



Pleistocene Specie Displacement of Elephas and Stegodonts in the Indian Subcontinent

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Abstract: The paper explores relationship between changing environments, vegetation and climates with respect to species displacement. It examines the emergence of new species in areas not native to them and they displace the preexisting similar families species by competing with them for resources and space. A compartitive study has been done of the isotope ratios between Indian localities of Siwaliks, Narmada and Manjra valleys and the Irrawaddy localities to understand specie displacement. Irrawaddy values for carbon are in the range $\delta^{13}C = -6.9\text{‰}$ to -0.8‰ and for oxygen the are $\delta^{18}O = -6.9\text{‰}$ to -5.5‰ , whereas the same taxa in Siwaliks has given the range for carbon $\delta^{13}C = -2.2\text{‰}$ to -1.2‰ and for oxygen $\delta^{18}O = -6.0\text{‰}$ to -5.0‰

The Late Pleistocene saw the dominance of the Elephas and the eventual dying out of the other grazer proboscideans such as the Stegodonts. The dominating proboscideans in the Late Pliocene to Early Pleistocene were the Stegodonts, particularly *Stegodon insignis*, *Stegodon orientalis*, *Archidiskodon planifrons*, *Elephas hysudricus* in the Mainland regions of Asia. In Java species such as *Stegoloxodon indonesicus*, *Sinomastodon bumiajuensis*, *Stegodon trignocephalus*, *Elephas hysudricus* were thriving. The $\delta^{13}C$ values generated from this taxa are slightly more positive and is in the range (-7.8‰ to 1.2‰). This shift is indicative of mixed diets and rise of specialized grazers, even then these values are not of pure C4 grazers. An increase in the $\delta^{18}O$ values is also seen, this is expected as the aridity increased the values recorded became higher in the range of (-6.9‰ to -2.2‰).

Keywords: Isotopes, Proboscideans, Megafaunal Extinctions.

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Introduction

The Indian Subcontinent is one of the few places where the order Proboscidea has flourished and still found today in the wild, also besides having a continuous presence they have displayed an intact and an uninterrupted fossil record. They have been found in areas where we cannot even fathom their

presence today. Interestingly the first ever scientific discovery of a fossil was that of vertebrae of an elephant. This find was from the Umer river in Narsinghpur in the Narmada valley (Spilsbury, 1833). The proboscideans have inhabited the subcontinent from Pliocene. During the Eocene they were extensively found and were in quite an abundance. However today we have only two surviving taxa, out of which one is still found here: the *Elephas maximus indicus*.

Proboscideans are the largest mammals on the planet and have a late appearance in the geological records. Nevertheless, 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.

The early members of some families like Gomphotheriidae, Choerolophodontidae, Amebelodontidae, Mammutidae show a relation with Phioma, this was a primitive ancestor of the proboscideans in Africa and was present during the early Oligocene (Sankhyan & Chavasseau 2018). Dental studies have revealed that the proboscideans of these above mentioned families had a complex pattern trefoil arrangement in its molars, which is also displaced horizontally as we see in many later members to the ones present today and also the tusk had a guillochage pattern arrangement (Sankhyan & Chavasseau 2018).

Miocene was a time for the proboscideans and its early members were able to move into and colonize Eurasia, two families are of particular importance - Elephantidae and Stegodontidae, individuals of these families had the most number of variations and were able to successfully radiate into many new regions, studies and fossil evidence has showed that the members of these two families had well developed dentition with respect to molars and used the anterior-posterior mechanism for mastication of food, the mandibles were reduced and had tusks, the skulls were quite big with pneumatized bones and had an superior position with respect to the gait (Sankhyan & Chavasseau 2018) (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).

