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# Vegetation of Northern Tanzania during the Plio-Pleistocene: A synthesis of the paleobotanical evidences from Laetoli, Olduvai, and Peninj hominin sites



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## ABSTRACT

More than 40 years of scientific investigations of the hominin bearing Plio-Pleistocene sediments of northern Tanzania have provided a number of paleobotanical data, which, taken as a whole, provide today a way to investigate vegetation changes between 4 and 1 Ma, at a time when our early ancestors emerged. Here, I have integrated the data from all vegetation proxies obtained for the paleontological sites of Laetoli, Olduvai, and Peninj (i.e. macroscopic plant remains, pollen and phytolith assemblages, carbon and oxygen isotopic ratios measured on carbonates, and organic biomarkers). This important, yet discontinuous botanical record suggests some similarities between past and present-day vegetation at the regional scale: Afromontane forests with *Olea*, *Podocarpus*, *Juniperus*, *Hagenia abyssinica* in the highlands, and wooded grasslands with grasses and drought-adapted *Acacia*, *Commiphora*, Cappariaceae, and Chenopodiaceae and/or Amaranthaceae in the lowlands were present in the southern Serengeti–Crater Highlands region since 4 Ma. Grasses of the C<sub>4</sub> photosynthetic type made their first appearance in the record at ~3.7 Ma, i.e. during the mid-Pliocene, ~700 ky before major pCO<sub>2</sub> and temperature decline. C<sub>4</sub> grasses became dominant in the vegetation soon after (~3.66 Ma), probably in response to reduced precipitation. At ~2.6 Ma, phytolith and isotope indicate grassland with abundant C<sub>4</sub> xerophytic grasses that document strong aridity during the Intensification of Northern Hemisphere Glaciation period (~2.7–2.5 Ma). After 2 Ma, the detailed and diverse record at Olduvai indicates complex vegetation patterns linked to oscillating precipitation, varying lake levels, and the presence of geological faults. Hence, despite low (basin-averaged) reconstructed paleo-precipitation amounts of ~250–700 mm/y, C<sub>4</sub>-grasslands, closed woodlands, wetlands, and palm-groves co-occurred on short spatial scales near saline Lake Olduvai. Freshwater wetlands and palm-rich woodlands occurred in highly localized areas on the lake margins, where aquifer barriers and/or outcrops caused by geologic faults allowed groundwater discharge. Botanical evidence of paleo-springs at Laetoli, Olduvai, and Peninj includes the marked presence of *Typha* (cattail) and *Hyphaene* (palm tree) in association with *Acacia* pollen grains, and (at Olduvai) abundant forest indicator phytoliths and organic and isotopic biomarkers. At Olduvai, freshwater wetlands were most developed when lake level and fluvial competence were low, i.e. during dry periods. When wet–dry climate variability was extreme in East Africa (~1.9–1.7 Ma), freshwater springs may therefore have offered a sustainable habitat (i.e. refuge) for several species, including hominins, and favored hominin and artifact concentration at these specific places, particularly during environmentally stressful times.

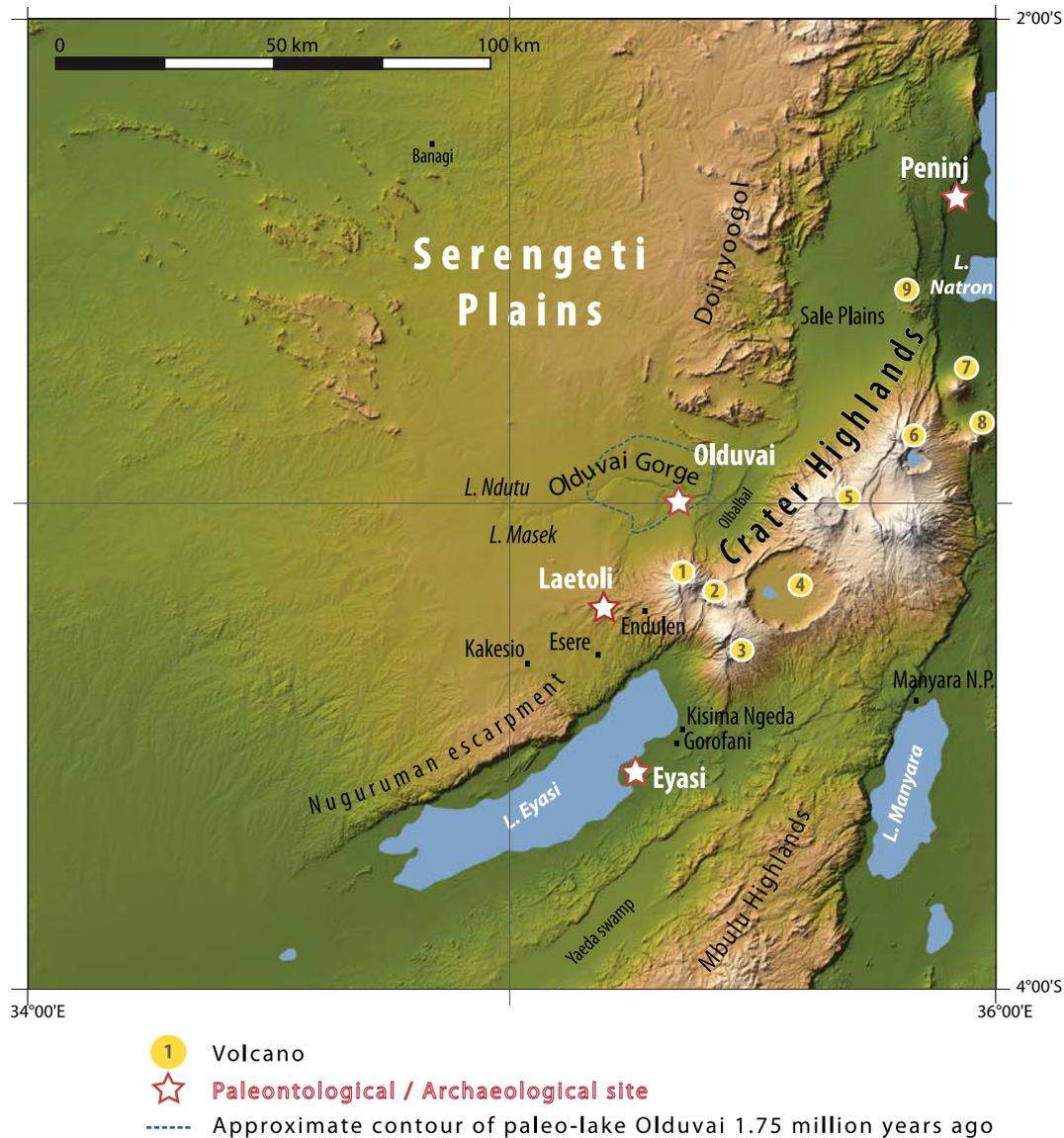
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## 1. Introduction

Northern Tanzania offers a 4 million year-long record of human evolution with as many as seven different hominin species found within the area encompassing the paleontological sectors of Laetoli, Olduvai Gorge, and Peninj (Fig. 1). Its location in the tectonically

active East African Rift System offers the advantage that the fossiliferous sedimentary units are relatively well time-constrained thanks to the numerous inter-embedded volcanic tuffs, most of which can be dated absolutely by K/Ar and <sup>40</sup>Ar/<sup>39</sup>Ar methods (retrospectives and latest dates: Deino, 2011, 2012). Hominin evolution and cultural emergence transpiring since the Late Pliocene in this region of East Africa can therefore be compared with large-scale environmental changes, such as global climate change and climate

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**Fig. 1.** Topographical map of the Serengeti–Crater Highlands region with the paleontological and archaeological sectors of Laetoli, Olduvai, Peninj, and Eyasi (stars). Numbered volcanoes are (1) Sadiman, (2) Lemagrut, (3) Oldeani, (4) Ngorongoro, (5) Olmoti, (6) Embagai, (7) Ol Doiyo Lengai, and (8) Kerimasi. This color-shaded relief image was acquired by the Shuttle Radar Topography Mission and is available on NASA's Earth Observatory website. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

variability inferred from long marine cores and ice cores from the polar caps (DeMenocal, 1995, 2004).

Hominin evolution that resulted in morphological, genetic, and neurobiological transformations as well as cultural developments was likely triggered by many interrelated factors (environmental, resource, social, competitive), the relative importance of which remains a well-studied and debated issue (e.g. Maslin and Christensen, 2007; Potts, 2013; Shultz and Maslin, 2013). In the 1960s, the savanna hypothesis suggested that increasing global aridity triggered the expansion of open grass savannas and prompted our early ancestors to adopt bipedalism (see review by Dominguez-Rodrigo, 2014). Among the factors responsible for the evolutionary process that lead to the emergence of hominins, Vermeij (1993) emphasized the importance of the biotic process of predator–prey coevolution. DeMenocal (1995, 2004) and Potts (1996), on the other hand suggested that climate change and increasing climatic variability since the Miocene 10 Ma favored evolution towards easily and rapidly adapting species. Richerson et al. (2008) concluded that both internal and external processes have played roles in human evolution.

They emphasized the possibility that climate deterioration has been the main driver of hominin evolution. Yet, the correlations between external (climatic, environmental) changes (e.g. increasing high-frequency environmental variation) and faunal changes (e.g. hominin evolution toward larger brains) are not straightforward (e.g. Shultz et al., 2012; Potts, 2013).

Vegetation is a key environmental factor that strongly determines the habitat of each species, including primates. The vegetal context of a site and a landscape fixes the type of resources available, as well as the spatial and temporal availability of those resources, and determines the type, presence, and abundance of predators and competitors (Hall et al., 1997; Manning et al., 2004). Vegetation therefore constitutes an important aspect of the paleo-environment to be reconstructed in order to discern among the potential factors that triggered hominin evolution.

Vegetation may be described using physiognomic criteria such as growth forms (e.g. tree, shrub, grasses), vertical structure (e.g. multi-story, single-story), horizontal cover (density, heterogeneity, the form and the relative contribution of woody plants versus

grasses, etc.). Vegetation may also be described using floristic criteria (e.g. species composition and abundance). These various aspects of vegetal cover determine the behavior of animal species both at the local and the landscape scales. They may therefore have played a role in shaping human behavior and, therefore, its evolution. But, which of these aspects of vegetation can paleobotanists and paleoecologists reconstruct? At what spatial scale should the paleobotanical data be interpreted?

