High-temperature environments of human evolution in East Africa based on bond ordering in paleosol carbonates

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Many important hominid-bearing fossil localities in East Africa are in regions that are extremely hot and dry. Although humans are well adapted to such conditions, it has been inferred that East African environments were cooler or more wooded during the Pliocene and Pleistocene when this region was a central stage of human evolution. Here we show that the Turkana Basin, Kenya—today one of the hottest places on Earth—has been continually hot during the past 4 million years. The distribution of ^{13}C-^{18}O bonds in paleosol carbonates indicates that soil temperatures during periods of carbonate formation were typically above 30 °C and often in excess of 35 °C. Similar soil temperatures are observed today in the Turkana Basin and reflect high air temperatures combined with solar heating of the soil surface. These results are specific to periods of soil carbonate formation, and we suggest that such periods composed a large fraction of integrated time in the Turkana Basin. If correct, this interpretation has implications for human thermophysiology and implies a long-standing human association with marginal environments.

continental paleoclimate | clumped isotopes | soil temperature | hominid | bipedal locomotion

The environmental context of human evolution in eastern Africa is widely believed to feature increased seasonal aridity and related habitat change from forested to more open, savanna-type ecosystems, in part owing to differential surface uplift associated with the creation of the East African Rift System (1). Fossil records of mollusks (2), mammals (3, 4), plants (5, 6), and carbon isotopes (indicative of tropical C_4 grasses) (7, 8) generally suggest that habitats became less wooded and more open during the Pliocene and Pleistocene. Less is known of the temperature history of Africa—or the continental tropics in general—during this time period. A land-based, high-resolution temperature record from eastern Africa, constructed using empirical paleotemperature proxies based on fossil pollen assemblages (6), suggests that late Pliocene temperatures were cooler than present. However, it is also commonly inferred that Africa was warmer in the past (3, 4, 9), on the basis of analogy with the record of cooling and increased glaciation in the Northern Hemisphere during the past 3 million years. Although there is ample evidence of environmental change in the tropics, including changes in the frequency spectrum and amount of dust transported from Africa to nearby seas (10), it is difficult to relate these records to temperature.

We address the temperature history of the Turkana Basin in northern Kenya (Fig. 1) by applying the carbonate clumped-isotope thermometer (11) to fossil soil (paleosol) carbonates. The Turkana Basin, whose present mean annual temperature of 29.2 °C places the region in the hottest ~1% of continental land areas (12) (Fig. 2), is a key locale in human evolution with a rich fossil record of hominins and associated fauna (13). Our geochemical approach is based on the temperature-dependent formation of ^{13}C-^{18}O bonds in carbonate minerals. Unlike the widely used δ^{18}O-in-carbonate paleothermometer, the clumped isotope approach requires no assumptions about the δ^{18}O of the water in which the mineral formed: A single laboratory measurement provides the formation temperature, δ^{13}C, and δ^{18}O of carbonate and allows for calculation of δ^{18}O of the parent water. This method conforms to a single calibration for a variety of carbonates, including inorganic calcite, corals, aragonitic fish otoliths, foraminifera, coccoliths, and mollusk and brachiopod shells (14), whereas kinetic effects and departure from the inorganic calibration line have been described in speleothems (15).

Past studies have not demonstrated conclusively whether clumped isotope temperatures of modern soil carbonates record modern ground temperatures, so this study includes an examination of recent soil carbonates from Kenya, Ethiopia, China, and the United States to investigate appropriateness of this proxy to the materials and locations of interest to us. Analysis of carbonatites and marbles indicates that solid-state ^{13}C-^{18}O reordering is negligible over geological timescales at temperatures cooler than ~250 °C (16). Preservation of Earth-surface temperatures in soil carbonates as old as 25 Ma and buried to depths of ~5 km (with associated burial temperatures of ~150 °C) demonstrates that this system can be refractory with respect to near-surface postdepositional alteration (17), although this issue must still be considered for our study, as near-surface processes such as dissolution and reprecipitation will reset the clumped isotope signal.

