $\delta^{13}C_{enamel}$ values versus age (Ma) showing close and forest ecology of middle Miocene. **B**. $\delta^{18}O_{enamel}$ values versus age (Ma) indicating the moisture conditions in middle Miocene. **C**. The niche partitioning in $\delta^{18}O_{enamel}$ versus $\delta^{13}C_{enamel}$ space among the suids, rhinocerotids, and deinotheres.

Discussion

The average $\delta^{13}C_{enamel}$ value of middle Miocene mammals (-12.2 ± 2‰) in our data overall indicates a diet composed of C_3 vegetation, which was likely present in the form of forests and woodlands (Kohn and Cerling 2002; Kohn 2010). Patnaik et al. (2019) report the range of $\delta^{13}C_{enamel}$ for large herbivores from -13.9 to -11.6‰ for middle Miocene Siwalik sub-Group

of India, which matches our results. The lowest $\delta^{13}C_{enamel}$ value in our results (-13.9‰) was recorded at ~13 Ma interval, whereas the highest value (-9.6‰) was recorded at ~12 Ma (Fig. 2, Table 1). This shows that the lower Chinji Formation was dominated by C_3 vegetation, likely present in the form of forestland, whereas the upper Chinji was dominated by C_3 open woodlands (Kohn and Cerling 2002; Kohn 2010). Thus, vegetation and habitat appear to have changed towards more

Table 1. $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ values for thirty enamel samples of fossil mammals from the middle Miocene Siwaliks of Pakistan. The ages of the samples have been calibrated according to Gradstein et al. (2012). Abbreviations: l, left; M/m, upper/lower molar; PM, upper premolar; r, right; V-PDB, Vienna Pee Dee Belemnite.

Sample ID	Family	Species	Horizon	Type of tooth	Age (Ma)	$\delta^{13}C_{enamel}$ V-PDB (‰)	$\delta^{18}O_{enamel}$ V-PDB (‰)
EB 470	Suidae	*Hyotherium pilgrimi*	upper Chinji	lM2	12.0	-10.3	-7.1
EB 471	Suidae	*Hyotherium pilgrimi*	upper Chinji	lM2	12.2	-9.6	-7.0
EB 472	Suidae	*Hyotherium pilgrimi*	upper Chinji	rP3	11.5	-11.1	-8.6
EB 473	Suidae	*Hyotherium pilgrimi*	upper Chinji	rm3	11.5	-12.1	-9.6
EB 474	Suidae	*Hyotherium pilgrimi*	upper Chinji	rm2	12	-12.25	-8.7
EB 475	Suidae	*Hyotherium pilgrimi*	upper Chinji	rM2	11.5	-11.8	-10.1
EB 476	Suidae	*Hyotherium pilgrimi*	upper Chinji	rM2	11.5	-10.4	-7.8
EB 477	Suidae	*Hyotherium pilgrimi*	upper Chinji	rM2	11.5	-12.45	-7.9
EB 478	Suidae	*Hyotherium pilgrimi*	upper Chinji	lM3	12.0	-11.2	-7.9
EB 479	Suidae	*Hyotherium pilgrimi*	upper Chinji	lM3	12.0	-10.9	-6.9
EB 480	Rhinocerotidae	*Chilotherium intermedium*	lower Chinji	lm2	13.6	-12.5	-11.3
EB 481	Rhinocerotidae	*Chilotherium intermedium*	lower Chinji	lM3	13.6	-12.2	-11.5
EB 482	Rhinocerotidae	*Chilotherium intermedium*	lower Chinji	lM3	12.6	-12.2	-12.7
EB 483	Rhinocerotidae	*Chilotherium intermedium*	upper Chinji	P4	11.6	-12.0	-9.6
EB 484	Rhinocerotidae	*Chilotherium intermedium*	lower Chinji	lM3	13.6	-12.5	-11.3
EB 485	Rhinocerotidae	*Chilotherium intermedium*	lower Chinji	rm2	13.8	-12.45	-11.9
EB 486	Rhinocerotidae	*Chilotherium intermedium*	lower Chinji	rM2	13.0	-11.9	-11.3
EB 487	Rhinocerotidae	*Chilotherium intermedium*	lower Chinji	lM2	12.8	-13.2	-11.5
EB 488	Rhinocerotidae	*Chilotherium intermedium*	lower Chinji	lM2	12.8	-11.6	-10.65
EB 489	Rhinocerotidae	*Chilotherium intermedium*	lower Chinji	rm3	12.8	-12.3	-12.1
EB 490	Deinotheriidae	*Deinotherium pentapotamiae*	upper Chinji	M2	11.6	-11.8	-9.1
EB 491	Deinotheriidae	*Deinotherium pentapotamiae*	upper Chinji	M3	11.6	-12.3	-10.45
EB 492	Deinotheriidae	*Deinotherium indicum*	lower Chinji	lm1	12.8	-13.8	-10.9
EB 493	Deinotheriidae	*Deinotherium indicum*	lower Chinji	lm2	12.8	-11.5	-10.5
EB 494	Deinotheriidae	*Deinotherium indicum*	lower Chinji	rM3	13.6	-13.2	-11.9
EB 495	Deinotheriidae	*Deinotherium indicum*	lower Chinji	rm3	13.6	-13.4	-10.7
EB 496	Deinotheriidae	*Deinotherium pentapotamiae*	upper Chinji	lm3	12.0	-11.3	-9.4
EB 497	Deinotheriidae	*Deinotherium pentapotamiae*	upper Chinji	lm3	11.6	-10.9	-8.6
EB 498	Deinotheriidae	*Deinotherium indicum*	lower Chinji	lm3	13.8	-13.25	-10.7
EB 499	Deinotheriidae	*Deinotherium pentapotamiae*	lower Chinji	lm3	13	-12.3	-10.5

