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Changing Diets Indicative of Changing Landscapes – A Study of Isotope Ratios from the Proboscideans of India

Sonika Sandhu[1] and Prof Vijay Sathe[2]

[1]*Subject Matter Head, Enroute Indian History, Janakpuri, Delhi.*
E-mail: sonika.sandhu@rocketmail.com
[2]*Former Professor in Archaeological Chemistry, Deccan College, Post Graduate and Research Institute Department of Ancient Indian History, Culture and Archaeology Deemed University, Pune, Maharashtra*

Abstract: *Stable Carbon and Oxygen isotope analysis was carried out on the proboscidean tooth enamel samples from the collection available at Deccan College Post-Graduation and Research Institute, Pune as part of doctoral studies. The collection comprises of various specimens of the Proboscidean community discovered from various fossil localities in the Siwaliks, Central Narmada Valley and the Manjra river valley. The specimens cover the periods from late Pliocene to upper Pleistocene. It was found that the carbon and oxygen data point towards a distinctive diet of the proboscideans in three different ages: The Miocene, The Pliocene and The Pleistocene. According to this the proboscideans of the Miocene were all browsers feeding on C3 plants, after the grassland spread and vegetation turnover of the Mid Miocene a diet change is also seen in the proboscides i.e., they begin to incorporate C4 plants in their diets and adapt to an intermediate or mixed feeding behavior. The Proboscideans of the late Pliocene to early Pleistocene were pure grazers feeding on exclusively C4 plants. Furthermore the Proboscideans of the late Pliocene to early Pleistocene were pure grazers feeding on exclusively C4 plants. This switch even brought a morphological change in the dentition of the proboscideans as they developed thinner enamels, higher hypsodonty and more plates to digest the tough silica rich grasses. By mid-Pleistocene the climate and seasonal cycle has stabilized and the proboscideans finding abundance of C3 plants or possibly competing with other grazers started to switch their diets again to C3 browsing. This diet shift is used extensively to build on past environment and vegetation patterns as well.*

Keywords: *Isotopes, Proboscideans, Narmada, Siwaliks, Palaeoenvironment*

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Introduction

The proboscideans have had an extensive and deep connect with the Indian Subcontinent. There have been nearly fifty members of this taxa which have made this region their home and are found in various parts of the sub-continent. The proboscideans have inhabited the subcontinent from Pliocene and during the Eocene they were extensively found. This can be attributed from the sediments and certain fossil localities of the Siwaliks which have given an in depth evidence and material to understand, analyze, document and build on their evolutionary history in Asia (e.g., Lydekker, 1880; Andrews 1904; Osborn 1933; Kumar & Badam 1982; Akbar et al. 2011; Sankhyan & Sharma 2014; Sankhyan & Chavasseau 2018; Abbas et al. 2018; Białas et al. 2021). The ability of a rapid evolution along with the capacity to easily colonize new geographical regions has made the proboscideans a valuable proxy and key marker for many stratigraphic studies, including understanding how past landscapes and environments evolved and existed (Maglio 1970; Shoshani & Tassy 1996).

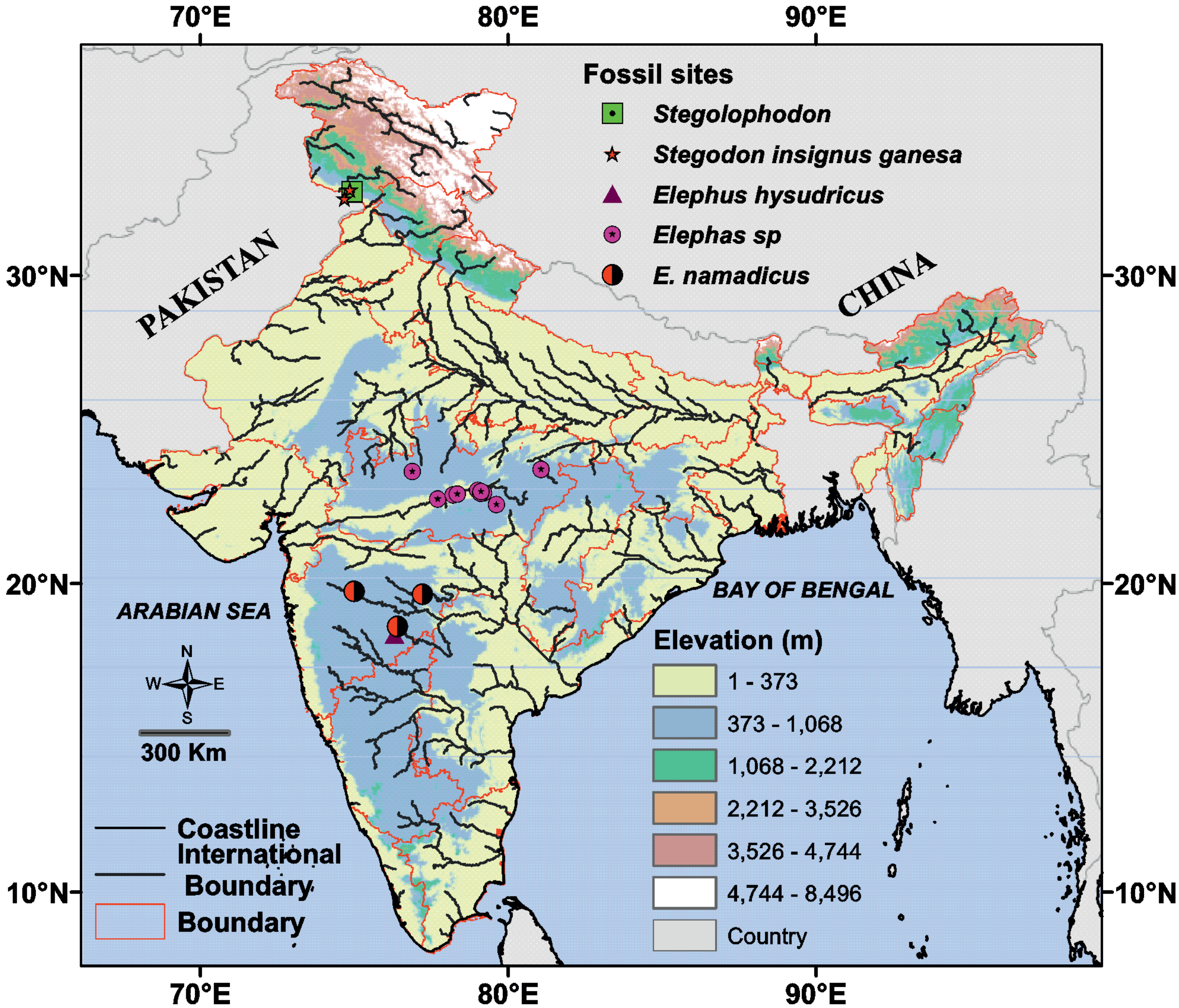
Four main species of Proboscidea have been reported from the quaternary deposit of India; *Stegodon insignus Ganesa, Elephas planifrons, Elephas hysudricus, Elephas namadicus* (Ganjoo 1989). These are also the species which have been investigated in this work. Enamel obtained from these have been investigated for isotope ratios to understand their diets and ecologies. The ratios obtained are compared to those of proboscideans from other localities. At present isotope studies are an excellent tool to study diets, ecologies, migrations, hereditary strategies, species biography, climate changes and shifts. Their use in the field of archaeology has grown exponentially over the last two decades. The primary advantage is that its ability to recognize multiple types of dietary inputs. Isotope studies also allows dietary composition and detect variation at individual levels. The famous sentence “ we are what we eat” is truly realized when it comes to isotope studies. Isotopes have also been used to understand and investigate the relationship between diet, social, economic and cultural process (Ambrose 1987; Koch et al. 1998; Feranec & MacFadden 2000; Hoppe & Koch 2006; Metcalfe & Longstaffe 2012, 2014

