
Insights from stable light isotopes on enamel defects and weaning in Pliocene herbivores

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A high prevalence of enamel hypoplasia in several herbivores from the early Pliocene Langebaanweg locality, South Africa, indicates general systemic stress during the growing years of life. The presence of several linear enamel hypoplasias per tooth crown in many teeth further suggest that these stress events may be episodic. The $\delta^{18}\text{O}$ values along tooth crowns of mandibular second molars of *Sivatherium hendeyi* (Artiodactyla, Giraffidae) were used to investigate the cause of the stress events in this tooth type. Results show that weaning in this fossil giraffid occurred at a similar ontogenetic age to that in extant giraffes, and that the observed enamel hypoplasia towards the base of this tooth type manifested post-weaning. Further, high-resolution oxygen isotope analyses across *S. hendeyi* third molars suggest that the entire development of defective tooth crowns occurred under conditions of increased aridity in which the cool, rainy part of the seasonal cycle was missing. The high prevalence of this defect in many herbivores suggests that climatic conditions were not favourable. This study reiterates the value of stable isotope analyses in determining both the behaviour of fossil animals and the environmental conditions that prevailed during tooth development.

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1. Introduction

Towards the end of the Miocene major changes in global climates and environments had profound effects on biological systems (Kurten 1972; MacFadden *et al* 1996; Janis *et al* 2000). By the early Pliocene, climates had become cooler, drier and more seasonal, with grasslands expanding to replace the tropical and subtropical forests characteristic of the Miocene (MacFadden *et al* 1996; Cerling *et al* 1997). At the same time, grazers with hypsodont dentition became more common in faunal assemblages (Janis 1993), including in the rich fossil assemblage at the early Pliocene site of Langebaanweg, South Africa (18°9'E, 32°58'S). The Langebaanweg assemblage includes a diverse collection of artiodactyls, of which the extinct giraffid, *Sivatherium hendeyi*, is most abundant. This

assemblage is unusual and unique. It is the only southern African site in the latest Miocene/early Pliocene epochs with a large assemblage of vertebrates, in which the introduction of several new forms of larger vertebrates is observed (Hendey 1984). That is, Langebaanweg is uniquely positioned at a time when Africa's rainforests were being replaced by grasslands, as a result of global climate changes. Second, a developmental tooth defect known as enamel hypoplasia was observed to be prevalent in *S. hendeyi* specimens during early excavations (Hendey 1981). It was suggested that these defects were the result of dietary stress related to the reduction of forest habitat and expansion of C₄ grasslands, to which, it was assumed, sivatheres were poorly adapted (Hendey 1981). According to the C₄ global expansion model (Cerling *et al* 1997), C₄ grasses could have reached mid-latitudes in southern

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Africa by the early Pliocene. C₄ grasses had reached similar latitude sites in South America by this time (MacFadden *et al* 1996), but carbon isotope evidence indicates that Langebaanweg remained a C₃ dominated habitat (Franz-Odenaal *et al* 2002). Hence, the high prevalence of enamel hypoplasia observed in *S. hendeyi* cannot be attributed to the C₃–C₄ grassland shift. This study shows that enamel hypoplasia is present, not only in *S. hendeyi*, but also in many other herbivores which were recovered from the Langebaanweg locality, suggesting systemic stress was experienced during the growing years of life in a large cohort of animals. Based on $\delta^{18}\text{O}$ values along tooth crowns of second molars of *S. hendeyi*, we show that weaning occurred at a similar ontogenetic age to that in extant giraffes, and that enamel hypoplasia in this tooth manifested itself post-weaning. In addition, high-resolution isotope analyses across third molars suggest a link between dental defects and a drier climate in which the cool, rainy part of the seasonal cycle was missing.

Since enamel is not remodelled during life, it provides a permanent non-specific record of events (mainly physiological) that occurred during tooth development. Linear enamel hypoplasia is caused by a disruption in ameloblasts that lay down the enamel matrix (Goodman and Rose 1990), resulting in defects. These defects manifest as a linear arrangement of pits or horizontal grooves across the tooth surface (figure 1). Systemic stress episodes that occur at a particular ontogenetic age affect all teeth developing at the time of the stress. Linear enamel hypoplasia has been linked to nutritional stress (Neiburger 1990; Goodman and Rose 1991; Dobney and Ervynck 2000), birth stress (Goodman and Rose 1991; Mead 1999), weaning stress (Goodman and Rose 1991; Dobney and Ervynck 2000), and stress associated with calf-cow separation (Mead 1999). Stress must reach a threshold level before ameloblasts are disrupted and a linear defect is manifested (Goodman and Rose 1990).