Preserved evidence of past vegetation in Northern Tanzania include silicified macro-remains such as pieces of woods, leaves, roots and silicified fruits (Bamford, 2005, 2011a, 2011b; Bamford et al., 2006, 2008; Albert and Bamford, 2012), organic micro-remains such as pollen grains (Bonnefille and Rioulet, 1980, 1987; Bonnefille et al., 1982; Bonnefille, 1984; Dominguez-Rodrigo et al., 2001a), and phytoliths (Dominguez-Rodrigo et al., 2001b; Albert et al., 2006, 2009; Bamford et al., 2006; Barboni et al., 2010; Ashley et al., 2010a, 2010b; Rossouw and Scott, 2011; Albert and Bamford, 2012). The carbon stable isotopes  $^{12}\text{C}$  and  $^{13}\text{C}$  were also measured in paleosol carbonated nodules, bulk organic matter, and lipid biomarkers to evaluate the relative abundance of  $\text{C}_3$  (mainly woody plants but also mesophytic and aquatic herbaceous) versus  $\text{C}_4$  plants (mostly tropical grasses, but also some sedges, and xerophytic dicots) (Cerling and Hay, 1986; Cerling, 1992; Sikes and Ashley, 2007; Magill et al., 2013a, 2013b). To date, plant macro-remains and pollen grains are the only fossils that provide insights into the floristic aspect of Plio-Pleistocene paleovegetation in this region because they allow taxonomical identifications sometimes up to the species-level. However, because they are generally transported (as it is the case for the fossil woods at Laetoli, and for pollen grains in general), these plant fossils cannot be used to reconstruct the “living distribution of taxa on a fine [spatial] scale” (Andrews and Bamford, 2008). On the contrary, phytolith assemblages are relatively poor taxonomical markers compared to pollen, yet their capacity to trace local changes in the density of the arboreal vegetation cover is superior (e.g. Bremond et al., 2005a). Both local and landscape scale aspects of the Plio-Pleistocene vegetation in this region of N Tanzania should therefore be revealed by the variety of vegetation proxies that was studied at Laetoli, Olduvai, and Peninj.

This paper is a review of the paleobotanical work carried out in northern Tanzania since the paleoanthropological sites were discovered in the early 1950s. It aims to consider the full paleobotanical record available to date for Laetoli, Olduvai, and Peninj, in order to provide an integrated paleovegetation reconstruction for the interval between 4 and 1 Ma, when Northern Tanzania hosted some of our early ancestors. As a complement to previous syntheses (Bonnefille, 1995, 2010; Andrews and Bamford, 2008; Peters et al., 2008; Jacobs et al., 2010), this review considers for the first time the phytolith record that is now available for Laetoli (Rossouw and Scott, 2011), Olduvai (Albert et al., 2006, 2009; Bamford et al., 2006; Barboni et al., 2010; Ashley et al., 2010a, 2010b; Albert and Bamford, 2012), and Peninj (Dominguez-Rodrigo et al., 2001b). It also considers the biomarker record recently obtained from Olduvai, which brings greater precision regarding climate and vegetation change in the Olduvai basin around 2.0–1.8 Ma (Magill et al., 2013a, 2013b, 2012). Unlike previous synthesis (e.g. Peters et al., 2008), the faunal data will not be discussed here, despite their value in characterizing paleoenvironments. This new synthesis considers the latest chronostratigraphy for Laetoli (Deino, 2011) and Olduvai (Deino, 2012).

## 2. Study area

The area under consideration here is located in the Eastern Branch of East African Rift Valley between 2–4°S and 34–36°E. It

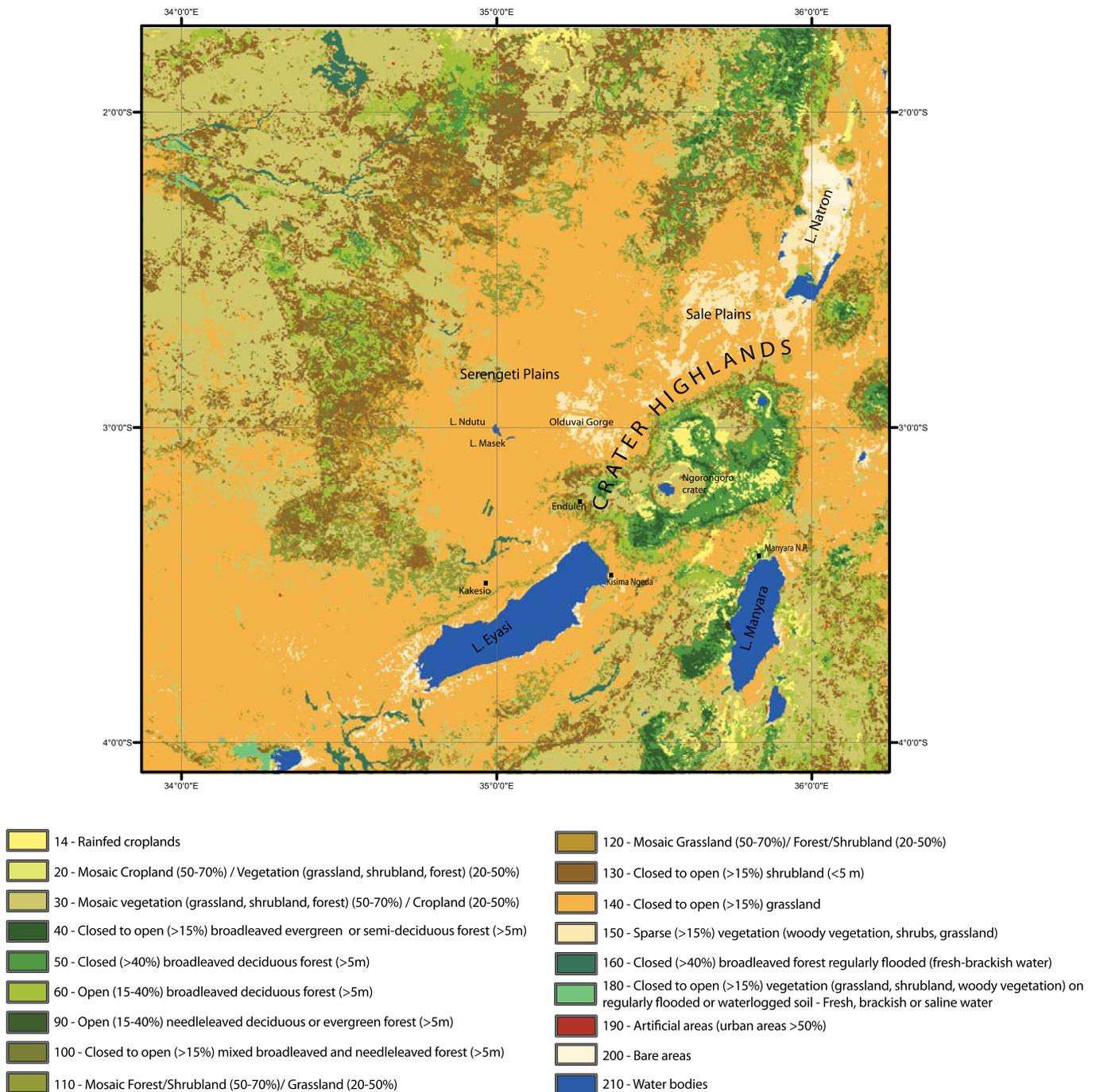
includes the Serengeti Plains, the Crater Highlands, and lakes Eyasi, Manyara, and Natron (Fig. 1). The Serengeti Plains cover most of the region. They lay west of the Crater Highlands at an elevation of about 1500–1800 m above the sea level (m asl). The Serengeti Plains include Olduvai Gorge (1350–1500 m asl), the Sale Plains, the Olbalbal depression, and the Doiyoogol Hills. The Crater Highlands (up to 3050 m asl) stretch along a SSW–NNE line which creates a rain shadow over the Eastern Serengeti Plains. Lake Manyara, Lake Eyasi, and Lake Natron lie at about 1000 m of elevation. Lake Manyara (saline/alkaline) and Lake Natron (saline) are located in Rift Valley at the foot of the major escarpment, while Lake Eyasi (saline/alkaline) lies along the Nguruman Escarpment between two branches of the Rift system.

### 2.1. Overview of the present-day climate and vegetation

The climate in this region is characterized by a bimodal rainfall regime controlled by the Indian Ocean and the seasonal migration of the Inter-Tropical Convergence Zone. Due to the steep relief, steep temperature and rainfall gradients trigger important vegetation changes over short distances. The rains mainly occur in March, April, and May, and again in November and December. The highest rainfall (750–1250 mm/y) occurs in the Crater Highlands, the Mbulu Highlands, the Doiyoogol Hills, and in the Western Serengeti (west of Lakes Masek and Ndotu). Medium rainfall (500–750 mm/y) occurs in the Eastern Serengeti Plains, the Sale Plains, around Lake Eyasi and Lake Manyara. Lowest rainfall (250–500 mm/y) occurs in the Rift Valley around Lake Natron, where evaporation is intense.

The modern vegetation in this region (Fig. 2) is determined by topography, present-day climate, and soil composition (Anderson, 2008). It is also strongly influenced by fire and grazing, which are both natural and anthropogenic (Holdo et al., 2009). The vegetation of this region was described and mapped in detail (Herlocker and Dirschl, 1972; Andrews and Bamford, 2008). It includes various types of deciduous bushlands and thickets with small *Acacia* (e.g. *A. tortilis*, *A. kikii*, *A. seyal*, *A. mellifera*) and *Commiphora* trees (e.g. *C. africana*, *C. madagascariensis*) that cover most of the region except the Serengeti Plains, where grasslands species (e.g. *Sporobolus marginatus*, *Digitaria macroblephara*, *Killinga* spp.) develop on soils derived from volcanic ash (Herlocker and Dirschl, 1972; White, 1983). Closed to open grasslands of short and medium-size grasses and sedges occur in the Serengeti Plains, the Endulen–Kakesio area, the Ngorongoro crater, on the Eyasi and Highland Plateaus, on Lake Eyasi and Lake Manyara flats. Shrublands and bushlands, with thorny usually deciduous small shrubs and trees (<8 m) that form discontinuous canopy, occur in Olduvai Gorge and on the western and northern sides of the Crater Highlands below ~2500 m in elevation. Mountain forests grow above 2500 m in elevation on the western wall of the Crater Highlands and on all slopes of the mountain peaks above the Highland plateau. Afro-montane vegetation occurs at lower elevation (~1600 m) on the moister eastern wall of the Crater Highlands.

In some very localized areas where freshwater seeps out of geologic faults, such as at Kisima Ngeda and Gorofani in the north-east of Lake Eyasi, near the village of Esere in the Laetoli area, and in the northwest of Lake Manyara and many other places not mapped here (Fig. 1), the vegetation is azonal, i.e. not in equilibrium with the regional climate. At the springheads of Lake Manyara, at the entrance of the Manyara National Park, a luxuriant evergreen forest develops despite the prevailing arid climate. Tall evergreen trees with buttresses and large leaves (meso- to macrophyllous) form a dense canopy with interlocking crowns. Small understory palms (*Phoenix reclinata*) are common, and the ground cover is made of Cyperaceae. Few hundred meters away from the influence of the



**Fig. 2.** Detailed vegetation map for the Serengeti–Crater Highlands region between 2–4°S and 34–36°E. Closed to open grasslands (#140-orange) and shrublands (#130-brown) cover most of the region. Closed broadleaved deciduous or semi-deciduous forests are restricted to the highlands and protected areas (#40, #50, #60). © ESA/ESA Globcover Project, led by MEDIAS-France/POSTEL. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

springs, the dense forest is sharply replaced by *Acacia xanthophloea*–*Hyphaene petersiana* woodlands and bushlands, where grasses and thorny low, multi-stemmed deciduous plants (e.g. the Cappariaceae *Salvadora persica* and *Maerua triphylla*) can resist prolonged periods of drought (Greenway and Vesey-Fitzgerald, 1969; Loth and Prins, 1986). At Kisima Ngeda, where the water supply from the underground is less important than at Manyara, the freshwater springs contribute to the development of tall *A. xanthophloea*–*H. petersiana* woodlands. Close-by, at Gorofani, remnants of evergreen forest can still be seen despite the heavy human disturbance. Although very localized in the landscape, these groundwater

discharge areas and associated azonal vegetal communities provide resources for the Hadzabe hunter-gatherers who live in the Eyasi area as well as for the recently arrived sedentary populations who grow various crops (e.g. onions, maize, sugar cane).