open ecological settings in the upper Chinji Formation. The shift to open woodland is also apparent in the suid $\delta^{13}C_{enamel}$ results, which return an estimate for suid diet of -22.7‰, assuming $e_{enamel-diet}$ = +13.1‰. (Kohn 2010; Cerling et al. 2015; Table 1). Moreover, the possibility of consumption of C_3 grasses cannot be ruled out as extant suids in eastern Africa also consume C_3 grasses but show a low-crowned dental morphology (Harris and Cerling 2002; Souron 2017).

These findings are supported by evidence presented in Quade and Cerling (1995), who reported $\delta^{13}C_{paleosol\ carbonate}$ values from Kamlial and Chinji formations ranging from -12.9 to -9.5‰, indicating a forestland and woodland environment. Further afield, Quade et al. (1995b) from Pasalar, Turkey, and Uno et al. (2016) from eastern Africa report the $\delta^{13}C$ values from paleosol and ungulate enamel, respectively. Both studies report a dominance of C_3 vegetation with very little or no C_4 vegetation during the middle Miocene time span.

The higher $\delta^{13}C_{enamel}$ values in suids compared to rhinocerotids and deinotheres indicate that this family preferred more

open areas for their feeding or browsed on a leafy vegetation. Tariq (2010) reports a frugivorous component to diets in suids on the basis of mesowear analysis. The mesowear analysis coupled with the morphological features of suid teeth (bunodont teeth with thick enamel) is in agreement with the hypothesis, based upon our $\delta^{13}C_{enamel}$ data, that suids of middle Miocene utilized C_3 plants in open habitats, including fruits, as their dietary resource and inhabited relatively more open areas (Tariq 2010; Aslam 2018; Waseem et al. 2020b).

