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Springs, palm groves, and the record of early hominins in Africa

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Highlights

- Groundwater systems locally create wet and wooded microhabitats in arid Eastern Africa.
- But, how important are groundwater-fed microhabitats to the early hominin record?
- Geological context, vegetation, and microfossils from modern springs were analyzed.
- Fossil springs were found associated with hominin remains in >50 different localities.
- Groundwater systems play essential roles at the species and ecosystem levels.

Abstract

Hominins evolved in Africa during a period of overall regional cooling, drying and increasingly variable climate. Despite prevailing regional aridity since the mid-Miocene, data show that early hominins *Sahelanthropus tchadensis*, *Orrorin tugenensis*, and *Ardipithecus ramidus* lived in environments made of mosaics of grasslands, mixed grasslands, woodlands, and forests, where wooded habitats were maintained by edaphic rather than regional (climatic) humidity. Groundwater systems (springs, seeps, shallow aquifers) and surface water (rivers, lakes), locally create wetter and more wooded environments in addition to that supported by precipitation alone. However, edaphically sustained woodlands are rare to missing in most published paleoecological interpretations of hominin archeological sites. To explore the importance of groundwater to the record of hominins in Africa, we provide newly acquired field data from spring sites in the Awash Valley, Ethiopia, and Lake Eyasi-Lake Manyara region, Tanzania, and re-evaluate published data from the *Ardipithecus*-bearing Aramis Member, Ethiopia.

Results show that 1) in arid Eastern Africa, a wide variety of microhabitats such as groundwater-fed wetlands, *Hyphaene* palm woodlands, *Phoenix reclinata* palm woodlands, and structurally complex and species-rich forest patches exist due to local variability of geologic, topographic and hydrologic conditions. 2) These microhabitats carry some characteristic pollen and phytolith signals, that may be easily masked by the signal of surrounding grass-dominated shrublands and grasslands. 3) The Aramis Member (Awash Valley, Ethiopia), which is to date, the best documented paleo-groundwater ecosystem, is not a riparian habitat. It is one of > 50 examples (within 22 geographically distinct areas) in Africa and the Middle East where evidence of groundwater systems co-exist with hominin and/or archeological remains. Springs are commonly localized features of limited area within a landscape, but provide ecological continuity through time and diverse microhabitats, some of which may be densely forested.

At the local scale, springs create microclimates, distinctive vegetation, and increase soil nutrients, species richness, structural complexity, and provide habitat for animals. At the landscape scale, they represent hydro-refugia favoring increased connectivity among animals and allowing migrations during dry periods. We conclude that in the East African Rift where low, highly seasonal rainfall and high evaporative demand limit vegetation growth in many areas, groundwater-fed zones create diverse microhabitats and play a major role in ecosystem functioning. It is likely that, within a context of increasing aridity and expansion of grass-dominated open habitats during the Mio-Pliocene, early hominins and many other animals viewed edaphically sustained woodlands as attractive habitats.

Keywords: Hominin; Paleoenvironment; *Ardipithecus*; Pliocene; Groundwater; Hydro-refugia

1. Introduction

The hominin phylogenetic tree is often put in parallel with records characterizing the global climate changes, such as the record of $\delta^{18}\text{O}$ a proxy for global ocean temperatures and polar ice volume (e.g. DeMenocal, 1995; Potts, 2013), or records of $\delta^{13}\text{C}$ in paleosols as a proxy for C_4 plant biomass abundance (e.g. Feakins and deMenocal, 2010; Levin, 2015; Quade et al., 1989). Climate above all environmental factors determines the spatial distribution of vegetation types at the continental and regional scales (e.g. Box, 1981; Pearson and Dawson, 2003), which subsequently determines the type of plant resources available to consumers as well as the spatial and temporal availability of those resources. It is thus hypothesized that large climatically driven vegetation changes, such as the spread of open habitats and the expansion of C_4 grass-dominated biomes were responsible for the Late Miocene mammalian evolution, including that of our lineage (see review on the origin of the savanna hypothesis by Bender et al., 2012, and references cited therein). In East Africa the expansion of C_4 grasses is approximately dated at 10 Ma (Feakins et al., 2013; Uno et al., 2016). This profound change in vegetation composition and structure at the continental scale likely induced a shift in the diet of Proboscideans which started to include C_4 plants in their (browsing) diet as early as 9.9 Ma, and became grazers at 7 Ma (Uno et al., 2016). Similarly, environmental change could have led some Primates to adopt terrestrial bipedalism, a purportedly cost effective locomotion in open environments (e.g. Sockol et al., 2007; Steudel-Numbers and Tilkens, 2004). This so-called savanna hypothesis that had germinated in our collective consciousness

since Lamarck published the first ideas in 1809 (Bender et al., 2012; Lamarck, 1809), has been challenged by some, as contextual data associated with Late Miocene and Early Pliocene hominins *Sahelanthropus tchadensis*, *Orrorin tugenensis*, and *Ardipithecus ramidus* indicate wooded and forested, rather than open environments (Pickford and Senut, 2001; Vignaud et al., 2002; White et al., 2009b). The savanna hypothesis is further challenged as it becomes clear that drivers of mammalian evolution cannot be reduced to one limited set of factors (climatically-driven biome changes) but rather by a complex interplay between biotic and abiotic factors (e.g. biotic interactions, tectonics) (e.g. Domínguez-Rodrigo, 2014; Richerson et al., 2008).

Hereafter fossil primate taxa (such as those cited above) for which published evidences suggest frequent bipedalism in terrestrial context will be referred to as 'early hominins'.

Arid and seasonal climatic conditions were established in North Africa by the Late Miocene (~ 7-11 Myr ago), likely following the shrinkage of Tethys Sea (Zhang et al., 2014). This aridification is attested by eolian dune deposits in the Lake Chad basin (Schuster, 2006), continental records (Moussa et al., 2016; Novello et al., 2015) and marine records of terrestrial vegetation (Feakins et al., 2013). As early as 12 Ma, pollen record xerophytic plant taxa of the *Acacia-Commiphora* Somalia-Masai steppes and bushlands similar to those occurring today, but in varying proportions of grasses, Amaranthaceae, and total arboreal pollen (Bonnefille, 2010; Feakins et al., 2013; Liddy et al., 2016). Faunal assemblages typical of the savanna biome were also well established in Central and Eastern Africa by 7 Ma (Kaya et al., 2018). Vegetation modeling indicates that

Pliocene climatic conditions in Central and Eastern Africa could only sustain dry open savanna vegetation and/or xerophytic shrubland biomes (Contoux et al., 2013; Salzmann et al., 2008). Although the abundance of grass and tree pollen from 6 to 4.5 Ma in the marine record DSDP231 indicates somewhat wetter conditions in eastern Africa than during the Plio-Pleistocene and the modern time, forested habitats that hosted arboreal primates and early hominins *Sahelanthropus tchadensis*, *Orrorin tugenensis*, and *Ardipithecus ramidus* were not widespread over the northern Africa mega-region (10-30°N) (Bonnefille, 2010; Liddy et al., 2016).

In arid regions, the heterogeneity of vegetation at the landscape scale is increased by the surface water (rivers, lakes) and groundwater systems (springs), which may sustain forested areas, locally. Savanna vegetation is patchy across scales ranging from 10s of meters (local site scale) to 10s of kilometers (landscape scale) (Caylor and Shugart, 2006). This is particularly true where, despite the regional arid climate that characterizes the East African Rift Valley, rivers, shallow aquifers, and groundwater discharge areas (base level seepage and/or springs flowing from fractured bedrock), trigger the local development of azonal woody vegetation, so called spring or groundwater-fed forests and woodlands (e.g. Greenway and Vesey-Fitzgerald, 1969).

The forested habitats interpreted for *Sahelanthropus tchadensis*, *Orrorin tugenensis*, and *Ardipithecus ramidus* were sustained by local (edaphic) rather than regional (climatic) humidity. In the Toros-Menalla paleontological area (Lake Chad basin, between 7.5 and 7 Ma) the inferred paleolandscape and paleovegetation contemporaneous of *Sahelanthropus* was a mosaic of diversely wooded habitats such as dense forest patches, palm groves, and mixed/grasslands (including aquatic grasslands), with forested habitats being most likely riparian forests sustained by local surface and groundwater fed systems, rather than by regional (climatic) humidity (Contoux et al., 2013; Novello et al., 2017; Vignaud et al., 2002). According to Novello et al. (2017), “the vegetation reconstructed at the type locality of *S. tchadensis* (TM266) is similar to modern palm grove formations with an arboreal cover percentage of at least 40%”, but as noted “It is

however difficult to assess whether this particular palm grove vegetation was really the preferred habitat of *S. tchadensis* or merely a random depositional environment in this complex landscape.” At Lukeino (Kenya, ~6 Ma), faunal assemblages and isotope data on herbivorous mammals indicate that the paleolandscape contemporaneous of *O. tugenensis* included open grassy woodlands as well as patches of forested habitats likely fringing the lake margin and streams that drained into the lake (Pickford and Senut, 2001; Roche et al., 2013; Senut, 2006). At Aramis (Middle Awash Valley, ~4.4 Ma), the inferred paleoenvironment contemporaneous of *A. ramidus* was also a mosaic of habitats. It included spring-fed forest patches and woodlands that graded into more open grasslands (Suwa and Ambrose, 2014; WoldeGabriel et al., 2009).

Groundwater discharge is a common phenomenon that occurs today throughout the East African Rift (see fig.1 in Cuthbert et al., 2017). It occurred in the Aramis Member paleolandscape, 4.4 Ma ago in Ethiopia (WoldeGabriel et al., 2009), as well as in Tanzania (Ashley et al., 2016, 2010a, 2010b; Barboni, 2014) and in Kenya (Ashley et al., 2004, 2002; Johnson et al., 2009; Owen et al., 2004). Cuthbert et al. (2017) showed that in East Africa, permanent springs are most abundant in the rift, and that more than 30% of these springs were likely to remain persistent through time even if the time needed for recharging the aquifers exceeds a precession cycle of 23,000 yrs. This time may be much shorter though; for example the groundwater seeping out in the Awash Valley today in the Filwoha area of Awash National Park is only 4500-5700 years old (Bretzler et al., 2011). Cuthbert’s modeling study, which couples a hydrogeological model with an agent-based model of hominin movement also, suggests that springs in the East African Rift likely favor north – south dispersal within the rift during dry periods, and act as hydro-refugia during driest periods. Hominin survival and dispersal, therefore, may be related to the presence of springs, and more generally to the rift hydrogeological context and hydrographic network (Cuthbert et al., 2017). Although the connection between hominin or archeological sites with water may appear as an evidence for some, few studies have actually analyzed the

potential impact of springs on archeological sites and hominin behavior. Ashley et al. (2009) and Deocampo and Tactikos (2010) showed that spatial concentration of stone artifacts and butchered bones are highest at spring sites, between ~1.8 and 1.75 Ma ago, and subsequent analyses at Olduvai confirm this pattern in older paleosurfaces (e.g. Arráiz et al., 2017; Ashley et al., 2010a; Egeland, 2014). Most recently, McCool (2018) showed that groundwater discharge in the Nile River was a more reliable water source for cultural groups in the valley during the early to mid-Holocene, than surface water. To our knowledge, however, there is no account of the number of archeological and hominin sites associated with groundwater-fed systems in Africa.

Phytolith analyses carried out at the early hominin sites of Toros Menalla (Chad) and Aramis (Ethiopia) document the presence of palms (Arecaceae), which are associated with geological evidence for groundwater at Aramis, but not at Toros Menalla (Novello et al., 2017; WoldeGabriel et al., 2009). At Aramis, the pollen record narrows down the palm identification to *Hyphaene* (WoldeGabriel et al., 2009). Palms were also found associated with evidence for groundwater at several sites of the Olduvai Gorge area (Tanzania) such as in Bed I paleosurfaces sampled at FLK Zinj-PTK-AMK and FLK N immediately below Tuff IC and Tuff IF, respectively (Albert and Bamford, 2012; Arráiz et al., 2017; Barboni et al., 2010). Palm phytoliths at Olduvai were also found associated with fluvial facies at HWK W and FLK S localities within the Tuff ID/IE interval, and a leaf imprint indicates the presence of *Phoenix reclinata* (Albert et al., 2018). The present-day distributions of *Hyphaene* and *Phoenix* species are different. Their occurrence in the fossil record may therefore indicate particular paleoenvironments. Groundwater discharge areas leave evidence in the geological record (e.g. tufa and carbonate layers with freshwater isotopic signal) (Ashley et al., 2014b, 2010b, 2010a). They potentially leave evidence in the paleovegetation micro-botanical record as well, but this has barely been analyzed to date.

The aim of this paper is to explore importance of groundwater, and of groundwater-associated woodlands and forests

to the record of hominins. It provides new data (field observations, pollen and phytolith data) on modern groundwater systems and their associated microhabitats from two regions in Eastern Africa where hominin and archeological sites are numerous. It provides a summary of the groundwater-fed paleoenvironment inferred for the *Ardipithecus*-bearing Lower Aramis member of the Central Awash Complex of the Middle Awash area (Ethiopia), the most intensively studied groundwater-associated hominin site. A survey of other hominin and archeological sites found in association with spring sites in Africa and the Middle East is also presented. The importance of groundwater-fed systems for species and ecological processes is discussed, as well as what it may imply for early hominins such as *Ardipithecus ramidus* at Aramis, 4.4 Ma ago.

2. Modern springs in East Africa: some case studies from Ethiopia and Tanzania

Fieldwork was carried out in Ethiopia and Tanzania, at modern spring sites, to document vegetation patterns, groundwater characteristics, geologic context, and to collect surface soil samples for phytolith and pollen analyses.

2.1. Field observations on geomorphology and vegetation

Springs and groundwater-fed wetlands in the East African Rift are generally found at the base of slopes and associated with faults (Cuthbert and Ashley, 2014; Olago et al., 2009). In the Awash River valley (Ethiopian Afar rift, Ethiopia), the three spring sites we visited occur in grabens, at the base of rift shoulders (between 750 and 550 m asl) (Fig. 1). Spring recharge occurs in the Western highlands and on nearby volcanoes at high elevation (> 2900 m asl). The slopes of the aquifers are important because the distance between the rift western flank where recharge occurs and grabens where springheads are located is short (50-90 km) (Fig. 1C). This part of the rift valley is characterized by tectonism and four recently active volcanoes (Chorowicz, 2005). At the three Ethiopian spring water was hot (>40-50°C) and pH about 8-9. In the Lake Eyasi – Manyara region (Gregory Rift, north Tanzania), the spring sites visited occur in grabens and at the base of slopes of the Ngorongoro Crater Highlands (Fig. 2).

Spring recharge occurs on the Ngorongoro Crater Highlands (>3000 m asl) located nearby (15-25 km from spring lines). At Lake Manyara and Lake Eyasi (Kisima Ngeda area) where large palm woodlands and wetlands occur (Fig. 2B), spring water is fresh (16-22 °C) and pH between 5 and 8. Some springs also occur on the western edge of Lake Manyara and northern and eastern edge of Lake Eyasi.

Depending on the geological context and/or on the spring discharge flux, we observed different spring habitats: herbaceous wetlands where groundwater table reached the surface (Fig. 1D, 3D, 4E), palm groves where groundwater was saline/alkaline and ca. 100 cm below the surface (Fig. 3, 4B, 4F-G), and evergreen forests where groundwater was fresh and most abundant (Fig. 4A, 4C). Vegetation at the spring sites we visited is azonal. It is strikingly different from vegetation in the surrounding landscape (Fig. 1D, 2C). The modern groundwater forest that occupies the northern end of saline Lake Manyara (Tanzania) is an excellent example of azonal vegetation (Fig. 2C, 4A). Plant species growing under the spring influence, make a dense forested patch of tall, evergreen trees, providing shade, cooler microclimate and micro-environment that are strikingly different than the nearby bushland (Fig. 4D), where deciduous spiny trees and shrubs, generally of low height except baobabs, offer little shade and protection against the heat of the day (Greenway and Vesey-Fitzgerald, 1969; Loth and Prins, 1986).