Results and Discussion

Recent Soil Carbonates. Climate data for recent soil carbonate localities are given in Table S1, and the temperatures of recent soil carbonates determined using the carbonate clumped isotope thermometer are shown in Fig. 3 and summarized in Table S2. For recent soil carbonates from Kenya and Ethiopia (tropical regions with little annual variability in temperature), we observe a close correspondence between soil temperatures inferred from the clumped isotope thermometer and mean annual air temperatures. For the higher latitude samples (California and China), clumped isotope temperatures are more similar to summer air temperatures, suggesting a seasonal bias in soil carbonate formation, possibly combined with an influence of solar heating in cases where the carbonates formed before or after warm-season air temperature maxima. Such seasonal bias in soil carbonate precipitation has been suggested on the basis of independent lines of evidence (18), and it appears that this will be an important

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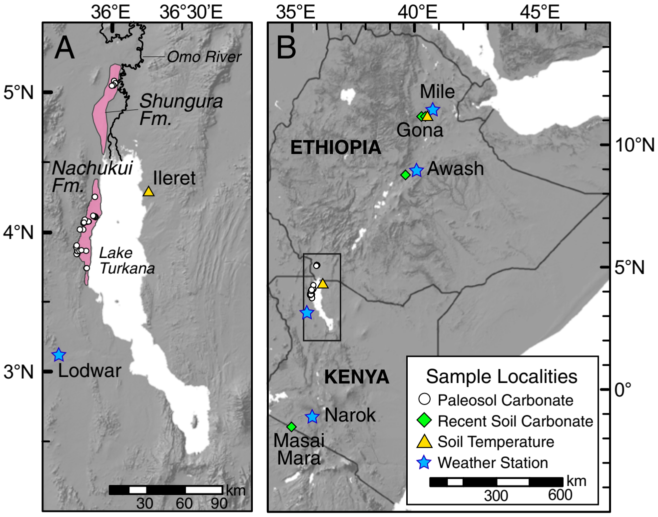

Fig. 1. Map of the study area in East Africa. (*A*) Detail map of the Turkana Basin showing sample locations for fossil paleosol carbonates (white circles). (*B*) Map of eastern Africa showing sample locations for recent soil carbonates (green diamonds), climate stations (blue stars), and locations of soil temperature measurements (orange triangles). Background images are shaded relief digital elevation models.

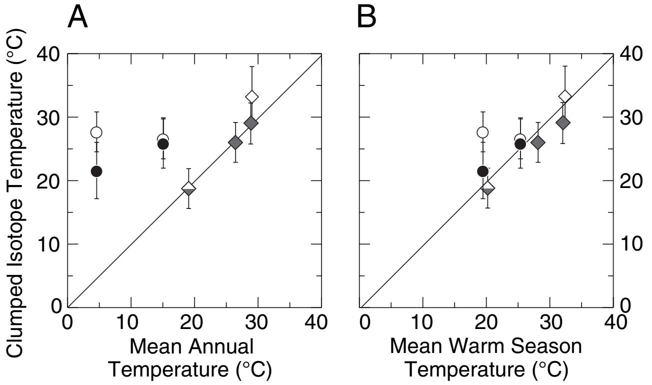

Fig. 3. (*A* and *B*) Clumped isotope temperatures of soil carbonates collected from recent soils from low latitudes (<12° absolute latitude, diamonds) and intermediate latitudes (34°N and 42°N, circles). Open, solid, and mixed symbols represent soil carbonates collected from <50 cm, ≥50 cm, or undocumented depth below the present soil surface. Error bars are SDs for soils with multiple depth-resolved samples or the average SD of replicate analysis for soils with single samples. (*B*) Mean warm season temperature is taken as the average temperature of the three warmest consecutive months of the year. The data are reported in Table S2.

consideration when applying the clumped isotope approach to soil carbonates formed in temperate climates. This seasonal bias should be less important in low latitudes where seasonality in temperature is minimal. For instance, the annual range in average monthly temperature near our study area at Lodwar, Kenya (Fig. 1) is 1.8 °C, and the average annual range for 14 meteorological stations across Kenya is 3.1 °C (19). However, seasonal variability in soil temperature may be larger owing to changes in soil moisture and insolation, as illustrated by soil temperature measurements near Lake Turkana (Fig. S1 and Table S3).

