Influences of dietary niche expansion and Pliocene environmental changes on the origins of stone tool making

Rhonda L Quinn, Jason Lewis, Jean-Philip Brugal, Christopher J Lepre, Alexandr Trifonov, Sonia Harmand

Title: Influences of dietary niche expansion and Pliocene environmental changes on the origins of stone tool making

Authors:
Rhonda L. Quinn[1,2], Jason Lewis[3], Jean-Philip Brugal[4], Christopher J. Lepre[2], Alexandr Trifonov[1], Sonia Harmand[3,5,6]

Authors' affiliations:
[1]Department of Sociology, Anthropology and Social Work, Seton Hall University, 400 South Orange Ave, South Orange, NJ 07079

[2]Department of Earth and Planetary Sciences, Rutgers University, 610 Taylor Road, Piscataway, NJ 08854

[3]Turkana Basin Institute and Department of Anthropology, Stony Brook University, Stony Brook, NY 11794-4364

[4]Aix Marseille Université, CNRS, Minist. Cult., UMR 7269 LAMPEA, Maison Méditerranéenne des Sciences de l'Homme, BP 647, 5 rue du Château de l'Horloge, F-13094, Aix-en-Provence Cedex 2, France

[5]CNRS, UMR 7055, Préhistoire et Technologie, Université Paris Ouest Nanterre La Défense, 21 allée de l'Université, 92023 Nanterre Cedex, France

[6]Institut Français de Recherche en Afrique (IFRA), UMIFRE, USR 3336, CNRS, Laikipia Road, Kileleshwa, Nairobi, Kenya.

*Corresponding Author:
Rhonda L. Quinn, Ph.D.
Department of Sociology, Anthropology and Social Work
Seton Hall University
400 South Orange Ave
South Orange, NJ 07079
Email: rhonda.quinn@shu.edu

Submitted to Palaeo3

Words: ~10673 (w/o abstract, references)
Tables: 1
Supplementary Tables: 2
Figures: 12

Keywords: Omo-Turkana Depression, paleosol isotopes, enamel isotopes, Pliocene climate, Lomekwi 3 archaeological site

Abstract

The world's oldest known stone tools discovered at the Pliocene site of Lomekwi 3 (LOM3) in the Nachukui Formation, northern Kenya, signals a prodigious behavioral change in the hominin lineage. LOM3, dated to 3.3 Ma, is significantly earlier than the first appearance of genus *Homo* and coincides with the onset of the Mid-Pliocene Warm Period, warranting new phylogenetic and environmental explanations for the origins of hominin stone tool making behaviors. Here we examined Pliocene paleoenvironments (4.3-3.0 Ma) within the Omo-Turkana Depression (OTD) with paleosol pedogenic carbonate (PC) and faunal enamel carbonate (EC) $\delta^{13}C$ and $\delta^{18}O$ values. Amidst the gradual shift toward more grassy environments, intranodular $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ variation slightly increased through time. Three of fourteen ungulate herbivore taxa yielded statistically significant increases in $\delta^{13}C_{EC}$ values. When all ungulate herbivore $\delta^{13}C_{EC}$ values are grouped by feeding categories (C_3-browsers, C_3-C_4-mixed feeders, C_4-grazers) there is evidence that the C_3-C_4-mixed feeding niche contracted and shifted toward the C_4-grazing niche as hominins expanded their dietary breadth during the middle Pliocene. Only one of nine taxa showed a significant decrease in $\delta^{18}O_{EC}$ values across the study interval. Abrupt, significant environmental perturbations are not evident during LOM3 times in the OTD, casting doubt on variability selection or pulsed humidity as selective forces for middle Pliocene technological innovations. We propose that a long-term feedback system involving gradual environmental changes and biotic dietary competition influenced a suite of hominin adaptations to a broad dietary niche, culminating in the origins of stone tool making behaviors.

1. Introduction

1.1 Repositioning the adaptive milestones of early African hominins

Stone tool making is characterized as a critical adaptive threshold, which once crossed, paved the way toward language, complex social interactions and global dispersal (Ambrose, 2001). The ability to make stone tools was originally thought to be one of the defining characteristics of genus *Homo*; its earliest member, *Homo habilis* ("handy man"), was named for the adaptation (Leakey et al., 1964). The origin and evolution of stone tool technologies associated with genus *Homo* have been linked to environmental perturbations (Clark, 1960; Potts, 1996, 1998, 2012, 2013; Potts et al., 2017; Ziegler et al., 2013). Potts and Faith (2015) showed that early members of genus *Homo* were bombarded with near consecutive periods of environmental instability during the late Pliocene-early Pleistocene associated with global climatic forcing factors via teleconnections to the tropics. Global climatic and large-scale environmental changes emphasizing the increasing presence of open and variable ("mosaic") landscapes were traditionally and continue to be evoked as primary selective pressures for hominin speciation events (Alemseged et al., 2020; Brain, 1981; Bromage and Schrenk, 1995; deMenocal, 1995, 2004; Stanley, 1992; Trauth et al., 2005, 2007, 2009; Vrba, 1985, 1995, 1999) and influences of specific adaptations including thermoregulation (Ruff, 1991, 1993; Ruff and Walker, 1993; Wheeler, 1991, 1992a, 1992b, 1994), energetic efficiency (Aiello and Wheeler, 1995; Aiello and Wells, 2002; Bramble and Leiberman, 2004; Leonard and Robertson, 1997; Wheeler, 1993), and encephalization (Ash and Gallop, 2007; Bailey and Geary, 2009; Shultz and Maslin, 2013).

Published in 2015 (Harmand et al., 2015) the Lomekwi 3 archaeological site, (LOM3; Figure 1) located in the Nachukui Formation of the Omo-Turkana Depression (OTD; northern Kenya-southern Ethiopia; Figure 2) and dated to 3.3 Ma, revealed that Pliocene hominins made stone tools substantially earlier than previously thought. As compared to the evidence of stone tool *use* with the discovery of cutmarked bone at Dikika dated to 3.4 Ma (McPherron et al., 2010), LOM3 provided evidence of stone tool *manufacturing*. Prior to the discovery of LOM3, the earliest known stone tool making behaviors were preserved at Gona (Ethiopia) and dated to 2.6-2.5 Ma (Semaw et al., 1997). The LOM3 site and the surrounding paleontological collecting area are substantially older than the known origins of genus *Homo* dated to 2.8 Ma from Ledi-Geraru (Ethiopia) (Villmoare et al. 2015). Genus *Homo* identified as the first, and perhaps only, stone toolmaker in the earliest Pleistocene has been questioned for some time (e.g., Panger et al., 2002; Susman, 1991), but these finds likely place the tools in the hands of australopithecine-like hominins. In eastern and north-central Africa, hominin species that date to the middle Pliocene have been designated as *Australopithecus afarensis* (Kimbel and Delezene, 2009), *A. deyiremeda* (Haile-Selassie et al., 2015), *A. bahrelghazali* (Brunet et al., 1996) and *Kenyanthropus platyops* (Leakey et al., 2001). Although specimens were initially identified as *A. afarensis* (Brown et al., 2001; Kimbel, 1988; Ward et al., 1999a), the majority of middle Pliocene hominin specimens found in the OTD has been designated as *K. platyops* (Wood and Leakey, 2011).

From excavations in 2011, 2012, and 2014, the West Turkana Archaeological Project (WTAP) recovered 165 surface and in situ artifacts at LOM3 (Harmand et al., 2015; Lewis and Harmand, 2016). WTAP excavations recovered cores and flakes that are

113 significantly larger than those from the Early Oldowan (Braun et al., 2019; Harmand et
114 al., 2015; Roche et al., 1999; Stout, 2010) and include heavy anvils, percussors, and
115 worked and split cobbles made predominantly from local basalts. Although the LOM3
116 artifacts do not indicate a mastery of stone knapping demonstrated by Oldowan
117 toolmakers, as detailed in Lewis and Harmand (2016), they provide evidence of
118 sensorimotor performance and an effective control of elementary percussive gestures
119 beyond what has been observed in chimpanzees either in the wild or during experiments
120 in captivity.

121 Stone tool making and use were not the only novel behaviors of Pliocene African
122 hominins. Several species show evidence for a significant dietary shift with the
123 incorporation of C_4 foods as revealed by stable carbon isotopic values of enamel
124 carbonate (denoted here as $\delta^{13}C_{EC}$) (Cerling et al., 2013b; Lee-Thorp et al., 1994;
125 Sponheimer and Lee-Thorp, 1999a). Middle Pliocene hominin $\delta^{13}C_{EC}$ values grouped by
126 identified species and/or separated into temporal bins (e.g., Patterson et al., 2019) show a
127 directional shift toward consumption of C_4 foods, which may have included C_4 sedges
128 and grass seeds, underground storage organs, termites and other arthropods, bird's eggs,
129 as well as C_3-C_4-mixed- and C_4-feeding vertebrates (Peters and Vogel, 2005; Sponheimer
130 and Lee-Thorp, 2003; Yaekel et al., 2007). There is also an increase in $\delta^{13}C_{EC}$ variance,
131 which has been interpreted to indicate dietary niche expansion relative to the earliest
132 hominins (i.e., *Ardipithecus* and *A. anamensis*) and extant chimpanzees (Antón et al.,
133 2014; Levin et al., 2015; Lee-Thorp et al., 2003, 2010; Sponheimer et al., 2013; van der
134 Merwe et al., 2003). The earliest mixed C_3-C_4 feeding hominins with measured $\delta^{13}C_{EC}$
135 values and identified to species are *A. bahrelghazali* at 3.6 Ma (Lee-Thorp et al., 2012),

A. afarensis at 3.4 Ma (Wynn et al., 2013), and in the OTD, *K. platyops* at 3.4 Ma (Cerling et al., 2013b) (Figure 3). Consumption of C_4 food resources by hominins has been found as early as 3.7 Ma at Woranso-Mille (Ethiopia); these hominin specimens were not identified to species but are likely australopithecines (Levin et al., 2015).

