Fine-scaled climate variation in equatorial Africa revealed by modern and fossil primate teeth

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Variability in resource availability is hypothesized to be a significant driver of primate adaptation and evolution, but most paleoclimate proxies cannot recover environmental seasonality on the scale of an individual lifespan. Oxygen isotope compositions (δ18O values) sampled at high spatial resolution in the dentitions of modern African primates (n = 2,352 near weekly measurements from 26 teeth) track concurrent seasonal precipitation, regional climatic patterns, discrete meteorological events, and niche partitioning. We leverage these data to contextualize the first δ18O values of two 17 Ma Afropithecus turkanensis individuals from Kalodirr, Kenya, from which we infer variably bimodal wet seasons, supported by rainfall reconstructions in a global Earth system model. Afropithecus δ18O fluctuations are intermediate in magnitude between those measured at high resolution in baboons (Papio spp.) living across a gradient of aridity and modern forest-dwelling chimpanzees (Pan troglodytes verus). This large-bodied Miocene ape consumed seasonally variable food and water sources enriched in 18O compared to contemporaneous terrestrial fauna (n = 66 fossil specimens). Reliance on fallback foods during documented dry seasons potentially contributed to novel dental features long considered adaptations to hard-object feeding. Developmentally informed microsampling recovers greater ecological complexity than conventional isotope sampling; the two Miocene apes (n = 248 near weekly measurements) evince as great a range of seasonal δ18O variation as more time-averaged bulk measurements from 101 eastern African Plio-Pleistocene hominins and 42 papionins spanning 4 million years. These results reveal unprecedented environmental histories in primate teeth and suggest a framework for evaluating climate change and primate paleoecology throughout the Cenozoic.

Climate seasonality is a potent driver of competition and natural selection (1), and is proposed to have influenced the origin and evolution of the great apes (2, 3), early hominins (4), and modern humans (5). Seasonal variation in water availability shapes the type and extent of savanna ecosystems (6), the expansion of which has exerted a profound effect on African faunal communities since the Late Miocene (7). In the Plio-Pleistocene, hominins occupied variably open environments (4, 8, 9), while African apes evolved (3, 10). The large-bodied Early Miocene ape Afropithecus turkanensis is of particular interest in this regard. Afropithecus is the oldest-known ape to possess anterior tooth specializations for hard-object feeding and thick molar cusp, as well as the first to have grown its molars over an extended period similar to modern African apes, features widely considered to be behavioral and developmental adaptations to durophagy and seasonal fallback food reliance (2, 11–14). Seasonal dietary resources are believed to have been important for later Eurasian apes of the Middle Miocene, and remain an important part of modern ape ecology (2, 14, 15).

Innovations in isotopic sampling methods now permit investigation of the seasonal ecology of extinct primates. While most paleoenvironmental proxies aggregate processes in sediments over thousands of years or longer—obscuring consequential trends in seasonality—ephemeral climate variation can be inferred from sequential changes in the composition of fossil teeth. Oxygen isotope compositions exhibit fluctuations that are recorded as teeth grow over time because hydroxyapatite mineral forms in equilibrium with body water δ18O values (16, 17). In tropical climates relevant to the evolution of apes, wet seasons result in low δ18O values, whereas during dry seasons the δ18O values of meteoric, surface and leaf waters increase (18–20). These patterns are influenced by

Significance

Environmental variability may have spurred unique adaptations among Miocene apes and later hominins, but this hypothesis has been impossible to test on the scale relevant to individual lifespans. We establish that oxygen isotope compositions in modern primate teeth record annual and semiannual seasonal rainfall patterns across a broad range of environments in equatorial Africa. We then document annual dry seasons experienced by the large-bodied Early Miocene ape Afropithecus turkanensis, which may explain its novel dental adaptations and prolonged development. By revealing real-time historical and prehistoric environmental variation on a near weekly basis, we demonstrate that extraordinary behavioral and ecological variability can be recovered from modern and fossil African primates.

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differences in moisture sources and surface evaporation, as well as by altitude, floral communities, and animals’ water tolerance, impacting mammalian $\delta^{18}O$ values across Africa at regional and local scales (18–25). It is possible to recover elements of this hydrological, physiological, and behavioral variability at high temporal resolution by sampling the rapidly mineralizing innermost enamel adjacent to the enamel–dentine junction (EDJ). This location averages far less time than other regions of the enamel, and $\delta^{18}O$ measurements can be coupled with daily incremental tooth formation to determine the timing of climatological and physiological events (17, 26–28). It remains unclear, however, to what extent primate enamel $\delta^{18}O$ values reveal specific meteorological histories, or how these values reflect hydrology at regional and continental scales.

