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# Enamel Hypoplasia Analysis in Giraffids to Compare Stress Episodes in Geological History of the Siwaliks of Pakistan

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**RMA did the research work and AMK and RMA drafted the manuscript. GR helped in improvement of the discussion and provided the literature, AMK and MK supervised the research work.**

**Key words**
**Artiodactyla, Enamel Hypoplasia, Miocene, Pleistocene, Stress.**

## ABSTRACT

Studies on dental enamel hypoplasia have been used by different paleontologists as stress indicator in evaluation of palaeo-environments. The present study involves the analysis of enamel hypoplasia in seven extinct giraffid species to determine and compare stress periods during the early Miocene to Pleistocene ages of the Siwaliks of Pakistan. Enamel hypoplasia is a tooth malady which is caused by the deficiency of food/nutrients. The feeding deficiency is directly linked to the physiological or environmental stress. In this study occurrence of enamel hypoplasia in giraffids has been observed in species of all time intervals between 18.3-0.6 Ma except the time 11.2-9.0 (late Miocene) that has no giraffids with this dental defect. The comparative percentage for occurrence of enamel hypoplasia in giraffids of these Siwalik deposits is early Miocene-early middle Miocene (29%), middle Miocene (20%), late Miocene-early Pliocene (15%), early Pliocene-late Pliocene (26%) and late Pliocene-early Pleistocene (10%). Prevalence of enamel hypoplasia indicates the existence of stress episodes and percentage displays the comparative intensity of these stresses in the Neogene and Quaternary period of the Siwalik region. These stress episodes are due to the climatic, vegetational, ecological and faunal changes during these time spans. These early Miocene to Pleistocene stress events may have played a key role in evolution and speciation of the Siwalik fauna especially the mammals.

## INTRODUCTION

Enamel defect studies can provide a unique perspective of environmental stress period present during the growing days of an extinct animal's life. Enamel is the hardest tissue of body and marks of enamel hypoplasia (EH) remain unaltered even during fossilization so it can be a highly admirable stress marker for the life history of an extinct animal.

EH is a type of enamel defect characterized by the thinning of enamel (Goodman and Rose, 1990). The formation of enamel can be categorized into two phases, first is named as secretary and second as maturation phase (Hillson, 1986). In the secretary phase enamel first caps top of the tooth crown and then move down along the sides of the crown. In the maturation phase the process of mineralization occurs on the tooth (Fig. 1). EH occurs during the secretary phase.

Areas missing enamel, single or multiple pits and vertical or horizontal groves are the three types of EH described by the FDI (Federation Dentaire International, 1982). The area missing enamel has advantage over other two types that it can be examined macroscopically. The age of animal during a particular stress episode in its eco-system can be accessed on the basis of position of area missing enamel on tooth crown relative to the tooth-crown junction (Goodman *et al*., 1980; Suckling, 1989). There are two types of area missing enamel, linear enamel hypoplasia (LEH) and semi-circular enamel hypoplasia (SEH). LEH is typically visible on a tooth's surface as one or more than one horizontal grooves and SEH is a tooth depression in semi-circular form in horizontal direction (Goodman and Rose, 1991; Skinner and Goodman, 1992). EH is caused by a physical disruption in the ameloblasts during the tooth development. This defect is usually co-related by a systemic stress (Franz-Odendaal *et al*., 2004). These systemic stresses mainly caused by the deficiency of food/nutrients. The feeding deficiency is directly linked to the physiological or environmental stress.

The studies about EH in extinct and extant species of ungulates have been carried out by different researchers in order to trace out the environmental conditions these species faced during their developmental and growth period (Franz-Odendaal, 2004; Franz-Odendaal *et al*.,

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2004; Mead, 1999; Niven *et al*., 2004; Roohi *et al*, 2015). This study of EH as a stress indicator in extinct giraffids is conducted in order to analyze the presence or absence of ecological stresses for giraffids in the Siwalik of Pakistan and to compare the intensity of these stresses among different formations of the Siwaliks. There is not yet any reported study of EH in Siwalik artiodactyles; this research work is the first attempt to analyze EH in giraffids of Potwar Plateau of the Siwaliks.

