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WERE LATE GOMPHOTHERES (PLIO-PLEISTOCENE) OF THE SIWALIKS AT MORE STRESS AS COMPARED TO EARLY GOMPHOTHERES (MIDDLE TO LATE MIOCENE)?

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ABSTRACT

Gomphotheres existed in the Siwaliks from the middle Miocene (14.2Ma) to the middle Pleistocene (0.8Ma) and became extinct later on. In this paper, we tried to discuss the reasons of such extinction of gomphotheres in the lower Pleistocene time span by considering Linear Enamel Hypoplasia (LEH) among 114 isolated tooth samples to assess whether ecological changes correlate with the stress factor in gomphotheres. For this purpose, the Siwalik gomphotheres were divided into two groups viz. early gomphotheres (middle Miocene to late Miocene) and late gomphotheres (Pliocene to middle Pleistocene). We presented the hypothesis, that as the gomphotheres are characterized by the brachydonty and relied on browsing for their feeding while inhabiting the semi forest land setting thus, expected to have higher stress in Plio-Pleistocene time span as vegetational change around ~6 Ma may have exerted stress on late gomphotheres. The results for the occurrence of frequency of LEH indicated severe ecological stress in late gomphotheres (33%). The significant differences were found ($P < 0.05$) among the early gomphotheres and late gomphotheres which can be correlated to the vegetational change from C_3 to C_4, higher aridity indices and intensified seasonality after the late Miocene vegetational shift which may have resulted in substantial faunal turnover, extinction and speciation. We assume that such palaeoecological changes forced a competition with more pronounced grazers like of family Elephantidae and Bovidae resulting in extinction of gomphotheres during the late Pleistocene in the Siwaliks of Pakistan.

Key words: Late Miocene, pliocene, stress, palaeohabitat, mammals.

INTRODUCTION

The Siwaliks of Pakistan ranges from the middle Miocene to the late Pleistocene time span and exhibit a rich vertebrate diversity including perissodactyls, artiodactyls, rodents, proboscideans, carnivores and hominids (Dennell et al., 2006; Badgley et al., 2008; Flynn et al., 2016). The Siwaliks display coarse and fine-grained sandstone, siltstone, claystone and conglomerates which are best represented in the western part of the sub-Himalaya (Roohi et al., 2015). The Potwar Plateau (Figure 1) has yielded a rich fossil record and has been a center of focus for palaeontologists from all over the globe from a century (Falconer and Cautley, 1868; Pilgrim, 1910, 1913, Sarwar, 1977; Barry et al., 1982, 2002, 2013 etc.). In this study, the samples have been taken throughout the Siwalik series to assess that how palaeoecological changes forged the phylogeny of gomphotheres.

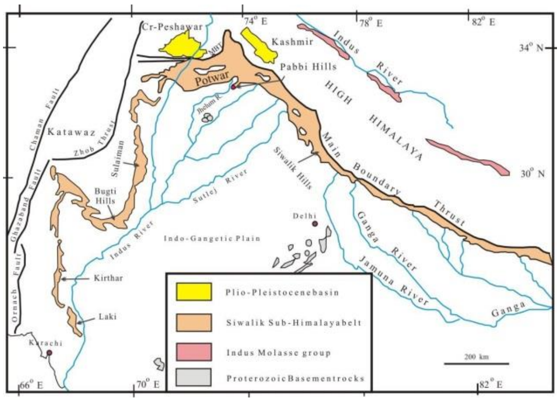

Figure 1: Generalized map of the Siwaliks indicating different basins (taken from Roohi et al., 2015).

Paleogeography of the Siwalik Gomphotheres

The order proboscidea includes both extinct and extant elephants and their relatives both on land (hyraxes) and in water (manatees and dugongs). The order proboscidea comprises of 10 families, 42 genera and 175 species and subspecies known from different biogeographic regions of the world (Shoshani and Tassy 2005). The Siwalik proboscideans are known by 4 families, 11 genera and about 22 species (Sarwar, 1977).

Gomphotheres were amongst the giant proboscideans recognized by their fossil record from the entire globe except from Australia and Antarctica (Shoshani, 1998). Gomphotheres were present during the middle Miocene (14.2Ma) to the middle Pleistocene (0.8Ma) in the Siwaliks (Table 1). Usually gomphotheres have two pairs of opposing lower and upper tusks. They have appeared and predominantly found in the earliest sediments of the early Miocene of Africa (~22.0 Ma) and migrated to Asia and Europe. These proboscideans are recognized as trilophodonts because of the presence of 3-plated primary two molars (m1 and m2). Tobien (1973) explained a simplified tooth structure linked to genus *Gomphotherium* with several crosswise ridges, comprising of a certain cone-like rudiments. The presence of trefoil structure is believed to be a characteristic of all bunodont mastodonts (Gomphotheriids), which can only be found on the worn molars thus, supporting the idea that these mastodonts were dominant browsers or somehow mixed feeders. This study deals with the hypothesis that, how ecological changes shape up the phylogeny of the Siwalik gomphotheres after the late Miocene transition (Cerling et al., 1993; Barry et al., 2002, 2013). The present work is the estimation of palaeoenvironmental stress among Gomphotheres before and after the transition.