## 2.2. Overview of the hominin record

So far, the hominin record for Northern Tanzania totals seven different species, which were found in Pliocene and Pleistocene sediments exposed at Laetoli, Olduvai Gorge, Peninj, and Lake Eyasi (Fig. 1). The hominin record for these sites is presented



chronologically in Fig. 3. The paleontological area of Laetoli, on the Eyasi Plateau, provided the oldest hominin, whose remains and footprints are attributed to *Australopithecus afarensis* dated ~3.85–3.63 million years (Ma) (Deino, 2011). *Paranthropus aethiopicus* was also found at Laetoli and is dated 2.66 Ma. Laetoli also provided remains of *Homo sapiens* dated about 88–132 ka (Harrison, 2011). Olduvai Gorge, in the Eastern Serengeti Plains ~50 km north of Laetoli, provided numerous faunal remains including three early hominin species: *Homo habilis*, *Paranthropus boisei* and *Homo erectus/ergaster* (Leakey and Leakey, 1964; Leakey, 1971; Clarke, 2012; Domínguez-Rodrigo et al., 2013). *P. boisei* and *H. habilis* were contemporaneous. They shared the same geographical area from ~1.9–1.6 Ma, and their remains were found in the same locations. Remains of *P. boisei* were also found in the paleontological area of Peninj, on the western bank of Lake Natron in sediments dated about 1.4 Ma (Leakey and Leakey, 1964; Isaac, 1965). The Ndotu beds in the area of Olduvai Gorge and Lake Ndotu provided hominin remains attributed to *Homo heidelbergensis*, approximately dated 400,000 years old (Rightmire, 1983). Lastly, remains of *H. sapiens* dated 80–132 ka were recovered from the north-eastern bank of Lake Eyasi (Domínguez-Rodrigo et al., 2008).

### 3. Methods applied for reconstructing paleovegetation

To date, the Plio-Pleistocene vegetation of northern Tanzania can be inferred from macro-botanical remains, pollen and phytolith assemblages, the ratio of stable carbon isotopes ( $^{13}\text{C}/^{12}\text{C}$ ), and organic biomarkers, which were studied at Laetoli, Olduvai, and/or Peninj. The paleobotanical record is presented in Fig. 3 on a time scale in parallel to the stratigraphy and to the hominin record at the three paleontological sites under focus. Some aspects of the past global and regional climate, as well as the regional geologic and volcanic activities are also given.

Macroscopic fossil plants were found preserved at various localities in the sectors of Laetoli and Olduvai. They were found most abundant and diverse at Laetoli, where casts of seeds and fruits, leaf impressions, and silicified wood were recovered mainly from the Upper Laetolil Beds in debris flow deposits (Bamford, 2011a, 2011b). At Olduvai, macro-botanical remains consist of silicified wood and root casts (Bamford, 2005; Bamford et al., 2006; Bamford et al., 2008).

Pollen grains are rarely found preserved at hominin sites. Yet, Bonnefille and collaborators obtained exploitable pollen assemblages from ten samples (over 40) collected in Lower and Upper Laetolil beds (Bonnefille and Riollet, 1987). Recently, additional efforts to obtain Pliocene pollen records from Laetoli proved unsuccessful (Rossouw and Scott, 2011). At Olduvai, where Bonnefille and collaborators initiated research in the 1970s, the efforts to obtain pollen assemblages were even less rewarding than at Laetoli: only 11 samples provided exploitable pollen assemblages over more than one hundred samples analyzed (Bonnefille and Riollet, 1980; Bonnefille et al., 1982; Bonnefille, 1984). Despite such a low number of productive samples, about 6000 pollen grains could be counted. The total list of fossil pollen for the Pleistocene at Olduvai includes 119 different taxa (Bonnefille, 1984). At Peninj, pollen grains were found preserved in only one sample from the Upper Humbu Formation (Domínguez-Rodrigo et al., 2001a). Because

pollen grains are easily transported by wind, rivers, and animals, pollen assemblages will therefore not strictly reflect the vegetation composition at the sampling site, but rather the vegetation at the landscape scale.

Phytolith research was successfully carried out at Laetoli by Rossouw and Scott (2011), who obtained 17 productive samples (over 41 samples collected) from the Lower and Upper Laetolil Beds, and the Upper Ndolanya Beds (about 4–2.66 million years). At Olduvai, phytolith research has concentrated on Upper Bed I (about 1.83–1.803 Ma, Deino, 2011; Barboni et al., 2010; Ashley et al., 2010a, 2010b) and Lower Bed II levels (about 1.785–1.74 Ma) (Albert and Bamford, 2012; Albert et al., 2009, 2006; Bamford et al., 2008, 2006) from the eastern paleolake margin. At Peninj, phytoliths were found preserved in one paleosol and on the sediment adhering to two bifacial tools (handaxes) (Domínguez-Rodrigo et al., 2001b) (Fig. 3). Phytoliths are well preserved in most environments (including paleosols) and are less prone to transport than pollen grains. The ongoing work on modern plants and soils in Africa contributes to improve the taxonomical and environmental identification of phytolith assemblages (Bremond et al., 2005a, 2005b, 2008a, 2008b; Barboni et al., 2007; Barboni and Bremond, 2009; Novello et al., 2012). Based on these studies, it is now possible to know if the paleovegetation at Plio-Pleistocene paleontological sites included woody plants (i.e. trees, shrubs, or woody herbs without distinctions), grasses, palms, or sedges, and to describe the paleovegetation in terms of density of the wood cover and grass dominance.

Stable carbon and oxygen isotopic composition of paleosol carbonates and bulk organic matter were analyzed in Olduvai samples from Bed I to Ndotu Beds (about 2 Ma to 100,000 years) (Cerling and Hay, 1986; Cerling, 1992, 1992; Sikes, 1994; Sikes and Ashley, 2007), and to a lesser extent at Laetoli in Lower and Upper Laetolil beds (Cerling, 1992). The exact stratigraphic position of the Laetoli isotope samples, however, is unknown (Fig. 3).

Organic (lipid) biomarkers preserved in the sediments may also be used as vegetation and climate proxies at hominin sites. This technique was recently applied in the sector of Olduvai. Stable hydrogen-isotope composition (expressed as  $\delta\text{D}$ ) was measured on lipid biomarkers (leaf waxes) preserved in the sediments of paleolake Olduvai (at locality 80, near the center of the paleolake), and provided estimates of mean annual precipitation for the period about 2.0–1.8 Ma (Magill et al., 2013b). Lipid biomarkers and their stable carbon isotopic signatures measured from the same sediments also provided a high-resolution record of vegetation changes (Magill et al., 2013a). At FLK Zinj archaeological site, sub-units of complex structural polymers (lignin) in plant tissues were found preserved in the paleosols capped by Tuff IC (approximately dated 1.848/1.832 Ma; Deino, 2012). These polymers allow distinguishing growth forms and record photosynthetic  $^{13}\text{C}$  discrimination, which provides additional evidence for site-scale (local) variations in the vegetation at FLK Zinj site (Magill et al., 2012).

The carbon isotopic composition of soil organic matter (bulk or biomarkers) and soil carbonates measures the proportion of  $\text{C}_3$  plants to  $\text{C}_4$  plants (e.g. Sikes and Ashley, 2007). Often overlooked is the fact that  $\text{C}_3$  plants are not only trees and shrubs (i.e. those contributing to the arboreal cover) but also sedges, *Typha*, many dicot herbs, and grasses (Poaceae) adapted to cool growing seasons,

**Fig. 3.** Summary of the Plio-Pleistocene paleobotanical record of Northern Tanzania, together with the hominin record and some keys events in global and regional climate, local climate as it may be inferred from extreme lake levels at Olduvai, and volcano-tectonic activity in the Eastern Branch of the East African Rift. The focus is on the paleontological sectors of Laetoli (Pliocene), Olduvai and Peninj (Lower Pleistocene). \* indicates that the positioning of carbon isotope samples within the Upper Ndolanya Beds and Laetolil Beds at Laetoli is imprecise. Numbers in bracket correspond to the paleobotanical references considered in this review (see list in Supplementary Table 1). Correspondence between lake levels and pollen samples at Olduvai was obtained by cross-checking stratigraphic positioning of the samples given in Bonnefille (1984) against the newly dated marker tuffs (Deino, 2012) and the detailed sedimentary record of Lowermost Bed II by Ashley et al. (2009). Positioning remains uncertain for samples RHCg, FCWc, and FCWa (†). Note that duration of high (+) and low (–) lake level phases is not accurately represented here (see e.g. Deino, 2012).

aquatic and shady environments (Tieszen et al., 1979; Livingstone and Clayton, 1980; Barboni and Bremond, 2009; Novello et al., 2012). Similarly, C<sub>4</sub> plants are not only savanna grasses, but also sedges (e.g. *Killinga*), non-graminoid herbs and dicots such as some species among the Acanthaceae (e.g. *Blepharis*), Amaranthaceae, Chenopodiaceae, Capparaceae (e.g. *Gynandropsis*), and Portulacaceae that occur in hot, dry and very sunny steppes and savannas (Pearcy and Ehleringer, 1984; Ehleringer et al., 1997; Sage, 2004). Stable carbon isotopic ratios measured on the total organic carbon (bulk) tend to overestimate C<sub>4</sub> inputs as a result of <sup>13</sup>C enrichment during the decomposition of organic matter (Wynn and Bird, 2007). Stable carbon isotopic ratios measured on leaf lipids (e.g.,  $\delta^{13}C_{31}$ ) can also overestimate C<sub>4</sub> inputs because macrophytes may assimilate inorganic carbon (e.g. bicarbonate). It seems that values for  $\delta^{13}C_{31}$  in arid environments are likely to be biased to wet conditions, when plants synthesize most leaf lipids (Post-Beittenmiller, 1996).

#### 4. Paleovegetation at Laetoli, 4–2 million years ago

Laetoli is a large sector that includes three main localities on the Eyasi Plateau: the newly designated Kakesio and Esere-Noiti localities and the fossil-rich locality of Laetoli, which has been prospected for fossils since the 1930s (Fig. 1). The Laetoli locality has produced a rich assemblage of fossil invertebrates, vertebrates, and mammals including three hominins (*Au. afarensis*, *P. aethiopicus*, and *H. sapiens*) and tracks of fossilized footprints of bipedal hominins, presumably of *Au. afarensis*. The Laetoli, Kakesio, and Esere-Noiti areas have also yielded important collections of fossil plants from the Pliocene-aged Lower and Upper Laetolil Beds and Upper Ndolanya Beds, which provide insights into the paleovegetation contemporaneous with our ancient ancestors who lived in this area 4 to 2 million years ago (Fig. 3). The fossil-rich Laetolil Beds were deposited (between 4.3 and 2 Ma) mainly in fluvial environment with some lacustrine sedimentation (Hay, 1987; Foster et al., 1997). The sedimentary beds are fossiliferous tuffs of Sadiman or Lema-grut volcanoes (Hay, 1976). Some of these volcanic tuffs made of natrocarbonatitic ashes (produced by some eruptions of the now extinct Sadiman volcano) provided a chronological framework for the archaeological remains (Deino, 2011), and allowed the preservation of animal footprints and impressions of raindrops (Hay, 1987).

