

Isotopic reconstructions of habitat change surrounding the extinction of *Sivapithecus*, a Miocene hominoid, in the Siwalik Group of Pakistan

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Abstract

This research presents an isotopic study of a wide range of mammalian taxa from the Miocene Siwalik Group of Pakistan, with a focus on two time intervals—9.3–9.2 Ma, when the hominoid *Sivapithecus* was present, and 8.1–8.0 Ma, shortly after *Sivapithecus* became extinct. The purpose of this investigation is to reconstruct the vegetation mosaic at both time levels in order to determine what *Sivapithecus* habitat was like and what changes in habitat and climate may have taken place by the time *Sivapithecus* went extinct. Both carbon and oxygen stable isotopes were sampled from inorganic carbonate in tooth enamel. Results indicate a vegetation mosaic of both closed and open habitat at both time intervals, but a decrease in forest accompanied by an increase in open habitat (including C₄ grasses) during the younger interval. Individuals from many species cluster with each other with respect to both carbon and oxygen isotope values, indicating a spectrum of feeding adaptations exploiting different parts of the habitat. Isotopic values for *Sivapithecus* suggest that it fed in the forest upper canopy. Taxa feeding in the most closed, wet habitat become extinct by 8.1 Ma. Furthermore, higher $\delta^{18}\text{O}$ values over time suggest a change in climate with a reduction in annual rainfall, perhaps accompanied by changes in precipitation sources or rainfall regime as well. These results suggest that forests became fragmented over time. While still present in the younger level, much of the forest was replaced by open habitat, including patches of C₄ grass. Forest loss and fragmentation is a likely cause of the extinction of *Sivapithecus*.

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1. Introduction

Sivapithecus is a Miocene hominoid found in the Siwalik sediments of Pakistan from around 13 Ma to 8.4 Ma (Barry et al., 2002). Its extinction roughly coincides with the disappearance of many other

Miocene apes throughout Europe, Asia, and Africa. Unlike most other Miocene hominoid localities, the Siwalik sequence spans nearly the past 20 million years, thus providing a rare opportunity to examine faunal and environmental changes throughout an ape's existence. This study uses carbon and oxygen stable isotopic compositions of tooth enamel carbonate from Siwalik large mammals to reconstruct and compare faunal paleodiets and habitats for two time intervals within the sequence—a period when *Sivapithecus* material is abundant and an interval shortly after *Sivapithecus* went

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Modern apes are found only in Africa and S.E. Asia where there is rainforest or at least gallery forest, and with few exceptions, where dry seasons last no longer than 4 months. Length of the dry period can have important consequences for apes because all except the mountain gorilla have diets specializing in ripe fruit. *Sivapithecus*' morphology 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 closer to 20 kg. *S. parvada* males were larger, approximating male orangutans (Kelley, 1986). Its molars are low and rounded with thick enamel, and dental microwear analyses suggest a diet of fruit with some hard-object feeding, similar to modern great apes (Kay, 1981; Nelson, 2003). Postcranially, however, *Sivapithecus* is similar to many other Miocene apes in resembling a monkey in many features, suggesting that it was a pronograde quadruped walking above branches more than suspending below them (Kelley and Pilbeam, 1986; Rose, 1986). A study of tooth development suggests that *Sivapithecus* had a life history pattern similar to that of modern apes, with a prolonged growth and maturation period relative to monkeys (Kelley, 1997). This life history pattern and morphology suggests that *Sivapithecus* was a large-bodied frugivore susceptible to periods of ripe fruit shortage. However, reconstructions of paleoprecipitation regimes based on oxygen isotopes of Siwalik equid teeth suggest that *Sivapithecus* experienced longer dry seasons than do modern apes, with dry seasons lasting 5 to 6 months, much like the climate regime in monsoon forests of southern China today (Nelson, 2005). Given the discrepancy between a frugivorous modern ape diet suggested by microwear and a precipitation regime that would likely not support modern ape habitat, this isotopic investigation seeks to reconstruct the vegetation mosaic as experienced by herbivorous mammals moving about the landscape.

Analyses of modern herbivores have shown that the carbon isotopic composition of body tissues reflects the carbon composition of vegetation eaten during tissue formation (DeNiro and Epstein, 1978; Van der Merwe and Vogel, 1978; Van der Merwe, 1982). Likewise, tissue oxygen isotope ratios provide information on the oxygen composition of water intake during develop-

ment (Longinelli, 1984; Luz et al., 1984; Luz and Kolodny, 1985). Tooth enamel in particular has been used to reconstruct paleodiets, habitats, and climatic change (Lee-Thorp et al., 1989; Cerling et al., 1997), for unlike fossilized bone, it is far less susceptible to diagenesis (Quade et al., 1992; Ayliffe et al., 1994; Wang and Cerling, 1994; Koch et al., 1997).

Carbon isotopes are informative for both paleodietary and paleohabitat reconstructions due to differences in carbon assimilation between different plants. Most terrestrial plants assimilate atmospheric CO₂ by one of two photosynthetic pathways. C₃ plants, which include almost all trees and shrubs, and only those grasses favored by cool, wet growing seasons, utilize the enzyme ribulose biphosphate carboxylase-oxygenase (Rubisco) to fix CO₂, forming a three-carbon sugar. C₄ plants, which include exclusively grasses and sedges growing in hot, dry habitats, use a different enzyme to fix CO₂, phosphoenolpyruvate (PEP) carboxylase, resulting in a four-carbon acid (Farquhar et al., 1989). These two photosynthetic pathways yield greatly different $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}$ is the ratio of ¹³C to ¹²C relative to a standard, in this case Pee Dee Belemnite or PDB), with C₃ plants falling between –22‰ and –35‰, and C₄ plants ranging between –10‰ and –15‰ (Bender, 1971; Vogel, 1980). A third photosynthetic pathway, known as CAM plants (crassulean acid metabolism) is ignored in this study, for they are xeric-adapted desert succulents not likely to have been present in significant abundance in the Siwaliks.

The non-overlapping $\delta^{13}\text{C}$ values of C₃ versus C₄ plants allows discrimination of browsing versus grazing diet from analyses of tooth enamel beginning with the first appearance of C₄ grasses in the Late Miocene. Enamel bioapatite records the carbon signal obtained from vegetation eaten, with an enrichment in $\delta^{13}\text{C}$ due to fractionation from metabolic processes. The enrichment factor for all taxa analyzed in this Siwalik study is assumed to be 14‰, as found by Cerling et al. (1999) in an extensive analysis of ungulates. It should be noted, however, that these ungulates were all ruminant foregut fermenters, and suids and primates may have slightly lower enrichment factors due to a different digestive system, though this remains to be determined. Thus, enamel with a $\delta^{13}\text{C}$ of –14‰ for any Siwalik taxa is taken to indicate a diet of plants averaging –28‰, or C₃ browse.

The C₃/C₄ distinction is useful for paleoenvironmental as well as dietary inferences, for the C₄ photosynthetic pathway is energetically expensive compared to the C₃ pathway and is only competitively advantageous in hot, dry climates. Carbon dioxide enters a leaf

through its stomata, but stomata must remain closed much of the time to conserve water in hot, dry climates. The enzyme used by C_4 plants has a higher affinity for CO_2 than does the C_3 enzyme, thus allowing the plant to take up more CO_2 when the stomata are open (Ehleringer et al., 1991). Furthermore, this concentrated version yields a ratio of CO_2 to O_2 high enough that little CO_2 is lost to photorespiration. These energetically expensive adaptations allow C_4 plants to function better than C_3 plants under high moisture stress during warm/hot growing seasons. However, because of the energetic tradeoff, C_4 plants are restricted to warm, relatively dry regions, with C_3 plants competitively superior in all other habitats.

Not only is the distinction between C_3 and C_4 significant, but the wide range of $\delta^{13}C$ values displayed by C_3 plants is an indication of vegetation type as well. Variability in $\delta^{13}C$ values among C_3 plants is a response to variation in irradiance and moisture stress as well as to CO_2 trapping under forest canopies (Ehleringer et al., 1986, 1987; Van der Merwe and Medina, 1989; Quade et al., 1995b). Ehleringer et al. (1987, 1986) studied monsoon forests in China and found that plants in relatively closed canopy versus open canopy differed in $\delta^{13}C$ values by several per mil on average. For any given plant species, individuals growing in open habitats yielded consistently higher $\delta^{13}C$ values than those growing under closed canopy, with those growing under intermediate coverage having intermediate $\delta^{13}C$ values. Habitat alone does not explain all of the variance, however. Ehleringer et al. (1986) found that among ten species, a range of 2–3‰ in carbon values was found for any given habitat (closed or open). When over 100 plant species were sampled in a subsequent study (Ehleringer et al., 1987), a range of 6–7‰ was found within a given habitat, though again, each species showed consistent enrichment with decreasing coverage. Thus $\delta^{13}C$ values of plants respond to differences in habitat, but habitat alone does not explain the entire variability of carbon values observed for C_3 plants.

Among herbivores feeding in different habitats (closed versus open), $\delta^{13}C$ values of tooth enamel respond to the differences in vegetation. Van der Merwe and Medina (1989) demonstrated that in a Brazilian rainforest, fauna foraging in forest openings showed a 2‰ enrichment in bone collagen relative to fauna foraging in relatively closed forest. Furthermore, in dense closed canopy forests in which little light penetrates to the ground, and exchange of CO_2 in forest floor air with open tropospheric air is inhibited, carbon values for both the vegetation and fauna feeding are even more depleted (Cerling et al., 1997). Medina et al. (1986)

reported vegetation $\delta^{13}C$ values as low as –36‰ for forest floor vegetation in Venezuela, compared to values as high as –29‰ at the upper canopy, while Harris and Cerling (2002) have found forest hog (*Hylochoerus*) enamel from the Ituri forest as low as –23‰, meaning it ate vegetation as low as –37‰. Thus $\delta^{13}C$ variability in C_3 plants translates into variability among fauna. Furthermore, very closed canopy forests yield a uniquely low $\delta^{13}C$ signal that should be detectable in the fossil record.

