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The Geological, Isotopic, Botanical, Invertebrate, and Lower Vertebrate Surroundings of *Ardipithecus ramidus*

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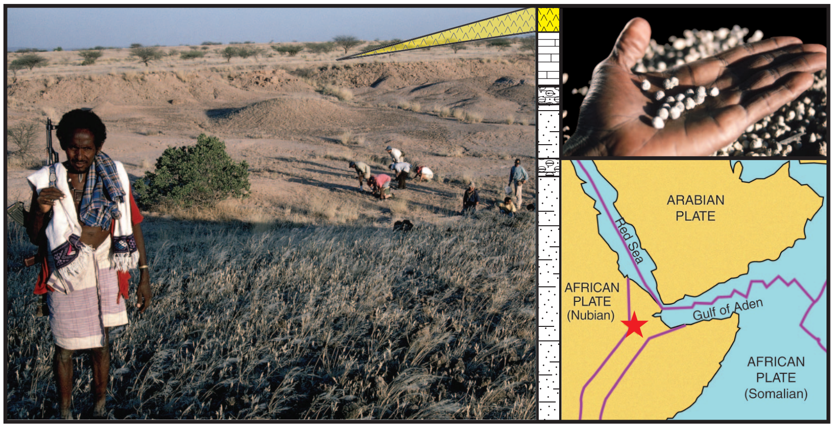
Ardipithecus ramidus was found in exposed sediments flanking the Awash River, Ethiopia. The local geology and associated fossils provide critical information about its age and habitat.

Most of Africa's surface is nondepositional and/or covered by forests. This explains why so many discoveries related to early hominid evolution have been made within eastern Africa's relatively dry, narrow, active rift system. Here the Arabian and African tectonic plates have been pulling apart for millions of years, and lakes and rivers have accumulated variably fossil-rich sediments in the Afar Triangle, which lies at the intersection of the Red Sea, Gulf of Aden, and Main Ethiopian Rifts (see map). Some of these deposits were subsequently uplifted by the rift tectonics and are now eroding. In addition, volcanoes associated with this rifting have left many widespread deposits that we can use to determine the age of these fossils using modern radioisotopic methods.



Map showing the Middle Awash area (star) and rift locations (red lines). Photo shows the 4.4 Ma volcanic marker horizon (yellow bed) atop the locality where the skeleton and holotype teeth of *Ar. ramidus* were discovered. Also shown are some of the fossil seeds.

Several of the most important hominid fossils have been found near the Afar's western margin, north and west of the Awash River (star on map), including Hadar (the "Lucy" site), Gona [known for the world's oldest stone tools at 2.6 million years ago (Ma)], and the Middle Awash (including Aramis). Cumulatively, these and nearby study areas in Ethiopia have provided an unparalleled record of hominid evolution.

Fossil-bearing rocks in the Middle Awash are intermittently exposed and measure more than 1 km in thickness. Volcanic rocks near the base of this regional succession are dated to more than 6 Ma. Its uppermost sediments document the appearance of anatomically near-modern humans 155,000 years ago. As is the case for many river and lake deposits, fossil accumulation rates here have been highly variable, and the distribution and preservation of the fossils are uneven. Alterations of the fossils caused by erosion and other factors further complicate interpretation of past environments. To meet this challenge, beginning in 1981, our research team of more than 70 scientists has collected 2000 geological samples, thousands of lithic artifacts (e.g., stone tools), and tens of thousands of plant and animal fossils. The emergent picture developed from the many Middle Awash rock units and their contents represents a series of snapshots taken through time, rather than a continuous record of deposition.

Ar. ramidus was recovered from one such geological unit, 3 to 6 m thick, centered within the study area. Here, the Aramis and adjacent drainage basins expose a total thickness of 300 m of sediments largely deposited in rivers and lakes, and on floodplains, between ~5.5 and 3.8 Ma. Within this succession, the *Ar. ramidus*–bearing rock unit comprises silt and clay beds deposited on a floodplain. It is bracketed between two key volcanic markers, each dated to 4.4 Ma. Their similar ages and sedimentology imply that the fossils themselves date to 4.4 Ma and were all deposited within a relatively narrow time interval lasting anywhere from 100 to 10,000 years. Today the unit is exposed across a 9-km arc that represents a fortuitous transect through the ancient landscape. The western exposure, in particular, preserves a rich assemblage of plant and animal fossils and ancient soils.

