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Enamel Hypoplasia in Siwalik Rhinocerotids and its Correlation with Neogene Climate

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Abstract.-The developmental or usage patterns experienced in the dentition by certain mammals during their growth or later in life often are preserved in their fossilized remains and have extensively been used in reconstructing life-history or the habitat in which the animals lived. One such, though lesser emphasized, feature is the enamel hypoplasia (EH), which is a failure for the enamel to form properly leaving distinct linear or curved marking(s) on the teeth. EH is caused by environmental or physiological stresses in an animal's life at that particular time when the growth was taking place. Hence, the EH analysis in a faunal accumulation has been used for providing a unique perspective into environmental conditions present during the growing years of an extinct animal's life. The present study on EH of Siwalik Rhinocerotids has proved to be an important tool for not only understanding their past life-history but also in reconstructing local palaeoenvironment and regional palaeoclimate of the region.

Key words: Perissodactyla, Fossil Teeth, Anomaly, Physiological stress, Palaeoenvironment.

INTRODUCTION

The Siwalik Group rocks constituting the Sub-Himalayan hill ranges have long been known to yield rich Neogene to Quaternary vertebrate fossil assemblages that represent dominantly mammalians fauna of multiple lineages, including rodents, artiodactyls, perissodactyls, proboscideans, carnivores and occasionally but of critical significance hominoid primates (Barry *et al.*, 2002; Siddiq *et al*., 2014). Rhinocerotids constitute a prominent group among the Siwalik Perissodactyla, first appearing around 35 Ma in the Bugti Hills, central Pakistan and continuing into the recent times. Rhinocerotid fossils are known from dental, cranial, and post-cranial elements which are considered to be of utmost importance for understanding their evolution and distribution in the Old World (Antoine *et al*., 2013; Khan, 2009). The Neogene to Quaternary Siwalik Group rocks have also been extensively studied for understanding the Himalayan orogenic system and the geomorphologic evolution of the South Asian landscape including the present-day drainage pattern (Khan *et al.*, 1997). In the past decade or so, a combination of functional analyses of some skeletal elements, meso- and micro-wear signatures of cheek teeth, and isotopic analyses of tooth enamel, coupled with oxygen and carbon isotopic composition of carbonate nodules in the fossil soil and trace elements in fine sediments have given unique insight on the evolution of the Neogene climate and specially the onset of present-day Monsoonal system in South Asia (Nelson, 2005). This paper describes a novel approach for understanding Neogene environmental and climate changes in the region by studying the dental developmental defect (enamel hypoplasia) recorded in Siwalik Rhinocerotids.

The several kilometer thick Siwalik sequence of coarse-grained (sandstone and conglomerate) and fine grained (siltstone and clay stone) sediments forming the southern hill-ranges of the Himalayas are best known from its western part (Fig. 1). The Siwaliks are often exposed as shallowly dipping undeformed rocks in low Sub-Himalayan hill ranges and are generally capped by hard resistant conglomerate-dominated Pleistocene beds (Lei, Mirpur, Dada Formation in Figure 2). Siwalik lithofacies include grey sandstones, red to brown siltstones and mudstones, and rare conglomerates. Formations have been defined on the basis of the