2. Species of Interest

2.1. A. 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. Unlike many other proboscideans it was not very widespread and has been reported from select localities around the world. The earliest record of this animal comes from Japan, on the river bed of Nakagawa river at Katsura village. It has been dated to mid Miocene (Yoshiki *et al.* 2013; Osborn 1929; Hooijer

1955; Bakr *et al.* 1966; Sarwar 1977; Koda 2003; Kalb *et al.* 1996a) . 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). In Siwaliks of Pakistan it has been found at the Lower Chinji horizon (Osborn 1929) . Interestingly *S.cautleyi* is the most primitive and ancient to these genera. From *S. cautleyi*, two lines of evolution can be derived. One leading to *S. daratensis* and the other to *S. latidens*. *S. daratensis* probably gave rise to *S. stegodontoids* while *S. latidens* to *S. cristatus* (Sarwar 1977)

2.1.B. STEGODONTS

Another specie of interest and relevance are the Stegodonts. They belong to the extinct sub family of ‘Stegodontinae’, comprising of two genera: Stegolophodons and Stegodonts. They were present from 11.6 m.y.a to late Pleistocene, with unconfirmed reports of regional survival till as late as 4100 yrs. ago. But this seems to be highly disputed. Falconer (1857) observed and proposed that they actually constitute the intermediate group of Proboscidea from which the specie spilt occurred between mastodons and true elephants. *Tetralophodont gomphotheres* most likely gave rise to both stegodontids and elephantids. The earliest known fossil is reported from Northern China dated to 5.5-6 m.y.a. From Indian subcontinent it has been reported from multiple localities and regions. The fossils of this specie from Indian subcontinent are of particular importance as they manifest and represent a nearly unbroken evolutionary passage from mastodons 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 Stegolophodons were of an Asian origin (H. Saegusa *et al.* 2005)

2.1.C.ELEPHAS

The origin of the present day Asian elephants *Elephas maximus* L is an interesting phenomenon, the name ‘elephas’ previously was used to denote and encompass many different types of fossil elephants, today however only a few members are included in this group (Maglio 1973). 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 latter branch culminated in the living Asiatic elephant, *Elephas*

3. Faunal Exchanges And Dispersals

Of interest are three events which led to the dispersal and radiation of proboscideans around the globe: The Proboscidean Datum Events:

Africa, the birthplace of proboscideans had largely been isolated during the Paleogene and early Miocene. The Tethys had acted as the barrier for Africa when it came to connectivity with Europe, Asia and the Indian Subcontinent. Hence the fauna on this continent had largely been endemic. Gradually because of plate tectonics and sea level changes including disappearance of the Tethys sea and emergence of the Himalayas and the Alps, fluctuating terrestrial connections were developed between Africa, India and Eurasia from time to time, as a result of which we see more frequent and equal number of faunal exchanges. These

faunal exchanges initially were termed as Proboscidean Datum Event and were thought to be a singular occurrence (Madden/Van Couvering 1976) but with more study and research three such events came to be identified (Thomas 1985) which later increased to a minimum of six such faunal exchanges (Van der made 1996, 1999). Fossil localities in the areas of Bugti and Zinda Pir dome are providing more and more evidence regarding the early contacts and exchanges between Africa, Indian Subcontinent and Eurasia for example an elephantid proboscidean incisor was unearthed from the strata here and dated to around 24 m.y.a, thus inconclusively proving that these faunal exchanges started much before than previously proposed (Antoine *et al.* 2003; Lindsay *et al.* 2005; Van der made 2010).

By 22 m.y.a many types of animals of Eurasian origin such as rodents, lagomorphs, chalicotheres, pigs, ruminants, rhinoceroses, carnivores etc had moved into Africa and the Indian subcontinent, amongst these animals at least one species of a proboscidean also reached the Indian sub-continent. This event has been given great importance and is comparable to the 'Great American Exchange' of the Eo-Oligocene transition (Van der made 2010).

The proboscidean Gomphotherium and Zygolophodon reached Europe and East Asia around 20-28 m.y.a, another faunal exchange took place two million years later around 16 m.y.a wherein the proboscidean Deinotherium entered into Europe simultaneously Choerolophodons and Zygolophodons may have arrived in eastern Asia (Van der made, 2010).