Fossilized wood, seeds, and phytoliths (hard silica parts from plants) confirm the presence of hackberry, fig, and palm trees. There is no evidence of a humid closed-canopy tropical rainforest, nor of the subdesertic vegetation that characterizes the area today. Invertebrate fossils are abundant and include insect larvae, broodballs and nests of dung beetles, diverse gastropods, and millipedes. The terrestrial gastropods best match those seen in modern groundwater forests such as the Kibwezi in Kenya. Aquatic lower vertebrates are relatively rare and probably arrived episodically during flooding of a river distal to the Aramis area. The most abundant fish is catfish, probably introduced during overbank flooding and/or by predatory birds roosting in local trees.

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.

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Sediments containing *Ardipithecus ramidus* were deposited 4.4 million years ago on an alluvial floodplain in Ethiopia's western Afar rift. The Lower Aramis Member hominid-bearing unit, now exposed across a >9-kilometer structural arc, is sandwiched between two volcanic tuffs that have nearly identical ^{40}Ar/^{39}Ar ages. Geological data presented here, along with floral, invertebrate, and vertebrate paleontological and taphonomic evidence associated with the hominids, suggest that they occupied a wooded biotope over the western three-fourths of the paleotransect. Phytoliths and oxygen and carbon stable isotopes of pedogenic carbonates provide evidence of humid cool woodlands with a grassy substrate.

Ardipithecus ramidus and abundant associated faunal and floral fossils were recovered from sedimentary rocks in the Central Awash Complex (CAC) of the Middle Awash study area. The CAC is a complexly faulted dome centered 25 km east of the western rift margin, Afar, Ethiopia. Today, 300 m of strata deposited between 5.6 and 3.9 million years ago (Ma) are exposed in the CAC (*1*). The hominid-bearing Lower Aramis Member of the Sagantole Formation lies midway in this stratigraphic succession and crops out along an erosional arc >9 km across, extending from the Ounda Sagantole drainage in the southeast to Aramis Locality 6 in the north, and to Kuseralee Locality 2 to the southwest (Fig. 1). Here, we describe regional and local geology, and present isotopic, paleobotanical, invertebrate, and lower vertebrate fossil evidence that illuminates local conditions at the time the vertebrate fossils were deposited.

Geology. The Aramis Member directly overlies the Gàala ("Camel") Tuff Complex (GATC), which has a ^{40}Ar/^{39}Ar age of 4.419 ± 0.068 Ma (*2*, *3*). This vitric tuff is 0.5 to 2 m thick and is rich in pumice and crystals. The Aramis Member includes light salmon (hue 5YR) to deep red-brown silt, clay, and sand of variable thickness and induration, deposited on a floodplain. These strata show a general increase in thickness toward the east, and they range from an average of 3 m up to 6 m. They are overlain by the Daam Aatu ("Baboon") Basaltic Tuff (DABT), which has a ^{40}Ar/^{39}Ar age of 4.416 ± 0.031 Ma (*1*). We define the Lower Aramis Member as the entirety of both tuffs and all sediments between them.

A patchwork of variably fossiliferous localities along the outcrop arc has yielded a combined total of more than 6000 individually cataloged vertebrate fossils between the widespread volcanic marker horizons. The vertebrate assemblages are in close association with sedimentological and structural information, botanical and invertebrate fossils, and oxygen and carbon isotopic data on pedogenic carbonates in soil horizons. Integration of these data allows reconstruction of the physical and biological aspects of the depositional setting.

The Middle Awash was a persistent sedimentary basin during the Pliocene (*4*). The basin axis during deposition of the entire Aramis Member was southeast of the *Ardipithecus* localities, as evidenced by deltaic and lake margin deposits generally disposed to the southeast, in the direction of paleocurrent orientations and erosional features. Active volcanic centers of the CAC were located to the south (*1*). Paleoenvironmental data and structural reconstructions suggest that the overall elevation may have been greater than today's ~600 m, although kinematic models are equivocal (*5*, *6*).

The lower tuff (GATC) is underlain by a widespread cobble conglomerate. In the central part of the exposure arc, fossiliferous Lower Aramis Member sediments comprise predominantly massive and bioturbated silty clays deposited primarily on a low-relief floodplain far from the main river channel(s). Reworked GATC pumices and glass are present locally, but evidence of channels is limited to rare sandstone lenses generally situated below the fossiliferous strata. Massive (<1.5 m thick), predominantly micritic carbonate horizons and nodules representing groundwater and pedogenic deposits pinch out laterally within clayey silts. These are also locally fossiliferous.