Thus, the presence of these defects in a population can provide a unique perspective into prevailing environmental conditions by indicating the health status during the early (growing) years of life. Few occurrences of linear enamel hypoplasia have been reported in non-primate fossil animals (Mead 1999; Dobney and Ervynck 2000; Niven 2002), yet analyses of this defect remain both a powerful and popular tool in anthropology (Goodman and Rose 1990).

2. Materials and methods

To investigate whether defects correlated with particular diets (i.e. nutritional stress), we first determined the extent of enamel hypoplasia in the Langebaanweg faunal assemblage. We examined almost 3000, mostly isolated, teeth from herbivores forming part of the large and diverse collection of vertebrate fossils from the fluvialite deposit

(Pelletal Phosphate Member) at Langebaanweg. The position and size of each defect was recorded and measured with digital callipers. Tooth hypoplastic area (THA) scores (after Enson and Irish 1995), indicating the percentage of total crown height that is defective, were calculated for each animal.

Using stable oxygen isotope ratios from enamel apatite carbonate, across defective tooth crowns, the timing and seasonality of the occurrence of these defects was established. All stable isotope values are reported relative to the PeeDee Belemnite standard in parts per mil (‰). Only unworn or very slightly worn teeth were selected for serial isotope analyses, and on an average, twelve samples were obtained per tooth crown. Serial samples were drilled in thin horizontal grooves ~ 1 mm apart across the entire tooth crown, from top to base. This approach enabled us to make some inferences about the cause of the observed stress episodes. It also provided us with fresh insight into the environmental conditions that prevailing at the time.

However, this approach has a drawback. Defects occur during the initial laying down phase of enamel, whereas apatite development and, hence, incorporation of carbonate proceeds from this point onwards until the end of mineralization. In domestic sheep, for example, three waves of mineralization occur (Suga 1982). Hence a defect at a certain position on the tooth crown represents a stress episode that occurred during the initial secretion of enamel protein, but the $^{18}\text{O}/^{16}\text{O}$ composition reflected at that point on the crown represents an accumulation of the isotope signal throughout the process of amelogenesis.

3. Results

An investigation of ~ 2000 mandibular teeth belonging to *S. hendeyi* showed that deciduous teeth were unaffected by linear enamel hypoplasia, whereas all permanent teeth had defects (Franz-Odenaal *et al* 2004). This finding indicates that throughout development of the adult dentition [which in extant giraffes commences pre-birth and ends at around 5–6 years (Hall-Martin 1976)], unfavourable and stressful conditions were experienced. Furthermore, 35% of *S. hendeyi* teeth have more than one defect on an individual tooth crown suggesting that stress episodes were also episodic. The distribution, incidence and size of linear defects in each tooth type are variable (Franz-Odenaal *et al* 2004) and suggest that the duration of the stress episodes varied at different times during ontogeny.

By extending this analysis to other herbivores, our results show that linear enamel hypoplasia is not confined to *S. hendeyi* but is present in almost all the herbivores from the Pelletal Phosphate Member at Langebaanweg (figure 2). Several distinct linear defects were observed in the continually erupting hippopotamus tusks, indicating that stress episodes were not confined to the developing years of an animal's life but that they also extended into adulthood.

The highest incidence of linear enamel hypoplasia (> 20%) was observed in the hippopotamus (Gen. and sp. undet.), sivathere (*S. hendeyi*), and reduncines (*Kobus*

sp.). The duration of the stress episodes (i.e. the width of each defect) is reflected by the THA score for each animal. Average scores indicate that the hippopotamus