On the basis of average $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ values, we may hypothesize that middle Miocene climate was sub-humid and animals drank from shaded water holes or rivers (Sanyal et al. 2010; Tada et al. 2016). If we use the equation for MAP calculation on the basis of $\delta^{13}C_{diet}$ following Kohn (2010), we can say that in middle Miocene of the Siwalik sub-Group of Pakistan MAP was lower than ~700 mm/year (see Kohn 2010: fig. 3). The average value of $\delta^{18}O_{enamel}$ (-9.9 ± 3‰) of all non-ruminant taxa is low, indicating sub-humid conditions (Fig. 2B) during the middle Miocene time span in the Siwalik sub-Group of Pakistan,

Fig. 3. Reconstruction of the middle Miocene ecology of the Siwaliks and relative habitat partitioning among three mammalian families based on the stable isotope data of carbon and oxygen. Deinotheres (**A**), rhinocerotids (**B**), and suids (**C**).

which is consistent with Indian contemporaneous sites (Patnaik et al. 2019). The low $\delta^{18}O_{enamel}$ values also probably indicate that in the middle Miocene, animals drank from relatively unevaporated water holes or rivers.

The $\delta^{18}O_{enamel}$ and $\delta^{13}C_{enamel}$ values increase gradually from ~14 Ma to ~11 Ma (Fig. 2A, B), culminating in more open environments supporting a woodland or perhaps minor C_4 vegetation (0–18% cover). However, the *Hyotherium pilgrimi* samples show higher $\delta^{13}C_{enamel}$ values in our data which may also imply that this response may be species specific. Even if we consider the values as species specific, the open ecology towards the end of middle Miocene is still supported as we consider that the studied suid species occupied more open areas similar to the late Miocene suids. However, suids in the late Miocene showed feeding in both open and closed environments (Nelson 2005, 2007).

Niche partitioning among middle Miocene mammals

The studied middle Miocene mammals show some degree of niche partitioning (Fig. 3). The deinotheres and rhinocerotids from middle Miocene of Indian Siwaliks show an average $\delta^{13}C_{enamel}$ values of -12.5‰ and -12.8‰, respectively, very close to the ranges in our results for these taxa (Patnaik et al. 2019), pointing to overall similar ecological and dietary preferences. The suids (average $\delta^{13}C_{enamel}$ = -11.2 ± 1.4‰) inhabited a woodland/forestland setting where they fed on C_3 vegetation consisting of plants, including fruits. They may have drunk from less shaded water holes as represented by their elevated $\delta^{18}O_{enamel}$ values (-8.1‰) compared to the other middle Miocene taxa (Fig. 2B, C). The rhinocerotids and deinotheres show similarly low (p >0.05) $\delta^{13}C$ values (-12.2‰ and -12.4‰, respectively), indicating that both families inhabited a forestland setting and browsed from understory vegetation (Fig. 2A, C), as reported by Patnaik et al. (2019) for contemporaneous Indian sites. However, the $\delta^{18}O_{enamel}$ values significantly differ between these two families (-11.3 ± 1.8‰ and -10.4 ± 1.7‰; Fig. 2B). Heissig (1972, 2003) reports that middle Miocene rhinocerotids of Pakistan preferred a habitat close to water bodies and Biasatti et al. (2018) report the same behavior for middle Miocene rhinocerotids of China. Thus, we may assume that middle Miocene rhinocerotids lived in habitats close to water, resulting in the lowest $\delta^{18}O_{enamel}$ values among all the middle Miocene taxa analyzed in this study. Deinotheres preferred a forested habitat where they had access to water but they did not live

very close to the water bodies like rhinocerotids as indicated by the $\delta^{18}O_{enamel}$ values (Fig. 3).

Conclusions

We analyzed thirty specimens belonging to three families of middle Miocene Siwalik sub-Group of Pakistan. On the basis of our results, we conclude that these middle Miocene species inhabited dense forests and woodlands where they fed on the C_3 vegetation and drank from shaded water resources like ponds or rivers which were frequently refilled by precipitation (Fig. 3). We did not find clear evidence of significant C_4 vegetation in their diet. The $\delta^{18}O_{enamel}$ results reveal that the environment was more humid at ~14 Ma and became less humid towards the upper Chinji Formation (12–11.2 Ma). In general, the middle Miocene Siwaliks of Pakistan were dominated by forests and woodlands with precipitation supporting a more evergreen ecology as in the middle Miocene of eastern Africa, India, and Nepal and present-day vegetation of Myanmar (Quade et al. 1995a, b; Uno et al. 2016).

