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Comment on the Paleoenvironment of *Ardipithecus ramidus*

Thure E. Cerling,^{1*} Naomi E. Levin,² Jay Quade,³ Jonathan G. Wynn,⁴ David L. Fox,⁵ John D. Kingston,⁶ Richard G. Klein,⁷ Francis H. Brown¹

White and colleagues (Research Articles, 2 October 2009, pp. 65–67 and www.sciencemag.org/ardipithecus) characterized the paleoenvironment of *Ardipithecus ramidus* at Aramis, Ethiopia, which they described as containing habitats ranging from woodland to forest patches. In contrast, we find the environmental context of *Ar. ramidus* at Aramis to be represented by what is commonly referred to as tree- or bush-savanna, with 25% or less woody canopy cover.

We welcome the contribution by White and colleagues (1–3) to the growing body of isotopic paleoenvironmental evidence for Africa. This data set supports, rather than refutes, existing interpretations for the environmental context of early hominins such as *Ardipithecus ramidus*. Before about 8 million years ago (Ma), Africa was mainly vegetated by C₃ plants, presumably forest and shrubland, with no evidence of open C₄ grasslands that are important today (4, 5). Globally, C₃ ecosystems retreated first in the tropics and later at the mid-latitudes, with C₄ grasses becoming increasingly important in local ecosystems between 8 and 3 Ma. Open grasslands emerged later in Africa, between 3 and 2 Ma depending on location.

This transitional state is readily apparent in isotopic and other data presented by White and colleagues for the Awash River basin in central Ethiopia. However, we disagree with their interpretation of the data, specifically their stress on the wooded nature of the paleoenvironment of *Ar. ramidus*. The following represents their views: “Our combined evidence indicates that *Ar. ramidus* did not live in the open savanna that was once envisioned to be the predominant habitat of the earliest hominids, but rather in an environment that was humid and cooler than it is today, containing habitats ranging from woodland to forest patches” (1) and “*Ar. ramidus* resided and usually died in a wooded biotope that included closed through grassy woodlands and patches of true forest [sensu (6)]. There is no evidence to associate this hominid with more open wooded grasslands or grassland savanna”

(3). In contrast, we find the environmental context of *Ar. ramidus* at Aramis to be represented by what is commonly referred to as “tree or bush savanna” with 25% or less woody canopy cover. The habitats involved probably ranged from riparian forest to grassland.

We adopt the United Nations Scientific and Cultural Organization (UNESCO) definitions for classification of African vegetation (6) used by White *et al.* (3) in which “forests have continuous stands of trees with overlapping crowns, forming a closed, often multistory canopy 10 to 50 m high; the sparse ground layer usually lacks grasses; closed woodlands have less continuous canopies and poorly developed grass layers; woodlands have trees with canopy heights of 8 to 20 m; their crowns cover at least 40% of the land surface but do not overlap extensively. Woodland ground layer always includes heliophilous (sun-loving, C₄) grasses, herbs/forbs, and incomplete small tree and shrub understories; scrub woodland has a canopy height less than 8 m, intermediate between woodland and bushland. As proportions of bushes, shrub, and grasses increase, woodlands grade into bushland/thickets or wooded grasslands. Wooded grassland is land covered with grasses and other herbs, with woody plants covering between 10 and 40 per cent of the ground. Grassland is land covered with grasses or other herbs, either without woody plants or the latter not covering more than 10 per cent of the ground.” The UNESCO classification does not include a definition of savanna because of its ambiguous use, but common usage of the term [e.g., (7, 8)] would include wooded grasslands and grasslands of the UNESCO terminology.

Our comments focus on material presented in (1–3): stable carbon isotopes in paleosols, oxygen isotopes of mammalian tooth enamel used to determine paleoaridity, carbon isotopes in mammalian tooth enamel, the relative abundance of micromammal fossils, and the relative abundance of phytoliths. These measures are independent of vertebrate morphologies as paleoenvironmental indicators.

Paleoecologic reconstruction at Aramis (1) relies heavily on the carbon isotopic composition of

paleosol organic matter and carbonate from paleosols at all nine sampled localities. Pedogenic carbonate forms in soils where evapotranspiration exceeds infiltration and is an indicator of water-stressed environments. In the tropics, pedogenic carbonates are found in most soils where rainfall is <1000 mm per year.