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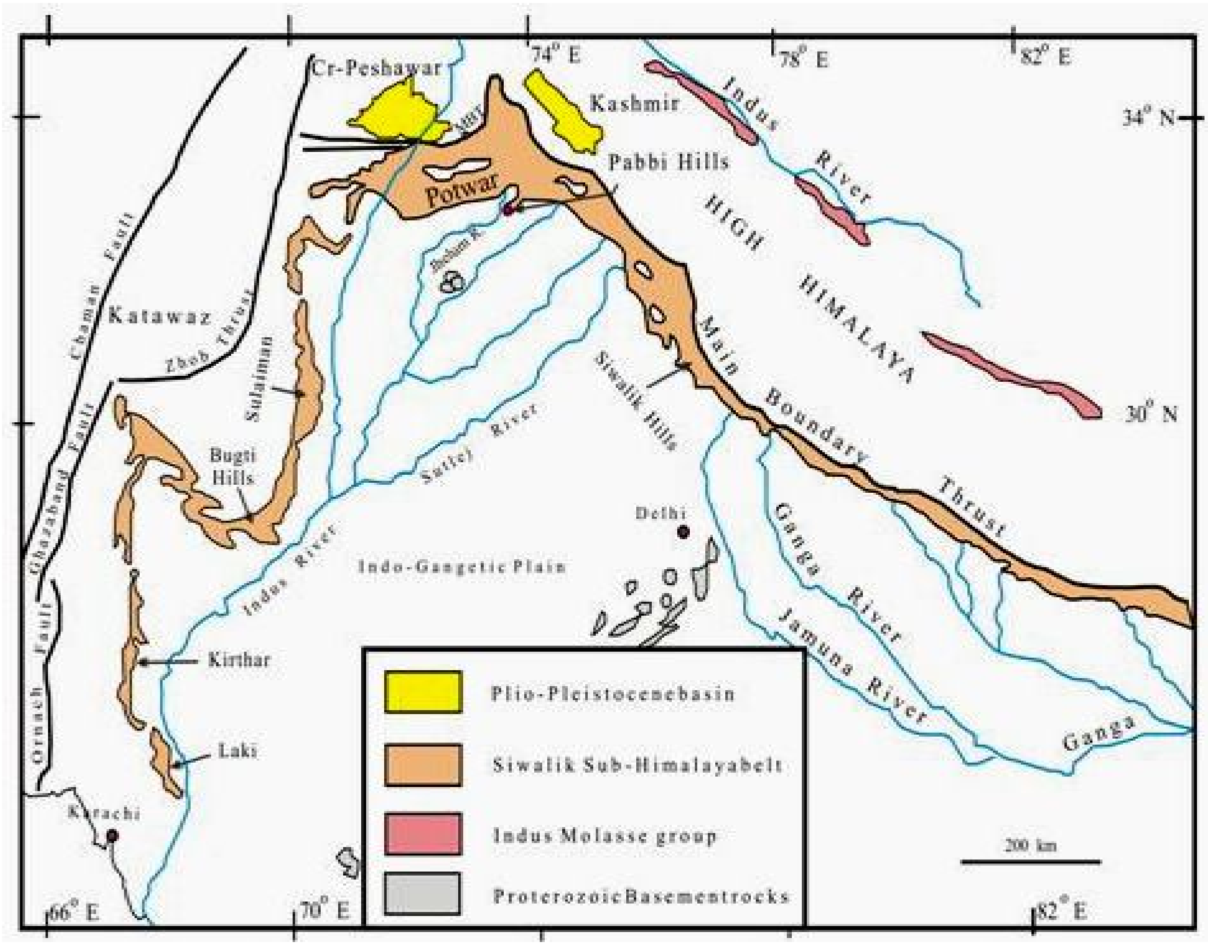

Fig. 1. Generalized geological map of Pakistan and northern India, showing distribution of the Neogene "Siwalik" and coeval rocks (Modified from Raza, unpublished).

relative proportions of coarse-grained facies (*i.e.*, sandstone and rare conglomerates) and fine-grained (siltstone, and rare clay) units, as well as the lateral extent and thickness of sandstone bodies (Fig.2). The environmental reconstructions of the Siwalik formations are based primarily on sedimentological evidence, using the Indus and the Gnages rives as modern analogues (Willis and Behrensmeyer, 1995). However, the older formations, namely Chitarwata, Gaj, basal Manchar and Murree formations (Fig. 2), were deposited in a mixed environment transitioning between marine, estuarine, and fluvial conditions. In the past 40 years whereas the Potwar Plateau has remained the focus of an extensive paleontological and sedimentological investigation, the coeval continental sediments of the Sulaiman Ranges, Bugti Hills and Kirthar Ranges have also been studied (Barry *et al*., 2002, Antoine *et al*., 2013; Raza *et al*., 1984, 2002; Hussain *et al*., 1992).

The Siwalik Group rocks are fairly fossiliferous throughout the Sub-Himalayan ranges but more specifically the bulk of the paleontological wealth came historically from the Potwar Plateau and the Siwalik Hills (Pilgrim, 1910, 1912; Falconer and Cautley, 1868).The extensive research in the past four decades in Pakistan not only expanded the collections known from the Potwar Plateau, Bugti Hills, and the Kirthar Ranges but also added fauna from the Sulaiman Ranges, Bhimber-Mirpur (Azad Kashmir) and the Pabbi Hills.