Enamel Hypoplasia as Stress Indicator

Enamel is the outermost whitish shell of tooth crown which is extremely mineralized and toughest tissue of the mammalian body (Shawashy and Yaeger, 1986; Kierdorf et al., 2012). Hypoplasia is the low or underdevelopment of a tissue or organ. Enamel Hypoplasia (EH) is a deficit of enamel thickness because of physiological faults that negotiate the deposition of ameloblasts through the secretory period of amelogenesis (Sarnat and Schour, 1941; Yaeger, 1980; Shafer et al., 1983; Guita, 1984). Simply, EH is known as the failure of tooth enamel to reach its normal thickness during its development on the tooth crown (Goodman et al., 1987; Goodman and Rose, 1991). It can appear as vertical or horizontal grooves or as discrete pin prick cavities, more or less encircling the tooth crown in an ordinary enamel (Figure 2,3,4), supposed to resemble with less severe stress (Ainamo, 1982). Typically, this kind of EH is attributed to an inadequate secretions of ameloblasts. It can be easily linked to myriad but is typically associated with malnutrition, febrile disease or infections (Suckling, 1989), which embraces an everlasting mark on the tooth. These everlasting marks can be evaluated both in bones and teeth and also in similar type of tissues in mammals.

The dispersal and morphology of EH on different types of mammalian dentition may identify the type of environmental stress, trauma and disease. These tooth developmental defects in mammals are believed to be noticeable components for the scale of the environmental stress from mild to severe morbidity and mortality (Skinner, 1996). These perturbations of EH can occur via three causal conditions: (1) systematic or physiological stress (nutritional stress, illness, weaning, parturition, and stress during cow calf separation) (2) hereditary anomalies or (3) localized trauma in emerging teeth at a specific ontogenetic age (Weinmann et al., 1945; Shawashy and Yaeger, 1986; Suckling, 1989) and are typically identified as linear enamel hypoplasia (LEH) (Neiburger, 1990; Mead, 1990; Goodman and Rose, 1990; Dobney and Ervynck, 2000; Lukacs, 2001; Franz-Odendaal et al., 2004). LEH is usually produced by the physiological or environmental stresses at a specific phase in an animal's life, at which the development, growth and eruption of tooth was taking place. On the basis of ease of examination, chronological array of its development, sensitivity, and failure to remodel, tooth enamel is endorsed to be a perfect tissue for recording any change in an animal physiology during its development (Kreshover, 1940; Massler et al., 1941; Sarnat and Schour, 1941). Hence, the width of depression mark, depth, and frequency of LEH reveal the duration, strength of severity, and the episodes of ecological stress (Shklar and McCarthy, 1976; Guita, 1984; Rose et al., 1985) respectively, which have been faced by an animal during its tooth enamel development. Thus, in this study we have utilized LEH to evaluate our hypothesis.

MATERIALS AND METHODS

The present study was conducted on a total of 114 tooth specimens from the fossilized family gomphotheriidae for the evaluation and correlation of dental enamel paleopathology (Linear Enamel Hypoplasia) to the Siwalik palaeoenvironment. The studied fossil material utilized for the analysis of LEH was taken from the Dr. Abu Bakr Fossil Display and Research Centre, and Fossil Research Centre Jhelum Campus, University of the Punjab, Lahore, Pakistan. The gomphotheres fossilized material was identified following the dental terminology of Tassy (1996). The tooth specimens consisting of worn enamel were omitted. The selected tooth specimens were examined by two raters having expertise in LEH analysis for the precision and to avoid any ambiguity. A 10-X hand lens for magnification was used for each tooth examination. A 50-watt variable incandescent light was used in laboratory examination of LEH, as samples were analyzed both in artificial and natural sunlight. The location of LEH on enamel of the tooth crown was measured starting from root crown junction (RCJ) towards the tip by using a White Worth digital vernier caliper. The distance was recorded in millimeters (mm). After quantitative examination of LEH, samples were shifted for pictorial presentation of paleopathology marks. A digital handheld camera "canon ECOS-350D" was being used for snapshots. The tooth specimens with unknown and erased catalogue were newly catalogued by giving the first alphabet of the family after Punjab University Palaeontological Collection (PUPC), and the numeric denominators for each unknown specimen as PUPC-G_1, PUPC-G_2 and so on.

The old abbreviation (UZ, University Zoology) was also considered. Cohen's Kappa (1960) statistics was performed as a statistical tool to observe the differences in opinion among both raters. The details of LEH results on gomphotheres teeth are provided in Table 1.

RESULTS

Prevalence of LEH by Taxon

The detailed information of LEH incidences in the family gomphotheriidae by taxon is grouped and summarized in table 1. The height, location, and magnitude of the LEH on each tooth specimen were greatly variable in the examined material (Table 2). A total of 101 gomphotheres comlete samples were analyzed consisting of 22 affected samples comprising of 21.78% of LEH. The generic analysis indicated that *Choerolophodon, Gomphotherium,* and *Protanancus* each have represented a single Siwalik` species *C. corrugatus, G. browni,* and *P. chinjiensis* that were revealed 16.33%, 31.82%, and 16.67%, of LEH, respectively. Only the Siwalik genus, *Anancus* represented by two species, *A. sivalensis* and *A. osborni* which showed 33.33% occurrences of LEH. Individually, both species consisted of 37.50% and 25% of LEH, respectively. The occurrence of LEH was observed maximum in genus *Anancus* (33.33%) and *Gomphotherium* (31.82%). The lowest occurrence of LEH was found in *Choerolophodon* (16.33%) and *Protanancus* (16.67%) which was almost equally distributed in both genera. The comparison of LEH in all the five Siwalik species of gomphotheres revealed the lowest amount 16.33% of occurrence of LEH in the individuals of *C. corrugatus,* whereas, the highest amount of occurrence 37.50% of LEH was found in individuals of *A. sivalensis*. The findings of these results from the above data sets in table 1 indicated that the members of *A. sivalensis* were more susceptible to the environmental stress as compared to the others.

