

Ancient diets indicate significant uplift of southern Tibet after ca. 7 Ma

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ABSTRACT

The uplift of the Tibetan Plateau plays a critical role in controlling global climate, yet the history of the Tibetan uplift is still a contentious issue. In particular, the elevation of the plateau during the Neogene—a crucial period in the development of the Asian monsoons and C₄ ecosystems—remains uncertain. Here we present carbon isotopic evidence, preserved in tooth enamel from 7-m.y.-old horses and rhinos from the high Himalayas, which indicates that, unlike modern herbivores in the area, these ancient mammals ate substantial amounts of C₄ grasses. The presence of significant amounts of C₄ grasses in the diets of these ancient mammals indicates that the climate in the area was much warmer and the elevation was much lower in the late Miocene than today. The carbon isotope data from the high Himalayas, after accounting for late Cenozoic global cooling and paleoatmospheric CO₂ levels, indicate that this part of southern Tibet was less than 2900–3400 m above sea level in the latest Miocene. This implies that the present elevation of the area must have been attained after 7 Ma, much later than generally believed.

Keywords: carbon isotopes, Tibetan Plateau, fossils, C₄ grasses, paleoclimate, elevation.

INTRODUCTION

The Tibetan Plateau is important for driving the modern Asian monsoons, with profound effects on global atmospheric circulation, climate, and erosion, as well as biological and ecological migration (Molnar and England, 1990; Quade et al., 1989; Raymo and Ruddiman, 1992; Prell and Kutzbach, 1992; Molnar et al., 1993; An et al., 2001; Qiu, 1990). However, the timing of the surface uplift of the Tibetan Plateau and how it was distributed both spatially and temporally are still hotly debated. It is generally believed that uplift of the Tibetan Plateau began ca. 50–60 Ma, and further significant increases in elevation of the region occurred in the Oligocene and Miocene, or more recently (e.g., Coleman and Hodges, 1995; Hsu, 1976; Yin and Harrison, 2000; Spicer et al., 2003). One view holds that rapid uplift of the Tibetan Plateau began in the early Miocene and that the present elevation of much of the high plateau was attained by ca. 8 Ma (e.g., Harrison et al., 1992; Dettman et al., 2001; Garzzone et al., 2000; Spicer et al., 2003; Currie et al., 2005). Another view (e.g., Zheng et al., 2000; Hsu, 1976) is that substantial uplift of the Tibetan Plateau occurred in the Plio-Pleistocene and that the area reached an elevation of 4000–5000 m by the end of the middle Pleistocene. The uplift of the Tibetan Plateau would have disrupted the west-to-east airflow across the Northern Hemisphere, initiated the monsoon-driven wind systems across southern and southeastern Asia, increased precipitation along the Himalayas, and prevented the entry of warm and humid monsoonal air from the eastern Pacific Ocean and Indian Ocean into a vast region on the north side of the high plateau. These changes in climate caused by the uplift of the Tibetan Plateau would have had significant impacts on ecosystems and environment in central Asia.

In this paper, we present a stable carbon isotopic record of paleodiet and paleoenvironment in the high Himalayas that is preserved in

bioapatite of fossil mammalian tooth enamel. Our carbon isotope data provide independent evidence that sheds new light on the debate concerning the timing of the uplift of the Tibetan Plateau.

STUDY SITE, SAMPLES, AND ANALYTICAL METHODS

Our fossil mammalian teeth were collected from the Gyirong Basin (28°46.13N, 85°17.84E) in the high Himalayas (Fig. 1). The Gyirong Basin is an intermountain basin located along the northern slope of Mount Xixabangma in the central Himalayas and has an area of ~200 km². The current elevation of the basin is ~4200 m. The average annual temperature in the basin is about –10 to 2 °C and the annual rainfall is 300–400 mm (Tibet Bureau of Surveying and Mapping, 2000). The area is essentially a desert with little vegetation except in low-lying areas adjacent to the Gyirong River. The basin contains thick late Cenozoic deposits that unconformably overlie Jurassic marine de-