3.1. Faunal Exchange Between Asia And North America: The Grand Coupure

An interesting event occurred at the end of Eocene at around (34-24 m.y.a), formation of the Atlantic ocean separated south America from Africa and during the Eocene North America from Europe, towards the end of Eocene and Oligocene extensive glaciations occurs on the Antarctica which locks the water of the world, this leads to a substantial decrease in the sea levels, leading to increased connectivity between land masses which previously had remained isolated and distanced due to water bodies. With increase in the available land animals of the time also moved into these new areas resulting in an intense faunal movement between Asia, North America and Europe, this even has been termed as the *Grand Coupure* (Van der made 2010)

3.1.a. Proboscidean Dispersals

The dispersals and the colonization by various animals occurred during the Mid-Miocene Climatic Optimum, at the time the global temperatures were lower as compared to the Eocene, this reduction in the temperatures is seen during the mid-Miocene around 16-17 to 12-14 m.y.a (Lear *et al.* 2000; Van der made 2010). However somewhere during the Mid Miocene the temperatures dropped again, this has been termed as the Mid-Miocene crisis (Van der made, 2010). This climate optimum led to the expansion of many continental as well as marine species northwards. Thermophile animals like reptiles and amphibians migrated into Europe, but as the climate optimum waned these species became extinct and were unable to permanently establish themselves (Böhme 2003; Van der made 2010). The mammals which migrated into new lands also seem to have followed suit, for example tringulids dispersed into Europe and thrived there but soon after became extinct after the climate optimum, during this Mid-Miocene optimum some proboscideans also reached Eurasia and thrived for a time but they too became extinct once the climate changed again (Van der made, 2010). Many African proboscideans did not venture into new lands as they hadn't yet developed different feeding strategies whereas the proboscideans which did actually migrate where browsers and were able to thrive for the time, until climate changed (Böhme 2003; Van der made 2010).

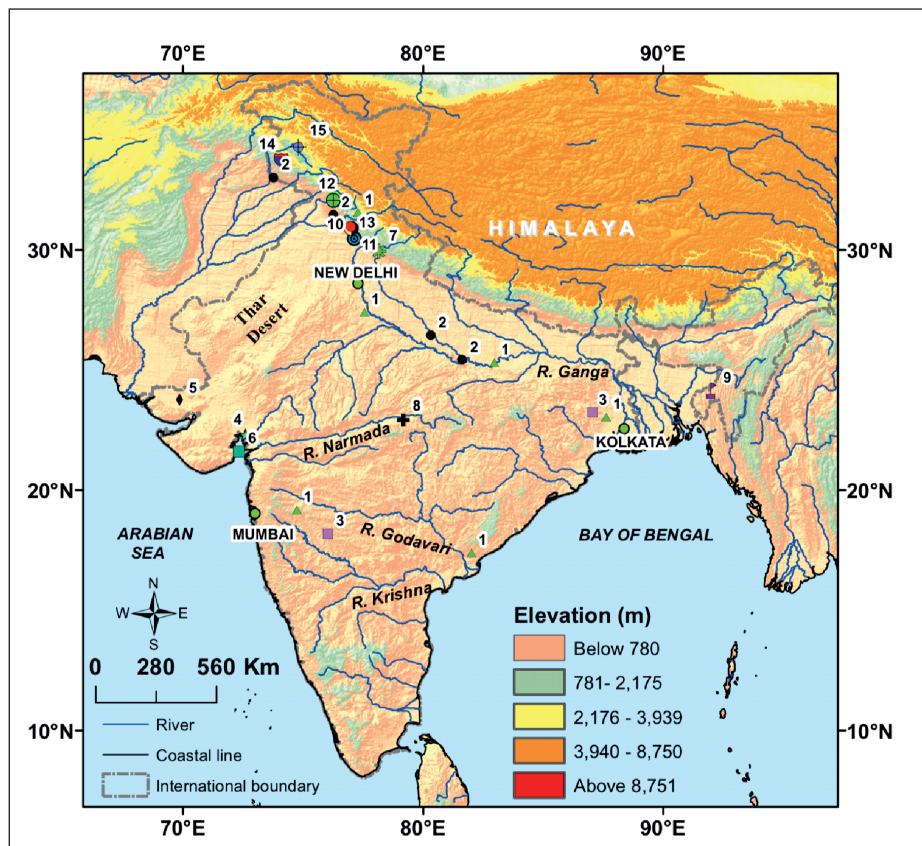
3.1.b. Arrival Of The Elephants In The Indian Subcontinent