Finally, we cannot rule out the possibility that apparent clumped isotope temperatures are influenced by kinetic effects during carbonate precipitation. However, the deep soil environment (~ >50 cm) is buffered from rapid changes in temperature, moisture, and pCO_2, and this buffer might reduce opportunities for calcite precipitation under nonequilibrium conditions. We observe some tendency for shallow soil carbonates (<45 cm) to record higher apparent "clumped isotope" temperatures than deep soil carbonates in recent soils (Fig. 3 and Table S2), although this pattern is poorly defined and is not observed in all samples.

Paleosol Carbonates. Isotopic analysis was restricted to carbonates collected from depths of ≥50 cm below the preserved upper surface of each paleosol horizon. The mass-47 enrichments of CO_2 extracted from paleosol carbonates (expressed as values of Δ_{47}, *Methods*) range between 0.58 and 0.63‰, indicating that soil temperatures during periods of carbonate formation were between 41 and 28 °C (Fig. 4 and Table S4). There are no clearly resolvable temporal trends in these data, and the mean temperature recorded by paleosol carbonates is 33.2 °C, or 4.0 °C higher than present-day mean annual temperature (MAT), and comparable to modern soil temperatures (Fig. S1 and Table S3). Because soil temperature at >50 cm depth represents a time-

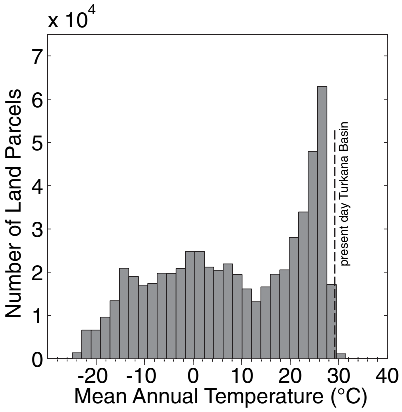

Fig. 2. Global distribution of mean annual temperatures. The histogram is a compilation of mean annual temperatures of all land parcels exclusive of Antarctica (10′ x 10′ grid) in the WorldClim global climatology (12). The Turkana Basin presently has a mean annual temperature of ~29 °C, ranking it among the hottest places on Earth.

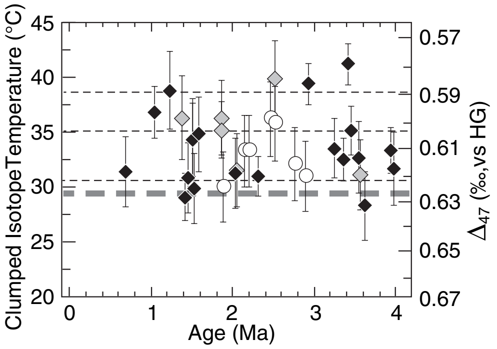

Fig. 4. Clumped isotope temperatures of paleosol carbonates from the Nachukui and Shungura formations (solid diamonds and open circles, respectively), Turkana Basin, Kenya, and Ethiopia. Results from nonpedogenic authigenic carbonates from the Nachukui Formation are shown by shaded diamonds. Error bars are SEs, calculated as detailed in *SI Text*. The thick dashed line represents the present-day mean annual air temperature in the study area (meteorological data from Lodwar, Kenya). The thin dashed lines represent the minimum, mean, and maximum soil temperatures observed at 50 cm depth over a 9-mo interval in the study area (Ileret, Kenya; Fig. S1 and Table S3). The data are reported in Table S4.

integrated average of daytime and nighttime soil surface temperatures, these temperatures indicate that daytime surface soil temperatures were well in excess of 28–41 °C.