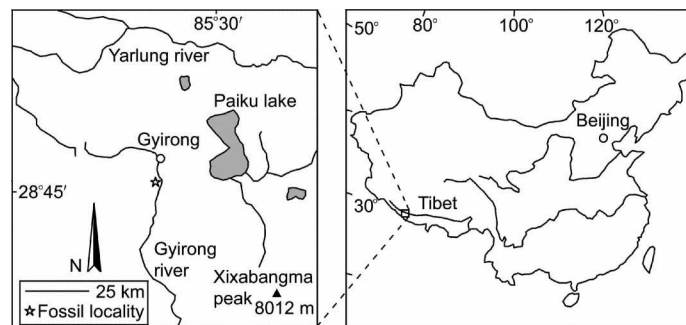


Figure 1. Location map showing the study site in the Gyirong Basin in Tibet, China.

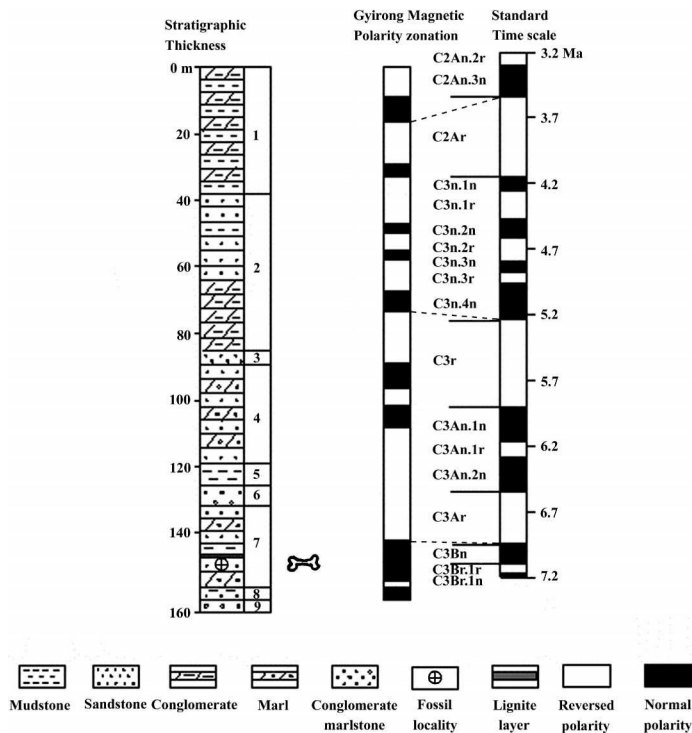


Figure 2. The lithostratigraphy and magnetic stratigraphy in the Gyirong Basin, Tibet (adapted from Yue et al., 2004). The age of the fossil layer is determined on the basis of paleomagnetic time scale and stratigraphic position.

posits (CAS, 1989). The late Cenozoic sequence—the Woma Formation—in the basin is well exposed in the badlands along the Gyirong River and consists primarily of lacustrine and fluvial deposits. An *Hipparion* fauna (CAS, 1989) was found in the lower Woma Formation in a fine sandstone layer at an elevation of 4384 m, ~300 m above the current valley floor. This layer contains the horse *Hipparion forstenae*, rhino *Chilotherium xizangensis*, artiodactyls *Metacervulus capreolinus*, *Palaeotragus microdon*, *Gazella gaudryi*, lagomorph *Ochotona guizhongensis*, rodent *Heterosminthus* sp., and carnivore *Hyaena* sp. (CAS, 1989). These fossil specimens are archived at Institute of Vertebrate Paleontology and Paleoanthropology in Beijing. Previous studies suggest that the *Hipparion* fauna in the Gyirong Basin was similar to the *Hipparion* fauna in northern China and represents a mixed habitat including dense forests and grasslands (CAS, 1989). A recent paleomagnetic study (Yue et al., 2004) of the lower Woma Formation suggests that the sandstone layer containing the *Hipparion* fauna was deposited in the late Miocene during chron 3Bn, ca. 7 Ma (Fig. 2).