1.2. Area of Study

The three important fossils localities: The Siwaliks, The Narmada valley and Manjra river valleys in Maharashtra, were chosen for this study (Map 1). These localities have also yielded significant number of fossil elephants.

1.2.a: Siwaliks

The Siwaliks represent the final and the southernmost phase of the upliftment of the Himalayas, The Siwaliks are positioned linearly along the entire length of the Himalayan foothills starting from the Indus in the west till the Brahmaputra in the east (Parmar 2013). The origin of the Siwalik sediments is dated from Middle Miocene (18 m.y.a) till about Late Pleistocene (0.22 m.y.a), these sediments were deposited by large fluvial systems analogous to some of the Himalayan rivers in the present day context, this group is identified on the basis of its sandstone-mudstone alternations, which are present throughout the Lower, Middle and in the Upper subgroups of the Siwaliks (Parmar 2013). The Jammu Siwaliks contain freshwater deposits in their sediments and this is their identifying feature, the succession here is about 7 km in its thickness, it has been dated to 18.3 m.y.a to 0.22 m.y.a (Johnson et al. 1985; Ranga Rao et al. 1988; Nanda 2013). The Siwaliks are further divided into three sub groups namely: the Upper, Lower and Middle (Nanda 2013). Of particular interest is the Khanpur formation from where the fossils examined have been discovered. Khanpur formation is the lowest formation of the Quaternary and its name is derived from the village nearby where it was identified - Khanpur (32°47’15”: 74°54’30”) and at Bajalta (32°45’30” : 74°56’15’). The Khanpur formation rests above Bantalao formation (Dhok pathan) near village Gungai (32°42’30”: 75°03’05”) with a conglomerate bed of 2m. These sediments have alternative beds of clay and sand, the clays are fine laminated and



Map 1: Map of the Indian Subcontinent with the studied fossil sites for this study. Map has been generated using ArcGis 10.3 (Hydrology toolbox) along with Coraldraw X3. Dem data resolution is 90m.

fissured and at places make sharp contact with the sand beds, the sand beds are of variable colour from reddish yellow to greenish brown, within the red clays there are deposits of bentonitic clay which is nearly 2.5 m in thickness (Ganjoo 1989)

1.2.b: Narmada

The Narmada valley has given the best and the most accurate Pleistocene Fluvial sequence regarding the Deccan localities in the Peninsular and Central parts of the Indian subcontinent, It has given the complete sequence of Quaternary deposit right from lower Pleistocene to Holocene (Khan & Sonakia 1992). Besides yielding this fluvial sequence it is also famous for being the richest source of vertebrate fossils, the fossils examined are dated to the Pleistocene age (Badam & Salahuddin 1982; Biswas 1997; Chauhan 2008), there are seven primary formations identified in the Narmada, these have been identified in the Central Narmada basin: the formations are- (Pilikarar, Dhansi, Surajkund, Baneta, Hirdepur, Baurus, Ramnagar), Surajkund and the Baneta formation have given the maximum number of fossils (Tiwari and Bhai 1997; Tiwari 2001). It has been observed that the vertebrate fossils tend to be found in the sedimentary matrix all over the Central Narmada Basin (Khatri 1966; Chauhan 2008).