At groundwater-fed wetlands we observed abundant aquatic herbs *Typha*, *Phragmites*, ferns and Cyperaceae species, and, some hydrophyte treelets such as *Sesbania sesban* (in Tanzania near Lake Eyasi) or *Tamarix* (in the Awash Valley). At spring sites where groundwater is very close to the surface (ca. 100 cm) we observed palm woodlands. Two genera, *Hyphaene* and *Phoenix* were commonly found at spring sites. In the Awash Valley, *Hyphaene thebaica* (doum palm) was found at Doho, and in the Filwoha area of the Awash National Park where it forms large groves over an area of several square kilometers (Fig. 3A, 3C). At Metaka, where the spring water merges with the Awash River, only a single *Hyphaene* tree was present. No palm trees were observed at Bilen, likely because of logging. In Tanzania, another species, *Hyphaene petersiana* was observed on the northeastern side of Lake Eyasi where it

forms a ~15 km-long woodland in association with the yellow bark *Acacia xanthophloea* (Fig. 2B). *Hyphaene petersiana* and *Phoenix reclinata* were both observed on the northwestern edge of Lake Manyara; *Phoenix* occurring under the tree canopy of the spring forest, while *Hyphaene* occur on open, dry grounds. In *Hyphaene* palm groves, we note that the abundance of grasses (Poaceae) in the understory is striking; see example from the Filwoha National Park in Ethiopia (Fig. 3A). Other characteristic trees occur at spring sites e.g. *Acacia xanthophloea*, *Rauvolfia caffra*, and *Tamarindus indica* in Tanzania, *Tamarix*, and *Ficus* spp. in Ethiopia, but *Typha*, Cyperaceae, Poaceae and palms of *Hyphaene* or *Phoenix* species are common to all sites. Palm groves and islands of *Phoenix reclinata* have also been observed along the Banagi and Bonar groundwater-fed rivers in the western Serengeti (Albert et al., 2015, and Ashley personal observations).

Hyphaene palm groves seem to develop where groundwater is saline and/or alkaline, whatever the groundwater temperature (cool or hot). We observed that *Hyphaene petersiana* occurs on dry grounds, but where water table is high (about 100 cm below the surface), at the ecotone between saline/alkaline Lake Eyasi and the Kisima Ngeda freshwater spring and wetland, in northern Tanzania. In the Awash Valley, *Hyphaene thebaica* may occur directly at the springheads, growing within the fractures of the basalt (Fig. 3D). Hence, the presence of *Hyphaene* at spring sites is linked to high water table and relatively high water salinity or alkalinity (Stauffer et al., 2014). Spring water temperature, which we measured to be up to 50°C does not seem to be a limiting factor for *Hyphaene*. *Phoenix reclinata*, on the contrary to *Hyphaene* species, favors less saline/alkaline but wetter (damp) soils and may occur in both open and shady habitats.

2.2. Pollen analyses

Pollen data are available for 20 surface soil samples, which we collected at several spring sites in the Awash Valley (5 samples, labeled BB17-#) and in the Eyasi – Manyara region (15 samples, labeled DB11-#). A surface soil sample consists of 20-30 sub-samples collected at random over an area of about 500 m² and combined. Soil samples (without litter) were collected 0 to 1 cm below surface following

classical sampling method (Bonnefille et al., 1999). Extractions and counting procedures also follow Bonnefille et al. (1999).

Modern pollen signal of groundwater forests and woodlands (Fig. 5, SOM 1). Herbaceous taxa such as *Typha*, Cyperaceae, and Poaceae, as well as the arboreal pollen of *Acacia*, occur in all 20 samples in various proportions: Cyperaceae being the most abundant taxon followed by Poaceae, *Typha*, and *Acacia* with average relative abundances of 33%, 12%, 11%, and 3% respectively. Herbaceous taxa such as Asteraceae, *Cyathula*-type *orthacantha*, *Achyranthes*-type *aspera* and other Amaranthaceae also occur in all samples albeit low relative abundances (<1-5%). In agreement with field observations, *Hyphaene*-type is most abundant in the palm woodlands from the Awash Valley and Lake Eyasi, while *Phoenix reclinata*-type is most abundant in samples from the Manyara spring-forest. Pollen taxa diversity is highest in the Manyara spring forest. Arboreal pollen taxa, palms excluded, however, never represent more than 35% of the total pollen assemblages, even in the Manyara forest samples. We note that *Celtis*, *Syzygium*-type *guineense* and *Ficus*-type (found as fossil seeds and wood in Aramis Member) only occur in samples from the most developed spring forest at Manyara; *Ficus*-type, however, also occurs in two samples from Eyasi palm woodlands (SOM 1).

2.3. Phytolith analyses

Samples analyzed for their pollen content were also analyzed for their phytolith content, except BB17-17. Extractions and counting procedure follow WoldeGabriel et al. (2009). The phytolith data obtained for these 14 samples were included in the African modern soil phytolith dataset, which initially was made up of 149 samples (Barboni et al., 2007; WoldeGabriel et al., 2009). In this previous dataset, not a single sample came from a groundwater-fed zone. We have augmented this dataset with 116 new data points including data from various African vegetation types where palms are well-represented such as in some West African gallery forests, desert oases, riparian palm islands from groundwater-fed rivers, and the spring-associated woodlands and forests (Albert et al., 2015; Arraiz, 2017; Novello, 2012; Novello et al., 2017). In addition to these, we included samples from zonal

vegetation types in Guinea, Chad, and Tanzania, which are more distinctly influenced by climatic than by edaphic factors. Fossil phytolith data such as Aramis can now be compared against a modern African dataset of 265 samples (SOM 2).

We have chosen to constrain our interpretations to phytolith morphotypes with clear taxonomic attribution, namely silica shorts cells for grasses (rondel, bilobate, polylobate, cross, saddle and crenate morphotypes) (e.g. Barboni and Bremond, 2009), globular decorated morphotypes for woody dicotyledons (representing trees and shrubs essentially) (Collura and Neumann, 2017), and globular echinate morphotypes for palms (e.g. Bamford et al., 2006). However, the rondel morphotype was excluded from the correspondence analysis (CA) as it prevented sample discrimination according to vegetation types, as also observed by Neumann et al. (2017). CA was run on raw phytolith counts, using modern surface soil samples as active variables, and Aramis samples (SA-#) as supplementary variables. We used R software using FactoMineR (for the analysis) and factoextra (for data visualization) (Kassambara and Mundt, 2017; Lê et al., 2008; R Core Team, 2018) (Fig. 6).

Modern phytolith signal of groundwater forests and woodlands (Fig. 6, SOM 2). Correspondence analysis of the African surface soil phytolith assemblages shows that Axis 1, which explains 29.2% of the total inertia, distinguishes forests and woodlands from grasslands. Axis 2 (20% of total inertia) separates low elevation from high elevation grasslands on the one hand, and, on the other hand, brings some discrimination among the wooded environments. Dispersion of the phytolith morphotypes about Axes 1 and 2 indicates that desert oases, *Raphia* swamp, groundwater forests and palm woodlands are characterized by the globular echinate phytoliths, while semi-deciduous forests and evergreen forests are characterized by phytolith assemblages with abundant globular granulate and smooth morphotypes. The cohort of phytoliths typical for lowland grasslands, the bilobate, cross, and saddle grass silica short cell morphotypes, are also typical for C4 grasses, while the crenate morphotypes is characteristic for high elevation grasslands where C3 Pooideae grasses dominate (Barboni and Bremond, 2009).

3. Fossil springs

3.1. Aramis Member, Awash Valley, Ethiopia

The *Ardipithecus*-bearing Lower Aramis member of the Central Awash Complex of the Middle Awash area (Ethiopia), dated 4.4 Ma, was thoroughly documented and provides the most complete set of geological, faunal, isotopic, and botanical data associated with the early hominin *Ardipithecus ramidus* (Louchart et al., 2009; Suwa et al., 2009; White et al., 2009b, 2009a; WoldeGabriel et al., 2009). From our point of view, it also provides a thoroughly documented multi-proxy record of a paleo-ecosystem associated with groundwater.

Geological evidence for groundwater in the Aramis member are described as follows by WoldeGabriel et al. (2009), which make no doubt that groundwater strongly influenced botanical and faunal assemblages:

"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, 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".

Over the 7 km-long west to east transect sampling Aramis paleolandscape, carbonate horizons are found at ARA-VP-17 and ARA-VP-6 localities capped by the Daam Aatu Basaltic Tuff, and about 70-80 cm below the DABT at KUS-VP-2 and SAG-VP-7 localities (WoldeGabriel et al., 2009, figure 1).

Calcite-replaced wood and endocarps were found preserved in the carbonate horizons of Aramis Member (mainly at ARA-VP-6 locality), and absent in the non-cemented sediments (WoldeGabriel et al., 2009). In agreement with geological and faunal evidence for negligible fluvial transport, the wood and seed specimens attributed to *Ficus*, *Syzygium cf. guineense*, and *Celtis* (Jolly-Saad and Bonnefille, 2012), therefore, could have been fossilized *in situ* or not far from the place of collection, i.e. not far from the spring resurgence. The Aramis pollen record, despite its paucity (only 16 grains found in just 4 samples over 40 tested), attests for the presence of *Hyphaene* (n = 2 at ARA-VP-6 and n = 2 at ARA-VP-1 TS) (WoldeGabriel et al., 2009). *Hyphaene* pollen type is produced by both *Borassus* and *Hyphaene*; however, *Borassus* palm trees do not occur at spring sites but in dryland savannas, on the contrary to *Hyphaene* species which grow at alkaline spring sites, preferentially on rocky grounds, and where water table is high (Edwards et al., 1997; Orwa et al., 2009). The presence of palms at Aramis is also attested by the phytolith record in which globular echinate phytoliths may represent up to 40% (WoldeGabriel et al., 2009). Pollen, relatively prone to transport, indicate that trees of *Myrica* and of *Hyphaene* palms were also part of the vegetation locally or in the landscape along with grasses and sedges (WoldeGabriel et al., 2009). *Myrica* species today occur in the Afromontane forests, while *Hyphaene* occur in the lowlands (up to 1400 m) (Orwa et al., 2009).

Aramis phytoliths assemblages indicate the presence of C₄ grasses, palms, woody plants, and sedges. Phytolith-inferred woody cover is heterogeneous among samples as it ranges from <40 % to ~65 % (WoldeGabriel et al., 2009). By comparison with our extended modern surface soil phytolith dataset, Aramis fossil phytolith assemblages (SOM 3) best compare with present-day lowland C₄-grasslands, groundwater forests and palm woodlands. Few samples (SA15, SA19, and SA39) show similarities with semi-deciduous forests and the

group of samples that includes Tree/Shrub savannas, ecotones, and the Awash riparian forest (Fig. 6).

Aramis paleosol carbonates, which were sampled over the Aramis 7 km-long west to east paleolandscape transect, exhibit $\delta^{13}\text{C}$ values ranging from -9.3‰ to -0.4‰, and $\delta^{18}\text{O}$ values ranging from -9.8‰ to -0.9‰ (WoldeGabriel et al., 2009) (reported in Fig.7). They indicate expanses of wooded grassland (tree or bush-savanna) where densely wooded habitats were likely of limited geographic extent (Cerling et al., 2010; WoldeGabriel et al., 2009). Wooded habitat, however, was inferred from multiple lines of evidence, such as the abundance of *Tragelaphus* (browsing antelope, kudu) and cercopithecoid monkeys (*Pliopapio alemui* and *Kuseracolobus aramisi*) which combined with other data show that “the large mammal biomass at Aramis was dominated by browsers and frugivores” (White et al., 2009a). Preferred wooded habitat was clearly inferred for the primates *Ardipithecus ramidus*, *Kuseracolobus aramisi* (colobine monkey) and *Pliopapio alemui* (a small baboon-like monkey), and *Tragelaphus* using carbon isotopes in enamel (Fig.7), tooth micro- and mesowear, craniofacial structure and masticatory apparatus, and tooth anatomy and proportions for the hominin, and microwear, mesowear, isotopes, and postcranial ecomorphology for cercopithecoids and kudus (White et al., 2015a, 2009a). The micro-mammal assemblage indicates a variety of biotopes ranging from locally present forests and/or well-developed mesic woodlands, to palm thickets /woodlands, savanna woodlands, dry scrub or even arid steppe. The assemblage also includes two taxa which present-day counterparts occur in mesic montane forests and uplands (Louchart et al., 2009). Regarding the bird assemblage, we note that among the Psittacidae, Apodidae and Passeriformes, which represent >43% of the identified avian specimens at Aramis (Louchart et al., 2009), several have modern species in Ethiopian lowlands that rely on the fruit bearing spring palm species *Hyphaene thebaica* (Ash and Atkins, 2010). At last, the terrestrial gastropods assemblage with *Maizania* from the *M. hildebrandti* group, *Limicolaria* sp. and *Chlamydarion* cf. *hians* bares resemblance with that of modern Kibwezi groundwater forest in southern Kenya (WoldeGabriel et al., 2009).

3.2. Hominin and archeological sites co-occurring with springs

Springs and groundwater-supported ecosystems may leave sparse evidence in the geologic record. Yet, evidence left is diverse and corresponds to *in situ* deposits, so important for paleoenvironment interpretation. They include terrestrial and aquatic plant remains such as pollen, phytoliths, seeds and other carbonated and silicified macro-remains as described in length here for Aramis Member, as well as algae (Ashley et al., 2016), and organic molecules (Magill et al., 2016). Evidence also include *in situ* terrestrial and aquatic animals (mollusks, crustaceans) (e.g. Pickford, 1995), and *in situ* minerals: chiefly carbonate, but also opal (silica), evaporates, sulphates, clay minerals (Cantonati et al., 2016; Pigati et al., 2014).

Copious literature documents hominin and/or archeological sites associated with evidence for groundwater, with no less than 50 different localities within 22 geographically different paleontological and archeological areas found throughout the East African Rift and beyond in the Arabian Peninsula, Jordanian, Iran, and Turkey (Fig. 8, Table 1). Among these, 12 are dated to > 1 Ma. In some cases, springs and hominin remains and/or artifacts may be found to co-occur in several stratigraphic levels within one paleontological area. At Olduvai Gorge for example, springs and hominin remains and/or artifacts were found to co-occur in no less than five different paleosurfaces between 1.85 and 1.34 Ma (Table 1).

Interestingly for the Pliocene, both fossiliferous areas in the Afar region with *Ardipithecus ramidus*, Gona and Aramis, have spring deposits (Semaw et al., 2005; WoldeGabriel et al., 2009). Despite different depositional environments at Gona and Aramis, *Ardipithecus* remains were found closely associated with tufa or groundwater carbonates. Spring deposits also occur at several sites with *Australopithecus* species in Ethiopia (Woranso-Mille) (Haile-Selassie et al., 2007), South Africa (Taung) (Hopley et al., 2013; McKee and Kuykendall, 2016) and plausibly in Tanzania as well. At Laetoli (Tanzania), geological evidence for groundwater was likely eroded although “pond deposits” were recognized (Ditchfield and Harrison, 2011, p. 74). We also suspect the presence of springs at Laetoli

because pollen taxa such as *Hyphaene* (spring palm tree) and the freshwater-loving *Typha* (cattail) occur in several samples (Barboni, 2014; Bonnefille and Riollot, 1987).

For the early Pleistocene, spring sites with hominin remains are found in Turkey (Kappelman et al., 2008; Lebatard et al., 2014; Vialet et al., 2012), the Syrian desert (Jagher et al., 2015), and in Tanzania with several sites throughout the 1.89 – 1.30 Ma interval at Olduvai Gorge (Ashley et al., 2016, 2014a, 2010a, 2010b, 2010c, 2009; Barboni et al., 2010; Deocampo et al., 2002; Garrett, 2017; McHenry et al., 2007), and possibly at Peninj as *Typha* pollen is abundant (Dominguez-Rodrigo et al., 2001). During the Middle and Upper Pleistocene, there is recurrent evidence for human presence at spring sites in the Saharan desert belt (Churcher et al., 1999; Dachy et al., 2018; Foulds et al., 2017; Hill, 2001; Inglis et al., 2017; Kleindienst et al., 2008; McCool, 2018; Nicoll et al., 1999; Smith et al., 2007, 2004; Wendorf et al., 1993), in northeast Ethiopia (Benito-Calvo et al., 2014; Gossa et al., 2012; Williams et al., 1977), in Kenya (Beverly et al., 2015; Johnson et al., 2009; Johnson and McBrearty, 2012; Tryon et al., 2014, 2012; Van Plantinga, 2011), and South Africa (Butzer, 1973; Porat et al., 2010). In South Africa, the massive tufa fan deposits spanning the length of the Ghaap Plateau escarpment (the Buxton Limeworks at Taung, and the Groot Kloof and Gorrokop at Ulco) have resulted from the discharge of groundwater-fed Thabaseek River since the Pliocene (review in Doran et al., 2015). The Buxton Limeworks are aggrading surface freshwater carbonate deposits at the edge of the Kalahari Desert that have preserved the Taung Child skull attributed to *Australopithecus africanus* (Dart, 1925), as well as traces of at least 17 Pleistocene and Holocene sites (Hopley et al., 2013; McKee, 1994; McKee and Kuykendall, 2016).