Carbonate deposits in some localities contain characteristic features of tufas (*7*), such as fossil gastropods and other invertebrates, abundant and uncrushed calcite-replaced vegetation, vertebrate remains, and eggshells (guinea-fowl size). These suggest that the carbonate horizons generally formed at or near the landscape surface. Evidence of spring activity includes several 1-m-wide banded travertine deposits associated with faults. A porous microcrystalline carbonate with dense concentrations of calcite isomorphs of plant parts forms a broad, low dome just north of ARA-VP-6. However, in almost all sections excavated for isotopic, phytolith, and pollen analysis, the carbonates lack diagnostic features of tufas. Their micritic textures and the presence of terrestrial soil invertebrate faunal activity (such as dung beetle brood burrows) suggest that the carbonate horizons are derived from groundwater carbonate that generally formed at or near the landscape surface in seasonally saturated soils near springs (fig. S1).

Paleosols in the Lower Aramis Member are primarily protosols and calcisols (*8*) and are most strongly developed just below the DABT. Protosols are 10 to 200 cm thick, with massive to single-grain structure and abundant root structures. Calcisols are 50 to 100 cm thick and contain subsurface horizons (Bk) displaying massive to angular blocky ped structures, weakly developed argillic cutans, and small (<5 mm across) calcareous nodules and tubules. The best-developed calcisols are present directly below the DABT. These nodules are most abundant to the north and may imply that it was slightly drier there. Sections at the southeast end of the exposure arc show weaker soil development, perhaps implying deposition in a predominantly wetter, more axial environment.

The DABT is poorly consolidated. The lower third (~15 to 20 cm) of the unit is composed of bedded and laminated gray basaltic glass lapilli and scoria. Given the geometry of its basal contact and lack of underlying incision, we interpret the DABT to have fallen across a dominantly low-relief landscape. Reworked clasts of the DABT are seen in only a few small shallow channels. The presence of paleosols and minor channels before deposition of the DABT indicates that sedimentation was intermittent and that streams only slightly incised this part of the basin. Sediments immediately overlying the DABT near

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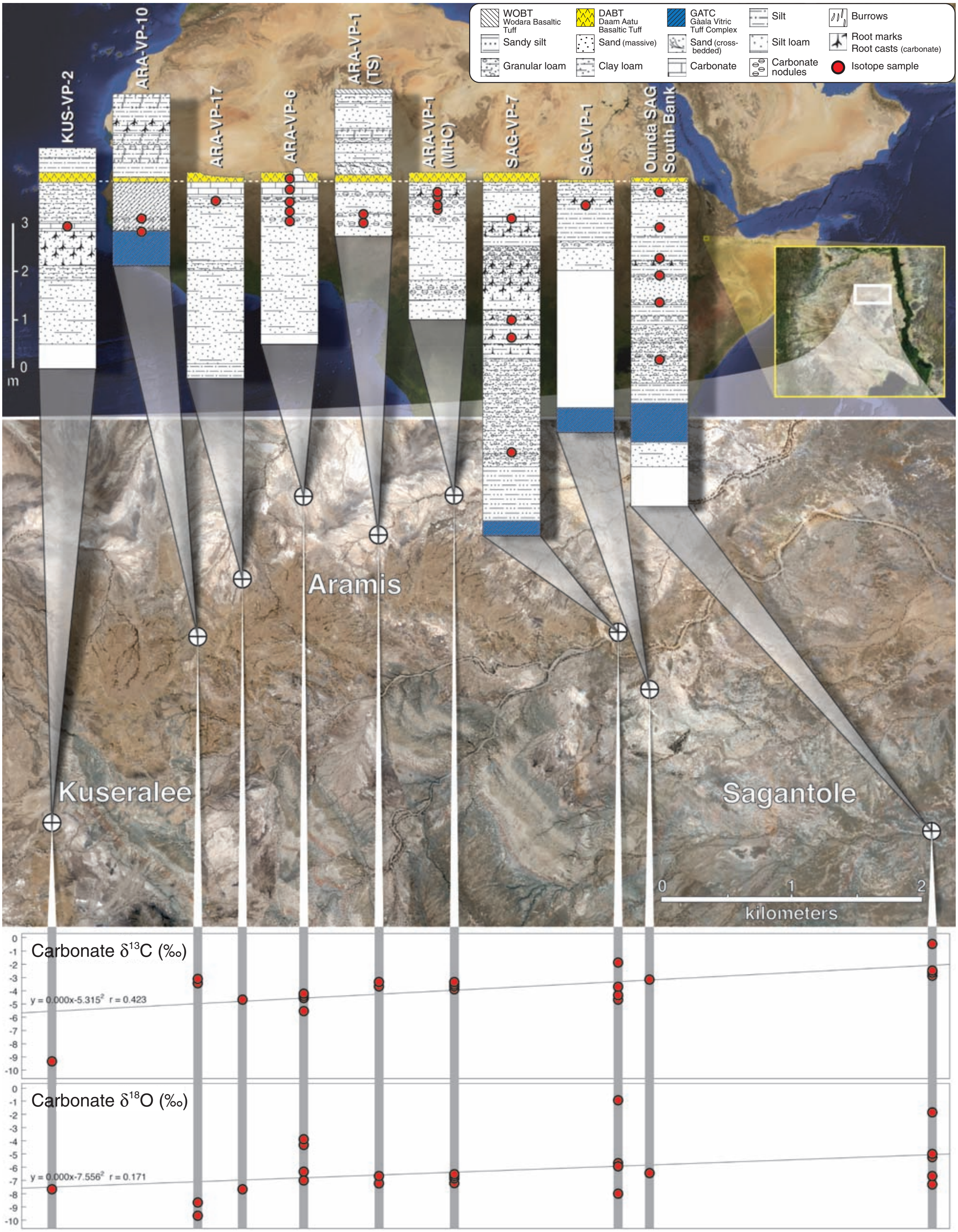

