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Extinction of Past Proboscideans from the Indian Subcontinent- Possible Reasons and Theories

DR. SONIKA SANDHU

Subject Matter Head, Enroute Indian History, Janakpuri, Delhi.

E-mail: sonika.sandhu@rocketmail.com

Abstract: *In this study, stable Carbon and Oxygen isotope analysis was carried out on the proboscidean tooth enamel samples from the DC collection available at Deccan College Post-Graduation and Research Institute, Pune. 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. The basic aim of this work was to reconstruct the interactions and relationships between environment change in the past, and the appearance and disappearance of various proboscideans associated. The idea was to gather an understanding of how the changing landscape actually affected the proboscidean populations and caused their disappearance in some regions whereas in certain other areas they continued to thrive and be present until recently.*

Keywords: *Isotopes, Proboscideans, Megafaunal Extinctions.*

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1.1. 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. proboscideans have inhabited the subcontinent from Pliocene. During the Eocene they were extensively found and were in quite an abundance.

The elephants as compared to many other animals seem to have evolved at a much faster rate. This 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 (Maglio 1970; Shoshani & Tassy 1996). Scholars (Shoshani & Tassy 1996 ; Sankhyan & Chavasseau 2018) have found three separate phases in their variation and radiations, which are as follows:.

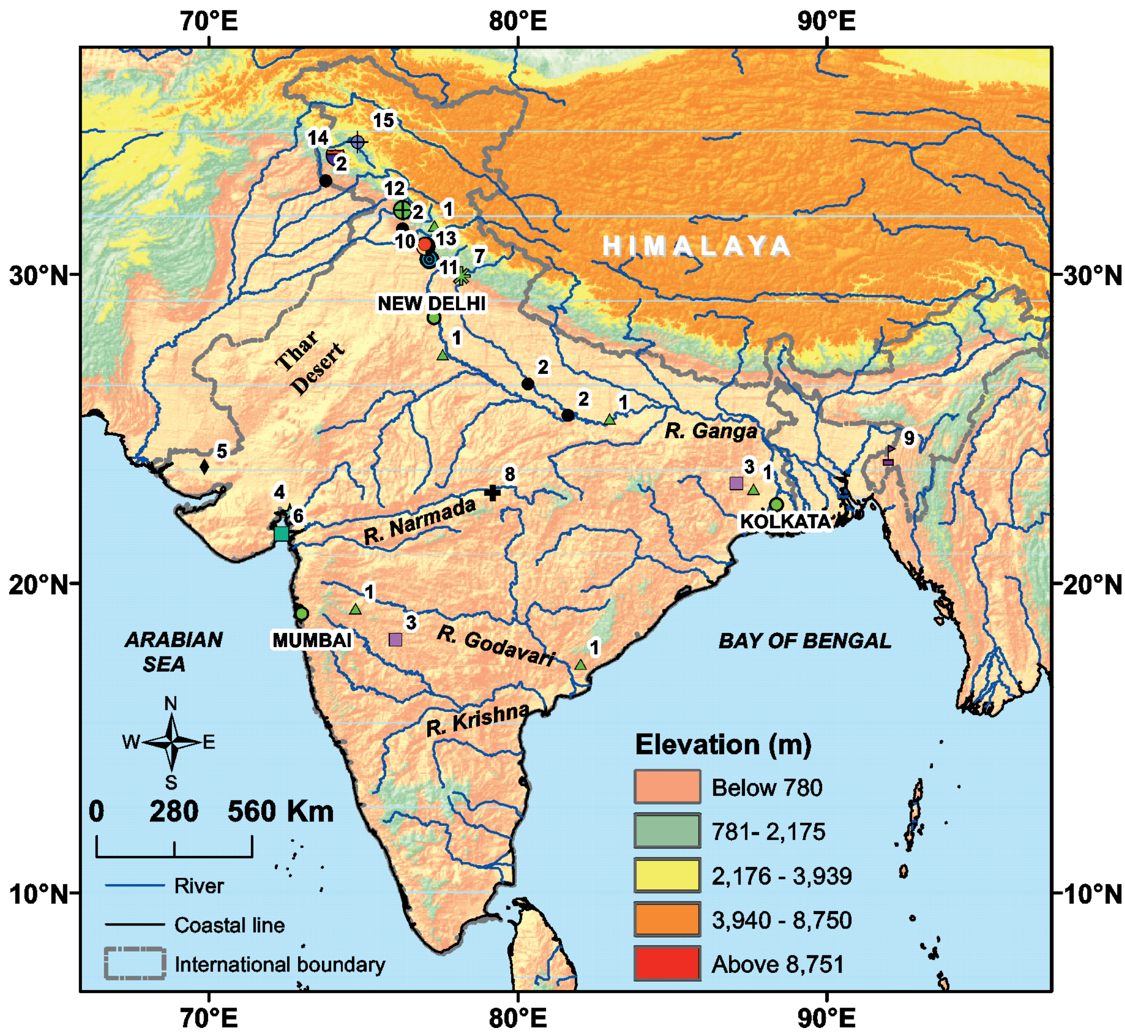
- During the Paleogene the ancient and early members of Proboscidea diverged in the Afro-Arabian areas.
- During the early Miocene, the Elephantimorpha displayed quite a bit of expansion and radiations around the world.
- Also during the Miocene again the families of Elephantidae and Stegodontidae further underwent development and diverged.