1.2.c: Manjra

Another river system which has yielded fossils in the peninsula is the Manjra river system. A major hill complex in the upper reaches of its basin are the Balaghat ranges, these ranges are an offshoot of the Western Ghats, this basin resembles a plateau and topography is of soft rolling undulating type (Dikshit 1970; Joshi et al. 1981) Studies have revealed that the middle and the upper parts of the Manjra river valley are composed of rocks of Cretaceous-Eocene, This river system is important as it has revealed a fossil assemblage which indicates to a very different ecosystem where hippos, tigers and elephants thrived in the past, very unlike its present day setting. The fossils of Manjra valley have been assigned to upper Pleistocene and some of the fossils are the ancient representatives of their modern day counterparts. The important fossiliferous localities on this river are: Dhanegaon, Wangdari, Tadula, Ganjpur, Yendikol. A total of 286 vertebrate fossils and 59 molluscans have been discovered from these sites (Joshi et al., 1981; Badam et al., 1984; Babar et al., 2011; Sathe 1989, 2004, 2015). The fossils have mostly been found in the alluvial sediments; these fossils are dated to late Pleistocene (Badam 1979; Kajale et al.1976; Joshi et al.1981; Badam et al. 1984; Sathe 1989, 2004, 2009, 2015)

2.1. Material & Methods

Serial sampling of tooth enamel provides an effective approach to reconstruct the long-term dietary and ecological use of mammals, during the time of tooth growth with higher precision (Fox and Fisher, 2004; Zazzo et al. 2006; Fox et al. 2007). This method is suitable for the huge molars of Proboscidea and has been successfully applied on extinct mammoths and mastodons to track individual life history for signatures related to climate change, seasonal dietary shifts, and tooth enamel growth rate among other scientific questions (Koch et al. 1998; Feranec & MacFadden, 2000; Hoppe and Koch, 2006; Metcalfe & Longstaffe, 2012, 2014)

2.2. Material

This collection of fossils housed in the Paleontology Laboratory of Deccan College Post Graduate and Research Institute was investigated. The collection has been built over the years by G.L.Badam, Z.D.Ansari, S.N.Rajaguru, Vijay Sathe, R.K. Ganjoo and Salahuddin during their field investigations in the Siwaliks, Narmada and Manjra river valleys:

2.3. Methods

These specimens were all members of Proboscidea and fell under the taxa of Stegodons and Elephas.

(a) Pre Treatment: A total of seven specimens were selected from the Deccan College repository for serial sampling. The general method for stable isotope sampling of tooth enamel followed Koch et al. (1997) . The lophs were selected on the basis of wear and tear and enamel exposure and condition. A sequence of horizontal bands of enamel was sampled from the top to the bottom through the whole enamel layer using a diamond drill. Only Enamel samples were used. Before the samples were drilled, the outer surface of each tooth was cleaned, abraded to reduce chances of any contamination. A Dremel hand drill with a diamond tip burr was used to mechanically separate the enamel from the dentine. Around 100mg of powdered enamel was obtained from each individual tooth, the collection was made serially from top to bottom. A distance of 1-2mm was maintained between each drilling position by using a Vernier caliper for measurement. The drill lines were perpendicular to the crown height. All the samples were collected in eppendorfs and were treated with 2% NaOCl (Natrium Hypochlorite) for 24 hrs. this is done to oxidize any organic resides which may hamper with the readings. Further the samples were treated with 0.1M CH3COOH (acetic acid) for another 24 hours to remove any exogeneous carbonates (Koch et al.1997). After this the samples were given a wash of deionized water and dried. Between the two chemical treatments the samples were also washed with this deionized water and each time dried before proceeding further. The powders obtained were tested for Carbon and Oxygen isotope analysis

(b) Carbon and Oxygen isotope measurements of its hydroxyapatite carbonate components The isotope measurements were carried out on a Delta V Plus Isotope Ratio Mass Spectrometer of Thermo Fisher Scientific at the Stable Isotope Laboratory of the Indian Institute of Tropical Meteorology in Pune, India. The treated enamel powders were made to react with a 100% Phosphoric acid at 25°C, the CO2 generated after this reaction was used to analyze the carbon and oxygen isotopes. The standards used were NBS-19 and PRL Lab Standard. The instrument was also checked and standardized for reproducibility and accuracy using a large number of primary and secondary laboratory standards of water and carbonate samples. The analytical precision (based on replicate analyses of NBS-19 and VSMOW and several other lab standards processed with each batch of samples) is ±0.1‰ for δ13C and ±0.2 for δ18O. Isotope ratios are expressed as δ18O and δ13C, and the units are per mil (‰) (Sharp 2007, Libes and Susan M.,1992). Oxygen and carbon isotopes are reported as d=[(Rsample/Rstandard)- 1]*1000 where R=13C/12C or 18O/16O, and reported against the VSMOW and VPDB scale for oxygen and carbon respectively (Chakraborty & Ramesh. 1992; Chakraborty et al. 2018; Sandhu et al. 2021).