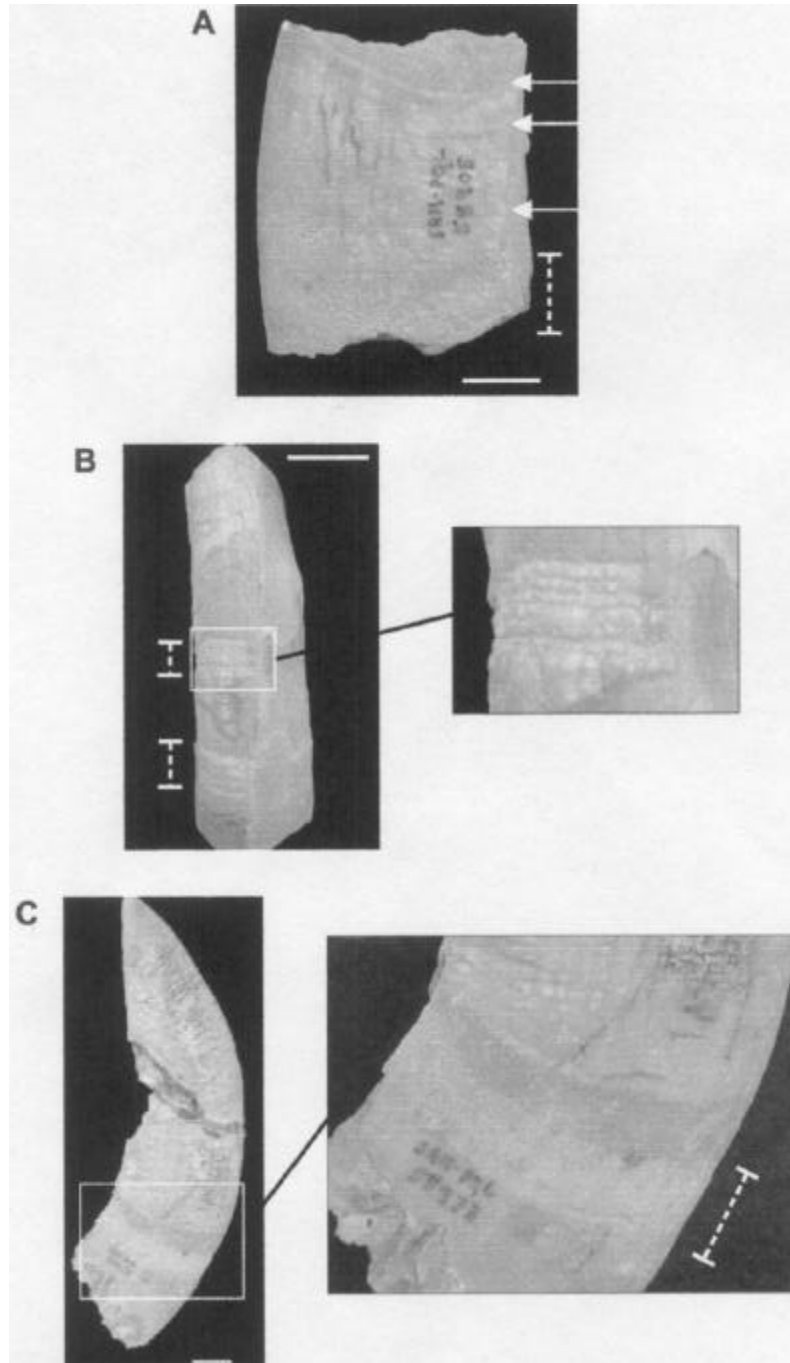


Figure 1. Hippopotamus teeth with linear enamel hypoplasia. (A) Tusk fragment (SAM PQL 58905), with several linear defects, the dashed vertical line indicates a wide band of pits whereas the other three defects (arrows) are fairly narrow. (B) Incisor fragment (SAM PQL 51371), dashed vertical lines indicate areas with linear grooves. (C) Tusk (SAM PQL 58973), dashed line indicates the width of a linear defect. Scale bars represent 1 cm. Sample accession numbers are from the South African Museum, Cape Town.

and reduncine were most severely affected (with scores greater than 35%).