1.2. Ancestors of Asian Proboscideans

In the Indian Subcontinent, they have been possibly present right from Neogene onwards, 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, analyse, document and build on their evolutionary history in Asia (MAP 1) (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). Subsequent studies on the proboscideans from Siwalik localities have led us to understand the rich and varied paleo diversity within this group (e.g., Tassy, 1983a-c) allowing us an insight into their evolution and radiation (Sankhyan & Chavasseau 2018). Some of the early key ancestors were as follows.

- STEGOLOPHODON: This proboscidean is of pure Asiatic origin and genus. It appeared on the scene in mid-Miocene and thrived during the Miocene-Pliocene epoch but towards the end of Pliocene it made its exit. It has been dated to mid Miocene (Yoshiki et al.2013; Osborn 1929; Hooijer 1955; Bakr et al.1966; Sarwar 1977; Koda 2oo3; Kalb et al. 1996a) . *Stegolophodon sahabianus* has been found. In India it has been found in the Siwalik sediments of Punjab and also from Piram islands in Gujrat (Lydekker 1886). The specie *Stegolophodon cautleyi* is native to the Indian subcontinent and is endemic to this region, this particular type has not been reported from anywhere else but the Siwaliks of India and Pakistan and the Piram islands of Gujrat (Khan et al. 2005).
- STEGODONTS: From Indian subcontinent it has been reported from multiple localities and regions. The fossils of this species are of particular importance as they manifest and represent a nearly unbroken evolutionary passage from mastodonts into true elephants. In India stegodonts are represented by: *S. insignis ganesa, S. bombifrons, S. bondolensis, S. aurorae, S. airawana, S. trigonoelephalus, S. orinthis shodoensis (*Kundal et al. 2017). Due to its impressive radiation, diversity and presence, most likely Stegodonts like Stegolophodonts were of an Asian origin (H. Saegusa et al. 2005)
- ELEPHAS: From the members of the Elephas group the Pleistocene species of *E. hysudricus* of the Indian subcontinent and *E. hysudrindicus* of S.E. Asia are at present the closest to the ancestry of the living species (Lister et al 2013). Elephas first appeared in the late Pliocene of Africa as a contemporary of Loxodonta and underwent a complex radiation in response to expansion into new geographic areas outside that continent; it is the most diverse of the generic groupings within the Elephantidae. Two major lines are recognized; one survived in Africa until very late Pleistocene times, and the other was Eurasiatic in distribution.

The question then arises, that despite such an extensive spread and a long history, Why did these species die out and become extinct? What possible factors led to their extinction?