1.2 Searching for environmental forces of hominin evolution

Finding evidence for stone tool making behaviors at 3.3 Ma potentially by australopithecine-like hominins complicates hypotheses of temporally discrete environmental perturbations as primary selective pressures for this adaptive milestone (Figure 4A-D). The formation of deep lakes forced by eccentricity-modulated precession has been proposed as a mechanism for environmental change influencing human evolution (Donges et al., 2011; Maslin et al., 2014; Trauth et al., 2005, 2007, 2009). Deep African lakes are interpreted to have occurred throughout the Pliocene (e.g., Trauth et al., 2005), but an identified lake phase in the OTD, Lake Lokochot (Feibel, 2011), ends approximately 200 Ka prior to the LOM3 site date (Figure 4D). Potts (1996, 1998) links high environmental variability to several hominin speciation events and technological innovations, but the middle Pliocene appears to encompass a long period of low climatic variability (Potts and Faith, 2015) (Figure 4C). Modeled global pCO_2 concentrations by Stap et al. (2016) (Figure 4A) suggests a steady decrease through time aligning with trends in sea level, temperature, and global ice volume (Figure 4B).

The LOM3 site is coincident with the start of the mid-Pliocene Warm Period (mPWP: 3.264–3.025 Ma: Dowsett et al., 2010; Haywood et al., 2010), which is commonly used as an analogue for anthropogenic conditions of today (Burke et al.,

159 2018). The mPWP is characterized as “a warm blip,” potentially ~2-3°C degrees warmer
160 in the tropics than present day (Haywood et al., 2013), high atmospheric CO_2 levels, and
161 low seasonal variability in rainfall (Pagani et al., 2010; Raymo et al., 1996). The warm
162 and wet Pliocene world (Salzmann et al., 2011) is often used to contrast environmental
163 proxy records of the late Pliocene when Earth begins its major climatic reorganization
164 near the onset of the Quaternary ice age (Maslin et al., 1998; Mudelsee and Raymo, 2005;
165 Shackleton and Opdyke, 1977; Willeit et al., 2015). Compared to the early Pliocene,
166 however, mPWP climatic proxy records appear to indicate relatively constant conditions
167 (Haywood et al., 2016). Permanent El Niño conditions are interpreted for the early and
168 middle Pliocene due to a deep eastern Pacific thermocline and shallow sea-surface-
169 temperature gradient across the equatorial Pacific (Fedorov et al., 2006; Molnar and
170 Cane, 2002; Wara et al., 2005).
171 Characterization of the LOM3 site environment with the pedogenic carbonate
172 $\delta^{13}C$-based paleo-shade proxy of Cerling et al. (2011) positioned the site in C_3-dominated
173 environments in the grassy woodland/bushland/shrubland category (fraction of woody
174 canopy cover, f_{WC} =60-40%) (Harmand et al., 2015). f_{WC} comparisons to other middle
175 Pliocene (3.4-3.2 Ma) eastern African hominin locales from the Awash Basin (Ethiopia),
176 Tugen Hills (Kenya), and elsewhere in the OTD found that none were significantly
177 different from one another, but all were woodier than the earliest Oldowan site of Gona
178 (Harmand et al., 2015). Study of the Fe oxides in paleosols from the northeast Turkana
179 Basin at 3.3 Ma indicate a mean annual rainfall estimate of 500-1000 mm/year (Lepre,
180 2019). These estimates are comparable to those interpreted for the middle Pliocene OTD
181 based on faunal ecomorphic analysis (Fortelius et al., 2016) and the $\delta^{18}O_{EC}$-based aridity

index (Blumenthal et al., 2017). Current OTD middle Pliocene environmental reconstructions imply that stone tool making occurred in more humid and closed environments than widely found for genus *Homo* (e.g., Plummer et al., 2009; Reed, 1997; Sikes, 1994; Sikes et al., 1999).

Additionally, through-time records show little evidence for substantial environmental shifts from the early to middle Pliocene, especially compared to the late Pliocene (Figure 5). From the compiled pedogenic carbonate (subscript PC) $\delta^{13}C$ datasets of the OTD, there is a gradual increase in grassy environments from 4-1 Ma (Figure 5A); however the largest increase occurs after 2 Ma (Cerling et al., 2011a,b; Levin et al., 2011). The compiled herbivore ungulate OTD $\delta^{13}C_{EC}$ database demonstrates a relatively steady increase in C_4-grazers from 4-1 Ma (Figure 5B); although sample sizes are not uniform and some time periods have small sample sizes, the trend appears gradual. Faunal abundance data of Bobe and Behrensmeyer (2004) from the Lower Omo Valley shows a major shift in grassland indicators after 3 Ma; the middle Pliocene appears stable (Figure 5C). Passey et al. (2010) estimated Plio-Pleistocene OTD soil temperatures with pedogenic carbonate clumped isotopes and found consistently high temperatures but no directional trend from 4-1 Ma (Figure 5D). Fortelius et al. (2016) estimated air temperatures in the OTD from 7-1 Ma via ecomorphic proxies and similarly found no directional shift through time. Blumenthal et al. (2017) found that aridity does not increase from 4-1 Ma, but rather variable water deficits are found throughout the OTD (Figure 5E). Fortelius et al. (2016) found a general decreasing trend in mean annual precipitation in the OTD based on ecometric analysis, but the largest decrease in rainfall was in the upper portion of the record from 3-1 Ma.

Detecting environmental change relevant to questions of human evolutionary milestones depends on the scale of each proxy record (e.g., Behrensmeyer, 2006; Kingston, 2007). Kingston (2007) and Potts (2012, 2013) suggested that, in order to test if key evolutionary events in the hominin lineage occurred during intervals of high (global/regional) climatic variability or in response to significantly increased aridity or humidity, climate proxy records from terrestrial hominin environments at resolutions of seasonal- to orbital-scale should be evaluated. The search for high-resolution records of environmental change relevant to patterns and processes of human evolution motivated the Hominin Sites and Paleolakes Drilling Project (HSPDP; Campisano et al., 2017; Cohen et al., 2009, 2016). The drill project comprised several fossil hominin locales in eastern Africa. In the OTD, however, the target interval was focused on the younger part of the record (Lupien et al., 2018; Sier et al., 2017) during the tenure of *Homo erectus* (Lepre and Kent, 2015). HSPDP environmental reconstructions reported to date suggest changes in vegetation structure and aridity were associated with the both high- and low-latitude climate forcing and coincide with major evolutionary events in genus *Homo* (e.g., Lupien et al., 2019; Potts et al., 2017). HSPDP cores from the Awash and Baringo Basins reached maximum depths that date to the middle/late Pliocene (Deino et al., 2019; Lupien et al., 2019; Westover et al., 2019), which are highly relevant for the environments during the rise of genus *Homo* but postdate the complete time interval of interest for Pliocene hominin diet change and stone tool making origins.

1.3. Approach of study

The early flickering of environmental interactions with unmodified or minimally

228 worked stones has not likely been discovered given the subtle archaeological traces and
229 current modes of field-based artifact search and recovery methods (e.g., McPherron et al.,
230 2011; Thompson et al., 2019). To date, LOM3 is the earliest known evidence for stone
231 tool making behaviors by early African hominins and represents an important datum to
232 identify selective pressures for this adaptation. Our approach in this study relies on
233 current data suggesting that hominin tool making behaviors arose within the 4-3 Ma
234 interval. Naturally, future archaeological discoveries may change the supposed time
235 period of interest, similar to the evidence that has come to light within the last decade
236 (Harmand et al., 2015; McPherron et al., 2010).

237 Since the original publication of the LOM3 site only included pedogenic
238 carbonate $\delta^{13}C$-based vegetation reconstructions and vertebrate specimen identification to
239 characterize the environment, we examined other proxy records to detect environmental
240 changes during the middle Pliocene. Paleosol $\delta^{13}C_{PC}$ values provide spatially limited (~1
241 m^2) and time averaged (~10^1-10^3 years) estimates of vegetation structure (Birkeland,
242 1999; Srivastava, 2001) and may not have the resolution to reveal the vegetation
243 structural diversity available with $\delta^{13}C_{EC}$ values of fauna (Du et al., 2019). Here we
244 contribute new $\delta^{18}O_{PC}$ data of paleosols and faunal $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ values of
245 specimens collected at LOM3 and in the surrounding paleontological collecting areas.

246 We focus on the interval of 4.3-3.0 Ma, which is before a major
247 paleohydrographic reconfiguration of the OTD (Lepre, 2014) and the detected significant
248 environmental changes there and across eastern Africa after 3 Ma (Cerling et al., 2011a,b;
249 Levin et al, 2011). At present and even with this study, sampling across the time
250 bracketing the rise of hominin tool making behaviors and dietary changes (4.3-3.0 Ma) is

not uniformly distributed, neither temporally nor spatially, primarily due to differential preservation of paleosols and fossil material suitable for isotopic analyses. Research focus has also impacted sample density. Much environmental research has historically focused on the rise and evolution of *Homo*. Early and middle Pliocene environments in eastern African hominin locales have been used as the "before" interval to emphasize the magnitude of directional shifts and changes in climatic variability in the "after" interval during the late Pliocene and early Pleistocene. We shifted the comparison to the early and middle Pliocene by examining isotopic proxy records in two 400-kya intervals of time (4.3-3.9 Ma and 3.4-3.0 Ma). These relatively large temporal bins are comparable to those used by Cerling et al. (2015) and have considerable sample sizes of paleosols (Harmand et al., 2015; Levin et al., 2011; Quinn and Lepre, 2020; Wynn, 2000, 2004) and faunal enamel datasets (Blumenthal et al., 2017; Cerling et al., 2015; Manthi et al., 2020; Negash et al., 2020; this study), including those of hominins (Cerling et al., 2013b). *Australopithecus anamensis* occurs in the OTD during 4.3-3.9 Ma (Leakey et al., 1995, 1998; Ward et al., 1999b, 2001), thus we use this species and time period as a comparison to gauge potentially new or different selective pressures on stone tool making behaviors preserved in the 3.4-3.0 Ma.

Although a comparison of all middle Pliocene eastern African hominin sites is a useful endeavor for looking at large-scale environmental shifts (e.g., Drapeau et al., 2014; Kingston and Harrison, 2007; Trauth et al., 2005), we focus our study on records in the OTD to minimize confounding influences on the proxy records used here as a function of the idiosyncratic geography and hydrology of different rift basins. Eastern African basins are variable with respect to temperature (Gebrechorkos et al., 2019), elevation (Junginger

and Trauth, 2013), and meteoric water sources (Levin et al., 2009), which in turn influence vegetation $\delta^{13}C$ and $\delta^{18}O$ values (Blumenthal et al., 2016; Sparks and Ehleringer, 1997; Tieszen, 1991; Yakir et al., 1990) and soil pore and surface water $\delta^{18}O$ values (Cerling, 1984; Dansgaard, 1964; Gat, 1996; Kim and O'Neil, 1997).