The Miocene Siwalik and coeval mammal

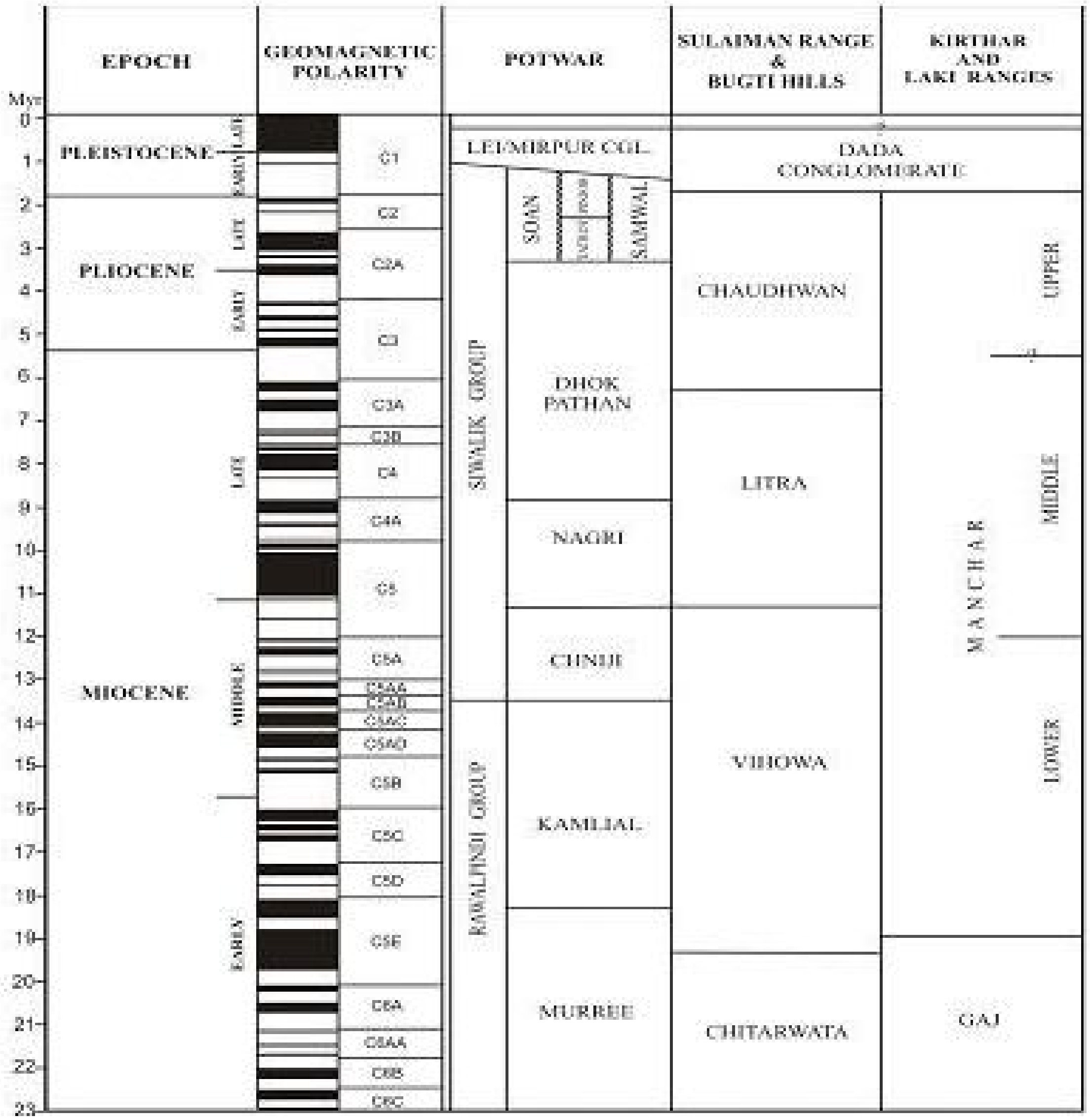

Fig. 2. Neogene Formations in various regions of the Indus Basin and correlation with European MN Zones. Compiled from Raza *et al*. (1984); Hussain *et al.* (1992); Barry *et al.* (2002) and Antoine *et al.* (2013).