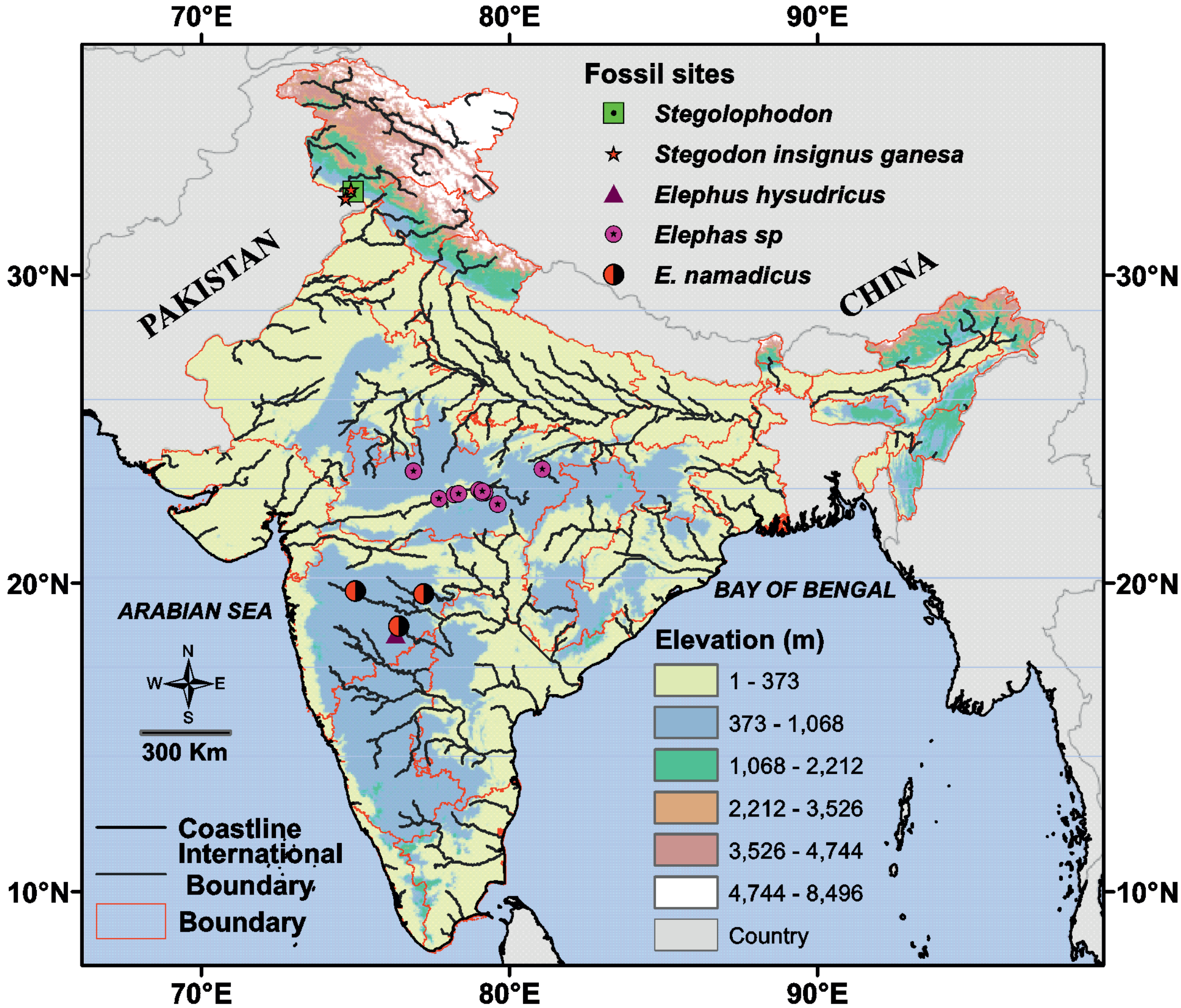
Map 1: Various localities from where proboscideans have been reported in the Indian Subcontinent. 1. Stegodon insignis Ganesa, 2. Hypselephus hysudricus, 3: Paleoloxodon namadicus, 4: Deinotherium angustedens, 5: Moertherium sp, 6: Deinotherium indicum, 7: Pentalophodon sivalensis, 8: Stegodon namadicus, 9: Trilophodon pandionis, 10: Stegodon k. puralensis, 11: Archidiskdon planifrons, 12: Stegodon bombifrons, 13: Anthracobune aijiensis, 14: Pentalophodon falconeri, 15: Paleoloxodon priscus. Map has been generated using ArcGIS 10.3 (Hydrology toolbox) along with CorelDRAW X3. Dem data resolution is 90m.

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 2). These localities have also yielded significant number of fossil elephants.

3. Materials and 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 extinctions and migrations. (Koch et al. 1998; Feranec & MacFadden, 2000; Hoppe and Koch, 2006; Metcalfe & Longstaffe, 2012, 2014)



Map 2: 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.

3.1. 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:

3.2. 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).

4. Results

Table 4.1 : 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

The above table summarizes the data generated from the specimens analyzed for this study, according to the readings obtained the following inferences can be drawn. The carbon isotope readings for Siwalik localities (Table 4.1) are in the range from 0.01 to 1.49, this is indicative of a grazing diet signal, and perhaps points to predominance of a C_4 vegetation, the climate at the time is an intermediate type, wherein seasonality is setting in and the monsoon is slowly gathering momentum. The correlation co efficient was calculated to be -0.38, which is also indicative of this slowly developing seasonality

The data coming from the Peninsular localities is in contrast with the Siwaliks, on one hand the Siwaliks were much drier whereas on the other the Narmada (and Manjra river valleys were experiencing wet climates with plentiful rainfall. Consequently the proboscidean population of these areas were primarily browsers and fed on C_3 vegetation of forests. The Narmada and The Manjra localities have a correlation factor of 0.67 and 0.42. This is indicative of a strong positive correlation is indicative of seasonal and varied diet, and most likely they were feeding on seasonally fresh fodder.