Here we first test whether primate enamel oxygen isotope compositions track meteorological histories in two baboons (Papio hamadryas) by contrasting enamel $\delta^{18}O$ measurements with concurrent local rainfall records. We quantify daily tooth growth rates to facilitate near weekly, fine-scale (approximately 15 to 20 μm) sequential $\delta^{18}O$ measurements over multiple years of formation using a sensitive high-resolution ion microprobe specialized for stable isotope analysis (SHRIMP-SI). Baboon individuals belonged to two troops relying upon different, nearby water sources—the shallow, saline Lake Basaka, and the Awash River, buffered by the upstream Koka Dam—permitting an examination of how local hydrology may mediate the incorporation of environmental signals into teeth. We then test whether enamel $\delta^{18}O$ values from primates in five populations across equatorial Africa evince broader regional patterns of rainfall seasonality and isotopic compositions. Long-term environmental comparisons have established that, relative to the eastern African Rift region and highlands, densely forested areas of western Africa have more consistent and higher annual rainfall, and rainfall $\delta^{18}O$ values are lower. In parts of eastern Africa, wet seasons are both annual and semiannual, and arid regions tend to experience variable and less rainfall overall; rainfall tends to have higher $\delta^{18}O$ values due, in part, to $^{18}O$-enriched moisture sources and evaporative effects (18, 22).

Finally, to improve the record of Early Miocene climate relevant to the environments in which apes originated and evolved, we investigate the oxygen isotope ecology of A. turkanensis and fossil herbivores from the circa 17 Ma Kenyan site of Kalodirr (11, 29, 30). Our two Afropithecus specimens derive from different stratigraphic levels within Kalodirr’s depositional sequence, allowing a test of the stability of the environments Afropithecus occupied over a portion of the Kalodirr Member. These results are compared to enamel $\delta^{18}O$ values from fauna sampled using traditional hand-drilled (bulk) carbonate methods, and contextualized with our analyses of modern African cercopithecoids and chimpanzees (Table 1). Values are also compared with simulations of seasonal Miocene rainfall and precipitation $\delta^{18}O$ from an Earth system model (31). Earth system models are three-dimensional numerical models of the global climate system that resolve the circulation and climate features of the atmosphere, ocean, and land surface. They are best known for their use in making future climate projections in response to anthropogenic emissions. For this study, we have modified an Earth system model, the National Center for Atmospheric Research Community Earth System Model (31), to simulate past climate conditions by incorporating nonvarying boundary conditions (e.g., atmospheric CO$_2$ levels, geography, bathymetry, surface elevations, surface types, glacial ice, aerosols, and solar luminosity) appropriate for the Miocene. The model simulates subdaily climate features at a horizontal resolution of 1.9°×2.5° in the atmosphere and 1°×1° in the ocean; however, in this study we focus on seasonal timescales. This integration of traditional and high spatial resolution stable isotope compositions, coupled with Earth system modeling, provides insights into the environmental conditions directly experienced by this important ancient ape.

### Results

#### Eastern African Modern Primates

We first establish an association between local monthly rainfall amounts, $\delta^{18}O$ measurements from an upstream water source, and $\delta^{18}O$ values from modern *P. hamadryas* tooth enamel formed concurrently. Primary monsoon rains arrive in Ethiopia’s Awash National Park in July and August, and are accompanied by a synchronous rapid decrease in rainwater $\delta^{18}O$ values in the Ethiopian highlands (Fig. 1A) (32, 33). $\delta^{18}O$ values were measured from several molars of two baboons that died in 1973; the formation of two of these molars during 1969 to 1971 facilitates comparison with measured local rainfall (Fig. 1A and B, SI Text Appendix, SI Text 1.1 and Figs. S1 and S2, and Dataset S1). The third molar (M3) cusp of baboon 73261, whose troop drank from Lake Basaka, reveals multiple $\delta^{18}O$ troughs with the same timing as