This range in $\delta^{13}C$ values for C_3 browse has in fact been used in reconstructing Miocene paleoenvironments. Quade et al. (1995b) have found consistent differences in $\delta^{13}C$ values between different Miocene browsers at Pasalar, a 15 Ma site in Turkey, suggesting that some taxa fed predominantly in open habitats, while others fed in closed habitats. Likewise, an isotopic study of fauna from Fort Ternan, a 14 Ma Kenyan site, yielded $\delta^{13}C$ values ranging from –13‰ to –8.6‰, suggesting a woodland/forest habitat with no closed canopy (Cerling et al., 1997).

In the Siwalik Group of Pakistan, carbon isotopes of paleosols, tooth enamel, and fossil avian eggshells have been used to reconstruct paleohabitats. Paleosol $\delta^{13}C$ ratios reflect the isotopic composition of vegetation growing above the site of soil formation, with about a 15‰ enrichment due to fractionation effects of gaseous diffusion and equilibrium exchange (Quade and Cerling, 1995; Quade et al., 1995a). Thus, soil carbonate formed in the presence of pure C_3 vegetation would have an average $\delta^{13}C$ (PDB) value of around –13‰, while pure C_4 biomass would yield values around +2‰. $\delta^{13}C$ values above –9‰ may indicate a small amount of C_4 (Quade et al., 1989; Quade and Cerling, 1995). Paleosol carbonates in the Siwalik Group indicate a relatively rapid shift in carbon values during the Late Miocene (Quade et al., 1989, 1992; Quade and Cerling, 1995). The results were originally calibrated to the Berggren et al. (1985) timescale but have since been recalculated by Barry et al. (2002) using the Cande and Kent (1995) timescale. The beginning of the paleosol carbon shift from C_3 to C_4 vegetation occurs around 8.1 Ma, and the biomass becomes pure C_4 by 5.9 Ma. However, this shift is complex, with low $\delta^{13}C$ values even after 7.4 Ma, indicating patches of C_3 , and higher values indicating pure C_4 grasslands as early as 6.8 Ma.

Previous tooth enamel and eggshell data have also shown this carbon transition from C_3 browse to mixed and C_4 grazing diets, with a distinct shift in $\delta^{13}C$ values after 8 Ma (adjusted to Cande and Kent, 1995), similar to the paleosol data (Morgan et al., 1994; Stern et al., 1994). These studies yield $\delta^{13}C$ values as high as –8‰

to -9% before the 8 Ma transition, suggesting C_4 graze may have been a minor component before 8 Ma. Only equids yield a clear C_4 grazing signal in their diets prior to 8 Ma, with a mixed C_3 – C_4 diet appearing as early as 8.7 Ma (Nelson, 2005). It is possible that these early C_4 grasses were simply not sampled in the paleosol record, or soils associated with this vegetation may not have preserved the carbonate nodules necessary for isotopic analyses.

In addition to carbon isotopes, oxygen isotopes are also useful in reconstructing diets and habitats as well as paleoclimatic change, but they have received less attention from paleontologists because their interpretation is not straightforward. The $\delta^{18}\text{O}$ value of body water, and hence tooth enamel, is determined largely by the oxygen isotopic composition of ingested water, both in drinking water and in plants eaten, with a minor contributing component being metabolic processes which vary among species (Luz et al., 1984; Luz and Kolodny, 1985). The $\delta^{18}\text{O}$ value of environmental water, in turn, is controlled by the $\delta^{18}\text{O}$ value of local precipitation, with water sources potentially later modified by evaporative effects (Longinelli, 1984; Quade et al., 1995a).

Due to evaporative effects, certain caveats must apply when interpreting oxygen ratios. These include differences between depleted permanent water sources and enriched ephemeral ones, differences between depleted well-shaded sources and enriched open sources, and potential similarities between depleted permanent sources and depleted well-shaded ones. Furthermore, there are differences between obligate drinkers versus animals that obtain all of their water from foliage. Herbivores that obtain most of their water from plant sources have oxygen values reflecting not only $\delta^{18}\text{O}$ values of local rainwater, but also environmental relative humidities which affect oxygen enrichment in plant leaves via evapotranspiration (Ayliffe et al., 1992). A sample across different Australian climates of macropods, known to obtain at least 40% of their ingested water from vegetation, yielded a range in $\delta^{18}\text{O}$ values of bone phosphate that was greater than the range of values for Australian rainwater (Ayliffe and Chivas, 1990). Thus differences in $\delta^{18}\text{O}$ values among fauna can often be interpreted in several different ways, including differences in habitat and differences in water dependence (Bocherens et al., 1996; Kohn, 1996; Sponheimer and Lee-Thorp, 1999).

Nonetheless, changes in $\delta^{18}\text{O}$ values over time can suggest changes in paleoclimates, and consistent differences in $\delta^{18}\text{O}$ values between taxa are useful for inferring closed versus open habitat preferences. For example, both Cerling et al. (1997) and Quade et al.

(1995b) found that Miocene giraffids at Fort Ternan and Pasalar yielded very high $\delta^{18}\text{O}$ values compared to contemporaneous fauna, consistent with feeding in dry, open canopy tops. These high values are also consistent with feeding habits of modern giraffes, who obtain much of their water from canopy foliage (Quade et al., 1995b; Zazzo et al., 2000). Furthermore, oxygen values at Pasalar, like the carbon values, were consistently different between some taxa, suggesting some were drinking in open habitats, others, in well-shaded areas (Quade et al., 1995b).

In addition to reconstructing vegetation mosaics via inter-species variability, changes in $\delta^{18}\text{O}$ values over evolutionary time suggest changes in climate, or more specifically, changes in temperature or rainfall regime. 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, oxygen values respond to seasonal variability in temperature, for temperature varies more on an annual basis than does amount of rainfall. In temperate regions, renewal of vapor from the air by condensation is affected by cooling; therefore, oxygen isotopes can track changes in temperature due to differences in evaporative pressure between ^{18}O and ^{16}O (Yurtsever and Gat, 1981). In the tropics, where rainfall is more variable than temperature, oxygen values track changes in rainfall, for ^{18}O precipitates more readily than ^{16}O ; therefore, the more it rains, the less ^{18}O is present in atmospheric water, and the more depleted subsequent precipitation becomes (Dansgaard, 1964).

Most research on changes in oxygen values over time in terrestrial records has involved studies of paleosols or fossil bivalve shells. Plants do not fractionate oxygen during water uptake; therefore, oxygen isotopic values of paleosols are determined only by the $\delta^{18}\text{O}$ value of meteoric water at the site, by the subsequent evaporation, and by temperature. In the Siwalik Group of Pakistan, paleosols indicate a shift in $\delta^{18}\text{O}$ values beginning around 9.15 Ma, with $\delta^{18}\text{O}$ values becoming higher over time (Quade et al., 1989; Quade and Cerling, 1995). This shift appears as suddenly as the carbon shift, but it precedes the carbon shift by 1.1 Ma. The oxygen shift also lasts longer than the carbon shift and appears to take place in phases, with most of the enrichment occurring by 8.0 Ma, and another pulse after 6.0 Ma. Quade and Cerling (1995) outline a number of possible factors that could have resulted in the enrichment, including an increase in temperature by 5 °C; a decrease in rainfall, with a reduction by 250 mm between 8.5 and 6 Ma; a change in the source of precipitation, with the rise of the Himalayas blocking northern storms, thus restricting rain

sources to the southern, more enriched storms; or more likely, a combination of factors including a decrease in rainfall and increasing seasonality of rainfall with increasing strength of the Asian monsoon. A study of oxygen isotopes in Siwalik equid teeth indicate a monsoonal rainfall regime as early as 10 Ma, with a decrease in rainfall occurring in phases, as suggested by paleosols (Nelson, 2005). The equid tooth study suggests a 375 mm decrease in rainfall from 10.0 to 6.3 Ma, enough to drive a transition in vegetation from moist- to dry-monsoonal forest. Finally, both Siwalik oxygen isotope studies are compatible with foraminiferal records which show the initiation of strong summer Arabian 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). Furthermore, Miocene deposits in Nepal show a 3‰ enrichment in oxygen isotopes of fossil bivalve

shells around 7.5 Ma, also suggesting aridification (Dettman et al., 2001).

The inferred increase in seasonality, aridification, and summer rainfall suggested by Siwalik paleosol, equid, and bivalve oxygen isotopes would have favored C_4 plants, and hence more open habitats, over C_3 plants and closed forest. The Siwalik sediments are ideal for analyzing climate, vegetation, and faunal change through time, for they comprise one of the best known terrestrial records spanning the past 20 million years. These sediments are well exposed throughout the Potwar Plateau of Pakistan with minimal deformation, great thickness, and lateral continuity allowing for detailed and temporally resolved studies of stratigraphic sections (Barry et al., 2002) (Figs. 1 and 2). The Siwalik fossil record now includes tens of thousands of specimens from over 1000 localities, with many of these localities dated to within a 100,000-year resolution (Barry et al., 2002).