Fig. 1. Satellite image of the ~9-km erosional arc exposing the *Ardipithecus*-bearing GATC-DABT horizon of the Central Awash Complex of the Middle Awash study area, Ethiopia. Isotopic data are shown. Values in the eastern sample sites indicate slightly more open habitat (where primate fossils were not found), a finding consistent with the macrobotanical and paleontological evidence.

the ARA-VP-1 (TS), ARA-VP-7, and ARA-VP-10 localities contain massive to weak, blocky, root-marked protosols overlain by alternating massive clayey silt and fine, well-sorted sand with tubular, subvertical 1- to 2-cm burrows. These features indicate that the water table was high and that the floodplain was aggrading more rapidly after deposition of the tuff, in accordance with faunal evidence that more aquatic and water-dependent mammals were more abundant above the DABT.

The time span represented by the fossiliferous sediments of the Lower Aramis Member (between the two tuffs) is difficult to ascertain. The dates for the two tephras are statistically indistinguishable, the difference between them only 0.003 ± 0.075 million years at 68% confidence. Thus, the dates suggest that, most probably, this interval represents a few thousand to perhaps at most 100,000 years. Paleosols in similar aggrading distal floodplain environments often indicate geologically short time spans. The fossil assemblages collected from between the two tuffs are consistent with environmental stability during the interval, and no evolutionary trends are evident (*9*). On the basis of analogous settings, these sediments probably represent deposition within 100 to 10,000 years (*10*) and their paleontological contents would qualify as a "within-habitat time-averaged assemblage" (*11*).

The depositional environment of the *Ar. ramidus* fossils in the CAC differs somewhat from that of penecontemporaneous Gona fossils ~70 km to the northwest. The Gona conspecifics were recovered in mixed-habitat faunas along the western basin margin where lake deposits interfinger with small fluvial channels or lap onto active basaltic cones and flows (*12*).

Stable isotopes. To further elaborate the conditions surrounding deposition of the hominid remains between the two tuffs, we analyzed carbon and oxygen isotopes (*13*, *14*) from paleosol carbonate, as well as carbon isotopes from associated organic matter (Fig. 1, figs. S1 to S3, and tables S1 and S2) (*15*). Plants using the C_3 photosynthetic pathway (such as trees, shrubs, and most herbaceous dicots; shaded forest understory; and cold-adapted tropical alpine and high-latitude grasses) have average $\delta^{13}C$ values of –26.5 per mil (‰). Tropical savanna grasses using the C_4 pathway have average $\delta^{13}C$ values of –12.5‰. Decomposing plant organic matter labels the soil with a similar isotopic composition (*16*). Disseminated organic carbon is present in trace amounts in ancient soils formed on volcanic parent materials, mainly in the allophane clay fraction (*17*), and in carbonate nodules (*18*). Trace amounts of organic carbon contamination, mainly from C_3-based petroleum products introduced after excavation, can substantially lower the $\delta^{13}C$ values of soils formed in paleoenvironments with C_4 plant biomass. We are confident that the procedures used to minimize contamination (table S2) (*15*) permit accurate reconstruction of the Aramis Member plant biomass isotopic composition.