3.1. Results

Table 3.1: Summary of data from Siwaliks, Central Narmada Valley and Manjra

S. no	*Taxa*	*Locality*	*Age*	*$\delta^{13}C$ (‰, VPDB) Mean: m Standard dev: d*	*$\delta^{18}O$ (‰, VPDB) Mean: m Standard dev: d*	*Diet Browser/ Grazer/ Mixed feeder*	*Environment Wet/ Dry/ Intermediate*
1.	Stegodon insignis/ ganesa n=3	Siwaliks	Lower Pleistocene	0.01 to 1.49, m 0.65, d 0.29	-5.52 to -4.36, m 5.03, d 1.42	Grazer	Intermediate
2.	Elephas Hysudricus n=2	Narmada	Lower Pleistocene	-9.82 to -10.07, m -9.76, d 0.53	-4.93 to -6.3, m -5.28, d 0.92	Browser	Wet
3.	Elephas namadicus, n=3	Manjra	Pleistocene	-8.02 to -11.04 m -9.80 d 0.39	-3.18 to -6.43 m -5.06 d 0.77	Browser	Wet

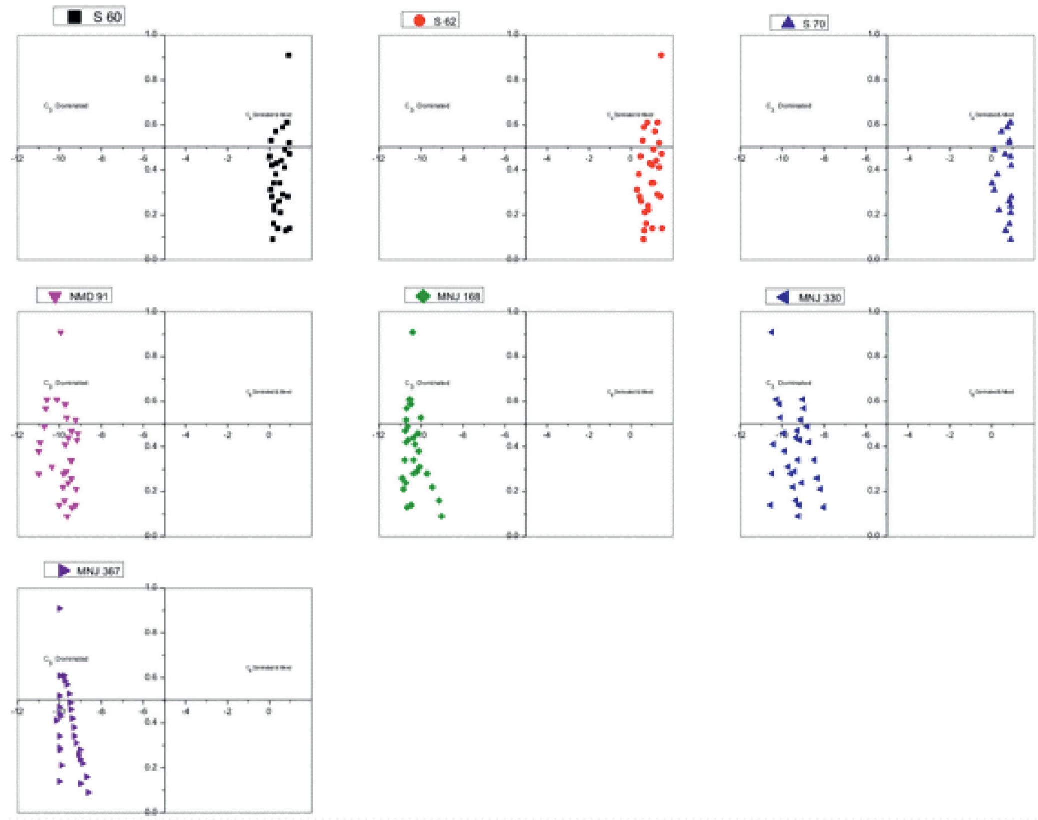


Fig 3.2 : δ13C data from each individual specimen from all the studied localities of Siwaliks, Narmada and Manjra River valley, the data has been extracted into layers