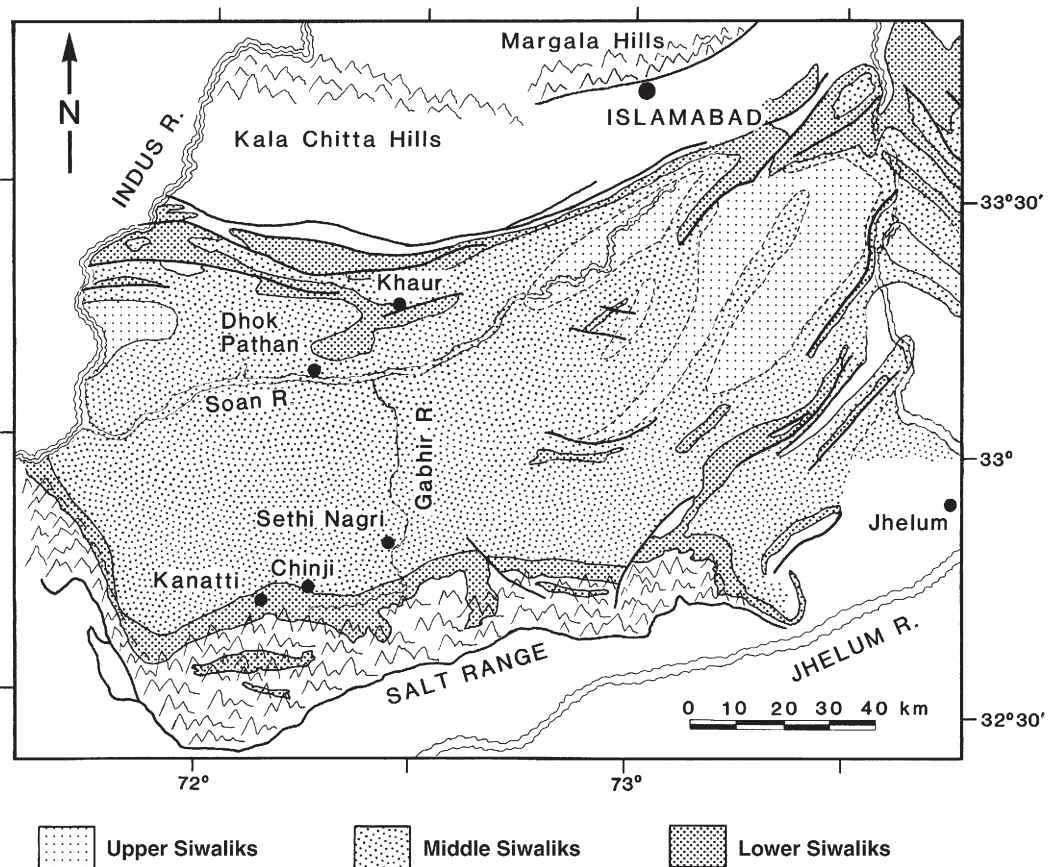


Fig. 1. The Siwalik sediments of northern Pakistan span hundreds of kilometers across the Potwar Plateau. Deposits and formations are named after nearby towns. Map copyright and courtesy of C.E. Badgley and *Palaeogeography, Palaeoclimatology, Palaeoecology*. From Badgley and Behrensmeier (1995).

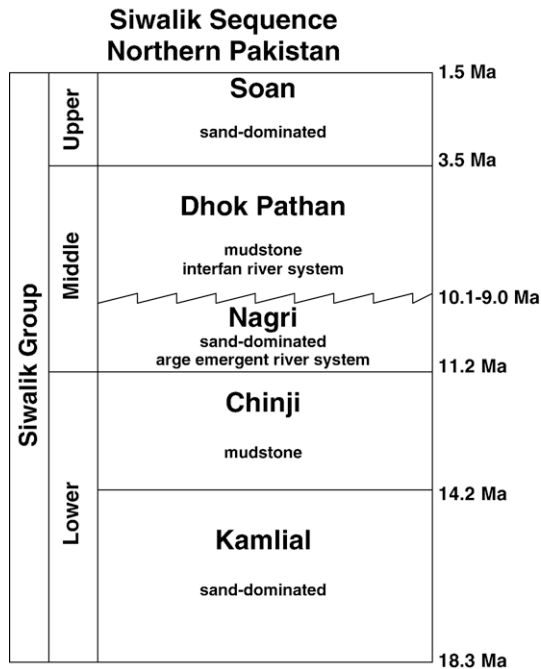


Fig. 2. Formations of the Siwaliks are characterized by kilometer-scale alternations in lithologies that represent changes in channel belts over time. Overlap in ages between the Nagri and Dhok Pathan represents time transgression.

This Siwalik isotopic investigation of mammalian tooth enamel seeks to reconstruct the C_3/C_4 transition over two time intervals in addition to changes in the ratio of closed to open habitat and any corresponding climatic shifts. This isotopic investigation seeks to determine what *Sivapithecus*' habitats were like and whether changes in habitat, such as loss of forest, led to its extinction.

2. Materials and methods

A total of 101 fossil teeth from 17 taxa were selected from two time intervals, 9.3–9.2 Ma, referred to here as the *Sivapithecus*-level (S-level), and 8.1–8.0 Ma, or the post-*Sivapithecus* level (PS-level). These intervals from the Dhok Pathan and Khaur regions of the Siwalik Group were chosen because both are comparably abundant in fossils and have been well surveyed (Figs. 1 and 2). Furthermore, much of the *Sivapithecus* material found comes from the S-level, suggesting this was a period of relative abundance for the ape, and *Sivapithecus* went extinct around 8.4 Ma, not long before the fossiliferous younger level was sampled. Thus from the two time intervals, environmental inferences can be made for the habitat when *Sivapithecus* was at its prime,

and again just after *Sivapithecus* went extinct. All teeth sampled were either premolars or molars, and all came from different individuals, except where noted for seven bovid specimens. Taxa represented include *Sivapithecus*, the suoids *Propotamochoerus hysudricus*, *Hippopotamodon sivalense*, *Tetraconodon magnus*, and *Schizochoerus gandakasensis*; anthracotheres (an extinct group possibly related to Hippopotamidae) *Microbunodon punjabiense* and *Merycopotamus* sp.; proboscideans known as gomphotheres and deinotherids; a giraffid *Bramatherium megacephalum*; rhinocerotids; a chalicothere (a fossil perissodactyl with long forelimbs and short hindlimbs); the bovids *Tragocericus* spp. and *Dorcadoxa porrecticornis*; the tragulids *Dorcabune nagrii* and *Dorcotherium majus*; and the equid genus *Hipparion*. The taxa included are all the large mammal herbivores present at the two levels which had enamel thick enough to sample. The large taxonomic range represents most of the community, with small mammals, carnivores, very small tragulids and bovids, and bovids of unknown taxonomy excluded.

Samples of pure enamel were removed from teeth using a Dremel high-speed rotary tool with a tungsten-carbide or diamond-impregnated bit. Samples were taken along the horizontal axis of the tooth from an area about the size of a grain of rice. In an initial isotopic analysis of some of the horse teeth, CO_2 was extracted from carbonate by reacting it with phosphoric acid and isolating it cryogenically. All other samples were run using an automated carbonate microsample device. For those samples extracted cryogenically, 30–50 mg of tooth enamel were ground, washed with 3% hydrogen peroxide for 1 h to remove organic matter, rinsed

Table 1
Comparison of cryogenic and automated carbonate microsample methods used to sample equid teeth

Specimen	Samples	Cryo $\delta^{13}C$	Auto $\delta^{13}C$	Cryo $\delta^{18}O$	Auto $\delta^{18}O$
Y11881	Same tooth	-10.8	-11.5	-6	-6
Y19810	Same tooth	-8.7	-9.2	-3.5	-2.6
Y49548	Same individual	-7.8	-7.8 to -5	-3.3	-3.2 to 0.6
Y50803	Same individual	-6.5	-7.6 to -5.4	-5	-2.7 to 0.4

The microsample method was used only for tooth profiles in which teeth were sampled at least twelve times down the length of the tooth. When the same tooth was sampled by both methods, the average for the same level along the length of the tooth is reported for the microsample profiles as for the one cryogenic sample. When different teeth from the same individual are sampled, the range for the microsample profiles is reported.