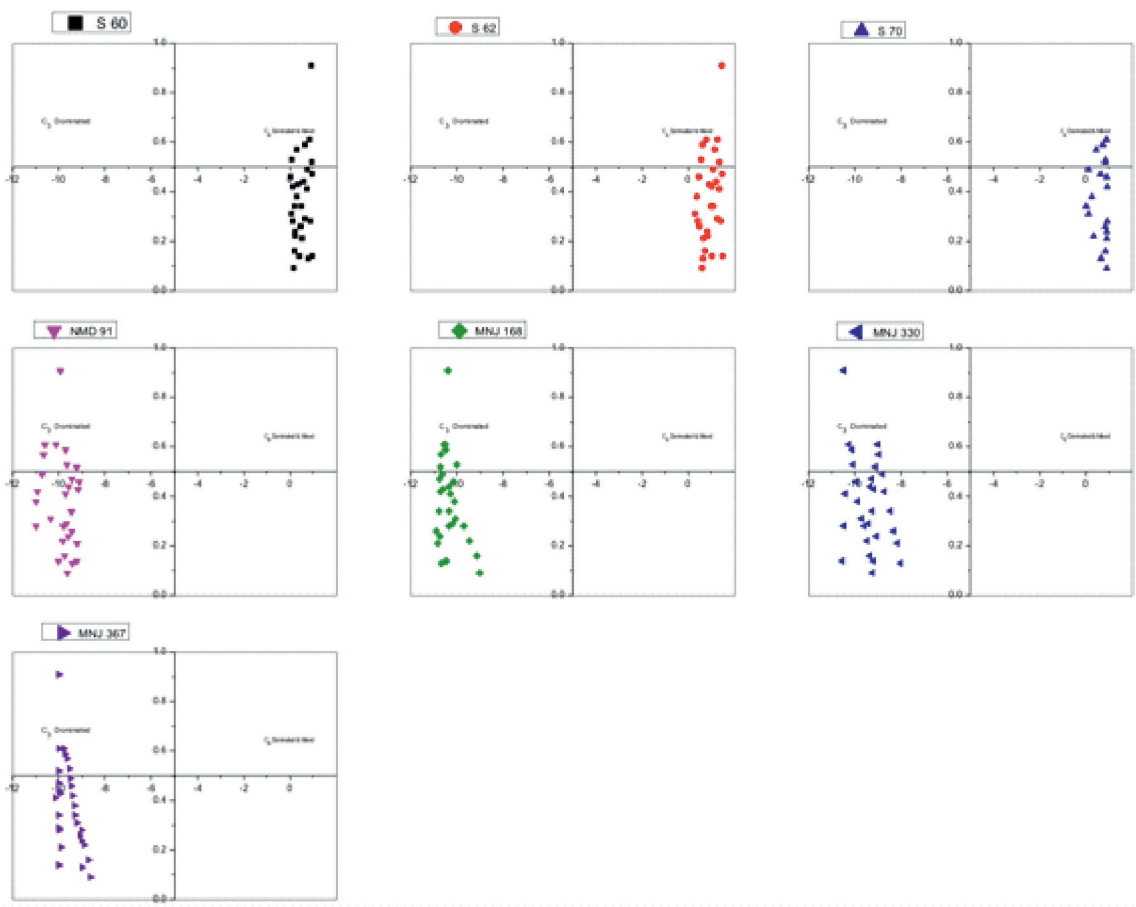


Fig 4.2 : δ^{13}C data from each individual specimen from all the studied localities of Siwaliks, Narmada and Manjra River valley, the data has been extracted into layers.

In this study the δ13C values of the early proboscideans of the Miocene such as Sinomastodons, Stegoloxodons, Platybelodon, *Stegodon orientalis, Stegoloxodon indonesia* are all C_3 browsers and derived their nutrition from dense woodlands and forests. The δ13C values of Stegoloxodons falls in the range of -14.1 to -12.8‰ indicative of a browsing based forest diet. The later proboscideans such as the *Palaeloxodon namadicus* (between -9.7 and -8.7‰) shows an inclination towards a mixed C_3-C_4 diet, similarly *Stegodons insignus*, *Elephas Hysudricus* are also showcasing a mixed diet but Elephas individuals in these times are flexible in their modes of nutrition and are incorporating both browsing and grazing strategies. Based on this data we can further predict and build on theories and factors for the extinctions of these species and what pushed them into niche environments.