4. Discussion

4.1. Modern analog groundwater-associated habitats

The pollen signal of the groundwater-supported habitats we sampled is characterized by the abundance of herbaceous taxa such as *Typha*, Cyperaceae, and Poaceae, while the abundance of arboreal taxa is low (<~35%),

except for *Acacia*, and palms *Hyphaene* and *Phoenix*. The Manyara forest for example, despite its closed, mostly evergreen canopy and important tree taxa diversity is characterized by low percentages of arboreal pollen, because Cyperaceae (sedges), which occur in enclosed swamp herbages (Fig. 5) contribute to disproportionately high pollen percentages (Fig. 6). Among the groundwater-associated habitats, therefore, forests may not show up in the fossil pollen record, which is likely to exacerbate the signal of wetlands, as it is dominated by herbaceous aquatic taxa. Woodlands and forests may also be outshined in the pollen record by the surrounding open and more largely widespread xerophytic vegetation, as some xerophytic taxa, notably Amaranthaceae occur in all surface samples, even in most forested sites. We note that although *Ficus*, *Celtis*, and *Syzgium* arboreal taxa were recorded in the pollen assemblages from the most developed forest of Manyara, these taxa are not unique to groundwater-fed forests as they also occur in riparian forests (Carr, 1998).

In the phytolith record, some, but not all groundwater-associated habitats carry a distinct phytolith signal. Wetlands, on the one hand, do not differentiate despite the fact that Cyperaceae produce typical (unique) morphotypes; the silicified papillae phytoliths of sedges were too poorly represented in the soil phytolith assemblages to allow discrimination (Fig. 6). Wetlands exhibit a phytolith signal indistinguishable from that of grasslands most likely also because our dataset was restricted to main phytolith categories. Novello et al. (2012) showed that distinguishing trapeziform grass silica short cell phytoliths within the bilobate, cross, and saddle categories could improve the identification of wetland grasses. Unfortunately, such distinction was not considered by all the authors who contributed to the African phytolith dataset presented here. Some groundwater-associated woodlands and forests, on the other hand, strongly discriminate because of the presence and relative abundance in the surface samples of globular echinate phytoliths, typical for palms (Arecaceae). It is the presence of palms in the vegetation that is well captured by the phytoliths and which, therefore, allows identifying some groundwater-associated woodlands and forests, such as the Manyara spring forest, the Eyasi

Acacia and palm woodland, a palm grove on a spring-fed river bank in the Serengeti, the Saharan oases, and some palm woodlands from the Awash River valley. We note, however, that despite the presence of palms in the vegetation, the relative abundance of globular echinate phytoliths was too low in several samples to allow discriminating some groundwater-associated palm woodlands: e.g. samples BB17-05 from a *Hyphaene thebaica* palm woodland in the Awash Valley, and MNY12-40 from Manyara forest (Fig.6). The systematic over-representation of palms in phytolith assemblages is, thus, not proven here. Other authors came to the same conclusion: although Arecaceae are large phytolith producers (Hodson et al., 2005), palms are not systematically over-represented in surface samples (Albert et al., 2015; Bremond et al., 2005; Novello, 2012; Novello et al., 2017). Yet, to our knowledge, a formal calibration between phytolith abundance and palm abundance in the vegetation has never been carried out.

Taphonomic issues affect phytolith assemblages, and dissolution affects phytolith morphotypes differently despite the fact that they all are composed of the same mineral (SiO_2 , nH_2O) and have similar range of solubility (Frayse et al., 2009, 2006). Phytolith dissolution starts at $\text{pH} > 8$, and preferentially affects morphotypes with a surface to bulk ratio > 1 , such as e.g. the silicified papillae (hat-shaped phytoliths) of Cyperaceae. Morphotypes with a surface to bulk ratio < 1 , such as the grass silica short cells and the globular echinate phytoliths of palms happen to be particularly stable (Cabanes and Shahack-Gross, 2015). In the 13 fossil phytolith assemblages from Aramis Member where hat-shaped phytoliths occur (WoldeGabriel et al., 2009), it is therefore likely that preservation was exceptional, and that the relative abundance of all morphotypes was preserved. We agree that a standardized phytolith solubility test as proposed by Cabanes and Shahack-Gross (2015) would allow evaluating the phytolith state of preservation for the whole Aramis dataset.

4.2. Identifying ancient groundwater-associated habitats in the geologic, isotopic, and faunal record

The groundwater-discharge zones are typically localized features that can be as small

as 10s of m^2 or a few kilometers² (Magill et al., 2016; Pigati et al., 2014). Groundwater-discharge zones, thus, could be completely missed when sampling paleoenvironments. Among the micro-habitats supported by groundwater, the least extensive are the forests, as they are the most demanding in terms of water amount, quality, and availability through time. Hence, although springs may be permanent features on the landscape lasting for hundreds of years, groundwater-supported wetlands and woodlands may leave only sparse evidence in the geologic record. At Aramis (4.4 Ma), for example, the woodland setting with forest patches that made the habitat of kudu and leaf- and fruit-eating primates including *Ardipithecus*, did leave a forest signal in the tooth enamel isotopic record of browsing taxa (White et al., 2009a), but not so in the pedogenic carbonates, as most $\delta^{13}\text{C}$ values cluster between -5‰ and -2‰ (WoldeGabriel et al., 2009). The discrepancy between the enamel and pedogenic carbonate isotopic datasets (Fig. 7) may be related to the fact that isotopic records of tooth enamel captures the herbivores' dietary preference over the herbivores' lifetime (1–10 years), while that of pedogenic carbonate averages environmental information over 100–1000 years (Du et al., 2019). It could also be related to the fact that forest patches at Aramis were too sparse compared to open (grass-prone) habitats in the landscape that was sampled, to significantly contribute to the isotopic record in carbonate nodules (Cerling et al., 2011). An alternative possibility, more convincing to our opinion, is that the carbonate nodules sampled in the Aramis member were diagenetically altered by groundwater, and that their carbon isotopic composition was overprinted by the groundwater own isotopic composition (Budd et al., 2002; Gallagher and Sheldon, 2016). In the case where the presence of groundwater is attested, $\delta^{13}\text{C}$ should be measured on organic biomarkers (leaf waxes) rather than on carbonate nodules, as they are too prone to having their $\delta^{13}\text{C}$ values reset by the groundwater carbon isotopic composition and the extent of water:rock interaction (Budd et al., 2002).

Groundwater-fed environments have tended to be overlooked and underappreciated in the geological record. Similarly, in the modern world, groundwater-fed habitats have

hardly been sampled to evaluate their proxy signature. The modern phytolith dataset initially used to interpret Aramis fossil data did not include any samples from groundwater micro-habitats (Barboni et al., 2007; WoldeGabriel et al., 2009), nor did the isotopic dataset assembled to provide a quantitative modern-based estimate of paleo tree cover at Aramis (Cerling et al., 2014, 2011, 2010). In this modern isotope dataset only one sample evaluates the isotopic signal of a groundwater-forest in Kenya (Mzima Springs, Tsavo West National Park), but not a single sample comes from palm-rich groundwater-associated woodlands, the most likely analog according to the whole Aramis dataset. The paleoenvironment of *Ardipithecus ramidus* at Aramis was interpreted as a distal floodplain with spring-fed forest patches within predominantly grassy woodland to wooded grassland habitats (Suwa and Ambrose, 2014; White et al., 2009b; WoldeGabriel et al., 2009). Yet in a discussion of the White et al. interpretation, Cerling et al. (2014, 2010) interpreted a tree- or bush-savanna and did not recognize the possibility of localized water sources unrelated to rivers and lakes. Cerling et al. (2014, 2010)'s interpretations were of a generalized landscape that was dry everywhere except perhaps along a riparian corridor. Yet, Aramis is not in a riparian setting (White et al., 2015b; WoldeGabriel et al., 2009). The importance of groundwater in providing relatively persistent additional moisture, therefore, still needs to be understood and acknowledged.

The Aramis groundwater-fed paleoecosystem included the early hominin *Ardipithecus ramidus*, as well as a diverse fauna of macrovertebrates characterized by the abundance of tragelaphine bovids and cercopithecoid primates (White et al., 2009a). Some bovid tribes are useful environment indicators: the grazing Alcelaphini, Antilopini and Hippotragini (AAH) indicate open grass-dominated habitats, the mixed feeders and browsing Tragelaphini and Aepycerotini (TA) indicate dry woodlands, and Reduncini and Bovini (RB) are usually associated with closed riparian habitats (Shipman and Harris, 1988; Vrba, 1980). At Aramis, tragelaphines represents 85%, aepycerotines 4%, reduncines <1% and all other tribes less than 10% of the

Bovidae. Aramis bovid assemblage does not compare to Olduvai Bed I and Bed II (Alcelaphini and Antilopini-rich), despite the recognized presence of groundwater-fed wooded and palm-rich micro-habitats (Albert et al., 2018; Arráiz et al., 2017; Ashley et al., 2010b; Barboni et al., 2010), nor to Shungura (mixed Reduncini and Tragelaphini) where fluvial and deltaic environments likely prevailed (Shipman and Harris, 1988). Aramis bovid assemblage is very different than many other Plio-Pleistocene sites by its marked abundance of tragelaphines (White et al., 2009a). The dominance of Tragelaphini at Aramis best compares with modern Kruger, Mkuzi and Timbavati national parks (N.P.) bovid data when comparison is restricted to AA, BR and TA tribes (Aramis data plotted on Shipman and Harris, 1988's ternary diagram, not shown). By considering all bovid tribes but Reduncini, however, Aramis data best compare with Manyara N.P. and Hwange N.P. (Dominguez-Rodrigo and Musiba, 2010). Manyara N.P. is definitely a groundwater-fed ecosystem, as described in length here. Hwange N.P. includes many spring areas (e.g. Sinamatella), and could therefore represent another potential faunal analog for Aramis.

In Aramis groundwater-fed ecosystem primates in the Cercopithecidae include a colobine monkey (*Kuseralocolobus aramisi*) and a small baboon-like monkey (*Pliopapio alemui*) (White et al., 2009a). Today, the Filwoha spring area in the Awash Valley doesn't host colobines, but Hamadryas baboons (*Papio hamadryas hamadryas*), which large group sizes may be explained by "the abundance of one food resource in particular, doum palm nuts" (i.e. *Hyphaene thebaica*) (Swedell, 2002). One colobine, *Colobus guereza* is found today in several Ethiopian regions largely at mid- and high-elevation (>1700 m up to 3300 m asl) and at low elevation in the Omo Valley and, presumably, the Awash Valley (Dunbar, 1975). This leaf-eating monkey, however, chiefly occupies riparian and gallery forests where its favorite food are leaves of *Celtis africana* and *Ficus* spp. (Dunbar, 1987; Dunbar and Dunbar, 1974), among many other species (Hussein et al., 2017). Understanding how critical the role of groundwater-fed habitats was to the Aramis faunal community, however, would require further investigations.

4.3. Why are springs ecological keystones?

Despite the fact that groundwater-fed areas leave well-recognized evidence in the geological record, their importance in defining the type of habitat available to hominins and other elements of the fauna is rarely recognized (but see Barboni, 2014; Beverly et al., 2015; Cuthbert et al., 2017; Deocampo and Tactikos, 2010; Djamali et al., 2018; Reynolds et al., 2011). Yet, we have shown here that the occurrence of springs is not anecdotal in the African hominin and human record (Table 1). Aramis site is just one among > 50 examples in Africa and the Middle East where springs or groundwater-fed areas co-occur with hominin and/or archeological remains. Here we discuss the importance of springs, and that springs are ecological keystones for species, and crucial environmental features that cannot be ignored in paleontology, and in paleoenvironmental studies aiming at reconstructing hominin paleo-habitats.

Springs in arid environments play key roles for species. In the discipline of conservation biology, small natural features like springs and riparian areas are considered ecological keystones because these sites have a disproportionate ecological importance to their size (Hunter Jr et al., 2017). Springs and groundwater-fed habitats have been recognized biodiversity hotspots in Europe (Cantonati et al., 2012), North America (Stevens and Meretsky, 2008), New Zealand (Collier and Smith, 2006), as well in tropical deserts in Africa (Suhling et al., 2006), Australia (Davis et al., 2017; Fensham et al., 2011; Murphy et al., 2015), and Central America (Bogan et al., 2014). In xeric regions, springs provide permanent source of water for vertebrates, and are used as mesic refugia by birds (e.g. Szaro and Jakle, 1985), elephants (e.g. Viljoen et al., 1990), as well as savanna chimpanzees (Kempf, 2009; Pruetz and Bertolani, 2009).

4.3.1. Springs provide a stable water resource

Groundwater-discharge zones may supply the critical need for water for plants and animals in arid regions, as springs persist throughout the year and throughout wet-dry climatic cycles. The presence and temporal persistence of springs depends on multiple factors. Cuthbert et al. (2017) showed that groundwater response

time is the primary factor controlling the presence and the persistence of active springs in the East African Rift, rather than rates of groundwater recharge. Groundwater response time depends on subsurface hydraulic properties of the aquifer and the topography (i.e. length scale and topographic gradient of the catchment area), two factors that are stable over 10^3 to 10^6 years-long periods. On the contrary, rates of groundwater recharge depend on climate, a factor that varies greatly over a range of timescales (from $<10^1$ to $>10^5$ years-long periods). Hence, topography and geology act as buffers; they prevent springs from responding directly to climate changes (Cuthbert et al., 2017). Springs may therefore guarantee a rather stable habitat. They provide ecological continuity through time. At Esere, near Laetoli paleo-anthropological area (northern Tanzania, Fig. 2B), an active spring occurs next to a ca 2 m –thick carbonated tufa mount attesting for the presence of a persistent fresh water spring in this area (dating of the carbonate in progress, Ashley, *unpublished*) (Fig. 9). Springs were likely present throughout the Late Pliocene – Early Pleistocene in this region of north Tanzania, where no less than three paleontological sites are known (Barboni, 2014).

4.3.2. Springs are controlled by geology and topography, and are independent of climate

Springs are more likely to play a crucial ecological role in regions with low annual rainfall, seasonal rainfall and periodic droughts because groundwater is protected from evaporation. At first glance, this is counter-intuitive as a reasonable assumption has been that more rainfall (recharge) would lead to more discharge (spring and groundwater seeps) and that climate variability is the dominant control on water availability. But, the persistence of springs is highly dependent on topographic and geologic factors, such as distance from recharge area, the topographic gradient and the transmissivity of the intermediary rocks and soils (Cuthbert et al., 2017). These physical controls buffer the impact of climate variability. A majority of the paleo-spring records at Olduvai Gorge are located in topographic low areas (playa lake basin), at the base the slope and formed during insolation minima during periods of low lake levels (Ashley et al., 2014b;

Cuthbert et al., 2017; Cuthbert and Ashley, 2014).

4.3.3. Springs generate distinct microclimates, distinct vegetation and distinct micro-habitats

The sustained water supply increases structural complexity because soil moisture triggers higher plant productivity. In East Africa, rainfall is mostly low (250-500 mm/yr) and highly seasonal, whereas evapotranspiration is high (~2500 mm/yr). As a consequence, shallow lakes are saline and net primary productivity is low compared to e.g. central West Africa (Brown et al., 2010). Vegetation growth is limited in many areas, and trees are generally scattered in the landscape. It is a region where climate deterministically supports low (<55%) tree cover (Staver et al., 2011). Tree cover >55% only occurs where rainfall is >750 mm/yr and dry season <7 months (Good and Caylor, 2011; Staver et al., 2011). Springs are eye-catching in the landscape, as they appear like vegetated island oases in an otherwise grass-dominated or bare landscape. Groundwater-fed areas are more vegetated than the surroundings; a contrast that is well marked on satellite images (Figs. 2, 3) (Reynolds et al., 2016). The size of a groundwater discharge area varies according to groundwater discharge rate and the geological setting, which may favor the development of a groundwater-fed river or more expansive wetland. In Africa, the greatest number of habitats are seen near water bodies, and decline with distance (O'Regan et al., 2016).