Table 2

Carbon and oxygen isotopic values for taxa in the S-level (9.3–9.2 Ma) and the PS-level (8.1–8.0 Ma)

Sample no.	Locality	Taxon	Age	$\delta^{13}\text{C}$ (PDB)	$\delta^{18}\text{O}$ (PDB)
Y47024	Y317	<i>Sivapithecus</i>	9.3–9.2	-12.4	-0.9
Y13933	Y260	<i>Sivapithecus</i>	9.3–9.2	-13.1	-1.9
Y47023	Y182	<i>Sivapithecus</i>	9.3–9.2	-12.8	-1.7
Y47021	Y182	<i>Sivapithecus</i>	9.3–9.2	-13.9	-6.0
Y13811	Y224	<i>Sivapithecus</i>	9.3–9.2	-12.7	-2.7
Y51694	Y545	Rhinoceros	8.1–8.0	-10.9	-3.3
Y51551	Y542	Rhinoceros	8.1–8.0	-11.7	-3.6
Y51734	Y889	Rhinoceros	8.1–8.0	-13.3	-4.3
Y51572	KL11A	Rhinoceros	8.1–8.0	-11.4	-3.2
Y51776	Y1000	Rhinoceros	8.1–8.0	-8.3	-3.4
SN2	Y260	Gomphothere	9.3–9.2	-12.0	-5.5
Y5290	Y211	Gomphothere	9.3–9.2	-12.0	-5.8
Y11022	Y313	Gomphothere	9.3–9.2	-11.6	-6.5
SN1	KL01	Gomphothere	9.3–9.2	-10.1	-4.1
Y51576	Y539	Gomphothere	8.1–8.0	-11.3	-5.9
Y51774	Y1000	Gomphothere	8.1–8.0	-12.0	-1.0
Y51559	KL11A	Gomphothere	8.1–8.0	-11.0	-7.0
Y51782	Y547	Gomphothere	8.1–8.0	-12.2	-6.6
Y51704	Y545	Gomphothere	8.1–8.0	-9.6	-3.9
Y16986	Y545	Deinotherium	8.1–8.0	-11.7	0.0
Y3548	Y163	<i>B. megacephalum</i>	9.3–9.2	-14.6	-2.0
Y16759	KL03	<i>B. megacephalum</i>	9.3–9.2	-13.2	-2.0
Y10296	Y309	<i>B. megacephalum</i>	9.3–9.2	-10.7	-1.9
Y40145	Y403	<i>B. megacephalum</i>	9.3–9.2	-10.2	-2.0
Y11678	Y317	<i>B. megacephalum</i>	9.3–9.2	-10.2	-3.2
Y5694	Y017	<i>B. megacephalum</i>	8.1–8.0	-14.2	1.3
Y18385	Y605	<i>B. megacephalum</i>	8.1–8.0	-10.7	-0.3
Y2798	Y019	<i>B. megacephalum</i>	8.1–8.0	-11.1	-0.2
Y18412	Y605	<i>B. megacephalum</i>	8.1–8.0	-10.9	-0.9
Y14502	Y269	<i>P. hysudricus</i>	9.3–9.2	-11.0	-6.9
Y41368	Y269	<i>P. hysudricus</i>	9.3–9.2	-12.9	-9.2
Y4554	Y182	<i>P. hysudricus</i>	9.3–9.2	-12.6	-5.4
Y6753	Y227	<i>P. hysudricus</i>	9.3–9.2	-11.0	-5.7
Y10224	Y309	<i>P. hysudricus</i>	9.3–9.2	-12.0	-8.4
Y11007	Y314	<i>P. hysudricus</i>	9.3–9.2	-11.2	-8.2
Y351	Y024	<i>P. hysudricus</i>	8.1–8.0	-10.5	-5.0
Y51554	Y542	<i>P. hysudricus</i>	8.1–8.0	-11.8	-4.0
Y51700	Y545	<i>P. hysudricus</i>	8.1–8.0	-11.8	-5.9
Y49515	Y599	<i>P. hysudricus</i>	8.1–8.0	-10.2	-3.6
Y31474	Y545	<i>P. hysudricus</i>	8.1–8.0	-11.0	-2.7
Y13524	Y239	<i>H. sivalense</i>	9.3–9.2	-10.8	-7.3
Y47176	Y159	<i>H. sivalense</i>	9.3–9.2	-11.4	-6.6
Y12708	Y260	<i>H. sivalense</i>	9.3–9.2	-11.7	-4.5
Y5276	Y211	<i>H. sivalense</i>	9.3–9.2	-9.4	-7.0
Y4226	Y182	<i>H. sivalense</i>	9.3–9.2	-10.8	-5.1
Y27915	Y260	<i>H. sivalense</i>	9.3–9.2	-11.2	-5.7
Y51745	Y599	<i>H. sivalense</i>	8.1–8.0	-10.8	3.5
Y330	Y017	<i>H. sivalense</i>	8.1–8.0	-11.1	-4.1
Y17069	Y315	<i>T. magnus</i>	9.3–9.2	-12.8	-3.4
Y4630	Y182	<i>S. gandakasensis</i>	9.3–9.2	-13.0	-5.1
Y14499	Y269	<i>S. gandakasensis</i>	9.3–9.2	-13.1	-9.2
Y5124	Y211	<i>M. punjabiense</i>	9.3–9.2	-11.5	-7.2
Y9799	Y269	<i>M. punjabiense</i>	9.3–9.2	-12.3	-5.8
Y11797	Y317	<i>M. punjabiense</i>	9.3–9.2	-12.1	-6.9
Y47066	Y317	<i>Merycopotamus</i>	9.3–9.2	-8.5	-5.8
Y27044	Y224	<i>Dorcabune nagrii</i>	9.3–9.2	-11.0	-6.5

Table 2 (continued)

Sample no.	Locality	Taxon	Age	$\delta^{13}\text{C}$ (PDB)	$\delta^{18}\text{O}$ (PDB)
Y6857	Y227	<i>Dorcabune nagrii</i>	9.3–9.2	-10.6	-2.4
Y11155	Y310	<i>Dorcabune nagrii</i>	9.3–9.2	-9.9	-1.6
Y10220	Y309	<i>Dorcabune nagrii</i>	9.3–9.2	-11.1	-8.2
Y10886	Y312	<i>Dorcatherium majus</i>	9.3–9.2	-10.6	-2.2
Y10965	Y314	<i>Dorcatherium majus</i>	9.3–9.2	-10.5	-3.6
Y7310	Y227	<i>Dorcatherium majus</i>	9.3–9.2	-12.7	0.5
Y50921	Y227	<i>Dorcatherium majus</i>	9.3–9.2	-10.6	-8.3
Y5567	Y310	<i>Dorcatherium majus</i>	9.3–9.2	-11.1	-5.6
Y499	Y024	<i>Dorcatherium majus</i>	8.1–8.0	-10.5	-3.8
Y16270	Y539	<i>Dorcatherium majus</i>	8.1–8.0	-8.8	-2.5
Y16236	Y540	<i>Dorcatherium majus</i>	8.1–8.0	-10.6	-1.7
Y49530	Y888	<i>Dorcatherium majus</i>	8.1–8.0	-9.9	-2.4
Y679	Y033	<i>Dorcatherium majus</i>	8.1–8.0	-10.5	-2.4
Y19770	Y240	Chalicothere	9.3–9.2	-11.0	-3.3
Y19802	Y182	Chalicothere	9.3–9.2	-11.1	-3.8
Y5127-	Y211	<i>Tragocericus</i>	9.3–9.2	-11.6	-6.7
M2					
Y5127-	Y211	<i>Tragocericus</i>	9.3–9.2	-11.5	-3.5
M3					
Y15118-	Y227	<i>Tragocericus</i>	9.3–9.2	-11.7	0.3
M3					
Y11593-	Y227	<i>Tragocericus</i>	9.3–9.2	-11.7	-4.4
M2					
Y11593-	Y312	<i>Tragocericus</i>	9.3–9.2	-10.7	0.7
M3					
Y9203-	Y017	<i>Tragocericus</i>	8.1–8.0	-11.0	-7.0
M2					
Y9203-	Y017	<i>Tragocericus</i>	8.1–8.0	-10.0	0.5
M3					
Y717011	Y545	<i>Tragocericus</i>	8.1–8.0	-12.4	-6.5
Y9208	Y017	<i>Tragocericus</i>	8.1–8.0	-10.3	0.1
Y51687	Y545	<i>Tragocericus</i>	8.1–8.0	-10.1	0.9
Y263-M2	Y017	<i>Tragocericus</i>	8.1–8.0	-11.1	-5.1
Y263-M3	Y017	<i>Tragocericus</i>	8.1–8.0	-9.8	-1.3
Y17007	Y545	<i>Tragocericus</i>	8.1–8.0	-12.0	-1.9
Y2817-	Y017	<i>D. porrecticornis</i>	8.1–8.0	-10.9	1.6
M2					
Y2817-	Y017	<i>D. porrecticornis</i>	8.1–8.0	-9.6	-3.6
M3					
Y461-M2	Y024	<i>D. porrecticornis</i>	8.1–8.0	-11.9	-3.2
Y461-M3	Y024	<i>D. porrecticornis</i>	8.1–8.0	-10.7	-8.0
Y9207-	Y017	<i>D. porrecticornis</i>	8.1–8.0	-10.3	-1.1
M2					
Y9207-	Y017	<i>D. porrecticornis</i>	8.1–8.0	-10.6	-4.3
M3					
Y49550	Y606	<i>D. porrecticornis</i>	8.1–8.0	-9.3	-3.2
Y19813	Y312	<i>Hipparion</i>	9.3–9.2	-9.5	-1.5
Y47080	Y312	<i>Hipparion</i>	9.3–9.2	-8.1	-2.6
Y19810 ^a	Y312	<i>Hipparion</i>	9.3–9.2	-9.2	-1.6
Y19810	Y312	<i>Hipparion</i>	9.3–9.2	-8.7	-3.5
Y46248	Y418	<i>Hipparion</i>	9.3–9.2	-9.1	-4.9
Y49674	Y542	<i>Hipparion</i>	8.1–8.0	-5.3	-1.3
Y18418	Y606	<i>Hipparion</i>	8.1–8.0	-7.7	-1.9
Y17859	Y599	<i>Hipparion</i>	8.1–8.0	-5.9	-2.7
Y49548 ^a	Y890	<i>Hipparion</i>	8.1–8.0	-6.5	-0.8
Y49548	Y890	<i>Hipparion</i>	8.1–8.0	-7.8	-3.3

^a Average of multiple samples taken along full length of tooth.

thoroughly with distilled water, and washed with 1 M acetic acid for 1 h to remove surficial carbonates, followed by a thorough rinse with distilled water and finally, ethanol. They were then reacted with 100% phosphoric acid at 25 °C for 48 h, and the evolved CO₂ was subsequently isolated cryogenically, reacted with Ag wool to remove any SO₂, and analyzed on a Finnigan delta S stable isotope ratio mass spectrometer. For all other samples, only 0.5–0.7 mg were required, and these samples were washed with 3% hydrogen peroxide for 15 min and rinsed, followed by 0.1 M acetic acid for 15 min and rinsed. Samples were then reacted with 100% phosphoric acid at 90 °C on the automated carbonate device interfaced with a Finnigan MAT 252 stable isotope ratio mass spectrometer. Isotopic ratios are presented in the per mil (‰) notation

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

where R_{sample} and R_{PDB} are the ratios $^{13}\text{C}/^{12}\text{C}$ (or $^{18}\text{O}/^{16}\text{O}$) in the sample and standard respectively, and the isotope reference standard is PDB. Oxygen values are reported assuming the acid-calcite fractionation factor for calcite of 1.00799.