4. Discussion

4.1 Enamel hypoplasia and nutrition

Nutritional stress is the most commonly reported cause for linear enamel hypoplasia (Goodman and Rose 1990). From $^{13}\text{C}/^{12}\text{C}$ analysis, we were unable to determine whether the incidence of defects correlated with dietary preference because of the C_3 -dominant environmental signature at Langebaanweg (Franz-Ondendaal *et al* 2002). Instead, we compared the fauna with their modern relatives or to similar species at other localities in Africa of a similar age. Conservative diets within fossil and extant Hippopotamidae (Bocherens *et al* 1996; Zazzo *et al* 2000) and Alcelaphinae (*Damalacra* sp.) (Zazzo *et al* 2000) suggest that these animals were almost exclusive grazers in

North and East Africa from ~ 5 Mya. Although the diets of fossil Giraffidae were probably highly heterogeneous (Solounias *et al* 2000), $^{13}\text{C}/^{12}\text{C}$ analysis of *Giraffa jumae* at the Pliocene site of Makapansgat (South Africa) has confirmed that this species was a browser (Sponheimer *et al* 2003). *Giraffa* cf. *jumae* is present at Langebaanweg. Both the Palaeotraginae and Sivatheriinae had grazing, mixed feeding and browsing members during the Miocene epoch (Solounias *et al* 2000) and their diets at Langebaanweg remain uncertain. The boselaphine (*Mesembriportax acrae*) was assumed to be a browser (Hendey 1983b). Data from other localities in Africa indicate that the reduncine (*Kobus* sp.), rhinoceros (*Ceratotherium praecox*) and bovine (*Simatherium demissum*) from this locality were either mixed feeders or grazers (Sponheimer *et al* 1999, 2001; Zazzo *et al* 2000). Our results indicate that animals that eat grass, such as hippopotamuses and alcelaphines (*Damalacra* sp.), are not equally affected with enamel hypoplasia defects, indicating that there is not a simple correlation between prevalence of linear

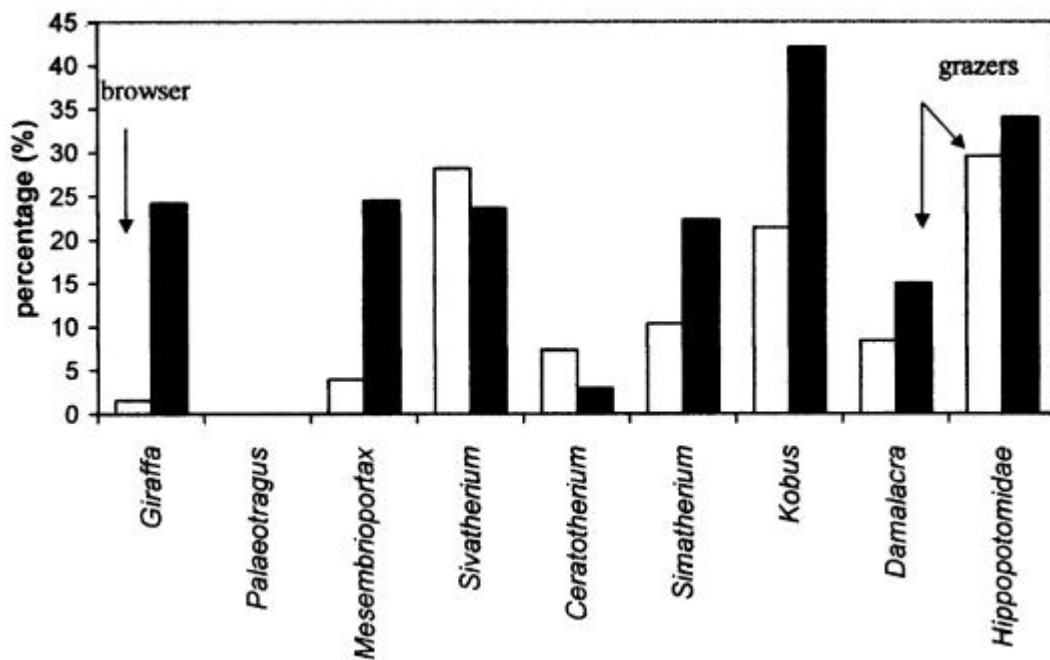


Figure 2. Linear enamel hypoplasia (LEH) in herbivores from the Pelletal Phosphate Member, Langebaanweg, South Africa. Open bars represent the percentage of teeth affected with LEH (i.e. incidence); closed bars represent the percentage of tooth crowns affected expressed as an average for the animal (i.e. average THA scores for each animal). Presumed browsers are on the left, expected grazers on the right, and animals with uncertain dietary habits in the middle. The sum of the widths of each defect on a tooth crown was divided by the crown height of each defective tooth, to give a THA score. Average scores for each animal were then calculated. Fragmented teeth were excluded from the analysis except for the hippo where large tusk fragments were included. Numbers in parenthesis indicate the number of permanent teeth analysed. Giraffids include *Giraffa* cf. *jumae* (259), *Palaeotragus* cf. *germaini* (24) and the sivathere *S. hendeyi* (1544). Other animals include the boselaphine *Mesembriportax acrae* (152), reduncine *Kobus* sp. (42), the rhinoceros *Ceratotherium praecox* (41), the alcelaphine *Damalacra* sp. (191), the bovine *Simatherium demissum* (116) and the Hippopotamidae (Gen and sp. undet.) (196).