At the local scale, springs increase soil moisture such as high-water demanding plants may grow even under arid climate. High soil moisture also favors the growth of tall trees, and evergreen (rather than deciduous) plants. Springs therefore favor the growth of azonal vegetation units, which are not in equilibrium with regional climate (e.g. Greenway and Vesey-Fitzgerald, 1969). Groundwater-fed areas support denser vegetation and taller trees than surrounding areas; the microclimate they provide contributes to buffer extreme temperatures and maintain moisture. Pruetz and Bertolani (2009) observed that spring-associated gallery forests, which provide the only permanent source of water and shade during the dry season can be considered as

“pseudo-home base for Fongoli chimpanzees at this time, as they move outwards from these areas in a radiating fashion to forage”.

Davis et al. (2013) showed that in arid Australian aquatic systems, perennial spring sites represent both ecological refuges for mobile taxa, and evolutionary refugia for species with low dispersal capabilities. Although this study focused on aquatic invertebrates, it presents a concept that could plausibly apply to vertebrates. Springs are likely to mitigate the impact of climate change on the dispersal of animals, hominins included, as they would provide potable water during dry periods, even in dry and very dry areas where many lakes are saline and rivers seasonal (Barboni, 2014; Cuthbert et al., 2017; Cuthbert and Ashley, 2014). In arid regions or during less favorable (more arid) climatic periods, groundwater springs may represent, for mobile taxa, ecological refuges or "stepping stones" between sites with more permanent water. Groundwater-fed sites in arid regions are also likely to contain relict and short-range endemic species as the habitats they provide is climatically decoupled (Davis et al., 2013; Harvey, 2002).

During arid climatic periods, spring sites could become sites of intense competition among species with overlapping ecological niches, therefore modifying the intensity of biotic interactions. At Olduvai, the paleosurface underlying Tuff IC dated ca 1.84 Ma ago (Deino, 2012), which includes evidence for springs and water holes bordered by palm groves (Arraiz, 2017; Ashley et al., 2010a; Dominguez-Rodrigo et al., 2010), has provided remains of three sympatric hominin species (*Paranthropus boisei*, *Homo habilis*, and likely *Homo erectus*) (Domínguez-Rodrigo et al., 2015). In this paleosurface were also recognized a carnivore kill site (AMK, Aramendi et al., 2017) and several hominin sites with evidence for carcass butchering such as FLK Zinj site and the newly discovered PTK and DS sites (Arraiz et al., 2017; Domínguez-Rodrigo and Cobo-Sánchez, 2017). These new finds are further evidence that, in Olduvai paleolake basin, freshwater springs were essential in the landscape for both hominins and other elements of the fauna. A review of lithic and faunal assemblages through Olduvai Bed I and Bed II (1.89 – 1.3 Ma) showed no correlation between

hominin sites and predator risk, and suggests instead, that water and tree cover “played more proximal roles” for Early Pleistocene hominins than carnivore avoidance (Egeland, 2014). Hence, although freshwater would attract both prey and predators, and would become places of intensified predation risk, the presence of trees likely offered a crucial advantage of safety for primates, including early hominins.

4.4. Perennial water at the continental scale: springs versus permanent rivers

We have found 50 hominin–spring associations and just 12 that include localities dated to >1 Ma (Fig.1, Table 1). Although it is likely that spring deposits may have been overlooked in some sites, this number is low compared with e.g. the ~110 hominin-bearing localities of the Plio-Pleistocene Shungura Formation in the Turkana Basin that do not seem to display evidence for groundwater-fed habitats (JR Boissérie, *pers. com*). Although the large hominin occurrence is the Omo Valley points to the importance of surface water and riparian micro-habitats rather than groundwater in this region, what it really means is that permanent water and the wooded micro-habitats it may sustain are the key parameters to the ecology and probably the dispersal of early hominins.

Perennial rivers on the one hand, and springs on the other hand both contribute permanent water and sustain wooded habitats, but at different temporal and spatial scales. The Shungura Formation is a continuous record of fluvial, deltaic, and lacustrine environments in the Omo Valley dating since the Pliocene to the mid-Pleistocene indicating that the river system was active even during driest periods (de Heinzelin, 1983; McDougall et al., 2012). It is likely that the Omo River has been active since relief was created, i.e. since the Ethiopian volcanic doming >23 million years ago (Rooney, 2017). Same reasoning applies to the Awash River. Permanent rivers, hence, are likely to provide highly stable water resource and wooded micro-habitats on much longer timescales (10^6 – 10^7 years) than springs, which start or cease being active according to much more 'frequent' intra-rift faulting and basin formation (10^3 – 10^6 years).

Permanent rivers, in addition, may represent hundreds of km-long wooded

corridors that could potentially connect different valleys through the highlands, making inter-regional dispersal possible for faunas favoring wooded habitats (and relatively tolerant to lower temperatures). Landscape heterogeneity (due to topography, volcanism, tectonism) in addition to the micro-habitat diversity created by the hydrographic network in the rift valleys break off the apparent homogeneity of the savanna biome at the regional scale (Bailey et al., 2011; Reynolds et al., 2015, 2011). Patterns of faunal diversity and their relationship with the heterogeneity of landscapes and habitats in various valleys during the Pliocene would be worth investigating.

5. Conclusions

The geological context, the present-day vegetation, and the pollen and phytolith signatures of several modern springs from two regions in Eastern Africa that have numerous paleoanthropological sites, namely the Awash Valley (Ethiopia) and the Crater Highlands Region (Tanzania) were sampled, generating new plant microfossil datasets of 20 pollen and 19 phytolith samples. The new phytolith dataset that we have combined with previously published data (Albert et al., 2015; Arraiz, 2017; Barboni et al., 2007; Novello, 2012; Novello et al., 2017) now makes up a dataset of 265 surface samples, which allows a more accurate interpretation of ancient spring and wetland environments in arid Africa.

Groundwater-associated forests, palm groves, and wetlands, despite being small natural features, play essential roles at the species and ecosystem levels, particularly in arid and sub-arid regions. Springs and groundwater-fed areas are spatially localized, but temporally persistent features that are independent of the regional climate drivers. They contribute to additional soil moisture that generates the development of species-rich and structurally complex microhabitats in arid regions.

Interpretation of the paleoecology suggests that in the East African Rift where low, highly seasonal rainfall and high evapo-transpiration limit plant growth in many areas, springs and groundwater-fed zones play a major role in ecosystem functioning. Springs are commonly localized features (oases) within a landscape;

they are limited in space, but yield a dependable daily supply of water and provide ecological continuity through time. At the local scale, springs create a microclimate, distinctive vegetation, increase soil nutrients, species richness, structural complexity, and provide habitat for animals. At the landscape scale, they represent hydro-refugia favoring increased connectivity among animals and allowing migrations during dry periods. Hence, the palm and grass-rich spring woodland that made up the habitat of *Ardipithecus ramidus* likely played a crucial role on the feeding ecology, locomotion, and evolutionary trend of this early hominin in northeastern Ethiopia and, potentially of other hominins elsewhere in East Africa.

Aramis paleoenvironment as inferred from the sampling of 9 km-long west-east transect in the Middle Awash Valley is interpreted as a mosaic of micro-habitats including forest patches and palm groves closely associated with the presence of groundwater, and open grasslands. Aramis wooded micro-habitats represent by no means the paleoenvironment at the landscape or regional scale, but localized, azonal patches of wooded vegetation within the much larger, climatically-driven, savanna biome.

More generally, our study shows that it is permanent water and the wooded micro-habitats that it may sustain that are likely the key parameters to the ecology and dispersal of early hominins. Hominin and faunal evolution in general was likely driven by a complex interplay between abiotic factors (tectonics, hydrography, climate) and biotic interactions at various spatial and temporal scales, and not simply by climatically-driven biome changes.

Research data

SOM 1. Site data and pollen counts for samples from the Awash Valley (Ethiopia) (samples BB17-) and from the region of Lake Eyasi - Lake Manyara (Tanzania) (samples DB11-). <http://dx.doi.org/10.17632/dsgd78tfjz.1> - file-12c6e371-ea9a-4502-87ce-7096c7f6214e

SOM 2. Site data and raw phytolith counts for 265 surface soil samples and for the 41 fossil samples from Aramis Member, Sagantole Formation. <http://dx.doi.org/10.17632/myg68hsjvf.1>

SOM 3. Site data and raw phytolith counts for the 41 fossil samples from Aramis Member, Sagantole Formation (partially published in WoldeGabriel et al., 2009).

<http://dx.doi.org/10.17632/4crtycn7rk.1>

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References

- Albert, R.M., Bamford, M.K., 2012. Vegetation during UMBI and deposition of Tuff IF at Olduvai Gorge, Tanzania (ca. 1.8 Ma) based on phytoliths and plant remains. *J. Hum. Evol.* 63, 342–350. <https://doi.org/10.1016/j.jhevol.2011.05.010>
- Albert, R.M., Bamford, M.K., Esteban, I., 2015. Reconstruction of ancient palm vegetation landscapes using a phytolith approach. *Quat. Int.* 369, 51–66.
- Albert, R.M., Bamford, M.K., Stanistreet, I.G., Stollhofen, H., Rivera-Rondón, C.A., Njau, J.K., Blumenshine, R.J., 2018. River-fed wetland palaeovegetation and palaeoecology at the HWK W site,

- Bed I, Olduvai Gorge. *Rev. Palaeobot. Palynol.*
<https://doi.org/10.1016/j.revpalbo.2018.09.010>
- Aramendi, J., Uribelarrea, D., Arriaza, M.C., Arráiz, H., Barboni, D., Yravedra, J., Ortega, M.C., Gidna, A., Mabulla, A., Baquedano, E., others, 2017. The paleoecology and taphonomy of AMK (Bed I, Olduvai Gorge) and its contributions to the understanding of the “Zinj” paleolandscape. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 488, 35–49.
- Arraiz, H., 2017. Paleovegetation and stone tool use at a selection of hominin sites and their associated landscapes from Olduvai Gorge (Tanzania): a study of plant microfossils (Doctorat). Universidad Complutense De Madrid, Madrid, Spain.
- Arráiz, H., Barboni, D., Ashley, G.M., Mabulla, A., Baquedano, E., Domínguez-Rodrigo, M., 2017. The FLK Zinj paleolandscape: Reconstruction of a 1.84 Ma wooded habitat in the FLK Zinj-AMK-PTK-DS archaeological complex, Middle Bed I (Olduvai Gorge, Tanzania). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* <https://doi.org/10.1016/j.palaeo.2017.04.025>
- Ash, J., Atkins, J., 2010. *Birds of Ethiopia and Eritrea: An Atlas of Distribution*. Bloomsbury Publishing.
- Ashley, G.M., Barboni, D., Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Diez-Martin, F., Barba, R., Baquedano, E., 2010a. A spring and wooded habitat at FLK Zinj and their relevance to origins of human behavior. *Quat. Res.* 74, 304–314. <https://doi.org/10.1016/j.yqres.2010.07.015>
- Ashley, G.M., Barboni, D., Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Diez-Martin, F., Barba, R., Baquedano, E., 2010b. Paleoenvironmental and paleoecological reconstruction of a freshwater oasis in savannah grassland at FLK North, Olduvai Gorge, Tanzania. *Quat. Res.* 74, 333–343. <https://doi.org/10.1016/j.yqres.2010.08.006>
- Ashley, G.M., Bunn, H.T., Delaney, J.S., Barboni, D., Dominguez-Rodrigo, M., Mabulla, A.Z.P., Gurtov, A.N., Baluyot, R., Beverly, E.J., Baquedano, E., 2014a. Paleoclimatic and paleoenvironmental framework of FLK North archaeological site, Olduvai Gorge, Tanzania. *Quat. Int.* 322–323, 54–65. <https://doi.org/10.1016/j.quaint.2013.08.052>
- Ashley, G.M., de Wet, C.B., Barboni, D., Magill, C.R., 2016. Subtle signatures of seeps: Record of groundwater in a Dryland, DK, Olduvai Gorge, Tanzania. *Depositional Rec.* 2, 4–21. <https://doi.org/10.1002/dep2.11>
- Ashley, G.M., De Wet, C.B., Dominguez-Rodrigo, M., Karis, A.M., O'Reilly, T., Baluyot, R., 2014b. Freshwater limestone in an arid rift basin: a goldilocks effect. *J. Sediment. Res.* 84, 988–1004.
- Ashley, G.M., Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Baquedano, E., 2010c. Sedimentary geology and human origins: A fresh look at Olduvai Gorge, Tanzania. *J. Sediment. Res.* 80, 703–709. <https://doi.org/10.2110/jsr.2010.066>
- Ashley, G.M., Goman, M., Hover, V., Owen, R., Renaut, R., Muasya, A., 2002. Artesian blister wetlands, a perennial water resource in the semi-arid rift valley of East Africa. *Wetlands* 22, 686–695. [https://doi.org/10.1672/0277-5212\(2002\)022\[0686:ABWAPW\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2002)022[0686:ABWAPW]2.0.CO;2)
- Ashley, G.M., Mworio, J., Muasya, A., Owen, R., Driese, S., Hover, V., Renaut, R., Goman, M., Mathai, S., Blatt, S., 2004. Sedimentation and recent history of a freshwater wetland in a semi-arid environment: Lobo Swamp, Kenya, East Africa. *Sedimentology* 51, 1301–1321. <https://doi.org/10.1111/j.1365-3091.2004.00671.x>
- Ashley, G.M., Tactikos, J.C., Owen, R.B.,

2009. Hominin use of springs and wetlands: Paleoclimate and archaeological records from Olduvai Gorge (similar to 1.79-1.74 Ma). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 272, 1–16. <https://doi.org/10.1016/j.palaeo.2008.10.016>
- Bailey, G.N., Reynolds, S.C., King, G.C.P., 2011. Landscapes of human evolution: models and methods of tectonic geomorphology and the reconstruction of hominin landscapes. *J. Hum. Evol.* 60, 257–280. <https://doi.org/10.1016/j.jhevol.2010.01.004>
- Bamford, M.K., Albert, R.M., Cabanes, D., 2006. Plio-Pleistocene macroplant fossil remains and phytoliths from Lowermost Bed II in the eastern palaeolake margin of Olduvai Gorge, Tanzania. *Quat. Int.* 148, 95–112. <https://doi.org/10.1016/j.quaint.2005.11.027>
- Barboni, D., 2014. Vegetation of Northern Tanzania during the Plio-Pleistocene: A synthesis of the paleobotanical evidences from Laetoli, Olduvai, and Peninj hominin sites. *Quat. Int., The Evolution of Hominin Behavior during the Oldowan-Acheulian Transition: Recent Evidence from Olduvai Gorge and Peninj (Tanzania)* 322–323, 264–276. <https://doi.org/10.1016/j.quaint.2014.01.016>
- Barboni, D., Ashley, G.M., Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Baquedano, E., 2010. Phytoliths infer locally dense and heterogeneous paleovegetation at FLK North and surrounding localities during upper Bed I time, Olduvai Gorge, Tanzania. *Quat. Res.* 74, 344–354. <https://doi.org/10.1016/j.yqres.2010.09.005>
- Barboni, D., Bremond, L., 2009. Phytoliths of East African grasses: An assessment of their environmental and taxonomic significance based on floristic data. *Rev. Palaeobot. Palynol.* 158, 29–41. <https://doi.org/10.1016/j.revpalbo.2009.07.002>
- Barboni, D., Bremond, L., Bonnefille, R., 2007. Comparative study of modern phytolith assemblages from inter-tropical Africa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 246, 454–470. <https://doi.org/10.1016/j.palaeo.2006.10.012>
- Bender, R., Tobias, P.V., Bender, N., 2012. The savannah hypotheses: origin, reception and impact on paleoanthropology. *Hist. Philos. Life Sci.* 147–184.
- Benito-Calvo, A., Barfod, D., McHenry, L.J., De la Torre, I., 2014. The geology and chronology of the Acheulean deposits in the Mieso area (East-Central Ethiopia). *J. Hum. Evol.* 76, 26–38.
- Beverly, E.J., Driese, S.G., Peppe, D.J., Johnson, C.R., Michel, L.A., Faith, J.T., Tryon, C.A., Sharp, W.D., 2015. Recurrent spring-fed rivers in a Middle to Late Pleistocene semi-arid grassland: Implications for environments of early humans in the Lake Victoria Basin, Kenya. *Sedimentology* 62, 1611–1635.
- Bogan, M.T., Noriega-Felix, N., Vidal-Aguilar, S.L., Findley, L.T., Lytle, D.A., Gutiérrez-Ruacho, O.G., Alvarado-Castro, J.A., Varela-Romero, A., 2014. Biogeography and conservation of aquatic fauna in spring-fed tropical canyons of the southern Sonoran Desert, Mexico. *Biodivers. Conserv.* 23, 2705–2748.
- Bonnefille, R., 2010. Cenozoic vegetation, climate changes and hominid evolution in tropical Africa. *Glob. Planet. Change* 72, 390–411. <https://doi.org/10.1016/j.gloplacha.2010.01.015>
- Bonnefille, R., Anupama, K., Barboni, D., Pascal, J., Prasad, S., Sutra, J.P., 1999. Modern pollen spectra from tropical South India and Sri Lanka: altitudinal distribution. *J. Biogeogr.* 26, 1255–1280. <https://doi.org/10.1046/j.1365-2699.1999.00359.x>