While two different methods were used to obtain the equid values, when both methods were performed on the same tooth or teeth from the same jaw, they yielded comparable results in almost all cases (Table 1). For Y50803, the $\delta^{18}\text{O}$ values from the two different methods could be very different due to the fact that for the cryogenic method, the sample was taken at the root of the tooth, and the root develops much later than the crown (Hillson, 1986). The cryogenic method did yield slightly more depleted $\delta^{18}\text{O}$ values for some of the other teeth as well, but the difference between the two methods is generally minimal.

3. Results and discussion

Carbon and oxygen results are first presented for the S-level to provide a reconstruction of the vegetation mosaic at a time when *Sivapithecus* was present. Results are then reported for the PS-level to reconstruct the vegetation mosaic just after *Sivapithecus* went extinct. Changes in habitat are then inferred from a comparison of the two time levels, and climatic changes are inferred from differences in oxygen isotopic values between the two levels.

Carbon values are interpreted based upon certain cutoff values for diets of C₃ versus C₄ vegetation as well as for closed versus open habitat. The $\delta^{13}\text{C}$ values for tooth apatite for pure C₃ modern diets in general range

from approximately –20‰ to –8‰, with the extremes representing distinctive habitats, low values very closed canopy rainforest and high values very open habitat (Cerling et al., 1997). A pure C₄ diet, on the other hand, yields $\delta^{13}\text{C}_{\text{(apatite)}}$ values from +1‰ to +4‰. Modern $\delta^{13}\text{C}$ values are depleted by 1.5‰ 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‰ today, or the most enriched pure C₃ diets, is comparable to a Miocene value of –6.5‰. For the purposes of this analysis, a cutoff $\delta^{13}\text{C}$ value of –7.5‰ is used to distinguish evidence of at least some C₄ in the diet. In terms of habitat, $\delta^{13}\text{C}$ values below –12‰ represent closed habitat, while those above –10‰ suggest affinities for more open habitat (Quade et al., 1995b).

3.1. The S-level (9.3–9.2 Ma)

The $\delta^{13}\text{C}$ results for the S-level fall between –14.6‰ and –8.1‰, for a range of 6.5‰ and a mean of –11.3‰, indicating a predominantly, if not entirely, C₃ habitat (Table 2 and Fig. 3). The highest values from the S-level are greater than –10‰ and therefore suggest that some animals, in this case *Hipparion*, an equid (average –8.9‰), and *Merycopotamus*, an anthracothere (–8.5‰), fed in open habitats, where plants are under high water and light stress. These results could also potentially indicate grazing on C₃ grasses if open C₃ grasslands were part of the Miocene landscape. Alternatively, the high values could suggest diets containing a small percentage of C₄ grass. The lowest $\delta^{13}\text{C}$ values, those below –12‰ (found for *Sivapithecus*, gomphotheres; the giraffid *Bramatherium*; the suoids *Propotamochoerus*, *Tetraconodon*, and *Schizochocerus*; the anthracothere *Microbunodon*; and the tragulid *D. majus*), are consistent with closed woodland or forest habitat, though none indicate a closed canopy with little light penetration or lack of exchange of forest and tropospheric CO₂.

The $\delta^{18}\text{O}$ values for the S-level fall between –9.2‰ and +0.7‰, for a range of 9.9‰, and an average of –4.5‰. For several taxa, individuals cluster in their $\delta^{13}\text{C}$ and/or $\delta^{18}\text{O}$ values, suggesting that they fed in particular parts of the habitat. For example, *Hipparion* specimens have the highest carbon and oxygen values, suggesting they prefer more open, drier patches of the vegetation mosaic. Furthermore, some taxa are isotopically distinctive from others (Fig. 4). These results are a good indication that true dietary signals are being preserved, for diagenetic alteration would have led to isotopic homogeneity rather than clustering by taxa. *Sivapithecus* yields some of the lowest $\delta^{13}\text{C}$ values

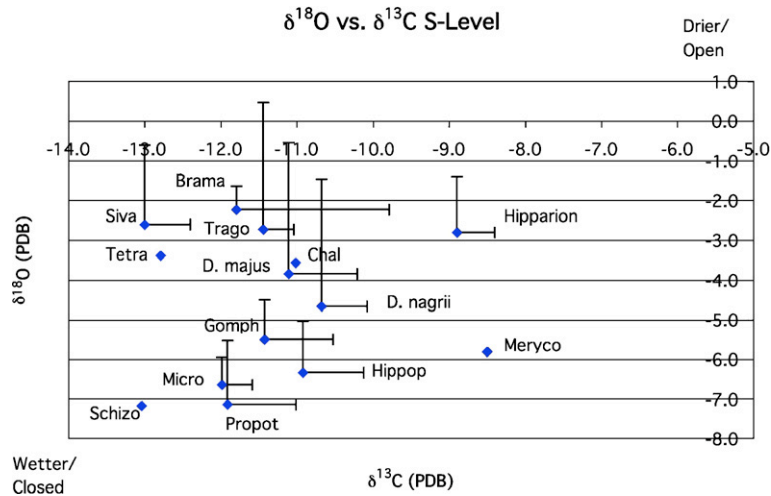


Fig. 3. Average carbon and oxygen isotopic values for each taxon in the S-level indicate a range of feeding adaptations exploiting different parts of the habitat. Taxa include *Sivapithecus*, the suoids *Propotamochoerus*, *Schizochocerus*, *Tetraconodon*, and *Hippopotamodon*; gomphotheres; the anthracotheres *Merycopotamus* and *Microbunodon*; the giraffid *Bramatherium*; the tragulids *Dorcabune nagrii* and *Dorcatherium majus*; the bovid *Tragocericus*; the equid *Hipparion*; and a chalicothere. One standard deviation is marked for taxa represented by at least three specimens. *Bramatherium* is similar to modern giraffes in high $\delta^{18}\text{O}$ values, indicative of feeding on upper canopy foliage. *Merycopotamus* is similar to hippopotamus today in high $\delta^{13}\text{C}$ values but low $\delta^{18}\text{O}$ values. *Hipparion* also fed in open habitat. *Schizochocerus*, *Propotamochoerus*, and *Microbunodon* fed in closed, wet forest. *Sivapithecus* fed in the upper canopy of forest.

for the S-level, with values around -13‰ , suggesting forest habitat, accompanied by some of the highest $\delta^{18}\text{O}$ values (around -2.6‰), suggesting that it obtained most of its water from enriched upper canopy vegetation, most likely including fruit, as suggested by microwear (Nelson, 2003). *Schizochocerus* and *Tetraconodon*, both suids, also yield $\delta^{13}\text{C}$ values around -13‰ , suggesting forest habitat for both, and *Schizochocerus* has the lowest $\delta^{18}\text{O}$ value, suggesting feeding

in closed, wet forest. Other notable habitat preferences include the anthracothere *Merycopotamus*. While represented by only one specimen, its carbon value suggests feeding in open habitat, while its oxygen value suggests an aquatic habitat or greater dependence on water than most other taxa. These results are compatible with hippopotamus behavior today, for they are aquatic by day and feed in open habitat at night. *Bramatherium* is isotopically similar to other fossil

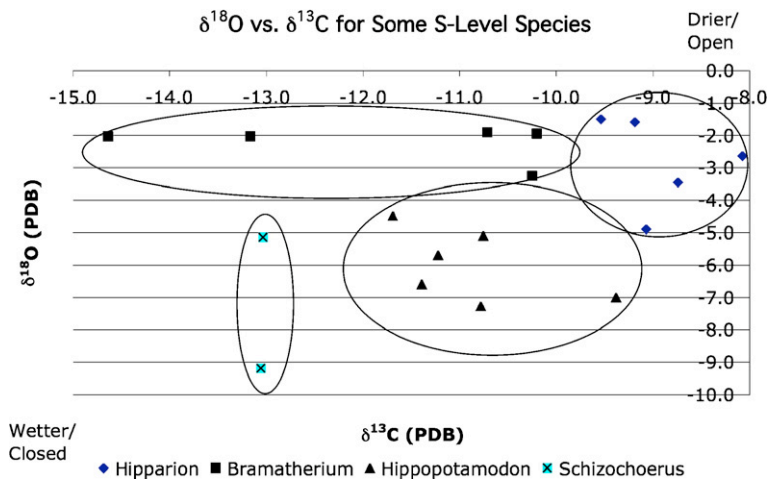


Fig. 4. An example of specimen clustering for four S-level species, suggesting a spectrum of feeding adaptations exploiting different parts of the habitat.