| Taxon                   | Region                        | Individual ID/accession | Teeth | Years sampled |
|-------------------------|-------------------------------|-------------------------|-------|---------------|
| *Papio hamadryas* sp.   | Awash National Park, Ethiopia | 73261                   | LM1-3 | 4.7           |
| *Papio hamadryas* sp.   | Awash National Park, Ethiopia | 73436                   | LM1-2 | 3.4           |
| *Papio anubis* sp.      | Awash National Park, Ethiopia | HT 17-02                | LM2-3 | 3.3           |
| *Papio anubis* sp.      | Awash National Park, Ethiopia | HT 18-02                | LM2-3 | 3.4           |
| *Papio anubis-hamadryas* sp. | Awash National Park, Ethiopia | HT 19-02                | LM2-3 | 2.5           |
| Theropithecus gelada    | Debre Highlands, Ethiopia     | HKU 0237                | LM2   | 2.2           |
| Theropithecus gelada    | Debre Highlands, Ethiopia     | HKU 0243                | LM3   | 2.9           |
| *Papio anubis*          | Bushenyi District, Uganda    | U9                      | LC, LM1-2 | 7.1           |
| *Papio anubis*          | Bushenyi District, Uganda    | U10                     | UC, UM1 | 2.2           |
| Chlorocebus tantalus tantalus | Bushenyi District, Uganda | HT 06-02                | LM1-3 | 4.0           |
| Chlorocebus tantalus tantalus | Bushenyi District, Uganda | HT 07-02                | LM1   | 1.0           |
| Cercopithecus mona       | Lama Forest, Benin           | HT 01-10                | LC, LM1 | 3.5           |
| Pan troglodytes verus    | Ganta Region, Liberia        | 7038                    | UM3   | 2.5           |
| Pan troglodytes verus    | Ganta Region, Liberia        | 7079                    | UM3   | 2.8           |
| Afropithecus turkanensis | Kalodirr, Kenya              | KNN-WK 17024            | LM2   | 2.7           |
| Afropithecus turkanensis | Kalodirr, Kenya              | KNN-WK 24300            | LM2   | 3.2           |
the primary rains of 1969 and 1970. The second molar (M2) cusp of baboon 73436, whose troop lived next to the Awash River, shows a steady increase in δ¹⁸O values over more than 8 mo that is consistent with the marked drought from September 1970 until May 1971, a period during which the minor seasonal rain failed to arrive. Values for this M2 finally declined, presumably with the onset of the 1971 rains.

While δ¹⁸O measurements of additional molars from these two individuals and other nearby wild baboons cannot be precisely anchored in time (and thus related to rainfall records), enamel δ¹⁸O means and ranges from a total of five individuals from Awash National Park are relatively consistent (Fig. 1C and SI Appendix, Figs. S1–S5). Their range of variation (on average 3.6‰) is slightly less than average seasonal rainfall δ¹⁸O variation of 4.9‰ in the Addis highlands, upstream from the Awash River (Fig. 1A). Major peaks and troughs in the enamel δ¹⁸O of Awash baboons show annual periodicities across most but not all molars (SI Appendix, Figs. S6–S10), while some teeth also record the semiannual rainfall periodicities present in this region of eastern Africa (22, 33).

When looking more broadly across eastern Africa, enamel δ¹⁸O values are highest in P. hamadryas baboons inhabiting arid scrubland where estimated rainfall δ¹⁸O values are also high (33, 34). Mean values are lower in teeth from two highland Theropithecus gelada individuals (24.8‰, n = 235 measurements) (SI Appendix, SI Text 1.2 and Figs. S11 and S12 1.2), where annual

![Figure 1](https://example.com/figure1.png)

**Fig. 1.** Primate enamel δ¹⁸O values reflect local seasonal rainfall and regional hydrology. (A) Seasonal meteoric precipitation amounts from the Awash National Park (blue trendline) are reflected by rainfall δ¹⁸O compositions from Addis Ababa (purple trendline) averaged over 1966 to 1973. Measured trends in water near the headlands of the Awash River are largely consistent with rainfall amounts in the national park over the lifetime of baboons studied here. (B) Three-sample moving average of weekly sequential enamel δ¹⁸O values (black trendline) from the M3 of 73261 (Upper) and M2 of 73436 (Lower), registered to contemporaneous local rainfall values over 1969 to 1971 (blue trendline). Error margins from the estimated duration of tooth development prior to death in 1973 precluded the calendar registration of earlier-forming molar teeth or more precise alignments of these teeth. (C) δ¹⁸O measurement ranges from cercopithecoid teeth (horizontal bars) at Awash in the Ethiopian Rift Valley (brown), Debre in the Ethiopian highlands (blue), Bushenyi District in Uganda (green), Lama Forest in Benin (yellow), and chimpanzee teeth from the Ganta region in Liberia (red). Means are shown as stars and 95th percentiles shown as darkened bar segments. On the y axis, mean estimated rainfall δ¹⁸O is shown for each of the five sites, demonstrating that primate enamel δ¹⁸O follows regional rainfall δ¹⁸O. Horizontal enamel δ¹⁸O bars are not scaled to the y axis. (D) Estimated mean annual rainfall δ¹⁸O (33–35) compared to enamel δ¹⁸O tooth means in this study.
rainfall is greater and rainfall $\delta^{18}$O values are correspondingly lower (inferred from nearby Addis and from regional rainfall $\delta^{18}$O models) (33–35). Enamel $\delta^{18}$O values are lowest in two Ugandan baboons (Papio anubis) from the Bushenyi District (21.8‰, $n = 544$ measurements) (SI Appendix, SI Text 1.3, and Figs. S1–S15), where rainfall mean $\delta^{18}$O values are also lowest. Two Bushenyi talanta monkeys (Chlorocebus tantalus) have slightly elevated $\delta^{18}$O values (23.0‰, $n = 267$ measurements) (SI Appendix, Figs. S16–S18) compared to the contemporaneous sympatric baboons, consistent with their relatively high ingestion of arboreal resources that are likely enriched in $^{18}$O (19, 20, 25). A pronounced but brief decline in $\delta^{18}$O values in one talanta monkey may correspond to a major rainstorm in April 1963 coincident with third molar formation (SI Appendix, Fig. S17); historical rainfall records document the end of a long drought at this time, and a 60-y low in rainfall $\delta^{18}$O measurements from nearby Entebbe (33).