Taphonomic and collector biases are also concerns when reconstructing vegetation structures with isotopic analyses of faunal remains (e.g., Robinson et al., 2017). Moreover, considering modern mammalian speciosity in Kenya alone (309 species, Musila et al., 2019) and herbivore ungulate population sizes (e.g., 10^2-10^4; Georgiadis, 2011), the number of enamel samples analyzed to date from eastern African fossil locales is miniscule. Due to preservation in and around the LOM3 site, we contribute a modest faunal enamel sample in order to make better comparisons to the early Pliocene OTD databases, but emphasize that larger sample sizes from many species are warranted to gauge the environmental context of Pliocene hominins.

2. The Omo-Turkana Depression

The OTD, also known as the Turkana Depression and the Turkana-Omo rift, extends across northern Kenya and southern Ethiopia (Figure 2) and lies within the eastern branch of the East African Rift System (EARS) between the Kenyan and Ethiopian domes (Ebinger et al., 2000; Knapp et al., 2020). The OTD is composed of several structural sub-basins within the tectonic complex associated with the development of the EARS (Feibel, 2011). The OTD presently contains one of the largest rift lakes, Lake Turkana, with an area of 7000 km^2 and a catchment surface of 130,800 km^2 (UNEP, 2004; Frostick, 1997). Today, the lake is a saline-alkaline and closed-basin lake that

297 receives over 90% of its water from rainfall over the Ethiopian Highlands, via the Omo
298 River, with minor inputs from the Turkwel and Kerio river systems (Yuretich, 1979;
299 Cerling, 1986). The general climate within the rift is arid to semi-arid and receives 250-
300 500 mm of rainfall annually (Nicholson, 1996). Air temperatures are hot, averaging 29°C
301 today, and have been estimated to 30-40°C during the Plio-Pleistocene (Passey et al.,
302 2010). The Omo River meander belt and delta, now situated in the Omo Valley and
303 northern Turkana Basin respectively, has gallery forests along its banks with depths of
304 about ~1 km, which transition to open grasslands along the floodplains (Carr, 1998).
305 Mudflats and grasslands surround present day Lake Turkana, and woody vegetation is
306 largely restricted to the deltaic systems and thin margins of perennial and ephemeral
307 tributaries (Mbaluka and Brown, 2016).
308 Holocene and late Pleistocene lacustrine proxy records demonstrate that Lake
309 Turkana's water levels and temperatures were responsive to regional-scale climatic
310 events such as the African Humid Period and precession-paced variations in solar
311 insolation (Halfman and Johnson, 1988; Forman et al., 2014; Garcin et al., 2012; Bloszies
312 et al., 2015; Morrissey et al., 2018; Morrissey and Scholz, 2014; Nutz and Schuster,
313 2016). A rich archaeological record of early pastoralists and fishing peoples suggests a
314 dynamic livelihood on these changing lakeshores (Ashley et al., 2011; Hildebrand et al.,
315 2018; Mirazón Lahr et al., 2016; Owen et al., 1982; Prendergast and Beyin, 2018; Wright
316 et al., 2015;).
317 Plio-Pleistocene sedimentary strata in the OTD, designated as the Omo Group (de
318 Heinzelin, 1983), begins circa 4.3 Ma when the region shifts from the volcanic activity of
319 mostly flood basalts to a depositional regime dominated by sedimentary clastic detritus

(Brown and McDougall, 2011; Bruhn et al., 2011). Omo Group Plio-Pleistocene environmental proxy records include those from the Kanapoi and Lothagam formations in the southwestern portion of the Turkana Basin, the Mursi Formation located in the Omo River Valley, the Koobi Fora Formation exposed along the northeast and southeast side of the Turkana Basin, and the Nachukui Formation along the northwest and southwest basin (Feibel et al., 1991; Feibel, 2003a, 2003b; Harris et al., 1988). Pliocene mudstones, sandstones, and conglomerates comprise the bulk of the Nachukui Formation's Lomekwi Member, which preserves the LOM3 site (Harmand et al., 2015). The Omo Group formations have been dated and correlated through a combination of tephrastratigraphy, radioisotopic ages, and paleomagnetic stratigraphy (Brown and Feibel, 1986, 1991; Feibel et al., 1989; Hillhouse et al., 1986; Lepre, 2014; Lepre and Kent, 2010, 2015; Lepre et al., 2011; McDougall, 1985; McDougall and Brown, 2006, 2008; McDougall et al., 2012), which has afforded a high degree of temporal resolution for several long records of terrestrial environments (Figure 5).

Late Pliocene and early to middle Pleistocene sedimentary records indicate the presence of large lakes. The longest in duration is Lake Lorenyang (Feibel, 1997) beginning at 2.14 Ma (Lepre, 2014) and extending to ~1.5 Ma (Feibel, 2011) and likely caused by the damning of the basin with the eruption of Mt. Kulal during the early Pleistocene (Bruhn et al., 2011). Fluctuations in lake levels during the early Pleistocene may have been influenced by orbitally-paced variations in water delivery to the Omo River source region in the Ethiopian Highlands (Boës et al., 2019; Joordens et al., 2011; Lepre et al., 2007; Nutz et al., 2017). The increasing abundance of C_4 grasslands in the basin during the early Pleistocene may have been partially influenced by paleogeographic

343 variations as the basin transitioned from fluvial- to lacustrine-dominated depositional
344 systems (Levin et al., 2011; Quinn et al., 2007; Wynn, 2004).
345 Early to middle Pliocene depositional environments in the OTD are largely
346 characterized as fluvial and dominated by the proto-Omo, -Kerio and -Turkwel rivers
347 (Feibel, 2011). Prior to the eruption of Mt. Kulal, the hydrological configuration is
348 reconstructed as an open system with an outlet to the Indian Ocean via the Turkana River
349 (Feibel, 1994). Short-term lakes of various sizes punctuated the Pliocene fluvial
350 landscapes as a function of accommodation space and sedimentation in the half-graben
351 basin. The estimated largest and deepest lake, Lake Lonyumun, reached an aerial expanse
352 of 9000 km^2 circa 4.1 Ma; another lake, Lake Lokochot, was likely shallower but nearly
353 reached a comparable aerial extent circa 3.5 Ma (Feibel, 1997). These large lakes show
354 evidence for deltaic sediments at the interface of emptying perennial rivers such as the
355 proto-Omo, -Kerio, and -Turkwel, similar to the modern deltas at the north and south
356 ends of Lake Turkana. Adjacent to the LOM3 site, the local paleogeography of the
357 northwest Turkana Basin included alluvial fans and other transverse drainages that likely
358 intersected at times with axial depositional systems, such as the proto-Omo River and
359 small ephemeral lakes (Harmand et al., 2015; Harris et al., 1988; Leakey et al., 2001).
360 The OTD preserves one of the most complete fossil and archaeological records of
361 Plio-Pleistocene hominin evolution. Sediments capture several key evolutionary
362 landmarks in the hominin lineage including the first appearance datum (FAD) of genus
363 *Australopithecus* (Leakey et al. 1995), FAD and the last appearance datum (LAD) of *K.*
364 *platyops* (Leakey et al., 2001), an early *Homo sp.* candidate FAD (Prat et al., 2005), *H.*
365 *rudolfensis* FAD (Leakey, 1973), *H. habilis* FAD and LAD (Spoor et al., 2007; Wood,

366 1991), the earliest Acheulean industry (Lepre et al., 2011), numerous Pleistocene sites
367 preserving Oldowan industry diversity through time (Braun et al., 2010; Delagnes and
368 Roche, 2005; Isaac, 1997; Harmand, 2007, 2009a,b; Mana et al., 2019; Roche et al.,
369 1999, 2003), and the focus of this study, the earliest lithic technology, known as the
370 Lomekwian (Harmand et al., 2015).
371
372 **3. Isotopic proxy records of terrestrial African environments**
373 *3.1 Pedogenic carbonate $\delta^{13}C$ and $\delta^{18}O$ analyses*
374 For nearly forty years, African terrestrial vegetation communities have been
375 reconstructed with measurements of $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ values preserved in paleosols
376 (Cerling, 1984, 1992a; Cerling et al, 1988). Thorough descriptions of these methods are
377 available elsewhere (e.g., Cerling et al., 2011a; Koch, 1998; Levin, 2015); here we briefly
378 describe the methods and data interpretation used in this study.
379 Globally C_3 and C_4 plants show normal and non-overlapping distributions (Sage
380 and Monson, 1999). C_3 plants (trees, shrubs, few sedges, and cool growing season
381 grasses) utilize the Calvin-Benson three-carbon photosynthetic pathway and discriminate
382 against the heavier of the two stable isotopes of carbon, ^{13}C. C_4 plants (most sedges and
383 warm season growing grasses) utilize the Hatch-Slack four carbon photosynthetic
384 pathway and allow some incorporation of ^{13}C. In eastern Africa, C_3 dicots from closed
385 and open canopy forests have lower $\delta^{13}C$ values (-31.4 ± 0.5 ‰, -27.8 ± 0.3 ‰,
386 respectively) than those of savanna and bushlands (-27.0 ± 0.2 ‰; Cerling et al., 2003c).
387 Mesic C_4 grasses (NADP subpathway) have an average $\delta^{13}C$ value of -11.8 ± 0.2‰; xeric
388 C_4 grasses utilizing the NAD and PCK subpathways have average $\delta^{13}C$ values of -13.1 ±