enamel hypoplasia and diet. Another cause for the systemic stress underlying the occurrence of these defects must exist. Differences in the prevalence of linear defects between taxa with similar diets may relate to differences in behaviour and/or tolerance levels for stressful conditions.

4.2 Enamel hypoplasia and weaning

Amongst the ~2000 *Sivatherium* teeth examined, only the upper third of the m1 is devoid of defects (Franz-Odendaal *et al* 2004) and since this tooth begins development before parturition, this portion of the tooth crown perhaps corresponds to a stress-free *in utero* period. In extant giraffes, it is well documented that weaning is reflected primarily in the later development of the m1 and in the earliest development of the m2, but the onset and duration of weaning varies greatly depending on the quality of available vegetation (Hall-Martin 1976). It is, however, not certain whether modern giraffes provide reasonable analogues for the timing of tooth development and weaning in extinct sivatheres. In an effort to ascertain when, in tooth ontogeny, weaning occurred in *S. hendeyi*, and whether the subsequent stress episodes were linked to seasonal changes, we turned to high-resolution intra-tooth $^{18}\text{O}/^{16}\text{O}$ sequences.

Both enamel phosphate (PO_4) and carbonate (CO_3) $d^{18}\text{O}$ closely reflect body water $d^{18}\text{O}$, although absolute $a_{\text{bw-PO}_4}$ and $a_{\text{bw-CO}_3}$ differ. Serial analyses from top to base of the tooth crown reflect seasonal changes during tooth development in modern and fossil animals (Koch *et al* 1989; Bryant *et al* 1994; Fricke and O'Neil 1996; Stuart-Williams and Schwarcz 1997; Feranec and MacFadden 2000; Balasse *et al* 2002). The weaning transition is detectable because milk is significantly enriched in ^{18}O compared to drinking water, resulting in higher $d^{18}\text{O}_{\text{CO}_3}$ in suckling calves compared to weaned calves and adults (Fricke and O'Neil 1996).

In the extant giraffe, relatively higher $d^{18}\text{O}$ values, reflecting suckling, were observed in the uppermost portion of an unworn m2 (figure 3A, arrow) as expected from their weaning behaviour (Hall-Martin 1976). Four out of five of the sivathere m2s have similar higher $d^{18}\text{O}$ values (figure 3B) indicating that, in most individuals, weaning was completed during development of the top of the tooth crown. Hence weaning in *S. hendeyi* occurred at a similar ontogenetic period to extant giraffes. Defects towards the base of the m1 (Franz-Odendaal *et al* 2004) might be associated with weaning as in humans (Goodman and Rose 1990) and pigs from archaeological sites (Dobney and Ervynck 2000), but linear defects present in the rest of the permanent dentition cannot be attributed to this particular systemic stress.