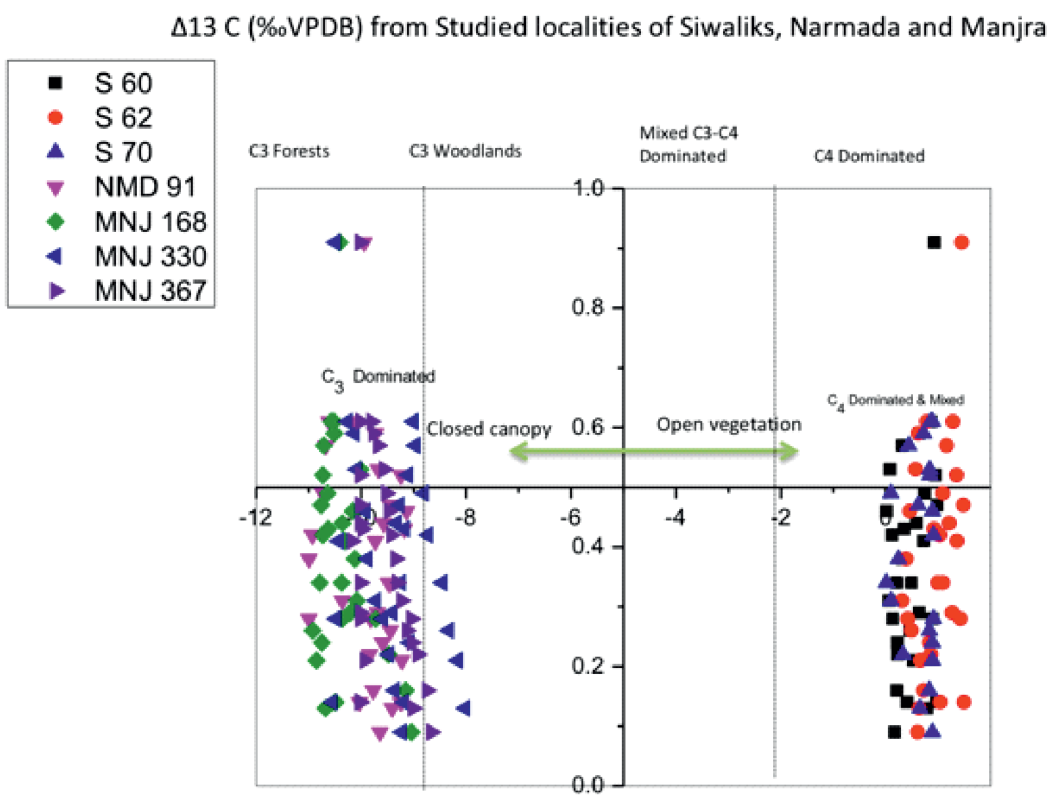


Fig 3.3: A graphical representation of the δ13C values from the localities of Siwaliks, Central Narmada valley and Manjra river valley showing the diet and vegetation of the studied specimens

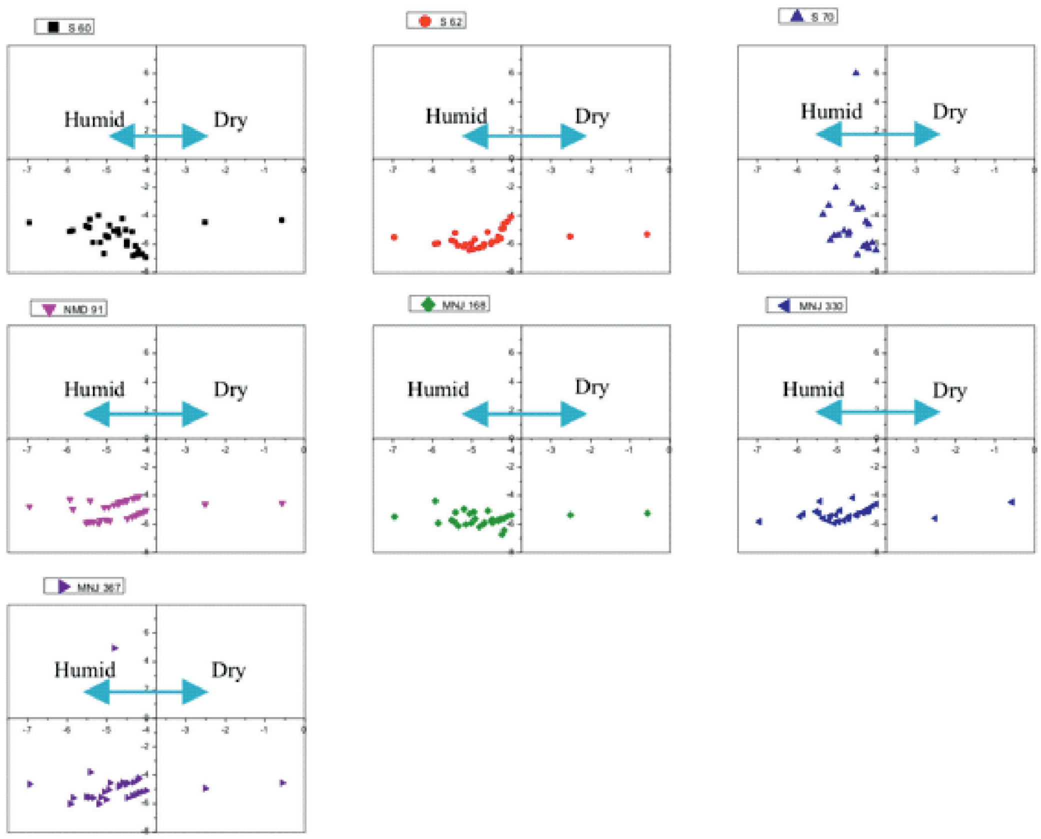


Fig 3.4 : δ^{18}O data from each individual specimen from all the studied localities of Siwaliks, Narmada and Manjra River valley, the data has been extracted into layers