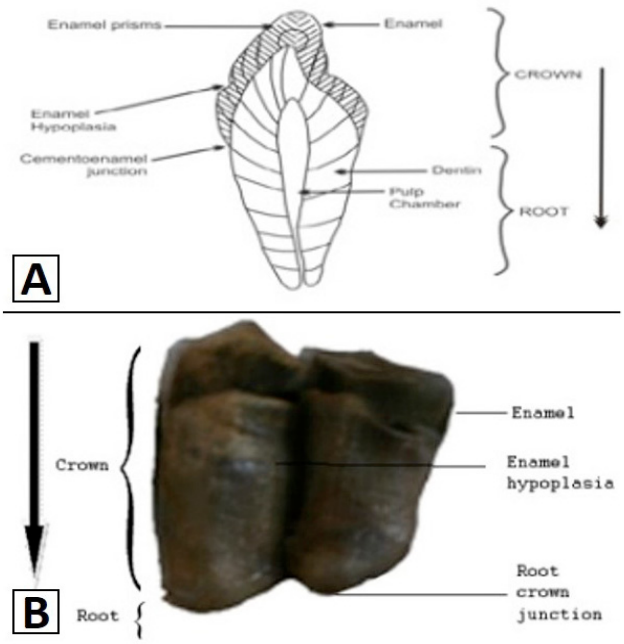


Fig. 1. A, hypothetical tooth demonstrating the process of enamel formation (Goodman and Rose, 1990; Franz-Odendaal *et al*., 2004); B, diagrammatic representation of giraffid molar. The vertical arrow indicates the direction of crown development (addition of enamel) from tip to base.

The Siwaliks collection of Indo-Pak sub-continent and Churia collection of Nepal is formed as a result of sedimentation of the Miocene to Pliocene originated rocks (Medlicott, 1864). For paleontologist the Indo-Pak hills of the Siwalik region are highly significant as from last 100 years it is a source for study mammalian fossilized fauna from early Miocene to Pleistocene. This mammalian fauna was originated from Asia and Europe (Pilbeam *et al*., 1977). Potwar Plateau of the province Punjab, Pakistan (Lat. 33° 00'' N; Long. 72° 30'' E) is a part of the Siwalik group ranges from Margala and Kala Chita hills to Salt range in north-south and from Jhelum River to Indus River in east-west direction (Fig. 2). This plateau has a depth of 5000-5500 m and an area of about 20,000 km$^2$ (Tripathi and Sharma, 1986). Potwar Plateau is further divided on the basis of faunal organization into Kamlial Formation, Chinji Formation (Lower Siwaliks), Nagri Formation, Dhok Pathan Formation (Middle Siwaliks) and Soan Formation (Upper Siwaliks). The Soan Formation is further divided into Tatrot, Pinjor and Boulder Conglomerates zones (Barry *et al*., 2002). The chronological ages of Kamlial Formation, Chinji Formation, Nagri Formation, Dhok Pathan Formation, Tatrot Formation and Pinjor Formation are 18.3-14.2 Ma, 14.2-11.2 Ma, 11.2-10.0 Ma, 10.0-3.3 Ma, 3.3-2.6 Ma and 2.6 to 0.6 Ma, respectively. Kamlial Formation (early Miocene-early middle Miocene) has river sediments containing many beds of conglomerates. Chinji Formation (middle Miocene) composed of red shale and fine to medium grained sandstone light gray to ash gray in color. The proportion of shale and sandstone varies in different areas of this Formation. Nagri Formation (late Miocene) is characterized by nodules containing red clays. Dhok Pathan Formation (late Miocene-early Pliocene) consists of orange, red clay and light gray sandstone (Khan, 2009). Pink granite containing rounded and sub angular pebbles, purple sandstone and many quartzites are the lithological properties of Tatrot Formation (early Pliocene-late Pliocene) (Siddiq *et al*., 2016). Pinjor Formation (late Pliocene-early Pleistocene) consists of brown mudstone, brown to grayish-brown sandstone and pebbles (Siddiq *et al*., 2014).

Five Siwaliks genera of order Artiodactyla and family Giraffidae namely *Progiraffa, Giraffokeryx*, *Giraffa*, *Bramatherium* and *Sivatherium* are included in the present study of EH for the prediction of climatic variations and ecological disturbances of the Neogene and Quaternary Siwaliks.