fauna includes species from at least 13 orders and more than 50 families (Flynn *et al.*, 1995; Barry *et al*., 2002; Raza *et al*., 2002; Lindsay *et al*., 2005; Antoine *et al*., 2013). At least nineteen of these families are currently present in the Indo-Pakistan subcontinent (Roberts, 1997; Nanda, 2008). The orders include Insectivora, Scandentia, Chiroptera, Pholidota, Primates, Rodentia, Lagomorpha, Creodonta, Carnivora, Tubulidentata, Proboscidea, Artiodactyla, and Perissodactyla. Among the Perissodactyla, the Rhinocerotidae occur very early in the sequence, in fact the earlyradiation in the Indian subcontinent is well recorded in the basal Chitarwata beds (*i.e*. the famous 'Bugti Bone beds' Pilgrim, 1912; Forster-Cooper, 1934) dated around 23 Ma (Antoine *et al.*, 2013). Rhinocerotids of the fauna from the Bugti Hills-Sulaiman Range have been classified into 13 species whereas Khan (2009), while revising the Siwalik Rhinocerotids from the Potwar Plateau, grouped them into 19 species (Fig. 3). The first author (Ghazala Roohi) examined all the rhinocerotid dental material known from the Siwalik and coeval rocks of Pakistan and Siwalik Hills (northern India) residing in the leading museums and institutions in France, UK, USA and Pakistan, namely the Pakistan Museum of Natural History Islamabad (PMNH); the Geological Survey of Pakistan, Islamabad (GSP); the Zoology Department of the Punjab University, Lahore (PUPC); Muséum National d'Histoire Naturelle Paris, France (MNHN); Museum d' Histoire Naturelle Toulouse, France (MHNT); American Museum of Natural History, New York, USA (AMNH); Peabody Museum Harvard University USA (PMHU); Yale Peabody Natural History Museum, USA (YPNHM) and the Natural History Museum London (NHM). The dental materials were examined visually and through magnifying glass to identify any dental defect in the enamel development, hypoplasia, and to record all contextual information.

Dental enamel hypoplasia (EH) is a thinning of tooth enamel resulting from disruptions in the enamel deposition by amelobalsts during crown development (Ensor and Irish, 1995). This results either in pits and grooves in areas of the tooth or in widespread absence of enamel as a linear band (Hillson, 2005; Larsen, 1997). The most visible deficiencies are in the form of linear band noted as linear enamel hypoplasia (LEH). Since hypoplastic defects are not erased unless the enamel itself is worn away, teeth provide an excellent record of the different types and degrees of environmental stress and influence of the metabolic conditions affecting tooth structure and tooth survival. LEH is a deficiency in enamel thickness occurring during tooth crown formation. It is typically visible on a tooth's surface as one; two or more horizontal (or transverse) grooves or lines (Fig.5). It may also be in the form of a linear array of pits, representing a deficiency of enamel formation visible on the outer enamel surface. It is the most commonly studied expression of EH. Other type of EH observed is semicircular enamel hypoplasia (SEH).

EH is caused by a physical disruption in the cells (ameloblasts) laying down the enamel (Goodman and Rose, 1990). The disruption is usually caused by systematic (metabolic) stress and this defect is manifested by thinning of the tooth enamel. Enamel essentially forms in two phases: a secretory and a maturation phase (Hillson, 1986). During the initial secretory phase, enamel laid down in an incremental fashion starting at the dentine-enamel junction and proceeding outwards and apically. Successive layers of enamel are deposited outside the initial apical enamel so that younger enamel is found toward the root (Fig. 4).The age at which the defect formed and the timing of the stress episode can be estimated from its position on the tooth crown relative to the root-crown junction. The width of the LEH relates to the duration of the stress episode and its depth is thought to be related to severity (Goodman *et al*., 1980; Suckling, 1989).

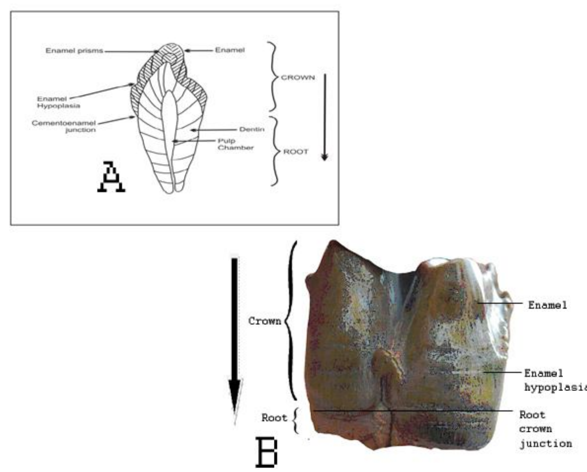

Fig. 4. (A) Hypothetical tooth demonstrating the process of enamel formation (Goodman and Rose, 1990; Franz-Odendaal*et al*., 2004). (B) Diagrammatic representation of Rhinocerotid molar. The vertical arrow (extreme left) indicates the direction of crown development (addition of enamel) from tip to base.