4.3 Enamel hypoplasia and climate

The clearest isotopic indicators of seasonal cycles are archived in the third molars (Fricke and O'Neil 1996), which develop well after weaning in giraffes (Hall-Martin 1976). To investigate whether defects were correlated with seasonality regime, we obtained a high-resolution $d^{18}\text{O}$ series from three normal and three defective *S. hendeyi* m3s (figures 4 and 5). Serial $d^{18}\text{O}_{\text{enamel}}$ measurements on modern and archaeological sheep and cattle from this area of South Africa showed seasonal cyclicity in which the cool, wet winter is recorded as low $d^{18}\text{O}$ values while the dry summer season values are higher (Balasse *et al* 2002). A similar cyclical pattern is observed in the sivathere normal teeth with seasonal amplitudes of more than 2‰ (figure 4). In m3s with linear enamel hypoplasia seasonal amplitude is reduced, mostly because the lower $d^{18}\text{O}$ (winter/rainy season) part of the cycle is missing (figure 5). The lowest seasonal amplitude of 0.9‰ occurs in tooth SAM PQL 62733/62 which has the broadest defect affecting over 36% of the tooth crown (figure 5A). In tooth SAM PQL 62733/61, seasonal amplitude is low (0.9‰) in the area with three narrow defects, while it is 1.7‰ in the broad basal portion of this tooth (figure 5B), which is similar to normal teeth. The pattern is less similar for tooth SAM PQL 62733/13, where a negative $d^{18}\text{O}$ shift corresponds with a linear enamel hypoplasia at the base of the tooth (figure 5C); nevertheless the seasonal pattern differs from that of the normal teeth. The results suggest that defective enamel co-occurs with a significant reduction in the overall seasonality, in which the wet season (winter) is completely or partly missing. Although several defects on a tooth crown suggest episodic stress event(s) interspersed with favourable conditions, these results suggest that development of the entire crown occurred under conditions of increased aridity or drought. The possibility that altered chemistry in defective areas could produce these differences in $d^{18}\text{O}$ is remote, since the defects manifest in the organic template and infrared microscopy shows the standard enamel apatite structure (figure 6).

It has been suggested that a strongly seasonal rainfall regime existed at Langebaanweg 5 Mya (Hendey 1983a), based on pollens (Scott 1995) and taphonomic context that suggests flood episodes (Hendey 1981). The $d^{18}\text{O}$ series for the six *S. hendeyi* m3s suggest two kinds of climate scenarios – one in which there were regular wet seasons, expected seasonal amplitudes, and no enamel hypoplasia, and the other where the wet season is missing, seasonal amplitude is low, and defects become prevalent. The latter suggests drier conditions. The inference that the stress agent was aridity is also supported by the distribution of stressed animals. The hippopotamus and reduncines, both of which are extremely water-dependant today, have

the highest incidence and average THA scores (figure 2). Probable browsers (*Giraffa* sp. and boselaphine) also have fairly high THA scores, indicating that not only was available drinking water limited but that the water content of browse was also reduced. Known grazers (e.g. *Damalacra* sp.) that would have been less dependent on water and possibly migratory have the lowest scores.

The large-scale climate changes at the end of the Miocene/early Pliocene placed many herbivores previously adapted to warmer, wetter and more stable environmental conditions, under stress (as noted by, for example, Janis 1993). Some of these lineages would have been able to adapt relatively quickly to the changing climatic conditions. Our results suggest that climatic conditions on both a large