Correlated to the Lower Laetolil Beds (about 4.1–4.0 Ma, Molle et al., 2011), the silicified fossil woods preserved in the volcanic debris flow deposits exposed in the Noiti locality (10 km south of the main Laetoli area) provide the oldest botanical record for northern Tanzania (Fig. 3). Unfortunately the fossilization process has not preserved the fine (discriminating) anatomical features required to identify the woods at the species level. Based on the broad preserved anatomical wood features, however, the paleobotanist in charge at Laetoli was able to select several most likely candidates for each specimen of fossil wood (Bamford, 2011a). These most likely candidates are present-day species which happen to represent a wide variety of vegetation types including deciduous woodlands, riverine woodland and gallery forest along watercourse or linked to springs, and wooded grassland. These vegetation types are observed today in the area (Andrews and Bamford, 2008). The fossil woods preserved in the volcanic deposits, however, are just one element of the paleoflora, which must have included also herbaceous plants and grasses. The presence of grasses in the paleovegetation is evident from the phytolith record from the same Noiti area (Rossouw and Scott, 2011) (Fig. 3). Grass phytoliths represent less than 50% of the total phytolith assemblage, which suggests woodland, bushland or shrubland, and wooded grassland. The  $\delta^{13}C_{\text{carbonate}}$  also indicate that C<sub>3</sub> plants were dominant over C<sub>4</sub> plants in the ecosystem during Lower and Upper Laetolil Bed time

(Cerling, 1992). The grass phytolith assemblages are rich in trapeziform polylobates (crenate) phytoliths, which are typical for Pooideae grasses that use the C<sub>3</sub> photosynthetic pathway (Barboni and Bremond, 2009; Rossouw and Scott, 2011). Hence both woody plants and grasses contributed to the pool of C<sub>3</sub> plants in the Laetoli area about 4 Ma (Fig. 3).

The presence and most likely the abundance of grasses in the paleovegetation at Laetoli is also attested to by pollen data (Bonnefille and Rioulet, 1987). The pollen data are from younger sediments at Laetoli localities 9s and 10 (similar to 3.83–3.86 Ma) and 22 (similar to 3.66–3.70 Ma) (Upper Laetoli Beds) (Deino, 2011) (Fig. 3). The pollen record represents few trees and shrubs (e.g. *Acacia*, *Commiphora*, *Rhus*) among which are several that originate in the Afromontane forest (*Olea*, *Podocarpus*, and *Juniperus*). The pollen record is dominated by grasses, and by herbs such as those occurring today in wooded grasslands. Pollen of *Hyphaene* and *Euclea* also indicate the presence of riparian or spring woodlands in the area (Andrews and Bamford, 2008).

The presence and abundance of fossil seeds attributed to small deciduous trees such as *Boscia coriacea* (between Tuff 5 and 8, similar to 3.63–3.79 Ma), *Ximania caffra* and *Cryocarpa latifolia* (between Tuff 5 and 6, similar to 3.70–3.79 Ma), and *Ximania americana* and *Celtis cf. africana* (between Tuff 6 and 7, similar to 3.66–3.70 Ma) suggest dry woodlands to moist or riparian woodlands (Bamford, 2011b). A deciduous flora is also indicated by the leaf impressions preserved on top of Tuff 8 (similar to 3.63 Ma) and which were tentatively identified to Euphorbiaceae (a very large botanical family which includes succulent, herbaceous as well as arboreal species that occur in very diverse environments). The leaves are relatively small (250–2000 mm<sup>2</sup>) with toothed and entire margins typical of deciduous floras in cool and/or dry environments (Bamford, 2011b).

The  $\delta^{13}C_{\text{carbonate}}$  at Laetoli ranges from about –8 to –5‰ in the Lower and Upper Laetolil Beds indicating that tropical grasses and/or sedges, Amaranthaceae, Chenopodiaceae, some Capparidaceae or Portulacaceae (all contributing to the C<sub>4</sub> biomass) were part of the ecosystem, but that they were less abundant than woody plants and/or C<sub>3</sub> grasses (contributing to the C<sub>3</sub> biomass). These values suggest grassy woodland before 3 Ma. After 3 Ma, the  $\delta^{13}C_{\text{carbonate}}$  values are much more positive (about –5 to +1‰). They record an increase in C<sub>4</sub> biomass, which implies that the paleovegetation was more open, like a wooded grassland or desert steppe during the Upper Ndolanya Bed time (Cerling, 1992) (Fig. 3).

At Laetoli, the phytolith assemblages record an interesting shift in the grass cover with the marked appearance of C<sub>4</sub> grasses after the deposition of Tuff 6 (~3.70 Ma), and relatively soon after, an increase in the grass cover relative to woody cover after the deposition of the Footprint tuff (Tuff 7, ~3.66 Ma) (Fig. 3). At the time of deposition of the Upper Ndolanya Beds (~2.60 Ma) the phytolith assemblage indicates wooded grassland with abundant C<sub>4</sub> xerophytic grasses. As noted, this shift towards more than 50% of C<sub>4</sub> biomass is also marked by the  $\delta^{13}C_{\text{carbonate}}$  values between the Laetolil and Ndolanya Beds (Cerling, 1992).

Altogether the Laetoli botanical record with its macro-botanical remains, pollen, and phytolith data suggests a variety of dry and moist woodlands, including riparian woodlands, as well as Afromontane forests on the close-by highlands. The fossil seeds, leaves, carbon isotopes and phytolith data suggest close woodlands with broadleaved deciduous trees and shrubs being more abundant than grasses. Until the deposition of Tuff 6 (~3.70 Ma), the woodland grasses were predominantly of the C<sub>3</sub> photosynthetic type, most likely of the Pooideae grass subfamily, such as those that thrive under low growing season temperatures, that is >2300 m asl in East Africa today. After the deposition of Tuff 6, the woodlands included not only C<sub>3</sub>-temperate grasses, but also C<sub>4</sub> grasses. Grasses

of the C<sub>4</sub> photosynthetic type thrive today at low elevation (< ~2300 m), preferentially in xeric (hot and dry environments) in East Africa (Tieszen et al., 1979; Livingstone and Clayton, 1980). The pollen data indicate that grasses were abundant in the vegetation at the landscape scale, along with herbs such as those occurring today in the Serengeti wooded grasslands (e.g. various Acanthaceae, Amaranthaceae, Asteraceae). Hence, it is most likely that *Au. afarensis* and later on *P. aethiopicus* occurred in a landscape with Afromontane forests occurring in the nearby highlands (within 50 km or more), and with dry woodlands, moist woodlands, wooded grasslands and grasslands occurring locally in the Laetoli area. Such mosaic of vegetation types can still be observed today in the Serengeti–Crater Highlands–Eyasi–Manyara region (Andrews and Bamford, 2008) (Fig. 2).

## 5. Paleovegetation at Olduvai and Peninj, 2–1 million years ago

### 5.1. Olduvai

Olduvai Gorge, in the Eastern Serengeti Plains (Fig. 1), exposes a 100-m thick sequence of deposits, including lacustrine, fluvial, wetland, aeolian, and pyroclastic sediments. Sedimentation occurred in a closed-basin lake between ~1.92 and ~0.2 Ma in a predominantly saline environment (Hay, 1976; Foster et al., 1997). The Olduvai deposits (and particularly Bed I) have produced an extremely rich assemblage of fossil vertebrates and mammals including four hominin species, representing nearly 2 Ma of hominin evolution: *P. boisei*, *H. habilis*, *H. erectus/ergaster*, and even modern *H. sapiens* (Fig. 3). In addition, stone artifacts have been recovered from all the Olduvai deposits, showing the evolution of tool technologies over time. At Olduvai, imbedded between the alluvial and lacustrine deposits, many of the volcanic tuffs could be dated and used as chronological markers for the archaeological sites (for review and latest dating see Deino, 2012).

The first paleobotanical record for Olduvai was obtained through the analysis of pollen grains, which, until recently were the only botanical evidence of what the vegetation may have looked like when *P. boisei* and *H. habilis* were present at Olduvai (Bonnefille and Riollet, 1980; Bonnefille et al., 1982; Bonnefille, 1984). The fossil pollen data from Bed I and Bed II indicate a paleovegetation dominated by grasses and sedges throughout the record, with relatively few arboreal plants. Arboreal pollen in the fossil assemblages represents drought-adapted trees and shrubs species of the Sudano-Zambesian phytogeographical zone (e.g. *Acacia*, *Commiphora*, *Alchornea*, *Capparidaceae*, *Ximenea*) and highland species from the Afromontane phytogeographical zone (e.g. *Olea*, *Juniperus*, *Podocarpus*, *Hagenia*). Apart from the abundance of *Typha*, which indicates the presence of freshwater source nearby, the fossil pollen data surprisingly shows little floristic difference with modern pollen assemblages from the present-day wooded grasslands surrounding Olduvai (Bonnefille, 1984). Yet, carbon isotopic studies of paleosols provide some evidence for substantial woody vegetation in some localities in the Olduvai Gorge, especially during Bed I and Bed II times (about ~1.8–1.2 Ma) (Cerling and Hay, 1986; Sikes, 1994; Sikes and Ashley, 2007) (Fig. 3). The carbon isotopic composition of paleosol carbonates at Olduvai shows an increase in the fraction of C<sub>4</sub> biomass that was first interpreted as an increase of grasses in the paleovegetation between 1.8 Ma and 500,000 years ago (Cerling and Hay, 1986; Cerling, 1992). More than 50% C<sub>4</sub> biomass was measured, indeed, in samples from Ndutu, Masek, and Bed III and IV, that is, after the end of Bed II (about 1.2 Ma). However, during Bed I and Bed II time, the isotopic composition of carbonates registers a great spatial variability in the fraction of C<sub>4</sub> biomass, which suggests heterogeneous vegetation such as

localized patches of woodland, shrublands or bushlands ( $\delta^{13}\text{C}_{\text{carb}}$  values ranging from  $-7.8$  to  $-5\text{‰}$ ) within a generally C<sub>4</sub>-grass dominated biome ( $\delta^{13}\text{C}_{\text{carb}}$  values ranging from  $-5$  to  $-0.5\text{‰}$ ). The greatest vegetation heterogeneity between samples from the same locality is observed during Upper Bed II time (e.g. at Locality 27 in the extreme east of the main gorge). Highest woody cover is inferred from lowest  $\delta^{13}\text{C}_{\text{carb}}$  values ( $\sim -7\text{‰}$ ) measured at localities 27, 33a, 33b, 34a in the east of the main Gorge during Bed II time and during Bed I time to a lesser proportion (Cerling and Hay, 1986; Sikes, 1994). It remains to be tested, however, through a phytolith analysis for example, if such low  $\delta^{13}\text{C}_{\text{carb}}$  values are to be attributed only to woody plants and to both woody plants and C<sub>3</sub> grasses. The presence of C<sub>3</sub> grasses cannot be ruled out as indicated by the phytolith analysis of FLK N in Upper Bed I (Barboni et al., 2010).