The LEH has been widely used as an indicator of a period of generalized physiological stress during tooth development in hominid and non-hominid primates (Goodman and Rose, 1990; Guatelli-Steinberg, 2000, 2003, 2004; King *et al*., 2002; Larsen, 1997; Moggi-Cecchi and Crivella, 1991; Skinner and Goodman, 1992; Skinner and Hopwood, 2004), domestic pigs and wild boar (Dobney and Ervynck, 2000; Dobney *et al*., 2004) and other extinct or extant ungulate species (Franz-

Odendaal, 2004; Franz-Odendaal *et al*., 2004; Mead, 1999; Niven *et al*., 2004). These studies demonstrated that the analysis of LEH is a useful means for retrospective assessment of the timing and intensity of systematic stress events during the period in which an individual's dentition is formed, and can thereby contribute to the understanding of past ecological and health conditions.

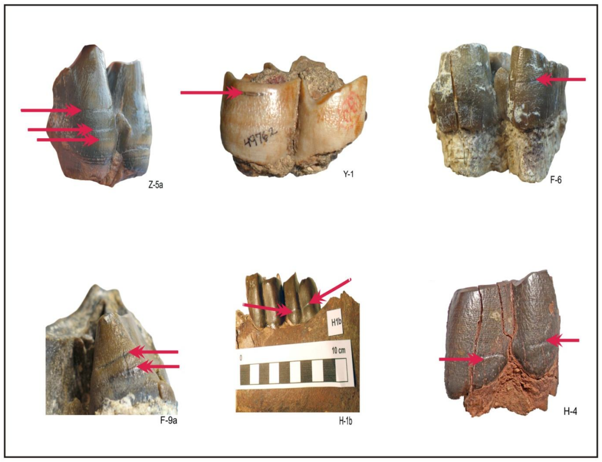

Fig. 5. **Z-5a** *Brachypotheriumperimense*, PUPC 07/152. Three LEH, 7, 10, 17 mm. **Y-1***B. fatehjangense*, YPM VP 049762. One LEH, 15 mm above the neck on the lingual side of m2.**F-6***Pleurocerosblanfordi*, Pak 1031.One, LEH 11 mm above the neck on the lingual side of P2. **F-9a** *Mesaceratherium welcommi*, Pak 1032b.Two LEH, 9, 16 mm on the protocone above the neck on the lingual side of M3. **H-1b** *Gaindatherium browni*, PMHU Y 24067b.Two LEH, 10 mm and 10 mm above the neck on the buccal side of m3; natural size.**H-4** *Rhinoceros* sp., PMHU Y 31182.Two LEH, 11, 9 mm above the neck on the buccal side of m2.

MATERIALS AND METHODS

A total of 846 fossils were carefully examined. These 846 fossil rhinocerotid teeth included 21 incisors, 2 canines, 43 deciduous premolars, 283 premolars, and 497 molars, calculated to be from at least 337 animals. Each tooth was examined visually (or by magnifying glass if needed) for the presence or absence of EH and description of each defect, its position on the tooth crown and the position of the defected tooth in each jaw were recorded. Dental terminology of Rhinocerotidae teeth for studying hypoplasia in this study follows that of Antoine *et al*. (2010). Enamel defects were further classified as LEH or SEH depression. Linear and semicircular defects on both lingual and buccal surfaces were also noted down. The height of LEH on the tooth crown from the root-crown junctions (neck) was measured. All measurements were taken in mm. EH analysis was based on Mead (1999).

RESULTS AND DISCUSSION

A fairly small number of fossil teeth were found with hypoplasia; 39 teeth from a total of 846 teeth (about 5%) had hypoplasia. The minimum number of individuals (MNI) of fossil rhino with EH was calculated to be 34 animals. These 34 animals belong to 14 species which are reported form a fairly wide region; from the Bugti Hills, to Potwar Plateau and eastwards to the Siwalik Hills. The hypoplasia occurrences in fossil rhino teeth are also found at almost all intervals of the Neogene period (Fig. 3). Occurrence of EH was observed on both lingual as well as buccal side of teeth. The results of this study indicate that hypoplasias on teeth can be single or multiple (Fig. 5). A maximum number of 07 LEH on a single tooth is observed in studied material.

The tooth distribution having hypoplasia in this study given in Table I shows that EH is most prevalent in dP4 (3 of 12, or 25%) as compared to other deciduous teeth, which is the last one to erupt among the deciduous teeth (Tong, 2001). It has also been noted that the EH in most of the teeth occurred at a late developmental stage as evidenced from position on the crown from the cementoenamel junction (*i.e.* neck) (Tables II-V). One possible inference, based on the developmental and eruption pattern of Recent Rhinos, is that EH occurred when the animal was not dependent upon mother's nutrition. Therefore, the animal was under some sort of physiological stresses perhaps triggered by external factors. However, one incidence of EH on DP3 (*B. perimense* (PMHU Y 53615), Table IV) may suggest that in some cases it could have been caused by nutritional stress to the mother.