## MATERIALS AND METHODS

The studied material includes fossilized teeth of seven species. *Progiraffa exigua* and *Giraffokeryx punjabiensis* belongs to genus *Progiraffa* and *Giraffokeryx* respectively, *Giraffa priscilla* and *Giraffa punjabiensis* are species of genus *Giraffa,* the higher taxon for species *Bramatherium megacephalum* and *Bramatherium grande* is *Bramatherium* and *Sivatherium giganteum* is the species of genus *Sivatherium*. The detail of the studied material along with results for occurrence of EH in these fossils is described in Table I. Severely damaged or worn teeth were excluded and only well preserved teeth were evaluated. The fossils used for analysis of EH are housed at the Dr. Abu Bakar Fossil Display and Research Center, Department of Zoology, University of the Punjab Lahore, Pakistan. The fossils were discovered from out crops of the Siwalik sedimentary deposits having age from early Miocene to Pleistocene.

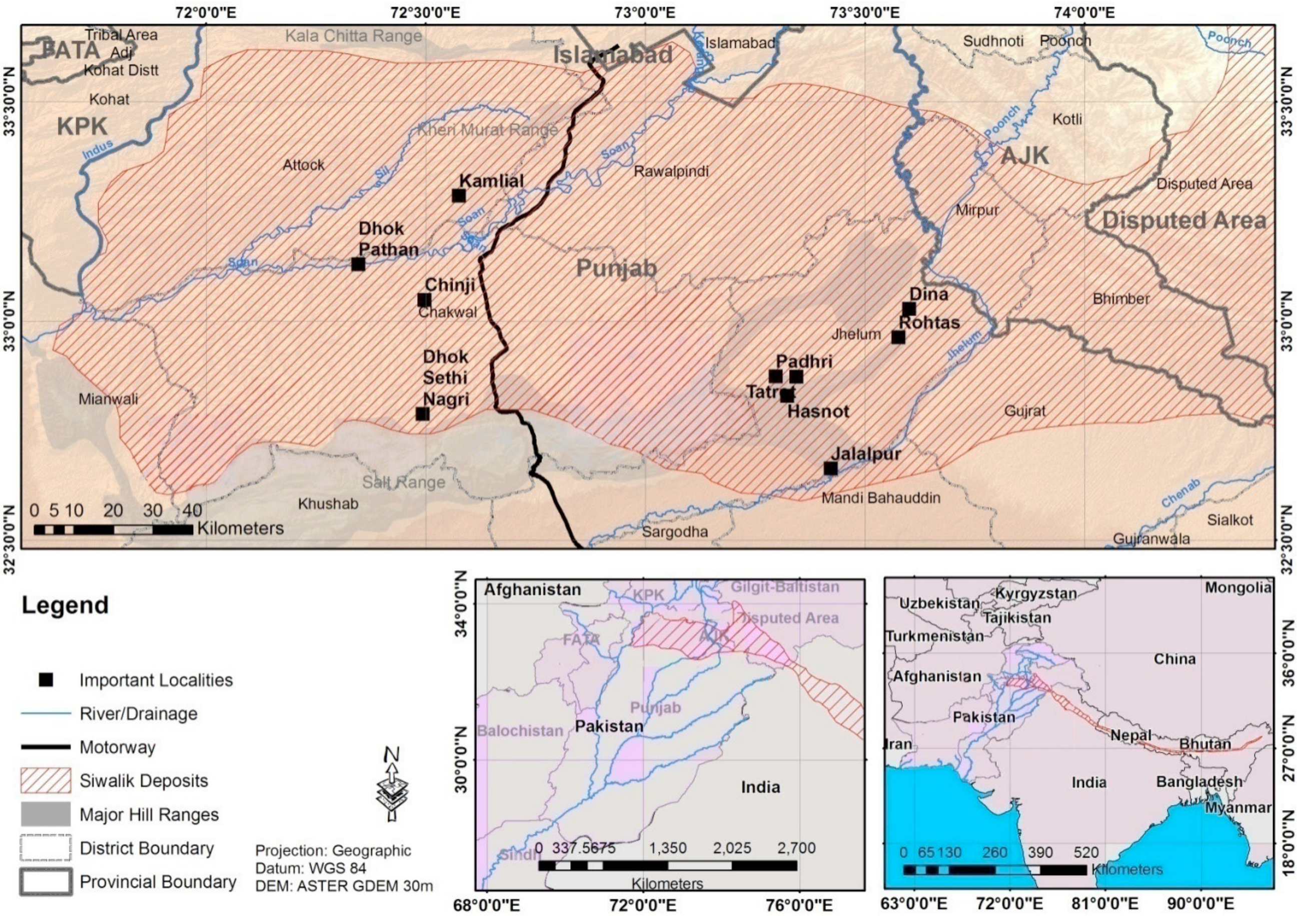


Fig. 2. Distribution of the Siwalik deposits in different areas of Pakistan.