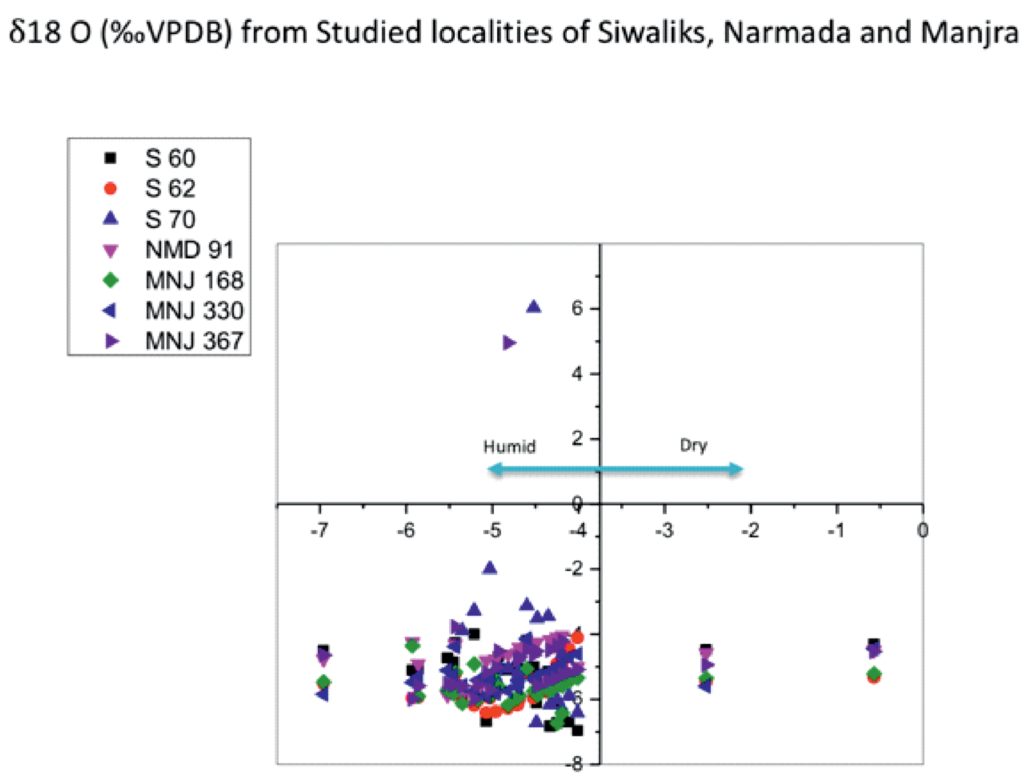


Fig 3.5: A graphical representation δ^{18}O of the values from the localities of Siwaliks, Central Narmada valley and Manjra river valley showing the general climatic conditions in terms of aridity and humidity

4.1. Discussion

Focusing specifically on the Siwaliks, the carbon δ13C values from the Late Pliocene to Early Pleistocene of the proboscideans (*Stegodon insignis, Archidiskodon planifrons and Elephas hysudricus*) have a more positive value than their previous periods. The reason for this is an increase in the C4 plants in their diets, most possibly the proboscideans of this age were mixed feeders or grazers but none of them were pure browsers. If we draw a conclusion based on the values then one can say that the animals were inhabiting an environment dominated by C4 vegetation, possibly like woodlands or a savannah like region. This dominance of the C4 plants is also confirmed by pedogenic analysis wherein an increase in the δ13C carbonate values was noted (Behrensmeyer et al. 2007; Puspaningrum 2016). Also in another study an increase in the C4 plant pollen was recorded in Upper Siwalik sediments (Figure 4.1)(Patnaik 2003; Puspaningrum 2016). The oxygen isotope values in the Pliocene till about Early Pleistocene are indicating a dry and an arid climate (Figure 4.2) , this may also be due to the weakening of the monsoon system. The weakening of the monsoon has been explained by extensive glaciation cycles which resulted in low sea levels. Together the isotope data in hand points to the general drying in localized areas and a transition from woodland forests to woody and open grasslands during the Late Pliocene till about Middle Pleistocene (Van Bemmelen 1949; Hall 1998, 2009, 2012a, 2013; Puspaningrum 2016). Keeping up with the global vegetation turnover even in India, by late Miocene the forests had given way to grasslands and the environment became arid and dry. Another event which further added to the aridity in the Siwaliks was the Himalayan upliftment. According to the results obtained and of other similar studies it can be safely concluded that in Late Miocene proboscideans were browsers and fed on C3 vegetation in closed canopied sub-tropical forests , somewhere between 8-7 m.y.a new proboscideans emerged on the scene, these were Stegolophodons, Stegodons, these new arrivals were also C3 browsers (Hoorn et al. 2000; Barry et al. 2002; Badgley).

The early Pliocene saw a grassland dominated landscape, the proboscideans of this age were all pure grazers and fed on a C4 diet (Figure 4.1) . The late Pliocene was a thriving age for the proboscidean community and multiple taxa such as the Stegodons, Anancus, Elephas (E. planiforns, E. hysudricus, E. platycephalus) roamed the grasslands. Out of these proboscideans Stegodonts stood out as the only one having a variable mixed diet of C3 browsing to mixed feeding to pure grazing (Quade et al.1992; Morgan et al.1994; Cerling et al.1999; Patnaik et al.2019). By the beginning of the Pleistocene the environment in the Siwaliks had changed again, from being arid and dry it now was dominated by wet grasslands, there were gallery forests and water bodies like ponds and swamps dotted the region also the monsoon by this time was much better established. The Proboscideans of this age namely *Elephas hysudricus,* Elephas sp etc. were all C4 grazers, an exception is the Elephas sp. from the Karewas of Kashmir, these Elephants seem to be browsing and not following the general norm of being a grazer. However by Middle Pleistocene the proboscidean diet had again changed from C4 grazer to now being a C3 browser (Phadtare et al.1994; Kotla et al. 2018; Kotlia 1990; Craig et al.2014; Patnaik et al. 2019).

4.1.a The Peninsular Localities From Narmada & Manjra River Valleys

Very few studies have been conducted in the Central Narmada region in terms of recreating the past vegetation and ecology. Based on a pollen study the following. According to this study, the landscape in the Middle Pleistocene, Central Narmada valley had been covered by non-arboreal plants, a swamp and marshy environment along the river bed. The starting of this period i.e. the Middle Pleistocene the landscape was ruled by grasses, sedges with very less arboreal elements. This kind of environment is characteristic of open grasslands. Over time there was an improvement in the climate and increase in