Prevalence of LEH by Tooth

Our results related to the frequency of LEH by tooth revealed considerable variations as summarized in Table 3. A total of 114 gomphotheriid isolated teeth were analyzed consisted of 24 affected individual teeth comprising of 20.05% of LEH. All the five species, *C. corrugatus, G. browni, P. chinjiensis, A. sivalensis,* and *A. osborni* belonging to the Siwalik family gomphotheridae were showed 16.36%, 28.57%, 15.79%, 37.50%, and 25.0 %, of the LEH, respectively. The findings showed that the lowest number of teeth defected with LEH were found 15.79% in *P. chinjiensis* and 16.36% in *C. corrugatus* whereas, the species *A. sivalensis* having 37.50% of LEH was found to have the highest number of defected teeth. The results for these observed defects of LEH in dentition of gomphotheres showed that the members of *A. sivalensis* were affected more severely by prevailing environmental conditions compared to other species analyzed in this Siwalik family. The frequency for the occurrence of LEH determined that there are maximum of three LEH's were found on a single tooth (PUPC-15/239) which showed that three different types of ecological stress incidents may have addressed that animal during his life history.

Table 1: Occurrence of EH in fossils of the family gomphotheriidae from middle Miocene to middle Pleistocene having an age of 15.2 - 1.6 Ma approx.

Species	Specimen	Locality	Age (Ma)	Enamel Hypoplasia		
				Tooth	Loph/lophid	Location
Gomphotherium browni	PUPC-15/14	Kanhatti	14.2-11.2	right m1	2nd lophid	One LEH 12.07mm above the RCJ
				left m1	1st lophid	One LEH 5.52 mm above the RCJ
	PUPC-15/218	Chabbar Syedan	14.2-13.0	m3	2st loph	One LEH 17.94 mm above the RCJ
	UZ-67/80	Pari Darweza (Kamlial zone)	15.2-11.0	M1	1st loph	One LEH 07.80mm above the RCJ
	PUPC-15/06	Chabbar Syedan	14.2-13.0	m1	1st and 2nd lophid	Two LEH's 10.53mm and 11.78mm above the RCJ
	UZ-68/810	Chinji	14.2-11.2	M2	1st lophid	Two LEH's 5.04mm and 12.97mm above the RCJ
	UZ-66/49	Chinji	14.2-11.2	m3	1st lophid	One LEH 40.24mm above the RCJ
	UZ-67/227	Chinji	14.2-11.2	m3	Last lophid	One LEH 22.10mm above the RCJ
Choerolophodon corrugatus	PUPC-14/39	Dhok Pathan	7.7-5.2	M1	2nd lophid	One LEH 5.02mm above the RCJ
				M2	3rd lophid	One LEH 10.12 mm above the RCJ
	PUPC-15/05	Markhal (Dhok Pathan)	7.7-5.2	m3	3rd lophid	Two LEH's 16.20mm and 21.07mm above the RCJ
	UZ-67/118	Dhok Pathan	7.7-5.2	dp4	1st lophid	Two LEH's 5.04mm and 12.97mm above the RCJ
	UZ-69/627	Vasnal, Bhelomar	14.2-11.2	m3	1st lophid	One LEH 17.03mm above the RCJ
	PUPC-15/239	Dhok Mila	11.2-9.0	M2	1st, 2nd , and 3rd loph	Four LEH's 36.16mm, 10.96mm, and

						5.0mm, above the RCJ
	UZ-68/816	Kanhatti	14.2-11.2	M2	2nd last loph	One LEH 23.94mm above the RCJ
	UZ-84/116	Lava, Dhok, Rehmat Ali	14.2-11.2	M2	Last loph	One LEH 37.16mm above the RCJ
	PUPC-15/204	Kanhatti	14.2-11.2	M1	2nd loph	Two LEH's 2mm and 3.57mm above the RCJ
Protanancus chinjiensis	UZ-69/626	Pari Darweza	14.2-11.2	m3	3rd lophid	One LEH 21.22mm above the RCJ
					4th lophid	One LEH 20mm above the RCJ
	UZ-47	Chinji bed (Chakwal)	14.2-11.2	M3	2st loph	One LEH 34.50mm above the RCJ
	PUPC-15/16	Chabbar Syedan	14.2- 11.2	m2	4th lophid	One LEH 6.63mm above the RCJ
Anancus osborni	PUPC-G_1 (A_1)	Chinji	14.2-11.2	M3	5th loph	One LEH 33mm above the RCJ
Anancus sivalensis	UZ (71/56)	Dhok Awan Tatrot zone Jhelum	3.6-2.58	m3	Last lophid	Two LEH's 7.90mm above the RCJ
	PUPC-(10/75)	Rohtas	2.58-1.6	m3	3rd lophid & Last lophid	Two LEH's 27.64mm above the RCJ 41.2mm above the RCJ
	PUPC-G_{12} (A_3)	Rohtas	2.58-1.6	m3	2nd last lophid	Two LEH's 32.60mm and 42mm above the RCJ
					Last lophid	One LEH 34.30mm above the RCJ

Table 2: Occurrence of LEH by taxon in fossil remnants of the Siwalik gomphotheres.