Table 5

Comparison of Miocene hominoid localities, including Ft. Ternan, represented by 21 specimens and 9 species; Pasalar, represented by 44 specimens and 16 species; and the S-level localities, represented by 54 specimens and 14 species

	Ft. Ternan	Pasalar	S-level
$\delta^{13}\text{C}$ values	−13.0 to −8.6	−13.5 to −9.0	−14.6 to −8.1
Range $\delta^{13}\text{C}$	4.4	4.5	6.5
Average $\delta^{13}\text{C}$	−10.8	−11.2	−11.3
$\delta^{18}\text{O}$ values	−0.7 to +4.2	−9.1 to +1.4	−9.2 to +0.7
Range $\delta^{18}\text{O}$	4.9	10.5	9.9
Average $\delta^{18}\text{O}$	1.5	−4.6	−4.5

Ft. Ternan data from Cerling et al. (1997). Pasalar data from Quade et al. (1995b). All data relative to the standard PDB.

tailed p -value corrected for ties: $Z = -2.46$; $p = 0.014$). *Schizochoerus* also has lower $\delta^{13}\text{C}$ values than all the other taxa in the S-level that range through the PS-level (average is -11.1% for all other taxa) ($Z = -2.04$; $p = 0.042$), as is *Sivapithecus* ($Z = -3.05$; $p = 0.002$). *Microbunodon*, an anthracothere that goes extinct before the PS-level, also has lower $\delta^{13}\text{C}$ values than most other taxa. *Hipparion* has higher $\delta^{13}\text{C}$ values than all other taxa, suggesting a preference for more open habitat.

There are differences in $\delta^{18}\text{O}$ values between taxa as well (Table 4). Both *Sivapithecus* and *Bramatherium*, the giraffe, yield higher $\delta^{18}\text{O}$ values than many other taxa, again consistent with both species obtaining much of their water from vegetation high in the upper canopy. The tragulids and bovid that did not differ significantly from *Sivapithecus* or *Bramatherium* may likewise have obtained much of their water from high-canopy fallen fruit, or the high values for these taxa may represent

drinking in open habitat, similar to *Hipparion*. The chalicothere has higher values than many of the other taxa. This large perissodactyl with long forelimbs and short hindlimbs may have fed and drunk in open habitats as well. Alternatively, it has been suggested that chalicotheres could stand bipedally and pull down leaves from high branches (Benton, 1990), a scenario consistent with the high $\delta^{18}\text{O}$ values. The suoids *Microbunodon*, *Hippopotamodon*, and *Propotamochoerus* yield lower $\delta^{18}\text{O}$ values than many other taxa, suggesting they preferred more closed habitat. Again, *Hipparion* has higher values than many other taxa suggesting an affinity for open habitat.

In addition to sampling a wide range of fauna, this investigation also sampled many fossil localities. A total of 38 localities or collecting levels were represented, 21 of which date to the S-level, with many sites represented by multiple specimens and taxa. While this study was not designed to profile individual sites, some initial inferences can be made from the data collected, including inferences about *Sivapithecus* habitat. Of the S-level sites, *Sivapithecus* is found at nine of them. Among these, the six sites represented by at least three specimens all contain at least one specimen other than *Sivapithecus* with a $\delta^{13}\text{C}$ value of -12% or lower, suggesting the presence of closed forest, and one site (Y182) includes *Schizochoerus*, the taxon with the lowest carbon and oxygen values thought to prefer closed, wet forest. Three of the nine sites (Y211, Y310, and Y317) also include a $\delta^{13}\text{C}$ value above -10% , indicating some open habitat present as well. All *Sivapithecus* sites contain specimens with at least the

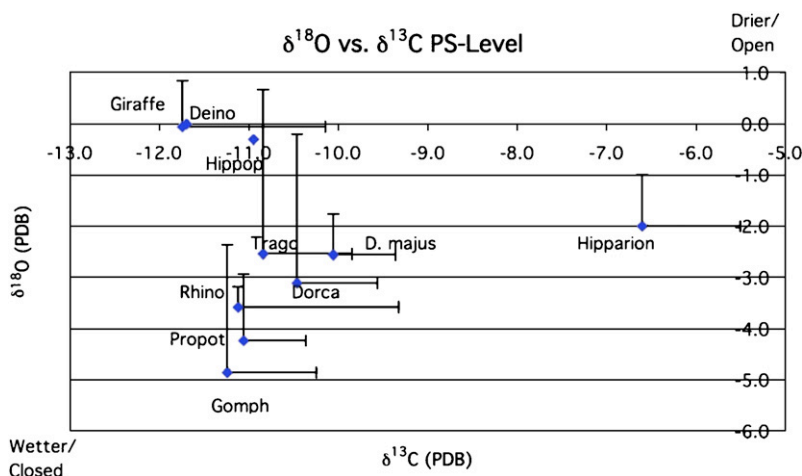


Fig. 5. Average carbon and oxygen isotope values for each taxon in the PS-level indicate a range of feeding adaptations exploiting different parts of the habitat. Taxa include gomphotheres and deinotheres; rhinoceros; the suids *Propotamochoerus* and *Hippopotamodon*; the tragulid *Dorcatherium majus*; the bovids *Tragocericus* and *Dorcadoxa*; the giraffid *Bramatherium*; and the equid *Hipparion*. One standard deviation is marked for taxa represented by at least three specimens.

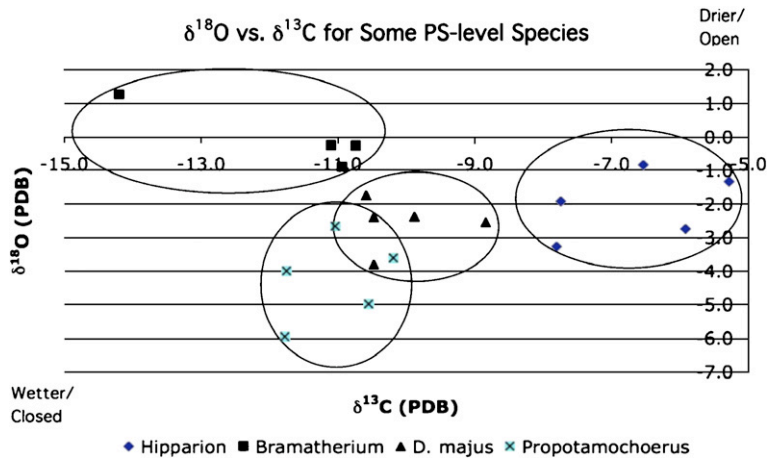


Fig. 6. An example of specimen clustering for four PS-level species, suggesting a spectrum of feeding adaptations exploiting different parts of the habitat.

with closed woodland or forest still present, but with some C_4 grasses as well. The fact that bovids, including *Dorcadoxa*, a reduncine (all grazers today), had not incorporated C_4 graze into their diets by 8.0 Ma suggests that while C_4 patches were present, they were not extensive.

The $\delta^{18}\text{O}$ values for the PS-level fall between -8.0‰ and $+3.5\text{‰}$ (compared to -9.2‰ to $+0.7\text{‰}$ for the S-level), for a range of 11.5‰ (versus 9.9‰) and an average of -2.7‰ (versus -4.5‰). Again, for several taxa, individuals cluster in their $\delta^{13}\text{C}$ and/or $\delta^{18}\text{O}$ values, suggesting they fed in particular parts of the habitat, and some taxa are isotopically distinct from

others (Tables 6 and 7, Fig. 6). *Bramatherium* and gomphotheres continue to yield low $\delta^{13}\text{C}$ values indicative of forest, and they are lower in $\delta^{13}\text{C}$ values than several other PS-level taxa, suggesting the number of forest taxa has decreased since the S-level. *Dorcadoxa* is the only species sampled which was not present during the S-level, and its average $\delta^{13}\text{C}$ values of -10.4‰ suggests this new species had an affinity for open woodland. *Hipparion* continues to yield higher $\delta^{13}\text{C}$ values than any other taxon, indicating that it fed in open habitat more often than other taxa.

Taxa cluster in oxygen values as well (Table 7). *Bramatherium* continues to yield higher $\delta^{18}\text{O}$ values

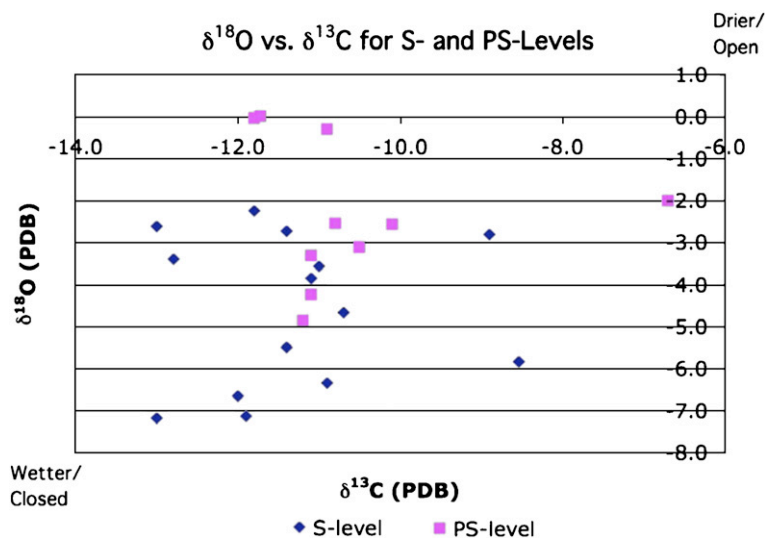


Fig. 7. Average values for each taxon in the S-level and the PS-level. A shift to more positive $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values over time suggests a decrease in forest habitat, an increase in open habitat, and possibly a shift in rainfall regime.