The Asian elephant is one of the largest terrestrial mammals in the world today, and is now an endangered species sporadically distributed in South and Southeast Asia (Maglio 1973; Shoshani & Eisenberg 1982; Shoshani & Tassej 1996). At present India is one of the major countries where the elephant species is still prevalent and has active populations in the wild.

Elephants have played an important part in the history of humankind particularly that of the people of the Indian subcontinent. Their presence has been recorded on rock paintings as seen on the Zoo rock from Bhimbetka, and even on the seals of the Indus valley particularly as on the ‘Pasupati Seal: which features an elephant along with buffalo, a deer and an early representation of Shiva (Rebecca & Sharma 2017). Around 300-350 extant and extinct members of Proboscidea have been recorded, out of which nearly 50 have been reported from the Indian subcontinent (Rai 2004). Proboscidean members from four orders, eight families and over fifty species have been discovered and reported from the Indian Subcontinent making it one of the proboscidean rich localities of the world. These have been studied and classified by Osborn 1921, 1936, 1942, Colbert 1935, Lydekker 1877, 1878, 1880, Maglio 1973, Simpson 1945, and Madden 1981 many others to name a few.

Areas of Proboscidean prominence in the Indian Subcontinent: (Rai, 2004).

Subathu group: formation of Himalaya. Lower to middle Eocene (50-30 m.y.a.)



Map 1: Various localities from where proboscideans have been reported. 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.

- Bugti beds of N.E. Baluchistan and Sind: Fatehjang zone
- Salt Range of Attock district of Punjab: Chinji stage (Middle Miocene 14-10 m.y.a.)
- Nagri and Dhok Pathan Stages of Middle Siwaliks: (upper Miocene 10-5 m.y.a)
- Salt range of Jhelum district of Punjab: Tatrot stage of Upper Siwaliks: upper Pliocene(5-2.6m.y.B.P)
- The Pinjor stage of the Siwaliks of Ambala District: Upper Pliocene (2.6-1.5 m.y.a)
- Potwar plateau of the Outer Himalayas of Jammu: Miocene
- The Piram beds of the Piram islands in Gujarat
- Indo gangetic alluvium of Uttar Pradesh, Bihar, West Bengal: Pleistocene (1.8-0.01 m.y.a)
- Narmada and Godavari systems: Upper Pliocene- Upper Pleistocene (2.6-1.5 m.y.a)

4. Comparative Results for Analysis

Table 1: Comparative Data from Siwaliks, based on the study done by Patnaik *et al.* 2019