**Western African Modern Primates.** Comparisons across equatorial Africa reveal that primate enamel $\delta^{18}$O values mirror regional hydroclimate and oxygen isotope systematics (Fig. 1 C and D and Datasets S1 and S2). Primate enamel $\delta^{18}$O values are highest in eastern Africa, where rainfall $\delta^{18}$O values are also high, and lower in western Africa (Fig. 1 C) (33–35). Mean enamel $\delta^{18}$O measurements correlate relatively closely with mean annual rainfall $\delta^{18}$O estimates (Fig. 1D); while the relationship between variability in tooth and rainfall oxygen isotope composition is positive, it is inconsistent (SI Appendix, Fig. S19).

Two M3s from broadly contemporaneous Liberian chimpanzees show mean $\delta^{18}$O values (18.3‰) lower than those of the Ethiopian rift baboons (25.6‰) and highland geladas (24.8‰), Ugandan baboons (21.6‰), and talanta monkeys (23.0‰) (SI Appendix, SI Text 1.4). Similar seasonal patterns are seen in both chimpanzees, with $\delta^{18}$O ranges of 7.9‰ and 8.7‰, respectively (Fig. 2, SI Appendix, SI Text 1.5, and Dataset S2). The M3 of individual 7038 was sampled over 2.5 y of continuous growth, revealing three discrete $\delta^{18}$O peaks that are likely capturing brief dry seasons. The M3 of individual 7079 yielded 2.8 y of records, revealing three dry seasons more prolonged than those experienced by 7038. Frequency analyses show 1.0-y periodicities in $\delta^{18}$O values in the molars of both individuals (SI Appendix, Fig. S20). Low enamel $\delta^{18}$O values and strong annual oscillations are consistent with records of high rainfall (approximately 1.880 mm annually) at the time of collection in the Ganta region of Liberia (36), similar to recent patterns from the Taï Forest, Ivory Coast (Fig. 2B) (37).

We also sampled one mona monkey (Cercopithecus mona) from Benin, where chimpanzees are now locally extinct. Its mean enamel $\delta^{18}$O value (19.8‰, $n = 181$ measurements) (SI Appendix, Fig. S21 and Dataset S1) is consistent with higher rainfall $\delta^{18}$O values in Benin compared to Ganta (33–35), and with feeding in a higher canopy niche relative to chimpanzees. Weekly $\delta^{18}$O measurements over 2.6 y of tooth formation reveal the same strongly annual seasonality as in the Liberian chimpanzees (SI Appendix, Fig. S22).