Acknowledgements

References

Andrade, J.L., De La Barrera, E., Reyes-García, C., Ricalde, M.F., Vargas-Soto, G., and Cervera, C.J. 2007. El metabolismo ácido de las crasuláceas: diversidad, fisiología ambiental y productividad. *Boletín de la Sociedad Botánica de México* 87: 37–50.

Aslam, S. 2018. *Dental and Cranial Morphological Studies Based on New Collection of Neogene Suids from the Siwalik Hills of Pakistan*. 206 pp. Unpublished Ph.D. Thesis, University of the Punjab, Lahore.

Badgley, C., Barry, J.C., Morgan, M.E., Nelson, S.V., Behrensmeyer, A.K., Cerling, T.E., and Pilbeam, D. 2008. Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. *Proceeding of National Academy of Science USA* 105: 12145–12149.

Barry, J.C., Behrensmeyer, A.K., Badgley, C.E., Flynn, L.J., Peltonen, H., Cheema, I.U., Pilbeam, D., Lindsay, E.H., Raza, S.M., Rajpar, A.R., and Morgan, M.E. 2013. The Neogene Siwaliks of the Potwar Plateau, Pakistan. *In*: X. Wang, L.J. Flynn, and M. Fortelius (eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*, 373–399. Columbia University Press, New York.

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. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37: 95–130.

Barry, J.C., Morgan, M., Flynn, L.J., Pilbeam, D., Behrensmeyer, A.K., Raza, S.M., Khan, I., Badgely, C., Hicks, J., and Kelley, J. 2002. Faunal and environmental change in the L=late Miocene Siwaliks of Northern Pakistan. *Palaeobiology* 28:1–72.

Bellasio, C., Quirk, J., and Beerling, D.J. 2018. Stomatal and non-stomatal limitations in savanna tress and C_4 grasses grown at low, ambient and high atmospheric CO_2. *Plant Science* 274: 181–192.

Ben-David, M. and Flaherty, E.A. 2012. Stable isotopes in mammalian research: a beginner's guide. *Journal of Mammalogy* 93: 312–328.

Biasatti, D., Yang, W., and Deng, T. 2018. Paleoecology of Cenozoic rhinos from northwest China: a stable isotope perspective. *Vertebrata PalAsiatica* 56: 45–68.

Bibi, F. 2007. Dietary niche partitioning among fossil bovids in late Miocene C_3 habitats: consilience of functional morphology and stable isotope analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253: 529–538.

Blumenthal, S.A., Levin, N.E., Brown, F.H., Brugal, J.P., Chritz, K.L., and Cerling, T.E. 2018. Diet and evaporation sensitivity in African ungulates: A comment on Faith (2018). *Palaeogeography, Palaeoclimatology, Palaeoecology* 506: 250–251.

Blumenthal, S.A., Levin, N.E., Brown, F.H., Brugal, J.-P., Chritz, K.L., Harris, J.M., Jehle, G.E. and Cerling, T.E. 2017. Aridity and hominin environments. *Proceedings of the National Academy Sciences* 114: 7331–7336.

Cerling, T.E. 1999. Paleorecords of C_4 plants and ecosystems. *In*: R.F. Sage and R.K. Monson (eds.), C_4 *Plant Biology*, 445–469. Academic Press, London.

Cerling, T.E. and Harris, J.M. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120: 347–363.

Cerling, T.E., Andanje, S.A., Blumenthal, S.A., Brown, F.H., Chritz, K.L., Harris, J.M., Hart, J., Kirera, F., Kaleme, P., Leakey, L., Meave, L., Levin, N.E., Manthi, F., Passey, B.H., and Uno, K.T. 2015. Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. *Proceeding of National Academy of Science USA* 112: 11467–11472.