TAXA	AGE	$d^{13}C$ VPDB (range, mean m and SD s)	$d^{18}O$ VPDB (range, mean m and SD s)	Diet Browser/ Grazer/ Mixed feeder	Environment
Gomphother (n 1/4 3)	Miocene	11.55‰ to 10.43‰, m -10.82, s 0.63	-10.36‰ to -9.49‰, m -9.83, s -0.46	Browser	Wet
Deinotheres (n 1/4 2)	Late Miocene	-13.33‰ to -12.95‰, m -13.14, s 0.27	-4.71‰ to -4.39‰, m -4.55, s 0.23	Browser	Intermediate
Gomphother (n 1/4 1)	Late Miocene	-10.99‰	-2.67‰	Browser	Intermediate
Gomphother (n 1/4 1)	Late Miocene	-10.81	-9.55	Browser	Wet
Stegodon (n 1/4 4)	Pliocene	-0.36 to -1‰, m 0.49, s 0.607152	-6.67‰ to -1.47‰, m -4.28, s 2.45	Grazer	Intermediate, Seasonal
Anacus	Pliocene	-0.13‰	-4.29‰	Grazer	Intermediate
<i>Elephas planifrons</i> (n 1/4 4)	Pliocene	-0.21‰ to -0.16‰, m -0.02, s 0.16	-6.81‰ to -4.42‰, m -5.7, s 1.09	Grazer	Intermediate
<i>Elephas planifrons</i>	Pliocene	-0.75 to 1-.31‰, m 0.10, s 0.18	5.59‰ to 2.71‰, m 4.49, s 0.82	Grazer	Intermediate seasonal
<i>Elephas hysudricus</i> (n 1/4 2)	Pliocene	3.33‰ to -0.16‰, m 1.75, s 2.24	-3.12‰ to -0.61‰, m -3.73, s 4.41	Grazer	Dry seasonal
<i>Elephas platycephalus</i>	Pliocene	0.83‰ to 0.5‰, m 0.72, s 0.11	-4.72‰ to -1.37‰, m -3.40, s 1.28	Grazer	Intermediate seasonal
Stegodon sp. (n 1/4 1)	Pleistocene	0.58‰,	-5.78‰,	Grazer	Intermediate
<i>Elephas planifrons</i> (n 1/4 3)	Pleistocene	-1.96‰ to -0.82‰, m -1.47, s 0.59	-6.85‰ to -4.89‰, m -5.63, s 1.06	Grazer	Intermediate
<i>Elephas hysudricus</i> (n 1/4 1)	Pleistocene	0.28‰	-4.29‰	Grazer	Intermediate
<i>Elephas</i> sp. (n 1/4 2)	Pleistocene	-0.63‰ to -0.72‰, m 0.05, s 0.95	-7.02‰ to -5.87‰, m -6.45, s 0.81	Grazer	Intermediate
<i>Elephas hysudricus</i>	Pleistocene	-9.20‰ to -8.77‰, m -8.99, s 0.15	-6.99‰ to -5.86‰, m -6.61, s 0.39	Browser	Wet
<i>Elephas hysudricus</i>	Pleistocene	-10.15‰ to -9.40‰, m -9.86, s 0.28	-6.96‰ to -6.24‰, m -6.69, s 0.34	Browser	Wet
<i>Palaeoloxodon namadicus</i> (n 1/4 3)	Pleistocene	-2.8‰ to -0.00‰, m -0.9, s 1.65	-2.7‰ to -0.10‰, m -1, s 1.49	Mixed Feeder	Intermediate to dry

