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# Paleoseasonality inferred from equid teeth and intra-tooth isotopic variability

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## Abstract

This research presents a study of intra-tooth isotopic variability measured in hypsodont equid teeth as a means of determining paleoseasonality. The purpose of this investigation is to determine whether *Sivapithecus*, a Miocene hominoid from the Siwaliks of Pakistan, lived in habitats characterized by a seasonal rainfall regime, and if so, what kind of forest is associated with this regime. Forest type, such as evergreen, semi-evergreen, moist deciduous, and dry deciduous, is largely determined by length of the dry period. Reconstruction of the rainfall regime therefore allows inferences of forest type in the fossil record. Seasonal rainfall regimes can be determined from oxygen stable isotopes, for oxygen isotopes track amount of rainfall in tropical regions. Sampling oxygen isotopes along the length of an equid tooth, which takes over a year to develop, therefore provides a record of seasonal isotopic changes in body water, which in turn reflect drinking water and ultimately precipitation. Carbonate oxygen results from Siwalik equid teeth spanning 10.0–6.3 Ma indicate a rainfall regime similar to that experienced by southern China monsoon forests today, with a monsoonal rainy season and a five-to-six month dry season. Furthermore, results suggest a seasonal birthing pattern for Siwalik equids and therefore predictable seasonal regime. These results indicate that *Sivapithecus* lived under a seasonal regime with dry periods longer than the maximum of 4 months that most great apes experience today. Therefore *Sivapithecus* may have experienced longer periods of low fruit availability than do modern apes. Either *Sivapithecus* differed in habitat requirements, or the forest differed in terms of the spatio-temporal variability of fruit compared to modern analogues. Over geologic time, annual rainfall appears to have decreased in the Siwaliks, beginning around the time *Sivapithecus* became extinct, but annual seasonality of rainfall does not change.

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## 1. Introduction

### 1.1. Modern ape habitat requirements

The Miocene was a period of dramatic evolutionary change within the hominoid clade, with the

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first undisputed appearance of ape species during the early Miocene, followed by a radiation of the clade throughout Africa, Europe, and Asia. By the end of the Miocene, however, most apes species had become extinct. Only the Siwalik sediments of Pakistan, spanning the past 20 million years, provide a nearly continuous record of faunal and environmental change documenting an ape clade throughout its radiation and extinction. Within this long terrestrial sequence, the hominoid genus *Sivapithecus* appears around 13 Ma and disappears around 8.4 Ma (Barry et al., 2002). The purpose of this investigation is to determine whether *Sivapithecus* had habitat requirements similar to those of modern apes, as well as to determine what roles changing habitat and climate, specifically increasing seasonality, may have played in its extinction. Seasonality of Miocene precipitation regimes, and types of forests associated with those regimes, will be interpreted from isotopic analyses of carbonate oxygen in fossil equid teeth.

In order to interpret the effects of changing environment on fossil hominoids, it is first necessary to understand the habitat and climatic requirements of modern apes. Extant apes are found only in Africa and S.E. Asia, and with few exceptions, their geographic ranges lie within a few degrees of the equator. Within the equatorial region, precipitation regimes are such that dry periods generally last no longer than 4 months. Length of the dry period can have important consequences for hominoids because all, except the mountain gorilla, have diets specializing in ripe fruits, and fruit temporal availability, density, and diversity often correlate negatively with length of dry seasons.

Within tropical Africa, availability of fruit varies seasonally, with fruit peaks coinciding with annual rainfall peaks in most regions (Badrian and Malenky, 1984; Tutin et al., 1991). Equatorial West and Central Africa experience two short relatively wet seasons and two short relatively dry ones annually, but even during the drier months, most regions remain humid (Walter et al., 1975). The vegetation of this region consists of evergreen forest and is inhabited by lowland gorillas, chimpanzees, and bonobos. Apes in these regions are never without ripe fruit, even in the driest season.

Among the African apes, only chimpanzees range outside tropical forests. In East Africa, the bimodal rainfall pattern is characterized by unequal peaks, namely a long rainy season and a short rainy season

(Kortlandt, 1983). Climate is no longer continuously humid, and a longer dry season results in less evergreen and more semi-evergreen and deciduous forests in East Africa (Walter et al., 1975; Walter and Breckle, 1984). Again, though, chimpanzees in these more seasonal East African forests are never without ripe fruit (Goodall, 1986; Wrangham et al., 1993).

A few chimpanzee populations live in regions which experience extensive dry periods of 5 months or more, but in these regions, such as Mt. Asserik in Senegal, population density is extremely low, and home ranges are large (McGrew et al., 1981). While these chimpanzees travel freely during the wet season to reach dispersed fruit, during the dry season, their ranges are confined primarily to gallery forest, or habitat similar to typical hominoid habitats (McGrew et al., 1981; Baldwin et al., 1982).

Southeast Asian dipterocarp rainforests differ dramatically from African ape habitats in phenology, with rainforests characterized by mast fruiting events in which a large number of trees fruit in synchrony about every 2–10 years (Knott, 1998). Time of fruiting is therefore very irregular rather than following an annual seasonal regime. Rainfall regimes are highly seasonal for these forests, however, due to the monsoonal system. Monsoonal rainfall patterns influence vegetation patterns in that forest type, such as evergreen versus deciduous forest, is largely determined by length of the dry season as well as total annual rainfall (Walter, 1973). The boundary between rainforest and monsoon forest formations is determined by evapotranspiration and availability of soil water and is therefore most closely related to length and severity of the dry season rather than total annual rainfall (Richards, 1996). Most evergreen rainforests are limited to regions which experience only a very short dry season of 2 months, if any dry season occurs at all. As length of dry season increases and annual rainfall amount decreases, a transition to moist deciduous and then to dry deciduous forest occurs (Walter and Breckle, 1984).

Among this spectrum of forest types, siamangs and orangutans are limited to rainforests, with only gibbons ranging into more seasonal forests, although their geographic range lies predominantly in rainforest as well. Both geographic range and day range among the S.E. Asian hominoids correlate negatively with body size, with gibbons having twice the day range of

siamangs (twice the body size of gibbons), and orangutans having the smallest day range. Gibbons travel greater daily distances in order to exploit small, scattered fruit patches, while siamangs travel half as far and feed at half as many sites, depending instead upon clumps of highly productive trees (MacKinnon and MacKinnon, 1978; Chivers, 1984). Orangutans have the greatest dependence on high average ripe fruit abundance, but they are able to store large amounts of energy as fat and therefore take advantage of periods of fruit superabundance, something not yet observed in gibbons (MacKinnon, 1977; Knott, 1998). Perhaps as a result of differences in fruit density needs, gibbons have the widest geographic distribution among the S.E. Asian hominoids and are found as far west as Assam and Bangladesh (Gittens and Tilson, 1984).

While gibbons do have the widest range, even they appear to be restricted to the more diverse and less seasonal forests (Kappeler, 1984).

Frugivorous apes thus show a number of different adaptations for dealing with the spatio-temporal variability of fruit. Some apes increase daily travel distance in order to find more fruit patches. This adaptation requires efficient locomotor adaptations such as brachiation in the lesser apes (Cannon and Leighton, 1994, 1996) and terrestrial adaptations such as knuckle-walking in African great apes. The orangutan, with neither of these locomotor adaptations, is able to take advantage of masts by fat storage. All apes rely on fallback foods during fruit shortages, with larger body size being an advantage, but the question remains—how long a period can a frugivorous ape rely on fallback foods? The evidence from modern ape habitats would suggest about 3 or 4 months for almost all populations.

### 1.2. *Sivapithecus*

Modern apes are thus restricted to regions where there is at least some gallery/rainforest and where rainfall usually exceeds 1500 mm, with dry periods lasting no more than 4 months. The morphology of *Sivapithecus* suggests many similarities to large-bodied frugivorous apes today but with some significant differences that may have resulted in different habitat requirements. *Sivapithecus sivalensis* males were about the size of male chimpanzees (40–50 kg),

while females were roughly the size of male baboons (20 kg). *Sivapithecus parvada* is the larger species, with males approximating male orangutans or female gorillas (Kelley, 1986). The molars of *Sivapithecus* are low and rounded with hyperthick enamel, resembling extant primates that feed on hard objects, such as fruits with tough rinds or nuts (Kay, 1981). Dental microwear analyses of molar occlusal surfaces suggest a diet similar to those of modern frugivorous apes, with some hard-object feeding (Nelson, 2003). *Sivapithecus*' cranio-facial morphology is heavily buttressed, suggesting an adaptation to either withstand prolonged cyclical loading or to generate high occlusal loads (Kelley and Pilbeam, 1986). Given that *Sivapithecus* molars most resemble those of frugivores, it is likely that these adaptations for heavy mastication may have related to fallback foods and that *Sivapithecus* diet consisted primarily of ripe fruit (Kelley and Pilbeam, 1986).

The postcranial skeleton of *Sivapithecus* suggests that it was a pronograde quadruped (similar to monkeys, walking above branches) like most other Miocene hominoids, but that it included some climbing in its locomotor repertoire as well (Rose, 1986). Features of the distal humerus, wrist bones, femur, foot, and ankle indicate a degree of mobility compatible with *Sivapithecus* being predominantly arboreal and above-branch, with some climbing behavior and little ape-like suspensory activity. While no features preclude terrestrial locomotion, *Sivapithecus* shows no specializations for extensive terrestriality (Kelley and Pilbeam, 1986).

Finally, an analysis of tooth development based up tooth enamel perikymata of a *Sivapithecus parvada* juvenile, the largest *Sivapithecus* species, indicates that this species had a life history pattern similar to that of modern great apes, with a prolonged growth and maturation period relative to monkeys (Kelley, 1997). This life history pattern, combined with the morphology of *Sivapithecus*, suggests that *Sivapithecus* was a large-bodied frugivore which would have been susceptible to periods of ripe fruit shortage. How, then, could *Sivapithecus* have dealt with the spatio-temporal variability of food resources? Given its body size, inability to brachiate, and lack of terrestrial specializations, it is unlikely that it could have traveled as extensively as gibbons or chimpanzees in search of fruit. With the life history pattern of a

great ape, a decrease in energy expenditure alone was probably not an option, at least for lactating females. Fat reserves are an adaptation to environments which experience extremes, such as temperate regions or the masting forests of S.E. Asia. Such seasonal extremes may have existed in *Sivapithecus*' habitat, but there is no current evidence for masting. Perhaps *Sivapithecus* had a greater toleration of toxins than modern apes, or, given the novel dietary adaptations suggested by the cranial and dental morphology, *Sivapithecus* may have relied upon different fallback foods, such as hard seeds and nuts, or may have relied upon them to a greater extent. Greater detail of *Sivapithecus*' habitat in terms of forest type and seasonality is needed to better understand its requirements, adaptations, and extinction.