Cerling, T.E., Harris, J.M., Ambrose, S.H., Leakey, M.G., and Solounias, N. 1997a. Dietary and environmental reconstruction with stable isotope analyses of herbivore tooth enamel from the Miocene locality of Fort Ternan, Kenya. *Journal of Human Evolution* 33: 635–650.

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., and Ehleringer, J.R. 1997b. Global vegetation change through the Miocene–Pliocene boundary. *Nature* 389:153–158.

Cerling, T.E., Hart, J.A., and Hart, T.B. 2004. Stable isotope ecology in the Ituri Forest. *Oecologia* 138: 5–12.

Channell, J.E.T., Ohneiser, C., Yamamoto, Y., and Kesler, M.S. 2013. Oligocene–Miocene magnetic stratigraphy carried by biogenic magnetite at sites U1334 and U1335 (equatorial Pacific Ocean). *Geochemistry, Geophysics, Geoecosystem* 14: 265–282.

Codron, J., Codron, D., Lee-Throp, J.A., Sponheimer, M., Bond, W.J., de Ruiter, D. and Grant, R. 2005. Taxonomic, anatomical, and spatio-temporal variations in the stable carbon and nitrogen isotopic compositions of plants from African savanna. *Journal of Archaeological Science* 32: 1757–1772.

Codron, D., Hull, J., Brink, J S., Codron, J., Ward, D., and Clauss, M. 2011. Effect of competition on niche dynamics of syntopic grazing ungulates: contrasting the predictions of habitat selection models using stable isotope analysis. *Evolutionary Ecology Research* 13 (3): 217–235.

Dansgaard, W. 1964. Stable isotopes in precipitation. *Tellus* 16: 436–468.

Decher, J. 1999. Book review: "The Kingdon Field Guide to African Mammals" by J. Kingdom. *Journal of Mammalogy* 80 (2): 692–693.

Deng, T. 2005. New discovery of *Iranotherium morgani* (Perissodactyla, Rhinocerotidae) from the late Miocene of the Linxia Basin in Gansu, China, and its sexual dimorphism. *Journal of Vertebrate Paleontology* 25: 442–450.

Dennell, R.W., Coard, R., and Turner, A. 2006. The biostratigraphy and magnetic polarity zonation of the Pabbi Hills, northern Pakistan: an Upper Siwalik (Pinjor Stage) upper Pliocene–Lower Pleistocene fluvial sequence. *Palaeogeography, Palaeoclimatology, Palaeoecology* 234: 168–185.

Domingo, L., Prado, J.L., and Alberdi, M.T. 2012. The effect of paleoeco-

logy and paleobiogeography on stable isotopes of Quaternary mammals from South America. *Quaternary Science Reviews* 55: 103–113.

Ehleringer, J.R., Lin, Z.F., Field, C.D., Sun, G.L., and You, L.Y. 1987. Leaf isotope ratios of plants from a subtropical monsoon forest. *Oecologia* 72: 109–114.

Faith, J.T. 2011. Late Quaternary dietary shifts of the Cape grysbok (*Raphicerus melanotis*) in Southern Africa. *Quaternary Research* 75: 159–165.

Faith, J.T. 2018. Paleodietary change and its implications for aridity indices derived from $\delta^{18}O$ of herbivore tooth enamel. *Palaeogeography, Palaeoclimatology, Palaeoecology* 490: 571–578.

Feranec, R.S. and MacFadden, B.J. 2006. Isotopic discrimination of resource partitioning among ungulates in C_3-dominated communities from the Miocene of Florida and California. *Paleobiology* 32: 191–205.

Flynn, L.J., Pilbeam, D., Barry, J.C., Morgan, M.E., and Raza, S.M. 2016. Siwalik synopsis: A long stratigraphic sequence for the later Cenozoic of South Asia. *Comptes Rendus Palevol* 15: 877–887.

Gradstein, F.M., Ogg, J.G., and Hilgen, F.J. 2012. On the Geologic Time Scale. *Newsletters on Stratigraphy* 45: 171–188.