389 0.3‰ and -12.9 ± 0.1‰, respectively (Cerling et al., 2003c) in eastern African savanna
390 environments. Vegetation $\delta^{13}C$ values are inferred from those measured in pedogenic
391 carbonate nodules (Cerling et al., 1992b; Cerling and Quade, 1993).
392 Pedogenic carbonates at depths greater than 30 cm in soils with relatively high
393 respiration rates incorporate CO_2 of decaying organic matter derived from surface
394 vegetation during soil development with an offset of 14-17‰ (Cerling, 1984, 1992b;
395 Cerling and Quade, 1993; Quade et al., 1989). Thus the $\delta^{13}C_{PC}$ values preserved in
396 paleosols are used to quantitatively measure the relative amounts of C_3 and C_4 vegetation
397 on the land surface during soil carbonate formation (Cerling, 1992a). Pedogenic
398 carbonates form in warm, dry periods and have been shown to overestimate C_4
399 contributions to paleovegetation (Breeker et al., 2009). Cerling et al. (2011b) derived a
400 regression equation to calculate the fraction of woody canopy cover (f_{WC}) from paleosol
401 carbonate $\delta^{13}C_{PC}$ values in order to categorize structure based on UNESCO
402 classifications of African vegetation. Cerling et al. (2015) describe the classification as
403 follows: 1) grassland: f_{WC} = 0-10%, 2) open wooded grassland: f_{WC} = 10-20%, 3)
404 wooded grassland: f_{WC} = 20-40%, 4) grassy woodland/bushland/shrubland: f_{WC} = 40-
405 60%, 5) woodland/bushland/shrubland: f_{WC} = 60-80%, 6) forest/closed forest: f_{WC} = 80-
406 100%.
407 $\delta^{18}O_{PC}$ values are controlled by soil pore water $\delta^{18}O$ values, temperature-
408 dependent isotopic fractionation during carbonate formation, evaporation rates and soil
409 moisture (Cerling, 1984; Kim and O'Neil, 1997). At depths greater than 30 cm, soil pore
410 water $\delta^{18}O$ values track those of meteoric water (Amundson and Wang, 1996; Cerling,
411 1984; Cerling and Quade, 1993). Soil pore water $\delta^{18}O$ values are controlled by several

412 factors including 1) evaporation relative to precipitation (i.e., aridity) (Cerling, 1984;
413 Cerling and Quade, 1993), 2) rainfall source $\delta^{18}O_{MW}$ values (Dansgaard, 1964; Ferretti et
414 al., 2003; Gazis and Feng, 2004), 3) air and soil temperatures (Breecker et al., 2009;
415 Cerling, 1984; Kim and O'Neil, 1997), or 4) some combination of these factors.
416 Advances in mass spectrometry have reduced the amount of carbonate required to
417 obtain reliable $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ results, thus it is common for a single pedogenic nodule
418 to be drilled and analyzed multiple times (e.g., database of Levin, 2013). Pedogenic
419 nodules form by accretion (Retallack, 2005; Wieder and Yaalon, 1982) and therefore
420 record several episodes of environmental conditions depending on nodule growth rate
421 and size. Sampling one nodule multiple times for $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ values potentially
422 reveals variability in vegetation structure and soil water during nodule formation. By no
423 means is this the ideal gauge of environmental variability; however, it has been an
424 underutilized dataset in paleoenvironmental research in eastern African hominin localities
425 that reflects aspects of past vegetation structure and climatic conditions not visible with
426 measures of bulk carbonate of one pedogenic nodule.
427
428 *3.2 Faunal $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ analyses*
429 Faunal enamel carbonate $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ values record $\delta^{13}C$ values of whole
430 diet and $\delta^{18}O$ values of body water, respectively, and thus have been used for some time
431 to reconstruct continental paleoenvironments (e.g., Koch, 1998). Fossil faunal $\delta^{13}C_{EC}$
432 values have been extensively used to estimate vegetation structures at Plio-Pleistocene
433 hominin locales relative to modern eastern African environments (Cerling et al., 2015;
434 Drapeau et al., 2014; Kingston and Harrison, 2007; Manthi et al., 2020; Wynn et al.,

435 2016; Negash et al., 2020). Based on $\delta^{13}C_{EC}$ values of herbivorous ungulate taxa,
436 specimens are assigned to one of three dietary groups: C_3-browsers, C_3-C_4-mixed feeders,
437 and C_4-grazers (Cerling et al., 2015). Relative percentages of the three feeding categories
438 are used to characterize the faunal community composition (e.g., Manthi et al., 2020;
439 Robinson et al., 2017). $\delta^{13}C_{EC}$ values of carnivores reflect the feeding category(ies) of
440 their prey, and of omnivores, a mixture of plant and prey $\delta^{13}C$ values (Lee-Thorp et al.,
441 1989).
442 $\delta^{13}C_{EC}$-based dietary reconstructions and by extension environmental
443 reconstructions are not without methodological assumptions. Cerling et al. (2015)
444 proposed the following $\delta^{13}C_{EC}$ values to delineate the three feeding categories of the
445 Artiodactyla, Perissodactyla and Proboscidea (APP) orders: C_3-browsers, $\delta^{13}C_{EC}$ <-8‰;
446 C_4 grazers, $\delta^{13}C_{EC}$ >-1‰; C_3-C_4-mixed feeders, $\delta^{13}C_{EC}$ between -8 and -1‰, which were
447 based on the large modern $\delta^{13}C_{EC}$ database of APP taxa, a pre-industrial CO_2 $\delta^{13}C$ offset
448 of 1.5‰, a $\varepsilon^*_{enamel\text{-}diet}$ value of 14‰. In fossil organisms, the $\varepsilon^*_{enamel\text{-}diet}$ value is based on
449 modern analogs. The use the $\varepsilon^*_{enamel\text{-}diet}$ value of +14‰ (e.g., Cerling et al., 2013b,
450 Manthi et al., 2020), is based on large ruminant and nonruminant mammals (Cerling and
451 Harris, 1999; Cerling et al., 2003a; Passey et al., 2005). Alternatively, Kellner and
452 Schoeninger (2007) suggested that the ε*enamel-diet value for a non-fermenting-gut
453 omnivore is +10‰; however, this $\varepsilon^*_{enamel\text{-}diet}$ value may be more applicable to members
454 of genus *Homo* than Pliocene hominins (Schoeninger, 2014). An $\varepsilon^*_{enamel\text{-}diet}$ value of
455 +13‰ (Cerling et al., 2004; Passey et al., 2005) has been utilized to characterize extant
456 primates (e.g., Loudon et al., 2016; Smith et al., 2010). Tejada-Lara et al. (2018)
457 suggested the $\varepsilon^*_{enamel\text{-}diet}$ value of mammalian herbivores is predicted by body mass and

458 gut physiology, producing $\varepsilon^*_{\text{enamel-diet}}$ values ranges between +9 and +16‰. The use of
459 specific $\varepsilon^*_{\text{enamel-diet}}$ values can impact dietary reconstructions (Quinn, 2019).
460 Notably, global CO_2 $\delta^{13}C$ values have changed through time (Tipple et al., 2010),
461 and thus through-time analyses of faunal $\delta^{13}C_{EC}$ values must consider specific CO_2 $\delta^{13}C$
462 offsets when differentiating diet categories (Uno et al., 2011; Garrett et al., 2015; Faith et
463 al., 2018). Vegetation structure also impacts dietary reconstructions by altering the end
464 members of C_3 and C_4 diets (Garrett et al., 2015). Moreover, Robinson et al. (2017) have
465 suggested that the methods of Cerling et al. (2015) artificially skew $\delta^{13}C_{EC}$-based
466 interpretations of feeding categories and general community structures because they do
467 not account for differential species abundances present in collector- and taphonomic-
468 biased faunal assemblages.
469 $\delta^{18}O$ values are preserved in both the carbonate (subscript EC) and phosphate
470 (subscript EP) phases of enamel and have been shown to resist diagenetic alteration
471 (Wang and Cerling, 1994); consequently faunal $\delta^{18}O_{EP/EC}$ analyses have been widely
472 employed for environmental reconstructions in deep time (Ayliffe and Chivas, 1990;
473 Ayliffe et al., 1992; Bryant et al., 1994, 1996; Kingston and Harrison, 2007; Koch et al.,
474 1989; Wang et al., 2007; Wang and Deng, 2005; Wynn et al., 2016). Mammalian $\delta^{18}O_{EC}$
475 values are derived primarily from drinking water, atmospheric O_2, and water consumed in
476 food (Bryant and Froelich, 1995; Kohn, 1996; Kohn and Cerling, 2002; Podlesak et al.,
477 2008).
478 In eastern African savanna environments, obligate drinkers have been shown to
479 have lower but overlapping $\delta^{18}O_{EP/EC}$ values than non-obligate drinkers (Bocherens et al.,
480 1996; Cerling et al., 2003b). Eastern African C_3-browsing and C_3-C_4-mixed-feeding

481 herbivore ungulates were found to have lower bone phosphate $\delta^{18}O$ values than C_4-
482 grazing ungulates (Kohn et al., 1996). As recently reviewed by Faith (2019), C_3-browsers
483 obtain substantial amounts of water from C_3 vegetation. C_4 grasses offer little water
484 content and therefore C_4-grazers typically obtain water from surface water sources, which
485 generally have lower $\delta^{18}O$ values than that of C_3 vegetation.

486 Sponheimer and Lee-Thorp (1999b, 2001) suggested that trophic level is
487 correlated with $\delta^{18}O_{EC}$ values in a modern sample of the Morea Estate mammals and
488 fossil fauna from Swartkrans and Equus Cave (South Africa). Few studies have aimed to
489 further test this prediction in modern eastern African ecosystems. One jackal from
490 Turkana (Cerling et al., 2003b) yielded a lower $\delta^{18}O_{EC}$ value than measured herbivores
491 but comparable values as elephant and black rhino. Lake Turkana hippos (Cerling et al.,
492 2003b), but not those inhabiting rivers (Blumenthal et al., 2017), yielded higher $\delta^{18}O_{EC}$
493 values than the one isotopically analyzed jackal. At Tsavo, lions (n=9) yielded lower
494 $\delta^{18}O_{EC}$ values than several herbivorous species, but showed no difference from those of
495 elephant and black rhino (Cerling et al., 2008).

496 Several studies in African forested environments have shown that $\delta^{18}O_{EC}$ values
497 of forest-living fauna vary with canopy height. For example, high canopy primates
498 achieve higher $\delta^{18}O_{EC}$ values than low canopy or ground dwellers in closed environments
499 (Cerling et al., 2004; Krigbaum et al., 2016; Nelson, 2013). This is because high canopy
500 leaves experience higher evapotranspiration than vegetation at low canopy and ground
501 levels in a forest (Sternberg et al., 1989), and those different vegetation $\delta^{18}O$ values are
502 transferred to consumers (Carter and Bradbury, 2016; Nelson, 2013). Additionally,
503 woodland- and grassland-dwellers achieve higher $\delta^{18}O_{EC}$ values than those living in

forests (Cerling et al., 2003a). This can result from drinking open habitat evaporative surface waters (Cerling et al., 2003a), but is also influenced by ingesting open habitat vegetation, which experiences higher rates of evapotranspiration (Belsky et al., 1989).