To place the isotope analysis in context, we present $\delta^{13}\text{C}$ of organic matter from modern tropical soils as related to measured woody canopy cover (Fig. 1A) and to commonly used ecosystem classifications (Fig. 1B). The fraction of C₄ biomass is not expected to be directly related to canopy gaps: Shade provided by the full to partial tree canopy reduces surface temperatures, which encourages growth of C₃ plants relative to C₄ plants. Figure 1A shows limited C₄ biomass until tree or woody canopy cover falls below 50% to 60%. Even in areas of limited tree or woody canopy cover, nonwoody C₃ forbs and herbs are present that contribute to soil organic matter; thus, open grasslands (<10% woody plants) may still have substantial C₃ biomass.

Figure 1C shows a histogram of the fraction C₄ biomass calculated in table S1 of (1) based on Aramis paleosols. Eighty-three of eighty-four analyses show C₄ biomasses exceeding 25%. Consideration of each site separately shows that there is no isotopic gradient from west to east (Fig. 2) and that all sites have median values between 40% and 60% C₄ biomass [calculations from (1)]. Such high estimates of the fraction of C₄ biomass are not consistent with the interpretation of “closed, wooded habitats” (3), but instead are compatible with a more open habitat where C₄ grass makes up 40 to 60% of the biomass or primary productivity.

Most Aramis paleosols have more than 40% C₄ biomass (78 of 84 values); Fig. 1A shows that this corresponds to woody canopy cover between 5 and 25%; Fig. 1B shows that this implies the types of vegetation described in the literature as tree-bush savanna, arid shrub savanna, edaphic grassland, bush savanna, or open savanna (references in Table 1). These correspond most closely to the UNESCO definition of wooded grassland or grassland, meaning none of the paleoenvironmental choices dictated by the Aramis results include the interconnected tree canopy (>60% woody canopy cover over extensive areas) required for interpretations of closed woodland or forest.

Paleosol carbonates from Aramis yield among the highest $\delta^{13}\text{C}$ values of all Pliocene sites in eastern Africa where pedogenic carbonates have been measured (9–14) and represent some of the highest abundances of C₄ biomass. Thus, Aramis has a higher fraction of grass and is more open than other hominin-bearing sites older than 4 Ma.

White *et al.* (3) use the Levin *et al.* (15) approach to estimate a water deficit of ~1500 mm per year, and we agree with their calculation. However, we do not agree that “therefore, Aramis was a generally dry woodland setting far from

¹Department of Geology and Geophysics, University of Utah, Salt Lake City, UT 84112, USA. ²Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, MD 21218, USA. ³Department of Geosciences, University of Arizona, Tucson, AZ 85721, USA. ⁴Department of Geology, University of South Florida, Tampa, FL 33620, USA. ⁵Department of Geology and Geophysics, University of Minnesota, Minneapolis, MN 55455–0231, USA. ⁶Department of Anthropology, Emory University, Atlanta, GA 30322, USA. ⁷Program in Human Biology, Stanford University, Stanford, CA 94305, USA.

*To whom correspondence should be addressed. E-mail: thure.cerling@utah.edu

riparian environments.” In the original study of the mammal $\delta^{18}\text{O}$ aridity index (15), the site giving the highest water deficit (1588 mm per year) was the Turkana region. Rivers in the Turkana region have narrow (10s to 100s of meters) riparian corridors abruptly grading into grassland or desert scrubland, an excellent example of a mosaic setting. Thus, the water deficit calculated by White *et al.* (3) is compatible with a riparian forest or woodland in an otherwise open bushland, woody grassland, or grassland as is found in the lower Omo Valley today. The high water deficit value (~1500 mm) at Aramis is similar to values in some of the hottest and driest parts of eastern Africa today, and it

contradicts the statement that *Ar. ramidus* lived “in an environment that was humid and cooler than it is today” (1).

More species of grazing ungulates have been recovered at Aramis than browsing ungulates. The absence of duikers (*Cephalophus* spp.) among the browsers argues against dense woodland or forest, whereas the dominance of kudu (*Tragelaphus*) need imply only riparian thicket (16). Specialized ambush predators in dense water-edge vegetation could explain the abundance of kudu and the even more striking abundance of primates (>35% of all specimens, including almost 6% hominins). White *et al.* (3) stress that the fossil fauna was heavily “ravaged” by carnivores be-

fore burial, suggesting that the fossil sites may represent a highly biased assemblage.