**Table I.- Studied fossils of the giraffids in the Siwalik formations from early Miocene to Pleistocene.**

| Studied Siwalik time intervals | Included species | Catalog number | Type of dentition | Presence/ Absence of EH |
|---|---|---|---|---|
| Early Miocene–early middle Miocene | *Progiraffa exigua* | PUPC 14/10 | I | 02 LEH |
| | | PUPC 09/11 | p2 | ………………. |
| | | | p3 | ………………. |
| | | PUPC 67/240 | p4 | 01 LEH |
| | | PUPC 14/71 | p4 | 01 LEH |
| Middle Miocene | *Giraffokeryx punjabiensis* | PUPC 66/95 | M1 | ………………. |
| | | | M2 | 01 LEH |
| | | | M3 | 03 LEH |
| | | PUPC 09/92 | P2 | ………………. |
| | | PUPC 11/65 | P3 | ………………. |
| | | PUPC 12/53 | P3 | ………………. |
| | | PUPC 94/10 | P4 | ………………. |
| | | PUPC 12/54 | M1 | 01 LEH |
| | | PUPC 09/93 | M2 | 01 LEH |

| **Studied Siwalik time intervals** | **Included species** | **Catalog number** | **Type of dentition** | **Presence/ Absence of EH** |
|---|---|---|---|---|
| Middle Miocene | *Giraffokeryx punjabiensis* | PUPC 69/37 | M2 | 02 LEH |
| | | PUPC 02/13 | M2 | ……………… |
| | | PUPC 09/93 | M2 | ……………… |
| | | PUPC 09/01 | M3 | 01 LEH |
| | | PUPC 10/14 | p3 | ……………… |
| | | | p4 | ……………… |
| | | | m1 | ……………… |
| | | | m2 | ……………… |
| | | | m3 | ……………… |
| | | PUPC 09/117 | p2 | ……………… |
| | | | p3 | ……………… |
| | | | p4 | 01 LEH |
| | | | m1 | 01 LEH & 01 SEH |
| | | | m2 | 02 LEH |
| | | | m3 | ……………… |
| | | PUPC 09/88 | p2 | ……………… |
| | | | p3 | ……………… |
| | | | p4 | 01 LEH |
| | | | m1 | 01 LEH |
| | | | m2 | ……………… |
| | | | m3 | ……………… |
| | | PUPC 14/143 | p3 | 01 LEH |
| | | PUPC 11/06 | p3 | 01 LEH |
| | | PUPC 09/47 | p4 | ……………… |
| | | PUPC 02/09 | m3 | ……………… |
| | | PUPC 09/95 | m3 | ……………… |
| | *Giraffa priscilla* | PUPC 11/31 | p4 | ……………… |
| | | | m1 | ……………… |
| | | PUPC 11/24 | m2 | ……………… |
| | | PUPC 02/15 | m3 | 01 LEH |
| Late Miocene | *Giraffokeryx punjabiensis* | PUPC 07/88 | P3 | ……………… |
| | *Giraffa punjabiensis* | PUPC 86/307 | m3 | ……………… |
| | *Bramatherium megacephalum* | PUPC 09/45 | P4 | ……………… |
| Late Miocene-early Pliocene | *Giraffa punjabiensis* | PUPC 86/84 | M1 | 02 LEH |
| | | | M2 | ……………… |
| | | | M3 | ……………… |
| | | PUPC 96/07 | m1 | ……………… |
| | | | m2 | ……………… |
| | | PUPC 83/737 | m2 | ……………… |
| | | PUPC 09/96 | m2 | ……………… |