- Bonnefille, R., Riollet, G., 1987. Palynological spectra from the Upper Laetoli Beds, in: Leakey, M.D., Harris, J.M. (Eds.), *The Pliocene Site of Laetoli, Northern Tanzania*. Oxford, pp. 52–61.
- Box, E.E., 1981. Macroclimate and plant forms: an introduction to predictive modeling in phytogeography, *Tasks for vegetation science*. Junk, The Hague.
- Bremond, L., Alexandre, A., Hely, C., Guiot, J., 2005. A phytolith index as a proxy of tree cover density in tropical areas: Calibration with Leaf Area Index along a forest-savanna transect in southeastern Cameroon. *Glob. Planet. CHANGE* 45, 277–293. <https://doi.org/10.1016/j.gloplacha.2004.09.002>
- Bretzler, A., Osenbrück, K., Gloaguen, R., Ruprecht, J.S., Kebede, S., Stadler, S., 2011. Groundwater origin and flow dynamics in active rift systems – A multi-isotope approach in the Main Ethiopian Rift. *J. Hydrol.* 402, 274–289. <https://doi.org/10.1016/j.jhydrol.2011.03.022>
- Brown, M.E., de Beurs, K., Vrieling, A., 2010. The response of African land surface phenology to large scale climate oscillations. *Remote Sens. Environ.* 114, 2286–2296. <https://doi.org/10.1016/j.rse.2010.05.005>
- Budd, D.A., Pack, S.M., Fogel, M.L., 2002. The destruction of paleoclimatic isotopic signals in Pleistocene carbonate soil nodules of Western Australia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 188, 249–273. [https://doi.org/10.1016/S0031-0182\(02\)00588-6](https://doi.org/10.1016/S0031-0182(02)00588-6)
- Butzer, K.W., 1973. Spring Sediments from the Acheulian Site of Amanzi (Uitenhage District, South Africa) 299–319.
- Cabanes, D., Shahack-Gross, R., 2015. Understanding fossil phytolith preservation: the role of partial dissolution in paleoecology and archaeology. *PloS One* 10, e0125532.
- Cantonati, M., Füreder, L., Gerecke, R., Jüttner, I., Cox, E.J., 2012. Crenic habitats, hotspots for freshwater biodiversity conservation: toward an understanding of their ecology. *Freshw. Sci.* 31, 463–480. <https://doi.org/10.1899/11-111.1>
- Cantonati, M., Segadelli, S., Ogata, K., Tran, H., Sanders, D., Gerecke, R., Rott, E., Filippini, M., Gargini, A., Celico, F., 2016. A global review on ambient Limestone-Precipitating Springs (LPS): Hydrogeological setting, ecology, and conservation. *Sci. Total Environ.* 568, 624–637.
- Carr, C.J., 1998. Patterns of vegetation along the Omo River in southwest Ethiopia. *Plant Ecol.* 135, 135–163.
- Caylor, K.K., Shugart, H.H., 2006. Pattern and process in savanna ecosystems, in: D’Odorico, P., Porporato, A. (Eds.), *Dryland Ecohydrology*. Springer, The Netherlands, pp. 259–281.
- Cerling, T.E., Brown, F.H., Wynn, J.G., 2014. On the environment of Aramis: A comment on White in Domínguez-Rodrigo. *Curr. Anthropol.* 55, 469–470. <https://doi.org/10.1086/677210>
- Cerling, T.E., Levin, N.E., Quade, J., Wynn, J.G., Fox, D.L., Kingston, J.D., Klein, R.G., Brown, F.H., 2010. Comment on the paleoenvironment of *Ardipithecus ramidus*. *SCIENCE* 328. <https://doi.org/10.1126/science.1185274>
- Cerling, T.E., Wynn, J.G., Andanje, S.A., Bird, M.I., Korir, D.K., Levin, N.E., Mace, W., Macharia, A.N., Quade, J., Remien, C.H., 2011. Woody cover and hominin environments in the past 6 million years. *Nature* 476, 51–56. <https://doi.org/10.1038/nature10306>
- Chorowicz, J., 2005. The East African rift system. *J. Afr. Earth Sci.* 43, 379–410. <https://doi.org/10.1016/j.jafrearsci.2005.07.019>
- Churcher, C.S., Kleindienst, M.R., Schwarcz, H.P., 1999. Faunal remains from a Middle Pleistocene lacustrine marl in Dakhleh Oasis, Egypt:

- palaeoenvironmental reconstructions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 154, 301–312. [https://doi.org/10.1016/S0031-0182\(99\)00104-2](https://doi.org/10.1016/S0031-0182(99)00104-2)
- Collier, K.J., Smith, B.J., 2006. Distinctive invertebrate assemblages in rockface seepages enhance lotic biodiversity in northern New Zealand, in: *Marine, Freshwater, and Wetlands Biodiversity Conservation*. Springer, pp. 223–248.
- Collura, L.V., Neumann, K., 2017. Wood and bark phytoliths of West African woody plants. *Quat. Int.*, 9th International Meeting of Phytolith Research (IMPR) 434, 142–159. <https://doi.org/10.1016/j.quaint.2015.12.070>
- Contoux, C., Jost, A., Ramstein, G., Sepulchre, P., Krinner, G., Schuster, M., 2013. Megalake Chad impact on climate and vegetation during the late Pliocene and the mid-Holocene. *Clim. Past* 9, 1417–1430.
- Cuthbert, M.O., Ashley, G.M., 2014. A spring forward for hominin evolution in East Africa. *PLOS ONE* 9, e107358. <https://doi.org/10.1371/journal.pone.0107358>
- Cuthbert, M.O., Gleeson, T., Reynolds, S.C., Bennett, M.R., Newton, A.C., McCormack, C.J., Ashley, G.M., 2017. Modelling the role of groundwater hydro-refugia in East African hominin evolution and dispersal. *Nat. Commun.* 8, 15696. <https://doi.org/10.1038/ncomms15696>
- Dachy, T., Briois, F., Marchand, S., Minotti, M., Lesur, J., Wuttmann, M., 2018. Living in an Egyptian Oasis: Reconstruction of the Holocene archaeological sequence in Kharga. *Afr. Archaeol. Rev.* 1–36.
- Dart, R.A., 1925. *Australopithecus africanus*: the man-ape of South Africa. *Nature* 115, 195–199.
- Davis, J., Pavlova, A., Thompson, R., Sunnucks, P., 2013. Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. *Glob. Change Biol.* 19, 1970–1984. <https://doi.org/10.1111/gcb.12203>
- Davis, J.A., Kerecsy, A., Nicol, S., 2017. Springs: Conserving perennial water is critical in arid landscapes. *Biol. Conserv.*, Small Natural Features 211, 30–35. <https://doi.org/10.1016/j.biocon.2016.12.036>
- de Heinzelin, J. (Ed.), 1983. The Omo Group, Musée Royal de l’Afrique Centrale, Annales, Série in 8: Sciences Géologiques.
- DeMenocal, P.B., 1995. Plio-Pleistocene African climate. *Science* 270, 53–59.
- Deocampo, D., Blumenshine, R., Ashley, G.M., 2002. Wetland diagenesis and traces of early hominids, Olduvai Gorge, Tanzania. *Quat. Res.* 57, 271–281. <https://doi.org/10.1006/qres.2001.2317>
- Deocampo, D.M., Tactikos, J.C., 2010. Geochemical gradients and artifact mass densities on the lowermost Bed II eastern lake margin (similar to 1.8 Ma), Olduvai Gorge, Tanzania. *Quat. Res.* 74, 411–423. <https://doi.org/10.1016/j.yqres.2010.09.004>
- Ditchfield, P., Harrison, T., 2011. Sedimentology, lithostratigraphy and depositional history of the Laetoli area, in: *Paleontology and Geology of Laetoli: Human Evolution in Context*. Springer, pp. 47–76.
- Djamali, M., Gondet, S., Ashjari, J., Aubert, C., Brisset, E., Longerey, J., Marriner, N., Mashkour, M., Miller, N.F., Naderi-Beni, A., Pourkerman, M., Rashidian, E., Rigot, J.-B., Shidrang, S., Thiéry, A., Gandouin, E., 2018. Karstic spring wetlands of the Persepolis Basin, southwest Iran: unique sediment archives of Holocene environmental change and human impacts. *Can. J. Earth Sci.* 55, 1158–1172. <https://doi.org/10.1139/cjes-2018-0065>
- Domínguez-Rodrigo, M., 2014. Is the “Savanna Hypothesis” a Dead Concept for Explaining the Emergence of the Earliest Hominins? *Curr. Anthropol.* 55,

- 59–81. <https://doi.org/10.1086/674530>
- Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Ashley, G.M., Diez-Martin, F., Barboni, D., Prendergast, M.E., Yravedra, J., Barba, R., Sanchez, A., Baquedano, E., Pickering, T.R., 2010. New excavations at the FLK Zinjanthropus site and its surrounding landscape and their behavioral implications. *Quat. Res.* 74, 315–332. <https://doi.org/10.1016/j.yqres.2010.07.003>
- Domínguez-Rodrigo, M., Cobo-Sánchez, L., 2017. A spatial analysis of stone tools and fossil bones at FLK Zinj 22 and PTK I (Bed I, Olduvai Gorge, Tanzania) and its bearing on the social organization of early humans. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* <https://doi.org/10.1016/j.palaeo.2017.04.010>
- Dominguez-Rodrigo, M., Lopez-Saez, J.A., Vincens, A., Alcalá, L., Luque, L., Serrallonga, J., 2001. Fossil pollen from the Upper Humbu Formation of Peninj (Tanzania): hominid adaptation to a dry open Plio-Pleistocene savanna environment. *J. Hum. Evol.* 40, 151–157. <https://doi.org/10.1006/jhev.2000.0440>
- Domínguez-Rodrigo, M., Musiba, C.M., 2010. How Accurate are Paleoecological Reconstructions of Early Paleontological and Archaeological Sites? *Evol. Biol.* 37, 128–140. <https://doi.org/10.1007/s11692-010-9087-2>
- Domínguez-Rodrigo, M., Pickering, T.R., Almécija, S., Heaton, J.L., Baquedano, E., Mabulla, A., Uribelarrea, D., 2015. Earliest modern human-like hand bone from a new >1.84-million-year-old site at Olduvai in Tanzania. *Nat. Commun.* 6, 7987. <https://doi.org/10.1038/ncomms8987>
- Doran, T.L., Herries, A.I., Hopley, P.J., Sombroek, H., Hellstrom, J., Hodge, E., Kuhn, B.F., 2015. Assessing the paleoenvironmental potential of Pliocene to Holocene tufa deposits along the Ghaap Plateau escarpment (South Africa) using stable isotopes. *Quat. Res.* 84, 133–143.
- Du, A., Robinson, J.R., Rowan, J., Lazagabaster, I.A., Behrensmeyer, A.K., 2019. Stable carbon isotopes from paleosol carbonate and herbivore enamel document differing paleovegetation signals in the eastern African Plio-Pleistocene. *Rev. Palaeobot. Palynol.* 261, 41–52. <https://doi.org/10.1016/j.revpalbo.2018.11.003>
- Dunbar, R. and P., 1975. Guereza monkeys will they become extinct in Ethiopia? *Walia* 1975, 14–15.
- Dunbar, R.I.M., 1987. Habitat quality, population dynamics, and group composition in *Colobus* Monkeys (*Colobus guereza*). *Int. J. Primatol.* 8, 299–329. <https://doi.org/10.1007/BF02737386>
- Dunbar, R.I.M., Dunbar, E.P., 1974. Ecology and Population Dynamics of *Colobus guereza* in Ethiopia. *Folia Primatol. (Basel)* 21, 188–208. <https://doi.org/10.1159/000155600>
- Edwards, S., Demissew, S., Hedberg, I., 1997. Flora of Ethiopia and Eritrea: volume 6. Hydrocharitaceae to Arecaceae. Addis Ababa Natl. Herb. Biol. Dep. Addis Ababa Univ.
- Egeland, C.P., 2014. Taphonomic estimates of competition and the role of carnivore avoidance in hominin site use within the Early Pleistocene Olduvai Basin. *Quat. Int., The Evolution of Hominin Behavior during the Oldowan-Acheulian Transition: Recent Evidence from Olduvai Gorge and Peninj (Tanzania)* 322–323, 95–106. <https://doi.org/10.1016/j.quaint.2013.11.021>
- Feakins, S.J., deMenocal, P.B., 2010. Global and African regional climate during the Cenozoic, in: Werdelin, L. (Ed.), *Cenozoic Mammals of Africa*. University of California Press, pp. 45–56.
- Feakins, S.J., Levin, N.E., Liddy, H.M., Sieracki, A., Eglinton, T.I., Bonnefille, R., 2013. Northeast African vegetation

- change over 12 m.y. *Geology* G33845.1. <https://doi.org/10.1130/G33845.1>
- Fensham, R.J., Silcock, J.L., Kerezszy, A., Ponder, W., 2011. Four desert waters: Setting arid zone wetland conservation priorities through understanding patterns of endemism. *Biol. Conserv.* 144, 2459–2467. <https://doi.org/10.1016/j.biocon.2011.06.024>
- Foulds, F.W.F., Shuttleworth, A., Sinclair, A., Alsharekh, A.M., Ghamdi, S.A., Inglis, R.H., Bailey, G.N., 2017. A large handaxe from Wadi Dabsa and early hominin adaptations within the Arabian Peninsula. *Antiquity* 91, 1421–1434. <https://doi.org/10.15184/aqy.2017.153>
- Fraysse, F., Cantais, F., Pokrovsky, O.S., Schott, J., Meunier, J.-D., 2006. Aqueous reactivity of phytoliths and plant litter: physico-chemical constraints on terrestrial biogeochemical cycle of silicon. *J. Geochem. Explor.* 88, 202–205.
- Fraysse, F., Pokrovsky, O.S., Schott, J., Meunier, J.-D., 2009. Surface chemistry and reactivity of plant phytoliths in aqueous solutions. *Chem. Geol.* 258, 197–206.
- Gallagher, T.M., Sheldon, N.D., 2016. Combining soil water balance and clumped isotopes to understand the nature and timing of pedogenic carbonate formation. *Chem. Geol.* 435, 79–91. <https://doi.org/10.1016/j.chemgeo.2016.04.023>
- Garrett, K.R., 2017. Multi-proxy reconstruction of a ~ 1.3 Ma freshwater wetland, Olduvai Gorge, Tanzania (MS Thesis). Rutgers University-Graduate School-New Brunswick.
- Good, S.P., Caylor, K.K., 2011. Climatological determinants of woody cover in Africa. *Proc. Natl. Acad. Sci.* 108, 4902–4907. <https://doi.org/10.1073/pnas.1013100108>
- Gossa, T., Sahle, Y., Negash, A., 2012. A reassessment of the Middle and Later Stone Age lithic assemblages from Aladi Springs, Southern Afar Rift, Ethiopia. *Azania Archaeol. Res. Afr.* 47, 210–222.
- Greenway, P.J., Vesey-Fitzgerald, D.F., 1969. Vegetation of Lake Manyara National Park. *J. Ecol.* 57, 127–149. <https://doi.org/10.2307/2258212>
- Haile-Selassie, Y., Deino, A., Saylor, B., Umer, M., Latimer, B., 2007. Preliminary geology and paleontology of new hominid-bearing Pliocene localities in the central Afar region of Ethiopia. *Anthropol. Sci.* 115, 215–222.
- Harvey, M.S., 2002. Short-range endemism amongst the Australian fauna: some examples from non-marine environments. *Invertebr. Syst.* 16, 555–570. <https://doi.org/10.1071/is02009>
- Hill, C.L., 2001. Geologic Contexts of the Acheulian (Middle Pleistocene) in the Eastern Sahara. *Geoarchaeology Int. J.* 16, 65–94.
- Hodson, M., White, P., Mead, A., Broadley, M., 2005. Phylogenetic variation in the silicon composition of plants. *Ann. Bot.* 96, 1027–1046. <https://doi.org/10.1093/aob/mci255>
- Hopley, P.J., Herries, A.I.R., Baker, S.E., Kuhn, B.F., Menter, C.G., 2013. Brief communication: beyond the South African cave paradigm--Australopithecus africanus from Plio-Pleistocene paleosol deposits at Taung. *Am. J. Phys. Anthropol.* 151, 316–324. <https://doi.org/10.1002/ajpa.22272>
- Hunter Jr, M.L., Acuña, V., Bauer, D.M., Bell, K.P., Calhoun, A.J., Felipe-Lucia, M.R., Fitzsimons, J.A., González, E., Kinnison, M., Lindenmayer, D., 2017. Conserving small natural features with large ecological roles: a synthetic overview. *Biol. Conserv.* 211, 88–95.
- Hussein, I., Afework, B., Dereje, Y., 2017. Population structure and feeding ecology of Guereza (*Colobus guereza*) in Borena-Sayint National Park, northern Ethiopia. *Int. J. Biodivers. Conserv.* 9, 323–333. <https://doi.org/10.5897/IJBC2017.1114>
- Inglis, R.H., Sinclair, A.G., Alsharekh, A.M., Barfod, D., Chang, H.C., Fanning, P.C., Al Othaibi, D.T., Robson, H.K.,