### 1.3. Climate and habitat changes in the Siwaliks of Pakistan

The extinction of *Sivapithecus* can be placed in a context of faunal and environmental change, for the Siwalik sediments span the past 20 million years, thus documenting the clade throughout its radiation and extinction. The Siwaliks are fluvial deposits exposed throughout significant areas of western and northern Pakistan, northern India, and Nepal. In Pakistan, sediments are particularly well exposed on the Potwar Plateau, where they are typically 2000–5000 m thick and comprise broad outcrop bands extending laterally for tens of kilometers (Barry et al., 1995). These outcrops span 18 Ma to less than 1 Ma, making the Potwar formations one of the longest, most fossiliferous terrestrial vertebrate sequences known. The Siwalik record now consists of more than 40,000 fossils representing hundreds of species from over 1000 localities, many of which have been dated to within a 100,000 year resolution.

Environmental changes in the Pakistan Siwalik sequence have best been documented by isotopic changes in paleosols, given the absence of a pollen record in Pakistan. Most terrestrial plants assimilate CO<sub>2</sub> by one of two photosynthetic pathways, and these different pathways fractionate carbon isotopes differently. C<sub>3</sub> plants include most trees and shrubs and some grasses which experience cool growing seasons. C<sub>4</sub> plants, on the other hand, are grasses and sedges which live in hot, drier environments, and

these plants have tissues enriched in <sup>13</sup>C relative to C<sub>3</sub> plants. Paleosol δ<sup>13</sup>C values reflect the isotopic composition of vegetation growing above the site (Cerling et al., 1989). When dated according to the Cande and Kent (1995) timescale, the Siwalik paleosol data indicate that C<sub>4</sub> plants appeared around 8 Ma, with the first C<sub>4</sub> dominated habitats at 7.37 Ma (Quade et al., 1989; Quade and Cerling, 1995). Communities composed of predominantly C<sub>3</sub> plants became diminished or disappeared around 7.0 Ma.

Carbon isotope ratios in mammalian tooth enamel corroborate the paleosol data. Early analyses of mammalian tooth enamel indicated a transition from C<sub>3</sub> dominated diets to mixed C<sub>3</sub>/C<sub>4</sub> diets and ultimately to C<sub>4</sub> dominated diets, with a major shift after 8 Ma (Morgan, 1994). The paleoenvironment was most likely a mosaic of C<sub>3</sub> and C<sub>4</sub> plants throughout the Late Miocene, but with increasing percentage of C<sub>4</sub> grasses after 8 Ma. Nelson (2003) also conducted an isotopic analysis of large mammalian tooth enamel from two fossiliferous time intervals—9.3–9.2 Ma, when *Sivapithecus* was present, and 8.1–8.0 Ma, shortly after *Sivapithecus* became extinct. Results indicated a vegetation mosaic of both open and closed habitats at both intervals, but a decrease in forest accompanied by an increase in open habitat (including C<sub>4</sub> grasses) during the younger interval. Isotopic values for *Sivapithecus* suggested that it fed in the forest upper canopy.

Changes in the vegetation mosaic probably related to changes in the depositional systems of the Pakistan Siwaliks during the Late Miocene as well as to changes in climate. Nagri Formation large emergent river systems were replaced by Dhok Pathan Formation interfan river systems beginning around 10.1 Ma (Willis and Behrensmeyer, 1995; Barry et al., 2002). After 9.0 Ma, these interfan river systems were less well drained, with more seasonally variable flow and more avulsions. Vegetation probably responded to specific local conditions, resulting in mosaics over distances of 100s of meters to a few kilometers (Barry et al., 2002).

The paleosol data also indicate a shift in δ<sup>18</sup>O values, beginning around 9.15 Ma, with samples becoming more enriched over time (Quade et al., 1989; Quade and Cerling, 1995). This shift has been interpreted as both a decrease in rainfall and increase in seasonality of rainfall. Foraminiferal records

indicate the beginning of strong summer Arabian Sea upwellings around 9.4 Ma, with continued strengthening until around 8.2 Ma, suggesting the beginning or at least major intensification of the South Asian monsoon (Kroon et al., 1991, corrected to Cande and Kent, 1995). Intensification of the monsoon may explain the oxygen shift in Pakistan, with intensification causing increased seasonality, aridification, and summer rainfall which would then favor C<sub>4</sub> plants and hence more open habitats, over C<sub>3</sub> plants and closed forest.

While no pollen has been found associated with the Pakistan Siwaliks, fossil wood in India indicates that tropical evergreen forests with rare moist deciduous taxa flourished in this region during the Middle Miocene (Prasad, 1993). Though poorly dated, these forests were probably present between 17 and 11 Ma. Moist deciduous taxa later dominate, and dry deciduous forests make their first appearance, but again this transition is poorly dated. Pollen and leaf fossils from Nepal also suggest that evergreen forests dominated the vegetation in this region during the Middle Miocene but were gradually replaced by semi-deciduous and dry deciduous forests between 11 and 6 Ma (Quade and Cerling, 1995). Work by Corvinus and Rimal (2001) provides a more detailed plant record of the Nepal Siwaliks. The Bankas formation, corresponding to Pakistan's Chinji Formation (14.2–11.2 Ma) (Barry et al., 2002), preserves leaves of tropical evergreen genera found today only in S.E. Asia, including *Dipterocarpus*. Moist deciduous elements make their first appearance in the lower Chor Khola, corresponding to the beginning of the Pakistan Nagri Formation at 11 Ma, though evergreen plants are still present. Evergreen taxa become rare and are replaced by a majority of moist deciduous and dry deciduous taxa in the Surai Khola, corresponding to the second half of Pakistan's Dhok Pathan Formation, roughly 7 Ma. A shift from moist to dry deciduous flora subsequently occurs in the Dobatta Formation, equivalent to the Pakistan Upper Siwaliks some time after 4 Ma. A high proportion of Nepal Middle Miocene paleosols are gleyed, suggesting swampy conditions. It should be noted that gleyed paleosols are absent from the Pakistan Siwaliks, however, indicating that Nepal was wetter than Pakistan during the Miocene, as it is today. If so, then the transition from evergreen to moist deciduous

to dry deciduous forests probably occurred slightly earlier in Pakistan compared to Nepal. The Nepal paleosols also show oxygen and carbon isotope shifts comparable to those seen in Pakistan, though the carbon shift is about 0.7 million years later in Nepal (Quade and Cerling, 1995).

Evidence from the Nepal Siwalik bivalves also indicates decreasing rainfall in the Late Miocene. Dettman et al. (2001) tracked  $\delta^{18}\text{O}$  values in fossil bivalves from the Siwalik sediments in Nepal from the past 10.7 million years and found evidence for wet–dry seasons in all shells, suggesting that the monsoon system was already in effect as early as 10.7 Ma. Furthermore, since 9.5 Ma, the magnitude of seasonal variability in  $\delta^{18}\text{O}$  values remained essentially unchanged.  $\delta^{18}\text{O}$  values before 7.5 Ma were lower than younger specimens, suggesting a decrease in rainfall beginning at 7.5 Ma. The decrease in rainfall in Pakistan, as inferred from the oxygen isotope shift observed in paleosols, therefore precedes the shift observed in Nepal by 0.5 Ma.

Finally, reconstructions of Siwalik paleoclimates with respect to rainfall are useful not only for inferring *Sivapithecus*' habitat preferences but also for determining the timing of inception and strengthening of the Asian monsoon. The S.E. Asian–S.W. Indian monsoon system today envelops the tropical and subtropical continents of Asia, Africa, and Australia. In India, moisture is carried from both the Arabian Sea on southwest winds and the Bay of Bengal on southeast winds during the summer, while winds blow across the dry Asian continent from the northeast in winter (Mooley and Shukla, 1987). Pakistan also receives these monsoonal rains, although in the more northern latitudes the monsoon rains arrive later and leave earlier than in more southern latitudes. Pakistan in addition receives supplemental rains during the winter from prevailing westerlies carrying moisture from the Mediterranean, Black, and Caspian seas (Murakami, 1987).

The Asian monsoon is driven largely by a land–ocean temperature gradient, which in turn is driven by the Tibetan Plateau (Webster, 1987). The plateau generates a high-altitude region of low pressure in the summer as it warms, thus pulling moisture-laden air masses from the ocean, and it subsequently generates a high-pressure region in the winter as it cools, returning moisture from the land back to the ocean.

Climatic modeling suggests that the Tibetan plateau had to be at least half its current height in order to drive a strong monsoonal system (Prell and Kutzbach, 1992). The timing of uplift of the plateau remains a point of contention, with estimates ranging from 40 to 3.4 Ma, but a range of evidence suggests that while uplift started around 50 Ma, a significant increase in altitude began around 10–8 Ma (Zhisheng et al., 2001).

#### 1.4. Reconstructing precipitation regimes using oxygen stable isotopes

The purpose of this investigation is to determine whether *Sivapithecus* habitats were characterized by a seasonal rainfall regime, and if so, what kind of forest is associated with this regime in the modern world. Another goal is to determine whether the rainfall regime changed during the later Miocene, for intensification of the Asian monsoon during the Late Miocene could have led to a greater degree of seasonality of precipitation and hence a change in vegetation.

Seasonality of precipitation and/or temperature can be tracked using stable oxygen isotopes. The  $\delta^{18}\text{O}$  value of precipitation is controlled by a number of factors, including ambient temperature and amount of rainfall. In temperate regions which experience a wide range of temperatures annually,  $\delta^{18}\text{O}$  values track monthly change in temperature due to differences in evaporative pressure between  $^{18}\text{O}$  and  $^{16}\text{O}$ , with enriched  $\delta^{18}\text{O}$  values during summer months. In tropical regions, where rainfall varies but temperature remains relatively constant,  $\delta^{18}\text{O}$  monthly values track rainfall (Gonfiantini, 1985; Njitchoua et al., 1999).  $^{18}\text{O}$  precipitates more readily than  $^{16}\text{O}$ ; therefore, the more it rains, the less  $^{18}\text{O}$  is present in atmospheric water, and the more depleted the precipitation becomes (Dansgaard, 1964). In monsoonal environments which experience both monthly differences in temperature as well as rainfall,  $\delta^{18}\text{O}$  values track rainfall, with precipitation greatly depleted during monsoonal months, in spite of high summer temperatures (Rozanski et al., 1993; Araguas-Araguas and Froehlich, 1998). For example, on the Tibetan Plateau, summer monsoonal rainfalls are depleted in  $^{18}\text{O}$  by more than 6‰ compared to winter rainfall, despite 10 °C higher summer temperatures (Araguas-

Araguas and Froehlich, 1998). Thus, in a monsoonal system, the precipitation amount effect overpowers the temperature effect.