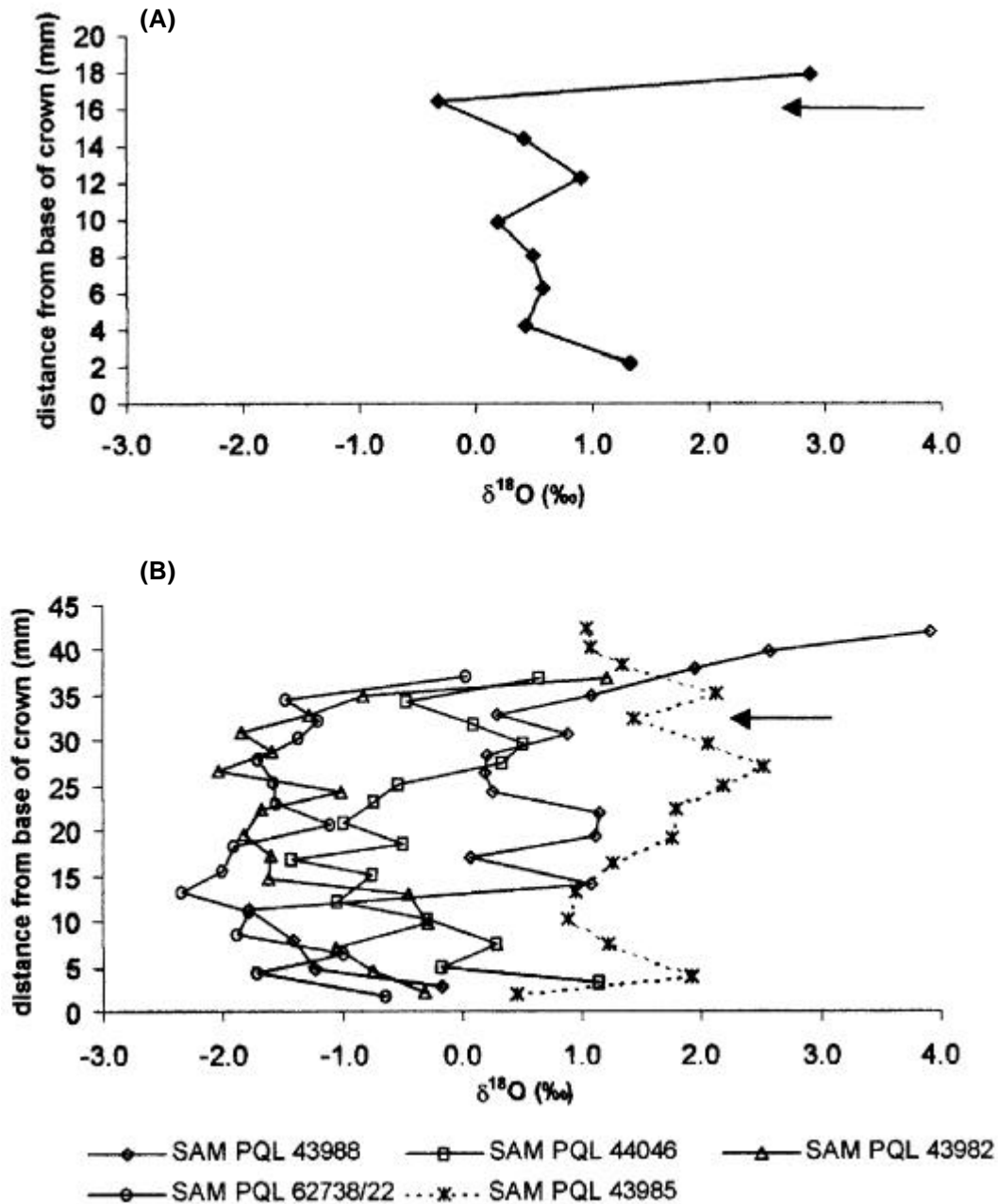


Figure 3. Stable oxygen isotopes along lower second molars. (A) Extant giraffe, *Giraffa camelopardalis*, and (B) the extinct giraffid, *S. henderyi*, showing similar enriched $\delta^{18}\text{O}$ values near the top of the tooth crown (arrows). Y-axis indicates direction of tooth development from top of the crown towards the base (0 mm).

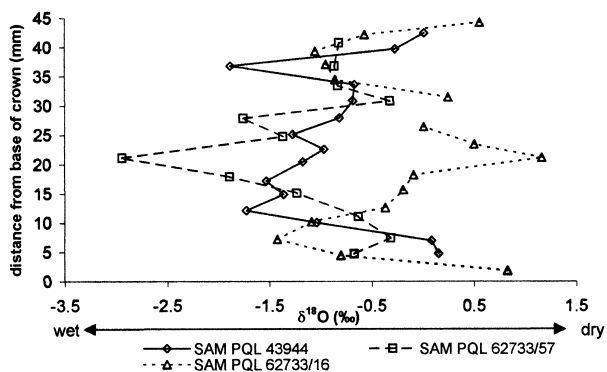


Figure 4. Stable oxygen isotopes along normal lower third molars of *S. hendeyi*. Y-axis indicates direction of tooth development from top of the crown towards the base (0 mm) and the X-axis indicates wetter/cooler (left) to drier/warmer (right) environments. One data point (in tooth SAM PQL 62733/16) could not be determined conclusively.