There are no clear relationships between soil temperature and orbital eccentricity, obliquity, precession, or solar insolation, although such analysis for the higher-frequency signals (precession and solar insolation) is limited by the ~40- to 100-ka age uncertainty of each sampling horizon (*SI Text*). There are no correlations between soil carbonate Δ_{47} and $\delta^{13}C$, $\delta^{18}O$, or calculated soil water $\delta^{18}O$. Additionally, there is no correlation between Δ_{47} and burial depth (Fig. 5) such as would be indicative of ^{13}C-^{18}O bond reordering at elevated temperatures during burial.

Climatic Significance of Ground Temperature. To interpret the isotopic paleotemperature record, we further consider how soil temperatures relate to air temperatures. To first order, soil temperature at ~50 cm depth approximates mean annual air temperature in tropical regions that exhibit little seasonal variation in air temperature, or seasonally averaged air temperature in regions with significant seasonality of temperature (20). Superimposed on the air temperature effect, solar heating of the soil surface acts to further elevate soil temperatures. This solar-heating effect is important to the interpretation of our data because it is the soil surface temperature, rather than air temperature, that is the dominant boundary condition controlling soil temperature at depth (20). This phenomenon is illustrated by measurements of soil temperature in immediately adjacent shaded and sunny locations (21, 22) and by contrasting temperatures of primary vs. disturbed tropical rainforest soils (Fig. S2). We logged soil temperatures at several sites relevant to this study (Table S3 and Fig. S1), including a 9-mo record at Ileret, Turkana Basin, Kenya. The average 50-cm-depth soil temperature at Ileret was 35 °C, or 4 °C higher than average air temperature measured in the same location. Daytime air temperatures were typically in the range of 35–40 °C, and heat flow calculations (23) suggest that daytime soil-surface temperatures were commonly in excess of 50 °C.

Plio-Pleistocene Paleoenvironments in the Turkana Basin. The similar-to-present soil temperatures indicated for the paleosol carbonates are inconsistent with cooler and more vegetated (shaded) conditions compared with the present day. And, because the present environment is already arid, sunny, and sparsely vegetated, there is little potential for additional solar heating. Thus, the Plio-Pleistocene environments recorded by clumped isotopes in paleosol carbonates were either similar to present environments or more vegetated but also warmer.

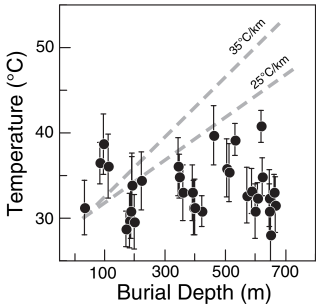

Fig. 5. Carbonate clumped isotope paleotemperatures (circles) and modeled maximum burial temperatures (dashed lines) plotted as a function of burial depth (Table S4). The burial temperatures are modeled for 35 °C/km and 25 °C/km geothermal gradients. There is no clear evidence of ^{13}C-^{18}O reordering in the paleosol carbonates resulting from diagenetic processes at depth (for example, dissolution/recrystalization, pressure solution, or other mechanisms of crystal coarsening).

As a limiting case of a "warmer and more vegetated" scenario, if the Turkana Basin was humid enough to be occupied by closed forest during the Pliocene and Pleistocene, soil temperatures would have been similar to air temperatures (because the forest canopy would make radiative heating negligible), and average air temperatures of ~33 °C would be required to explain our carbonate clumped isotope thermometry results. To place this temperature into context, today <1% of all tropical landmass (30°N to 30°S) has a mean annual temperature >30 °C, and of that receiving enough precipitation to support rainforest (here taken as >1,500 mm annually), <1% has a mean annual temperature >28 °C (12). Excluding gallery forest, we know of no forested site with MAT warmer than 30 °C.