Since 2005, fossil woods, root casts, phytoliths, and more recently biomarkers provide additional information regarding the paleovegetation at Olduvai during Bed I and Bed II time (about 1.83–1.785 Ma). Phytoliths and biomarkers proxies, along with new geological evidence confirm that, locally, at several sites within the area of Olduvai the paleovegetation was indubitably very different 1.8 to 1.3 million years ago, because of the presence of (potentially large) groundwater-discharge areas (freshwater swamps, springs) (Deocampo, 2002; Ashley et al., 2009, 2010a, 2010b, 2010c; Barboni et al., 2010; Magill et al., 2012, 2013a, 2013b). Contrary to pollen data, which include an allochthonous regional component, these botanical markers are more prone to provide a signal from the local vegetation. The fossil wood was identified as *Guibourtia coleosperma* or possibly *G. schliebenii*, which are medium size trees of the Caesalpiniaceae family. *Guibourtia schliebenii* grows today in southwest Tanzania, but *G. coleosperma* is only present in mixed woodlands and bushlands of the arid Kalahari sands (Bamford, 2005). Other macro-botanical remains from Olduvai were hardly identified beyond the family level. Yet, the presence of sedges (Cyperaceae) and the cattail *Typha* in some areas (Bamford, 2012) further attest that permanent freshwater was available in localized areas within in the Gorge during Upper Bed I and Lower bed II time (Barboni et al., 2010; Ashley et al., 2010b).

Phytolith analyses of two well-constrained stratigraphic and archaeological levels namely FLK N capped by Tuff IF (about  $1.803 \pm 0.002$  Ma) and FLK Zinj capped by Tuff IC (about  $1.832 \pm 0.003$  Ma) have provided botanical evidences for spring-associated woodlands in Olduvai Gorge (Ashley et al., 2010b; Ashley et al., 2010c; Barboni et al., 2010). Phytolith assemblages at the exact location of the tufa spring deposits happened to be rich in globular granulate and other forest-indicator phytoliths, as well as in blocky phytoliths such as those that are produced by some sedges (Novello et al., 2012). Away from the thick carbonate beds (tufa), the phytolith assemblages were rich in grass phytoliths. The phytolith-inferred paleovegetation for FLK N and FLK Zinj archaeological site is spatially heterogeneous, with patches of dense woody vegetation that may be forest, woodland, or bushland with scattered palm trees within a grass-dominated biome similar to wooded grassland. A locally dense vegetation with palms and sedges but few grasses in the vicinity of freshwater springs is a paleoenvironmental context associated with a paleolake that is analogous to the present setting around lakes Manyara and Eyasi, which are also saline and/or alkaline (Fig. 1) (Barboni et al., 2010).

A study of lipid biomarkers recently provided a high-resolution record of ecosystem variability for the 2.0–1.8 Ma interval in the Olduvai area. First, it showed that the region was generally arid, with mean annual precipitation fluctuating between ~250 and 700 mm/y during this time period (Magill et al., 2013b). Second, it provided another direct line of botanical evidence that closed woodlands were present in localized areas, and that vegetation near Olduvai paleo-lake rapidly shifted from closed C<sub>3</sub> woodlands

to open C<sub>4</sub>-dominated grasslands (Magill et al., 2013a). Vegetation was therefore heterogeneous on both temporal and spatial scales but only in some highly localized areas within the Olduvai Basin. The apparent discrepancy between the pollen data, which argue for a landscape dominated by grasses (Bonniefile, 1984), and the phytolith data, which argue for the presence of localized patches of dense vegetation near water-discharge areas (Barboni et al., 2010; Ashley et al., 2010a, 2010b), is therefore resolved.

## 5.2. Peninj

Peninj is another Pleistocene site which has preserved some remains of *P. boisei* dated ~1.5 Ma and abundant stone artifacts of the Acheulian stone tool industry (Leakey and Leakey, 1964; Isaac, 1965; Isaacs and Curtis, 1974). It is located on the northwestern side of Lake Natron near the Peninj River (Fig. 1). Sedimentation at Peninj occurred in the closed-basin lake in a saline-alkaline environment between 1.7 and 1.2 Ma (Foster et al., 1997). The only pollen assemblage obtained from the Upper Sands with Clay unit (USC) that make up the upper section of the Humbu Formation indicates that the paleoenvironment in the Peninj area was dominated by grasses. Pollen of *Typha* and *Cyperaceae* (sedges) indicate the presence of local freshwater swamps, but the vegetation at the landscape scale is interpreted as savanna grassland, where trees and shrubs of *Acacia*, *Commiphora*, and *S. persica* were scarce compared to grasses (Dominguez-Rodrigo et al., 2001a). This result is in agreement with the only phytolith assemblage obtained from the artifact-bearing paleosol (Dominguez-Rodrigo et al., 2001b). The assemblage is dominated by saddle-type phytoliths, which are typical for C<sub>4</sub>-grasses adapted to xeric and open environments (Barboni and Bremond, 2009). The paleovegetation 1.5 Ma ago near Lake Natron, therefore, was probably very much like the present-day vegetation.

At Peninj, the study of plant remains was also carried out on stone artifacts in order to investigate the stone tool function. Plant fibers and the phytoliths recovered on the sediment matrix adhering to the handaxes showed marked differences with the phytoliths from the paleosols, which yield unambiguous evidence of their function as woodworking tools (Dominguez-Rodrigo et al., 2001b).

## 6. Discussion

The north Tanzanian botanical record spans ~4 Ma, with most data available between ~4–3.6 Ma and ~2–1 Ma (Fig. 3). It offers the potential to provide a snapshot of what paleovegetation looked like before and after some major climatic changes occurred, i.e. during the Pliocene when climate was globally warmer and *p*CO<sub>2</sub> levels were high, and during the Lower Pleistocene when strong wet–dry variability characterized East Africa following the intensification of the Walker Circulation (e.g. Ravelo et al., 2004; Trauth et al., 2005; Maslin and Christensen, 2007). Unfortunately, little data is available on the paleovegetation to document the potential impact of the gradual onset of the continental ice sheets and rapid decline of *p*CO<sub>2</sub> ~2.5 Ma, and the Mid-Pleistocene Revolution after ~1 Ma (Maslin and Christensen, 2007). The north Tanzanian botanical record synthesized here, however, offers new evidence that the structural development of the East African Rift influenced vegetation changes in the past, both at the regional and local scales.

### 6.1. Rain shadow effect of the Crater Highlands

The paleogeography of the Serengeti–Crater Highlands region, which encompasses the paleontological sectors of interest, varied in response to dynamics of the East African Rift System (EARS), which triggered important volcanic activity, topographical movements,

and faulting throughout the region over the last 4–5 million years (e.g. Hay, 1976; Foster et al., 1997). The volcanic activity has been intense along the southeast margin of the Serengeti Plain during the last 4 Ma with no less than ten volcanoes occurring within 100 km around Olduvai and Laetoli (Fig. 1). Several large volcanoes including Ngorongoro, Olmoti, Embagai, and probably Lemagrut and Oldeani were formed between 2.5 and 1.7 Ma (Fig. 3). Volcanoes such as Ngorongoro, which may have reached an elevation of 4500 m before the collapse of the caldera (Hay, 1976; Mollel, 2007), created the Crater Highlands, prominent landforms along the southeast margin. The uplift of these landforms shaped the landscape through the development of relief, which must have influenced the local rainfall patterns by reducing the moisture available for rain on the eastern sides of the mountains (rain shadow effect), such as it occurred elsewhere along the East African Rift during the Late Cenozoic (Trauth et al., 2005; Sepulchre et al., 2006). The paleobotanical record shows that, at Laetoli, trees and shrubs were already adapted to drought ~4 Ma, as indicated by their preserved anatomical features that (mostly) infer arid/xeric habitats with warm mean annual temperature (>13 °C) (Bamford, 2011a), and grasses were already present in the Pliocene xerophytic woodlands, shrublands, or bushlands. However, grasses were most likely of the Pooideae family that exclusively uses the C<sub>3</sub> photosynthetic pathway (Fig. 3) (Rossouw and Scott, 2011).

### 6.2. Appearance and expansion of C<sub>4</sub> grasses

Increased regional aridity caused by the (gradual or rapid?) uplift of the Crater Highlands since ~4 Ma may have played a role in the appearance of C<sub>4</sub> grasses in North Tanzania between 3.70 and 3.66 Ma, and in their expansion after 3.66 Ma (Fig. 3). Such shift from C<sub>3</sub> to C<sub>4</sub> grasses, and shortly after from dominant C<sub>3</sub> biomass to dominant C<sub>4</sub> biomass, however, is difficult to interpret since it may suggest a change from cooler to warmer climatic conditions, or increased aridity, and reduced *p*CO<sub>2</sub>, or a combination of factors (Pearcy and Ehleringer, 1984). Multi proxy reconstruction indicates that, five million years ago, *p*CO<sub>2</sub> was similar to today (~384 ppm), and that a rapid decline from this value to pre-industrial *p*CO<sub>2</sub> (~275–285 ppm) occurred in parallel with Northern Hemisphere ice growth from 3.2 to 2.8 Ma (Seki et al., 2010). The C<sub>3</sub>/C<sub>4</sub> shift observed in N Tanzania therefore pre-dates by some 700,000 years the *p*CO<sub>2</sub> decline. Mid-Pliocene (4.5–3 Ma) was also characterized by higher sea levels (10–20 m), reduced Antarctic ice cover, and warmer temperatures (+3 °C) on a global average (Ravelo et al., 2004). Biome reconstructions and model simulations for the mid-Pliocene (3.6–2.6 Ma) further indicate that climate was generally warmer, but also drier between 15°S and 15°N in East Africa (Salzmann et al., 2008). Therefore, increased aridity in North Tanzania (following or being accentuated by the uplift of the Crater Highlands) is likely what gave C<sub>4</sub> grasses a competitive advantage over C<sub>3</sub> grasses. Other factors, e.g. herbivores, fire, were probably also at play. Yet, their importance in explaining grass and, more generally paleovegetation changes in the savanna realm of East Africa remains to be quantified. It is likely that modeling will help in this task, providing that vegetation models will be able to take into account the functional traits of grasses (e.g. C<sub>4</sub> photosynthesis, quick resprouting after fire, high wet-season growth rates) that gives them a significant competitive advantage over woody plants in savannas ecosystems (e.g. Edwards et al., 2010).