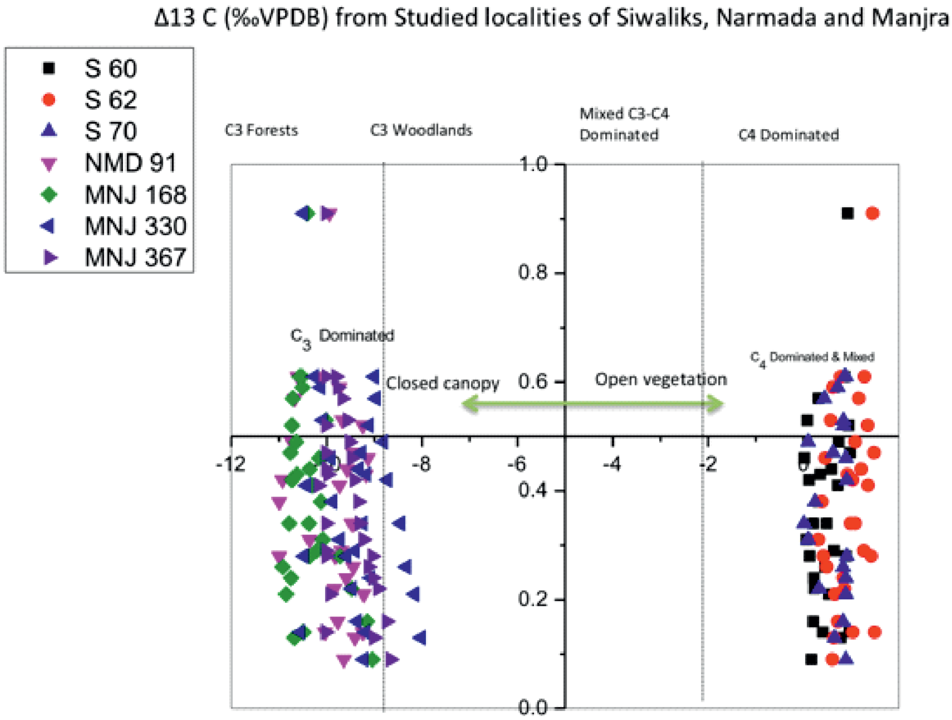


Fig 4.3: A graphical representation of the $\delta^{13}C$ values from the localities of Siwaliks, Central Narmada valley and Manjra river valley showing the diet and vegetation of the studied specimens.