The number of variables controlling faunal $\delta^{18}O_{EC}$ values impacts the method's usefulness for assessing environmental change. For example, water dependency and behavioral variables (Kohn et al., 1996) also influence $\delta^{18}O_{EC}$ values, which act to reduce $\delta^{18}O_{EC}$ distinctions between herbivore feeding categories (Bocherens et al., 1996; Cerling et al., 2003b). Moreover, Kohn (1996), Kohn et al. (1996), and Schoeninger et al. (2000) emphasize that behavioral variables unknown, and perhaps unknowable, in fossil species such as activity times, night feeding, and shade-seeking behaviors can influence $\delta^{18}O_{EC}$ values.

Several studies from eastern African hominin sites have shown that analyzing $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ values of mammalian taxa from discrete stratigraphic intervals captures a large range of available resources via different dietary behaviors practiced by various species (Du et al., 2019; Kingston and Harrison, 2007; Lehmann et al., 2016; Patterson et al., 2019; Robinson et al., 2016; Wynn et al., 2016). If diagenetic alteration of tooth enamel is negligible, $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ analyses of individual specimens record diet and water intake over the duration of enamel formation (10^0-10^1 years), which represents a small amount of time in contrast to the formation times of pedogenic carbonates (10^1-10^3 years). Spatially, however, faunal $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ values record information from across the range of animal movements, which vary by species and span 10^1-10^2 km^2 (Estes, 1991). In a similar approach to measuring intranodular variability, faunal isotopic variation measured in several specimens from individual taxonomic

groups serves as a proxy of dietary selectivity or flexibility (methods of Groenewald et al., 2020). Combining the two distinct yet complementary proxy records from paleosols and faunal specimens makes visible different aspects of the local and regional environments.

4. Materials and Methods

4.1. Pliocene OTD $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ analyses

We present new $\delta^{18}O_{PC}$ values (nodules=23, analyses=47) from LOM3 (see sampling described in Harmand et al., 2015; Supplementary Table 1). We combine $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ data and compare across two 400-kyr intervals, 4.3-3.9 Ma (n=70) and 3.4-3.0 Ma (n=77). Published $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ values from the OTD are drawn from the Kanapoi Formation (data from Quinn and Lepre, 2020; Wynn, 2000), the Koobi Fora Formation (data from Cerling et al., 1988; Levin et al., 2011), and the Nachukui Formation (data from Harmand et al., 2015; Levin et al., 2011; Wynn, 2004). OTD $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ data used in this study have been compiled into a publicly available database (Levin, 2015). f_{WC} values were estimated after methods of Cerling et al. (2011). We utilized standard variation of intranodular $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ values from these two intervals, 4.3-3.9 Ma (n=38) and 3.4-3.0 Ma (n=33), to represent environmental variability (data from Harmand et al., 2015; Levin et al., 2011; Quinn and Lepre, 2020; this study).

4.2. Pliocene OTD faunal $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ analyses

549 We add faunal $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ values (taxa =8, n =28) from LOM3 to
550 published OTD faunal $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ values. We limited enamel sampling to APP
551 specimens identifiable at taxonomic levels of tribe or lower. We also analyzed
552 crocodylians from the site for $\delta^{18}O_{EC}$ values to proxy meteoric water $\delta^{18}O$ values (e.g.,
553 Amiot et al., 2007). We combine $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ data of specimens collected from five
554 geologic formations in the Omo Group: Kanapoi Formation (data from Cerling et al.,
555 2013b; Manthi et al., 2020 and references therein), Koobi Fora Formation (data from
556 Blumenthal et al., 2017 and references therein; Cerling et al., 2013b, 2015 and references
557 therein; Schoeninger et al., 2003), Shungura Formation (data from Cerling et al., 2015;
558 Negash et al., 2020), Mursi Formation (data from Drapeau et al. 2014), and the Nachukui
559 Formation (data from Blumenthal et al., 2017 and references therein; Cerling et al.,
560 2013b, 2015 and references therein) and compare data of taxonomic groups. Fourteen
561 ungulate herbivore taxa (4.3-3.9 Ma, n=212; 3.4-3.0 Ma, n=197) were utilized for
562 assessing change in $\delta^{13}C_{EC}$ values, and 8 ungulate herbivore taxa and Crocodylia (4.3-3.9
563 Ma, n=134; 3.4-3.0 Ma, n=139) for comparing $\delta^{18}O_{EC}$ values (Table 1). After Cerling et
564 al. (2015) we distinguish two Rhinocerotidae taxa based on bimodal $\delta^{13}C_{EC}$ values,
565 Rhinocerotidae (G) and Rhinocerotidae (B), to denote grazing (cf. *Ceratotherium*) and
566 browsing (cf. *Diceros*) forms, but without the proper morphological indicators for
567 taxonomic designations.
568 Given the small sample sizes of individual taxa and the lack of representation by
569 numerous species in the sample, we use pairwise non-parametric comparisons of $\delta^{13}C_{EC}$
570 and $\delta^{18}O_{EC}$ values grouped by taxon present in both time intervals. We assess variability
571 in food and water inputs by comparing interquartile ranges of $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ values

of each taxonomic group separated into the two temporal bins. After Cerling et al. (2015), we place the taxonomic and temporal groups along the spectrum of $\delta^{13}C_{EC}$ values designated as separate feeding categories. However, we also consider canopy effects on vegetation $\delta^{13}C$ values (Kohn, 2010) and separate the C_3 browser category into "forest" C_3 browsers and "woodland" C_3 browsers. We define forest C_3-browsers when $\delta^{13}C_{EC}$ values drop below -14‰. This is based on the average plant $\delta^{13}C$ value of five lowland tropical closed canopy forests in Africa (-30.6‰) (data from: Loango National Park, Côte d'Ivoire, -30.5±3.5‰, Oelze et al., 2014; Tai Natural Park, Côte d'Ivoire, -30.8±4.1‰, Fahy et al., 2013; Ituri Forest, DRC, -31.2±2.8‰, Cerling et al., 2004; Salonga National Park, DRC, -29±2.7‰, Oelze et al., 2011; Kakamega Forest, Kenya, -31.4±0.5‰, Cerling et al, 2003c) and a correction for the Pliocene atmospheric CO_2 $\delta^{13}C$ offset of 2.3‰ (Tipple et al., 2010). We use the term "woodland" for C_3-feeders exploiting the more open C_3 biome resources; $\delta^{13}C_{EC}$ values range from -8‰ to -14‰. Based on Tipple et al. (2010), the time periods compared in this study vary only by 0.2‰ and therefore we do not change our feeding category demarcations through time. We also compare feeding categories through time by combining $\delta^{13}C_{EC}$ values and gauge change in mean $\delta^{13}C_{EC}$ values and variance (similar to methods of Sealy et al., 2020).

4.3. Mass Spectrometry

Pedogenic nodules were cross-sectioned and sampled for microcrystalline calcite with a 0.5 mm carbide drill bit (Foredom Series), avoiding surface and sparry calcite. We subsampled nodules twice and averaged the subsample values. Enamel samples from LOM3 were also sampled with a rotary drill affixed with a diamond drill bit (Foredom

595 Series). We eroded the outer layer of enamel prior to collecting enamel powders,
596 avoiding discolorations/inclusions and taking advantage of natural breaks. Enamel
597 samples were pretreated with a buffered acetic acid, pH = 5.0 (after Cerling et al., 2013b;
598 Koch et al., 1997). All analyses were conducted at the Stable Isotope Laboratory at
599 Rutgers University on a FISIONS Optima Mass Spectrometer with an attached Multi-
600 Prep device. All samples were reacted in 100% phosphoric acid at 90°C for 13 minutes.
601 Values for $\delta^{18}O_{PC}$ are reported in delta notation (per mil, ‰) versus V-PDB through
602 analysis of NBS-19; error for $\delta^{18}O_{PC}$ is <0.05‰. Enamel samples that yielded >10%
603 carbonate content were excluded from the study due to the likelihood of the presence of
604 non-structural carbonate (methods after Cerling et al., 2013b, 2015).
605
606 **5. Results**
607 *5.1. Pliocene OTD $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ values*
608 Summary data for the compiled Pliocene OTD $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ values for the
609 two time intervals are shown in Figures 6-8. $\delta^{13}C_{PC}$ values show a slight (0.9‰) but
610 statistically significant (t test, $p<0.05$) increase from the 4.3-3.9 Ma interval to the 3.4-3.0
611 Ma interval. Using the methods of Cerling et al. (2011b), the average $\delta^{13}C_{PC}$ increase of
612 0.9‰ equates to an 8% decrease in f_{WC}. The dominant vegetation structural category is
613 reconstructed as grassy woodlands/ bushland/shrubland in both time periods. $\delta^{18}O_{PC}$
614 values show a change by only 0.1‰ between the 4.3-3.9 Ma and the 3.4-3.0 Ma intervals,
615 and this is not statistically significant (Figure 7). Intranodular $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ standard
616 deviations and interquartile ranges are slightly higher in the 3.0-3.4 Ma interval than in

617 the 4.3-3.9 Ma interval, averaging 0.1 and 0.3 respectively (Figure 8), and both are
618 statistically significant (t test, $p<0.05$).
619
620 *5.2. Pliocene OTD faunal* $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ *values*
621 Pliocene OTD faunal $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ values are listed in Table 1, and box plots
622 are illustrated in figures 9 and 10. Pairwise comparisons of $\delta^{13}C_{EC}$ values for each of the
623 14 herbivore ungulate taxonomic groups examined across the two time intervals yielded
624 statistical significance for three taxa (Mann-Whitney U, $p<0.05$, Figure 9). Antilopini,
625 Aepycerotini and *Notochoerus* shift within the C_3-C_4 mixed feeding category toward
626 more C_4-feeding. None of the herbivorous species yielded statistically significant changes
627 in interquartile range (f test, $p=0.10$) in the 3.4-3.0 Ma interval. Figure 11 plots
628 probability densities of all herbivore ungulate $\delta^{13}C_{EC}$ values separated into the three
629 feeding categories (C_3-browsers, C_3-C_4-mixed feeders, C_4-grazers). The position and
630 shape of the plots illustrate a slight directional shift toward more C_4 consumption
631 especially within the C_3-C_4-mixed-feeding category. C_3-C_4-mixed feeders show
632 significant changes in mean and median $\delta^{13}C_{EC}$ values (t test, $p<0.000$; Mann-Whitney U,
633 $p<0.01$) and variance (f test, $p=0.04$).
634 Pairwise comparisons of $\delta^{18}O_{EC}$ values for each of the 10 herbivore ungulate
635 taxonomic groups examined across the two time intervals yielded statistical significance
636 for only one taxa (Mann-Whitney U, $p<0.05$, Figure 10). Alcelaphini yielded a
637 statistically significant decrease in $\delta^{18}O_{EC}$ values (Mann-Whitney U, $p<0.01$). Giraffidae
638 and Aepycerotini yielded lower $\delta^{18}O_{EC}$ mean values, but do not achieve statistical