### 6.3. Comparison with the general trend of increasing aridity since ~4.3 Ma

A continuous biomarker record from marine sediments off NE Africa (DSDP site 231) indicates that C<sub>4</sub> biomass expanded

relative to C<sub>3</sub> biomass in two phases during the last 12 Ma (with a reversal ~4.3 Ma), first between 12 and 4.5 Ma, then between 4.3 and 1 Ma, while the abundance of grass pollen decreased (Feakins et al., 2013). Grass pollen decreased relative to an increase in Chenopodiaceae/Amaranthaceae. C<sub>4</sub> grasslands may therefore have become less widespread than other C<sub>4</sub> vegetation types i.e. steppes or xerophytic bushlands when aridity increased (Bonnefille, 2010) following the onset of continental ice sheets since 5 Ma (Ravelo et al., 2004). The north Tanzanian paleobotanical record indicates that shrublands with C<sub>3</sub> grasses (>3.7 Ma) were replaced by shrublands with abundant C<sub>4</sub> grasses (~3.62 Ma), then by C<sub>4</sub> wooded grasslands (~2.66 Ma), which continued to be present at Laetoli and at Olduvai, and probably in the whole region after 2 Ma until present (Fig. 3) (Cerling and Hay, 1986; Rossouw and Scott, 2011; Magill et al., 2013a). On the contrary to the record for NE Africa, the increased C<sub>4</sub> biomass in N Tanzania is not characterized by increased in the relative abundance of Chenopodiaceae/Amaranthaceae pollen, which remain <5% at Laetoli, and <3–20% at Olduvai, and phytolith data do not exclude the presence of C<sub>3</sub> Pooidae grasses at Olduvai at the time of deposition of Tuff IF (newly dated at ~1.803 Ma; Deino, 2012) (Barboni et al., 2010). Regional differences therefore existed between Ethiopia and Tanzania in the vegetation response to increasing global aridity, which favored C<sub>4</sub> grasses in Tanzania but C<sub>4</sub> steppes or xerophytic bushlands in Ethiopian lowlands.

#### 6.4. Lower Pleistocene strong wet–dry variability (~1.9–1.7 Ma) and paleoenvironmental changes in the Olduvai Basin

The intensified Walker Circulation that followed the onset of continental ice sheets was accompanied by ~200-ky-long phase of high moisture availability in E Africa, and strong wet–dry variability. This period was characterized by drops in the East Mediterranean marine dust abundance, increased occurrence of sapropels in the Mediterranean Sea, and the formation of lakes in East Africa where volcano-tectonic processes linked with the EARS contributed to creating closed basins in the eastern and western branches of the Rift. There were large (but relatively ephemeral) deep freshwater lakes in the Kenyan and Ethiopian Rifts, but shallow, saline and alkaline lakes in north Tanzania (i.e. paleo-lake Olduvai, L. Natron, L. Eyasi, and L. Manyara) (e.g. Maslin and Christensen, 2007; Trauth et al., 2005, 2007; Feakins and Demenocal, 2010). In Tanzania this period also saw the formation of additional large and up to 4500 m high volcanoes in the Crater Highlands (e.g. Hay, 1976; Foster et al., 1997). In the botanical record it is not clear if this orographic change significantly increased aridity (by accentuating the rain shadow effect). The strong wet–dry rainfall climate variability between ~1.9–1.7 Ma, however, triggered rapid paleoenvironmental changes in the Olduvai Basin and nearby highlands. Paleo Lake Olduvai level fluctuated as much as 3 m, and its diameter varied from 7 to 15 km (Hay, 1990). Paleo lake Olduvai exposed a broad lake-margin zone at times of low lake levels, and remained shallow and saline-alkaline even during high levels (Hay, 1976; Hay and Kyser, 2001). Based on lithology, clay mineralogy, and geochemical proxy analyses, several major high and low lake levels were recognized in Bed I and Lower Bed II (Hay and Kyser, 2001; Sikes and Ashley, 2007; Deino, 2012) (Fig. 3). Lake level fluctuations, as well as paleosol development on lake margin flats were linked with rapid and drastic changes in rainfall/moisture availability in response to combined astronomical forcing effects of eccentricity (~100 ky cycle) and precession of the equinox (19 and 23 ky cycles) (linked to precession cycles) (Ashley, 2007; Deino, 2012; Beverly et al., 2014).

#### 6.5. Vegetation dynamic at Olduvai during the Lower Pleistocene strong wet–dry variability period (1.9–1.7 Ma): the role of geological faults in buffering regional drought

Paleovegetation changes associated with these extreme lake level variations can be confidently inferred from samples collected immediately below the dated tuffs or close by, although contemporaneity can only be assessed if there was contact with the tuff (Deino, 2012), e.g. for pollen samples FLKNNc, FLKa, FLKN1i, VEKa (Bonnefille, 1984), phytolith samples from FLK Zinj level 22, FLK N (Barboni et al., 2010; Ashley et al., 2010a), and from Tuff IF (Albert and Bamford, 2012) (Fig. 3). Paleovegetation changes associated with extreme lake level variations can also be confidently inferred from pollen samples collected in Lowermost Bed II in the Junction area at Olduvai, which sedimentary record was studied in detail (Liutkus and Ashley, 2003; Ashley et al., 2009). Paleovegetation changes associated with low lake levels are characterized by higher pollen abundance of xerophytic and halophytic taxa (e.g. *Suaeda*, Chenopodiaceae, Amaranthaceae, Portulacaceae), Sudano-Zambezian arboreal taxa (e.g. *Dombeya*, *Syzygium*, *Acacia*), and *Typha* relative to Poaceae and Afromontane taxa (~40% and <2%, respectively). On the contrary, Poaceae and Afromontane taxa are found in higher proportions (~70% and ~15%, respectively) during periods of high lake levels (Bonnefille, 1979, 1984; Bonnefille and Riollet, 1980). The increased abundance of Sudano-Zambezian arboreal taxa during dry periods may seem counterintuitive since they occur today in areas with annual precipitation >800 mm/y (White, 1983). Bonnefille (1984) interpreted variations in the arboreal Sudano-Zambezian pollen frequencies as changes in the “density of the tree cover in the extra-local wooded grassland” and changes in the Afromontane pollen frequencies as changes in the “extension of the forest among the regional vegetation”. Magill et al. (2013a,2013b) and Sikes and Ashley (2007) reconstructed mean annual precipitation averages of 200–700 mm/y, up to 800 mm/y for the period ~2–1.8 Ma. Today in tropical and subtropical regions of Africa, Australia, and South America, the probability for >20% tree cover vegetation with such low rainfall is <30% even under low fire regime (Hirota et al., 2011; Staver et al., 2011). Hence, it is unlikely that regional paleo-precipitation changes in the Olduvai basin produced significant changes in the lowland tree cover at the landscape scale, and that reduced precipitations favored Sudano-Zambezian species. Reduced regional precipitations, however, would have had an impact (reduction, species changes) on Afromontane forests from the nearby highlands. The increased relative abundance of Sudano-Zambezian species during dry periods (with inferred precipitation ~200 mm/y), however, can be explained by the presence of groundwater discharges areas (springs, wetlands...) in the east and southwestern side of the lake, which formed when lake level was low. Freshwater springs were more prone to favor the development of wetlands during periods of lake regression and low fluvial competence, i.e. during dry periods (Deocampo, 2002), as shown by geological, isotopic, biochemical, and lithological evidence which indicate that large (>1 km) freshwater wetlands affected the sedimentary and volcanic deposits of Olduvai beds I and II at specific periods only (Hay, 1990; Deocampo and Ashley, 1999a; Deocampo, 2002; Liutkus and Ashley, 2003; Liutkus et al., 2005; Ashley et al., 2009, 2010a, 2010b).

In basins with low-gradient margins (e.g. L. Eyasi, L. Natron, L. Makat in Ngorongoro Crater), freshwater wetlands start to form in playa margins when regression exposes lake flats and allows the water table to become emergent, and when faults and dikes act as aquifer outcrops or barriers which force water to the surface (Deocampo and Ashley, 1999b; Deocampo, 2002). Emergent water table allows several-km-long *A. xanthophloea* and *Hyphaene* palm

groves to occupy the northeaster playa margin of L. Eyasi today, despite annual precipitation <750 mm/y. Similarly at Manyara, an evergreen forest develops at the foothills of the rift escarpment only in the area where groundwater seeps out (Loth and Prins, 1986; and personal observations). Phytolith data from FLK Zinj and FLK N archaeological sites indicate dense tree and palm cover in localized areas within 50–100 m of tufa (spring) deposits and grasslands elsewhere, during low lake level periods at ~1.848/1.832 Ma and ~1.803 Ma when Tuff IC and IF were deposited (Barboni et al., 2010; Ashley et al., 2010a, 2010b). By now, it is clear that paleontological and archaeological sites in Olduvai Bed I and II (about 2.0–1.0 Ma) occurred close to freshwater springs and wetlands (Ashley et al., 2009, 2010c; Deocampo and Tactikos, 2010).

#### 6.6. How vegetation changes in N Tanzania may be related to human evolution: the example of *P. boisei*

Carbon and oxygen isotope studies of the tooth enamel of *P. boisei* specimens from all over East Africa, including Olduvai, indicate that its diet was essentially made of C<sub>4</sub> plants (~80%) unlike that of any other fossil hominin, but similar to that of grass-eating animals (e.g. warthogs, hippos), and that it was also strongly water-dependent (Van der Merwe et al., 2008; Cerling et al., 2011; Ungar and Sponheimer, 2011). Similar analyses conducted on *H. habilis* specimens from Olduvai indicate that its diet included <50% of C<sub>4</sub> plants (Van der Merwe et al., 2008; Ungar and Sponheimer, 2011). Hence, *P. boisei* and its contemporary *H. habilis* had very contrasting diets despite living in the same area. The geological and paleobotanical evidence of fresh-water springs and spring-associated woodlands at FLK N and FLK Zinj sites suggest spring-woodland/forest in a grass-dominated biome. Such an ecosystem offers contrasting plant distributions over the landscape because of the presence and proximity of freshwater springs. The paleobotanical data support the hypothesis that *P. boisei* and *H. habilis* may have occupied different ecological niches within the same area. If *P. boisei* was a C<sub>4</sub> sedge consumer as suggested, then its occurrence and probably its eventual extinction may be directly linked to spring occurrence, and therefore to tectonic and faulting activity of the Serengeti–Crater Highlands region. It is interesting to note in this respect, that *P. boisei* last occurrence datum in the Tanzanian record is ~1.2 Ma (e.g. Potts, 2013), when a major phase of rift faulting that strongly modified the landscape and hydrogeology occurred in the Crater Highland Region (Hay, 1990; Foster et al., 1997).

## 7. Conclusion

Human evolution has been challenged by environmental factors and the botanical record for northern Tanzania provides important insights on one key feature: the vegetation. The botanical record for Plio-Pleistocene northern Tanzania suggests some similarity between past and present-day vegetation at the landscape scale, with the continuous presence of drought-adapted trees and shrubs in the lowlands, and Afromontane forests in the highlands since 4 Ma in the Serengeti–Crater Highlands region. Yet, by considering the full botanical record available to date, we see that major vegetation changes affected this region, and that the EARS structural development played a major role in triggering these changes, both at the regional scale by controlling precipitation and Afromontane forests distribution, and at the local scale by creating a unique hydrological context that allowed the formation of “oases”.