Harris, J.M. and Cerling, T.E. 2002. Dietary adaptations of extant and Neogene African suids. *Journal of Zoology* 256: 45–54.

Heissig, K. 1972. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan, 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. *Bayerische Akademie der Wissenschaften Mathematisch Naturwissenschaftliche Klasse, Abhandlungen, Neue Folge* 152: 1–112.

Heissig, K. 2003. *Change and Continuity in Rhinoceros Faunas of Western Eurasia from the Middle to the Upper Miocene.* 89 pp. EEDEN, Stará Lesná.

Hynek, S.A., Passey, B.H., Prado, J.L., Brown, F.H., Cerling, T.E., and Quade, J. 2012. Small mammal carbon isotope ecology across the Miocene–Pliocene boundary, northwestern Argentina. *Earth and Planetary Science Letters* 321–322: 177–188.

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. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37: 17–42.

Khan, A.M. 2009. *Taxonomy and Distribution of Rhinoceroses from the Siwalik Hills of Pakistan.* 182 pp. Unpublished Ph.D. Thesis, University of the Punjab, Lahore.

Khan, M.A., Batool, A., Nayyer, A.Q., and Akhtar, M. 2013. *Gazella lydekkeri* (Cetartiodactyla: Ruminantia: Bovidae) from the Middle Siwaliks of Hasnot (late Miocene), Pakistan. *Pakistan Journal of Zoology* 45: 981–988.

Khan, A.M., Iqbal, A., Waseem, M.T., Ahmad, R.M., and Ali, Z. 2020. Palaeodietary and palaeoclimatic interpretations for herbivore fauna from late Pliocene to early Pleistocene Siwaliks of Pakistan. *Journal of Animal and Plant Sciences* 30: 355–363.

Koch, P.L. 1998. Isotopic reconstruction of past continental environments. *Annual Review of Earth and Planetary Science* 26: 573–613.

Koch, P.L. 2007. Isotopic study of the biology of modern and fossil vertebrates. *In*: R.H. Michener and K. Lajtha (eds.), *Stable Isotopes in Ecology and Environmental Science*, 99–154. Blackwell Publishing, Boston.

Kohn, M.J. 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. *Proceedings of the National Academy Sciences* 107: 19691–19695.

Kohn, M.J. and Cerling, T.E. 2002. Stable Isotope Compositions of Biological Apatite. *In*: M.J. Kohn, J. Rakovan, and J.M. Hughes (eds.), Phosphates—Geochemical, Geobiological, and Materials Importance. *Reviews in Mineralogy and Geochemistry* 48: 455–488.

Kohn, M.J., Schoeninger, M.J., and Valley, J.W. 1996. Herbivore tooth oxygen isotope compositions: effects of diet and physiology. *Geochimica et Cosmochimica Acta* 60: 3889–3896.

Koch, P.L., Tuross, N., and Fogel, M.L. 1997. The effects of sample treat-

ment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. *Journal of Archaeological Science* 24: 417–429.

Larramendi, A. 2016. Shoulder height, body mass, and shape of proboscideans. *Acta Palaeontologica Polonica* 61: 537–574.

Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., and Ehleringer, J.R. 2006. A stable isotope aridity index for terrestrial environments. *Proceedings of the National Academy Sciences* 103: 11201–11205.

MacFadden, B.J. and Cerling, T.E. 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: a 10 million-year sequence from the Neogene of Florida. *Journal of Vertebrate Paleontology* 16:103–115

MacFadden, B.J. and Higgins, P. 2004. Ancient ecology of 15-million-year old browsing mammals within C_3 plant communities from Panama. *Oecologia* 140: 169–182.

Medrano, H. and Flexas, J. 2000. Fotorrespiración y mecanismos de concentración del dióxido de carbono. *In*: J. Azcón-Bieto and M. Talón (eds.), *Fundamentos de Fisiología Vegetal*, 187–201. McGraw-Hill Interamericana, Madrid.