Some previous studies have suggested that rainforest habitat existed in the Turkana Basin as recently as the late Pliocene, on the basis of occurrences of fossil animals (4) and plants (5) with closed-forest affinities. However, there is abundant coexisting evidence of drier habitats in the Turkana Basin. For example, soil carbonates, which are uncommon in regions receiving >1,000 mm of rainfall per annum (24), are common throughout Pliocene-aged sediments in the Turkana Basin, including the Nachukui and Shungura Formations examined here. Fossil ungulate taxa specialized for grazing are common in the Turkana Basin fossil record, and carbon isotope analyses of their tooth enamel, and also paleosol carbonates (Table S4), confirm that C_4 grasses were an important part of these ecosystems (25). The coexisting evidence for humid and dry habitats suggests that these habitats were juxtaposed in space, in time, or both. A probable explanation is that gallery forest existed alongside the ancient Omo River—as it does today—and that it fluctuated in extent as climate cycled between humid and arid phases.

Climate Variability and Periods of Soil Carbonate Formation. Orbital-scale climate variability is well documented in this low-latitude setting (10) and has been cited as an important factor in shaping the course of human evolution (9). An intrinsic feature of our soil temperature proxy is that it records soil temperature during times of carbonate mineralization. Therefore it is important to examine whether these soil carbonates formed under a wide range of prevailing climates, or under a restricted range of prevailing climates. Paleosol carbonates are common in the Pliocene and Pleistocene strata of the Turkana Basin, and because the depositional regime was primarily fluvial, soils would have existed at all times and places except in the vicinity of active channels. Therefore, if soil carbonates formed only under very specific conditions, we would expect paleosol carbonates to be present in only a small fraction of paleosols. Although there are not yet quantitative data on the fraction of paleosols with soil carbonates, it is our experience that most of the paleosols host paleosol carbonates. In addition, the $\delta^{13}C$, $\delta^{18}O$, and Δ_{47} values of the paleosols are variable on short (<100 ka) timescales, indicating that soil carbonates formed under a variety of prevailing vegetation types, hydrological conditions, and temperatures. Although the relatively low sampling resolution and sample age uncertainties (~40–100 ka) (26, 27) do not permit correlation to precessional cycles, the resolution and dating are sufficient to show that soil carbonates developed under a range of eccentricity configurations. Finally, the $\delta^{13}C$ and $\delta^{18}O$ values show clear secular trends indicating a progressive increase through time of C_4 grasses ($\delta^{13}C$) and a major change in regional circulation, humidity, or basin hydrology ($\delta^{18}O$) after 2 Ma (ref. 7 and Table S4). These lines of evidence collectively suggest that soil carbonates formed under a variety of prevailing conditions. Because soils and soil carbonates develop over long timescales (10^2–10^5 y) (28) and are common throughout strata in the Turkana Basin (8), they must record a suite of frequently recurring environmental conditions.

Implications for Human Thermophysiology. This temperature record is relevant to the evolutionary origin or maintenance of a unique suite of adaptations that permit humans to remain active under high ambient heat loads. For example, upright posture in hot, open environments confers thermophysiological advantages to bipedal hominins owing to reduced interception of direct solar radiation and to displacement of the body away from the near-surface environment, which may be excessively hot due to solar heating (29). Derived human traits such as very little body hair, high sweating capacity, and high surface area to volume ratio are also advantageous for daytime activity in hot, arid climates (30), and temperature is a central variable in hypotheses of behaviors such as long-distance scavenging and persistence hunting (31). However, the thermoregulatory advantages of these adaptations arise primarily under very hot, sunny conditions (29, 32, 33). Our results suggest that such conditions were relevant to human ecology in the Turkana Basin, either directly within or at the spatial or temporal margins of human-preferred habitats.