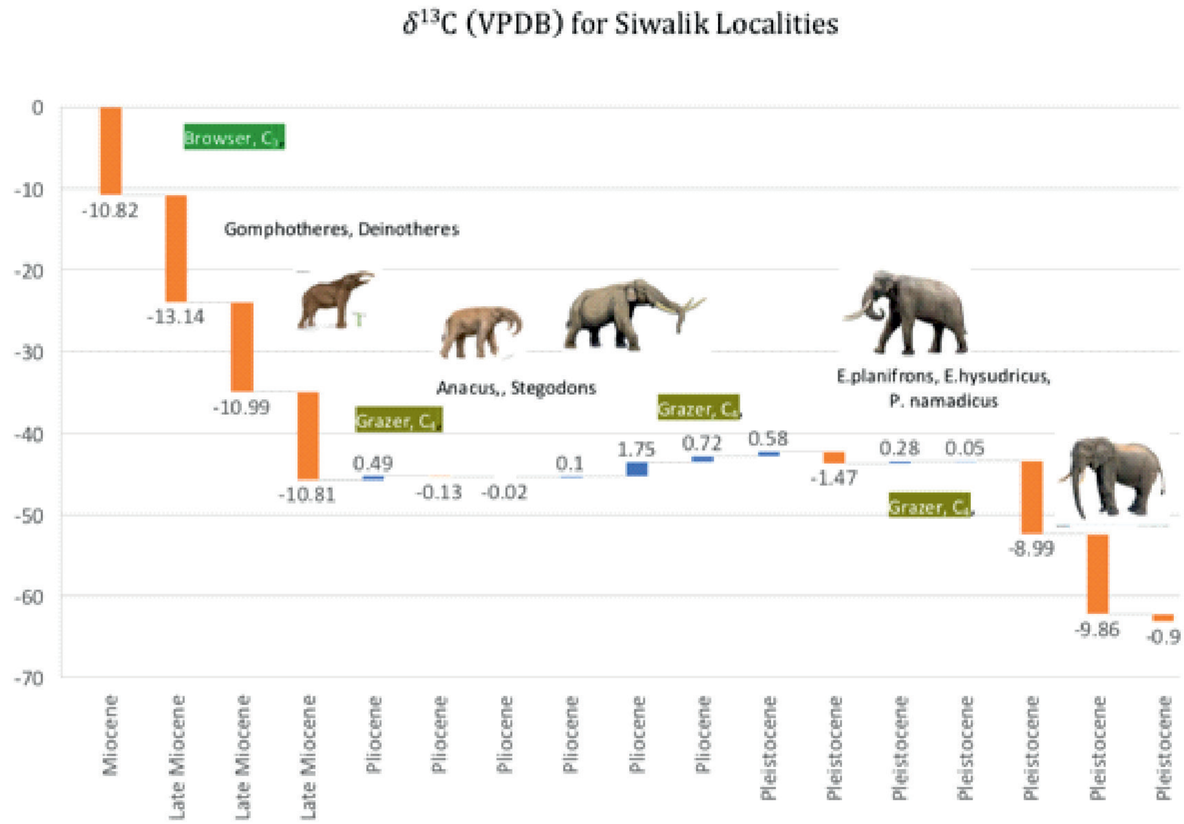


Fig 4.1: A graphical representation of the δ^{13}C data (Source: Patnaik et al. 2019) of the various Proboscidean populations from the Siwaliks

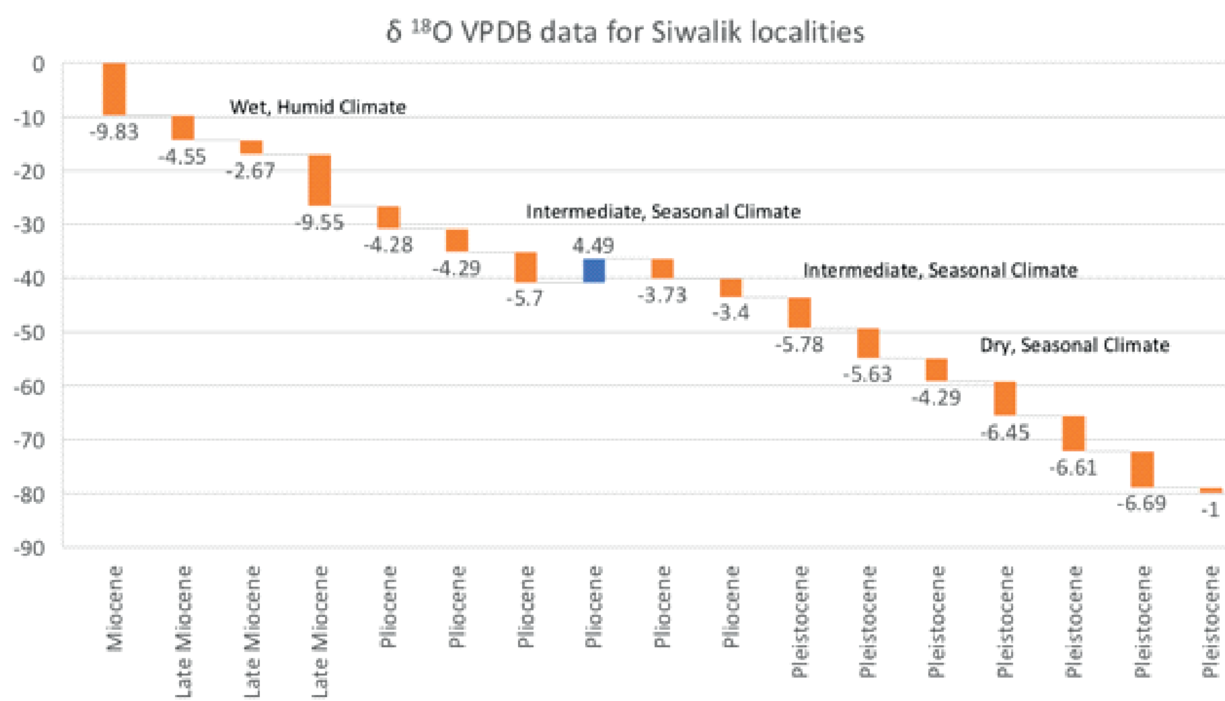


Fig 4.2: A graphical representation of the δ^{18}O data (Source: Patnaik et al. 2019) of the various Proboscidean populations from the Siwaliks, depicting the general trend in the aridity and the subsequent seasonality and drying of the region