**A. turkanensis and Associated Fauna.** Afropithecus specimens KNM-WK 17024 and KNM-WK 24300 were collected from the middle and upper layers of the Kalodirr Member of the Lothidok Formation, respectively (Fig. 3 A and B). Specimen KNM-WK 17024 derives from a fossiliferous locality in the middle of the Kalodirr Member known as “Bone Hill,” whose precise age is unknown but is bounded by the tuff at the base of the member (17.5 ± 0.2 Ma) and the Naserte Tuff above (16.8 ± 0.2 Ma) (Fig. 3B) (30). KNM-WK 24300 was recovered from sediments immediately below the Naserte Tuff, and we therefore estimate the age to be slightly older than 16.8 Ma. Fine-scaled enamel $\delta^{18}$O measurements show ranges of 3.3‰ (KNM-WK 17024, $n = 113$) and 5.5‰ (KNM-WK 24300, $n = 135$), or 8.4‰ across both teeth combined (Fig. 3G, SI Appendix, SI Text 1.6, and Dataset S3). The higher $\delta^{18}$O values and larger $\delta^{18}$O range in KNM-WK 24300 (21.4 to 26.9‰) compared to KNM-WK 17024 (18.5 to 21.8‰) suggest a landscape for the individual in the upper layer that was more seasonally variable, and possibly drier, which is discussed...
further below. KNM-WK 24300 appears to have experienced three prolonged dry seasons over 3 y, with the second lasting 7 to 9 mo. The M2 of individual KNM-WK 17024 appears to show two sustained dry periods over 2.5 y. The strongest seasonal oscillations are annual in KNM-WK 17024 (1.0 y) and subannual in KNM-WK 24300 (0.7 y), although KNM-WK 24300 also records a sharp secondary peak at 1.0 y (Fig. 4 A).

Enamel carbonate $\delta^{18}$O values from Kalodirr terrestrial herbivores ($n = 66$ individuals) (SI Appendix, SI Text 1.7 and 1.8 and Dataset S4; see Materials and Methods for carbonate-bioapatite comparison) demonstrate that anthracotheres ($n = 8$) have the lowest $\delta^{18}$O values (mean 17.9‰, Vienna Standard Mean Ocean Water, VSMOW), consistent with an aquatic or semiaquatic ecology (38). In contrast, suids ($n = 7$), hyraxes ($n = 7$), rhinocerotids ($n = 7$), and giraffids ($n = 5$) have higher $\delta^{18}$O values (means 19.7 to 19.8‰, consistent with terrestrial browsing. Anthracotheres—taxa most likely to reflect site hydrology due to inferred semiaquatic behaviors—have elevated $\delta^{18}$O values in the upper portion of the sequence, suggesting a hydrological shift, and possibly drier conditions in younger deposits. This would be consistent with the elevated $\delta^{18}$O values observed in the younger Afropithecus specimen (KNM-WK 24300). Mean $\delta^{18}$O values from both Afropithecus individuals are elevated by 3.2‰ compared to contemporary Kalodirr terrestrial herbivores (SI Appendix, Fig. S23). This difference is similar to that observed between chimpanzees and terrestrial herbivores at Kibale, Uganda (2.2‰) (SI Appendix, Fig. S24) (25), supporting the fidelity of niche reconstruction from fossil enamel $\delta^{18}$O values at Kalodirr.

To further evaluate seasonal $\delta^{18}$O oscillations observed in Afropithecus molars, we deploy a water isotope-enabled Earth system model (31) to predict seasonal rainfall patterns on a similarly detailed scale. The model fully resolves atmosphere, ocean, and land surface processes, and is framed by Miocene paleogeography, bathymetry, atmospheric CO$_2$, and ice volumes (SI Appendix, SI Text 1.9). Due to the significant influence of Earth’s orbital configuration on low-latitude precipitation, we ran

![Figure 3](https://doi.org/10.1073/pnas.2123366119)
simulations under two different orbital configurations, a “control” run with modern orbital parameters and a “high insolation” run with orbital parameters that maximize Northern Hemisphere summer insolation. In the control, the model predicts semianual rains at Kalodirr 17 Ma, consistent with the high-resolution tooth δ18O measurements and periodograms from *Afropithecus* individual KNM-WK 24300 (Fig. 4). In the high insolation run, the model predicts a continuous wet season from May to November with greater maximum rainfall, resembling the more annual pattern observed in individual KNM-WK 17024. Under control conditions, simulated precipitation δ18O values at Kalodirr have a seasonal range of approximately 2.7‰ with a maximum during April to June and a minimum in November to January; this range increases to 9.0‰, with high insolation.

**Discussion**

**Primate Enamel δ18O Values Track Equatorial African Hydrology.** We have established that oxygen isotope compositions in primate teeth reflect environmental gradients in rainfall amount, altitude, and aridity. Enamel δ18O values are highest in the arid Ethiopian rift, intermediate in Uganda, and lowest near the Guinean coast, mirroring continental-scale rainfall δ18O patterns (Fig. 1) (15, 33–35). Comparisons of primate populations in the same region show that local topography impacts δ18O values, as expected given rainout of air masses over rising altitudes (15, 20); highland gelada values are lower than lowland rift baboons. When populations are compared from the same location near Bushenyi District, Uganda, we find that enamel δ18O values segregate with ecological niches. Higher δ18O values among tantalus monkeys relative to local baboons (Fig. 2C) suggest the preferential consumption of arboreal resources, as is the case with other African primates feeding at different canopy heights (19, 23–25).