Genus	**Species**	**Animals**	**Animals with LEH**	**%age of LEH by species**	**%age of LEH by genus**
Gomphotherium	*G. browni*	22	7	31.82	31.82
Choerolophodon	*C. corrugatus*	49	8	16.33	16.33
Protanancus	*P. chinjiensis*	18	3	16.67	16.67
Anancus	*A. osborni*	4	1	25.00	33.33
	A. sivalensis	8	3	37.5	
Total		101	22	21.57	21.57

Table 3: Occurrence of LEH by tooth (species, genera, and family) in fossil remnants of the Siwalik gomphotheres.

Genus	**Species**	**Teeth**	**Teeth with LEH**	**%age of LEH by species**	**%age of LEH by genus**	**%age of LEH in early and late gomphotheres**
Gomphotherium	*G. browni*	28	8	28.57	28.57	
Choerolophodon	*C. corrugatus*	55	9	16.36	16.36	20.48
Protanancus	*P. chinjiensis*	19	3	15.79	15.79	
Anancus	*A. osborni*	4	1	25.0	33.33	22.58
	A. sivalensis	8	3	37.5		
Total		114	24	20.05	20.05	

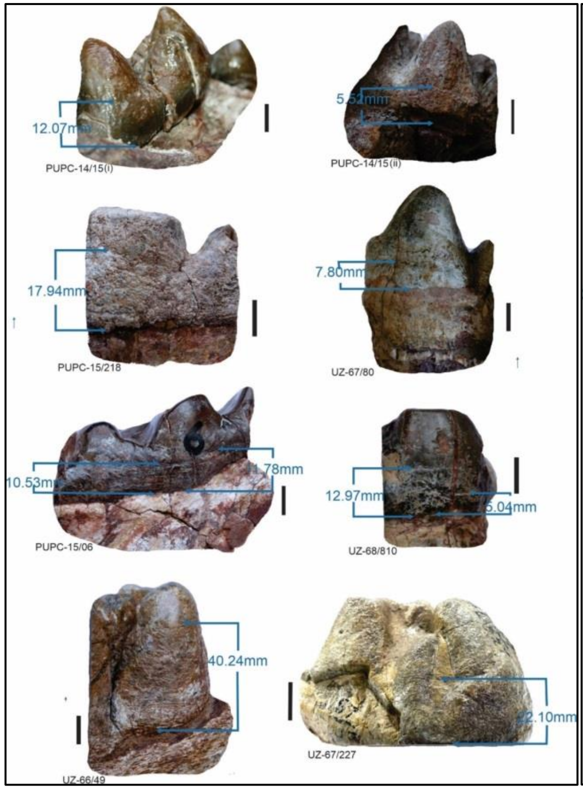

Figure 2: Position of EH in teeth of the proboscidean family gomphotheriidae; catalogue PUPC-15/14 to UZ-67/227 in "*Gomphotherium browni*".

Scale bar = 10 mm

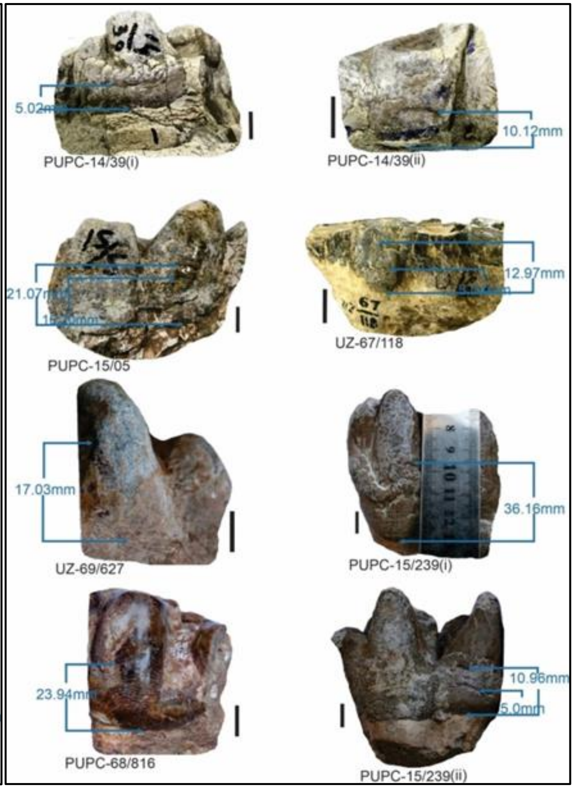

Figure 3: Information of EH from neck to the malady, catalogue PUPC-14/39 to PUPC-15/204 in "*Choerolophodon corrugatus*".