Soil carbonate $\delta^{13}C$ values are typically enriched by 14 to 17‰ relative to those of organic matter (*19*). Lower Aramis Member organic $\delta^{13}C$ values range from –21‰ to –15‰, and carbonate $\delta^{13}C$ values range from –6.5‰ to –0.5‰ (table S1). The mean difference between carbonate and included disseminated organic matter $\delta^{13}C$ values ($\Delta^{13}C$) is 13.8‰ and the median is 14.3‰. This is within the range expected for well-preserved paleosols (*19*). Oxygen isotope ratios of pedogenic carbonate nodules reflect those of soil water. The isotopic composition of meteoric waters is controlled by polar ice volume, altitude, temperature, humidity, and evapotranspiration (*20*–*22*). Preferential evaporation of isotopically "light" water ($H_2{}^{16}O$) leads to isotopic enrichment of remaining water in near-surface soils (*20*). Pedogenic carbonate $\delta^{18}O$ values are thus highest in hot, arid habitats and at low latitudes and altitudes (*14*, *16*).

These data reflect woodland to grassy woodland savanna floral habitats with 30% to 70% C_4 plants. Carbonate $\delta^{13}C$ and $\delta^{18}O$ values increase axially from west to east across this outcrop arc (Fig. 1). These data are consistent with sedimentological, taphonomic, paleobotanical, and paleontological indicators in suggesting more open, exposed, probably grass-dominated habitats for the localities at the eastern pole of the erosional arc of localities (toward the paleo-depocenter)