In addition to reflecting broad environmental trends, primate oxygen isotope compositions reveal specific meteorological histories and human alteration of the hydrological landscape. Awash baboon values are largely consistent with contemporaneous records of steep gradients in local rainfall and the δ18O values of precipitation in the upstream highlands (Fig. 1 A and B). Within the Awash individuals, enamel δ18O values differ between one baboon that drank from the shallow mineral Lake Basaka and another with year-round access to the Awash River. The latter individual’s isotopic compositions were likely buffered by the operation of the Koka Dam and reservoir upriver, with a total volume approximately five times that of Lake Basaka. Differences in the enamel δ18O profiles of two baboons experiencing similar rainfall histories, but living adjacent to different water bodies, suggests that local hydrology is a potent mediator between rainfall and body water isotope compositions. These differences also reveal how human alterations of the hydrological landscape can influence the body chemistry of local wildlife.

Our data show seasonal patterns consistent with trends in western and central Africa; enamel δ18O measurements in the chimpanzees and mona monkey reveal annual wet seasons, consistent with dominant rainfall patterns in this region (33–37). Rainfall seasonality, rainfall δ18O variation, and local variability in river water δ18O are estimated to be high in portions of the Gulf of Guinea (18, 33–35), likely contributing to the large enamel δ18O ranges in Liberian chimpanzees. Variable drinking and foraging behaviors may further contribute to enamel δ18O variability: across Africa, chimpanzees acquire water from rivers, streams, tree hollows, soaked wood, and underground tubers (39). Chimpanzees in the nearby Taï Forest consume at least 263 plant species with strong seasonal preferences (40). Primate enamel δ18O values may serve as faithful proxies for local hydrology and environmental variation despite the complexity of feeding behaviors (21, 24, 25, 37, 39, 40), because primates rely on plant resources with isotopic compositions that are exquisitely sensitive to local temperature, humidity, and evapotranspiration (40, 41). In summary, primate enamel δ18O profiles capture local environmental variation and broad rainfall patterns across Africa, demonstrating their utility for climatic and hydrological reconstruction.

**Climatic Drivers of Miocene Ape Evolution.** The two *Afropithecus* specimens collected from different layers in the Kalodirr Member show enamel δ18O profiles consistent with semiannual
Fig. 5. High-resolution δ18O samples from primate teeth reveal extensive lifetime climate variation relative to singular and aggregate bulk samples. (A) Conventional δ18O measurements from 62 teeth (red circles) of 33 chimpanzees reveals variation of only 2.7‰ (47). In contrast, high-resolution oxygen δ18O measurements of two chimpanzee molars (light blue bars) from the same population span 8.7‰. The gray circle is the single bulk measurement of chimpanzee 7079 (from ref. 47) converted from a carbonate measurement, as detailed in SI Appendix, SI Text 1.8. (B) δ18O ranges from two Afropithecus molars (dark blue) compared to (C) ranges derived from of bulk carbonate samples of 101 fossil hominins in the Turkana Basin over a 4-million-y period (45, 46) and (D) 42 bulk-sampled fossil Theropithecus individuals from an approximately 3-million-y period in the Turkana Basin (48). δ18O ranges of Afropithecus shown in B, shaded green across C and D for comparison.

and annual dry seasons of variable intensity. As in modern ecosystems where arboreal primate δ18O values are elevated relative to sympatric terrestrial herbivores, enamel δ18O values of Afropithecus are higher than other fossil taxa at Kalodir (SI Appendix, Figs. S23 and S24), supporting reconstructions of their arboreal feeding ecology (2, 12, 13, 30). Sustained durations of high δ18O values suggest longer dry seasons for Afropithecus than those experienced by Liberian chimpanzees, and the semianual wet seasons seen in the younger specimen (KNM-WK 24300) resemble rainfall patterns like those sampled from primate teeth in arid regions of the contemporary eastern African Rift (Fig. 4A).