If volcanoes strongly transformed the landscape and modified the regional climate, the faulting triggered by the opening of the East African Rift is another geological factor that affected both fauna and flora. Faulting linked to the development of the East African Rift led to the slow tilting of the Olduvai basin towards the East, which

in turn led to the displacement of Paleolake Olduvai to the East and, eventually, to its disappearance (about 1.2 Ma) and to the erosion of Olduvai Gorge (since 500,000 yrs) (Hay, 1976; Foster et al., 1997; Hay and Kyser, 2001). Faulting modified the nature of the stream drainage within the Olduvai Basin, not only by displacing the drainage sump to the east (Hay, 1976), but also by creating aquifer outcrops or barriers that forced groundwater to the surface, therefore leading to the development of freshwater wetlands (Deocampo and Ashley, 1999b; Deocampo, 2002). Freshwater wetlands occurred at Olduvai, at Peninj, and probably elsewhere in the Rift given the tectonic context favorable to close-basin sedimentation and faulting. Occurrence and abundance of freshwater spots interspersed along the Rift would have allowed faunal (including hominin) movements at the regional scale. However, the timing and patterns of faunal movements (theoretically caused by freshwater and resource availability) in relation with the wet–dry climate fluctuations still requires more paleoenvironmental and archaeological studies to be elucidated. During wet periods, lake levels were high, groundwater-fed wetlands rare or absent, but freshwater was potentially more available from rivers. Animals would therefore prefer to occupy areas other than those around the saline lake. On the contrary, during dry periods, lake levels were low, freshwater wetlands were most expanded, while riverbeds were mostly dry. During dry periods, faunal movements would then be towards the contracted lake where those oases occurred. Dry periods would have drawn a large variety of animals to those highly localized wetlands and groundwater woodlands, and therefore enhanced species interactions and competition at places like Olduvai lake margins. If springs allowed the development of wetlands and groundwater forests and woodlands at places like Olduvai, that are arid today, then human evolution and hominin biogeography is closely linked to the tectonic activity of the East African Rift System.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quaint.2014.01.016>.

## 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. *Journal of Human Evolution* 63, 342–350.
- Albert, R.M., Bamford, M.K., Cabanes, D., 2006. Taphonomy of phytoliths and macroplants in different soils from Olduvai Gorge (Tanzania) and the application to Plio-Pleistocene palaeoanthropological samples. *Quaternary International* 148, 78–94.
- Albert, R.M., Bamford, M.K., Cabanes, D., 2009. Palaeoecological significance of palms at Olduvai Gorge, Tanzania, based on phytolith remains. *Quaternary International* 193, 41–48.

- Anderson, T.M., 2008. Plant compositional change over time increases with rainfall in Serengeti grasslands. *Oikos* 117, 675–682.
- Andrews, P., Bamford, M.K., 2008. Past and present vegetation ecology of Laetoli, Tanzania. *Journal of Human Evolution* 54, 78–98.
- Ashley, G., 2007. Orbital rhythms, monsoons, and playa lake response, Olduvai Basin, equatorial East Africa (ca. 1.85–1.74 Ma). *Geology* 35, 1091–1094.
- Ashley, G., 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. *Quaternary Research* 74, 304–314.
- Ashley, G., 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. *Quaternary Research* 74, 333–343.
- Ashley, G., 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. *Journal of Sedimentary Research* 80, 703–709.
- Ashley, G., 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). *Palaeogeography, Palaeoclimatology, Palaeoecology* 272, 1–16.
- Bamford, M.K., 2005. Early Pleistocene fossil wood from Olduvai Gorge, Tanzania. *Quaternary International* 129, 15–22.
- Bamford, M.K., 2011a. Fossil woods. In: Harrison, T. (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context, Geology, Geochronology, Paleocology and Paleoenvironment*, vol. 1. Springer Science + Business Media B.V., Dordrecht, pp. 217–233.
- Bamford, M.K., 2011b. Fossil leaves, fruits and seeds. In: Harrison, T. (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context, Geology, Geochronology, Paleocology and Paleoenvironment*, vol. 1. Springer Science + Business Media B.V., Dordrecht, pp. 235–252.
- Bamford, M.K., 2012. Fossil sedges, macroplants, and roots from Olduvai Gorge, Tanzania. *Journal of Human Evolution* 63, 351–363.
- 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. *Quaternary International* 148, 95–112.
- Bamford, M.K., Stanistreet, I.G., Stollhofen, H., Albert, R.M., 2008. Late Pliocene grassland from Olduvai Gorge, Tanzania. *Palaeogeography, Palaeoclimatology, Palaeoecology* 257, 280–293.
- Barboni, D., Ashley, G., 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. *Quaternary Research* 74, 344–354.
- Barboni, D., Bremond, L., 2009. Phytoliths of East African grasses: an assessment of their environmental and taxonomic significance based on floristic data. *Review of Palaeobotany and Palynology* 158, 29–41.
- Barboni, D., Bremond, L., Bonnefille, R., 2007. Comparative study of modern phytolith assemblages from inter-tropical Africa. *Palaeogeography Palaeoclimatology Palaeoecology* 246, 454–470.
- Beverly, E.J., Ashley, G.M., Driese, S.G., 2014. Reconstruction of a Pleistocene paleocatena using micromorphology and geochemistry of lake margin paleo-Vertisols, Olduvai Gorge, Tanzania. *Quaternary International* 322–323, 78–94.
- Bonnefille, R., 1979. Méthode palynologique et reconstitutions paléoclimatiques au Cénozoïque dans le Rift East Africain. *Bulletin Societe Géologique France* 21, 331–342.
- Bonnefille, R., 1984. Palynological research at Olduvai Gorge. In: Lea, J.S., Link Powars, N., Swanson, W. (Eds.), *National Geographic Society Research Reports* 17, Washington, DC, pp. 227–243.
- Bonnefille, R., 1995. A reassessment of the Plio-Pleistocene pollen record of East Africa. In: Vrba, E., Denton, G., Partridge, T., Burckle, L. (Eds.), *Paleoclimate and Evolution, Paleoclimate and Evolution with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 299–310.
- Bonnefille, R., 2010. Cenozoic vegetation, climate changes and hominid evolution in tropical Africa. *Global and Planetary Change* 72, 390–411.
- Bonnefille, R., Lobreau, D., Riollet, G., 1982. Fossil pollen of Ximenia (olacaceae) in the Lower Pleistocene of Olduvai, Tanzania – paleological implications. *Journal of Biogeography* 9, 469–486.
- Bonnefille, R., Riollet, G., 1980. Palynologie, végétation et climats de Bed 1 et Bed 2 à Olduvai, Tanzanie. In: Leakey, R.E., Ogot, B.A. (Eds.), *Presented at the Proceedings of the 8th Pan-African Congress of Prehistory and Quaternary Studies*. Tillmiap, Nairobi, pp. 123–127.
- 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.
- Bremond, L., Alexandre, A., Hely, C., Guiot, J., 2005a. 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. *Global and Planetary Change* 45, 277–293.
- Bremond, L., Alexandre, A., Peyron, O., Guiot, J., 2005b. Grass water stress estimated from phytoliths in West Africa. *Journal of Biogeography* 32, 311–327.
- Bremond, L., Alexandre, A., Peyron, O., Guiot, J., 2008a. Definition of grassland biomes from phytoliths in West Africa. *Journal of Biogeography* 35, 2039–2048.
- Bremond, L., Alexandre, A., Wooller, M.J., Hely, C., Williamson, D., Schafer, P.A., Majule, A., Guiot, J., 2008b. Phytolith indices as proxies of grass subfamilies on East African tropical mountains. *Global and Planetary Change* 61, 209–224.
- Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeography Palaeoclimatology Palaeoecology* 97, 241–247.
- Cerling, T.E., Hay, R.L., 1986. An isotopic study of paleosol carbonates from Olduvai Gorge. *Quaternary Research* 25, 63–78.
- Cerling, T.E., Mbua, E., Kirera, F.M., Manthi, F.K., Grine, F.E., Leakey, M.G., Sponheimer, M., Uno, K.T., 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proceedings of the National Academy of Sciences of the United States of America*. <http://dx.doi.org/10.1073/pnas.1104627108>.
- Clarke, R.J., 2012. A *Homo habilis* maxilla and other newly-discovered hominid fossils from Olduvai Gorge, Tanzania. *Journal of Human Evolution* 63, 418–428.
- Deino, A., 2011. <sup>40</sup>Ar/<sup>39</sup>Ar dating of Laetoli, Tanzania. In: Harrison, T. (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context, Geology, Geochronology, Paleocology and Paleoenvironment, Vertebrate Paleobiology and Paleoanthropology*, vol. 1. Springer Science + Business Media B.V., pp. 77–97.
- Deino, A., 2012. <sup>40</sup>Ar/<sup>39</sup>Ar dating of Bed I, Olduvai Gorge, Tanzania, and the chronology of early Pleistocene climate change. *Journal of Human Evolution* 63, 251–273.
- DeMenocal, P.B., 1995. Plio-Pleistocene African climate. *Science* 270, 53–59.
- DeMenocal, P.B., 2004. African climate change and faunal evolution during the Pliocene-Pleistocene. *Earth and Planetary Science Letters* 220, 3–24.
- Deocampo, D., Ashley, G., 1999a. Siliceous islands in a carbonate sea: modern and Pleistocene spring-fed wetlands in Ngorongoro Crater and Oldupai Gorge, Tanzania. *Journal of Sedimentary Research* 69, 974–979.
- Deocampo, D., Ashley, G., 1999b. Sedimentology, Geochemistry, and Paleohydrologic Potential of Groundwater Wetlands in East African Lacustrine Basins. In: *Presented at the International Union for Quaternary Research, XV Congress*, Durban, South Africa, p. 52.
- Deocampo, D.M., 2002. *Sedimentary Processes and Lithofacies in Lake-Margin Groundwater-fed Wetlands in East Africa*.
- 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. *Quaternary Research* 74, 411–423.
- Dominguez-Rodrigo, M., February 2014. Is the “savanna hypothesis” a dead concept for explaining the emergence of early hominins? *Current Anthropology* 55 (1), 59–81.
- Dominguez-Rodrigo, M., Lopez-Saez, J.A., Vincens, A., Alcalá, L., Luque, L., Serrallonga, J., 2001a. Fossil pollen from the Upper Humbu Formation of Peninj (Tanzania): hominid adaptation to a dry open Plio-Pleistocene savanna environment. *Journal of Human Evolution* 40, 151–157.
- Dominguez-Rodrigo, M., Serrallonga, J., Juan-Tresserras, J., Alcalá, L., Luque, L., 2001b. Woodworking activities by early humans: a plant residue analysis on Acheulian stone tools from Peninj (Tanzania). *Journal of Human Evolution* 40, 289–299.
- Dominguez-Rodrigo, M., Mabulla, A., Luque, L., Thompson, J.W., Rink, J., Bushozi, P., Diez-Martin, F., Alcalá, L., 2008. A new archaic *Homo sapiens* fossil from Lake Eyasi, Tanzania. *Journal of Human Evolution* 54, 899–903.
- Dominguez-Rodrigo, M., Pickering, T.R., Baquedano, E., Mabulla, A., Mark, D.F., Musiba, C., Bunn, H.T., Uribelarrea, D., Smith, V., Diez-Martin, F., Pérez-González, A., Sánchez, P., Santonja, M., Barboni, D., Gidna, A., Ashley, G., Yravedra, J., Heaton, J.L., Arriaza, M.C., 2013. First partial skeleton of a 1.34-million-year-old *Paranthropus boisei* from Bed II, Olduvai Gorge, Tanzania. *PLoS One* 8, e80347.
- Edwards, E.J., Osborne, C.P., Stroemberg, C.A.E., Smith, S.A., Bond, W.J., Christin, P.-A., Cousins, A.B., Duvall, M.R., Fox, D.L., Freckleton, R.P., Ghannoum, O., Hartwell, J., Huang, Y., Janis, C.M., Keeley, J.E., Kellogg, E.A., Knapp, A.K., Leakey, A.D.B., Nelson, D.M., Saarela, J.M., Sage, R.F., Sala, O.E., Salamin, N., Still, C.J., Tipler, B., Consortium, C.G., 2010. The origins of C-4 grasslands: integrating evolutionary and ecosystem science. *Science* 328, 587–591.
- Ehleringer, J.R., Cerling, T.E., Helliker, B.R., 1997. C4 photosynthesis, atmospheric CO<sub>2</sub>, and climate. *Oecologia* 112, 285–299.
- 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.
- Foster, A., Ebinger, C., Mbede, E., Rex, D., 1997. Tectonic development of the northern Tanzanian sector of the East African Rift System. *Journal of the Geological Society* 154, 689–700.
- Greenway, P.J., Vesey-Fitzgerald, D.F., 1969. Vegetation of Lake Manyara National Park. *Journal of Ecology* 57, 127–149.
- Hall, L.S., Krausman, P.R., Morrison, M.L., 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* 25, 173–182.
- Harrison, T., 2011. Hominins from the Upper Laetoli and Upper Ndolanya Beds, Laetoli. In: Harrison, T. (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context, Fossil Hominins and the Associated Fauna*, vol. 2. Springer Science + Business Media B.V., Dordrecht, pp. 141–188.
- Hay, R.L., 1976. *Geology of the Olduvai Gorge: a Study of Sedimentation in a Semi-arid Basin*. University of California Press.
- Hay, R.L., 1987. Geology of the Laetoli area. In: Leakey, M.D., Harris, J.M. (Eds.), *Laetoli: a Pliocene Site in Northern Tanzania*. Clarendon, Oxford, pp. 23–47.
- Hay, R.L., 1990. Olduvai Gorge: a case history in the interpretation of hominid paleoenvironments in East Africa. In: Laporte, L.F. (Ed.), *Establishment of a Geologic Framework for Paleoanthropology*, pp. 23–37.
- Hay, R.L., Kyser, T.K., 2001. Chemical sedimentology and paleoenvironmental history of Lake Olduvai, a Pliocene lake in northern Tanzania. *Geological Society of America Bulletin* 113, 1505–1521.
- Herlocker, D.J., Dirschl, H.J., 1972. Vegetation of the Ngorongoro Conservation Area, Tanzania. In: *Canadian Wildlife Service Report Series No. 19*.