These climate-sensitive changes in meteoric water, or water that participates in atmospheric circulation, then become incorporated into an animal's water source and ultimately into its body water.  $\delta^{18}\text{O}$  values of tooth enamel reflect the isotopic composition of water ingested by an animal during enamel formation (Longinelli, 1984; Luz et al., 1984). Multiple studies have shown that inter- and intra-tooth variation in isotopic composition of carbonate and phosphate oxygen in both modern and fossil taxa represents the intra-annual seasonal oscillations that the animal experienced (Koch et al., 1989; Bryant et al., 1994, 1996a,b; Fricke and O'Neil, 1996; Fricke et al., 1998; Sharp and Cerling, 1998; Gadbury et al., 2000; Fox and Fisher, 2001). Submillimeter samples of tooth enamel taken throughout the length of a hypsodont tooth, such as an equid's which takes a year or more to develop, can therefore provide a record of annual seasonality (Cerling and Sharp, 1996; Sharp and Cerling, 1996).

Unlike carbon isotopic values, no universal fractionation factors apply between diet and tooth enamel for fauna in general, because fractionation of oxygen isotopes between body and environmental drinking water is dependent on the rates of drinking and respiration (Luz et al., 1984). Furthermore, certain caveats must be considered in inferring precipitation values from tooth enamel. First, like carbon isotopes, oxygen values of vegetation respond to differences in environment. In more open habitats, where plants are under irradiance and moisture stress, both carbon and oxygen values become enriched relative to more closed habitats (Ehleringer et al., 1986, 1987; Sternberg et al., 1989). Therefore, herbivores which obtain a significant amount of their water from vegetation will have  $\delta^{18}\text{O}$  values which reflect not only the  $\delta^{18}\text{O}$  value of local precipitation but also values from leaves that are enriched due to evapotranspiration. Preferential evaporation of  $^{16}\text{O}$  can elevate  $\delta^{18}\text{O}$  values of leaf water by 10‰ or more (Dongmann et al., 1974). Thus while  $\delta^{18}\text{O}$  values of precipitation are the predominant control over  $\delta^{18}\text{O}$  values of body water, relative humidity can be a factor in arid and semi-arid environments and with animals that obtain most or all of their body water from vegetation (Ayliffe and

Chivas, 1990; Ayliffe et al., 1992). These factors can be minimized by analyzing animals that drink daily and have high water turnover rates, such as zebra or horses, who will therefore have a body water composition more sensitive to surface water composition. All Siwalik precipitation regimes are inferred from equid teeth to minimize evapotranspiration effects.

In addition to evapotranspiration effects,  $\delta^{18}\text{O}$  values of plant water can differ between  $\text{C}_3$  plants and  $\text{C}_4$  grasses.  $\text{C}_4$  plants preferentially undergo evapotranspiration late in the day when it is drier and therefore have higher  $\delta^{18}\text{O}$  values. In arid settings, this difference can be as high as 10‰ (Sternberg et al., 1984), though in cooler, more humid environments, it is less than 1‰ (Epstein et al., 1977). It is unlikely that the Siwaliks were arid during the Late Miocene, and the  $\delta^{18}\text{O}$  difference between  $\text{C}_3$  and  $\text{C}_4$  plants would therefore have been closer to 1‰ than to 10‰. Nonetheless, oxygen values for Siwalik equids eating different amounts of  $\text{C}_3$  browse and  $\text{C}_4$  graze can be compared, for carbon values are collected for each specimen as well as oxygen.

Another consideration is how accurate an animal's water source will reflect the  $\delta^{18}\text{O}$  values of local precipitation. Water sources, such as rivers, respond to changes in  $\delta^{18}\text{O}$  values of precipitation, but their seasonal response may be attenuated with respect to rainfall. River water comprises both surface run-off of precipitation and groundwater. Where surface run-off predominates, river water  $\delta^{18}\text{O}$  values track rainfall. This signal becomes dampened, however, as groundwater becomes more of a source, for most groundwater bodies are isotopically constant and reflect the average annual isotopic composition of precipitation (Fritz, 1981; Gat, 1981). Furthermore, in arid zones, evaporation can enrich  $\delta^{18}\text{O}$  values. A study of rivers in North Central Africa, however, suggests that even in arid regions where evaporation is responsible for most seasonal variations, these waters respond strongly to monsoon rains, closely approaching the  $\delta^{18}\text{O}$  of rainfall during the monsoonal months (Fontes et al., 1970; Fritz, 1981). Smaller bodies of water, such as ephemeral drinking pools, experience rapid volume turnover, thereby reducing the effect of evaporation and allowing them to more accurately reflect  $\delta^{18}\text{O}$  values of precipitation (Koch et al., 1989). Thus, while Siwalik equids which drank from

shallow pools are likely to yield  $\delta^{18}\text{O}$  values reflective of the isotopic composition of rainfall, individuals which drank from larger, buffered bodies of water or from springs will yield an attenuated signal.

Finally, Bryant et al. (1994, 1996a) have suggested that mother's body water and physiology could affect teeth which develop before weaning, with weaning occurring at 9 to 15 months of age. In horses and zebras, first molars mineralize before weaning, and second molars mineralize around the age of weaning. All other premolars and molars mineralize after weaning. These authors therefore suggest excluding M1s and M2s from climatic reconstructions, even though they did not find a consistent pattern in  $\delta^{18}\text{O}$  values from M1 to M3 molars in Oligocene and Miocene horses (Bryant et al., 1996a). Gadbury et al. (2000) also report no differences between molar positions of Early Holocene bison teeth and suggest that there is no significant difference in the  $\delta^{18}\text{O}$  value of body water obtained from the mother versus water obtained from post-weaning dietary intake. This Siwalik study incorporates all molars.

## 2. Materials and methods

A total of 29 Hipparionini teeth spanning 10.3 to 6.3 Ma were sampled from the Siwalik record for carbon and oxygen isotopes. This sample includes specimens from localities also bearing *Sivapithecus* specimens. Fifteen of these teeth are represented by intra-tooth profiles, with each profile consisting of 13 to 23 samples spanning 33 to 53 mm from occlusal surface to root. These teeth included P3s, P4s, and all molars. Samples were removed from teeth using a Dremel high-speed rotary tool with a tungsten-carbide or diamond-impregnated bit. Tooth profiles were analyzed using the automated carbonate micro-sampler method. For each of these samples, 0.5–0.7 mg was required, and these samples were washed with 3% hydrogen peroxide for 15 min to remove organic material and then rinsed, followed by 0.1 M acetic acid for 15 min to remove surficial carbonates and then rinsed. Samples were then reacted with 100% phosphoric acid at 90 °C on an automated carbonate device interfaced with a Finnigan MAT 252 stable isotope ratio mass spectrometer. For the remaining 14 teeth sampled before the automated carbonate device

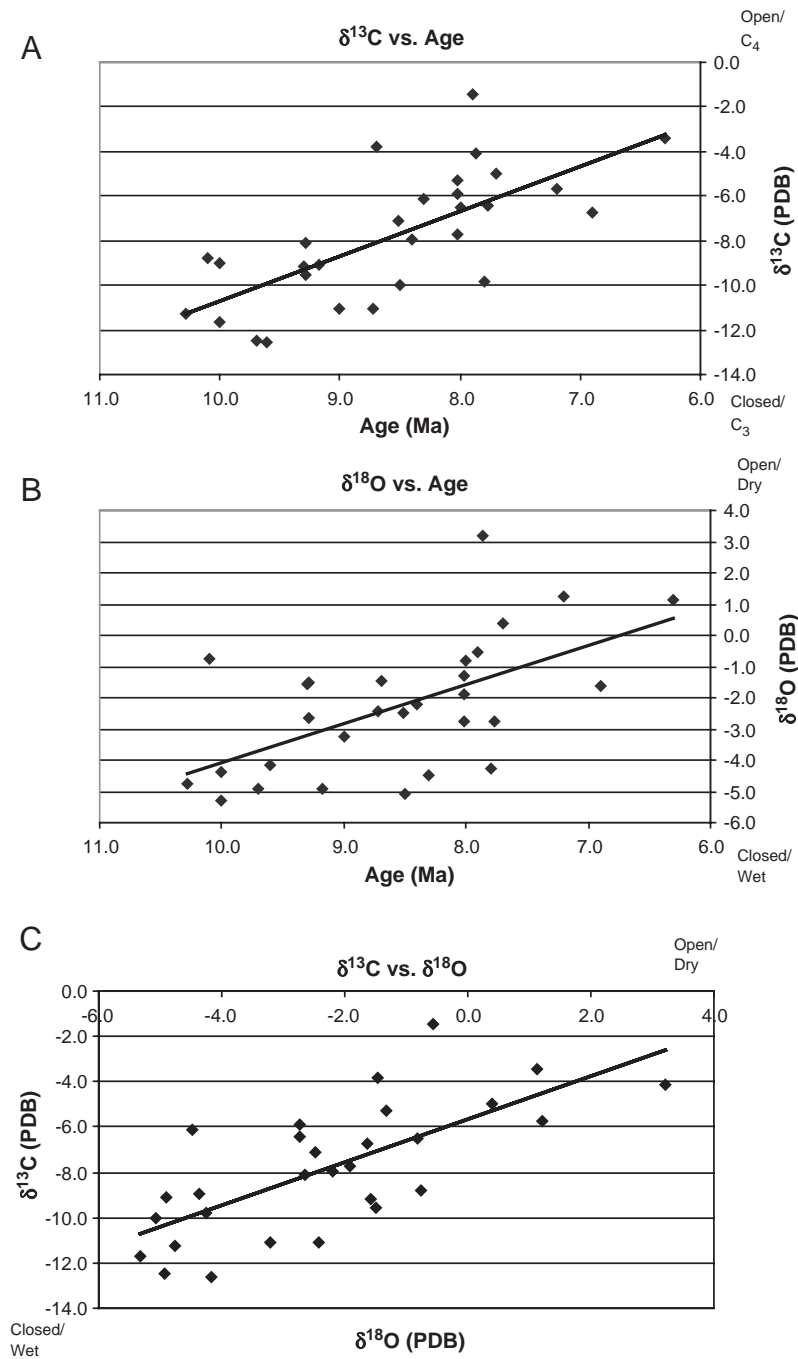


Fig. 1. A.  $\delta^{13}\text{C}$  values become more enriched over time, indicating a transition from closed to open habitat for horses, with a dietary transition to include C<sub>4</sub> grasses. Adjusted  $R^2=0.48$ ;  $p<0.0001$ . B.  $\delta^{18}\text{O}$  values also become enriched over time, indicating a transition from relatively wet habitat to dry habitat for horses. Adjusted  $R^2=0.32$ ;  $p=0.0009$ . C.  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values show a positive relation, indicating more closed habitats are wetter or less evaporative, while more open habitats are drier or more evaporative. Linear regression: adjusted  $R^2=0.48$ ;  $p<0.0001$ .

was available, CO<sub>2</sub> was extracted from carbonate by reacting it with phosphoric acid and isolating it cryogenically. For these samples, 30–50 mg of tooth enamel was ground, washed with 3% hydrogen peroxide for 1 h and rinsed, and then washed with 1 M acetic acid for 1 h and rinsed. They were then reacted with 100% phosphoric acid at 25 °C for 48 h, and the evolved CO<sub>2</sub> was subsequently isolated cryogenically, reacted with Ag wool to remove any SO<sub>2</sub>, and analyzed on a Finnigan delta S stable isotope ratio mass spectrometer.