| Studied Siwalik time intervals | Included species | Catalog number | Type of dentition | Presence/ Absence of EH |
|---|---|---|---|---|
| Late Miocene-early Pliocene | *Bramatherium megacephalum* | PUPC 87/218 | M2 | ……………… |
| | | PUPC 97/17 | p3 | ……………… |
| | | | p4 | ……………… |
| | | | m1 | 02 LEH |
| | | | m2 | ……………… |
| | | | m3 | 01 LEH |
| | | PUPC 67/77 | p2 | ……………… |
| | | | p3 | ……………… |
| | | | p4 | ……………… |
| | | PUPC 09/78 | m1 | 01 LEH |
| | | | m2 | ……………… |
| | | PUPC 06/10 | M2 | 01 LEH |
| | | PUPC 06/11 | m3 | ……………… |
| | | PUPC 95/24 | d1 | ……………… |
| | *Bramatherium grande* | PUPC 68/189 | M2 | ……………… |
| | | PUPC 69/156 | M3 | 03 LEH |
| | | PUPC 83/267 | m2 | ……………… |
| | | | m3 | 01 LEH |
| | | PUPC 10/46 | m2 | 01 LEH |
| | | PUPC 10/47 | m3 | ……………… |
| | | PUPC 09/17 | m3 | 01 LEH & 01 SEH |
| | | PUPC 67/446 | m3 | ……………… |
| Early Pliocene-late Pliocene | *Sivatherium giganteum* | PUPC 14/30 | I | 01 LEH |
| | | PUPC 67/26 | M2 | 02 LEH |
| | | PUPC 13/50 | M2 | ……………… |
| Late Pliocene-early Pleistocene | *Sivatherium giganteum* | PUPC 13/33 | I | ……………… |
| | | PUPC 14/23 | M1 | ……………… |
| | | PUPC 67/29 | M2 | 01 LEH |
| | | PUPC 67/156 | M2 | ……………… |

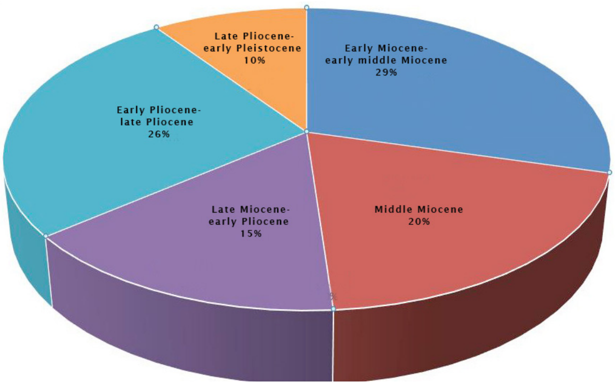


Fig. 3. Comparison of percentage for occurrence of EH in giraffid species in different epochs of the Siwaliks of Pakistan.

Each tooth was observed visually by using magnifying glasses for the presence or absence of EH. Description of each defect, its position on the tooth crown and the position of the defected tooth in each jaw were recorded. EH observation was based on Mead (1999). Dental terminology of giraffid tooth for studying EH in this experiment follows that of Khan *et al*. (2010). LEH and SEH defects on both lingual and buccal surfaces were noted down. The position of EH on the tooth crown heights from the root-crown junctions (neck) was measured using Vernier caliper. All measurements were taken in mm.

## RESULTS

Out of 83 studied fossilized teeth 28 (34%) has EH. The prevalence of EH in premolars is 06 out of 27 (22%), for molars this value is 21 out of 52 (40%), for incisor this value is 01 out of 03 (33%). These EH possessing fossils belong to species that are reported form a fairly wide region of the Siwalik Hills. The comparative percentage for prevalence of EH in studied specimens of giraffid species inhabiting the Neogene and Quaternary ecosystems of the Siwalik Hills of Pakistan is given in Figure 3.