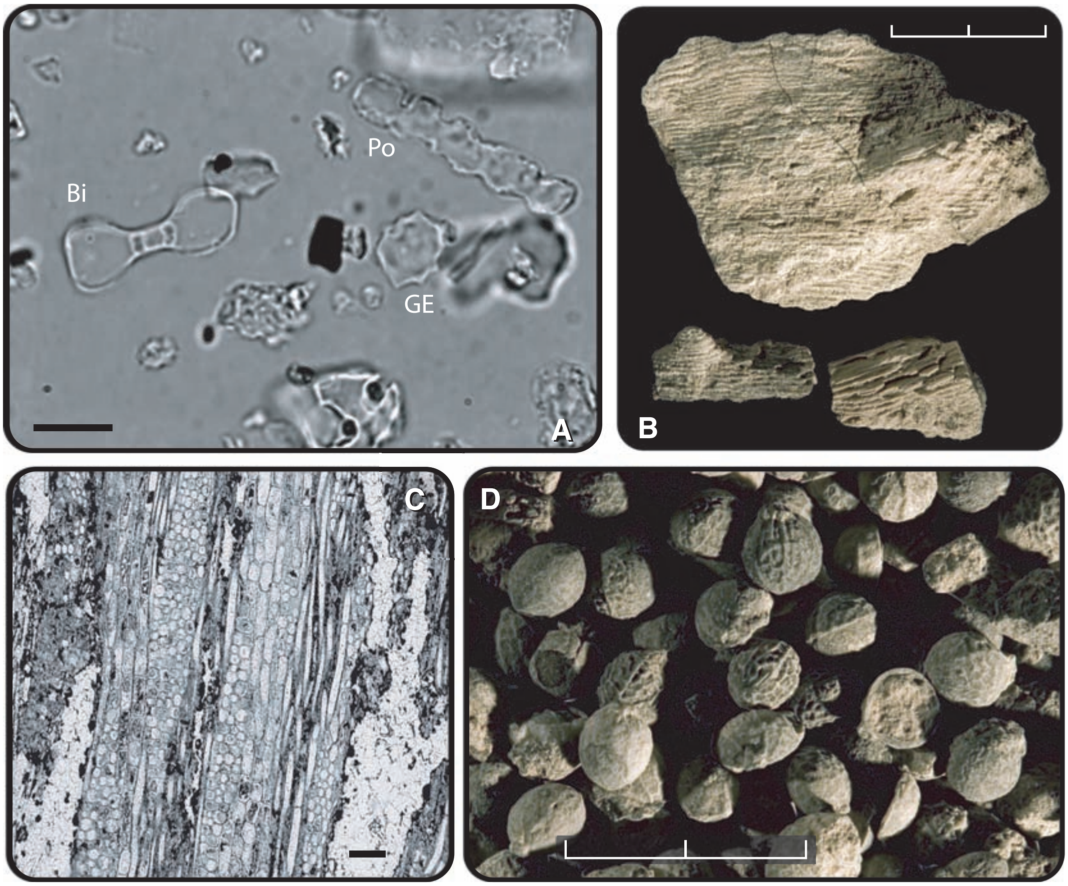

Fig. 2. Fossilized botanical remains from the Lower Aramis Member. Wood and seeds are ubiquitous at the *Ardipithecus*-bearing localities of the Lower Aramis Member. (**A**) Silica bodies (phytoliths). The bilobate (Bi) and polylobate (Po) types are from grasses (Poaceae); the globular echinate (GE) is from palms (Palmae). Scale bar, 10 μm. (**B**) Fossil wood. Scale bar, 2 cm. (**C**) Tangential microscopic section: general view showing disposition of rays of fossil wood specimen from ARA-VP-6, identified as the fig tree *Ficoxylon* sp. Scale bar, 108 μm. (**D**) Fossilized *Celtis* (hackberry) seeds. Scale bar, 2 cm.

(*9*, *23*). None of the primate fossils, micromammals, birds, or macrobotanical remains were found in the 2.5-km stretch of Lower Aramis sediment outcrops southeast of the easternmost *Ardipithecus*-bearing locality (SAG-VP-7).

Paleobotany. Many carbonate horizons between the two tuffs contain abundant calcite-replaced wood and endocarps (Fig. 2). In the noncemented sediments, these macrobotanical remains are typically decalcified and sometimes appear during excavation as white streaks or manganese stains. The ubiquitous fossil wood generally lacks the internal structure needed to achieve reliable taxonomic identification, except for one specimen attributed to the fig *Ficoxylon*. Endocarps of hackberry fruits attributed to *Celtis* sp. (*24*) are well preserved and abundant, but there is an inherent preservational bias because these are easily fossilized (*25*, *26*). Therefore, these trees cannot be assumed to have dominated the vegetation. *Celtis* trees are tolerant of a wide range of environmental conditions; their immature leaves are eaten by chimpanzees (*27*).

We analyzed a variety of silt, clays, and carbonate samples (including splits of the isotopic samples) for pollen, but found none. However, a few grains were extracted from sediment within the *ARA-VP-1/401* mandible, as well as from carbonate matrix encasing seeds and two coprolites from ARA-VP-6. The ARA-VP-6 grains are attributed to *Myrica* (*n* = 6), *Borassus/Hyphaene* (*n* = 2), Poaceae grass (*n* = 4), and Cyperaceae (*n* = 2), and the ARA-VP-1 grains to *Borassus/Hyphaene* (*n* = 2). *Myrica*, *Celtis*, and palm tree pollen was recovered both below and above the Lower Aramis Member, and these trees were part of the arboreal vegetation in the region between 4 and 5 Ma. Contemporaneous pollen data recovered from marine sediment deposited in the Gulf of Aden indicate that these trees were widespread and are associated with other components of today's afromontane flora (*28*).

Given the paucity of pollen, we extracted and analyzed phytoliths in the same samples (Fig. 2, fig. S4, and table S3) (*15*). Phytoliths produced by grasses (Poaceae) differ in shape and size from those produced by other plants, including woody dicotyledons (most trees and shrubs) and palms (*29*). Their abundance, relative to the abundance of globular phytoliths from woody dicots and palms, has been used to estimate tree cover on the basis of reference assemblages in modern soils (*30*). We recovered and recognized 96 phytolith types from 38 samples from the strata between the two tuffs. Types included globular ones typical of palms [globular echinate (*31*)], woody dicotyledons [globular granulate and smooth, produced by trees and shrubs (*32*)], grass silica short cells (64 different types), grass bulliform and hair cells, and some rare sclerids and tracheids. The relative abundance of globular phytoliths over grass phytoliths suggests an open grassland southeast of SAG-VP-7, with a maximum tree cover of <40%. West of SAG-VP-7, an estimated maximum tree cover of ~65% is suggested by some samples at KUS-VP-2, ARA-VP-10, and ARA-VP-1 (TS).