Isotopic ratios are presented in the per mil (‰) notation

$$\delta^{18}\text{O} \text{ (or } \delta^{13}\text{C}) = (R_{\text{sample}}/R_{\text{PDB}} - 1) \times 1000$$

where  $R_{\text{sample}}$  and  $R_{\text{PDB}}$  are the ratios  $^{18}\text{O}/^{16}\text{O}$  (or  $^{13}\text{C}/^{12}\text{C}$ ) in the sample and standard respectively, and the isotope reference standard is PDB (Pee Dee Belemnite). Oxygen values are reported assuming the acid-calcite fractionation factor for calcite.

### 3. Results and discussion

#### 3.1. Compilation of equid teeth sampled

When all horse teeth are compiled, with average  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values reported for tooth profiles, and individuals sampled by both methods represented only by the profile averages to avoid repetition, there are 29 *Hipparion* teeth which span 4 Ma (10.3–6.3 Ma). Among these teeth, both carbon and oxygen values correlate negatively with age (Spearman rank correlation: carbon  $t^* = -0.687$ ;  $p = 0.000$ ; oxygen  $t^* = -0.509$ ;  $p = 0.005$ ), indicating a shift to more open and drier habitats over time (Fig. 1A,B). This conclusion is further supported by a positive correlation between carbon and oxygen values ( $t^* = 0.0719$ ;  $p = 0.000$ ), indicating open habitats are also drier, while closed habitats are wetter or are undergoing less evaporative effects (Fig. 1C).

Carbon values are interpreted based upon certain cutoff values for diets of C<sub>3</sub> versus C<sub>4</sub> vegetation as well as for closed versus open habitat. The  $\delta^{13}\text{C}$  values for tooth apatite for pure C<sub>3</sub> modern diets in general range from approximately  $-20\text{‰}$  to  $-8\text{‰}$ , with the extremes representing distinctive habitats,

depleted very closed canopy rainforest and enriched very open habitat (Cerling et al., 1997). A pure C<sub>4</sub> diet, on the other hand, yields  $\delta^{13}\text{C}_{\text{(apatite)}}$  values from  $+1\text{‰}$  to  $+4\text{‰}$ . Modern  $\delta^{13}\text{C}$  values are depleted by  $1.5\text{‰}$  relative to Miocene values due to a shift in atmospheric carbon isotope ratios since the industrial revolution and burning of fossil fuels. Therefore, a value of  $-8\text{‰}$  today, or the most enriched pure C<sub>3</sub> diets, is comparable to a Miocene value of  $-6.5\text{‰}$ . For the purposes of this analysis, a cutoff  $\delta^{13}\text{C}$  value of  $-7.5\text{‰}$  is used to distinguish evidence of at least some C<sub>4</sub> in the diet. In terms of habitat,  $\delta^{13}\text{C}$  values below  $-12\text{‰}$  represent closed habitat, while those above  $-10\text{‰}$  suggest affinities for more open habitat (Quade and Cerling, 1995).

Different teeth suggest a range of habitats exploited by Siwalik equids (Figs. 1A, 2, Table 1). Two teeth dated to 9.7 and 9.6 Ma have carbon values less than  $-12\text{‰}$ , suggesting an affinity for closed habitat. The first clear evidence of C<sub>4</sub> graze appears at 8.7 Ma, with a range of  $-4.4\text{‰}$  to  $-3.1\text{‰}$  in this profiled tooth. While these values indicate some C<sub>4</sub> graze in the diet throughout the entire tooth, they also reflect a strong C<sub>3</sub> component as well. Teeth dated to 10.1 and

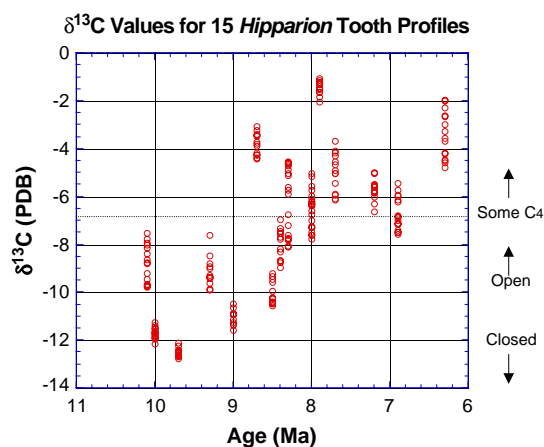


Fig. 2.  $\delta^{13}\text{C}$  (PDB) values for horse profiles indicate enrichment, and hence more open habitat and C<sub>4</sub> graze, over time. Each column of circles represents all samples from one tooth. The most depleted teeth, or those in relatively closed habitat, have the smallest ranges in carbon values. The first clear evidence for incorporation of C<sub>4</sub> graze into horse diets (greater than  $-7.5\text{‰}$ ) appears at 8.7 Ma, but all teeth have a C<sub>3</sub> component as well. Note that the 10.1 Ma tooth is remarkably enriched compared to teeth at 10.0 and 9.7 Ma. This tooth is a locality which lithologically resembles younger, more open habitats as well.

Table 1  
 $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  (PDB) values of 15 *Hipparion* teeth sampled throughout the length of the tooth

Specimen	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
10.1 $\delta\text{C}$	-8.4	-8.0	-7.8	-7.5	-7.9	-8.8	-9.4	-9.8	-9.7	-9.7		-9.6	-9.2	-8.8	-8.6	-8.2								
$\delta\text{O}$	0.3	0.3	-0.7	-1.1	-1.6	-2.2	-2.0	-1.1	0.3	-0.5		-0.4	-0.9	-0.9	0.0	-1.6								
10.0 $\delta\text{C}$	-11.4	-11.7	-11.7	-11.9	-11.9	-11.7	-11.9	-11.8	-12.1	-11.9	-11.6	-11.7	-11.6	-11.5	-11.8	-11.3	-11.4	-11.5						
$\delta\text{O}$	-6.1	-6.8	-6.5	-6.2	-5.5	-5.6	-5.0	-5.0	-4.6	-4.1	-3.9	-3.9	-4.1	-4.4	-5.3	-6.2	-6.3	-6.1						
9.7 $\delta\text{C}$	-12.4	-12.5	-12.7	-12.6	-12.7	-12.6	-12.5	-12.5	-12.5	-12.7		-12.5	-12.4	-12.1	-12.2	-12.5								
$\delta\text{O}$	-4.3	-3.9	-4.0	-4.3	-4.8	-4.7	-4.3	-5.3	-4.9	-5.3		-6.1	-5.8	-6.0	-5.2	-4.7								
9.3 $\delta\text{C}$	-9.6	-7.6	-9.4	-9.3	-8.9	-9.0	-9.0	-9.4	-9.3	-8.8	-8.5		-9.4	-9.9	-9.9	-9.9								
$\delta\text{O}$	-1.0	-0.4	-0.5	-1.7	-1.1	-1.0	-1.1	-1.7	-1.6	-2.0	-2.5		-2.4	-2.8	-2.1	-2.0								
9.0 $\delta\text{C}$	-11.1	-10.9	-10.9	-11.4	-10.9	-10.9	-10.9	-10.6	-10.9	-11.2	-11.3	-10.5	-11.6	-11.6										
$\delta\text{O}$	-1.4	-1.7	-2.1	-2.3	-2.4	-3.6	-3.3	-3.3	-4.2	-4.0	-4.5	-3.2	-4.8	-4.3										
8.7 $\delta\text{C}$	-3.2	-3.5	-3.7	-4.2	-4.4	-4.3	-4.4	-3.9	-4.2	-3.8	-3.4	-3.4	-3.1											
$\delta\text{O}$	-3.4	-3.1	-2.9	-2.9	-2.5	-1.6	-1.3	0.0	-0.1	0.0	-0.5	-0.2	-0.5											
8.5 $\delta\text{C}$	-9.2	-9.3	-9.3	-9.5	-9.6	-10.0	-10.2	-10.2	-10.4	-10.6	-10.5	-10.4	-10.4	-10.3	-10.2									
$\delta\text{O}$	-4.7	-5.2	-5.3	-5.9	-6.1	-5.9	-5.9	-5.7	-5.2	-4.8	-4.7	-4.4	-3.8	-3.9	-4.5									
8.4 $\delta\text{C}$	-7.5	-7.5	-7.7	-7.3	-7.3	-7.8	-8.3	-8.7	-9.0	-8.8	-8.7	-8.2	-7.5	-6.9										
$\delta\text{O}$	-2.3	-2.2	-2.3	-2.7	-3	-3.1	-3.4	-2.9	-2.8	-2.0	-1.4	-0.9	-1.2	-0.7										
8.3 $\delta\text{C}$	-5.0	-4.6	-4.5	-4.6	-4.9	-4.6	-4.7	-5.1	-5.6	-5.7	-5.9	-6.7	-7.2	-7.8	-7.8	-8.1	-8.1	-7.7	-7.6					
$\delta\text{O}$	-3.6	-3.9	-4.0	-3.9	-4.2	-4.4	-4.7	-5.3	-5.0	-5.7	-5.9	-5.5	-5.3	-4.5	-3.8	-3.8	-3.8	-4.1	-4.0					
8.0 $\delta\text{C}$	-6.1	-6.2	-6.3	-6.3	-6.8	-7.3	-7.6	-7.8	-7.6	-7.5	-7.2	-7.3	-7.0	-6.6	-6.3	-6.2	-6.0	-5.6	-5.2	-5.0		-5.7	-6.4	
$\delta\text{O}$	-0.7	-0.7	-1.2	-0.9	-1.0	-0.9	-0.1	-0.5	-0.4	-0.5	-0.4	-0.4	0.0	0.5	0.6	-0.2	-1.6	-1.8	-1.0	-1.0		-2.7	-3.2	
7.9 $\delta\text{C}$	-1.3	-1.3	-1.1	-1.4	-1.6	-1.5	-1.3	-1.1	-1.2	-1.5	-1.3	-1.2	-1.5	-1.6	-1.8	-2.0								
$\delta\text{O}$	-1.5	-1.3	-0.6	-0.4	-0.1	-0.5	-0.6	-0.2	-0.4	-1.0	0.5	0.0	-0.6	-1.1	-0.5	-0.6								
7.7 $\delta\text{C}$	-3.7	-4.3	-4.1	-4.6	-5.0	-5.4	-5.9	-6.1	-6.1	-5.9	-4.5	-5.0	-4.9	-4.2										
$\delta\text{O}$	0.4	-1.0	-0.6	-0.3	-0.5	0.7	0.1	1.0	0.9	0.6	2.3	1.4	0.1	0.3										
7.2 $\delta\text{C}$	-6.6	-6.3	-6.0	-5.8	-5.6	-5.6	-5.8	-5.5	-5.8	-5.6	-5.5	-5.5	-5.0	-5.0	-5.9									
$\delta\text{O}$	1.6	1.5	1.1	1.3	1.3	1.8	1.9	1.8	1.7	1.4	1.0	1.2	-0.2	0.8	0.2									
6.9 $\delta\text{C}$	-6.2	-6.1	-6.0	-5.7	-5.4	-5.9	-6.8	-7.1	-7.5	-7.6	-7.4	-7.2	-7.1	-6.8	-6.9	-7.5	-7.0							
$\delta\text{O}$	-2.7	-2.0	-2.1	-1.1	-1.0	-1.4	-2.0	-1.8	-2.0	-2.1	-1.9	-1.5	-1.1	-1.7	-1.8	-0.9	-0.4							
6.3 $\delta\text{C}$	-1.9	-2.0	-2.3	-2.6	-3.0	-3.3	-3.6	-2.6	-4.5	-4.8	-4.6	-4.2	-4.2	-4.5	-3.7									
$\delta\text{O}$	2.0	0.7	1.3	1.8	2.0	1.7	2.0	1.3	1.1	1.1	6.0	0.1	0.4	1.7	-0.9									