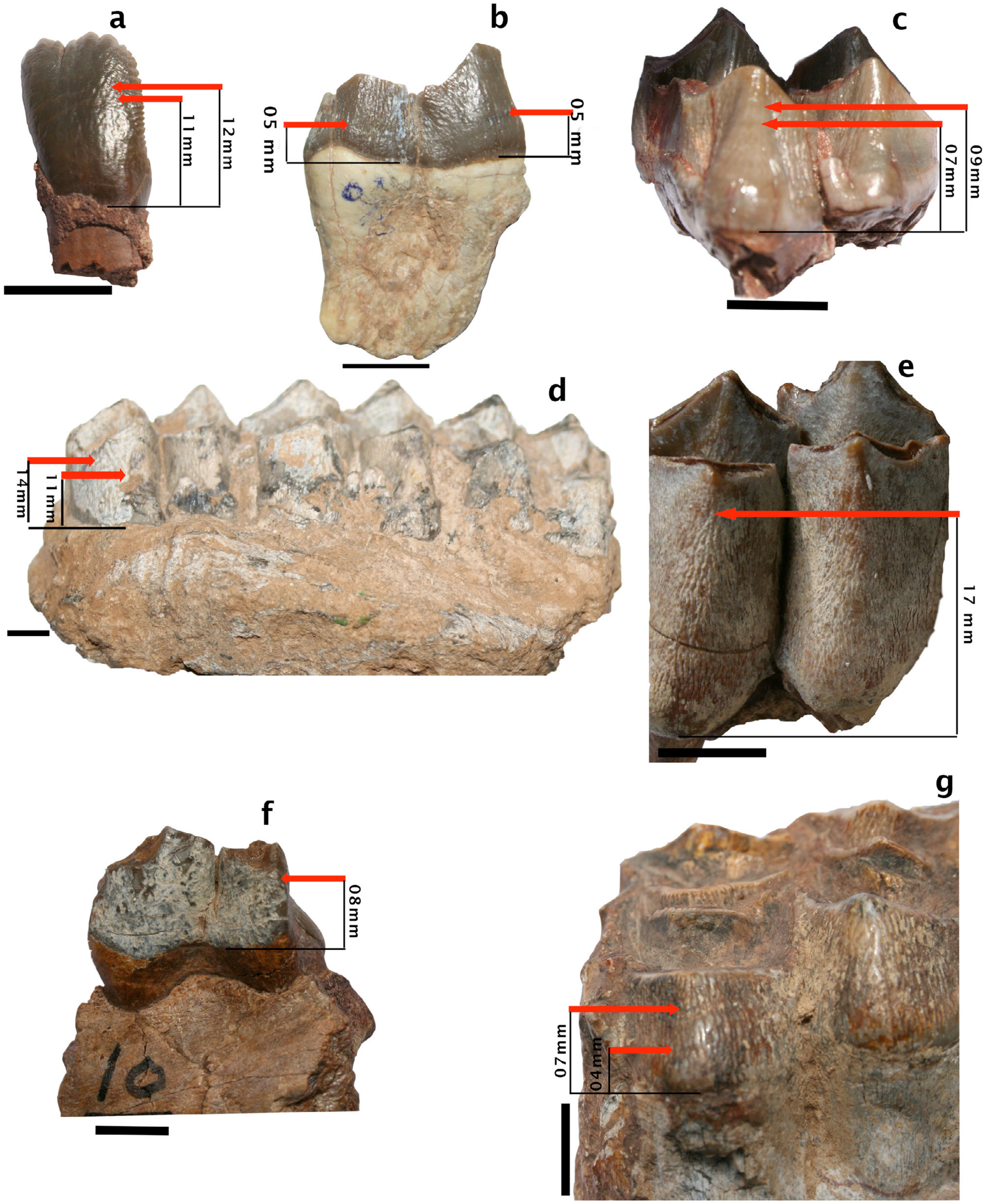


Fig. 4. EH in giraffid species of the Siwaliks: a, *Progiraffa exigua;* b, *Giraffa priscilla;* c, *Giraffokeryx punjabiensis;* d, *Giraffa punjabiensis;* e, *Bramatherium megacephalum;* f, *Bramatherium grande;* g, *Sivatherium giganteum.*

Occurrence of EH was observed in all the seven studied species as shown in Figure 4. The results of this study indicate that hypoplasia on teeth can be single or multiple LEH and/or SEH (Fig. 4). The maximum marks of EH observed in current study on a single tooth are 04 in number.