We note also that the interpretations of $\delta^{13}\text{C}$ data from browser tooth enamel are misleading. White *et al.* (3) state that “relatively low primate, giraffid, tragelaphine, and *Deinotherium* $\delta^{13}\text{C}$ values indicate that small patches of closed canopy forests were present,” but the enamel $\delta^{13}\text{C}$ values of the browsing animals from Aramis are considerably enriched in ^{13}C compared with analogs of these animals that live in closed canopy forests today (17). The $\delta^{13}\text{C}$ values from Aramis are consistent with browsing herbivores that live in a range of environments from woodlands to savanna.

The genera *Uranomys* and *Praomys* make up ~50% of the micromammalian fauna and are described as preferring biotopes associated with abundant C_4 grasses (2). Predator bias is offered to explain their frequency in what is interpreted as woodland. However, strong representation of *Uranomys* and *Praomys* is also consistent with the high fraction of local C_4 biomass estimated from local soils using carbon isotopes. If Louchart *et al.* (2) attribute the relative abundance of these grassland microfauna to predator bias and reject them as indicators of Aramis habitat, then they must also reject the environmental importance of the other rarer species that derive from the same barn owl accumulations and from which the authors infer woodland habitats.

We agree that “[M]odern studies on present-day vegetation demonstrate that...surface soil phytolith assemblages reproduce aspects of the vegetation such as tree cover and the relative abundance of C_3 and C_4 grasses” (1). Phytolith data [table S2 in (1)] show that the average phytolith abundance for 32 samples is $60 \pm 17\%$ grasses, $11 \pm 8\%$ palms, and $29 \pm 15\%$ dicots (Fig. 3). These data strongly suggest that grasses were a very important component of the vegetation at Aramis. The abundance of nonarboreal phytoliths is inconsistent with a predominantly woodland environment. As with the isotopic paleosol data, phytolith assemblages across the landscape do not vary substantially from west to east (Fig. 2).

WoldeGabriel *et al.* (1) state that “The abundance of arboreal phytoliths suggests tree cover ranging from a present-day mosaic of semi-deciduous forest and grassland to semi-deciduous woodland”. This is quite different from “habitats ranging from woodland to forest patches” (1) and, to us, does not appear to agree with the conclusion that “...early hominids did not evolve in response to open savanna or mosaic settings” (3).

Middle Awash now joins several other projects in Africa in which the paleoenvironmental context for fossil remains is coming into sharp focus. Evidence from Aramis and elsewhere clearly shows that open savanna grassland was not the environmental context of *Ardipithecus*. Savanna grassland became widespread much later in

Fig. 1. Relationships between the fraction of C_4 biomass from Aramis paleosols, $\delta^{13}\text{C}$ of soil organic matter in modern ecosystems, ecosystem classification, and percentage of woody canopy cover. Orange band in panels (A) to (C) represents >80% of the paleosol-derived C_4 estimates in (1). (A) Relationship between $\delta^{13}\text{C}$ in modern tropical soils (growing season temperature >15°C) and the fraction of woody canopy cover as determined in the field on an aerial basis. Data from (8, 18, 19); blue line is second-order polynomial fit to data. Percentage cover shown for 10, 25, 50, and 100% cover as 8-m diameter crown height for 1 ha area. (B) $\delta^{13}\text{C}$ values for soil organic matter from different tropical ecosystems as described by the respective authors (sources described in Table 1). Bars show the average values and ± 1 SD. (C) Histogram of C_4 values calculated for 84 stable isotope analyses of paleosols from Aramis sites. Values used are those calculated in (1) (Table 1). Relationship between percentage of C_4 in (C) and $\delta^{13}\text{C}$ values [(A) and (B)] are as defined in (1).