- Shuttleworth, A., Stone, A., Bailey, G.N., 2017. Preliminary Report on UK-Saudi 2017 Fieldwork At Wadi Dabsa, Asir Province, Saudi Arabia (Fieldwork report). University of York.
- Jagher, R., Elsuede, H., Le Tensorer, J.-M., 2015. El Kowm Oasis, human settlement in the Syrian Desert during the Pleistocene. *L'anthropologie* 119, 542–580.
- Johnson, C.R., Ashley, G.M., De Wet, C.B., Dvoretzky, R., Park, L., Hover, V.C., Owen, R.B., McBrearty, S., 2009. Tufa as a record of perennial fresh water in a semi-arid rift basin, Kapthurin Formation, Kenya. *Sedimentology* 56, 1115–1137.
<https://doi.org/10.1111/j.1365-3091.2008.01022.x>
- Johnson, C.R., McBrearty, S., 2012. Archaeology of middle Pleistocene lacustrine and spring paleoenvironments in the Kapthurin Formation, Kenya. *J. Anthropol. Archaeol.* 31, 485–499.
- Jolly-Saad, M.-C., Bonnefille, R., 2012. Lower Pliocene Fossil Wood from the Middle Awash Valley, Ethiopia. *Palaeontogr. Abt. B* 43–73.
- Kappelman, J., Alçiçek, M.C., Kazancı, N., Schultz, M., Özkul, M., Şen, Ş., 2008. First *Homo erectus* from Turkey and implications for migrations into temperate Eurasia. *Am. J. Phys. Anthropol.* 135, 110–116.
- Kassambara, A., Mundt, F., 2017. Factoextra: extract and visualize the results of multivariate data analyses.
- Kaya, F., Bibi, F., Žliobaitė, I., Eronen, J.T., Hui, T., Fortelius, M., 2018. The rise and fall of the Old World savannah fauna and the origins of the African savannah biome. *Nat. Ecol. Evol.* 2, 241.
- Kempf, E., 2009. Patterns of Water Use in Primates. *Folia Primatol.* 80, 275–294.
- Kleindienst, M.R., Schwarcz, H.P., Nicoll, K., Churcher, C.S., Frizano, J., Giegengack, R., Wiseman, M.F., 2008. Water in the desert: first report on Uranium-series dating of Caton-Thompson's and Gardner's 'classic' Pleistocene sequence at Refuf Pass, Kharga Oasis, in: *The Oasis Papers 2. Proceedings of the Second International Conference of the Dakhleh Oasis Project*. Oxbow Books Oxford, pp. 25–54.
- Lamarck, J.-B. de, 1809. *Philosophie zoologique, ou exposition des considérations relatives à l'histoire naturelle des animaux*. Dentu.
- Lê, S., Josse, J., Husson, F., 2008. FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.* 25, 1–18.
- Leakey, M.D., 1971. *Olduvai Gorge: Excavations in Bed I and II, 1960-63*. Cambridge University Press.
- Lebatard, A.-E., Alçiçek, M.C., Rochette, P., Khatib, S., Vialet, A., Boulbes, N., Bours, D.L., Demory, F., Guipert, G., Mayda, S., 2014. Dating the *Homo erectus* bearing travertine from Kocabaş (Denizli, Turkey) at at least 1.1 Ma. *Earth Planet. Sci. Lett.* 390, 8–18.
- Levin, N.E., 2015. Environment and climate of early human evolution. *Annu. Rev. Earth Planet. Sci.* 43, 405–429.
<https://doi.org/10.1146/annurev-earth-060614-105310>
- Liddy, H.M., Feakins, S.J., Tierney, J.E., 2016. Cooling and drying in northeast Africa across the Pliocene. *Earth Planet. Sci. Lett.* 449, 430–438.
<https://doi.org/10.1016/j.epsl.2016.05.005>
- Loth, P.E., Prins, H.H.T., 1986. Spatial patterns of the landscape and vegetation of Lake Manyara National Park. *ITC J.* 2, 115–130.
- Louchart, A., Wesselman, H., Blumenshine, R.J., Hlusko, L.J., Njau, J.K., Black, M.T., Asnake, M., White, T.D., 2009. Taphonomic, avian, and small-vertebrate indicators of *Ardipithecus ramidus* habitat. *SCIENCE* 326.
<https://doi.org/10.1126/science.1175823>
- Magill, C.R., Ashley, G.M., Domínguez-Rodrigo, M., Freeman, K.H., 2016.

- Dietary options and behavior suggested by plant biomarker evidence in an early human habitat. *Proc. Natl. Acad. Sci.* 113, 2874–2879.
- McCool, J.-P., 2018. Carbonates as evidence for groundwater discharge to the Nile River during the Late Pleistocene and Holocene. *Geomorphology*. <https://doi.org/10.1016/j.geomorph.2018.09.026>
- McDougall, I., Brown, F.H., Vasconcelos, P.M., Cohen, B.E., Thiede, D.S., Buchanan, M.J., 2012. New single crystal $^{40}\text{Ar}/^{39}\text{Ar}$ ages improve time scale for deposition of the Omo Group, Omo–Turkana Basin, East Africa. *J. Geol. Soc.* 169, 213–226.
- McHenry, H.M., Brown, C.C., McHenry, L.J., 2007. Fossil hominin ulnae and the forelimb of *Paranthropus*. *Am. J. Phys. Anthropol. Off. Publ. Am. Assoc. Phys. Anthropol.* 134, 209–218.
- McKee, J.K., 1994. Catalogue of fossil sites at the Buxton Limeworks, Taung. *Palaeontol. Afr.* 31, 73–81.
- McKee, J.K., Kuykendall, K.L., 2016. The Dart Deposits of the Buxton Limeworks, Taung, South Africa, and the context of the Taung *Australopithecus* fossil. *J. Vertebr. Paleontol.* 36, e1054937.
- Moussa, A., Novello, A., Lebatard, A.-E., Decarreau, A., Fontaine, C., Barboni, D., Sylvestre, F., Bourlès, D.L., Paillès, C., Buchet, G., others, 2016. Lake Chad sedimentation and environments during the late Miocene and Pliocene: New evidence from mineralogy and chemistry of the Bol core sediments. *J. Afr. Earth Sci.* 118, 192–204. <https://doi.org/10.1016/j.jafrearsci.2016.02.023>
- Murphy, N.P., Guzik, M.T., Cooper, S.J.B., Austin, A.D., 2015. Desert spring refugia: museums of diversity or evolutionary cradles? *Zool. Scr.* 44, 693–701. <https://doi.org/10.1111/zsc.12129>
- Neumann, K., Fahmy, A.G., Müller-Scheeßel, N., Schmidt, M., 2017. Taxonomic, ecological and palaeoecological significance of leaf phytoliths in West African grasses. *Quat. Int.* 434, 15–32. <https://doi.org/10.1016/j.quaint.2015.11.039>
- Nicoll, K., Giegengack, R., Kleindienst, M.R., 1999. Petrogenesis of artifact-bearing fossil-spring tufa deposits from Kharga Oasis, Egypt. *Geoarchaeology-Int. J.* 14, 849–863.
- Novello, A., 2012. Les phytolithes, marqueurs des environnements mio-pliocènes du Tchad. reconstitution à partir du signal environnemental des phytolithes dans l’Afrique subsaharienne actuelle (Doctorat). Université de poitiers, Poitiers, France.
- Novello, A., Barboni, D., Berti-Equille, L., Mazur, J.-C., Poilecot, P., Vignaud, P., 2012. Phytolith signal of aquatic plants and soils in Chad, Central Africa. *Rev. Palaeobot. Palynol.* 178, 43–58. <https://doi.org/10.1016/j.revpalbo.2012.03.010>
- Novello, A., Barboni, D., Sylvestre, F., Lebatard, A.-E., Paillès, C., Bourlès, D.L., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2017. Phytoliths indicate significant arboreal cover at *Sahelanthropus* type locality TM266 in northern Chad and a decrease in later sites. *J. Hum. Evol.* 106, 66–83. <https://doi.org/10.1016/j.jhevol.2017.01.009>
- Novello, A., Lebatard, A.-E., Moussa, A., Barboni, D., Sylvestre, F., Bourlès, D.L., Paillès, C., Buchet, G., Decarreau, A., Düringer, P., Ghienne, J.-F., Maley, J., Mazur, J.-C., Roquin, C., Schuster, M., Vignaud, P., 2015. Diatom, phytolith, and pollen records from a $^{10}\text{Be}/^{9}\text{Be}$ dated lacustrine succession in the Chad basin: Insight on the Miocene–Pliocene paleoenvironmental changes in Central Africa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 430, 85–103.
- Olago, D., Opere, A., Barongo, J., 2009. Holocene palaeohydrology, groundwater and climate change in the lake basins of

- the Central Kenya Rift. *Hydrol. Sci. J.* 54, 765–780.
<https://doi.org/10.1623/hysj.54.4.765>
- O'Regan, H.J., Wilkinson, D.M., Marston, C.G., 2016. Hominin home ranges and habitat variability: Exploring modern African analogues using remote sensing. *J. Archaeol. Sci. Rep.* 9, 238–248.
<https://doi.org/10.1016/j.jasrep.2016.06.043>
- Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., Simons, A., 2009. Agroforestree database: a tree species reference and selection guide version 4.0. World Agrofor. Cent. ICRAF Nairobi KE.
- Owen, R.B., Renaut, R.W., Hover, V.C., Ashley, G., Muasya, A.M., 2004. Swamps, springs and diatoms: wetlands of the semi-arid Bogoria-Baringo Rift, Kenya. *Hydrobiologia* 518, 59–78.
<https://doi.org/10.1023/B:HYDR.0000025057.62967.2c>
- Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* 12, 361–371.
- Pickford, M., 1995. Fossil land snails of East Africa and their palaeoecological significance. *J. Afr. Earth Sci.* 20, 167–226.
- Pickford, M., Senut, B., 2001. The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya. *Comptes Rendus Académie Sci.-Ser. IIA-Earth Planet. Sci.* 332, 145–152.
- Pigati, J.S., Rech, J.A., Quade, J., Bright, J., 2014. Desert wetlands in the geologic record. *Earth-Sci. Rev.* 132, 67–81.
<https://doi.org/10.1016/j.earscirev.2014.02.001>
- Porat, N., Chazan, M., Grün, R., Aubert, M., Eisenmann, V., Kolska Horwitz, L., 2010. New radiometric ages for the Fauresmith industry from Kathu Pan, southern Africa: Implications for the Earlier to Middle Stone Age transition. *J. Archaeol. Sci.* 37, 269–283.
- Potts, R., 2013. Hominin evolution in settings of strong environmental variability. *Quat. Sci. Rev.* 73, 1–13.
<https://doi.org/10.1016/j.quascirev.2013.04.003>
- Pruetz, J.D., Bertolani, P., 2009. Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savanna-mosaic environment: Implications for hominin adaptations to open habitats. *PaleoAnthropology* 252–262.
<https://doi.org/10.4207/PA.2009.ART33>
- Quade, J., Cerling, T.E., Bowman, J.R., 1989. Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. *Nature* 342, 163–166.
<https://doi.org/10.1038/342163a0>
- R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reynolds, S.C., Bailey, G.N., King, G.C.P., 2011. Landscapes and their relation to hominin habitats: Case studies from *Australopithecus* sites in eastern and southern Africa. *J. Hum. Evol.* 60, 281–298.
<https://doi.org/10.1016/j.jhevol.2010.10.001>
- Reynolds, S.C., Marston, C.G., Hassani, H., King, G.C., Bennett, M.R., 2016. Environmental hydro-refugia demonstrated by vegetation vigour in the Okavango Delta, Botswana. *Sci. Rep.* 6, 35951.
- Reynolds, S.C., Wilkinson, D.M., Marston, C.G., O'Regan, H.J., 2015. The ‘mosaic habitat’ concept in human evolution: past and present. *Trans. R. Soc. South Afr.* 70, 57–69.
- Richerson, P.J., Bettinger, R.L., Boyd, R., 2008. Evolution on a Restless Planet: Were Environmental Variability and Environmental Change Major Drivers of Human Evolution?, in: *Handbook of Evolution*. Wiley-VCH Verlag GmbH, pp. 223–242.
- Roche, D., Ségalen, L., Senut, B., Pickford,

- M., 2013. Stable isotope analyses of tooth enamel carbonate of large herbivores from the Tugen Hills deposits: Palaeoenvironmental context of the earliest Kenyan hominids. *Earth Planet. Sci. Lett.* 381, 39–51.
- Rooney, T.O., 2017. The Cenozoic magmatism of East-Africa: Part I — Flood basalts and pulsed magmatism. *Lithos* 286–287, 264–301. <https://doi.org/10.1016/j.lithos.2017.05.014>
- Salzmann, U., Haywood, A.M., Lunt, D.J., Valdes, P.J., Hill, D.J., 2008. A new global biome reconstruction and data-model comparison for the Middle Pliocene. *Glob. Ecol. Biogeogr.* 17, 432–447. <https://doi.org/10.1111/j.1466-8238.2008.00381.x>
- Schuster, M., 2006. The Age of the Sahara Desert. *Science* 311, 821–821. <https://doi.org/10.1126/science.1120161>
- Semaw, S., Simpson, S.W., Quade, J., Renne, P.R., Butler, R.F., McIntosh, W.C., Levin, N.E., Dominguez-Rodrigo, M., Rogers, M.J., 2005. Early Pliocene hominids from Gona, Ethiopia. *Nature* 301–305.
- Senut, B., 2006. Bipédie et climat. *Comptes Rendus Palevol* 5, 89–98.
- Shipman, P., Harris, J.M., 1988. Habitat preference and paleoecology of *Australopithecus boisei* in Eastern Africa. *Evol. Hist.* “robust” *Australopithecines* 343–381.
- Smith, J.R., Giegengack, R., Schwarcz, H.P., McDonald, M.M.A., Kleindienst, M.R., Hawkins, A.L., Churcher, C.S., 2004. A reconstruction of Quaternary pluvial environments and human occupations using stratigraphy and geochronology of fossil-spring tufas, Kharga Oasis, Egypt. *Geoarchaeology* 19, 407–439. <https://doi.org/10.1002/gea.20004>
- Smith, J.R., Hawkins, A.L., Asmerom, Y., Polyak, V., Giegengack, R., 2007. New age constraints on the Middle Stone Age occupations of Kharga Oasis, Western Desert, Egypt. *J. Hum. Evol.* 52, 690–701.
- Sockol, M.D., Raichlen, D.A., Pontzer, H., 2007. Chimpanzee locomotor energetics and the origin of human bipedalism. *Proc. Natl. Acad. Sci.* 104, 12265–12269.
- Stauffer, F.W., Ouattara, D., Stork, A.L., 2014. *Palmae*, in: Lebrun, J.-P., Stork, A.L. (Eds.), *Tropical African Flowering Plants: Monocotyledons 2. Conservatoire et Jardin botaniques de la Ville de Genève, Switzerland*, pp. 326–354.
- Staver, A.C., Archibald, S., Levin, S.A., 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334, 230–232. <https://doi.org/10.1126/science.1210465>
- Steudel-Numbers, K.L., Tilkens, M.J., 2004. The effect of lower limb length on the energetic cost of locomotion: implications for fossil hominins. *J. Hum. Evol.* 47, 95–109.
- Stevens, L.E., Meretsky, V.J., 2008. *Aridland springs in North America: ecology and conservation*. University of Arizona Press.
- Suhling, F., Sahlén, G., Martens, A., Marais, E., Schütte, C., 2006. *Dragonfly Assemblages in Arid Tropical Environments: A Case Study from Western Namibia*. *Biodivers. Conserv.* 15, 311–332. <https://doi.org/10.1007/s10531-005-2007-6>
- Suwa, G., Ambrose, S.H., 2014. Reply to Cerling et al. *Curr. Anthropol.* 55, 473–474.
- Suwa, G., Kono, R.T., Simpson, S.W., Asfaw, B., Lovejoy, C.O., White, T.D., 2009. Paleobiological Implications of the *Ardipithecus ramidus* Dentition. *Science* 326, 94–99. <https://doi.org/10.1126/science.1175824>
- Swedell, L., 2002. Ranging behavior, group size and behavioral flexibility in Ethiopian hamadryas baboons (*Papio hamadryas hamadryas*). *Folia Primatol. (Basel)* 73, 95–103.
- Szaro, R.C., Jakle, M.D., 1985. Avian use of a desert riparian island and its adjacent