Scale bar = 10 mm

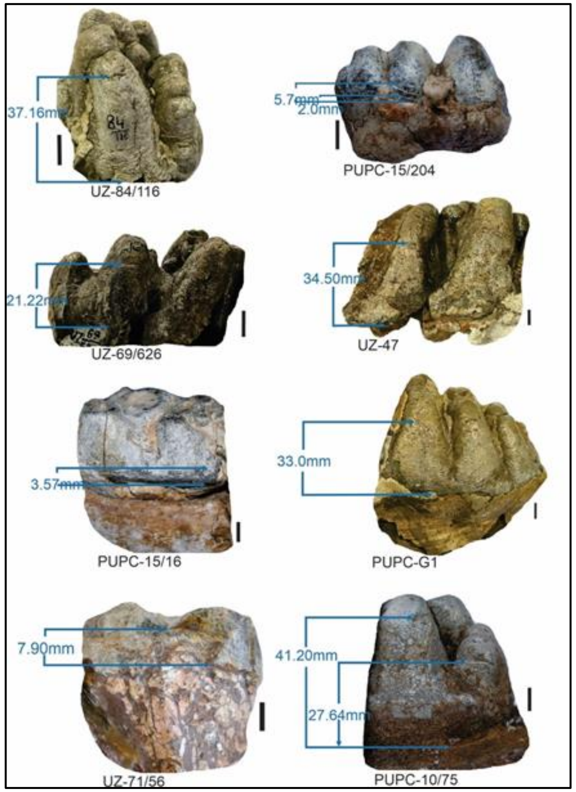

Figure 4: Detail of EH in the species of *Anancus* and *Protanancus,* UZ-69/626 – PUPC-10/75.

Scale bar = 10 mm

Interpretation of kappa: an Inter-rater reliability

The software version **“IBM SPSS statistics-20”** was used to calculate the significant/ non-significant differences in the analyzed data. The Cohen’s Kappa (1960) statistics was used for the description of agreement or disagreement between the two raters, observing the presence of LEH, a major descriptive of ecological stress in mammals. The calculation of “K” value indicated that there was a perfect agreement in both analyses where K=0.898 was present in the tooth material analyzed in natural sunlight whereas the value K=0.874 for the samples observed in artificial 50-watt incandescent light. The value $p > 0.05$ indicated that the difference in opinion between the two observers was non-significant during the analysis of LEH in gomphotheres.

DISCUSSION

Linear enamel hypoplasia is a systemic physiological perturbation which has been associated to the palaeoenvironmental stability of a taxon in a particular time span. In the Siwaliks of Pakistan, the stratigraphic range of Gomphotheriidae has been considered from the middle Miocene (14.2Ma) to the middle Pleistocene (0.8 Ma) as given in Table 5. Total four genera of the Siwalik Gomphotheres were used for the analysis of LEH. Among these four lineages, *Choerolophodon*, *Gomphotherium*, and *Protanancus* are reported from the middle Miocene deposits while the fourth lineage, *Anancus* is reported from the Pliocene deposits of the Siwaliks. The two taxa, *Gomphotherium*, and *Protanancus* disappeared during the late Miocene whereas; *Choerolophodon* and *Anancus* extinct during the Pliocene and Middle Pleistocene of the Siwaliks, respectively, as indicated in Figure 5.

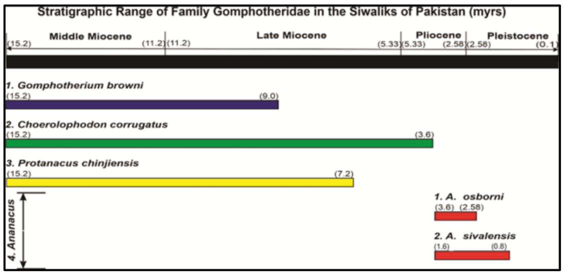

Figure 5: The stratigraphic range of genera of gomphotheres in the Siwaliks of Pakistan (Behrensmeyer and Barry 2005; Abbas et al., 2018).

The overall results of linear enamel hypoplasia in both early and late gomphotheres are sufficient to understand the stressful palaeoclimatic and paleoecological conditions which were responsible for the either migration or extinction of gomphotheres from the Siwalik sub-Group of Pakistan. The comparisons of LEH showed that each of the taxa had different levels of adaptations to the changing ecological conditions, depending on their dietary habits. The tooth examination of *Protanancus* and *Gomphotherium* indicated that these are the primitive taxa with the presence of lower incisors and less advanced lophodont teeth. The loss of lower incisors in proboscideans is one of the characteristics supposed towards novelty. The early gomphotheres, gomphotherium and protanancus clear have lower incisors, which can be considered as primitive character (Göhlich, 1999). The pronounced occurrence of LEH (20.05%) in gomphotheres similar to the family giraffidae (Ahmad et al., 2018) with 34% indicated that the less advanced teeth in these animals (brachydont) were responsible to impede their feeding habits on hard and coarse vegetation during the late Miocene. Herbert et al., (2016) reported that the late Miocene had warm and much drier environmental conditions with enhanced seasonality (Nelson, 2005). In the Siwaliks sub-Group, C_3 forests were gradually replaced by C_4 savannahs during the late Miocene (8.5 to 6.0 Ma) (Morgan et al., 2009; Waseem et al. 2021). During this vegetational turnover, few mammalian lineages evolved and strived for their survival but several others went extinct (Barry et al., 2002; Badgley et al., 2008). The simplest tooth structure of protanancus and gomphotherium out of all these Siwalik gomphotheres indicated that they browsed on leaves or shoots. Similarly, the long term warm and dry ecological conditions of the late Miocene also reduced the amount of available water resources both from environment and diet, forcing them towards extinction or migration (Böhme et al., 2008; Scheiter et al., 2012).