the overall temperature which drove the turnover in the landscape from an open grassland to Savannah type environment with increase in the number of trees and shrubs. However even during this time the grasses were in the majority, other proxy data of this period has revealed that by late Pleistocene the open grasslands had given way to wooded grasslands (Patnaik 2000; Verma & Rao 2011).During the latter part of Pleistocene the effects of the Last Glacial Maximum (18-22 kyr B.P), were being felt in the Narmada valley and a reduction in the overall vegetation cover has been recorded (Bradley 1966). The arboreal growth during this time declines, grasses showed stunted growth but on the contrary plants of the family Amaranthaceae, Chenopodiaceae thrived and achieved their maximum growth potential (Allen 1982; Elmoslimany 1990; Prabhu et al.2004; Fay et al.2005; Verma & Rao 2011). Other proxy data from the time has revealed that during Late Pleistocene the region around present day Hathnora had a dry climate with more aridity, the reason for this was the low precipitation received in the summer monsoon and more in the winters, which would be effected by the LGM event (Singh et al.1974; Bryson & Swain 1981, Singh et al.1990; Patnaik et al.2009; Verma & Rao 2011). But this condition was remedied once the LGM event had passed, the upper Pleistocene in the area is marked with a boom in the diversity of flora and increase in their occurrences, from woodland grasslands the environment now was that of a tree savannah with a warm and moist conditions, number of trees increased but also the grasses also showed substantial growth further indicating a moist climate (Bryson & Swain 1981; Singh et al.1990; El Moslimany 1990; Caratini et al.1994; Gasse & Van Campo 1994; Verma & Rao 2011). Around ~ 15 ka yr BP an increase in the humidity levels across is also documented in other areas such as the Didwana lake in the Thar desert, further an increase in the density and occurrences of sedges, and aquatic herbs also display a rise in the humidity levels across (Wasson et al.1984; Singh et al.1990; Verma & Rao 2011). Coming to the Holocene, by early Holocene an increase in the vegetation is seen again, now specifically the arboreals are thriving, this period also witnesses the rise of deciduous forests as they begin to colonize and invade the grasslands, and now the vegetation in the region has again changed to a mixed tropical deciduous forest. This change has been recorded somewhere around 11000-8500 yr B.P, as the monsoon further becomes stronger. This period of strong monsoons, thriving vegetation is again categorized under a climate optima phenomenon (Bryson & Swain 1981; Van Campo 1986 ; El-Moslimany 1990; Kumaran et al.2005; Overpeck et al.1996; Verma & Rao 2011). After this Climate Optima event, a reduction in vegetation is again recorded, and a cooler and more arid climate prevailed, this change in the climate and vegetation is being attributed to the 8.2 ka yr BP worldwide cooling event (Alley et al.1997; Mayew ski et al.2004; Gupta et al. 2003; Verma & 167 Rao 2011). By 5100 yr BP the vegetation had changed again this time to dry deciduous forests. This change is suggestive of a change in the climate again more specifically to reduction in the monsoon (Fleitmann et al.2003; Verma & Rao 2011).

Is the Diet Shift amongst Proboscideans because of Climate and Vegetation change? It has been found that during the Middle Miocene and early Pliocene the Proboscidean community of the said localities were entirely dependent on a C3 vegetation. The proboscideans of this age lived in dense forests and moved between open woodlands and grasslands with patches of woodlands. By late Miocene (~8 m.y.a) the first major vegetation turnover is occurring and the shift in the vegetation cover in Asia from predominantly C3 to C4 begins, this shift in the vegetation has been possibly attributed to the aridification of Central Asia because of the Himalayan upliftment and intensification of the Asian Monsoon system. There are some advantages that the C4 plants have over the C3 plants particularly in monsoon based climates, at higher temperatures the C4 plants are more efficient regarding CO_2 -H_2O interaction at the time of photosynthesis (Ehleringer 1978; Quade & Cerling 1995). As a result the C4 plants function better during warm and dry growing seasons of the monsoon climates, which is also reason why C4 plants are seen in the riverine regions in the low altitude areas of the Indian Subcontinent (Quade & Cerling 1995). Pollen studies and evidence from the Siwaliks also backs this concept of Miocene grassland expansion. Based on this data it seems that grasses began to appear in Jammu region somewhere during early middle Miocene, following this trend a marked increase in the Graminaceous pollen occurs.

5. Conclusion

The conclusion that we can draw from this is that most likely the physical environmental change led to a shift in the grazing behavior and modified feeding strategies and procurement of proboscideans, as a consequence of their new feeding habits more and more open habitats and grasslands were developed and maintained. During the Middle Pleistocene a change in the diets of the proboscideans is being recorded, this change is primarily being recorded in the *Elephas maximus* samples wherein it shows a completely different diet as compared to its ancestors in the Pliocene and early to middle Pleistocene period, what is seen is that these elephants of the Middle Pleistocene had begun foraging and feeding in closed canopy forests, also as per the negative values of the carbon and oxygen isotopes the climate also seems to have become more warmer and humid.

Acknowledgments

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