Conclusions

The data presented here demonstrate that clumped isotope temperatures of recent soil carbonates are related to climate and environment. The effects of solar heating or, conversely, shade are important to the interpretation of clumped isotope temperature data, and seasonality of carbonate precipitation is an important factor in temperate climates, where soil carbonates appear to record warm season temperatures. This seasonal bias is less apparent in tropical latitudes, where seasonality in air temperature is typically less than a few degrees.

The temperatures of carbonate formation inferred for Pliocene and Pleistocene paleosol carbonates from the Turkana Basin are similar to present-day soil temperatures. Because both air temperature and solar radiation control soil temperature at depth, these data are inconsistent with the hypothesis that past environments were cooler and more vegetated than today (at least, during periods of soil carbonate formation) and suggest that past environments were similar to, or warmer and more vegetated than, present-day environments. Thus, for example, modern Kenyan savanna environments like Nakuru, Maasai Mara, or Amboseli are not particularly good analogs for Turkana Basin paleoenvironments, because their temperatures are far lower (MAT = 17, 19, and 25 °C, respectively) than those inferred here (~ ≥30 °C). If past environments were more vegetated, a more suitable analog may be the grassland–bush–gallery forest environment typical of the lower Omo River valley north of Lake Turkana.

It is likely that numerous independent factors were involved in the evolutionary origin and maintenance of traits such as bipedal locomotion, slender body form, reduction of functional body hair, and high sweating capacity. Whereas our data are silent on the *importance* of ambient temperature in shaping human evolution, they comprise a necessary prerequisite for beginning to evaluate temperature-related hypotheses.

Methods

Carbonate nodules were collected from paleosols that are interbedded with fluvial, alluvial, and lacustrine sediments of the Nachukui and Shungura Formations in northern Kenya. These were collected ≥50 cm below the preserved upper surfaces of soil horizons. A small number of nonpedogenic carbonates were sampled, including crack-fill and ledge-type cements. Soil carbonates collected from recent soils included nodular, pendant (clast-coating), and crack- and ledge-type morphologies. Subsamples were examined and fine-grained (micritic) fractions were selected for isotopic analysis. The micritic texture of the fossil soil carbonates is similar to that observed for recent soil carbonates, suggesting that they were not recrystallized during burial. Isotopologue measurements were carried out using an automated carbonate device (Fig. S3) coupled to a Thermo MAT 253 mass spectrometer at the California Institute of Technology. Briefly, samples were reacted at 90 °C in 100% H_3PO_4, and the CO_2 product was purified by passage through multiple cryogenic traps, including a Porapak-Q gas chromatograph (GC) column held at −20 °C. Mass 44-normalized ion ratios of all stable CO_2 isotopologue masses (45/44, 46/44, 47/44, 48/44, and 49/44) were measured, and the parameter Δ_{47} was calculated as

$$\Delta_{47} = \left[\left(\frac{R^{47}}{R^{47*}} - 1\right) - \left(\frac{R^{46}}{R^{46*}} - 1\right) - \left(\frac{R^{45}}{R^{45*}} - 1\right)\right] \times 1,000,$$

where

$$R^{i} = \frac{\text{mass } i}{\text{mass } 44}.$$

The parameter R^{i*} is analogous to R^{i}, but corresponds to ratios for the same sample with a stochastic distribution of isotopologues. All data were normalized to CO_2 gases heated to 1,000 °C to achieve stochastic distribution of isotopologues. A correction of +0.081‰ was applied to all Δ_{47} data to account for the difference in phosphoric acid reaction temperature between this study (90 °C) and that of the original temperature calibration (25 °C; ref. 11) (Table S5). Finally, small (typically $<<\pm 0.02$‰) corrections were applied based on deviations from accepted values of in-house standards analyzed concurrently with the samples (Fig. S4; Dataset S1). Detailed methods are provided in *SI Text*.

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