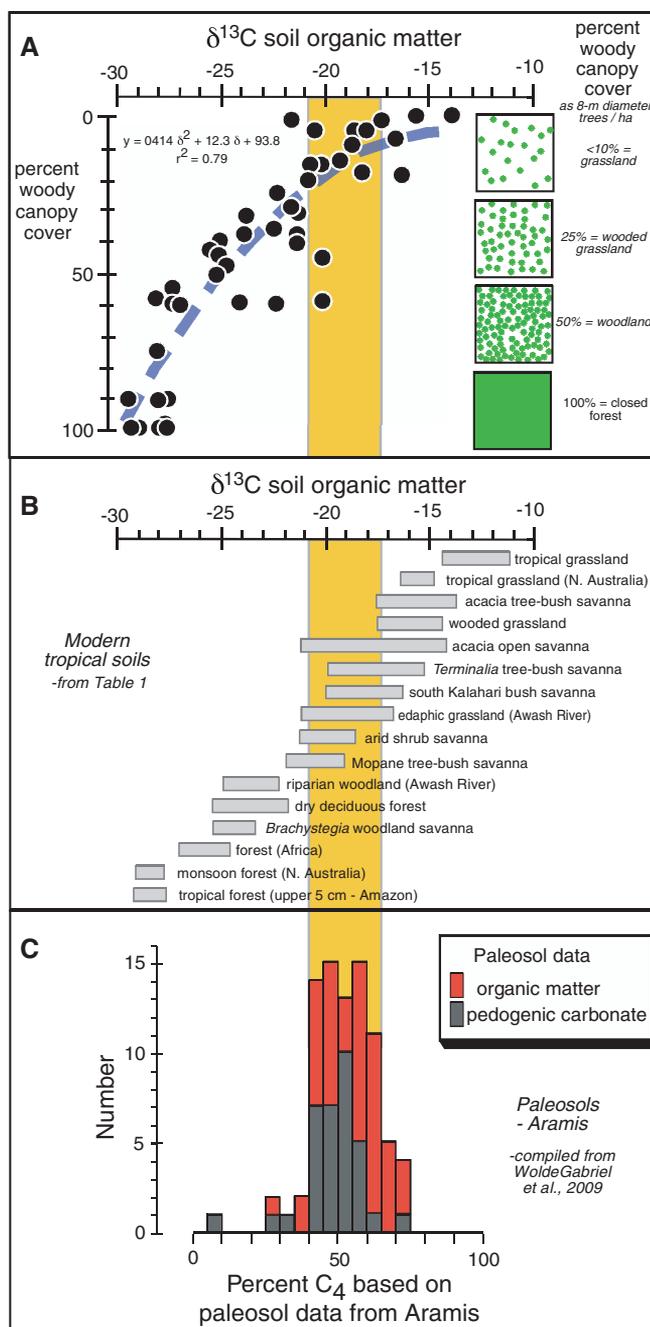


Fig. 2. Geographic variation of percent C₄ from paleosols [data from table S1 in (1)] and the range of grassy phytoliths found in 32 paleosol surface samples [data from table S2 in (1)] in the Aramis region. Percentage of C₄ values shown as a box-and-whisker diagram with the region between the 25th and 75th percentiles shaded in yellow. The total range of percentage of phytoliths is shown shaded in blue; range is given because many sites had from 1 to 3 samples, so percentile values could not be computed.