- scrub habitat. *The Condor* 87, 511–519.
<https://doi.org/10.2307/1367948>
- Tryon, C.A., Faith, J.T., Peppe, D.J., Keegan, W.F., Keegan, K.N., Jenkins, K.H., Nightingale, S., Patterson, D., van Plantinga, A., Driese, S., Johnson, C.R., Beverly, E.J., 2014. Sites on the landscape: Paleoenvironmental context of late Pleistocene archaeological sites from the Lake Victoria basin, equatorial East Africa. *Quat. Int.* 331, 20–30.
- Tryon, C.A., Peppe, D.J., Faith, J.T., Van Plantinga, A., Nightingale, S., Ogondo, J., Fox, D.L., 2012. Late Pleistocene artefacts and fauna from Rusinga and Mfangano islands, Lake Victoria, Kenya. *Azania Archaeol. Res. Afr.* 47, 14–38.
<https://doi.org/10.1080/0067270X.2011.647946>
- Uno, K.T., Polissar, P.J., Jackson, K.E., deMenocal, P.B., 2016. Neogene biomarker record of vegetation change in eastern Africa. *Proc. Natl. Acad. Sci.* 113, 6355–6363.
<https://doi.org/10.1073/pnas.1521267113>
- Van Plantinga, A., 2011. Geology of the Late Pleistocene artifact-bearing Wasiriya beds at the Nyamita Locality, Rusinga Island, Kenya (Master’s Thesis). Baylor University, Waco, TX.
- Vialet, A., Guipert, G., Alcicek, M.C., 2012. Homo erectus found still further west: reconstruction of the Kocabaş cranium (Denizli, Turkey). *Comptes Rendus Palevol* 11, 89–95.
- Vignaud, P., Düringer, P., Mackaye, H.T., Likius, A., Blondel, C., Boissérie, J.-R., de Bonis, L., Eisenmann, V., Etienne, M.-E., Geraads, D., Guy, F., Lehmann, T., Lihoreau, F., Lopez-Martinez, N., Mourer-Chauviré, C., Otero, O., Rage, J.-C., Schuster, M., Viriot, L., Zazzo, A., Brunet, M., 2002. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. *Nature* 418, 152–155.
<https://doi.org/10.1038/nature00880>
- Viljoen, P.J., Bothma, J., Du, P., 1990. Daily movements of desert-dwelling elephants in the northern Namib Desert. *South Afr. J. Wildl. Res.* 20, 69–72.
- Vrba, E.S., 1980. The significance of bovid remains as indicators of environment and predation patterns, in: Behrensmeyer, A.K., Hill, A.P. (Eds.), *Fossils in the Making*. University of Chicago Press, Chicago, pp. 247–272.
- Wendorf, F., Schild, R., Close, A., Associates (Eds.), 1993. *Egypt during the last interglacial: The Middle Paleolithic of Bir Tarfawi and Bir Sahara East*. New York: Plenum. Plenum Press, New York.
- White, T.D., Ambrose, S.H., Suwa, G., Su, D.F., DeGusta, D., Bernor, R.L., Boissérie, J.-R., Brunet, M., Delson, E., Frost, S., Garcia, N., Giauartsakis, I.X., Haile-Selassie, Y., Howell, F.C., Lehmann, T., Likius, A., Pehlevan, C., Saegusa, H., Semprebon, G., Teaford, M., Vrba, E., 2009a. Macrovertebrate Paleontology and the Pliocene Habitat of *Ardipithecus ramidus*. *SCIENCE* 326, 87–93.
<https://doi.org/10.1126/science.1175822>
- White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C.O., Suwa, G., WoldeGabriel, G., 2009b. *Ardipithecus ramidus* and the paleobiology of early hominids. *Science* 326, 75–86.
<https://doi.org/10.1126/science.1175802>
- White, T.D., Lovejoy, C.O., Asfaw, B., Carlson, J.P., Suwa, G., 2015a. Neither chimpanzee nor human, *Ardipithecus* reveals the surprising ancestry of both. *Proc. Natl. Acad. Sci.* 201403659.
- White, T.D., Suwa, G., Ambrose, S.H., 2015b. Reply to Cerling et al. *Curr. Anthropol.* 56, 447–448.
- Williams, M.A.J., Bishop, P.M., Dakin, F.M., Gillepsie, R., 1977. Late Quaternary lake levels in southern Afar and the adjacent Ethiopian Rift. *Nature* 267, 690–693.
- WoldeGabriel, G., Ambrose, S.H., Barboni, D., Bonnefille, R., Bremond, L., Currie, B., DeGusta, D., Hart, W.K., Murray, A.M., Renne, P.R., Jolly-Saad, M.C., Stewart, K.M., White, T.D., 2009.

The geological, isotopic, botanical, invertebrate, and lower vertebrate surroundings of *Ardipithecus ramidus*. Science 326.

<https://doi.org/10.1126/science.1175817>
Zhang, Z., Ramstein, G., Schuster, M., Li,

C., Contoux, C., Yan, Q., 2014. Aridification of the Sahara desert caused by Tethys Sea shrinkage during the Late Miocene. Nature 513, 401.

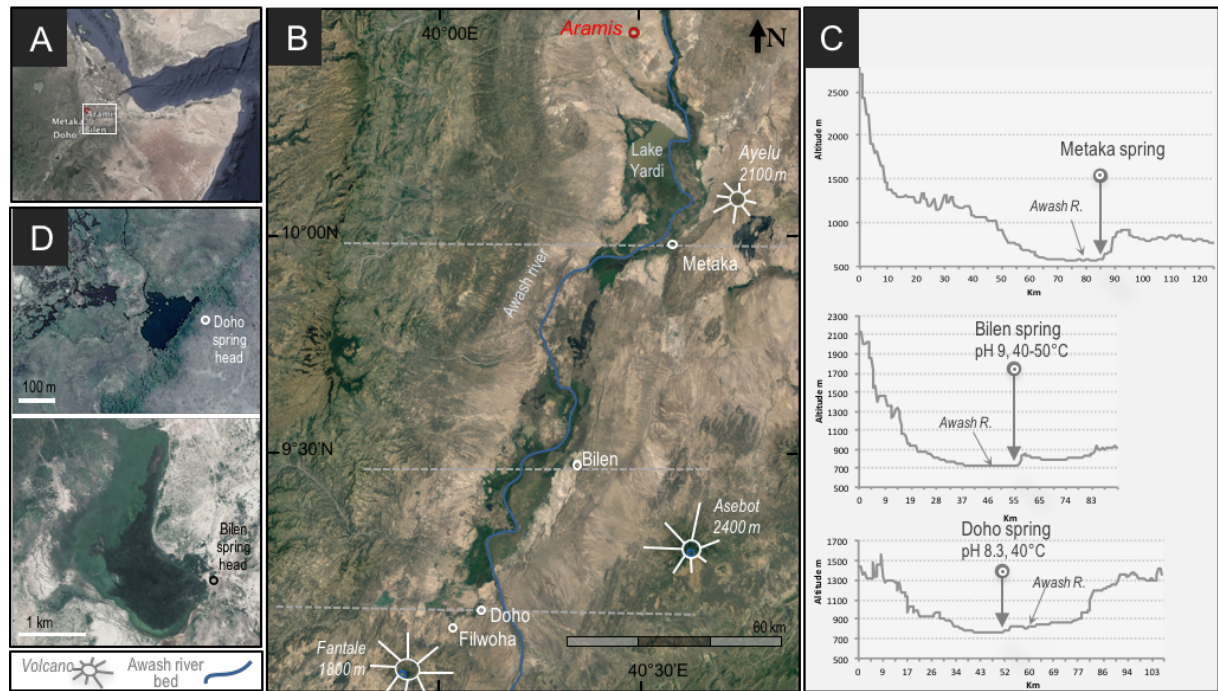


Figure 1. Springs in the Awash Valley, Afar region, Ethiopia. (A) Position of the Awash Valley. (B) Satellite view (Landsat / Copernicus image from GoogleEarth, 2018) with position of volcanoes, Awash River, and the four spring sites visited in 2018: Filwoha, Doho, Bilen and Metaka. (C) Elevation profiles from west to east cutting through the rift valley at the latitude of Metaka, Bilen and Doho. Elevation profiles were obtained using Zonums free software. (D) Close-ups show sharp vegetation changes at the spring sites.

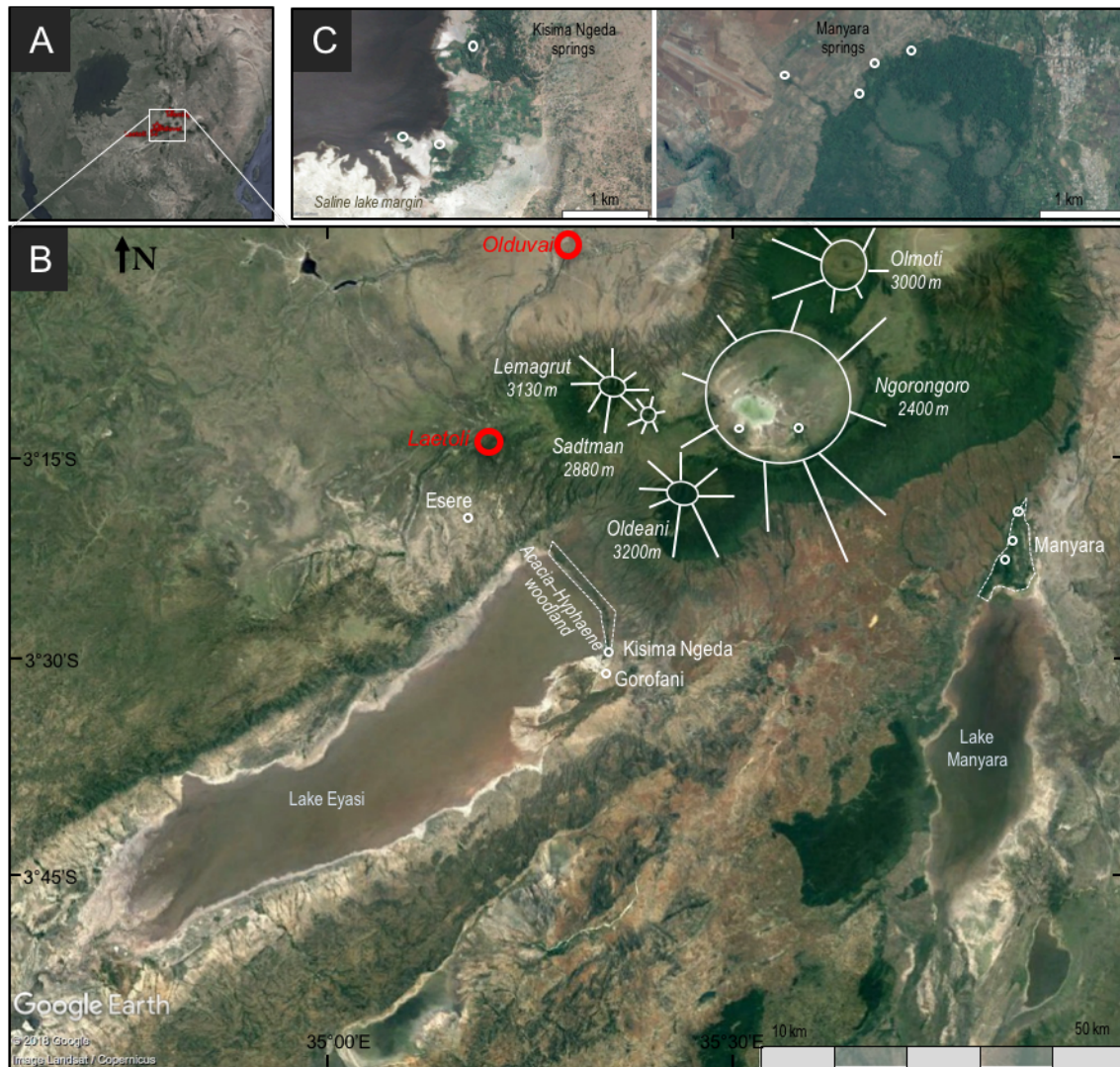


Figure 2. Springs in the Ngorongoro – Lake Eyasi – Lake Manyara region, north Tanzania. (A) General view. (B) Satellite view (Landsat / Copernicus image from GoogleEarth, 2018) with position of volcanoes, saline lakes Eyasi and Manyara, and the spring sites visited several times since 2012, mainly Kisima Ngeda and Manyara spring forest. Red circles indicate paleontological sites of Olduvai and Laetoli. (C) Close-ups show sharp vegetation changes at the spring sites, located at the foothills of Oldeani and Ngorongoro Highlands.



Figure 3. Photographs of modern spring palm woodlands of the Awash Valley, Ethiopia. A) Palm spring woodland with abundant grasses and some *Acacia* and Capparidaceae shrubs, Filwoha area, Awash National Park; B-D) Doho spring area, B) *Hyphaene thebaica* palms, *Acacia nilotica* and exotic *Prosopis* trees in the background at the base of the basaltic high, Cyperaceae on damp to wet soils; C) view from the basaltic high showing the extent of the spring woodland, patches of *Typha* and of grasses occur within the palm woodland, D) *Hyphaene thebaica* palm trees growing at the spring head, Doho Lodge.



Figure 4. Photographs of the modern azonal (spring) and zonal vegetation in the northwestern edge of Lake Manyara (A-D) and of northeastern edge of Lake Eyasi (E-H), Tanzania. A: Spring forest with abundant evergreen trees, understory includes sedges (foreground) and *Phoenix reclinata* palm treelets (background)– ground was damp; B: Woodland with *Hyphaene petersiana* palm trees and various shrubs at the southern edge of the spring forest –ground dry; C: Evergreen forest growing along one of the spring-fed rivers reaching Lake Manyara floodplain; D: *Acacia* – *Commiphora* thicket-woodland on the distal floodplain of Lake Manyara; E: Freshwater wetland on Lake Eyasi floodplain near Kisima Ngeda spring with *Typha*, sedges, and the small halophytic tree *Sesbania sesban*; F: Lake Eyasi floodplain with *Acacia xantophloea* and *Hyphaene petersiana* woodland on the right; G: close-up on the *Acacia xantophloea* and *Hyphaene petersiana* woodland; H: zonal scrubland with rare grass patches and the cactoid *Euphorbia candelabrum*. Photos by the authors, except F and G (M. Dominguez-Rodrigo).