We analyzed 46 fossil enamel samples from primarily horses and rhinos and a few unidentified herbivores collected from the *Hipparion* sandstone layer in the Gyirong Basin. In addition, we analyzed 26 modern herbivore teeth from the area. All enamel samples were prepared following a treatment procedure described in Wang and Deng (2005). The treated enamel samples were analyzed for their carbon and oxygen isotopic ratios using a Gas Bench II Autocarbonate device connected to a Finnigan MAT Delta Plus XP stable isotope ratio mass spectrometer at Florida State University. Isotope data are reported in the standard notation as $\delta^{13}\text{C}$ relative to the international carbonate standard PDB (Peedee belemnite). The analytical precision (based on replicate analyses of carbonate standard NBS-19 and our lab standards processed with each batch of samples) is $\pm 0.1\%$ or better.

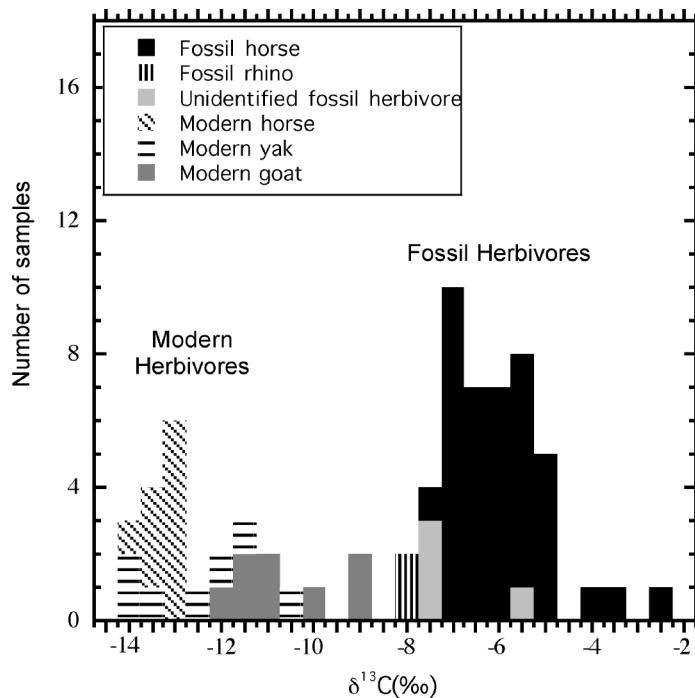


Figure 3. Stable carbon isotopic composition of tooth enamel from both modern and ancient herbivores in the Gyirong Basin in the high Himalayas.

RESULTS AND DISCUSSION

Carbon Isotopes, Diets, and Habitats of Herbivores in the Gyirong Basin

Fossil mammalian tooth enamel is an important archive of paleodiet and paleoenvironment and has been shown to retain its original carbon isotopic composition during diagenesis (Wang and Cerling, 1994; Cerling et al., 1997). Specifically, the carbon isotopic composition of tooth enamel from herbivores records the isotopic composition of their plant foodstuffs offset by a biochemical fractionation of $\sim 14\%$ (Cerling et al., 1997). Most plants photosynthesize by one of two pathways: the C_3 pathway or the C_4 pathway. C_3 plants use the C_3 photosynthetic pathway and include trees, shrubs, forbs, and cool-season grasses. C_4 plants use the C_4 photosynthetic pathway and are mostly grasses that favor warm growing seasons. Because C_3 plants discriminate more against the heavy ^{13}C isotope during photosynthetic fixation of CO_2 than do C_4 plants, C_3 and C_4 plants have very different carbon isotopic compositions. The $\delta^{13}\text{C}$ values of C_3 plants range from -22% to -34% , with an average of -27% , whereas C_4 plants have $\delta^{13}\text{C}$ values of -9% to -17% , averaging -13% (O'Leary, 1988). Therefore, the relative proportion of C_3 and C_4 vegetation in an animal's diet can be determined by analyzing the stable carbon isotopic composition of its tooth enamel. Animals that eat C_3 vegetation typically have $\delta^{13}\text{C}$ values of -9% to -16% ; animals that eat C_4 plants have $\delta^{13}\text{C}$ values between -1% and $+2\%$; and mixed feeders that eat both fall somewhere in between these two extremes (Cerling et al., 1997).