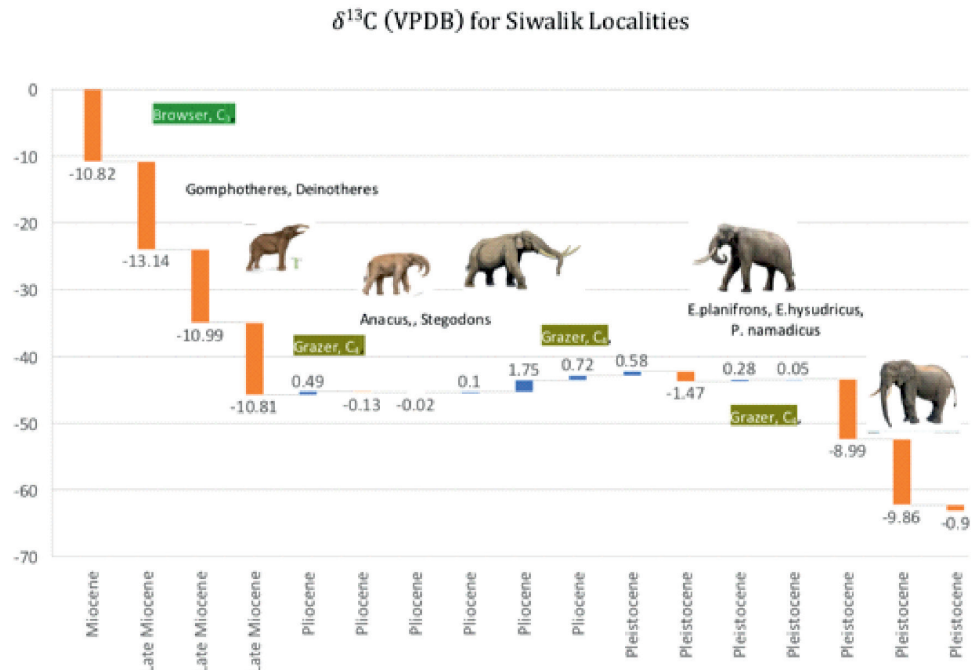


Fig. 1: A graphical representation of the δ¹³C data (Source: Patnaik *et al.* 2019) of the various Proboscidean populations from the Siwaliks

Table 2: Data from Mainland Asia, Irrawaddy based on the study by Puspaningrum 2016

TAXA	AGE	δ13C (‰, VPDB) Mean: m Standard dev: d	δ18O (‰, VPDB) Mean: m Standard dev: d	Diet Browser/ Grazer/ Mixed feeder	Environment Wet/Dry/ Intermediate
Platybelodon cf. grangeri n=6	Middle Miocene and Early Pliocene	-9.7 to -8.8, m -9.2, d 0.3	-9.3 to -5.8, m -7.2, d 1.4	Browser	Open woodland biomes, humid conditions
Sinomastodon sp. n=3	Middle Miocene and Early Pliocene	-12.8 to -11.3, m -12.9, d 0.7	-7.2 to -5.6, m -6.4, d 0.8	Browser	dense forest and woodland vegetation Humid conditions
Stegolophodon cf. stegodontoides n=6 Irrawaddy	Middle Miocene and Early Pliocene	-12.4 to -6.1, m -10.9, d 2.4	-8.8 to -6.1, m -7.4, d 0.9	Browser	dense forest and woodland vegetation Humid conditions
Stegodon insignis/ganesa n=3 Siwaliks	Late Pliocene to Early Pleistocene	-6.9 to 1.2, m -0.6, d 1.7	-6.4 to -5.0, m -5.8, d 0.8	mixed C3-C4 and dominant C4 diet range	
Archidiskodon planifrons n=2	Late Pliocene to Early Pleistocene	-0.2 to 1.1, m 0.5, d 0.9	-5.4 to -2.2, m -3.8, d 2.3	Grazer	
Palaeoloxodon namadicus n=4	late Early and Middle Pleistocene	-7.8 to -5.8, m -6.4, d 1	-5.9 to -3.0, m -4.2, d 1.2	Grazer	
Elephas hysudricus n=2	Late Pliocene to Early Pleistocene	-2.8 to 0.1, m -4.2, d 2.1	-6.8 to -4.5, m -5.7, d 1.6	mixed C3-C4 and dominant C4 diet rang	
Elephas maximus n=13	Late Pleistocene and Present	-16.21 to -8.70, m -13.1, d 2.6	-7.8 to -4.4, m -6.0, d 1.1	Browser	Increased Humidity

5. Discussion

5.1.a. Inter & Intra Specie Competition Amongst Proboscidea

Some of the early members of Proboscidea were all exclusively C3 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 paleosols in the Siwalik, a steady increase in the $\delta^{13}\text{C}$ 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 C3 dominated environment with a C4 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 Stegodonts had evolved and adapted their diets and switched their feeding behaviour 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 C4 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 C4 vegetation, because before the Pliocene the *Elephas* are absent from Asia and only start moving out once C4 grasslands have taken hold of the environment. To further add to this the morphology of the *Elephas* molars are more suited to the C4 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 Stegodonts in the early Pleistocene. The Sinomastodons had similar diets with the Stegodonts and possibly their extinction is not due to the vegetation change but competition by Stegodonts. In comparison the Stegodonts 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).