## DISCUSSION

In case EH was an inherited disorder in extinct giraffids, than the animal having inherited EH should have all teeth showing signs of EH (Stewart and Poole, 1982; Franz-Odendaal *et al*., 2004). In this study occurrence of EH was observed in six out of seven jaw fragments. No any species has a jaw with all teeth affected by EH indicating that observed EH was not inherited but due to some type of environmental or nutritional stress during growth and development period of these animals. Mead (1999) analysis of EH in *Teleoceras* (Miocene rhinoceroses) evidenced 19% EH in this species. A comparative study of EH in Siwalik rhino also manifested that 05% teeth of Rhinocerotidae has EH (Roohi *et al*., 2015). while comparatively high EH was observed in *Sivatherium hendeyi* (Pliocene giraffid) by Franz-Odendaal *et al.* (2004), nearly same is the case observed in studied girrafid species 34% teeth are affected showing that EH is competitively more prevalent in members of family Giraffidae than that of Rhinocerotidae that indicates that environmental modification during geological time scale in different regions cause comparatively more stress to giraffids. All the observed EH are horizontal and there is no any case of vertical EH (Fig. 4). These results support Franz-Odendaal *et al.* (2004) as they also only observed horizontal EH marks in extinct giraffids.

In giraffids first erupted tooth is first molar around the age of one year and premolars developed at the late stages of animal growth at the age of five to six years (Hall-Martin, 1976; Franz-Odendaal *et al*., 2004) The occurrence of EH in the first molar of *Giraffokeryx punjabiensis, Giraffa punjabiensis* and *Bramatherium megacephalum* as shown in Table I provide the evidence of very early defects in extinct species. Poor maternal diet and/or premature birth are significant etiologies for these early defects. Presence of EH in premolars of varied species as narrated in Table I shows that studied species of giraffids were facing a nutritional or environment stress in their mature ages as well. Presence of more than one LEH in one tooth indicates seasonal stresses during the life history of these animals.

*Data interpretation in regional context*

*Progiraffa exigua* is an early-middle Miocene species (Aftab *et al*., 2016). The studied specimens of this species are from early Miocene-early middle Miocene sediments.