The $\delta^{13}\text{C}$ values of tooth enamel samples from modern domesticated horses (*Equus caballus*), yaks (*Bos mutus*), and goats (*Capra hircus*) in the Gyirong Basin range from -9.0% to -14.2% (Fig. 3), with a mean value of $-12.2\% \pm 1.5\%$ ($n = 26$), indicating a pure C_3 diet consistent with the current dominance of C_3 vegetation in the area. One modern yak tooth from Little Gyirong, which is located south of the Gyirong Basin and at a much lower elevation of 2700 m, also yielded a pure C_3 diet-signal with a $\delta^{13}\text{C}$ value of -13.1% . Fossil tooth enamel from horses in the Gyirong Basin, on the other hand, have $\delta^{13}\text{C}$ values ranging from -2.4% to -8.0% (Fig. 3), with a mean of $-6.0\% \pm 1.1\%$, indicating that these ancient horses were feeding

on both C₃ and C₄ vegetation with ~30%–70% C₄ grasses in their diets, assuming pure C₃ and C₄ end-member enamel $\delta^{13}\text{C}$ values of -12‰ and $+2\text{‰}$, respectively (Cerling et al., 1997). Fossil rhino enamel samples have a mean $\delta^{13}\text{C}$ value of $-7.9\text{‰} \pm 0.1\text{‰}$, also indicating a mixed C₃–C₄ diet with ~30% C₄ plants. The presence of significant amounts of C₄ grasses in the diets of these seven-million-year-old mammals indicates that C₄ grasses were an important component of local ecosystems in the area at that time. The local ecosystems in the Gyirong Basin in the latest Miocene likely included grasslands and/or wooded grasslands that had significant amounts of C₄ grasses, which is consistent with forested grassy plains and shrubby grassland habitats represented in pollen analyses (CAS, 1989).

Implications for Tectonic Evolution of Southern Tibet

The presence of significant C₄ biomass in the Gyirong Basin in the latest Miocene has important implications for the tectonic evolution of the Himalayas. C₄ plants have the ability to concentrate internal leaf CO₂ before carbon is fixed by the normal C₃ photosynthetic cycle (Ehleringer et al., 1991). This mechanism provides C₄ plants a competitive advantage over C₃ plants at low atmospheric CO₂ (<500 ppmV) levels (Ehleringer et al., 1991). The ability to increase internal leaf CO₂ concentration also allows C₄ plants to decrease their stomatal conductance, effectively increasing their water-use efficiency (Ehleringer et al., 1991). Such adaptations offer an advantage in hot, high-light, and water-stressed environments (Ehleringer et al., 1991). The C₄ photosynthetic pathway is therefore believed to have evolved from the more primitive C₃ photosynthetic pathway as an adaptation to low atmospheric CO₂, high temperature, and water-stressed conditions (Cerling et al., 1997; Ehleringer et al., 1991).