Stable isotope studies have reveals that during the Middle Pleistocene all herbivores whether it be proboscideans, cervids or bovids were primarily grazers and inhabited and were dependent on the vast open grasslands prevalent at the time. The extinction of the Stegodonts coincides with the shift in the climate from a dry arid landscape to one with higher levels of humidity, at this time the vegetation cover began to change again from C4 to mixed and then finally to C3 again. Stegodonts since Pliocene were

basically grazers and had over the generations become highly skilled in this endeavour. This change in the vegetation cover, plus inter specific competition by *Elephas* and some early Hominin activities may have cumulatively led to their disappearance (Scheart 2003, 2005; Puspaningrum 2016).

The isotopic data has indicated that the *Elephas* and *Palaeoloxodon* members were successfully able to adapt and thrive in the C3 environment and hence this could not have been the reason for their extinction instead other factors like over hunting, predation could have led to their loss in numbers and disappearance. India lacks any concrete evidence in this regard due to absence of any Hominin finds but in Java the remains of these proboscideans are commonly found together with artefacts indicative of some hominin activities and tasks (Puspaningrum 2016).

5.1.b. 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 and in this study a distinct change in the diets of the Proboscideans concerned, forcing them to either adapt or become extinct. Low crowned proboscideans such as *Platybelodons*, *Stegolophodons*, primitive stegodonts had dentition more suitable to C3 diets but as the vegetation cover switched to C4 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 C4 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 their 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. A line of two on enamel histology as genetic response to rapid morphological change can be given here.

Now a second vegetation change took place towards the end of Middle Pleistocene wherein C4 dominated plant cover reverted back to C3 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 C3 diet is what has continued till present and today the proboscidean of India *Elephas maximus* is a C3 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 *Sinomastodons* 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. Comparable Data from Other Proboscidean Localities

Fossils often are chance finds and although there are regions which have a higher scope of recovering them, still one can never be sure and also one cannot control the taxa which would be discovered, because of this generally studies such as this one wherein only one taxa is being looked into, the greatest drawback is in the number of samples of generated, as this solely depends on the fossils available and found of the given taxa. In order to supplement and to gain & give a clear picture, data from comparable studies are often sought, sometime the fossil data is also compared with their modern descendants. This study has included data from other proboscidean localities from Siwaliks and some regions of South East Asia (Irrawaddy and Java), besides the targeted regions. The sites have been compared for temporal and spatial paleo vegetational and dietary implications for the Proboscideans from across the Indian Subcontinent and even from south east Asia. These localities are chosen keeping in mind the present day spread of the Asian elephants, and besides Siwaliks all the above mentioned regions have had active populations of Elephants.

5.2.a. Data From the Siwaliks

For this the primary source of data came from the study done by Rajeev Patnaik and his colleagues (2019). This study includes a large body of samples housed at the Museum of the Centre of Advanced Study in Geology in Panjab University. Besides generating carbon and oxygen isotope data from fossil proboscideans they have even looked into the ratios coming in from modern day samples of elephants from Sukumar and others (Sukumar *et al.* 1987; Sukumar & Ramesh 1992). Based on the isotope data and ratios, Patnaik *et al.* (2019) have proposed that in the Siwaliks the early proboscideans such as the Gomphotheres and *Deinotherium indicum* were C3 browsers. Both these proboscideans resided in open forests and were dependent on fresh water from forest channels and streams, this data is in concurrence with the results of the present study as well. During the late Pliocene the Stegodonts were the primary proboscideans, the proboscideans showcased a mixed feeding strategy and switched between grazing and browsing. The vegetation at this time is of open grasslands interspersed with gallery forests. Another proboscidean of the time *Anancus* also followed a similar feeding strategy

and switched between grazing in the open grasslands to browsing in the forests. Of particular interest is *Elephas planifrons* which was a grazer under seasonal conditions. *Elephas hysudricus* was again predominantly a grazer but inhabited the rid and dry regions. As per Patnaik and his colleagues a high seasonality was possibly the reason for such kind of variable and opportunistic dietary habits. During the Early Pleistocene Stegodons were present in the Siwaliks and constitute the Pinjor fauna. which were primarily C4 grazers and so were the various species of Elephas present (Patnaik *et al.*2014a,b; Patnaik *et al.*2019).