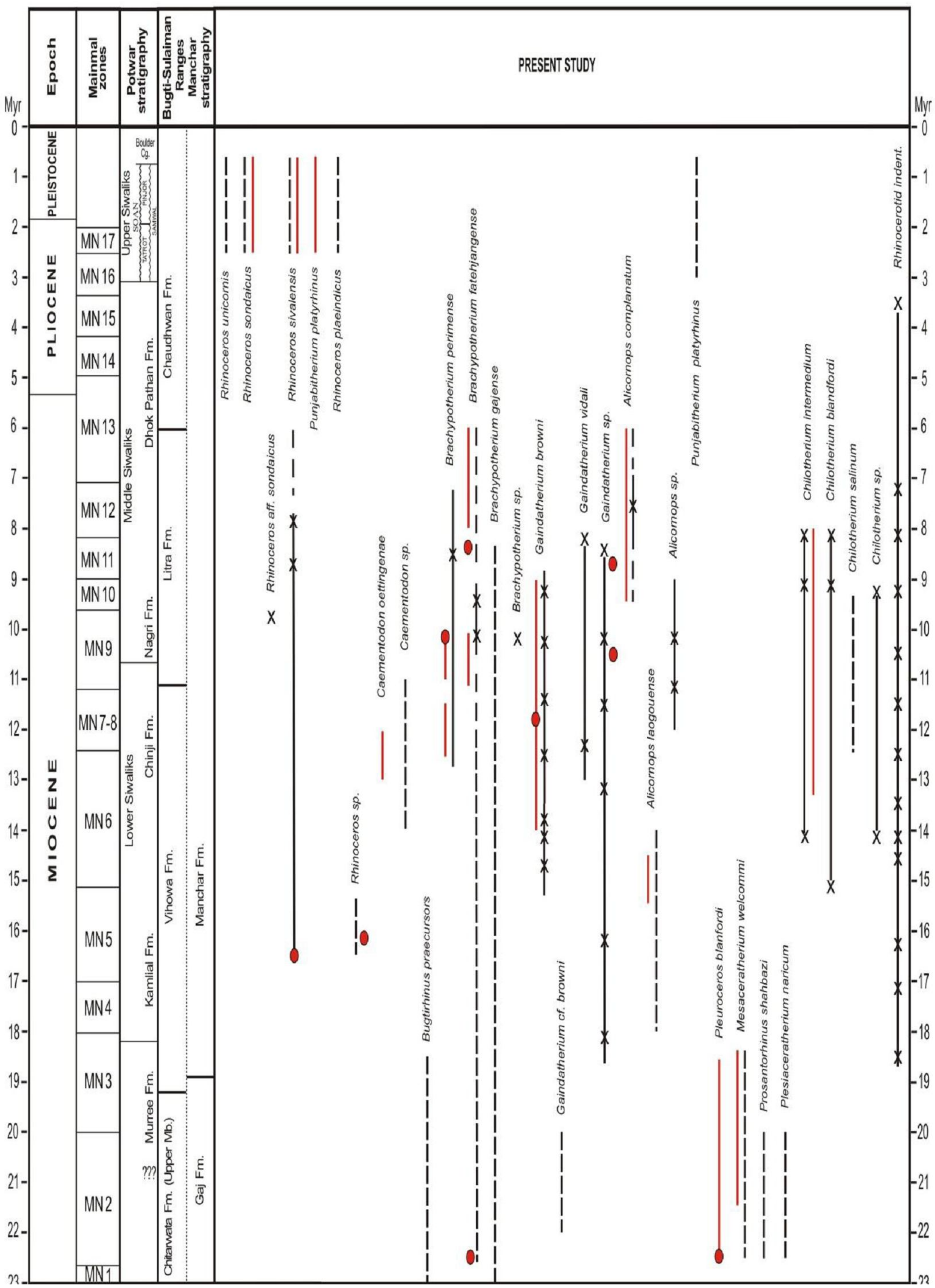

Fig. 3. Biostratigraphical ranges of Rhinocerotidae (this study) from the Neogene “Siwaliks” of Pakistan and the Siwalik Hills (India). Biostratigraphic ranges of rhinocerotids in this study are estimated from various sources (Colbert, 1935; Hussain *et al*., 1992; Barry *et al*., 2002; Nanda, 2008; Khan, 2009; Antoine *et al*., 2013). The red line in the individual taxon range shows the occurrence of EH, whereas, black lines indicate the ranges studied without EH. Cross and circles indicate exact ages of the specimens studied.