Samples begin at the occlusal surface and are numbered consecutively, ending at the cervical margin. Missing values represent unsuccessful analyses on the mass spectrometer.

9.3 Ma also show enriched  $\delta^{13}\text{C}$  values ( $-7.5\%$  and  $-7.6\%$  respectively) which could reflect a small component of  $\text{C}_4$  graze or alternatively, a diet of  $\text{C}_3$  plants in open habitats. Teeth subsequent to the first evidence of  $\text{C}_4$  graze at 8.7 Ma, or those sampled at 8.5, 8.4, and 8.3 Ma, indicate periods of the year in which no  $\text{C}_4$  component is present, suggesting  $\text{C}_4$  patches were small or greatly dispersed. It is not until 8.0 Ma that all horse profiles yield evidence of a  $\text{C}_4$  component throughout the entire tooth, suggesting permanent patches of  $\text{C}_4$  grass. Still, a 7.8 Ma tooth sampled once yielded low carbon ( $-9.8\%$ ) and oxygen ( $-4.3\%$ ) values, suggesting some horses continued to feed only on  $\text{C}_3$  plants at least part of the year in somewhat less open and wetter or less evaporative habitat.

Like carbon values, oxygen values are lower in older specimens than in younger (Fig. 1B, Table 1). In six teeth dating to 9.6 Ma or older, all but one have  $\delta^{18}\text{O}$  values less than  $-4\%$ . The exception is from a 10.1 Ma locality (Y258), and its enriched  $\delta^{13}\text{C}$  values throughout the length of the tooth ( $-9.8\%$  to  $-7.5\%$ ) indicate feeding in open habitat where evaporative effects could result in enriched  $\delta^{18}\text{O}$  values, both from evaporated water bodies and open-habitat vegetation. These values are consistent with lithological evidence that this locality was unusually open, resembling localities in the Dhok Pathan Formation interfan river system even though it came from the Nagrii Formation large emergent river system. Thus isotopic evidence from this locality (Y258) suggests that vegetation responded to specific local conditions, which would have resulted in local vegetation mosaics as well as mosaics spanning several kilometers.

The first high  $\delta^{18}\text{O}$  values appear consistently at 9.3 Ma, although low values are also present consistently until 8.3 Ma. Eleven teeth fall between 9.3 and 8.3 Ma, with four teeth yielding  $\delta^{18}\text{O}$  values below  $-3\%$ . From 8.0 Ma and later, of 12 teeth, all but one tooth has become enriched (greater than  $-3\%$ ) with consistently highly enriched values, but again the tooth sampled once at 7.8 Ma that was mentioned earlier does have a low oxygen value.

These results suggest that while some open habitat and some more wooded habitats were present throughout the four million years sampled, a transition to a greater proportion of open, drier habitats occurred first between 9.6 and 9.3 Ma, with a second transition

to even more open and drier habitats between 8.3 and 8.0 Ma. This vegetation shift was most likely accompanied by a decrease in rainfall as well, and variability in oxygen values between 9.3 and 8.3 Ma may represent variability in climate. Alternatively, the non-monotonic shift observed in oxygen values could be the result of diagenetic alteration of some of the teeth. However, in an isotopic study of a wide range of Siwalik large mammalian fauna, including equid specimens reported in this analysis, different taxa were isotopically distinctive from others in both carbon and oxygen (Nelson, 2003). These results are a good indication that true dietary signals are preserved, for diagenetic alteration would have led to isotopic homogeneity rather than clustering by taxa, especially with teeth collected from the same stratigraphic beds.

Finally, when the 29 teeth are divided into those present before the extinction of *Sivapithecus* (10.3–8.4 Ma,  $n=16$ ) and those present afterwards (8.3–6.3 Ma,  $n=13$ ), there is a significant enrichment in carbon values with time, from an average  $\delta^{13}\text{C}$  value of  $-9.5\%$ , indicating no graze on average, to an average of  $-5.7\%$ , indicating some graze on average ( $Z=-3.68$ ;  $p=0.0002$ ). Likewise, there is a significant enrichment of  $\delta^{18}\text{O}$  values from  $-3.2\%$  on average to  $-1.1\%$  on average ( $Z=-2.55$ ;  $p=0.011$ ). This  $2.1\%$  increase is consistent with the  $2.3\%$  increase seen in the all-inclusive taxa comparison between the *Sivapithecus*-level and the Post-*Sivapithecus*-level examined by Nelson (2003). This consistency suggests that mammalian teeth across a range of taxa are detecting a shift in the rainfall regime as well as a shift in the vegetation mosaic.

### 3.2. Intra-tooth sampling profiles

Teeth analyzed in this study included P3s, P4s, and all molars. Kruskal–Wallis 1-Way ANOVAs indicated no significant differences in high, low, mean, or range of carbon or oxygen values based on tooth position, suggesting there were no weaning effects on  $\delta^{18}\text{O}$  values. In fact, M1s and M3s yielded overlapping oxygen curves in comparisons of a 10.0 Ma M3 and an 8.5 Ma M1 and again between a 7.2 Ma M3 and a 6.3 Ma M1 (Fig. 3).

As in the 29 horse teeth sample, average  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for each tooth show a positive correlation

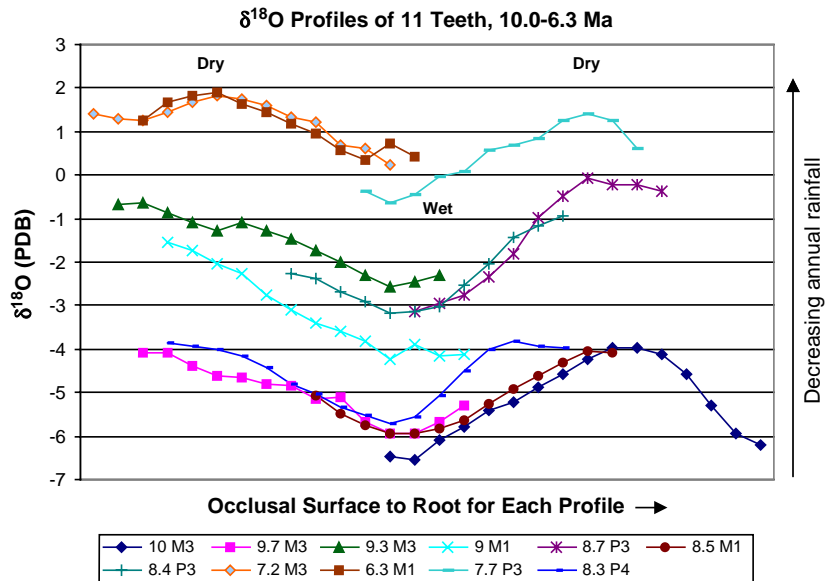


Fig. 3. When  $\delta^{18}\text{O}$  profiles are combined for the 10 teeth which made up half of the annual seasonal cycle and the one tooth (8.3 Ma) which incorporated the full annual cycle, a full annual cycle results which becomes enriched over time, suggesting a decrease in rainfall, while maintaining the same shape, implying the same seasonal regime. Profiles are represented by three-point running averages. For any given curve, crests represent dry seasons and troughs represent rainy seasons.

(Spearman rank correlation:  $t^* = 0.78$ ;  $p = 0.001$ ). This correlation suggests that over time, amount of annual rainfall decreased, changes in contributions from different precipitation sources may have occurred, and habitats became more open and included patches of  $\text{C}_4$  grass by 8.7 Ma. However, within *individual* profiles, there is not a consistent relationship between carbon and oxygen values (Table 1). Trends within teeth include increasing  $\delta^{13}\text{C}$  with increasing  $\delta^{18}\text{O}$ , decreasing  $\delta^{13}\text{C}$  with increasing  $\delta^{18}\text{O}$ , or no pattern at all. The fact that carbon and oxygen did not correlate or show consistent trends *within* teeth suggests that the  $\delta^{18}\text{O}$  curves are not indicative of movement from closed to open habitat or shifts from  $\text{C}_3$  to  $\text{C}_4$  diets within the time span of tooth development, for if that were the case, carbon and oxygen should show a positive correlation. Rather, the oxygen curves are indicative of annual changes in precipitation.

Intra-tooth variability in oxygen values follows a trend among consecutive samples most likely representing seasonal fluctuations in precipitation (Fig. 3). One tooth (8.3 Ma) has an oxygen curve which incorporates a distinguishable, complete seasonal cycle, beginning with enriched values representing

the dry season, followed by depleted values indicative of the wet season, followed by a return to enriched values and the dry season. This annual regime was captured over a tooth length of 50 mm. Another tooth (10.0 Ma) nearly captures a complete cycle, from one dry season to the next, over a tooth length of 46 mm. Other teeth, sampled over shorter lengths, captured only a portion of the cycle, either the dry season before the onset of heavy rains, or the rainy season and subsequent drying.