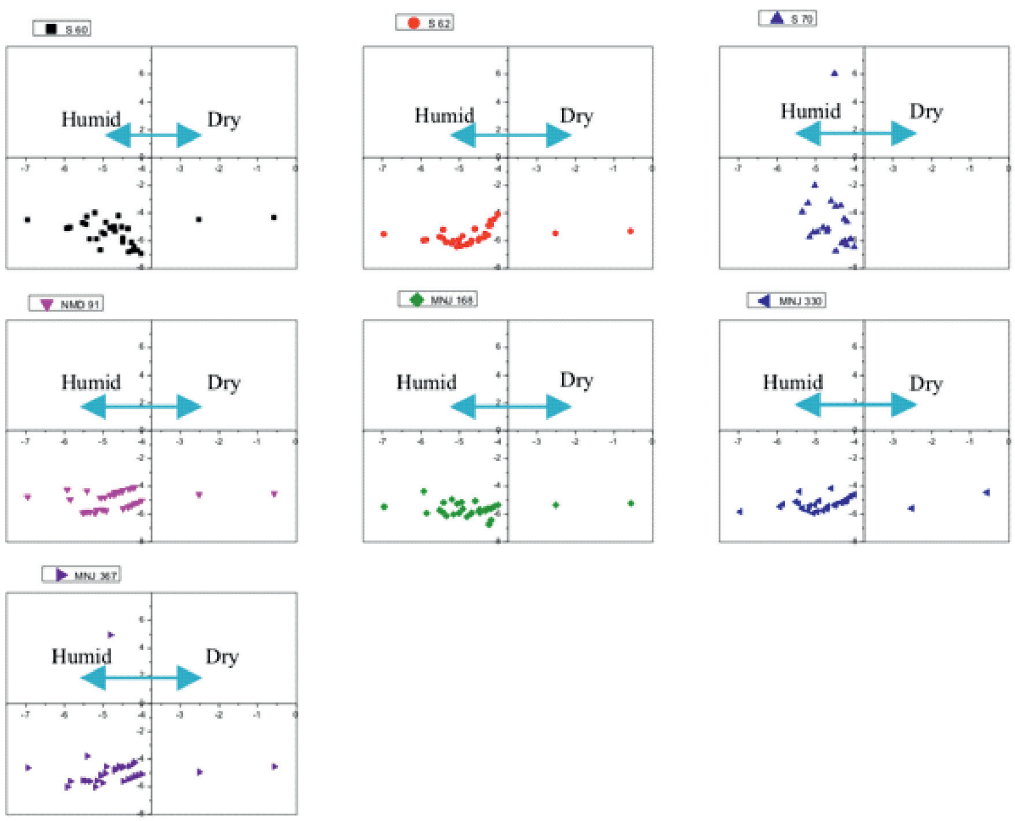


Fig 4.4 : $\delta^{18}O$ data from each individual specimen from all the studied localities of Siwaliks, Narmada and Manjra River valley, the data has been extracted into layers.

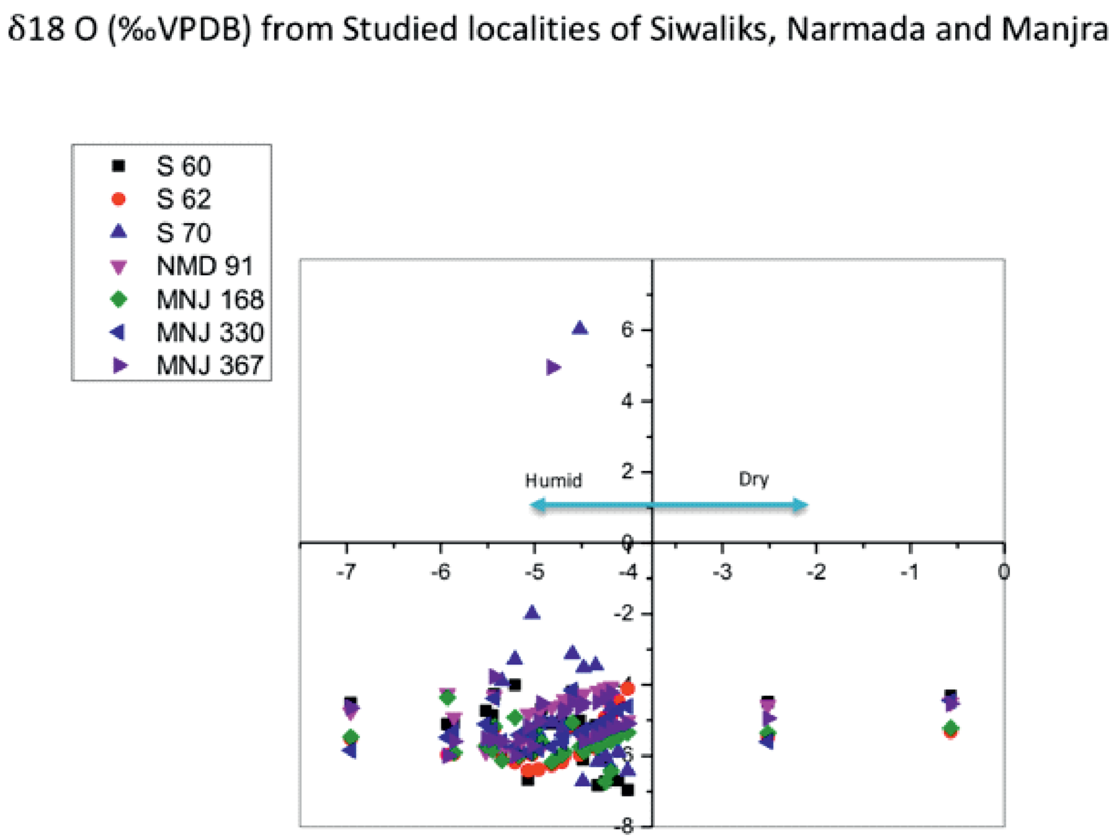


Fig 4.5: A graphical representation $\delta^{18}O$ of the values from the localities of Siwaliks, Central Narmada valley and Manjra river valley showing the general climatic conditions in terms of aridity and humidity.