5.2.b.Data From Mainland Asia: Sunda land regions, Java, Irrawaddy

Expanding the comparative study a bit more, another work from localities outside India was considered and closely studied. Out of the localities given in the said work, only three regions have been short listed for a comparative study. According to this study the general observations regarding the ratios and conclusions drawn from them are as follows: the $\delta^{13}\text{C}$ values from most of the sites in mainland Asia, be it in India, China, Thailand, Myanmar etc. falls in the range of -17.2 to 2.3 ‰(enamel, VPDB), within this range all diets conform to C3, C4 and mixed. The $\delta^{13}\text{C}$ values of the early proboscideans of the Miocene such as Sinomastodons, Stegolophodons, Platybelodon, *Stegodon orientalis*, *Stegoloxodon indonesia* are all C3 browsers and derived their nutrition from dense woodlands and forests. The $\delta^{13}\text{C}$ 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 C3-C4 diet, similarly *Stegodons insignis*, *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 . Elaborating a little more on this work, as mentioned above the early Proboscideans were all C3 browsers and fell in the range of (-12.9‰ to -6.1‰). The only exception to this exclusive C3 browser community is the Stegolophodons which have showcased a mixed diet in the Irrawaddy region. During the middle Miocene the dominant proboscideans were the Platybelodons, Whose habitat during this time was an open woodland type with dense interspersed forests. This particular proboscid chose to feed open woodlands while the other herbivore taxa of the day chose the opposite. The $\delta^{18}\text{O}$ values of the early proboscideans fall in the range of - 9.3‰ to -4.0‰; these values are indicative of a wet and a humid environment (Puspaningrum 2016)

The dominating proboscideans in the Late Pliocene to Early Pleistocene were the Stegodonts, particularly *Stegodon insignis*, *Stegodon orientalis*, *Archidiskodon planifrons*, *Elephas hysudricus* in the Mainland regions of Asia. In Java species such as *Stegoloxodon indonesicus*, *Sinomastodon bumiajuensis*, *Stegodon trignocephalus*, *Elephas hysudridcus* were thriving. The $\delta^{13}\text{C}$ values generated from this taxa are slightly more positive and is in the range (-7.8‰ to 1.2‰). This shift is indicative of mixed diets and rise of specialized grazers, even then these values are not of pure C4 grazers. An increase in the $\delta^{18}\text{O}$ values is also seen, this is expected as the aridity increased the values recorded became higher in the range of (-6.9‰ to -2.2‰). Focusing on one of the shortlisted localities; Java, here the $\delta^{13}\text{C}$ values of the early proboscideans are within the range (-14.1‰ to -12.1‰) indicating a C3 browsing diet, this is expected as at this time Java has dense forest cover and thicket, as younger samples were studied a mixed diet emerged indicating a mixed or a primarily C4 diet subsequently as the time passed and the forest cover gave way to open grasslands.

The locality of Irrawaddy is interesting, here *Stegodon insignis* was present during the Late Pliocene period. The same taxa is also recorded in the Siwalik groups; however the difference comes in the carbon and oxygen values and are lower than the ones recorded at Siwaliks. The

Irrawaddy values for carbon are in the range $\delta^{13}\text{C} = -6.9\text{‰}$ to -0.8‰ and for oxygen the are $\delta^{18}\text{O} = -6.9\text{‰}$ to -5.5‰ , whereas the same taxa in Siwaliks has given the range for carbon $\delta^{13}\text{C} = -2.2\text{‰}$ to -1.2‰ and for oxygen $\delta^{18}\text{O} = -6.0\text{‰}$ to -5.0‰ (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 C3 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.

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