Morgan, M.E., Behrensmeyer, A.K., Badgley, C., Barry, J.C., Nelson, S., and Pilbeam, D. 2009. Lateral trends in carbon isotope ratios reveal a Miocene vegetation gradient in the Siwaliks of Pakistan. *Geology* 37: 103–106.

Morgan, M.E., Kingston, J.D., and Marino, B.D. 1994. Carbon isotopic evidence for the emergence of C4 plants in the Neogene from Pakistan and Kenya. *Nature* 367: 162–165.

Nelson, S.V. 2005. Paleoseasonality inferred from equid teeth and intra-tooth isotopic variability. *Palaeogeography, Palaeoclimatology, Palaeoecology* 222: 122–144.

Nelson, S.V. 2007. Isotopic reconstructions of habitat change surrounding the extinction of *Sivapithecus*, a Miocene hominoid, in the Siwalik Group of Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 243: 204–222.

Patnaik, R., Singh, N.P., Paul, D., and Sukumar, R. 2019. Dietary and habitat shifts in relation to climate of Neogene–Quaternary and associated mammals of Indian Subcontinent. *Quaternary Science Reviews* 224: 105968.

Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.D., Roeder, B.L., and Ehleringer, J.R. 2005. Carbon isotope fractionation between diet, breath CO_2, and bioapatite in different mammals. *Journal of Archaeological Science* 32: 1459–1470.

Pérez-Crespo, V.A., Carranza y Castañeda, O., Arroyo-Cabrales, J., Morales-Puente, P., Cienfuegos-Alvarado, E., and Otero, F.J. 2017. Diet and habitat of unique individuals of *Dinohippus mexicanus* and *Neohipparion eurystile* (Equidae) from the late Hemphillian (Hh3) of Guanajuato and Jalisco, central Mexico: stable studies isotopes. *Revista Mexicana de Ciencias Geológicas* 34: 38–44.

Pilgrim, G.E. 1937. Siwalik antelopes and oxen in the American Museum of Natural History. *Bulletin of American Museum of Natural History* 72: 729–874.

Quade, J. and Cerling, T.E. 1995. Expansion of C_4 grasses in the late Miocene of northern Pakistan: Evidence from stable isotopes in paleosols. *Palaeogeography, Palaeoclimatology, Palaeoecology* 115: 91–116.

Quade, J., Cater, J.M.L., Adam, J., and Harrison, T.M. 1995a. Late Miocene environmental change in Nepal and the northern Indian subcontinent: Stable isotopic evidence from paleosols. *GSA Bulletin* 107: 1381–1397.

Quade, J., Cerling, T.E., and Bowman, J.R. 1989. Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. *Nature* 342: 163–166.

Quade, J., Cerling, T.E., Andrews, P., and Alpagut, B. 1995b. Paleodietary reconstruction of Miocene faunas from Paşalar, Turkey, using stable carbon and oxygen isotopes of fossil tooth enamel. *Journal of Human Evolution* 28: 373.

Quade, J., Cerling, T.E., Barry, J., Morgan. M.M., Pilbeam, D.R., Chivas. A.R., Lee-Thorp, J.A., and Van der Merwe, N.J. 1992. A 16 Ma record of paleodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. *Chemical Geology* 94:182–192.

Sánchez, B. 2005. Reconstrucción del ambiente de mamíferos extintos a

partir del análisis isotópico de los restos esqueléticos. *In*: P. Alcorno, R. Redondo, and J. Toledo (eds.), *Nuevas técnicas metodológicas aplicadas al estudio de los sistemas ambientales: los isótopos estables*, 49–64. Universidad Autónoma de Madrid, Madrid.

Sanyal, P., Bhattacharya, S.K., Kumar, R., Ghosh, S.K., and Sangode S.J. 2005. Palaeovegetational reconstruction in Late Miocene: a case study based on early diagenetic carbonate cement from the Indian Siwalik. *Palaeogeography, Palaeoclimatology, Palaeoecology* 228: 245–259.