The lineage, *Choerolophodon* from the late gomphotheres was found with 16.36% of LEH close to *Protanancus* (15.97%). The absence of lower incisors can be considered as the more advanced character compared to *Protanancus* and *Gomphotherium* as it enabled *Choerolophodon* maintained its survival throughout the middle Miocene and disappeared by the Pliocene strata (15.2 – 5.3 Ma) of the Siwaliks (Abbas et al., 2018). The existence of this genus until the Pliocene indicates that this group of gomphotheres has strived because of having more advanced tooth structure with higher hypsodonty indices. However, these land mammals somehow shifted their dietary niche from browsing towards mixed feeding (browsing/grazing). The extinction of *Choerolophodon* by the early Pliocene of the Siwaliks can be attributed to the large scale C_3/C_4 transition and climatic variations. The Miocene – Pliocene boundary ~5.3 Ma demonstrated the stages of many C_4 ecological events (Hynek et al., 2012). The fourth studied Siwalik lineage, Anancus appeared during the late Pliocene (~3.6 Ma) and became extinct during the Pleistocene (~0.8 Ma) (Khan et al., 2011). The highest occurrence of LEH (33.33%) in the genus *Anancus* shows that this lineage was remained under highly intense ecological conditions which can also be observed in the late Miocene.

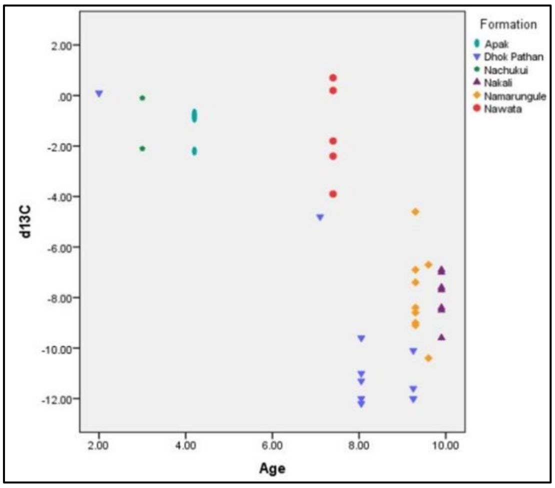

Figure 6: A comparative picture of carbon isotope values of gomphotheres among different formations (Data taken from Cerling et al., 1999; Nelson, 2007 and Uno et al., 2011).

The episodes of climatic variation profoundly affected the distribution and evolution of both plant and animal communities during the mid-Pleistocene times (Head et al., 2008). On average, the long-term ice volume of the globe was increased between 1.25 Ma to 700 ka which was linked with major cooling episodes (Clark et al., 2006). During the Middle Pleistocene (1.6 Ma), the forest succession was subsequently interrupted by a brief period of open vegetation of colder and drier continental climate, followed by a new vegetational cycle (Ravazzi and Strick, 1995). The unstable ecological conditions of the middle Pleistocene with substantial glaciation, prevailing ice sheaths and cooling regimes were responsible for the vanishing of *Anancus*. The simple and smooth tooth structure (Khan et al., 2011) indicate that the evolution was not as fast as vegetational change, hence confronted complications in shifting themselves on C_4 food choices and became extinct from the Siwaliks during the Pleistocene. The stable isotope values of carbon (Figure 6) indicate that the late Miocene vegetational transition (Cerling et al., 1993; Nelson, 2007; Badgley et al., 2008; Sanyal et al., 2010) forced the gomphotheres to adapt towards the C_4 grazing behavior while their low hypsodonty indices and less specialized teeth were not much in line with this transition. We assume, that due to such disadvantages, gomphotheres could not compete the coexisting specialized grazers (e.g. elephantids and bovids) which had specialized dentition and thus, became extinct towards the end of the Pleistocene.

CONCLUSION

Current study concludes that the proboscidean family Gomphotheriidae was severely affected because of changing paleoecological condition, during the late Miocene to the middle Pleistocene of the Siwalik sub-Group of Pakistan. The maximum occurrence of LEH found in the genus *Gomphotherium* and *Anancus* can been associated with their migration or extinction during the late Miocene and middle Pleistocene, respectively. Very high prevalence of LEH in the late Gomphotheres signals towards the stressful paleoecological conditions with limited food and water resources, limiting the survival of gomphotheres in the Siwaliks. Hence, it can be assumed that the late Miocene (7.2 – 5.3 Ma) and middle Pleistocene (2.58-1.6 Ma) time spans were the time of substantial modification in regional climate and ecology that may have reduced suitable habitats for gomphotheres pushing them gradually towards migration and extinction from the Siwalik sub-Group of Pakistan.

Authors Contribution

MA and AMK generated the idea, MA and RMA conducted the analysis as two raters, MA and MTW drafted the manuscript, MI and MA formatted the file, AI and AR organized the taxonomic identifications, and MA and MTW made the tables and figures.

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REFERENCES

Ahmad RM, Khan AM, Roohi G, Akhtar M (2018). Study enamel hypoplasia in giraffids to compare stress episodes in geological history of the Siwaliks of Pakistan. Pak J Zool., 50(1): 149-158.

Abbas SG, Khan MA, Babar MA (2018). New materials of Choerolophodon (Proboscidea) from Dhok Pathan Formation of Siwaliks, Pakistan. Vertebrata Pal Asiatica., 56(4): 295-305.

Ainamo J, Asikainen S, Paloheimo L (1982). Gingival bleeding after Chlorhexidine mouthrinses. J Clin Periodontol., 9(4): 337-345.

Badgley C, Barry JC, Morgan ME, Nelson SV, Behrensmeyer AK, Cerling TE, Pilbeam D (2008). Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. Proc. Natl Acad Sci USA., 105: 12145-12149.