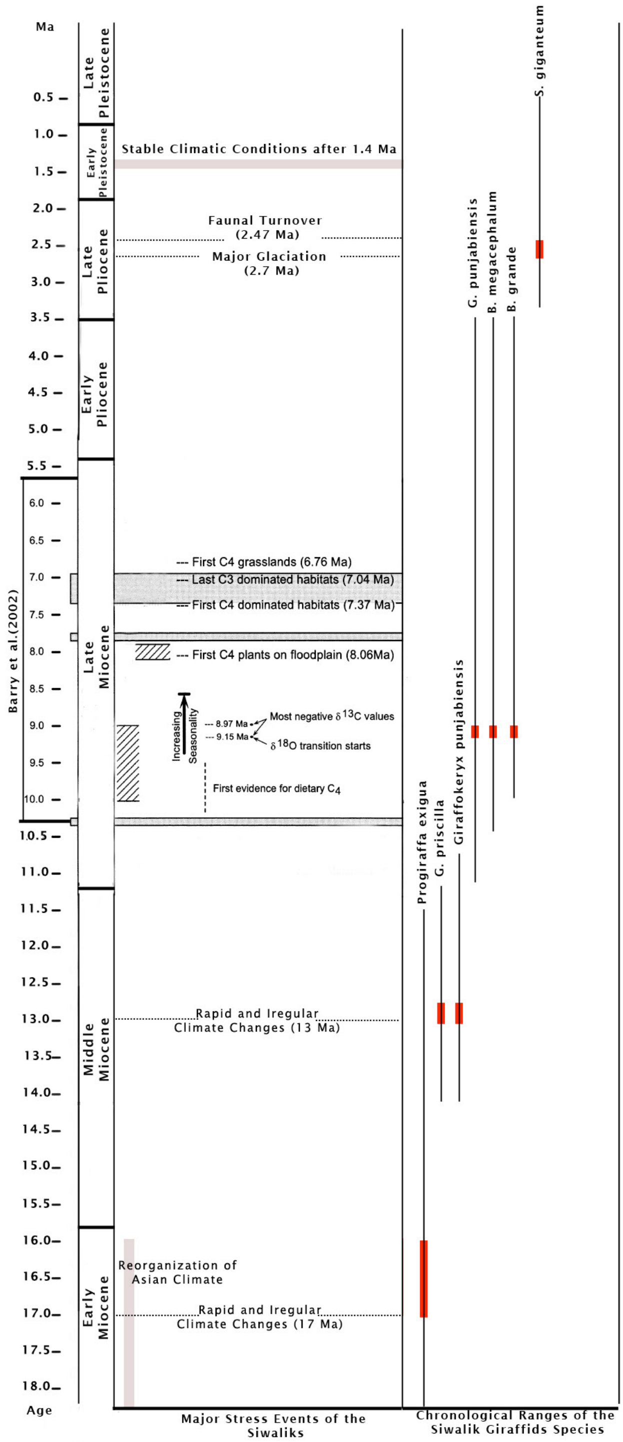


Fig. 5. Comparison of EH in giraffid species having different chronological distributions in the Siwaliks of Pakistan, Red areas in figure indicate the geological time for occurrence of EH in these species (Data for events and ages is taken from Barry and Flynn (1990), Barry *et al.* (2002), Dennell *et al.* (2006) and Lisiecki *et al.* (2007)).

The highest comparative percentage of EH (29%) is detected in early Miocene-early middle Miocene epoch (Figs. 3 and 5). The tectonic factors of early Miocene origin provided a noteworthy threshold for the Asian climate reorganization. There were rapid and irregular climate changes during 17 Ma. The early Miocene is a time for transition of Paleogene to Neogene deposits, one of the major climatic turn over (Barry and Flynn, 1990; Barry *et al*., 2002). All these factors collectively contributed for the exceeded value of EH occurrence in early Miocene-early middle Miocene Siwalik fauna.

*Giraffokeryx punjabiensis* and *Giraffa priscilla* are the species of middle Miocene fresh water deposits of Eurasia (Colbert, 1935; Khan *et al*., 2010). Both these species have EH (Figs. 3 and 5). The comparative percentage of EH in individual of middle Miocene species of the Siwaliks is 20% indicating that middle Miocene is a period of high stress episodes during the evolution of Siwalik mammals. The middle Miocene is a period of stress due to rapid and irregular climate changes at 13 Ma. The increased ratio of disappearance and appearance during this period indicates a rapid change in environment that ultimately is responsible for nutritional and ecological stress to the middle Miocene species (Barry and Flynn, 1990; Barry *et al*., 2002).

Three species were analyzed in late Miocene interval for EH. No EH is observed in these species this provides an idea of comparatively stress free environmental conditions for giraffids during 11.2-9.0 Ma time period of late Miocene epoch.

15% comparative EH is observed in late Miocene to early Pliocene fossils of *Giraffa punjabiensis, Bramatherium megacephalum* and *Bramatherium grande* (Figs. 3 and 5). This dental defect in these species is due to various stress events during late Miocene to early Pliocene time span. Average species duration decreased significantly in the late Miocene due to increase frequency of environmental disturbances. There was very marked cooling in late Miocene after 6.5 Ma, this cooling episode had a vital role in development of these environmental changes (Barry and Flynn, 1990).

Stress episodes are also analyzed in *Sivatherium giganteum*, a Pliocene to early Pleistocene species (Khan *et al*., 2011). There was an increase in cooling trends and glacial cycle amplitude in Plio-Pleistocene time span. The asymmetric saw tooth type glaciation pattern of these ages is one of the motives for climate dynamics. 2.5 Ma transition is considered as a major contributor for this climate dynamics (Lisiecki and Raymo, 2007). According to Dennell *et al*. (2006) there were shifts towards more arid conditions during 1.8, 1.7 and 1.0 Ma. The comparative percentage for stress indicated by EH is 26% and 10% for early Pliocene-late Pliocene and late Pliocene-early Pleistocene, respectively. The stable climatic conditions of Pinjor Formation are responsible for this percentage difference in the two regions.

## CONCLUSION

All the developmental signatures of EH on the teeth strongly favor that the hypoplasia is in fact related with environmental stress, which might have affected the nutrition and the food availability. This aspect, taken in conjunction with other environmental interpretations based on paleo-dietary inferences deciphered from the meso- and micro-wear analysis of cheek teeth of several other mammalian groups as well as the changes in stable carbon and oxygen isotopes analyses on carbonate nodules of paleosols, could be lead towards a better understanding of the local environment and regional climate changes during the Neogene in South Asia. EH presence in fossils of studied giraffid species of Neogene deposits of the Siwaliks indicates that there were a number of vegetational and climatic changes in these ecosystems during the history of earth that have a major contribution in the evolution, extinction and migration of extinct mammalian species.

*Statement of conflict of interest*

Authors have declared no conflict of interest.

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