Table I.- **Occurrences of EH on different teeth in the studied fossilized Rhino specimens.**

Dentition	i	c	Dp1	DP2	DP3	DP4	P1	P2	P3	P4	M1	M2	M3
Total studied teeth	21	2	11	7	13	12	25	69	93	96	178	129	190
Teeth having EH	---	--	1	---	1	3	---	3	5	7	6	5	8

Table II.- **Occurrences of EH on different teeth in fossilized Rhino specimens of three species having an age of around 23-20 Myr.**

Species	Specimen	Enamel Hypoplasia		
		Tooth	Cusp	Location
Brachypotherium fatehjangense	MNHN, (15400)	dp4	Hypoconid	One LEH 7 mm above the neck
	MHNT, (Pak 1069)	m1	Hypoconid	One LEH 13 mm above the neck
	PUPC(07/170)	P4	Protocone	Two SEH 5 and 7 mm above the neck
	PUPC (07/173)	DP4	Protocone	Three SEH 5, 7 and 11 mm above the neck
	YPM VP (049762)	m2	Ectoconid	One LEH 15 mm above the neck
Mesaceratherium welcommi	MHNT (Pak 1032b)	M3	Protocone	Two LEH 9 and 16 mm above the neck
			Metaloph	Three LEH 14, 15 & 16 mm above the neck
Pleuroceros blanfordi	MHNT (Pak 1031)	P2	Protocone	One LEH 11 mm above the neck
	MHNT (Pak 46 D)	M1	Protocone	One LEH 5 mm above the neck

Data interpretation in regional context

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 used towards a better understanding of the local environment and regional climate changes during the Neogene in South Asia.

The rhinocerotid dental material examined and analyzed in this study ranges in age from ~25 Myr to about 2 Myr and covers a wider geographical region from the Bugti Hills in central Pakistan to the Pabbi Hills in north-eastern Pakistan. The early 19th century rhinocerotid collection from the Siwalik Hills in northern India, described by Falconer and Cautley and presently housed in the British Museum of Natural History, was also studied. This study, thus, includes 14 Rhino species having EH from the earliest radiation in the late Oligocene in the Bugti Hills to the still living *Rhinoceros sondaicus* in the Pleistocene rocks of the Pabbi Hills and the Siwalik Hills (Fig. 3).

The Rhino species with EH are apparently more prevalent at four time periods; around 23-20 Myr, ~16 Myr, 12-8 Myr and ~2 Myr. It is noteworthy that there were at least 9 species of Rhinocerotids in the 23-20 Myr interval, but only 3 of them, namely *Brachypotherium fatehjangense*, *Pleuroceros blanfordi* and *Mesaceratheruim welcommi* were found to have hypoplasia (Table II).

Table III.- Occurrences of EH on different teeth in fossilized Rhino specimens of two species having an age of ~16 Myr.

Species	Specimen	Enamel Hypoplasia		
		Tooth	Cusp	Location
Rhinoceros sp.	PMHU (Y 31182)	m2	Paraconid	One LEH 11 mm above the neck
Alicornops laogouense	PUPC (07/47)	M1	Hypoconid	One LEH 9 mm above the neck
			Protocone	One LEH 14 mm above the neck
			Hypocone	One LEH 12 mm above the neck

Table IV.- Occurrences of EH on different teeth in fossilized Rhino specimens of six species having an age of 12-08 Myr.