Barry JC, Behrensmeyer AK, Badgley C, Flynn LJ, Peltonen H, Cheema IU, Pilbeam D, Lindsay EH, Raza SM, Rajpar AR, Morgan ME (2013). The Neogene Siwaliks of the Potwar Plateau, Pakistan. In: Wang X, Flynn LJ, Fortelius M. (Eds.), Fossil mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press New York. Pp: 373–399.

Barry JC, Lindsay EH, Jacobs LL (1982). A biostratigraphic zonation of the middle and upper Siwaliks of the Potwar Plateau of northern Pakistan. Palaeogeogr Paleoclimatol Paleoecol., 37(1): 95-130.

Barry JC, Morgan ME, Flynn LJ, Pilbeam D, Behrensmeyer AK, Raza SM, Khan IA, Badgley C, Hicks J, Kelley J (2002). Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. Paleobiol., 28: 1–71.

Behrensmeyer AK, Barry J (2005). Biostratigraphic surveys in the Siwaliks of Pakistan: A method for standardized surface sampling of the vertebrate fossil record. Palaeontol Electron., 8(1): 1-24.

Böhme M, Ilg A, Winklhofer M (2008). Late Miocene "washhouse" climate in Europe. Earth Planet Sci Lett., 275(3-4): 393-401.

Cerling TE, Harris JM, Leakey MG (1999). Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. Oecologia., 120(3): 364-374.

Cerling TE, Wang Y, Quade J (1993). Expansion of C_4 ecosystems as an indicator of global ecological change in the late Miocene. Nat., 361: 344-345.

Clark PU, Archer D, Pollard D, Blum JD, Rial JA, Brovkin V, Mix AC, Pisias NG, Roy M (2006). The middle Pleistocene transition: characteristics, mechanisms, and implications for long-term changes in atmospheric pCO_2. Quat Sci Rew., 25(23–24): 3150-3184.

Cohen J (1960). A coefficient of agreement for nominal scales. Educ Psychol Meas., 20: 37-46.

Dennell RW, Coard R, 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. Palaeogeogr Palaeoclimatol Palaeoecol., 234: 168-185.

Dobney K, Ervynck A (2000). Interpreting Developmental Stress in Archaeological Pigs: the Chronology of Linear Enamel Hypoplasia. J Archaeol Sci., 27(7): 597–607.

Falconer H (1868). Palaeontological Memoirs and notes of the Late Hugh Falconer with a biographical sketch of the author. Vol. 2. Murchison, R. Hardwicke, London: Pp: 548.

Falconer H (1857). On the species of Mastodon and Elephant Occurring in the Fossil State in Great Britain Part Mastodon. Q J Geol Soc Lond., 13: 307-360.

Flynn LJ, Pilbeam D, Barry JC, Morgan ME, Raza SM (2016). Siwalik synopsis: A long stratigraphic sequence for the later Cenozoic of South Asia. Comptes Rendus Palevol., 15: 877-887.

Franz-Odendaal, TO (2004). Enamel hypoplasia provides insights into early systemic stress in wild and captive giraffes (Giraffa camelopardalis). J Zool Lond., 263: 197–206.

Göhlich UB (1999). Order proboscidea. The Miocene land mammals of Europe., 157-168.

Goodman AH, Allen LH, Hernandez GP, Amador A, Arriola LV, Chavez A, Pelto GH (1987). Age at Development of Enamel Hypoplasias in Mexican Children. Am J Phy Anthropol., 72(1): 7-19.

Goodman AH, Rose JC (1990). Assessment of Systemic Physiological Perturbations From Dental Enamel Hypoplasias and

Associated Histological Structures. Yearb Phys Anthropol., 33: 59-110.

Goodman AH, Rose JC (1991). Dental enamel hypoplasias as indicators of nutritional status. Adv DentAnthropol., 279-293.

Guita JL (1984). Oral Pathology, 2nd Ed. Balti- mnrc: Willianx and Wilkins.

Head MJ, Pillans B, Farquhar SA (2008). The Early–Middle Pleistocene Transition: characterization and proposed guide for the defining boundary. Episodes., 31(2): 255-259.

Herbert TD, Lawrence KT, Tzanova A, Peterson LC, Caballero-Gill R, Kelly CS (2016). Late Miocene global cooling and the rise of modern ecosystems. Nat Geosci., 9(11): 843-847.

Hynek SA, Passey BH, Prado JL, Brown FH, Cerling TE, Quade J (2012). Small mammal carbon isotope ecology across the Miocene-Pliocene boundary, northwestern Argentina. Earth Planet Sci Lett., 321: 177-188.

Khan MA, Akhtar M, Iliopoulos G (2012). Tragulids (Artiodactyla, Ruminantia, Tragulidae) from the Middle Siwaliks of Hasnot (Late Miocene), Pakistan. Rivista Italiana di Paleontologia e Stratigrafia., 118(2): 325-341.

Kierdorf H, Witzel C, Upex B, Dobney K, Kierdorf U (2012). Enamel hypoplasia in molars of sheep and goats, and its relationship to the pattern of tooth crown growth. J Anat., 220(5): 484–495.

Kreshover SJ (1940). Histopathologic studies of abnormal enamel formation in human teeth. Am J. Orthod., 26: 1083-1101.