5. Discussion

The Indian Subcontinent has a documented presence of the proboscidean lineage right from the early Eocene. Four genera from its very first family Anthracobuniidae have been reported. The species of these four genera have all been more or less found in the northern reaches and frontiers of the subcontinent possibly indicative of their dispersal. The finds have come from areas of West Punjab in present day Pakistan and from the Subathu Formation of Kalakot from Jammu & Kashmir. Even members of Moeritheriidae which flourished from 37-33 m.y.a have been reported from western Kachchh (Bajpai et al. 1989). Besides these very ancient members, we also have some fossils from families like Brevirostrinae which is represented by three genera in the Indian Subcontinent, these are: Anancus, Pentalophodon, Synconolophus. These generally have been found in Mio-Pliocene deposits (Rai 2004). Besides having the living population of the present day proboscidean *Elephas maximus indicus*, Indian Subcontinent also boasts of the presence of its earliest member: Archidiskdon. They first appeared in Pliocene and were discovered from the Pinjor horizon of the upper Siwaliks near Kalka, Siswan, Chandigarh (Hooijier 1955; Rai 2004). All these species over time became extinct, the only living members at present belong to Elephantidae.

5.1. Adaptation And Extinction Of Proboscideans In The Localities Studied

In This Study A definite transformation and turn over in the plant cover have been recorded in the Middle Miocene which has produced effects till today, the most profound effect this turnover has brought in is possibly the extinction of certain mega herbivores forcing them to either adapt or become extinct. Low crowned proboscideans such as Platybelodons, Stegolophodons, primitive stegodonts had dentition more suitable to C_3 diets but as the vegetation cover switched to C_4 they died out during the early Pleistocene. However today we still find proboscideans amongst us is because their succeeding generations started evolving and began including more and more C_4 plants in their diets to an extent that their later progenies showcased grazing as their main feeding behavior. This change in their feeding habits to include more grasses in the diets is reflected in the dental morphologies of the late proboscideans. Members of advanced Stegodont taxa and Elephantidae family had to adapt and cater to more coarse grazing, they modified there dentition accordingly and started showcasing horizontal displacement of the molars. An increase in the size of the molars was also seen along with more lophs and ridges, the enamel became thinner and the hypsodonty index also went up. Now a second vegetation change took place towards the end of Middle Pleistocene wherein C_4 dominated plant cover reverted back to C_3 dominated cover, at this time proboscideans like Stegodonts in places like Java became extinct but in the other localities they again adapted to a browsing method, on the other hand there some proboscideans like the Elephas even though they were not excellent grazers started to prefer browsing, this preference is not so much guided by vegetation change but more so because of the increasing competition and perhaps predation. This C_3 diet is what has continued till present and today the proboscidean of India *Elephas maximus* is a C_3 feeder primarily but can become mixed feeder if the opportunity arises and more nutrition is promised.

From the data, evidence and previous work discussed above it is quite clear that the extinctions which occurred within the proboscidean community is not only because of a change in vegetation cover however factors such as competition from other herbivores or within themselves, predation could have also amounted to their habitat loss and leading up to their disappearance from the environment all together. In other words, it is not one but a combination of multiple factors and events which drove them into oblivion. This idea is further corroborated by the fact that within the proboscideans there were members which were flexible in their feeding habits (Stegoloxodon, Stegodon, Sinomastodons) and could have easily sustained the changes in vegetation but even they went extinct. A good example is of Sinomastodonts which initially must have faced stiff competition from Stegodonts and late even elephas and eventually died out in places where these two proboscideans began to make their mark, as compared to the Sinomastodons both the Stegodonts and Elephas were well adapted to grazing and could easily adapt and evolve to the changing vegetation in the regions at the time (Zhang et al.2016; Puspaningrum 2016).

Regarding the predation and overkill hypothesis, except Hathnora in the Central Narmada Valley none of these sites have yielded hominin remains or evidence of butchery or hunting in Indian context (Sathe & Paddayya 2013) supports humans as responsible factors for its extermination. Drawing analogies from Java and Flores, one can say that the two studied taxa viz. Stegodonts and Elephant species co-existed with hominins for almost a millennia without causing any extinction event. But this hypothesis is sound when talking about hominins. When it comes to Homo sapiens studies have shown that once they started increasing in number and colonizing more and more areas certain species of proboscideans like *Stegodont orientalis, Elephas hysudricus* and *Elephas maximus* disappeared from the localities. Therefore possibly Homo sapiens would have over utilized and exhausted the local resources, may have also caused modification in the environment by their activities like use of fire, would have led to the habitat loss for large animals like elephants and would have pushed them in the niches and fringes of the habitat they once had ruled, this has been seen in present day elephants who have remain hidden in the forested regions of Asia in an attempt to escape human predation and modification in an attempt to survive this ever growing threat of *Homo sapiens* on the horizon.