- Hirota, M., Holmgren, M., Van Nes, E.H., Scheffer, M., 2011. Global resilience of tropical forest and savanna to critical transitions. *Science* 334, 232–235.
- Holdo, R.M., Holt, R.D., Fryxell, J.M., 2009. Grazers, browsers, and fire influence to extent and spatial pattern of tree cover in Serengeti. *Ecological Applications* 19, 95–109.
- Isaac, G.L., 1965. The stratigraphy of the Peninj Group and the provenance of the Natron Australopithecine mandible. *Quaternaria* 7, 101–130.
- Isaacs, G.L., Curtis, G.H., 1974. Age of early Acheulian industries from the Peninj Group, Tanzania. *Nature* 249, 624–627.
- Jacobs, B.F., Pan, A.D., Scotese, C.R., 2010. A review of the Cenozoic vegetation history of Africa. In: Werdelin, L. (Ed.), *Cenozoic Mammals of Africa*. University of California Press, pp. 57–72.
- Leakey, L.S.B., Leakey, M.D., 1964. Recent discoveries of fossil hominids in Tanganyika: at Olduvai and near Lake Natron. *Nature* 202, 5–7.
- Leakey, M.D., 1971. *Olduvai Gorge*. Cambridge University Press.
- Liutkus, C., Ashley, G., 2003. Facies model of a semiarid freshwater wetland, Olduvai Gorge, Tanzania. *Journal of Sedimentary Research* 73, 691–705.
- Liutkus, C., Wright, J., Ashley, G., Sikes, N., 2005. Paleoenvironmental interpretation of lake-margin deposits using delta C-13 and delta O-18 results from early Pleistocene carbonate rhizoliths, Olduvai Gorge, Tanzania. *Geology* 33, 377–380.
- Livingstone, D.A., Clayton, W.D., 1980. An altitudinal cline in tropical African grass floras and its paleoecological significance. *Quaternary Research* 13, 392–402.
- Loth, P.E., Prins, H.H.T., 1986. Spatial patterns of the landscape and vegetation of Lake Manyara National Park. *ITC Journal* 2, 115–130.
- Magill, C.R., Ashley, G.M., Barboni, D., Freeman, K., 2012. High-resolution Reconstruction of Early Human Habitats at FLK Zinjanthropus (Olduvai Gorge, Tanzania): Biomarker, Stable Isotope and Phytolith Evidence. In: Presented at the Did Climate Change Shape Human Evolution Symposium. Columbia University's Lamont-Doherty Earth Observatory, Palisades NY, USA.
- Magill, C.R., Ashley, G.M., Freeman, K.H., 2013a. Ecosystem variability and early human habitats in eastern Africa. *Proceedings of the National Academy of Sciences of the United States of America* 110, 1167–1174.
- Magill, C.R., Ashley, G.M., Freeman, K.H., 2013b. Water, plants, and early human habitats in eastern Africa. *Proceedings of the National Academy of Sciences of the United States of America* 110, 1175–1180.
- Manning, A.D., Lindenmayer, D.B., Nix, H.A., 2004. Continuum and Umwelt: novel perspectives on viewing landscapes. *Oikos* 104, 621–628.
- Maslin, M.A., Christensen, B., 2007. Tectonics, orbital forcing, global climate change, and human evolution in Africa: introduction to the African paleoclimate special volume. *Journal of Human Evolution* 53, 443–464.
- Mollet, G.F., 2007. Petrochemistry and Geochronology of Ngorongoro Volcanic Highland Complex (NVHC) and its Relationship to Laetoli and Olduvai Gorge, Tanzania. ProQuest.
- Mollet, G.F., Swisher, C.C., Feigenson, M.D., Carr, M.J., 2011. Petrology, geochemistry and age of Satiman, Lemagurut and Oldeani: sources of the volcanic deposits of the Laetoli area. In: Harrison, T. (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context, Geology, Geochronology, Paleoenvironment and Paleoenvironment*, vol. 1. Springer Science + Business Media B.V., Dordrecht, pp. 99–119.
- 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. *Review of Palaeobotany and Palynology* 178, 43–58.
- Pearcy, R.W., Ehleringer, J., 1984. Comparative ecophysiology of C<sub>3</sub> and C<sub>4</sub> plants. *Plant Cell Environment* 7, 1–13.
- Peters, C., Blumenshine, R., Livingstone, D.A., Marean, C.W., Harrison, T., Armour-Chelu, M., Andrews, P., Bernor, R.L., Bonnefille, R., Werdelin, L., 2008. Paleoenvironment of the Serengeti-Mara ecosystem. In: Sinclair, A.R.E., Packer, C., Mduma, S.A., Fryxell, J.M. (Eds.), *Serengeti III: Human Impacts on Ecosystem Dynamics*. University of Chicago Press, Chicago, pp. 47–94.
- Post-Beittenmiller, D., 1996. Biochemistry and Molecular Biology of Wax Production in plants. *Annual Review of Plant Physiology and Plant Molecular Biology* 47, 405–430.
- Potts, R., 1996. Evolution and climate variability. *Science* 273, 922–923.
- Potts, R., 2013. Hominin evolution in settings of strong environmental variability. *Quaternary Science Reviews* 73, 1–13.
- Ravelo, A.C., Andraesen, D.H., Lyle, M., Olivarez Lyle, A., Wara, M.W., 2004. Regional climate shifts caused by gradual global cooling in the Pliocene epoch. *Nature* 429, 263–267.
- 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.
- Rightmire, G.P., 1983. The Lake Nduut cranium and early Homo sapiens in Africa. *American Journal of Physical Anthropology* 61, 245–254.
- Rossouw, L., Scott, L., 2011. Phytoliths and pollen, the microscopic plant remains in Pliocene volcanic sediments around Laetoli, Tanzania. In: Harrison, T. (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context, Geology, Geochronology, Paleoenvironment and Paleoenvironment*, vol. 1. Springer Science + Business Media B.V., Dordrecht.
- Sage, R.F., 2004. The evolution of C<sub>4</sub> photosynthesis. *New Phytologist* 161, 341–370.
- 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. *Global Ecology and Biogeography* 17, 432–447.
- Seki, O., Foster, G.L., Schmidt, D.N., Mackensen, A., Kawamura, K., Pancost, R.D., 2010. Alkenone and boron-based Pliocene pCO<sub>2</sub> records. *Earth and Planetary Science Letters* 292, 201–211.
- Sepulchre, P., Ramstein, G., Fluteau, F., Schuster, M., Tiercelin, J.-J., Brunet, M., 2006. Tectonic uplift and eastern Africa aridification. *Science* 313, 1419–1423.
- Shultz, S., Maslin, M., 2013. Early human expansion and dispersal influenced by African climate pulses. *PLoS One* 8, e76750.
- Shultz, S., Nelson, E., Dunbar, R.I.M., 2012. Hominin cognitive evolution: identifying patterns and processes in the fossil and archaeological record. *Philosophical Transactions, Royal Society B, Biological Sciences* 367, 2130–2140.
- Sikes, N.E., 1994. Early hominid habitat preferences in East Africa: paleosol carbon isotopic evidence. *Journal of Human Evolution* 27, 25–45.
- Sikes, N.E., Ashley, G.M., 2007. Stable isotopes of pedogenic carbonates as indicators of paleoenvironment in the Plio-Pleistocene (upper Bed I), western margin of the Olduvai Basin, Tanzania. *Journal of Human Evolution* 53, 574–594.
- 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.
- Tieszen, L.L., Senyimba, M.M., Imbamba, S.K., Troughton, J.H., 1979. The distribution of C<sub>3</sub> and C<sub>4</sub> grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia* 37, 337–350.
- Trauth, M.H., Maslin, M.A., Deino, A., Strecker, M.R., 2005. Late Cenozoic moisture history of East Africa. *Science* 309, 2051–2053.
- Trauth, M.H., Maslin, M.A., Deino, A.L., Strecker, M.R., Bergner, A.G.N., Dühnforth, M., 2007. High- and low-latitude forcing of Plio-Pleistocene East African climate and human evolution. *Journal of Human Evolution* 53, 475–486.
- Ungar, P.S., Sponheimer, M., 2011. The diets of early hominins. *Science* 334, 190–193.
- Van der Merwe, N.J., Masao, F.T., Bamford, M.K., 2008. Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. *South African Journal of Science* 104, 153–155.
- Vermeij, G.J., 1993. *Evolution and Escalation: An Ecological History of Life*. Princeton University Press.
- White, F., 1983. *The Vegetation of Africa, a Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa (3 Plates, Northwestern Africa, Northeastern Africa, and Southern Africa, 1:5,000,000)*. United Nations Education, Science, and Cultural Organization, Paris.
- Wynn, J.G., Bird, M.I., 2007. C<sub>4</sub>-derived soil organic carbon decomposes faster than its C<sub>3</sub> counterpart in mixed C<sub>3</sub>/C<sub>4</sub> soils. *Global Change Biology* 13, 2206–2217.