Table 8

Comparison of average $\delta^{13}\text{C}$ values for taxa sampled in both the S-level (9.3–9.2 Ma) and the PS-level (8.1–8.0 Ma)

Taxon	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$	Mann–Whitney
	S-level	PS-level	
Gomphothere	–11.4 (4)	–11.2 (5)	ns
Bramatherium	–11.8 (5)	–11.8 (4)	ns
Propotamochoerus	–11.8 (6)	–11.1 (5)	ns
Hippopotamodon	–10.9 (6)	–10.9 (2)	ns
Dorcatherium majus	–11.1 (5)	–10.1 (5)	$Z=-2.03$; $p=0.042$
Tragoceridus	–11.4 (5)	–10.8 (8)	ns
Hipparion	–8.9 (5)	–6.7 (5)	$Z=-2.45$; $p=0.014$

ns=not significant.

Number of samples in parentheses. For all taxa, carbon values either do not change or they become enriched over time. For all taxa, isotopic values either do not change or become enriched over time.

than most other taxa, again suggesting feeding from the enriched upper canopy. *Propotamochoerus* continues to yield lower $\delta^{18}\text{O}$ values than some taxa, suggesting that it still preferred more closed, less evaporative habitats. *Hipparion* still has higher $\delta^{18}\text{O}$ values than several taxa, also indicative of open habitat.

3.3. Comparison of the S-level and the PS-level

When all specimens are combined per level, the PS-level $\delta^{13}\text{C}$ values are significantly higher ($Z=-2.64$, $p=0.008$). When horses, the only substantial C_4 grazers, are removed from both levels (resulting in a range of -14.6‰ to -8.5‰ for the S-level and -14.2‰ to -8.3‰ for the PS-level), this difference is still significant ($Z=-2.79$, $p=0.005$). When $\delta^{18}\text{O}$ values

are combined for all taxa for each level, the PS-level taxa are again significantly higher with respect to those from the S-level ($Z=-3.09$; $p=0.002$). Both the carbon and oxygen isotopes therefore indicate a drier, more open habitat with a changing climate by 8.1 Ma (Fig. 7).

The enrichment of 1.8‰ in $\delta^{18}\text{O}$ between the different levels, if used as an estimate for change in meteoric water, can be interpreted as a change in temperature using an equation by Dansgaard (1964):

$$\delta^{18}\text{O}_{\text{meteoric water}} = 0.69T - 13.6\text{‰}$$

where T = mean annual air temperature.

Using this equation, the 1.8‰ enrichment translates into about a 3 °C increase in mean annual temperature, if temperature was the only climatic factor to change. Likewise, if change in precipitation was the only factor, then at tropical latitudes where there is a linear relationship between average monthly rainfall and its mean monthly $\delta^{18}\text{O}$ value, about a -1.5‰ shift per 100 mm, then the 1.8‰ enrichment translates into about a 120 mm reduction in rainfall.

These temperature and precipitation changes, when compared to climatic data from evergreen, semi-evergreen, moist-, and dry-monsoon forests of India today, are not enough to account for major changes in vegetation within these ecosystems. For example, there is a 3 °C spread between evergreen and semi-evergreen forests, but monsoonal forests fall between these values, making any interpretation of small temperature changes ambiguous. Amount of precipitation varies considerably more between the modern ecosystems, however, with a reduction of over 1000 mm between evergreen and

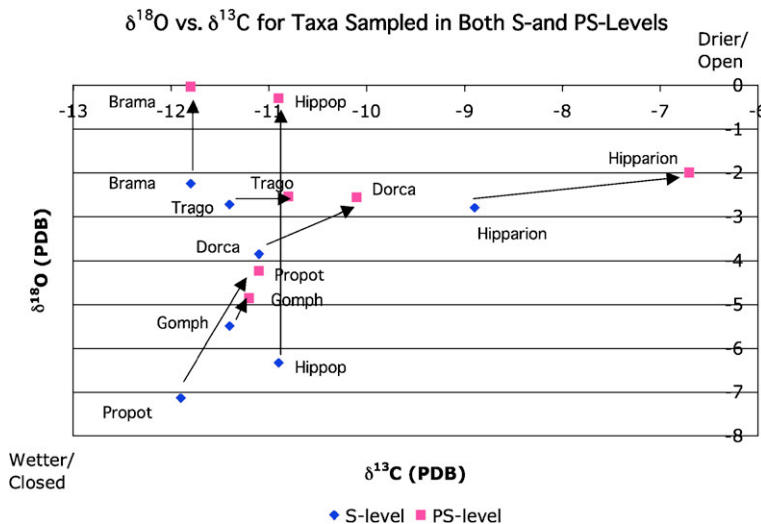


Fig. 8. Changes in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for taxa sampled in both the S-level (9.3–9.2 Ma) and the PS-level (8.1–8.0 Ma).

Table 9

Comparison of average $\delta^{18}\text{O}$ values for taxa sampled in both the S-level (9.3–9.2 Ma) and PS-level (8.1–8.0 Ma)

Taxon	$\delta^{18}\text{O}$ S-level	$\delta^{18}\text{O}$ PS-level	Mann–Whitney
Gomphothere	–5.5 (4)	–4.9 (5)	ns
<i>Bramatherium</i>	–2.2 (5)	–0.033 (4)	$Z = -2.49$; $p = 0.013$
<i>Propotamochoerus</i>	–7.3 (6)	–4.2 (5)	$Z = -2.37$; $p = 0.018$
<i>Hippopotamodon</i>	–6.0 (6)	–0.3 (2)	$Z = -2.00$; $p = 0.046$
<i>Dorcatherium majus</i>	–3.9 (5)	–2.6 (5)	ns
<i>Tragoceridus</i>	–2.7 (5)	–2.5 (8)	ns
<i>Hipparion</i>	–2.8 (5)	–2 (5)	ns

ns = not significant.

Number of samples in parentheses. For all taxa, oxygen values become enriched over time.

semi-evergreen, a further reduction of over 400 mm from semi-evergreen to moist-monsoonal, and another reduction of 250 mm from moist- to dry-monsoonal. Furthermore, for any of these ecosystem types, precipitation values can have 500 to over 1000 mm ranges (Walter, 1973).

Thus a reduction of 120 mm is not substantial enough to cause a major shift in vegetation unless accompanied by other climatic or atmospheric changes. The most important single determining factor of the modern forest types is length of the dry period, or seasonality of rainfall. The oxygen enrichment of the Siwalik Group cannot be interpreted solely as a shift to summer rains, for heavy summer rains of monsoons are greatly depleted relative to winter rains due to the amount effect mentioned earlier. An increase in seasonality, when combined with other factors such as decrease in rainfall or change in precipitation source, could have accounted for both the carbon and oxygen shifts observed. However, reconstructions of precipitation regimes for the Siwalik Group based upon oxygen isotope analyses of equid teeth indicate a monsoonal seasonal rainfall regime with reduction in rainfall over time but no changes in seasonality (Nelson, 2005).

The decrease in rainfall could have been more substantial than detected in this analysis. According to the Siwalik precipitation study, summer rain differed from winter rains in $\delta^{18}\text{O}$ values by 2.5‰ (Nelson, 2005). Some of the variability observed in oxygen values in this faunal analysis is likely the result of sampling different seasons of the year for different specimens. This seasonal variability may have confounded differences in amount of rainfall if samples from the different time levels were skewed to different seasons.

In addition to changes in the vegetation mosaic and climate, changes in feeding behavior or habitat preferences can be studied for individual taxa. For seven of the species studied, specimens were available for both stratigraphic levels. When average $\delta^{13}\text{C}$ values are compared for each taxon between the two levels, taxa become either enriched or have the same value from the S-level to the PS-level (Table 8, Fig. 8). For *D. majus* and *Hipparion*, the enrichment is significant, suggesting a shift in feeding to more open habitats. When average $\delta^{18}\text{O}$ values are likewise compared for the seven taxa, all show enrichment from the S-level to the PS-level, with significantly enriched values for *Bramatherium* and the two suids *Propotamochoerus* and *Hippopotamodon*, suggesting a shift to more open habitat or a shift in climate (Table 9, Fig. 8).

While larger sample sizes are needed for a more accurate analysis, range of isotopic values, and hence niche breadth, and changes in breadth over time can also be evaluated per taxon as a preliminary study (Table 10). *Bramatherium* exhibits a wide range of carbon values in both levels, indicative of feeding throughout the forest canopy, while its oxygen range is relatively small, suggesting that it obtained most of its water from enriched canopy leaves rather than watering holes. Rhinos also show a wide range of carbon values but a small range of oxygen values. Modern rhinos are highly omnivorous, feeding on fruits, leaves, branches, shrubs, and grass in a range of habitats (Kingdon, 1997; Nowack, 1999). Miocene rhino carbon values are compatible with the modern analogue. Furthermore, modern rhinos depend upon bodies of water for temperature control, digestion, and scent communication (Kingdon, 1997). The low Siwalik

Table 10

Range (per mil) of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values per taxon for both the S-level (S) and the PS-level (PS)

Taxon	Range $\delta^{13}\text{C}$ S	Range $\delta^{13}\text{C}$ PS	Range $\delta^{18}\text{O}$ S	Range $\delta^{18}\text{O}$ PS
Rhino	NA	5 (5)	NA	1.1 (5)
Gomphothere	1.9 (4)	2.6 (5)	2.4 (4)	6 (5)
<i>Bramatherium</i>	4.4 (5)	3.5 (4)	1.3 (5)	1.1 (4)
<i>Propotamochoerus</i>	1.9 (6)	1.6 (5)	3.8 (6)	3.2 (5)
<i>Hippopotamodon</i>	2.3 (6)	0.3 (2)	2.8 (6)	7.6 (2)
<i>Schizochocerus</i>	0.1 (2)	NA	4.1 (2)	NA
<i>Microbunodon</i>	0.8 (3)	NA	1.4 (3)	NA
<i>Dorcabune nagrii</i>	1.2 (4)	NA	6.6 (4)	NA
<i>Dorcatherium majus</i>	2.2 (5)	1.8 (5)	8.8 (5)	2.1 (5)
Chalicothere	0.1 (2)	NA	0.5 (2)	NA
<i>Tragoceridus</i>	1 (5)	2.6 (8)	7.4 (5)	7.5 (8)
<i>Dorcadoxa</i>	NA	2.6 (7)	NA	9.6 (7)
<i>Hipparion</i>	1.4 (5)	2.5 (5)	3.4 (5)	2.5 (5)

Number of specimens given in parentheses.

oxygen results are compatible with water dependence, and the small range of values are compatible with dependence on large bodies of water that would have been buffered from seasonal changes in $\delta^{18}\text{O}$ values. Notable taxa with large ranges in oxygen include both tragulids and bovids in the S-level and bovids in the PS-level, suggesting they are obtaining water from more varied sources than other taxa, either due to use of both open and closed habitats, or to obtaining some forest floor food as well as fruits that fell from the upper canopy.