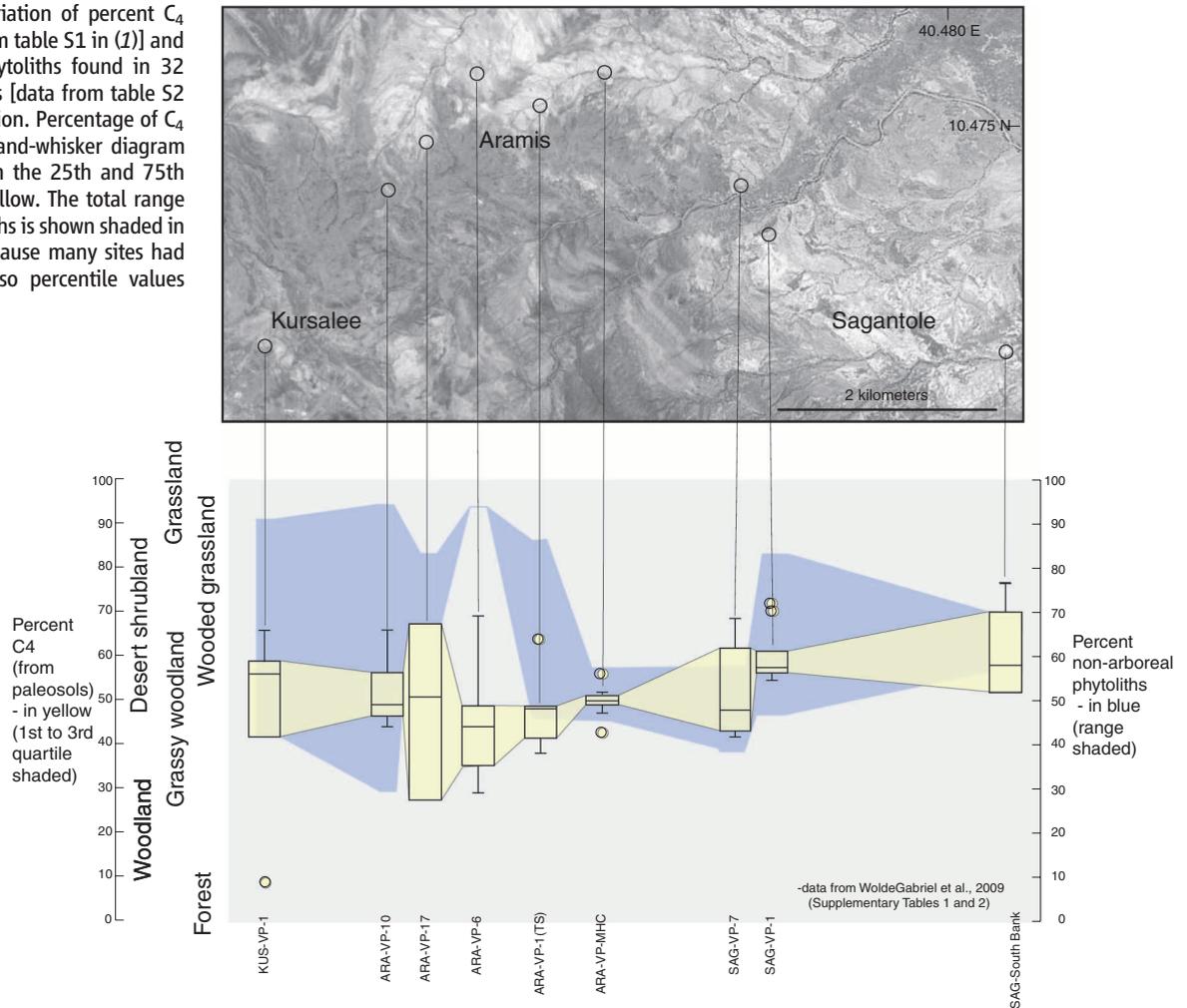


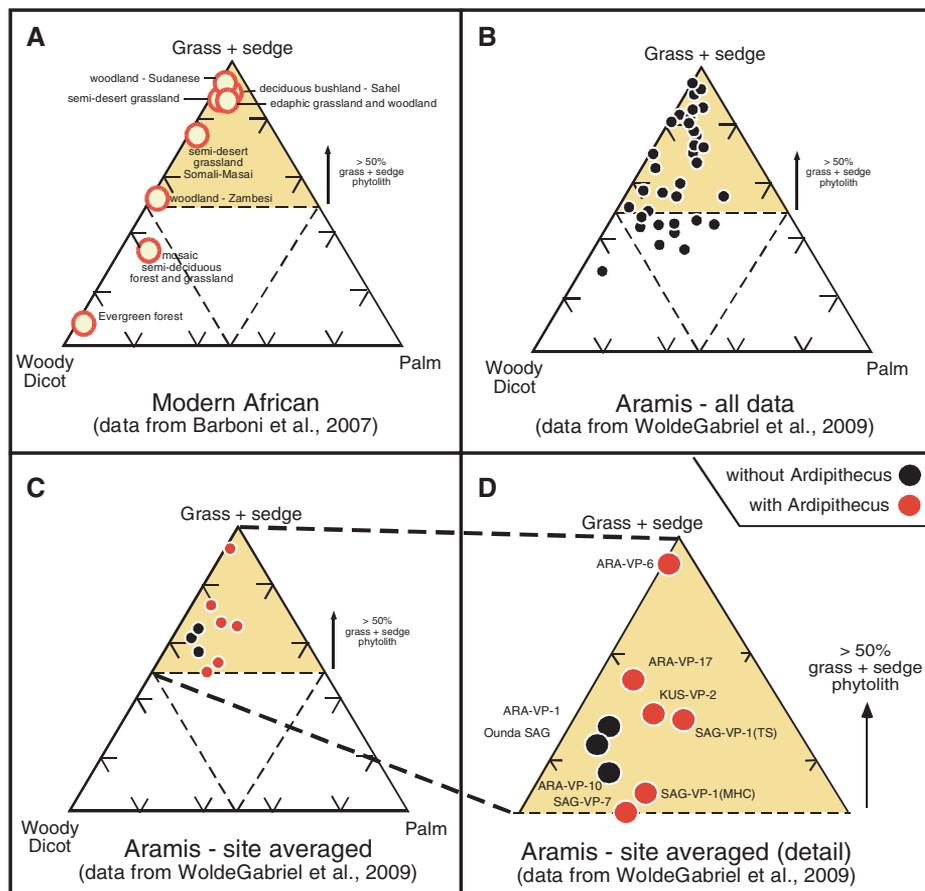
Table 1. Modern soil organic matter from tropical ecosystems as described in the references listed in the table. The average of all values is reported unless otherwise specified. SD, standard deviation; *n*, number of soil samples analyzed. No corrections have been made for age of soil organic matter; samples within one profile are not weight-percent averaged.