On the basis of the geology, phytoliths, fossils, and isotopic data, we infer that the local Pliocene vegetation included abundant palms and trees or shrubs as well as grasses (as would be characteristic of semi-deciduous woodlands and open forests for at least part of the year). Palms were present at all localities over the 9-km outcrop arc but were probably most abundant (despite potential overrepresentation) near the ARA-VP-1 and SAG-VP-7 localities. There is no evidence for lowland humid Guineo-Congolian rainforest, subdesertic arid vegetation, or highland C-3 Pooideae grasses (*15*) in the Lower Aramis Member or from younger or older sediments of the CAC. Evidence for *Celtis*, *Myrica*, and palm trees fits well with the presence of a groundwater-supported grassy woodland to forest.

Invertebrate fossils. The invertebrate fauna of the GATC-DABT *Ar. ramidus*–bearing biotope (especially ARA-VP-1 and -6) includes fossilized insect larvae, dung beetle broodballs and nests, diverse gastropods, millipedes, and a small centipede (Fig. 3). The millipedes belong to Spirostreptida, a large order common in a wide variety of modern African habitats from savanna to forests. Pupal cases (calcite-replaced inclusions weathered from carbonate) are common, but taxonomic identification has not proven possible. Dung beetle broodballs from the Lower Aramis Member average 3 to 5 cm in diameter and have walls 5 to 7 mm thick. Up to 15 of these have been found together in chambers excavated into host deposits (fig. S1). Rare larger balls up to 7 cm in diameter indicate a larger species. Dung beetles exist wherever large mammals occur in Africa (*33*).

Terrestrial gastropods are useful indicators of vegetation patterns, rainfall, altitude, and temperature (*34*). Their fragile shells do not withstand hydraulic transport well, so given their embedding fine-grain sediment of the Lower Aramis