Some taxa show a change in range of their carbon or oxygen values, suggesting a shift in niche (Table 10). *Tragoceridus* and *Hipparion* show an increase in breadth of carbon values, with the PS-level range being more than a per mil greater than the S-level samples. This increase might indicate a slightly greater use of more varied habitats. It should also be noted that *Dorcadoxa*, the PS-level bovid that was not present during the S-level, shows the greatest range in oxygen values (9.6‰) compared to any other taxa in either level, suggesting that this new species exploited a range of habitats including both closed and open. If *Dorcadoxa* and the increased niche breadth inferred for PS-level *Tragoceridus* and *Hipparion* are representative of fauna in general for that time level, it suggests that in this time of climatic change and a more varied vegetation mosaic, fauna are becoming more generalized in their habitat preferences. The one taxon which showed a drastic reduction in its oxygen range in the PS-level is *D. majus*, the one tragulid sampled still present from the S-level. This decrease suggests a reduction in niche breadth, perhaps due to competition with other taxa such as bovids, or perhaps due to loss of preferred habitats.

3.4. Comparison of paleosol carbonate and enamel

With respect to the vegetation mosaic, paleosol carbon isotopic values from previous studies directly represent vegetation growing above the soil, averaged over 10^2 – 10^4 years. Oxygen values are determined by the $\delta^{18}\text{O}$ value of meteoric water, the degree to which this water undergoes evaporative effects, and by temperature (Quade and Cerling, 1995). Tooth enamel values, on the other hand, represent only the particular diet of the animal at a single point in time. These two approaches thus provide two views of the paleovegetation at the time, one a broad-scale record of vegetation across the paleoecosystem, the other a fine-scale record as seen by the herbivorous mammals who could move about the landscape and feed from specific patches of vegetation.

A total of 101 fossil teeth were sampled between 9.3 and 8.0 Ma, while only 12 paleosol carbonate samples

have been analyzed between the ages of 9.4 and 8.0 Ma (Quade and Cerling, 1995). Carbon values of tooth enamel for the S-level (9.3–9.2 Ma) ranged from -14.6‰ to -8.1‰ . Paleosol carbonates between 9.4 and 9.2 Ma range between -12.6‰ and -10‰ . The enrichment factor for $\delta^{13}\text{C}$ values between vegetation and paleosol carbonate is about 15‰, compared to 14‰ for enamel. A subtraction of 1‰ from paleosol values is therefore needed to compare them to enamel, shifting their range to -13.6‰ to -11‰ . Both methods therefore detect forest and woodland, but only enamel analyses detected open habitat. This discrepancy is likely due to the very small paleosol sample size, but could suggest that open habitats were not an extensive part of the ecosystem. At the PS-level (8.1–8.0 Ma), enamel yielded a range of $\delta^{13}\text{C}$ values between -14.2‰ and -5.3‰ . Paleosol samples fall between -11.6‰ and -8.9‰ (or -12.6‰ to -9.9‰ to compare to enamel values). Again, enamel analyses detected more forest and more open habitat than did paleosol analyses, and only enamel analyses detected the presence of C_4 grasses. This discrepancy is also likely due to the small paleosol sample size, but it could also suggest that both forests and C_4 grasses were not extensive at this time level. Alternatively, it is possible that not all vegetation types preserved the carbonate nodules necessary for paleosol isotopic analyses.

S-level enamel samples ranged in $\delta^{18}\text{O}$ values between -9.2‰ and $+0.7\text{‰}$, while paleosol values from previous studies ranged between -9.9‰ and -5.4‰ (Quade and Cerling, 1995). Many factors could have led to enrichment of oxygen values in enamel with respect to meteoric water values, including enrichment due to metabolic processes, feeding on enriched vegetation, and drinking from bodies of water undergoing evaporation. Only evaporation and temperature affect paleosol carbonate oxygen values. Therefore, the best comparison between results from these two methods lies in the lowest $\delta^{18}\text{O}$ values. These low values, -9.2‰ for enamel and -9.9‰ for paleosols, are very similar, suggesting that these values provide the best approximation of unevaporated soil water for this time interval. Enamel and paleosol low $\delta^{18}\text{O}$ values are again very similar at the PS-level (-8.0‰ and -8.9‰ respectively), also suggesting the best approximation of unevaporated soil water. The difference between S- and PS-level low samples suggests an enrichment of at least 1‰ for soil water over time, probably more so given groundwater is buffered, and is likely an indication of a shift in the rainfall regime with a decrease in annual rainfall, possibly in conjunction with other atmospheric or climatic changes.

4. Conclusions

These isotopic results indicate a shift in vegetation and climate over the course of about 1.1 Ma between the S-level and the PS-level. While a mosaic of habitats is represented in both levels, there appears to have been more closed forest in the S-level and less open habitat compared to the PS-level. While closed forest is still present in the PS-level, much of it has been replaced by open habitat, including some patches of C₄ grass. These C₄ patches of grass were probably not extensive, however, given no bovids, including a reduncine, had incorporated C₄ graze into their diets yet. The extinction of S-level taxa with the greatest preferences for closed forest, including *Sivapithecus*, suggests that closed forests, while still present in the PS-level, had become greatly diminished or fragmented.

The decrease in annual rainfall suggested by this analysis may have been sufficient to cause the shift in proportions of closed versus open habitat observed, but it was not sufficient to cause major transitions in forest type when compared to forests in India today. An alternative modern habitat comparison might be a river delta system such as the Amazon or Okavango. These regions are characterized by very fertile soils with year-round water availability, and they can support greater spatial and temporal availability of fruits and thus support frugivorous fauna year-round. Furthermore, many of the wetter delta regions, such as Manu National Park in Peru, are characterized by heavy tree fall, low canopy, and an understory of vines (Terborgh, 1990). This vegetation mosaic is consistent with the mosaic inferred from the isotopic analyses, and lianas might provide a pathway for *Sivapithecus* to travel throughout the canopy.

Alternatively, the vegetation mosaic may have resembled deltas in more semi-arid regions, such as the Okavango. The Okavango receives only 500 mm of rainfall a year, considerably less than predicted for the Siwalik Group (McCarthy and Ellery, 1993, 1998). Yet, given annual flooding from Angolan highlands, this region supports a vegetation mosaic which includes evergreen forest. The vegetation mosaic occurs on a small scale, with both forests and open grasslands occurring on individual islands, and these islands range in size from 100 m in diameter to hundreds of kilometers wide (Ellery et al., 1993). Evergreen forests occur on island perimeters, and trees remain green yearlong due to groundwater uptake (Ellery et al., 1993; Ringrose, 2003). Vegetation becomes more open toward the interior of islands, with C₄ grasslands or no vegetation at all in the center of islands (Ellery et al., 1993, 2003). The Okavango is home to frugivorous baboons today, and its plant species include

those eaten by modern chimpanzees as fallback foods, such as figs and papyrus (Ellery et al., 1993; McCarthy and Ellery, 1998; Ellery et al., 2003).

Lithological evidence from the Siwalik Group suggests that the delta scenario is a viable hypothesis for the paleohabitat of *Sivapithecus*. The Siwalik Group was deposited in a fluvial system comparable in size to the Ganges or Indus today and were likely part of the paleo-Ganges drainage system (Beck and Burbank, 1990; Barry et al., 2002). Deposits include channels of both large and small streams and rivers as well as floodplain, and temporal changes in the fluvial system occurred periodically, with shifts from interfan systems with smaller streams to larger emergent river systems and vice versa (Willis and Behrensmeyer, 1995; Barry et al., 2002). Associated with these fluvial shifts, the mosaic of the physical habitat varied in scale from tens to hundreds of kilometers in small channel systems to hundreds to thousands of kilometers in large channel systems. Throughout the Siwalik sequence, paleosol morphology suggests seasonal fluctuations in the water table, which could have resulted from a monsoonal rainfall regime and/or flooding events (Behrensmeyer et al., 1995). A decrease in types of paleosols is observed after 9.0 Ma and is associated with a diminished network of small channels (Barry et al., 2002). This decrease suggests a reduction in habitat diversity which may have resulted in the extinction of many Siwalik frugivores, including *Sivapithecus*.

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