Our Earth system model shows that Early Miocene rainfall at Kalodir could be semianual or annual depending on the orbital configuration, consistent with Afropithecus seasonal δ18O profiles. The lower rainfall δ18O range simulated by our model under “control” orbital conditions appears consistent with the measured δ18O range in KNM-WK 17024. Simulated higher amplitude rainfall δ18O variation under conditions of high Northern Hemisphere insolation suggests that orbitally-forced climate differences may explain the higher enamel δ18O variation in KNM-WK 24300 relative to KNM-WK 17024. Additional factors may also contribute to differences between Afropithecus individuals, including variation in aridity and vegetation over time, or in temperature and global ice volume, although ocean δ18O records during this period indicate relative stability preceding the Miocene Climatic Optimum (42). Behavior and site hydrology could also influence δ18O values, analogous to differences between baboons drinking from varied water sources in the Awash National Park (Fig. 1).

The environmental variation that we have reconstructed using δ18O values and Earth system modeling supports the suggestion that Afropithecus’ distinct tooth and jaw morphology allowed it to exploit seasonally variable and fallback resources (2, 14). Hard-object feeding (durophagy) in Afropithecus is well supported by facial musculature and skeletal buttressing, as well as a suite of dental characteristics including thick enamel (2, 11–14). For example, its canine placement and premolar size would have allowed for consumption of fruit protected by hard shells, nuts, or other mechanically demanding objects (11, 13). Characterizations of enamel thickness place Afropithecus at the high-end of Early Miocene and extant ape values (12), very similar to modern hard-object feeding mangabeys (43), though Afropithecus’ anterior dentition is morphologically distinct from mangabeys. Miocene apes may have also relied on cognitive adaptations for survival in challenging seasonal environments, differentiating them from cercopithecoidea, which are thought to have responded to similar pressures with more rapid reproduction and anatomical specializations for folivory (3, 10). Social learning and extractive and cognitive behaviors needed to exploit seasonally variable and spatially complex resources likely required an extended developmental period (2, 3, 10–12, 15). Similar isotopic studies of Early and Middle Miocene apes Ekembo, Proconsul, Equatorius, and Kenyapithecus would provide important context about the relationship of these features to varied environments in eastern Africa, as well as heavily debated adaptations found in early hominins (2, 4, 8, 9).

Implications for the Study of Primate and Hominin Paleoecology. Stable isotope measurements of drilled (bulk) enamel samples have contributed to the discovery of niche differentiation between fossil apes and hominins within their faunal communities (25, 44–46). Nevertheless, bulk stable isotope sampling may not reveal individual behavioral flexibility, nor population- or species-level seasonal variability, because bulk samples incorporate enamel formed over much longer periods of time than values from high spatial-resolution measurements (16, 17, 26–28, 45). We first illustrate this through the example of Liberian chimpanzees. Our high-resolution sampling of the
M3s from two individuals (n = 255 measurements) reveals δ18O ranges (7.9‰ and 8.7‰) that are about three times larger than the range derived from bulk carbonate δ18O sampling of 33 individuals in this community (2.7‰, n = 62 teeth/measurements) (Fig. 5A) (47). A single bulk δ18O measurement of the M3 of chimpanzee 7079 yielded a phosphate-equivalent value of 19.4‰ (SI Appendix, SI Text 1.5 and 1.8) (47), while our 111 near weekly measurements from this same tooth produced a range of 13.1 to 21.8‰, with clear seasonal cycles over nearly 3 y (Fig. 2). Neandertal teeth previously examined with this high-resolution approach also revealed a similar expansion in δ18O ranges relative to bulk samples, subsuming variation presumed to have distinguished different phases of local occupation (28).

Importantly, the two Afropithecus molars reveal isotopic variation that is nearly equal to bulk δ18O values from 101 Turkana Basin hominins spanning 4 million y (Fig. 5C) (43, 44). Similar δ18O measurements from 42 Turkana Theropithecus specimens also show a narrower range of variation than the Afropithecus molars (Fig. 5D) (48). Simply stated, bulk sampling of fossil primates (including hominins) is underrepresenting environmental variation and behavioral complexity. Microsampling oxygen isotopes in primate teeth complements bulk approaches that explore population or species-level differences, and in this context can reveal crucial seasonal variation in the local hydrology and behavior of individuals. Future studies may elucidate details of past regional climates and even specific meteorological events, and will underpin the recovery of an extraordinary degree of ecological information from extinct taxa, including our primate ancestors.

Materials and Methods

Primate samples are detailed in SI Appendix, SI Text. Thin-section production of Afropithecus is described in Smith et al. (49), chimpanzees in Smith et al. (50), and baboons in Dirks et al. (32); all formation times were revisited and updated here by T.M.S. following analytical procedures in Smith et al. (28). Daily growth lines were measured along enamel prisms from their initial formation over the dentine horn until an accentuated line was encountered, yielding the formation time of the corresponding segment of the EDJ. This process was then repeated while mapping the successive positions of the enamel growth front (expressed as accentuated lines) until the enamel cervix was reached, yielding a total time of molar cusp formation (SI Appendix, Figs. S26 and S27).