Ecosystem	Locality	$\delta^{13}\text{C}$ (per mil)	SD	<i>n</i>	Ref.
Tropical forest (upper 5 cm)	Brazil	-28.4	0.8	18	(18)
Monsoon forest	Australia	-28.4	0.7	12	(21)
Forest	Kenya, Congo	-25.6	1.4	6	(22, 23)
<i>Brachystegia</i> woodland savanna	Zambia	-24.9	1.0	271	(24)
Dry deciduous forest	Botswana	-23.7	1.9	4	(8)
Riparian woodland	Ethiopia	-23.6	1.4	11	(10)
Mopane tree-bush savanna	Botswana	-20.7	1.3	44	(8)
Arid shrub savanna	Botswana	-19.8	1.5	4	(8)
Edaphic grassland	Ethiopia	-18.8	2.5	8	(10)
South Kalahari bush savanna	Botswana	-18.2	1.8	22	(8)
<i>Terminalia</i> tree savanna	Zimbabwe	-17.6	2.4	18	(7)
Acacia open savanna	Botswana	-17.2	3.5	296	(24)
Wooded grassland	Kenya	-16.2	1.7	11	(22, 25)
Acacia tree-bush savanna	Zimbabwe	-15.7	2.0	23	(7)
Tropical grassland	Australia	-15.5	0.8	9	(21)
Grassland savanna	Kenya, Congo, Tanzania	-13.8	1.3	8	(22, 23, 25)

Africa. However, we do not agree that a “closed wooded habitat” is indicated at Aramis. If woodland or closed forest habitat was indeed present as suggested in (1–3), it must have been of such limited geographic extent as to leave no evidence in paleosol geochemistry or in phytolith assemblages. This might be found in a riparian corridor bordered by mixed and more open environments, including woody grasslands with <25% canopy cover; such open environment areas are commonly described as “savanna.” Any such riparian habitat is likely to be restricted in scope in the context of the overall geographic distribution of a floodplain environment. In the locations where most of the *Ar. ramidus* remains were found, the tree canopy would not have been interconnected over extensive areas.

The Middle Awash reconstruction has been used to challenge the long-standing “savanna hypothesis” that states that bipedalism, among other human traits, evolved in response to the progressive expansion of grasslands and savannas (wooded grasslands) in Africa after 8 Ma. Although we do not judge the validity of the savanna hypothesis, we note that from the stable

Fig. 3. Ternary plot of phytoliths with apices of grass/sedge (all Poaceae and Cyperaceae), palm (globular echinate), and arboreal phytoliths/woody dicots (parallel-piped, globular granulate, globular smooth, and other forest indicators) as defined by (1). Most phytolith assemblages are dominated (>50%) by grass (and sedge) phytoliths; only 1 sample is dominated (>50%) by woody dicot phytoliths. (A) Modern phytoliths from African environments (20). (B) Fossil phytoliths from Aramis (1). (C) Fossil phytoliths from Aramis grouped by locality [average values given for each site reported in (1)]. (D) Enlargement of (C) shows that all sites are dominated (>50%) by grass/sedge phytoliths and non-*Ardipithecus*-bearing sites are not substantially different from *Ardipithecus*-bearing sites.



isotopic record, the connection between bipedalism and C₄ grass expansion starting in the late Miocene and continuing in the Pliocene remains a viable idea. Previous work has suggested that the period 8 to 4 Ma records a major ecologic transition globally as well as locally in Ethiopia. The data from Aramis reinforce this view.

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26. We thank M. Bird and L. Martinelli for assistance.

30 November 2009; accepted 26 April 2010
10.1126/science.1185274