The 45–50 mm/year rate of enamel formation suggested by Siwalik teeth is greater than the 35–40 mm/year rates described in two other horse and bison tooth studies (Fricke and O'Neil, 1996; Sharp and Cerling, 1998). In those studies, young adult or unerupted teeth were analyzed, whereas this Siwalik study used worn teeth (except for the 8.0 Ma tooth). This difference in time representation suggests that either Siwalik equids differed from modern equids and bison in rate of enamel formation or that amount of time sampled per length of tooth is dependent upon which portion of the tooth is analyzed. Striae of Retzius, or enamel bands, are laid down at a constant rate, but because the occlusal surface of tooth crowns

develops at a faster rate than the remaining tooth, striae are laid down at steeper angles in the crown, or more parallel to the enamel surface. Angle of striae then decreases from crown to root and becomes more perpendicular to the enamel surface (Hillson, 1986; Beynon et al., 1998; Fitzgerald, 1998; Shellis, 1998). This means that surficial sampling of enamel, with each sample covering several millimeters of enamel drilled down almost to the dentine layer, could capture more striae, and hence more time, at the crown. Worn teeth, while requiring more tooth surface to capture a full seasonal cycle, have an advantage in that the original occlusal surface with more angled striae has been worn away so that each sample incorporates less striae, and hence less time-averaging occurs per isotopic sample.

The oxygen isotopic curves from the 11 teeth spanning different seasons (dry-to-wet or wet and subsequent drying) can be combined to form complete seasonal cycles (Fig. 3). Justification for this combination is threefold. First, when combined, the curves from the 9.7 Ma tooth and the 8.5 Ma tooth overlap by seven samples along the trough (peak of the wet season), and these consecutive samples yield identical  $\delta^{18}\text{O}$  values. Tooth profiles which also overlap in

values and closely track the same trajectory include the 10.0 and 8.5 Ma teeth, the 8.7 and 8.4 Ma teeth, and the 7.2 and 6.3 Ma teeth. Furthermore, the resulting combined curves are very similar to the curve from the one tooth (8.3 Ma) that yielded the full seasonal cycle. The 8.3 Ma tooth curve is slightly shorter in length (about 15 samples as opposed to around 19), but this it to be expected given the time-averaging which would result from a single tooth due to sampling multiple striae of Retzius, as mentioned earlier. The fact that teeth from different individuals spanning millions of years follow identical trajectories sample by sample and in many cases yield identical  $\delta^{18}\text{O}$  values sample by sample indicates that despite caveats in interpreting oxygen isotopes, and potential for variability between teeth due to horse behavior or tooth histology, intra-tooth sampling of oxygen isotopes in hypsodont teeth can yield reconstructions of paleoprecipitation regimes.

Four teeth did not fit this general pattern (Fig. 4). Differences could have arisen at any or all of three of the following levels: 1) sampling the tooth could have resulted in greater time-averaging; 2) individual horse behavior may have differed, including more migratory patterns, buffered water sources, or a greater contri-

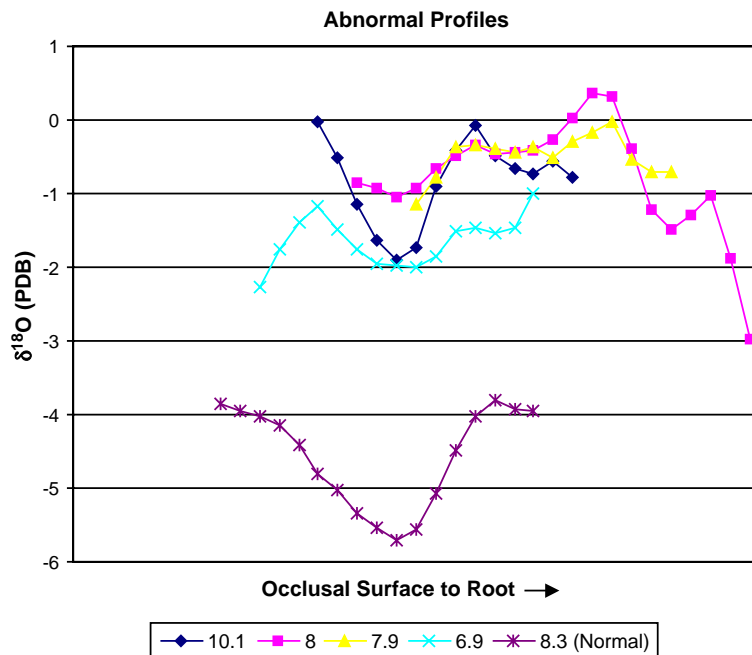


Fig. 4. Four teeth yielded  $\delta^{18}\text{O}$  curves which did not fit the shape of the curve generated by all other teeth (represented by the 8.3 Ma curve).

bution of vegetation to body water; and 3) there could have been differences in amount of rainfall or length of the wet or dry seasons in the particular year represented by the specimen. The fact that each of these four teeth still show fluctuations in  $\delta^{18}\text{O}$  values suggests that diagenesis is not a factor, for diagenesis should lead to homogeneity within a tooth.

Among the 11 teeth which did yield the consistent annual precipitation curve, the full seasonal cycle is represented by about 19 samples, with consecutive samples creating a similar pattern (Fig. 3). Amplitudes fall between approximately 2–3‰. These results suggest little to no change in the difference in amount of rainfall between dry and wet months over time, or changes in the seasonality of rainfall. However, the oldest teeth (10.0 and 9.7 Ma) yield the lowest  $\delta^{18}\text{O}$  values, between about –4‰ and –6‰, while the most positive curves, with  $\delta^{18}\text{O}$  values between +2‰ and 0‰, consist of the youngest teeth (7.7, 7.2, and 6.3 Ma). These results suggest a transition from closed habitat to more open habitat over time, accompanied by and associated with a decrease in rainfall over time, although the seasonal cycle itself, including its amplitude, does not appear to change. Teeth intermediate in age fall between these  $\delta^{18}\text{O}$  values, but not in chronological order, suggesting that the climatic shift was not monotonic.

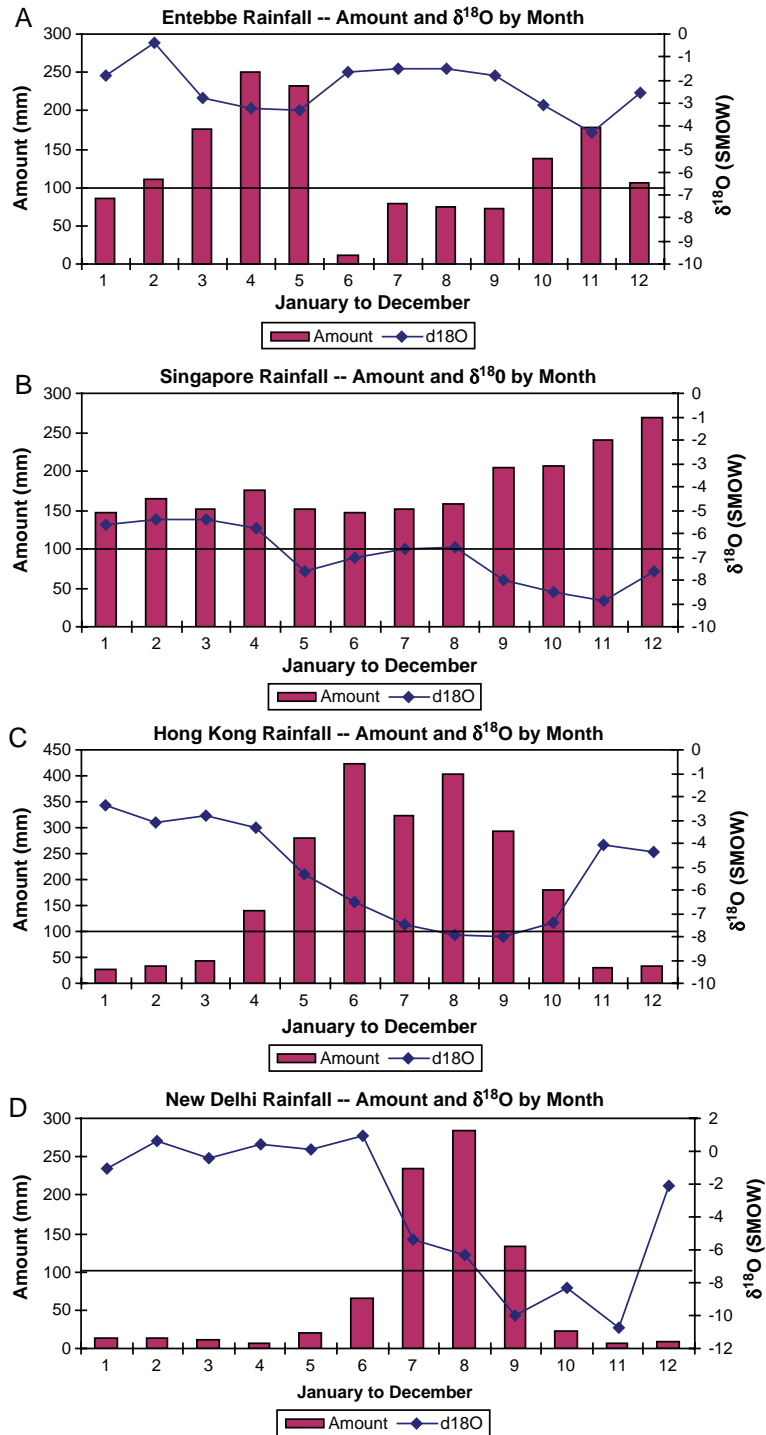
The actual  $\delta^{18}\text{O}$  values of the equid tooth profiles cannot be compared to modern precipitation values, for they are enriched due to evaporative effects on both water and vegetation consumed by the equids. Faunal isotopic analyses of a range of Siwalik large mammals indicate that *Hipparion* always inhabited the most open, most evaporative environments relative to other taxa, with more enriched  $\delta^{18}\text{O}$  values than most other taxa (Nelson, 2003). Furthermore, the actual amplitude of the tooth profiles most likely represents a minimum amplitude of the precipitation  $\delta^{18}\text{O}$  values rather than the full amplitude, for some

buffering of water sources, some buffering due to vegetation contributions to body water, and possibly some time-averaging due to sampling multiple striae may have occurred. However, the fact that the shape of the seasonal curve does not change throughout the record, including the amplitude and the distance between highest and lowest values (measured by number of samples), suggests that the shape of the curve can be compared to modern precipitation  $\delta^{18}\text{O}$  profiles.

The International Atomic Energy Agency (IAEA) has collected monthly precipitation amounts and  $\delta^{18}\text{O}$  values (weighted for amount) of precipitation for many locations around the world. These modern profiles include an African city in a region of evergreen and semi-evergreen rainforests characterized by a bimodal distribution of rainfall (Fig. 5A), S.E. Asian cities in evergreen rainforest regions with greater than 100 mm rainfall every month of the year (Fig. 5B), S.E. Asian cities in monsoonal forest regions with distinct wet/dry months due to the Asian monsoon (Fig. 5C), and an Indian city which also experiences a monsoonal climate, but with more dry months than wet per year (Fig. 5D).