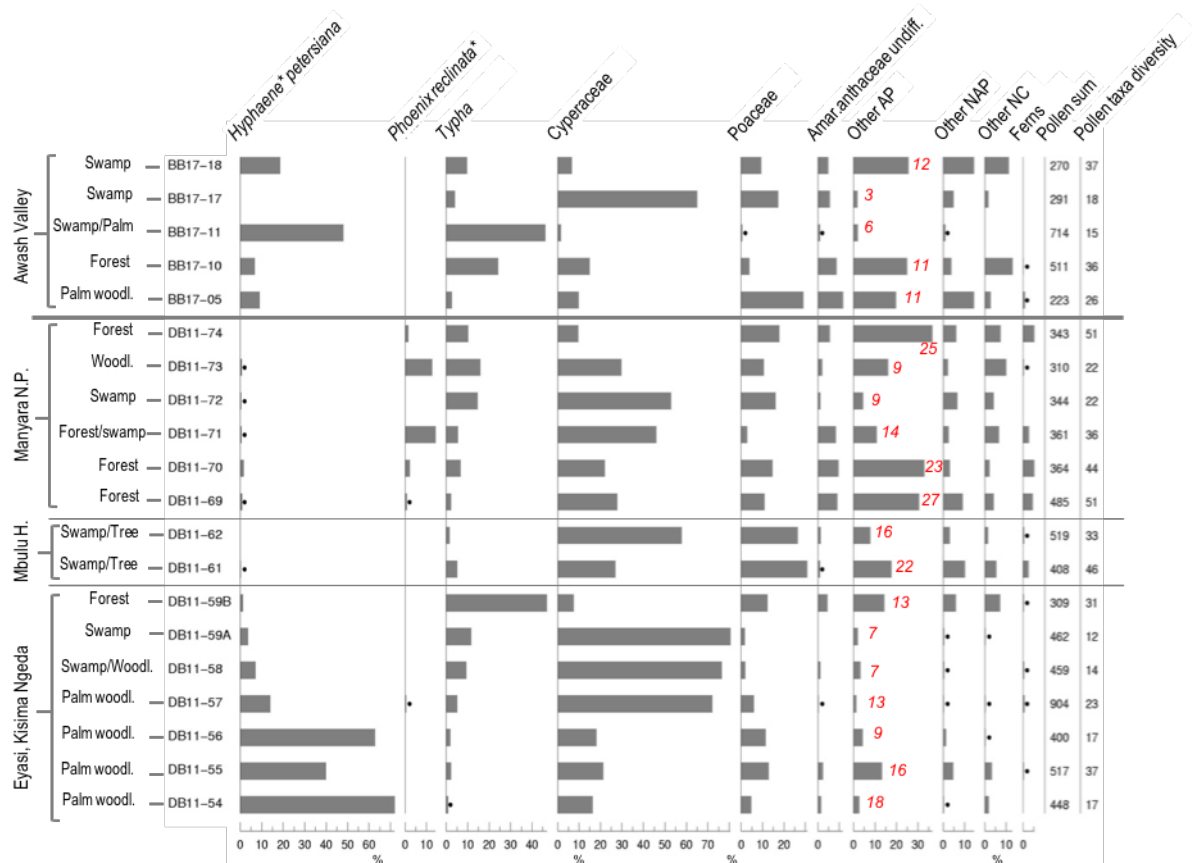


Figure 5. Pollen spectra from modern spring sites in Ethiopia and Tanzania. Numbers in red indicate pollen diversity among arboreal taxa. * means type, *Hyphaene-type petersiana* for example. Percentages <0.5% are marked by a black dot. Details regarding site location and pollen counts are given in SOM1.

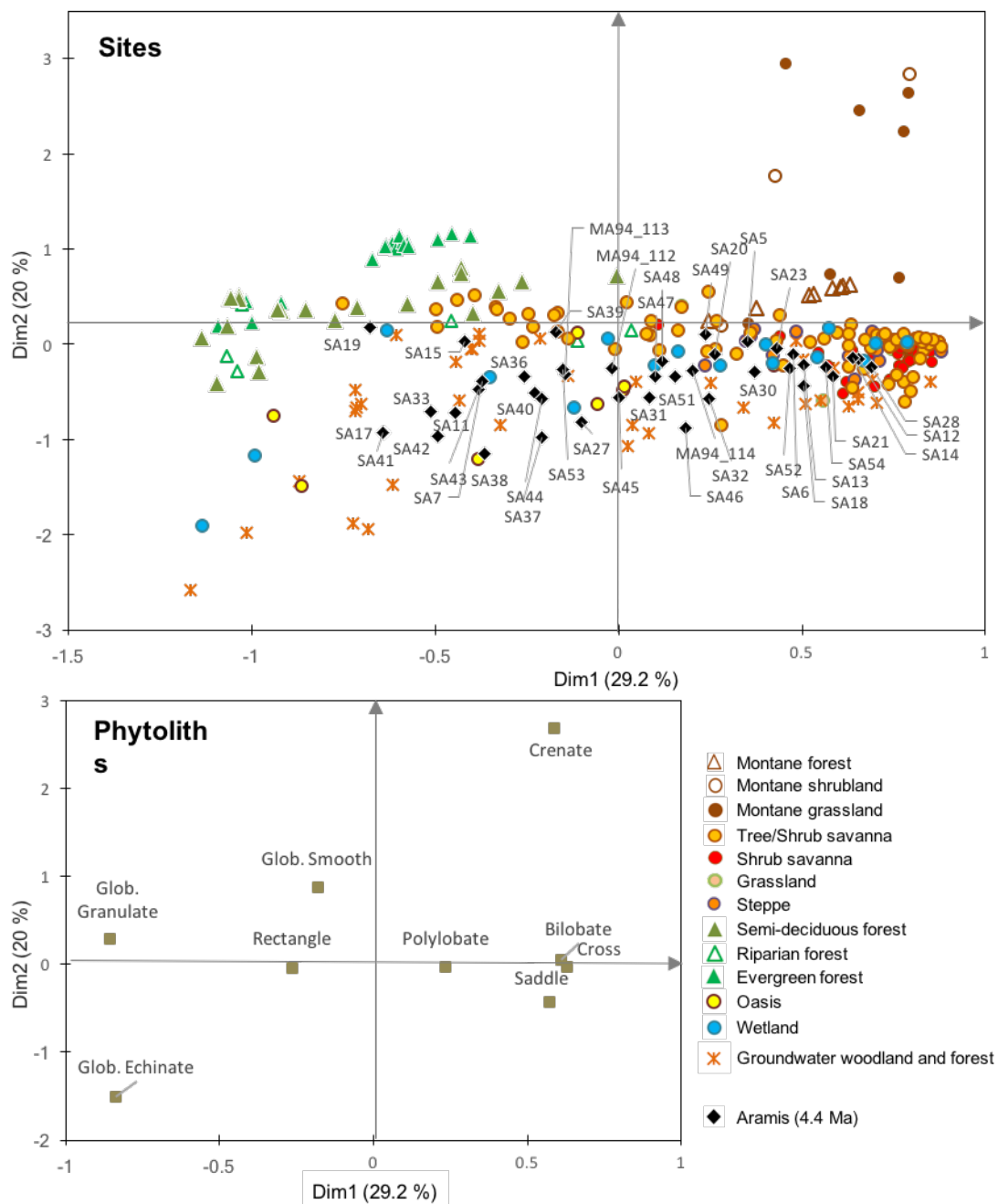


Figure 6. Correspondence analysis ordination diagram of 265 modern sites and 9 phytolith morphotypes. Fossil Aramis data points used as supplementary (passive) variables in the CA are shown as black diamonds.

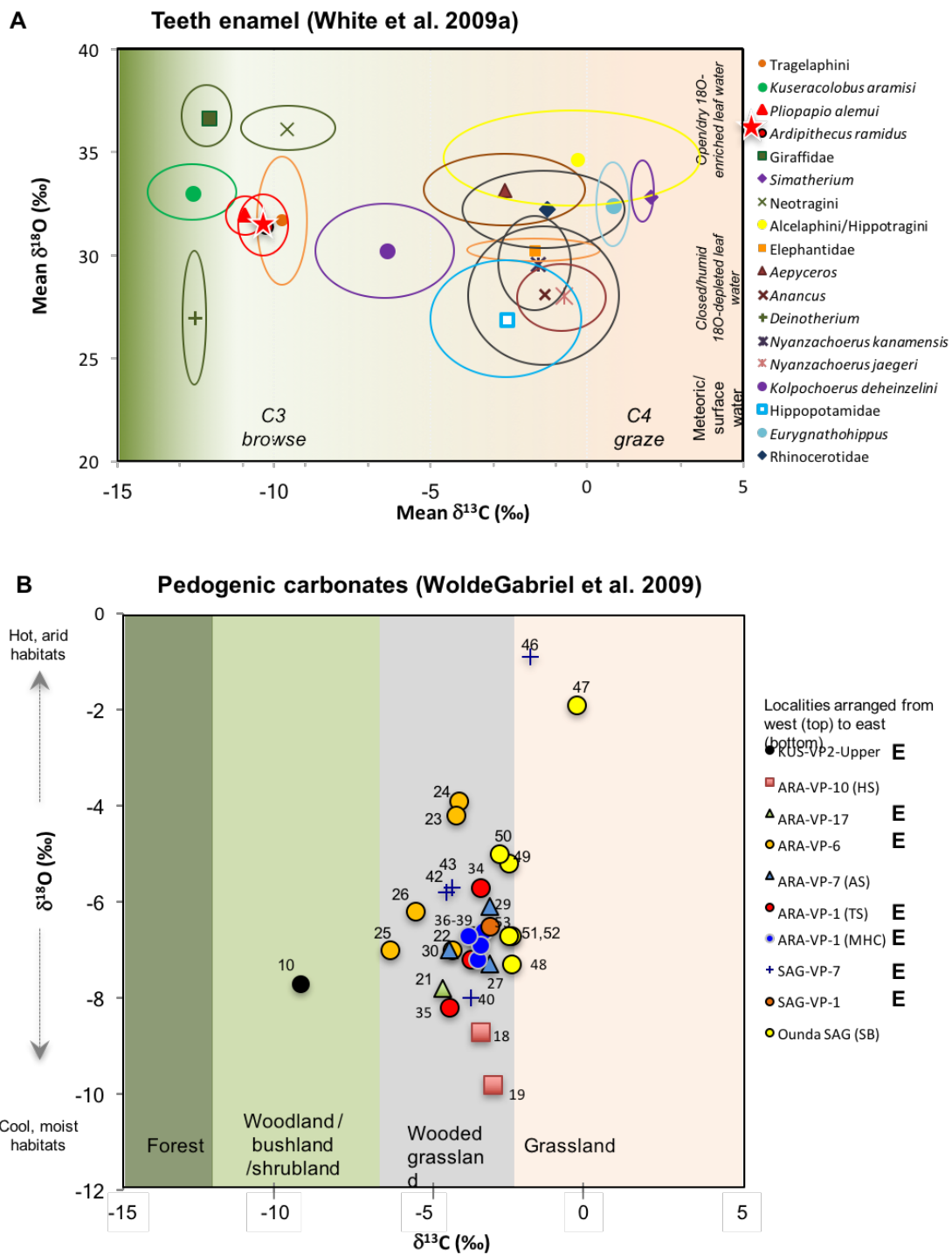


Figure 7. Aramis isotopic data $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ on teeth enamel and pedogenic carbonates. Data and inferred C_3/C_4 diets are from White et al. (2009a) and WoldeGabriel et al. (2009). Probable vegetation type inferred from $\delta^{13}\text{C}$ values according to Cerling et al. (2011).

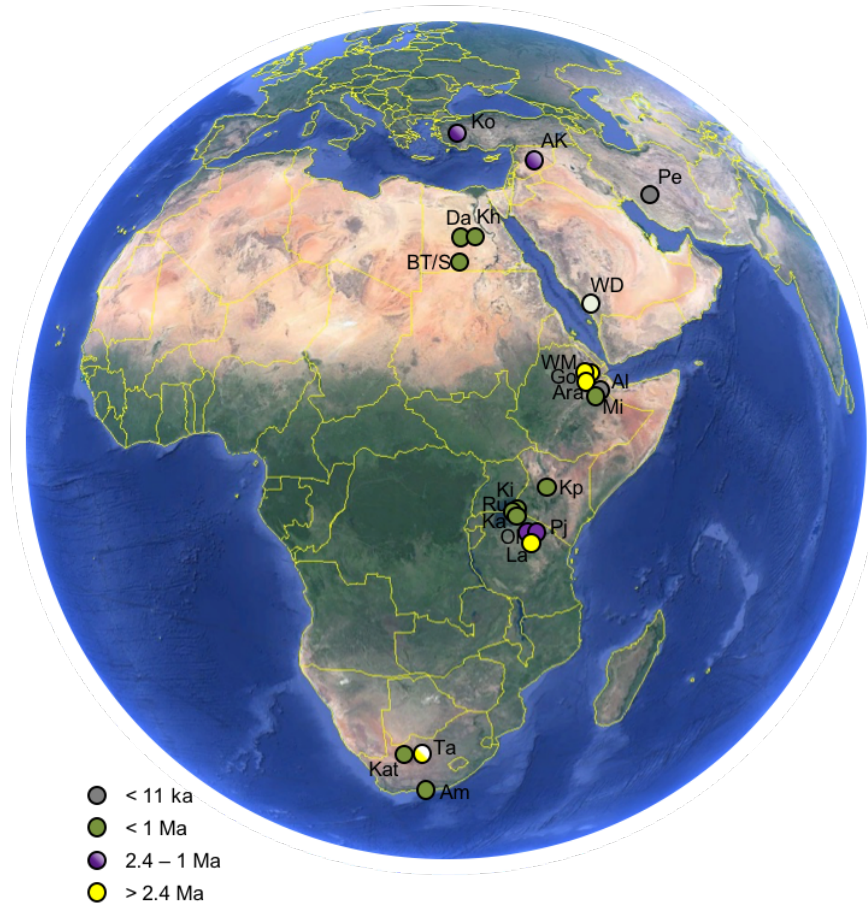


Figure 8. Position of the sites with early hominin remains and/or artifacts found associated with coeval geological evidence for springs. Google Earth map (Data SIO, NOAA, U.S. Navy, NGA, GEBCO; Image IBCAO, Image Landsat / Copernicus).

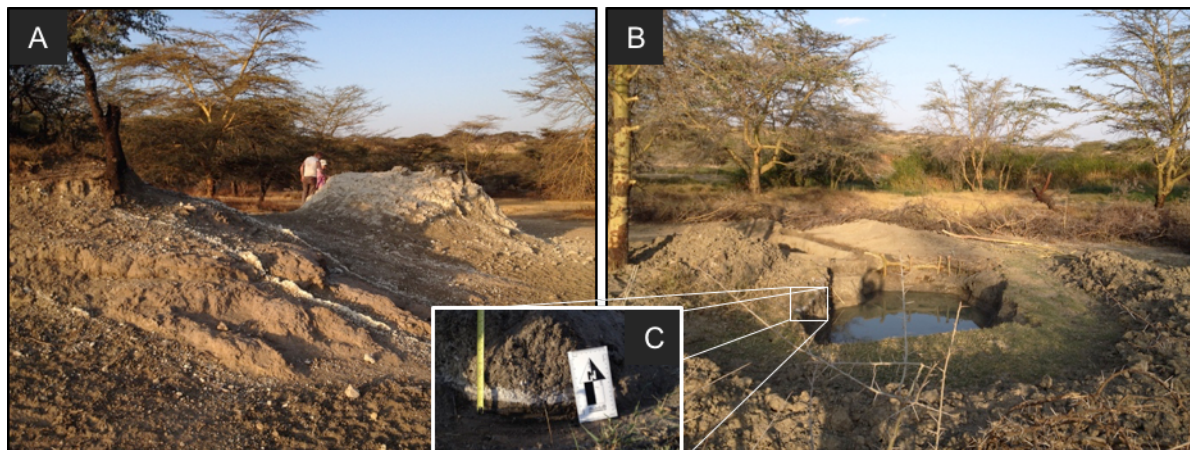


Figure 9. Photographs of fossil and modern spring at Esere, near Laetoli area, north Tanzania. (A) Carbonate mount with carbonate-encrusted plant remains, which attest to the presence of a fossil spring (dating of carbonate, in progress). (B) Modern, active spring adjacent to the carbonate mount. In the foreground, the water hole dug by herders shows that groundwater is <1 m below the surface. In the background, where spring water naturally reaches the surface, *Typha* reeds and sedges occur. (C) Micritic carbonate bed within the soil.