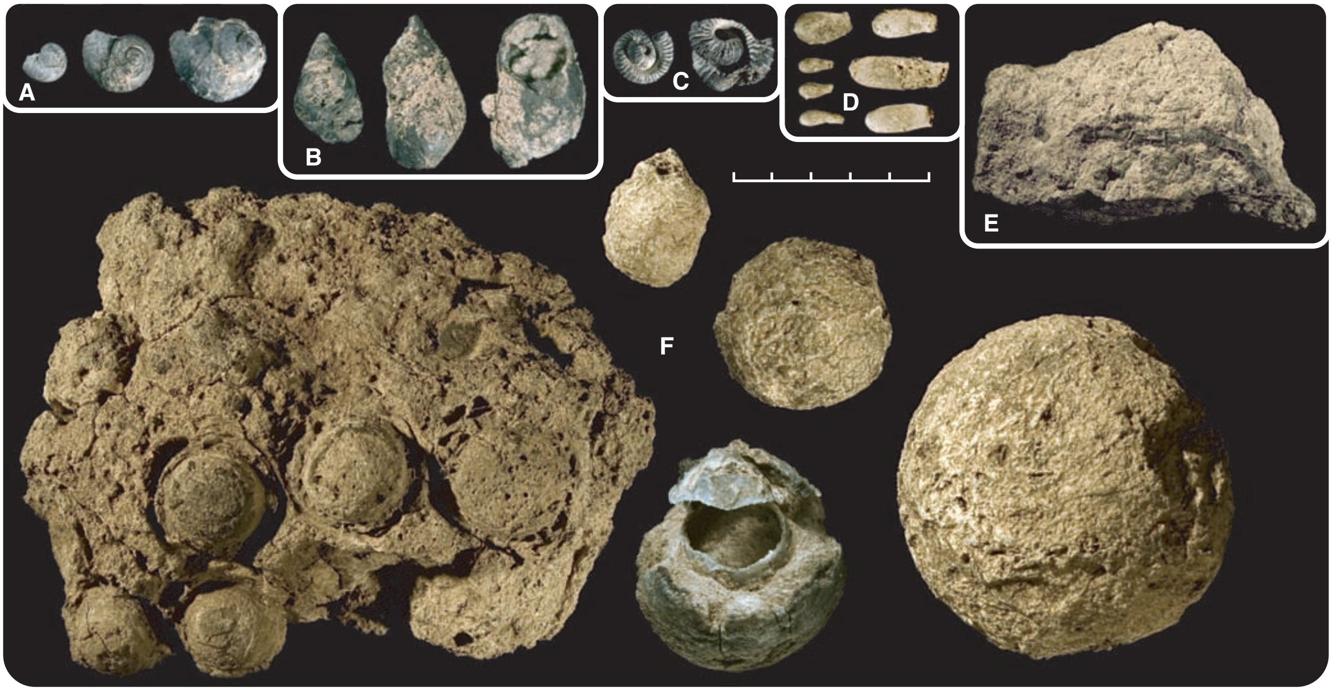

Fig. 3. Fossilized invertebrate remains and traces from the Lower Aramis Member. (**A**) Gastropods: ARA-VP-6 *Maizania* sp. (**B**) Gastropods: ARA-VP-6 *Limicolaria* sp. (**C**) Millipedes: ARA-VP-1. (**D**) Larvae: ARA-VP-6. (**E**) ARA-VP-6 centipede. (**F**) Dung beetle broodballs and nest, ARA-VP-6. Scale bar, 5 cm.

Member, the overall land snail assemblage can be considered to be locally derived (*35*). The presence of millipedes, insect cocoons, and solitary bee brood cells reinforces this conclusion. The most common gastropod (34 of 40 identified specimens) is *Maizania* from the *M. hildebrandti* group, followed by *Limicolaria* sp. ($n = 5$), and a single specimen of *Chlamydarion* cf. *hians*. This Aramis land snail assemblage resembles that of modern groundwater forests, such as the Kibwezi in Kenya (*34*). This lowland forest in a regionally semi-arid area thrives because it has a high water table, an analogy consistent with geological evidence from the Lower Aramis Member. Before poaching, its larger mammal composition appears to have been structured analogously to the similarly primate-rich Aramis assemblage.

Lower vertebrates. Of 275 identified Lower Aramis Member fish specimens, the dominant genus is the catfish *Clarias* ($n = 175$), followed by *Barbus* ($n = 20$) and the family Cichlidae ($n = 21$). These are shallow-water fish, the former capable of tolerating highly deoxygenated waters and a wide temperature range.

The giant terrestrial tortoise *Geochelonia* is present, along with *Pelusios* (African mud turtle or hinged terrapin), Cyclanorbinae (flapshell softshell turtle), and *Pelomedusa* (African helmeted turtle). Crocodiles are present and represented by scutes and teeth indistinguishable from those of extant Nile crocodiles. Remains of lizards, snakes, and frogs were recovered, particularly at the ARA-VP-6 microfauna quarry. The Lacertilia sample includes representatives of Varanidae (cf. *Varanus*) and Iguanidae (cf. chameleons, among others). The Serpentes sample includes at least cf. Pythoninae. Given the marked differences in habitat preferences typically seen even within genera of lizards and snakes, their use in paleoecological reconstruction is limited.

Chelonian, crocodylian, and osteichthyan skeletal elements are readily recognizable even when highly fragmentary, so their abundance (number of identified specimens) in a fossil assemblage is almost always inflated relative to their ecological abundance. Even so, these taxa are rare in the Lower Aramis Member vertebrate assemblage relative to other Middle Awash strata and other Pliocene hominid localities (except Laetoli). Most of these aquatic species presumably appeared episodically on the Aramis floodplain during times of over-bank flooding, although it is possible that some fish represent raptor meals—an interpretation supported by the lack of articulated elements of these taxa at *Ardipithecus* localities.

The relatively thin Lower Aramis Member stratigraphic interval, exposed in an erosional 9-km arc of localities between the rift margin to the west and the basin axis to the east, provides a paleotransect through a 4.4-Ma Pliocene landscape. The largely aggradational plain centered at Aramis and adjacent to the low northern slopes of the emerging CAC was subject to alluvial flooding that embedded a rich faunal and floral community containing *Ardipithecus*. Evidence of wooded environment is present and seems to have prevailed during this interval across the *Ardipithecus*-bearing localities that constitute the western three-fourths of this transect (*9*, *23*). The demonstrable co-occurrence of elements of a wooded biotope—including large and small mammals, birds, soil isotopes, gastropods, and micro- and macrobotanical remains—suggests that this floodplain, and the community it supported, constituted a wooded biotope rather than that of a grassland savanna in the localities that contain *Ardipithecus*.

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Supporting Online Material

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References

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