The first thing to note is that the Siwalik precipitation curve is not bimodal and is therefore more similar to Asian curves. Among the Asian curves, those in regions which never experience dry months (months receiving less than 100 mm of rainfall) show variability in  $\delta^{18}\text{O}$  values, but this variability does not show clear seasonal trends. However, cities in monsoonal regions which experience 4 to 5 considerably dry months per year show a distinct seasonal difference in  $\delta^{18}\text{O}$  values which results in a U-shaped curve. There is a small plateau of enriched values representing dry months, followed by a gradual decline in values as rainfall increases, which represents the onset of the monsoon. This decline ends in a trough which represents several

Fig. 5. A. Typical monthly rainfall amount and  $\delta^{18}\text{O}$  (SMOW) values for Entebbe, Uganda (IAEA, 1981). Entebbe represents the bimodal annual rainfall regime of East Africa. There are two drops in  $\delta^{18}\text{O}$  values which correspond to the two rainy seasons. B. Singapore represents East Asian regions in which monthly rainfall amounts never fall below 100 mm (IAEA, 1981). While  $\delta^{18}\text{O}$  (SMOW) values vary, they do not follow a distinct seasonal trend. C. Hong Kong experiences a very monsoonal rainfall regime, with 5–6 months of little rainfall, and the remaining months experiencing very heavy rainfall.  $\delta^{18}\text{O}$  (SMOW) values show a U-shaped trend (IAEA/WMO 2001; IAEA, 1981). D. New Delhi, India experiences the Asian monsoon, with several months of very heavy rainfall, but 9 months of very little rainfall. Consequently,  $\delta^{18}\text{O}$  (SMOW) values show a plateau of enriched values, followed by a very sharp drop, followed by a very sharp rise (IAEA, 1981). The Siwalik  $\delta^{18}\text{O}$  curve most resembles Hong Kong, representing a monsoonal rainfall regime with five-to-six month dry season and several months of very heavy rainfall.



months of extremely heavy rainfall, followed by a gradual rise in  $\delta^{18}\text{O}$  values representing decrease in rainfall as the monsoon recedes. Finally, in the monsoonal environment characterized by more dry months than wet, the precipitation isotopic curve also indicates seasonal transitions, although different from the wet monsoonal curves. In New Delhi, which experiences around nine dry months per year, there is a long plateau of enriched values representing dry months, followed by a very sharp drop to depleted values, representing the onset of the monsoon. These depleted values last only a few months, however, before the curve rises very sharply, representing a return to dry months as the monsoon recedes.

The Siwalik precipitation curve is U-shaped, with small enriched plateaus, a gradual increase in precipitation, a short trough, and a gradual rise in values (Fig. 3). This curve looks very much like the wet monsoonal environments of southern China today. It does not look like the curves which result from heavy rainfall year-round, nor does it resemble curves resulting from annual rainfall regimes characterized by more dry months than wet. Furthermore, it reflects a seasonal trend which characterizes places with months considerably drier than 100 mm rainfall and with dry periods of 5 to 6 months.

These results indicate seasons of very heavy rainfall in combination with seasons of considerably less rainfall, or the pattern of monsoonal climates today. These results therefore suggest that the Asian monsoon was probably already in place by 10.0 Ma, and that throughout the record from 10.0 to 6.3 Ma the Siwaliks experienced heavy monsoonal rainfall for at least several months, with 5 to 6 months of dry season per year. The fact that some teeth incorporated only the dry-to-wet transition, while others incorporated both the full wet season and the transition to the dry season suggests that the transition from dry-to-wet took a longer period of time than the transition of wet-to-dry. This discrepancy could represent similarity to the timing of the monsoon in India today, where onset of the monsoon is gradual, but it recedes very quickly (Mooley and Shukla, 1987).

The overall pattern from 10.0 to 6.3 Ma of increasing  $\delta^{18}\text{O}$  values over time but with maintenance of the same magnitude of seasonal variability (amplitude) is the same as the pattern yielded by Nepal bivalve shells spanning 9.5 to 3.1 Ma (Dettman

et al., 2001). Increasing  $\delta^{18}\text{O}$  values suggest a decrease in amount of annual rainfall over time, but no change in curve shape suggests no change in rainfall regime with respect to number of dry vs. wet months. Thus both the Pakistan equid teeth and the Nepal bivalves suggest a monsoonal seasonal regime was established in Asia by 10.0 Ma, and any changes that took place in that regime occurred after the ages sampled in these studies, namely after 6.3 Ma in Pakistan and after 3.1 Ma in Nepal.

These results suggest that *Sivapithecus* lived under a more seasonal rainfall regime than any great ape experiences today, with the exception of the Mt. Asserik chimpanzees (McGrew et al., 1981; Baldwin et al., 1982). Only a few gibbon populations are able to inhabit monsoonal forests today (Chivers, 1984; Kappeler, 1984). These results therefore suggest that either *Sivapithecus* had habitat requirements different from those of modern apes, or alternatively, Siwalik forests under a monsoonal rainfall regime differed in the spatio-temporal availability of fruit compared to modern analogues, thus providing habitat that could support a great ape.

### 3.3. Seasonal birthing

Eleven of fifteen teeth yielded the same seasonal curve, suggesting that not only is the curve an accurate representation of the rainfall regime, but that the rainfall regime was generally highly predictable, a further indication of a monsoonal environment. If rainfall regime was in fact predictable, and if resource availability tracked rainfall, seasonal birthing could track them both. The horse teeth sampled in this study are worn, preventing estimates of crown formation time, but timing of when crown formation stops can be estimated from the final samples from each tooth, those taken at the cervical margin. The sample from this study includes three P3s, two P4s, three M1s, two M2s, and five M3s. When final samples are compared per tooth type, a seasonal signal is apparent, with crown termination ending during particular seasons for each tooth position, although termination time is not completely consistent among the M1s (Fig. 6). All P3s stop crown formation during the dry season. Among P4s, one of the two teeth yields an abnormal curve, but both teeth complete formation during the dry season. Among M1s, two teeth complete develop-

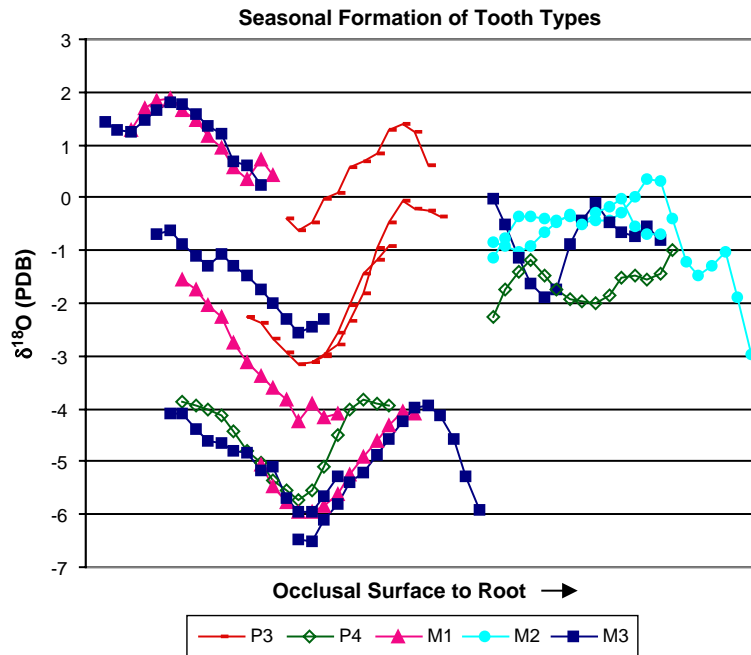


Fig. 6. Profiles of P3s and P4s end around the crest, or most enriched  $\delta^{18}\text{O}$  values, indicating crown completion during the dry season. Profiles of M1s, M2s, and M3s almost all yield curves which end around the trough, or most depleted  $\delta^{18}\text{O}$  values, suggesting crown completion during the wet season. One M1 indicates crown completion during the dry season.

ment during the wet season, while one clearly stops formation during the dry season. The M2s are represented by two teeth with abnormal curves, but they track one another, suggesting similar timing of development, and they complete development during the onset of the wet season. Finally, among the M3s, two teeth complete development during the early wettest season, two stop during the late wettest season, and one tooth is again an abnormal curve.

Among Burchell's zebra today, births can occur in any month, but most births occur during the wet season (Nowack, 1999). The Siwalik teeth are compatible with this flexible pattern of seasonal birthing. The abnormal M1 tooth suggests a different season of development than all other teeth, but there could have been a difference in hypsodonty undetectable in worn teeth. Alternatively, that M1 could have been misidentified to tooth position, but the only other tooth position possible is an M2, and it does not fit the pattern of M2s either. Finally, Hillson (1986) reports crown formation times in cattle, which are also hypsodont and act as a good proxy for horses. In cattle, crown completion occurs between birth and 0.5

years for M1, 0.5–1 year for M2, 1–1.5 years for P3, and 1.5–2 years for P4s and M3s. The Siwalik teeth follow this pattern when mapped onto a two-year seasonal curve, and depleted  $\delta^{18}\text{O}$  values at crown completion time in M1s suggest most births take place around the wet season (Fig. 7).

The pattern of tooth development suggested by isotopic analyses can be compared to two Siwalik fossil juvenile equid maxilla represented by premolars and molars with teeth in different stages of development. In specimen Y49606 from locality Y894 dated to 9.6 Ma, only the M1 and M2 have erupted. P2 and M3 are close to the occlusal surface, but P3 and P4 are far from the occlusal surface. Crown formation has completed in all teeth except the M3. Roots have formed only in the M1. This pattern of development suggests that M1 is completed first, followed by M2, with P2 the next tooth to develop. P3 and P4 appear to develop around the same time, after P2 development, with M3, the only tooth with the crown not yet completed, being the last tooth to develop.

Likewise, specimen Y262 from locality Y017 dated to 8.0 Ma, is represented by deciduous P2,

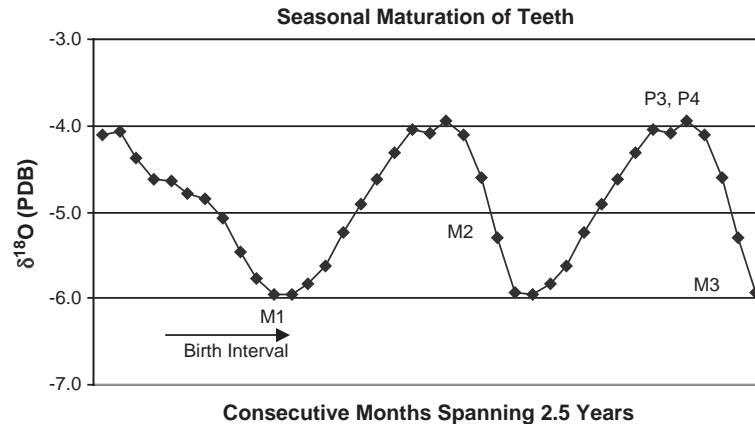


Fig. 7. Timing of crown completion can be inferred from tooth profiles, and when mapped onto a 2.5 year seasonal curve generated from replicating a general Siwalik curve, suggests birthing in the wet season for *Hipparion* with a tooth development trajectory similar to but possibly longer than that of modern cattle (also hypsodont).