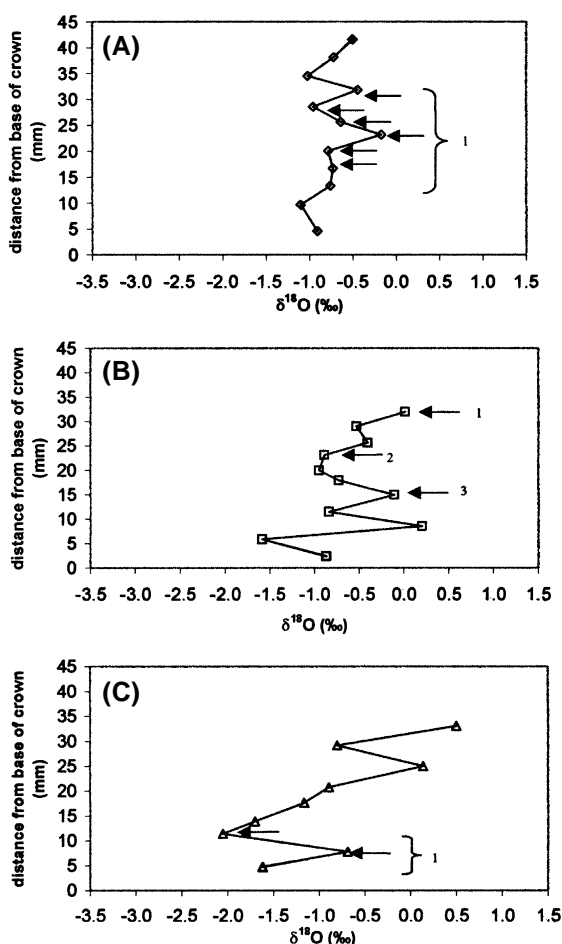


Figure 5. Stable oxygen isotopes along lower third molars of *S. hendeyi* with linear enamel hypoplasia. (A) SAM PQL 62733/62, (B) SAM PQL 62733/61, and (C) SAM PQL 62733/13. The position of the defects on each tooth is indicated with arrows. (A) Has one broad defect, (B) has three narrow defects and (C) has one medium-sized defect towards the base of this tooth. For a detailed explanation of the axes refer to figure 4.

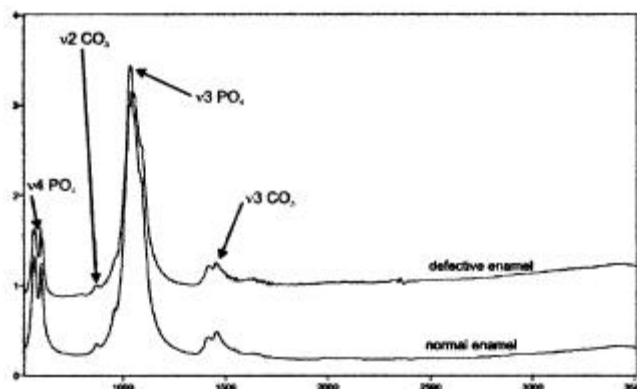


Figure 6. Fourier transform infrared spectroscopy of normal and defective *S. hendeyi* enamel, SAM PQL 43928 and SAM PQL 44053 respectively. The position and amplitude of peaks is characteristic of different kinds of apatites (LeGeros 1981, 1991; Sponheimer and Lee-Thorp 1999). The characteristic enamel apatite pattern (Sponheimer and Lee-Thorp 1999) is found in both defective and normal *S. hendeyi* enamel from Langebaanweg, South Africa.

and small time-scale (i.e. during the life of an individual) were highly variable. The high incidence of enamel hypoplasia linked to frequent drought episodes suggests that these highly variable climatic conditions were new to animals living in the late Miocene/early Pliocene, and that many of the animals (particularly those dependent on drinking water) suffered as a result. The unique (geographical and chronological) position of Langebaanweg, right at the time when global climates were changing, enables us to gain insight into the prevailing environmental conditions and their effects on terrestrial fauna. The only other site in southern Africa containing large vertebrate fauna in roughly this time period is located in the site of Sterkfontein, almost 50 km to the northwest of Johannesburg, in the interior of South Africa. The age of Member 2 and the Jacovic Cavern has been estimated to be about 4.2 Mya from cosmogenic nuclide and palaeomagnetic dating (Partridge *et al* 2003). Although several hominids, not yet identified to species, have been discovered in Member 2 and the Jacovic Cavern, only the latter reportedly contains a range of large vertebrates (Partridge *et al* 2003).

5. Conclusions

Our results indicate a correlation between the presence of linear enamel hypoplasia in a large early Pliocene faunal assemblage and reduced seasonality (aridity) in Southern Africa. These adverse climatic conditions persisted from development and throughout adulthood, and placed several herbivores under severe systemic stress that ultimately resulted in the manifestation of linear enamel hypoplasia.

In addition, we show that high-resolution isotope analyses can provide otherwise unobtainable insights into the weaning behaviour of extinct animals and can be used as a tool to understand the environmental contexts under which developmental dental disease manifests.

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