5.2. Inter & Intra Specie Competition Amongst Proboscidea

Some of the early members of Proboscidea were all exclusively C_3 feeders, they all had low crowned teeth with few plates and ridges in each molar, the enamel was thick and the hypsodont index was low, some of these early members were the gomphotheres, Stegodonts, Sinomastodons, Stegolophodons and Platybelodons (Liu et al.2009; Puspaningrum 2016)

According to the isotope studies conducted on the palaeosols in the Siwalik, a steady increase in the $\delta^{13}C$ values of the carbonates has been recorded. Interestingly this increase in the values is corresponding to the rise in the pollen record of plants of Poaceae and Graminae family, this is a clear proof of the displacement of the C_3 dominated environment with a C_4 grassland (Quade et al.1989; Quade & Cerling 1995; Behrensmeyer et al.2007; Puspaningrum 2016). Also around this time we see the rise of some mixed feeders in the area as well, however as compared to the other parts of Asia the turnover to open grassland was much more intense in the Siwaliks leading to the extinction of many obligate browsers like Suids and Tragulids (Morgan et al.1994; Barry et al.2002; Badgley et al.2002; Puspaningrum 2016).

The isotopic studies and results conducted in various parts of Asia have suggested that out of the Proboscideans present during the turnover period it seems members of only Stegodons had evolved and adapted their diets and switched their feeding behavior from that of a browser to a mixed feeder and finally becoming a grazer. This change is corroborated by physical and morphological changes as well and the later members of this genus which were predominantly grazers. Clear morphological changes were seen in the type of dentition which the later members of this genus developed, namely; increase in the number of plates and ridges in each molar, an increase in the hypsodont index, these changes in teeth are basically modifications which would allow the animal to chew and masticate the abrasive C_4 grasses and also ensure that the tooth does not get worn out early (Lister 2013; Puspaningrum 2016).

The radiation, of the family Elephantidae is actually coinciding with the spread of the C_4 vegetation, because before the Pliocene the Elephas are absent from Asia and only start moving out once C_4 grasslands have taken hold of the environment. To further add to this the morphology of the Elephas molars are more suited to the C_4 grasses as they showcase a high hypsodont index, thin enamel and large number of ridges and plates per molar. Of interest is the extinction of the *A.planifrons* from Siwaliks after 2.6 m.y.a even though it was well adapted to grassland and was a grazer, their extinction overlaps with arrival of the *Elephas hysudricus* and Cervids. Thus possibly *A. planifrons* could not compete with the growing number of Elephas and Cervus in the environment (Barry et al.1985; Hussain et al.1992; Basu 2004; Nanda 2002; Patnaik & Nanda 2010; Puspaningrum 2016). Another proboscidean which suffered a similar fate was the Sinomastodons which went extinct on the arrival of the Stegodons in the early Pleistocene. The Sinomastodons had similar diets with the Stegodons and possibly their extinction is not due to the vegetation change but competition by Stegodons. In comparison the Stegodons were more efficient grazers with more suited dental morphology as their molars were larger and had a higher hypsodont index than the Sinomastodons (Zhang et al.2016; Puspaningrum 2016).

The Late Pleistocene saw the dominance of the Elephas and the eventual dying out of the other grazer proboscideans such as the Stegodons, the *Elephas maximus* became the premier proboscidean during this age. The carbon isotope ratios of this time all indicate towards a shift back in the C_3 diet with more negative values being recorded. The range of these values is -16.2‰ to -7.7‰, even the oxygen values become lower and are recorded in the range -9.5‰ and -4.4‰. This lowering of the oxygen values is indicative of an increase in the humidity levels (Puspaningrum 2016)

6. Conclusion

The conclusion that we can draw from this is that the physical environmental change led to a shift in the grazing behaviour and modified feeding strategies, this invariably would have affected their numbers and would have caused new radiations and adaptations to be developed, in order to survive new feeding habits in more open grasslands would be needed to be developed. Also inter and intra specie competition along with increasing presence of Homo sapiens would have further caused a strain on the proboscidean populations. The slow birth rate and recovery rate would have also invariable led to their extinctions over a long period.

7. Acknowledgment

I would like to extend my gratitude to Indian Institute of Tropical Meteorology (Pune), for allowing me access to the instrument used for analysis. I would also like to thank the Paleontology laboratory at Deccan College Post Graduate and research Institute for furnishing me with the samples and fossils for this study.

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