639 significance (Mann-Whitney U, $p<0.08$). Pairwise $\delta^{18}O_{EC}$ interquartile ranges vary
640 widely, but none were significantly different from one another (f test, $p>0.05$).
641
642 **6. Discussion**
643 *6.1. Environmental change during the origins of stone tools*
644 Environmental proxy data from the Pliocene OTD confirms the modest
645 directional shift to higher abundances of C_4 vegetation through time. Average f_{WC}
646 decreased by 8%, and three herbivore ungulate taxa showed increases in C_4 consumption.
647 Modern species opportunistically shift their diets in response to resource availability
648 (e.g., Cromsigt and Olff, 2006; du Toit, 2003; Illius and O'Connor, 2000; Kartzinel et al.,
649 2015; Owen-Smith, 1997) and therefore can track changes in vegetation structure. Three
650 Pliocene fossil taxa consuming more C_4 plants may indicate a higher abundance of C_4
651 grasslands during the 3.4-3.0 Ma interval in general agreement with f_{WC} estimates.
652 However, faunal $\delta^{13}C_{EC}$ values are also a reflection of species interactions (Buschke et
653 al., 2015) and resource partitioning of C_3 and C_4 vegetation by herbivore competitors
654 (e.g., Codron et al., 2011; Davis et al., 2017; Feranac et al., 2007; Malindie et al., 2020),
655 which makes quantifying C_4 grass abundance with faunal $\delta^{13}C_{EC}$ values a difficult task.
656 As shown by Uno et al. (2011), Patterson and others (2017, 2019), and Negash et al.
657 (2020) in different portions of the OTD, dietary shifts by herbivore ungulates toward
658 greater C_4 consumption were highly variable in tempo and mode. Moreover, through-
659 time faunal $\delta^{13}C_{EC}$ data show that the dietary niches of many individual taxa were
660 relatively constant during the Pliocene and did not undergo significant transitions into the
661 C_4 biome until after 3 Ma (Negash et al., 2020). Although none achieve statistical

662 significance, Aepycerotini and *Notochoerus* may have become more dietarily selective
663 during the middle Pliocene, whereas Tragelaphini, like hominins, may have become more
664 opportunistic (e.g., Groenewald et al., 2020) (Figure 9). Based on the combined ungulate
665 herbivore $\delta^{13}C_{EC}$ values, it appears that the C_3-C_4 mixed feeding niche contracted over
666 this study interval (Figure 11), which may have been due to reductions in C_3 resource
667 availability and/or increased competition.

668 Unchanging $\delta^{18}O_{EC}$ values in taxa whose modern descendants tend to be water
669 dependent (e.g., Hippopotamidae, Crocodylia, Deinotheriidae, Elephantidae) suggests
670 that meteoric water $\delta^{18}O$ values did not significantly change over the two time intervals.
671 Hippopotamidae $\delta^{18}O_{EC}$ values reflect the $\delta^{18}O$ values of the water in which they swim
672 and thus have been suggested as faithful records of meteroric water $\delta^{18}O$ values (Cerling
673 et al., 2008; Levin et al., 2006). Crocodylia $\delta^{18}O_{EC}$ values, which also mirror meteoric
674 water $\delta^{18}O$ values (Amiot et al., 2007), are comparable to those of Hippopotamidae. OTD
675 Deinotheriidae and Elephantidae, perhaps similar to elephants today (Estes, 1991), likely
676 spent a significant portion of time in surface waters as well. Notably, Elephantidae
677 $\delta^{18}O_{EC}$ values are significantly higher than those of Deinotheriidae, which may reflect
678 differences in diet (e.g., Faith, 2019), gut physiology (Hempson et al., 2015), or body size
679 (Bryant and Froelich, 1995; Longinelli, 1984; Luz et al., 1984), but neither revealed
680 change in pairwise comparisons.

681 Of the taxa that yielded lower $\delta^{18}O_{EC}$ values in the 3.4-3.0 Ma interval, (e.g.,
682 Giraffidae, Alcelaphini, Aepycerotini), only Giraffidae was categorized as evaporation-
683 sensitive (ES) in the $\delta^{18}O_{EC}$-based aridity index of Levin et al. (2006) and refined by
684 Blumenthal et al. (2017). But notably, the decrease in Giraffidae $\delta^{18}O_{EC}$ values was not

685 statistically significant. As mentioned, Faith (2019) cautions that $\delta^{18}O_{EC}$-based water
686 deficit estimates based on herbivore ungulate species with changing diets, such as
687 Tragelaphini, may mimic changes in water deficits as more C_4-grazing triggers more
688 surface water drinking. The relatively lower $\delta^{18}O_{EC}$ values of Aepycerotini may have
689 been a by-product of higher C_4 consumption (e.g., Faith, 2019). The drop in $\delta^{18}O_{EC}$
690 values in Alcelaphini is accompanied by a slight decrease in $\delta^{13}C_{EC}$ values, which is
691 opposite of that predicted for changes in drinking behavior. Modern Alcelaphini taxa
692 vary in water dependency and tolerance for arid habitats and are not identified as ES taxa
693 (Levin et al., 2006). According to Estes (1991), few species live in arid areas without
694 access to water; those that do (e.g., hartebeests in the Kalahari) dig up roots and tubers or
695 feed on melons to access water. As a C_4-grazer, OTD Alcelaphini likely obtained their
696 water from surface sources due to the low water content in grasses. Reduced $\delta^{18}O_{EC}$
697 values imply that surface drinking water sources shifted to lower $\delta^{18}O$ values.
698 Alcelaphini $\delta^{18}O_{EC}$ values may have tracked changes in local water sources such as
699 floodplain lakes and small distributaries that are more susceptible to evaporative
700 fluctuations than large rivers.
701 Using the criterion of Faith (2019), Giraffidae, which does not change its diet
702 over the two time intervals, is ostensibly a good candidate for accurate water deficit
703 calculations. Although our pairwise comparison did not yield statistical significance,
704 Blumenthal et al.'s (2017) aridity index based on the Hippopotamidae-Giraffidae
705 equation yielded water deficits from Kanapoi (~4.1 Ma, 1315±994 mm/year), Allia Bay
706 (3.9 Ma, 500±1315 mm/year) and the Lomekwi member (3.4 Ma, 1±892 mm/year),
707 demonstrating increasingly more humid conditions across 4.3-3.0 Ma study interval.

708 Whether this potential humidity trend was caused by local or regional climatic forcing is
709 unknown. Donges et al. (2011) found that the interval of 3.33-3.28 Ma shows evidence
710 for decreasing sea-surface temperatures, lower surface air temperatures and changes in
711 the evaporation-precipitation balance. They suggest that under these conditions, eastern
712 Africa underwent a significant humid period, pointing to the Awash Basin's lacustrine
713 phase as evidence for increased rainfall. As mentioned, the OTD does not show evidence
714 for a lacustrine phase during LOM3 times; however, Giraffidae $\delta^{18}O_{EC}$ values may
715 indicate slightly more humid conditions. Clearly additional enamel samples of Giraffidae
716 are needed from the early and middle Pliocene in the OTD to further test this finding.
717 It is noteworthy that OTD $\delta^{18}O_{EC}$ values appear to track changes in humidity that
718 were not recorded in $\delta^{18}O_{PC}$ values, which may indicate that changes in humidity were
719 minor. However, $\delta^{18}O_{PC}$ values have several influences, which may have acted in concert
720 to blur environmental signals. Koch (1998) suggested that increased $\delta^{18}O_{PC}$ values can be
721 a by-product of grassland expansion. Relatively more C_4 vegetation in grass form results
722 in increased light stress and less soil moisture relative to soils formed under tree cover.
723 As a result, a decrease in soil moisture caused by a reduction in woody cover could have
724 counteracted the increase in precipitation on $\delta^{18}O_{PC}$ values during the middle Pliocene.
725 Increasing standard deviations of $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ values within nodules
726 suggest that variations in vegetation structure and climatic conditions marginally
727 increased across the two time intervals. While intranodular isotopic variability is not a
728 seasonal proxy, higher environmental variability on the order of nodule formation times
729 (100s-1000s years) may indicate more fluctuating environments during the 3.4-3.0 Ma
730 interval. This pattern of increasing variability is not predicted based on the African dust

731 records (Potts and Faith, 2015) and may suggest other controls on climatic variability in
732 the region during the middle Pliocene such as sea-surface temperature (Fedorov et al.,
733 2013) or the Indian Ocean Dipole (Marchant et al., 2007). The increase in standard
734 deviation, however, is ≤0.3‰ for both isotopic systems, which is negligible with respect
735 to significant changes in OTD environments. For example, variations in $\delta^{13}C_{PC}$ values of
736 0.3‰ would not result in significant changes in vegetation structure with the paleoshade
737 proxy (Cerling et al., 2011b). Although HSPDP did not target the Pliocene sediments in
738 the OTD, increase sampling density throughout the Pliocene sequence and additional
739 climate proxy records on seasonal and other short-term time scales (e.g., Ascari et al.,
740 2018; Blumenthal et al., 2019; Macho et al., 2003) are warranted to further test if
741 environmental variability increased through time by amplitudes impacting environmental
742 conditions.