Lukacs JR (2001). Enamel Hypoplasia in the Deciduous Teeth of Great Apes: Variation in Prevalence and Timing of Defects. Am J of Phys Anthropol., 116: 199–208.

Massler M, Schour I, Poncher HG (1941). Developmental pattern of the child as reflected in the calcification pattern of the teeth. Am J Dis Child., 62(1): 33-67.

Mead AJ (1990). Enamel hypoplasia in Miocene rhinoceroses (Teleoceras) from Nebraska: evidence of severe physiological stress. J Vert Paleontol., 19: 391-397.

Morgan ME, Behrensmeyer AK, Badgley C, Barry JC, Nelson S, Pilbeam D (2009). Lateral trends in carbon isotope ratios reveal a Miocene vegetation gradient in the Siwaliks of Pakistan. Geology. 37(2): 103-106.

Neiburger EJ (1990). Enamel hypoplasias: Poor indicators of dietary stress. Am J Phys Anthropol., 82: 231-232.

Nelson SV (2007). Isotopic reconstructions of habitat change surrounding the extinction of Sivapithecus, a Miocene hominoid, in the Siwalik Group of Pakistan, Palaeogeogr Palaeoclimatol Palaeoecol., 243: 204–222.

Nelson SV (2005). Paleoseasonality inferred from equid teeth and intra-tooth isotopic variability. Palaeogeogr Palaeoclimatol Palaeoecol., 222(1-2): 122-144.

Pilgrim GE (1910). Notices of new mammalian genera and species from the Tertiaries of India. Rec Geolog Surv India., 40: 63-71.

Pilgrim GE (1913). The correlation of the Siwalik with mammal horizons of Europe. Rec Geolog Surv India., 43: 264-325.

Ravazzi C, Strick MR (1995). Vegetation change in a climatic cycle of Early Pleistocene age in the Leffe Basin (Northern Italy). Palaeogeogr Palaeoclimatol Palaeoecol., 117: 105-122.

Roohi G, Raza SM, Khan AM, Ahmad RM, Akhtar M (2015). Enamel

Hypoplasia in Siwalik Rhinocerotids and its Correlation with Neogene Climate. Pak J Zool., 47(5): 1433-1443.

Rose JC, Condon K, Goodman AH (1985). Diet and dentition: developmental disturbances. In RI Gilheri and 33 Prehistoric Diets. New York: Academic Press. 281-306.

Sanyal P, Bhattacharya SK, Kumar R, Ghosh SK, Sangode SJ (2004). Mio-Pliocene monsoonal record from Himalayan Foreland basin (Indian Siwalik) and its relation to the vegetational change. Palaeogeogr Palaeoclimatol Palaeoecol., 205(1-2): 23-41.

Sarnat BG, Schour I (1941). Enamel hvuoplasias (chronic enamel aplasia) in relationship to systemic diseases: a chronological, morphological and etiological classification. J Am Dent Assoc., 28: 1989-2000.

Sarwar M (1977). Taxonomy and the distribution of the Siwalik Proboscidea. Bulletin of the department of zoology, university of the Punjab, Lahore, NS., 10:1-172.

Scheiter S, Higgins SI, Osborne CP, Bradshaw C, Lunt D, Ripley BS, Taylor LL, Beerling DJ
(2012). Fire and fire-adapted vegetation promoted C4 expansion in the late Miocene. New
Phytologist., 195(3): 653-666.

Shawashy M, Yaeger J (1986). Enamel. In SN Bhaskar (ed.): Orban's Oral Histology and Embryology. St. Louis: CV Mosby. 45-100.

Shoshani J. 1998. Understanding proboscidean evolution: a formidable task. Trends Ecol Evol., 13(12): 480-487.

Shoshani J, Tassy P (2005). Advances in proboscidean taxonomy and classification, anatomy and physiology, and ecology and behavior. Quat Int., 126: 5–20.

Skinner K (1996). Developmental Stress in Immature Hominines from Late Pleistocene Eurasia: Evidence from Enamel Hypoplasia. J Archaeol Sci., 23: 833–852.

Suckling G (1989). Developmental defects of enamel-historical and present-day perspectives of their pathogenesis. Adv Dent Res., 3: 87-94.

Tassy P (1996). Dental homologies and nomenclature in Proboscidea. – In: Shoshani J. and Tassy P. (eds). The Proboscidea. Evolution and Palaeoecology of Elephants and their Relatives. Oxford University Press, Oxford, New York, Tokyo. Pp: 21-25.

Tobien H (1973). The Structure of the Mastodont Molar (Proboscidea, Mammalia); Part 1: The Bunodont Pattern. Mainzer Geowissenscha-ftliche Mitteilungen., 2: 115-137.

Uno KT, Cerling TE, Harris JM, Kunimatsu Y, Leakey MG, Nakatsukasa M, Nakaya H (2011). Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. Proc Natl Acad Sci., 108: 09-14.

Waseem MT, Khan AM, Ghaffar A, Iqbal A, Ahmad RM (2021). Palaeodietary and Palaeoclimatic Reconstruction for Late Miocene Hipparionines from the Siwaliks of Pakistan. Pak J Zool., 1-9.

Weinmann J, Svoboda J, Woods R (1945). Hereditary disturbances of enamel formation and calcification. J Am Dent Assoc., 32(7): 397-418.

Yaeger J (1980). Enamel. In SN Bhaskar (ed): Orban’s Oral Histology and Embroyology (9th Ed). St. Louis: C.V. Mosby. Pp: 46-106.