P3, and P4 caps, all occluded, and by the M1 and M2. The M1 has erupted, but roots are not yet complete. M2 has not yet reached the occlusal surface. This specimen, like the previous specimen, suggests that M1 is the first tooth to complete development, followed by M2, with premolars developing later. Both specimens are compatible with the tooth development sequence suggested by the isotopic analyses.

#### 4. Conclusions

Eleven of fifteen tooth profiles indicate that intra-tooth sampling of hypsodont teeth can yield accurate representations of the seasonal trends in precipitation. This study indicates that in worn teeth, a greater length of enamel is needed than was suggested by original studies, greater, in fact, than most worn teeth permit. However, by sampling multiple teeth which include an array of premolars and molars, different portions of the annual seasonal signal can be pieced together. Furthermore, this study suggests that there is no detectable weaning effect and all molars can be analyzed.

Change in amount of annual rainfall over time can be estimated by comparing  $\delta^{18}\text{O}$  values of the wettest months and again for the driest months between the most depleted curves, representing the oldest samples, and the most enriched curves, representing the youngest samples. These differences are 5.3‰ and 5.8‰ respectively. An average increase of 5.6‰ can

be translated to a decrease in annual rainfall using the Dansgaard (1964) relationship which indicates a  $-1.5\text{‰}$  shift with every 100 mm of rainfall added in the tropics. This relationship suggests that over the time span of 10.0–6.3 Ma, rainfall in the Siwaliks decreased by approximately 375 mm.

This decrease in rainfall can be interpreted by comparisons of different ecosystems in India today. In a compilation of Indian forests, for those which experience five-month dry periods, a difference of 700 mm in annual rainfall separates semi-evergreen from moist-monsoon forest, and about 300 mm separate moist- from dry-monsoon forest (Walter, 1973). For those forests which experience six-month dry periods, 500 mm separate semi-evergreen and moist-monsoon forests; 400 mm separate moist- and dry-monsoon forest. Savannas in India occur only in regions where at least 7 months of the year are dry, and those regions receive on average several hundred millimeters less rainfall than dry-monsoonal forests.

The Siwalik seasonal precipitation curve interpreted from the tooth profiles most resembles rainfall regimes of southern China today, where monsoonal forests occur. These regions typically experience five-to-six month dry seasons. The decrease in rainfall suggested by the enrichment of  $\delta^{18}\text{O}$  values over time was sufficient, according to modern Indian forest habitats experiencing similar dry periods, to drive a transition in vegetation from moist- to dry-monsoonal forest over time.

The seasonal regime of all the teeth profiled indicate that onset of the Asian monsoon likely occurred prior to 10.0 Ma. A further indication of a monsoonal environment, or one with highly predictable seasons, is a seasonal birthing signal suggested by different tooth positions among the profiles, with most births occurring in the wet season, as African zebras today. This precipitation regime is more seasonal than any great ape experiences today, with the exception of the Mt. Asserik chimpanzees. Therefore, either *Sivapithecus* differed in habitat and feeding requirements from modern apes, or the Miocene forests differed from modern forests in some way which allowed for less variable fruit availability. Dental microwear analyses of Siwalik fauna suggest that *Sivapithecus* and many of its contemporaneous mammalian species were as frugivorous as their rainforest counterparts (Nelson, 2003). One possible scenario that would allow a Miocene monsoon forest to support rainforest species is if *Sivapithecus* inhabited gallery forests, or forests associated with rivers, and these gallery forests were more extensive in the Miocene Siwaliks than in any regions inhabited by great apes today. Forests of modern river basins such as the Amazon or Okavango are characterized by fertile soils which can support greater spatial and temporal availability of fruits and thus might support frugivorous fauna year-round.

While the  $\delta^{18}\text{O}$  values of the profiles indicate a transition from closed to open habitat as well as a decrease in rainfall over time, the youngest curve to fall among the lowest values occurs at 8.3 Ma, suggesting loss of closed habitat around the time *Sivapithecus* went extinct (8.4 Ma) as well as an initial decrease in rainfall. Furthermore, all three samples at 7.7 Ma or younger make up the most positive profiles, indicating a second transition well after *Sivapithecus* went extinct, most likely suggesting a transition from wet- to dry-monsoonal forest accompanied by a decrease in rainfall, with this transition occurring around the time that paleosol carbon isotopes detect the first  $\text{C}_4$  grasses. This transition also coincides with the 7.5 Ma decrease in rainfall detected in the Nepal bivalve shells (Dettman et al., 2001).

Finally, the isotopic results of this equid tooth study can be incorporated into previous isotopic analyses of Siwalik paleosols which were used to

reconstruct vegetation mosaic patterns as well as climate change (Quade and Cerling, 1995). With respect to the  $\text{C}_3/\text{C}_4$  transition, paleosol samples first detect isotopic evidence for  $\text{C}_4$  grasses on the floodplain at 8.1 Ma. The first indisputable dietary evidence for  $\text{C}_4$  graze in mammalian teeth occurs in the 8.7 Ma equid tooth, but somewhat enriched carbon values as early as 9.3 Ma suggest  $\text{C}_4$  grasses may have been a very small component of some diets prior to 8.7 Ma, in agreement with tooth analyses conducted by Morgan (1994). Evidence from the 8.7 Ma equid tooth, sampled multiple times along the length of the tooth, indicates that both  $\text{C}_3$  and  $\text{C}_4$  plants contributed to the diet year-round. However, equid teeth sampled similarly at 8.5, 8.4, and 8.3 Ma indicate periods of the year in which no  $\text{C}_4$  component is present. It is not until 8.0 Ma and later that intra-tooth sampling of every equid tooth detects a  $\text{C}_4$  graze component year-round, that is, in every sample taken from the tooth. Thus, both paleosol and equid enamel isotopic samples indicate the first permanent  $\text{C}_4$  patches around 8.0 Ma or slightly earlier. Even at 8.0 Ma, however, no bovids sampled were feeding on any  $\text{C}_4$  graze, suggesting that  $\text{C}_4$  grasses did not become extensive until some time after 8.0 Ma (Nelson, 2003). Paleosols indicate the first  $\text{C}_4$  dominated habitats around 7.4 Ma, with the last  $\text{C}_3$  dominated habitats at 7.0 Ma and the first  $\text{C}_4$  grasslands at 6.8 Ma (Quade and Cerling, 1995, corrected to Cande and Kent, 1995; summarized in Barry et al., 2002).

Paleosol oxygen isotopic analyses provide evidence of climatic change, with enrichment of  $\delta^{18}\text{O}$  values over time. This shift is sporadic, with both depleted and enriched values present through much of the record, similar to the fluctuating pattern of enrichment detected in horse tooth profiles between 9.3 and 8.4 Ma. These fluctuations probably reflect a highly variable vegetation mosaic, with horses drinking in both closed and open habitats, as well as potential fluctuations in annual rainfall amounts. The oxygen transition begins in the paleosols at 9.2 Ma, with the first  $\delta^{18}\text{O}$  values that are more positive than  $-8\text{‰}$  (Quade and Cerling, 1995, corrected to Cande and Kent, 1995; summarized in Barry et al., 2002). Among the 11 horse tooth profiles that yielded seasonal curves apparently unaffected by tooth histology or buffered water sources, the first shift from depleted curves to moderately enriched ones occurs at

9.3 Ma, in accordance with the 9.2 Ma initial transition observed in the paleosols. Within the paleosol record, almost all samples are greatly enriched after 8.0 Ma compared to older samples. Within the horse tooth profiles, the last depleted curve occurs at 8.3 Ma, and the first highly enriched curve occurs at 7.7 Ma, thus bracketing the enrichment shift observed in the paleosol record. A 3.7‰ enrichment is observed in Late Miocene paleosols. This shift is less than the 5.6‰ shift observed in the horse tooth profiles, but the paleosol shift is confounded by annual seasonal differences, whereas the profiles allow comparisons of particular seasons, such as shifts in  $\delta^{18}\text{O}$  values of the driest or wettest months over time.

Finally, morphology of paleosols corroborates evidence for both a decrease in rainfall throughout the Siwaliks and a seasonal rainfall regime throughout the Late Miocene. Clay minerals from Middle Miocene paleosols older than 14 Ma are dominated by kaolinite, which is present in Indian soils in wet climates (greater than 1000 mm rainfall per year). Kaolinite becomes less dominant over time, suggesting a decrease in rainfall over time (Quade and Cerling, 1995). Furthermore, Quade and Cerling (1995) suggest that the presence of soil carbonates from 12 to almost 2 Ma establishes an upper boundary of 1250 mm annual rainfall throughout the Siwaliks, given that carbonates are not generally present in soils in North America and Europe where rainfall exceeds this amount. This suggested cap on rainfall amounts is compatible with a monsoon forest scenario for the Siwaliks. Finally, in the Chinji Formation (14.2–12 Ma), soil morphology indicates periods of intense oxidation (Behrensmeyer et al., 1995). Behrensmeyer et al. (1995) suggest that a monsoonal rainfall regime with prolonged dry seasons would have promoted seasonal fluctuations in the water tables and resulted in the observed oxidation of organic materials.

Thus isotopic analyses of Siwalik equid teeth, in conjunction with isotopic paleosol evidence from the Siwaliks as well as isotopic analyses of bivalves in Nepal, suggest that the Late Miocene was characterized by a seasonal rainfall regime which was likely monsoonal, with a decrease in rainfall over time accompanied by forest fragmentation and replacement by open habitat, including  $C_4$  grasses. A decrease in rainfall began around 9.3 Ma and took place in

phases, with a second significant decrease in rainfall between 8.0 and 7.7 Ma.  $C_4$  grasses appeared on the floodplain by at least 8.7 Ma, but patches of  $C_4$  grass did not become extensive until after 8.0 Ma. As forests were replaced by more open habitat, closed-habitat species and frugivorous species became extinct. Dental microwear analyses of Siwalik mammals indicate that frugivore extinctions also occurred in phases according to thresholds for different species, with the first phase of most susceptible species including the large-bodied frugivorous hominoid *Sivapithecus* (Nelson, 2003).

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