Sanyal, P., Sarkar, A., Bhattacharya, S.K., Kumar, R., Ghosh, S.K., and Agarwal, S. 2010. Intensification of monsoon, microclimate, and asynchronous C_4 appearance: isotopic evidence from the Indian Siwalik sediments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 296: 165–173.

Sarwar, M. 1977. Taxonomy and distribution of the Siwalik Proboscidea. *Bulletin Department of Zoology University of the Punjab Lahore* 10: 1–172.

Shoshani, J. and Tassy, P. 2005. Advances in proboscidean taxonomy & classification, anatomy & physiology, and ecology & behavior. *Quaternary International* 126–128: 5–20.

Sorkin, B. 2008. A biomechanical constraint on body mass in terrestrial mammalian predators. *Lethaia* 41: 333–347.

Souron, A. 2017. Diet and ecology of extant and fossil wild pigs. *In*: M. Melletti and E. Meijaard (eds.), *Ecology, Conservation and Management of Wild Pigs and Peccaries*, 29–38. Cambridge University Press, Cambridge.

Sponheimer, M. and Lee-Thorp, J. A. 1999. Oxygen isotopes in enamel carbonate and their ecological significance. *Journal of Archaeological Science* 26: 723–728.

Tada, R., Zheng, H., and Clift, P.D. 2016. Evolution and variability of the Asian monsoon and its potential linkage with uplift of the Himalaya and Tibetan Plateau. *Progress in Earth and Planetary Science* 3: 4.

Tariq, M. 2010. *Palaeoenvironmental Study of Pakistan Siwaliks*, 78–122. Unpublished Ph.D. Thesis, Government College University, Lahore.

Tejada-Lara, J.V., MacFadden, B.J., Bermudez, L., Rojas, G., Salas-Gismondi, R., and Flynn, J.J. 2018. Body mass predicts isotope enrichment in herbivorous mammals. *Proceedings of the Royal Society B* 285 (1881), 20181020.

Tipple, B.J., Meyers, S.R., and Pagani, M. 2010. Carbon isotope ratio of Cenozoic CO_2: a comparative evaluation of available geochemical proxies. *Paleoceanography* 25: PA3202.

Uno, K.T., Cerling, T.E., Harris, J.M., Kunimatsu, Y., Leakey, M.G., and Nakatsukasa, M. 2011. Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. *Proceedings of National Academy of Science* 18: 1–6.

Uno, K.T., Polissar, P.J., Jackson, K.E., and de Menocal, P. 2016. Neogene biomarker record of vegetation change in Africa. *Proceedings of National Academy of Science* 113: 6355–6363.

Waseem, M.T., Khan, A.M., Ghaffar, A., Iqbal, A., and Ahmad, R.M. 2020a. Palaeodietary and palaeoclimatic reconstruction for late Miocene hipparionines from the Siwaliks of Pakistan. *Pakistan Journal of Zoology* [published online, https://dx.doi.org/10.17582/journal.pjz/20180314070354].

Waseem, M.T., Khan, A.M., Quade, J., Krupa, A., and Dettman, D.L. 2020b. Stable isotope analysis of middle Miocene faunal communities from the Siwaliks (Pakistan). *In*: E. Vlachos, D. Crespo, C. Martinez-Perez, H.G. Ferron, J.L. Herraiz, A. Gamonal, F.A.M. Arnal, F. Gasco, and P. Citton (eds.), *2nd Palaeontological Virtual Congress*, 199.

White, T.D., Ambrose, S.H., Suwa, G., Su, D.F., DeGusta, D., Bernor, R.L., Boisserie, J.-R., Brunet, M., Delson, E., Frost, S., Garcia, N., Giaourtsakis, I.X., Haile-Selassie, Y., Howell, F.C., Lehmann, T., Likius, A., Pehlevan, C., Saegusa, H., Semprebon, G., Teaford, M., and Vrba, E. 2009. Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. *Science* 326: 67–93.