In the modern world, the distribution of C₄ grasses is controlled by temperature, seasonality of precipitation, and, of relevance here, elevation. C₄ grasses dominate grasslands with warm growing seasons, whereas C₃ grasses dominate grasslands with cool growing seasons (Ehleringer, 1978; Collatz et al., 1998). Photosynthetic models predict a crossover temperature above which C₄ grasses have a competitive photosynthetic advantage over C₃ grasses and below which C₃ species are favored. The crossover temperature increases with increasing atmospheric partial pressure of carbon dioxide—*p*CO₂ (Cerling et al., 1997; Collatz et al., 1998). Model analyses of current plant distributions suggest a mean temperature of 22 °C for the warmest month as the crossover temperature at the present-day *p*CO₂ (Collatz et al., 1998). In addition to favorable temperatures, C₄ plants require sufficient precipitation (>25 mm monthly) during the warm growing season (Collatz et al., 1998).

Today, C₄ grasses are common in low-elevation (<2500 m) tropical to temperate ecosystems but are not present or are rare in high-latitude and/or high-altitude (>3000 m) environments (i.e., cooler temperatures) and in Mediterranean climates (characterized by winter precipitation) (Cerling et al., 1997; Tieszen et al., 1979; Hofstra et al., 1972; Boutton et al., 1980). Although C₄ grasses have been discovered on the Tibetan Plateau, they account for negligible amounts of the biomass (e.g., Deng and Li, 2005). Evidence suggests that C₄ grasses expanded rapidly between 8 and 4 Ma, perhaps in response to a reduction in atmospheric CO₂ concentration to close to the present-day levels (Cerling et al., 1997). Because C₄ vegetation is not observed in the soil record or in mammalian diets in Asia until ca. 7–8 Ma or later (e.g., Cerling et al., 1997; Wang and Deng, 2005), the presence of significant amounts of C₄ vegetation in the diets of fossil herbivores itself provides an independent age constraint suggesting a maximum age of 7–8 Ma for these fossils from the Gyirong Basin, which is consistent with the age estimate based on the magnetic stratigraphy and fossils.

Our new carbon isotope data from the high Himalayas provide

unequivocal evidence for the presence of C₄ grasses in eastern Asia in the late Miocene. The precise timing and rate of C₄ expansion in eastern Asia cannot be determined at this point. Nonetheless, our finding that C₄ grasses were an important component of local ecosystems in the latest Miocene in the Gyirong Basin is significant, indicating that the area had a much warmer climate and a much lower elevation during the late Miocene than today. Our results contradict interpretations based on carbonate $\delta^{18}\text{O}$ data (e.g., Garzzone et al., 2000; Currie et al., 2005). However, our reconstruction of paleoenvironment in the high Himalayas is supported by paleobotanical and mammalian fossil evidence from other basins on the Tibetan Plateau (Hsu, 1976; CAS, 1989). Our argument for a lower elevation is also supported by the paleosol carbonate $\delta^{13}\text{C}$ data from the Thakkhola graben west of the Gyirong Basin (Garzzone et al., 2000). Although Garzzone et al. (2000) interpret their paleosol carbonate $\delta^{18}\text{O}$ data from the Thakkhola graben as indicative of unchanging, high elevation since the late Miocene, their paleosol carbonate $\delta^{13}\text{C}$ data clearly indicate the presence of C₄-dominated grasslands with C₄ grasses accounting for as high as 100% of the biomass in the area in the late Miocene. The mean $\delta^{18}\text{O}$ value of tooth enamel from fossil horses in the Gyirong Basin ($-17.0\text{‰} \pm 1.5\text{‰}$) is significantly (t-test, $t = 7.1$, d.f. = 38, $p < 0.0001$; Wilcoxon-Mann-Whitney test, $p < 0.0001$) higher than that of modern horses ($-19.1\text{‰} \pm 0.6\text{‰}$) in the Gyirong Basin, which appears to be consistent with the interpretation of a lower elevation in the late Miocene from the $\delta^{13}\text{C}$ data. However, caution must be used in any quantitative interpretation of $\delta^{18}\text{O}$ records from fossil enamel and other carbonates such as soil carbonates in terms of paleometeoric water and paleoelevation. First of all, $\delta^{18}\text{O}$ values of enamel and soil carbonates do not directly measure the oxygen isotopic composition of meteoric water. Second, while carbon isotopic ratios of enamel are resistant to diagenetic alteration, oxygen isotopic ratios of enamel carbonates (and other carbonates) could be altered during diagenesis (e.g., Wang and Cerling, 1994). Third, even if we assume that $\delta^{18}\text{O}$ values of enamel carbonates and soil carbonates record the $\delta^{18}\text{O}$ of paleometeoric water, application of modern precipitation $\delta^{18}\text{O}$ -elevation relationships to the distant past is not warranted. Studies (e.g., Johnson and Ingram, 2004; Thompson et al., 2000) have shown that oxygen isotopic ratios of precipitation in China display a high degree of spatial and temporal variability, which is related to a complex array of factors including temperature, precipitation amount, and the source and rainout history of air mass as well as monsoon intensity. The intensity of the Asian summer monsoon is well known to have varied greatly on decadal to annual time scales and between glacial and interglacial periods (e.g., Thompson et al., 1989, 2000). Over longer time scales, changes in solar insolation, land albedos, ice volume, snow cover, atmospheric CO₂ levels, and sea surface temperatures all contribute to monsoon variability (Prell and Kutzbach, 1992). Because the $\delta^{18}\text{O}$ of precipitation at any given site in this region is somewhat affected by modern monsoon intensity, which is highly variable, it is not justified to use modern empirical relationships in any quantitative interpretation of $\delta^{18}\text{O}$ paleorecords. For example, ice core records from the Dasuopu Glacier in the Himalayas show that $\delta^{18}\text{O}$ of precipitation at that site varied from -14‰ to -26‰ in the last millennium (Thompson et al., 2000). If we were to use the empirical $\delta^{18}\text{O}$ -elevation relationship given in Garzzone et al. (2000), the $\delta^{18}\text{O}$ variation observed in the ice cores in the Himalayas would suggest a very recent change in elevation of 4138 m!