743 We interpret subtle changes in C_4 abundances and potentially a slight increase in
744 humidity in the OTD for the middle Pliocene compared to the early Pliocene, which
745 provides support for decoupling the link between aridity and C_4 grassland spread (e.g.,
746 Blumenthal et al., 2017; Levin, 2015; Polissar et al., 2019). The increasing trend of
747 eastern African C_4 vegetation appears related to the long-term decrease in atmospheric
748 pCO_2 (Faith et al., 2018; Polissar et al., 2019). Observably, vegetation communities are
749 not passive responders to changing environmental conditions, but rather compete with
750 one another for substrate, water, and sunlight (Bond, 2008; Bond et al., 2003; Ludwig et
751 al., 2004). In the OTD, the hydrological regime was dominated by the large meander belt
752 of the proto-Omo River and punctuated with lake phases, which in turn provided
753 changing conditions of water availability, substrate, and sedimentation. Avulsing river

754 and fluctuating lake margin landscapes may have offered a competitive advantage for C_4
755 vegetation during the Pliocene without an increase in aridity per se.
756
757 *6.2. Pliocene hominin dietary niche expansion and stone tool origins*
758 Modern savannas support a higher secondary productivity than woodlands and
759 forests (data compiled in Leonard et al., 2003). Reasons for this relationship are
760 multifaceted and involve the interplay of vegetation structure, effective rainfall, feeding
761 behaviors, and fire, among others (Hempson et al., 2015; Sankaran et al., 2005). The
762 Pliocene OTD C_3-C_4 feeding niche sustained a high number of herbivore ungulate species
763 (Cerling et al., 2015; Manthi et al., 2020; Negash et al., 2020) similar to other eastern
764 African Pliocene hominin locales (Kingston and Harrison, 2007; Robinson et al, 2017).
765 The move by many eastern African mammalian species into open woodlands and
766 grasslands was variable (Negash et al., 2020; Ségalen et al., 2007; Uno et al., 2011) but
767 perhaps represents responses by some herbivores to reduce competition (e.g., Kartzinel et
768 al., 2015; Malindie et al., 2020). OTD hominins' diets generally followed the trend of
769 increasing C_4 resources locally, which implies opportunistic foraging with changing food
770 abundances. Recently, however, Wynn et al. (2020) interpreted that the varied timing of
771 dietary shifts by hominins, non-hominin primates, and herbivore ungulates in the OTD
772 toward C_4 consumption signals behavioral changes rather than the tracking of C_4 resource
773 abundances per se. The increasing database of OTD faunal $\delta^{13}C_{EC}$ values supports the
774 hypothesis that hominins experienced a "protracted" adaptation to the widespread
775 presence of C_4 resources available by the late Miocene and early Pliocene (Ségalen et al.,
776 2007).

Biotic competition for the broad C_3-C_4 feeding niche may have been one of the selective pressures for stone tool making behaviors. As viewed in the temporal bins, *K. platyops* shared its general diet shift toward a greater reliance on C_4 plants with three ungulate herbivore C_3-C_4 mixed feeders in the OTD (Figure 9). Several ungulate herbivores and *Theropithecus*, the large-bodied baboon, had occupied the C_4 biome for some time (Cerling et al., 2013a; Uno et al., 2011). As many researchers have suggested, stone tools may have offered enhanced efficiency for processing vegetation (e.g., Brain, 1985; Dominguez-Rodrigo et al., 2001; Goren-Inbar et al., 2002; Hardy et al., 2015; Keeley and Toth, 1981; Panger et al., 2002; Schick and Toth, 1993; Sept, 1986, 1994). Notably, the combined ungulate herbivore $\delta^{13}C_{EC}$ data show evidence for dietary niche contraction within the C_3-C_4 mixed feeding niche in the 3.4-3.0 Ma interval. In contrast, hominins expand dietary breadth from a woodland C_3-browser to a broad C_3-C_4-mixed feeder, possibly filling the dietary niche left vacated by some of the C_3-C_4-mixed feeders, especially Antilopini, Aepycerotini, and *Notochoerus* (Figures 9 and 11).

Hominins, like humans and primates today, are thought to have been obligate drinkers (Grine et al. 2012; Lee-Thorp et al., 2010) and thus the average 2‰ decrease in $\delta^{18}O_{EC}$ values between *A. anamensis* and *K. platyops* suggest drinking behaviors changed. In the OTD, Quinn (2015) suggested that the presence of Lake Lonyumun during *A. anamensis'* times might have provided an ^{18}O-enriched source of drinking water resulting in higher $\delta^{18}O_{EC}$ values for *A. anamensis*. In contrast, *K. platyops* was imbibing primarily from the relatively unevaporated proto-Omo River and tributaries due to the OTD's hydrological configuration in the middle Pliocene. The lack of significant changes in Hippopotamidae $\delta^{18}O_{EC}$ values through time in the OTD (Harris et al., 2008)

and also shown here with other water dependent taxa (Crocodylia, Deinotheridae, Elephantidae) implies that $\delta^{18}O$ values of meteoric waters did not significantly shift over the two time intervals (Figure 10) and thus changing water sources appears a less likely scenario for the middle Pliocene. It appears that humidity increased over the study interval, which may have influenced the change in hominin $\delta^{18}O_{EC}$ values if a substantial amount of ingested water was derived from plant resources similar to other water-independent taxa (Figure 10).

Dietary changes could have lowered *K. playtops'* $\delta^{18}O_{EC}$ values such as feeding on ground level food resources in closed woodland settings (e.g., Nelson, 2013) or on wetland sedges and underground storage organs (e.g., Lee-Thorp, 2011). Changes in feeding and activity times could have also impacted *K. playtops'* $\delta^{18}O_{EC}$ values (e.g., Kohn, 1996; Schoeninger et al., 2000). Additionally, lower $\delta^{18}O_{EC}$ values indicate that *K. platyops* may have increased its water dependency by drinking a higher proportion of surface waters than ingesting water contained in vegetation. The relationship between lower $\delta^{18}O_{EC}$ values and increasing C_4 grass consumption as shown for Tragelaphini by Faith (2019) and here with Aepycerotini aligns with the dietary increase of C_4 resources by hominins.

Prior to the LOM3 publication (Harmand et al. 2015), Macho (2014) proposed that the increase in C_4 food consumption by Pliocene hominins was in part selected by an increase in predation as evident by an increasing speciosity of members of the Order Carnivora in the OTD and other eastern African hominin locales circa 3.6 Ma (data from Werdelin and Lewis; 2005, 2013). More frequent terrestriality practiced by habitual bipeds in the context of increased predation risk was thought to have been a prime mover

of diet change. Likewise, predation pressure could be viewed as an influence for the origins of stone tool making. However, Werdelin clarified the increase in speciosity during the middle Pliocene was caused by the "Laetoli effect" (commentary section of Thompson et al., 2019), a by-product due to a high preservation rate at one site. Moreover, Faurby and others (2020) recently demonstrated that Plio-Pleistocene Carnivora, specifically large-bodied species, across eastern Africa underwent a reduction in abundance, which they argue was influenced by competition with hominins (but see Faith et al., 2018). This decreasing trend in Carnivora began as early as 4 Ma, and notably, much of these data derive from the OTD. Faurby et al. (2020) assert that carnivores were outcompeted for animal food resources by hominins who engaged in scavenging of carcasses, stealing from carnivore kills (kleptoparasitism), or hunting behaviors. The authors suggest that hunting is a less likely explanation until hominins achieve body size and morphology for endurance hunting like that observed in genus *Homo* (e.g., Bramble and Lieberman, 2004) and/or the use of stone tools.

Tool-related activities by *Homo* (Blumenschine and Selvaggio, 1988; Braun et al., 2010; Bunn, 1981, 1994; Bunn and Kroll, 1986; Dominguez-Rodrigo et al., 2005; Pobiner et al., 2008; Potts and Shipman, 1981) and *Australopithecus* (de Heinzelin et al., 1999 McPherron et al., 2010) have been associated with animal carcass nutrient acquisition. Thompson et al. (2019) proposed that the Human Predatory Pattern (HPP) involving the scavenging of animals of equal or greater body size arose in Pliocene hominins with percussion-based marrow extraction of animal carcasses, rather than flake-tool assisted meat procurement like that interpreted for early *Homo*. The timing in the decrease of carnivore speciosity in the OTD is suggestive of direct competition between

carcass-scavenging hominins and sympatric predators beginning with *A. anamensis* and increasing throughout the Plio-Pleistocene (Faurby et al., 2020). Recent $^{44}Ca/^{42}Ca$ analysis, typically a proxy used to distinguish herbivory from carnivory, did not distinguish *A. anamensis* from *K. platyops*, and both species have $^{44}Ca/^{42}Ca$ values overlapping those of *Homo* sp., *Theropithecus*, and some eastern African carnivores (Martin et al., 2020). Indeed, discerning different dietary components of omnivorous primates requires multiple lines of evidence; we suggest that an increase in faunivory by *K. platyops* is consistent with the decrease of $\delta^{18}O_{EC}$ values relative to those of *A. anamensis* (e.g., Sponheimer and Lee-Thorp, 1999b, 2001). Although many variables could have influenced Pliocene hominin $\delta^{18}O_{EC}$ values (Faith, 2019; Lee-Thorp et al., 2010; Quinn, 2015), we cannot discount the possibility that faunivory via scavenging behaviors was one of several potential $\delta^{18}O_{EC}$-lowering factors.

Temporally discrete and sizable environmental events between 3-2 Ma are well documented in eastern Africa (Alemseged et al., 2020; Levin et al., 2011; Robinson et al., 2017; Wynn et al., 2016), but the adaptive morphological transitions from genus *Australopithecus* to *Homo* during this time appear less punctuated (Antón et al., 2014; Kimbel and Villmoare, 2016) than once characterized (McHenry and Coffing, 2000). Brain size and hand morphology did not cross a significant grade-level threshold with the first appearance of genus *Homo*, rather these adaptations were rooted in *Australopithecus* (Kimbel and Villmoare, 2016). Dietary niche expansion may have also occurred as a gradual increase in C_4 food consumption beginning with *A. anamensis*. The initial dietary interpretations of *A. anamensis* concluded that the earliest biped consumed 0-10% of C_4 foods (Cerling et al., 2013b), similar to that of modern savanna chimps (Loudon et al.,

2016). However, unlike savanna chimps, *A. anamensis'* dentognathic morphology was adapted for processing hard/tough foods (Grine et al., 2012; Macho et al., 2005; Ward et al., 1999b, 2001; White et al., 2006). Although microwear data contrast those of dentognathic morphology and imply soft foods were regularly consumed (Grine et al., 2012), *A. anamensis'* dental microwear patterns are similar to those of the C_3-C_4 mixed feeding *A. afarensis* (Grine et al., 2006; Ungar et al., 2010). Quinn (2019) reanalyzed the $\delta^{13}C_{EC}$-based C_4 consumption percentage of *A. anamensis* in the OTD informed by Pliocene CO_2 $\delta^{13}C$ values and vegetation structural categories and suggested that C_4 resources may have been more regular components in the earliest habitual biped (i.e., ~20% C_4 diet), constituting an stepwise increase from a purely C_3 diet to a C_3-C_4 mixed diet. Moreover, Blumenthal et al. (2020) has found high intra- and inter-annual $\delta^{13}C_{EC}$ values with laser ablation techniques in specimens of *A. anamensis* and *K. platyops*, suggesting seasonal fluctuations in resource use. Thus hominins' dietary forays into the C_3-C_4 biome may be characterized as incremental increases in dietary breadth throughout the early Pliocene, reaching the broad C_3-C_4 mixed diet in the middle Pliocene.