Species	Specimen	Enamel Hypoplasia		
		Tooth	Cusp	Location
Caementodon oettingenae	AMNH (19591a)	P4	Metacone	One LEH4 mm above the neck
Chilotherium intermedium	PUPC (07/95)	m2	Hypoconid	Two LEH 10 and 18 mm above the neck
			Protoconid	One LEH10 mm above the neck
	PUPC (07/94)	p3	Protoconid	One LEH9 mm above the neck
			Hypoconid	One LEH7 mm above the neck
Gaindatherium sp.	PMHU (Y 7079)	dp1	Entoconid	One LEH5 mm above the neck
			Metaconid	One LEH5 mm above the neck
	MNHN (15551)	m1	Paraconid	One SEH5 mm above the neck
	MNHN (10468)	P4	Metacone	One LEH5 mm above the neck
Gaindatherium browni	PUPC(07/147)	P4	Protocone	Two LEH5 and 9 mm above the neck
	PMNH (MUS-106)	p3	Protoconid	One LEH10 mm above the neck
			Hypoconid	One LEH11 mm above the neck
		p4	Protoconid	One LEH8 mm above the neck
			Hypoconid	One LEH7 mm above the neck
	PMHU (Y 24067 b)	m3	Protoconid	One LEH10 mm above the neck
			Hypoconid	One LEH10 mm above the neck
Alicornops complanatum	MHNT (Pak 1606)	p4	Paraconid	One LEH10 mm above the neck
			Hypoconid	One LEH5 mm above the neck
		m3	Paraconid	One LEH13 mm above the neck
Brachypotherium perimense	PUPC(07/74)	p2	Metaconid	One LEH15 mm above the neck
	PUPC(07/152)	DP4	Hypocone	Three LEH 7, 10 &17 mm above neck
			Protocone	Four LEH 9, 14, 17 & 22 mm above neck
	PUPC (07/126)	P2	Hypocone	One SHE 8 mm above the neck
	PUPC(68/826)	M3	Protocone	One LEH15 mm above the neck
	PUPC(07/54)	p3	Hypoconid	Two LEH 10 and 20 mm above neck
		m1	Hypoconid	Two LEH 10 and 15 mm above neck
	PUPC(68/529)	M3	Ecto-Metaloph	One SEH 18 mm above neck
	PMHU (Y 53615)	dp3	Paraconid	One LEH 10 mm above the neck

Table V.- Occurrences of EH on different teeth in fossilized Rhino specimens of three species having an age of ~02Myr.

Species	Specimen	Enamel Hypoplasia		
		Tooth	Cusp	Location
Punjabitherium platyrhinus	NHM (17996)	p3	Paraconid	One LEH 4 mm above the neck
			Hypoconid	One LEH 5 mm above the neck
	NHM (28911- cast)	p3	Protocone	One LEH 23 mm above the neck
			Hypocone	One LEH 23 mm above the neck
		M1	Protocone	One LEH 28 mm above the neck
Rhinoceros sondaicus	PUPC (2010/68)	m3	Metaconid	One LEH 8 mm above the neck
Pleuroceros blanfordi	PUPC (07/39)	m2	Entoconid	One LEH 15 mm above the neck
	PUPC (07/38)	M2	Protocone	One LEH 15 mm above the neck
		M3	Protocone	One LEH 12 mm above the neck
	NHM (39647)	P4	Protocone	One LEH 5 mm above the neck
	PMHU (Y 28225)	M3	Protocone	Two LEH 23 and 32 mm above neck

It can be postulated that the low incidence of hypoplasia may be related to stable subtropical to tropical climatic conditions during the Early Miocene time. The 17-15 Myr intervalwas the warmest period in the Neogene; establishment of a coolerregime developed over millions of years, and was in evidence at about 10 Myr (Flower and Kennett, 1995; Zachos*et al*., 2001). *Rhinoceros* sp. and *Alicornopsla ogouense* are the two species in which prevalence of EH is found at an age of ~16 Myr (Table III). The 16 to 12 Myr period records no hypoplasias in any of the well sampled lineages. This corresponds in large part to the Chinji Formation, which records rich faunas and apparently stable, equable conditions (Raza *et al*., 1984).

A maximum number of 6 species out of 15, namely *Caementodon oettingenae, Chilotherium intermedium*, *Gaindatherium* sp., *Gaindatherium browni*, *Alicornops complanatum* and *Brachypotherium perimense*, reported in the 12-8 Myr period have hypoplasia (Table IV). The Late Miocene was a period of intense climatic changes including the appearance and expansion of the C4 plants; visible signs of seasonality and the establishment of South Asian monsoonal system (Badgley *et al*., 2008). The Siwalik faunas from the Potwar Plateau also show major faunal turnover during this period (Barry *et al*., 2002). Rhinos being dominantly browsers must have suffered the most as the habitats shrank and became fragmented by increasing seasonality (Nelson, 2005). *Brachypotherium fatehjangense*, though a long ranging species since 23 Myr, showed more incidence of EH, and apparently could not cope with the changing environment, going extinct at around 8 Myr. Studies done on dental micro-wear and oxygen and carbon isotopes on tooth enamel on a few other Siwalik mammals (bovids, Hipparion, Sivapithecus, etc.) also point towards a time of ecological stress for these animals (Nelson, 2007; Morgan *et al*., 1994).

The Pliocene changing environment affected three species, *Rhinoceros sondaicus*, *R. sivalensis* and *Punjabitherium platyrhinus*, showing EH (Table V). It can be argued that climate, especially seasonality with prolonged drought periods, might have been the cause of stress for these animals.

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