In temperate environments today, C₄ grasses are abundant in warmest months below 1500 m elevation, but they either disappear completely or account for negligible amounts of the total biomass at elevations above 2500 m (Boutton et al., 1980). Even in the tropics, grasslands above 3000 m elevation are dominated by C₃ grasses with no or insignificant amounts of C₄ grasses (Tieszen et al., 1979; Hofstra et al., 1972). Assuming that the atmospheric *p*CO₂ level in the late

Miocene was about the same as it is today (Pagani et al., 1999) and that the average temperature lapse rate of 6.5 °C/km elevation applies to the past, 6 °C warmer temperatures in the late Miocene (Shackleton and Kennett, 1975) could extend the upper range of C₄-dominated grasslands to 2423 m at midlatitudes and to 2923 m in the tropics. If the temperature was 9 °C warmer (extreme scenario) in the late Miocene (Shackleton and Kennett, 1975), the upper range of C₄-dominated grasslands could extend to 2885 m at midlatitudes and to 3385 m in the tropics. It has been suggested that warmer than modern climatic conditions for the high elevations on the southern Tibetan Plateau, as indicated by a change in flora from thermophile species to those characteristic of cooler environments (Hsu, 1976; CAS, 1989), simply reflect global cooling trends since the Miocene (Molnar and England, 1990; Garzzone et al., 2000). However, using a secular change in temperature of 6–9 °C since the late Miocene (Shackleton and Kennett, 1975), global cooling clearly cannot explain the existence of significant C₄ grasses at elevations over 4000 m in the Himalayas. Our new carbon isotope data indicate that the elevation of the Gyirong Basin must have been lower than ~2900–3400 m, most likely lower than ~2400–2900 m, in the late Miocene and that the present elevation of the area was attained after ca. 7 Ma. Therefore, our carbon isotope data, along with other fossil evidence (Hsu, 1976; CAS, 1989), argue strongly for the attainment of current high elevation in this part of southern Tibet after 7 Ma.

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