SHRIMP measurement methods also follow those detailed in Smith et al. (28). Briefly, oxygen isotope ratios were measured using the SHRIMP SI at the Australian National University. Glass-mounted polished sections of the Afropithecus fossils and modern primates (Table 1) were cleaned with petroleum spirit, RBS detergent solution, and Millipore water, dried for ≥24 h in a 60°C vacuum oven, and coated with a thin (approximately 10 nm) layer of high-purity Al (and/or Au) before being placed in the SHRIMP SI under high vacuum for approximately 12 h prior to analysis by secondary ion mass spectrometry (SIMS). An approximately 1.5-μm, 15-kV beam of positive Cs ions was used to sequentially sputter a series of approximately 15- to 20-μm diameter spots in the innermost enamel adjacent to the EDJ from the dentine horn to the cervix. Negative O secondary ions were extracted at 10 kV, mass separated at approximately 3000R (M/ΔM) and measured in current mode using a multiple collector equipped with dual Faraday cups (resistors 107Ω for 18O, 105Ω for 16O). Charge on the sample surface was neutralized using a 1.2-kV focused electron beam. Each analysis consisted of 2-min preconditioning, during which electronbeam baselines were measured, followed by optimization of the beam steering and 6 × 20-s measurements of 16O/18O ratios, giving a spot uncertainty of approximately 0.1‰ (15E, 18O c. 1.5 GHz). Corrections for electron-induced secondary ion emission were made based on measurements before and after each analysis. δ18O values were calculated relative to mineral apatite standard Durango3 (9.8‰, VSMOW) that was measured repeatedly over the course of ~14 to 24-h period of data collection for each tooth (2 SD, approximately 0.5‰). Measurement spots were spaced as far apart as 300 μm near the dentine horn, and reduced to 25 to 30 μm apart toward the cervix, with spacing calculated to maintain near weekly sampling across all teeth.

In order to assess time-dependent patterns of tooth δ18O measurements, we used a frequency analysis algorithm known as the Lomb-Scargle periodogram (51). The Lomb-Scargle algorithm takes measurements that have been sampled unevenly or irregularly over a given interval, and estimates the power of sine wave periods within a given range to produce the temporal patterns present within those measurements. The method estimates periodicities that underlie more complex signals in a manner similar to Fourier transformations. For each tooth we calculated a fourth-order polynomial function predicting the timing of formation in days from the distance in mm along the tooth EDJ; this function was fitted using day of formation and EDJ length data (Datasets S1-S3). The function was then used to convert distances from SHRIMP measurements into estimates of days of tooth formation. Paired δ18O measurements and day of formation estimates were provided to the Lomb-Scargle periodogram algorithm hosted by the AstroPy 4.0.1 library run with Python 3.1. For individuals with teeth that formed over 600 d or more, periods from 0 to 500 d were analyzed for each tooth, and the maximum power of each period was reported in years.

Kaloldir herbivore teeth were placed in stratigraphic sequence using GPS locations on the basis of work by Boschetto et al. (52). Only specimens showing no or little visible diagenetic alteration were selected for isotopic analysis. Superficial enamel was removed and discarded by rotary drill, and then enamel powder samples were collected from the clean surface. Samples were not pretreated prior to analysis. Carbonate δ18O values were measured by Jason Curtis at the University of Florida, Gainesville, using a Finnigan-MAT 252 IRMS coupled with a Kiel III carbonation preparation device. Approximately 600 μg per analysis of sample and 30 to 50 μg of NBS-19 standard were reacted with purified phosphoric acid for 470 s to release CO2 for isotopic measurement. Carbonate δ16O V-PDB values were converted to bioapatite-equivalent values by subtracting 8‰ following the procedure outlined in the SI Appendix, SI Text 1.8, and then placed on a VSMOW scale; original and transformed data are given in Dataset S4.

We performed paleoclimate simulations using the fully coupled water isotope-enabled Community Earth System Model by the National Center for Atmospheric Research (31), with Miocene boundary conditions (e.g., atmospheric CO2 levels, geography, bathymetry, surface elevations, surface types, glacial ice, aerosols, and solar luminosity). Further details can be found in SI Appendix, SI Text 1.9.

Data Availability. All study data are included in the main text and supporting information.

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