In a common thread, we suggest a gradual and stepwise but not necessarily abrupt behavioral shift underpins the earliest known stone tool making behaviors as represented by LOM3. Tools are used by extant chimpanzees to forage (Boesch and Boesch, 1990; Haslam, 2014; Haslam et al., 2009; Marchant and McGrew, 2005); thus tool-assisted foraging may be a shared ape-human behavioral trait also present in the earliest hominins (Toth and Schick, 2009). As Thompson et al. (2019) proposed, the use of unmodified stone for carcass marrow extraction might have been practiced throughout the early Pliocene without visible archaeological traces. Stone tool making (Harmand et al., 2015)

892 and use (McPherron et al., 2010) became archaeologically visible when hominins began
893 to knap stones deliberately to produce sharp flakes. Although this step does not meet
894 Shea's (2017) criteria of obligatory and repeated-form stone tool making as seen in late
895 Pleistocene *Homo*, LOM3 artifacts may mark the beginnings of *habitual* tool-assisted
896 foraging behaviors for the purposes of extracting nutrients from a wide range of vegetal
897 resources as well as animal carcasses. Clearly, additional lines of evidence including
898 more archaeological occurrences are needed to test this hypothesis. Nevertheless, we
899 interpret that mounting evidence suggests that hominins may have expanded their dietary
900 niche in the early Pliocene with an incremental increase in C_4 food consumption and
901 carcass scavenging potentially with unmodified stone tools. The origins of stone tool
902 making behaviors enabled hominins to increasingly outcompete other C_3-C_4-mixed
903 feeders (Figures 9, 11) and perhaps carnivores. We assert that the earliest tool making
904 was an important step in human evolution but constitutes one of several adaptations for
905 enhancing foraging efficiency as Pliocene hominins incrementally expanded their dietary
906 niche into the C_3-C_4 biome and gradually encroached on the carnivore guild.
907 Figure 12 illustrates a (food-centric) feedback loop hypothesizing the adaptive
908 relationships between the environment, dietary niche expansion, morphological
909 adaptations and the origins of stone tool making. The construction of the model was
910 influenced by several contributions to paleoanthropology (Aiello and Wheeler, 1995;
911 Bromage and Schrenk, 1995; Faurby et al., 2020; Kimbel and Villmoare, 2016; Kingston,
912 2007; Leonard and Robertson, 1997; Leonard et al., 2003; Shipman and Walker, 1995;
913 Thompson et al., 2019). Gradual but consistent environmental change and biotic
914 competition served as selective factors for hominins to expand the dietary niche to

include foraging C_3-C_4 plants and carcass scavenging. Incremental changes in foraging across habitats with different and more variable food properties (e.g., hardness, caloric and macronutrient contents) and procurement requirements (e.g., stone percussion) influenced a mosaic suite of morphological changes to the body and brain including but not limited to habitual bipedal locomotion, a masticatory apparatus for hard, tough, and abrasive foods, hand morphology for object manipulation, and an increased brain size. (Un)modified stone-assisted percussion-based, food-getting behaviors were also influenced by food properties and procurement requirements. Moreover, changes in morphology and stone tool making behaviors, in turn, enhanced foraging efficiency and continued to increase hominins' capacity for dietary niche expansion. Gradual environmental changes in the early Pliocene and occurring throughout the middle Pliocene did not necessarily evoke abrupt changes to hominin morphology and diet, but provided consistent changes to resource abundances, shaping biotic competition. Likewise, stone tool-making behaviors involving rudimentary but deliberate core and flake technology do not represent the start of a new dietary niche, but the result of a long-term and stepwise adaptive zone throughout the Pliocene.

7. Conclusions

OTD environments shifted incrementally toward more open biomes but with slightly more humid conditions across the early and middle Pliocene. Some aspects of the environment became marginally more variable as indicated by intranodular $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ values, but these changes are modest. Three herbivore ungulate taxa accompanied hominins in their increasing consumption of C_4 resources over the study interval.

Notably, the C_3-C_4 feeding niche contracted through time, which was then occupied by broad C_3-C_4-mixed feeding hominins. No climatic changes are indicated with $\delta^{18}O_{PC}$ values from the early to middle Pliocene, but faunal $\delta^{18}O_{EC}$ values signal a slight increase in humidity. The drop in hominin $\delta^{18}O_{EC}$ values suggests an increase in water dependency as a function of increasing C_4 consumption, but also may have tracked the vegetation $\delta^{18}O$ decrease and/or the consumption of animal products. The gradual increase in C_4 vegetation detected across this time interval is consistent with the long-term decrease in pCO_2; however, the evidence for a slight uptick in humidity suggests that C_4 grassland spread was not accompanied by aridification. To date, OTD proxy records do not indicate the types of habitat changes predicted by variability or pulsed selection hypotheses per se (e.g., Maslin et al., 2014; Potts and Faith, 2015; Schultz and Maslin, 2013), but rather point to gradual, long-term environmental shifts. Making stone tools to more efficiently and effectively access foods provided the earliest knappers with a competitive edge relative to the established C_3-C_4 feeding guild members including carnivores. We assert that hominin dietary niche expansion in the Pliocene, involving a wide range of plant foods and possibly carcass scavenging, was not a punctuated event but rather a series of incremental steps as hominins became increasingly more reliant on tool-assisted foraging, which culminated in stone tool making origins.

Acknowledgments

We thank the office of the President of Kenya, the Ministry of Education, Science and Technology, the National Council for Science and Technology (NCST/RCD/12B/012/25) and the Kenya National Museums, especially

961 Frederick Kyalo Manthi, for fieldwork and sampling collection permissions. We thank
962 the Mission Préhistorique au Kenya/West Turkana Archaeological Project, funded by the
963 French Ministry of Foreign Affairs (Nu681/DGM/ATT/RECH, Nu986/DGM/DPR/PRG),
964 and the French National Research Agency (ANR-ARCHOR-12-CULT-0006; ANR-
965 HOMTECH-17-CE27-0005). The generous and ongoing support of the Turkana Basin
966 Institute facilitated this research project and aided with fieldwork. We thank
967 Richard Mortlock and James Wright in the Geochemistry Laboratory, Department of
968 Earth and Planetary Sciences, Rutgers University for mass spectrometry. Laboratory and
969 student educational support was provided by the National Science Foundation to RLQ
970 (NSF-CAREER, BCS-145527). The US Embassy in Nairobi provided support to JEL for
971 travel and logistics. Numerous researchers provided methodological tools, invaluable
972 datasets and environmental insights for the OTD, which made inferences such as these
973 possible, especially Thure Cerling.

974
975

References

Aiello, L.C., Wells, J.C.K., 2002. Energetics and the evolution of the genus *Homo*. Ann. Rev. Anthropol. 31, 323-338.

Aiello, L. C., Wheeler, P., 1995. The expensive-tissue hypothesis. Curr. Anthropol. 36, 199–211.

Alemseged, Z., Wynn, J.G., Geraads, D., Reed, D., Barr, W.A., Bobe, R., McPherron, S.P., Deino, A., Alene, M., Sier, M.J., Romani, D., Mohan, J., 2020. Fossils from Mille-Logya, Afar, Ethiopia, elucidate the link between Pliocene environmental changes and Homo origins. Nature Comm. 11, 2480.

Ambrose, S.H., 2001. Paleolithic technology and human evolution. Science 291, 1748-1753.

Amiot, R., Lecuyer, C., Escarguel, G., Billon-Bruyat, J.-P., Buffetaut, E., Langlois, C., Martin, S., Martineau, F., Mazin, J.-M., 2007. Oxygen isotope fractionation between crocodilian phosphate and water. Palaeogeog, Palaeoclim, Palaeoecol, 243, 412-420.

Amundson, R.G., Wang, Y., 1996. The relationship between the oxygen isotopi composition of soil CO_2 and soil water. IAEA, Isotopes Water Res. Manage. 1, 315-332.

Antón, S.C., Potts, R., Aiello, L.C., 2014. Evolution of early Homo: an integrated biological perspective. Science 345,1236828.

Ascari, S., Njau, J.K., Sauer, P.E., Polly, P.D., Peng, Y., 2018. Fossil herbivores and crocodiles as paleoclimatic indicators of environmental shifts from bed I to Bed II times of the Olduvai Gorge, Tanzania. Palaeogeog, Palaeoclim, Palaeoecol, 511, 550-557.

Ash, J., Gallup, G., 2007. Paleoclimatic variation and brain expansion during human evolution. Hum. Nat. 18, 109–124.

Ashley, G.M., Ndiema, E.K., Spencer, J.Q.G., Harris, J.W.K., Kiura, P.W., 2011. Paleoenvironmental context of archaeological sites, implications for subsistence strategies under Holocene climate change, northern Kenya. Geoarchaeol., 26, 809-837

Ayliffe, L.K., Chivas, A.R., 1990. Oxygen isotope composition of the bone phosphate of Australian kangaroos: potential as a palaeoenvironmental recorder. Geochim. Cosmochim. Acta 54, 2603-2609.

Ayliffe, L.K., Lister, A.M., Chivas, A.R., 1992. The preservation of glacial-interglacial climatic signatures in the oxygen isotopes of elephant skeletal phosphate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 99, 179-191.

Bailey, D. H. Geary, D. H., 2009. Hominid brain evolution: testing climatic, ecological,

and social competition models. Hum. Nat. 20, 67–79.

Behrensmeyer, A.K., 2006. Climate change and human evolution. Science 311, 476-478.

Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S.J., Ali, A.R., Mwonga, S.M., 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. J. Appl. Ecol. 26, 1005–1024.

Birkeland, P.W., 1999. Soils and Geomorphology. Oxford University Press, New York.

Bloszies, C., Forman, S.L., Wright, D.K., 2015. Water level history for Lake Turkana, Kenya in the past 15,000 years and a variable transition from the African humid period to holocene aridity. Glob. Planet. Change, 132, 64-76

Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. Nature 333, 763-765

Blumenthal, S.A., Cerling, T.E., Chritz, K.L., Lee-Thorp, J.A., Manthi, F., Strum, S. 2020. Seasonal-scale variability in diets of hominins from Turkana, Kenya. Am. J. Phys. Anthropol. 171, 31.

Blumenthal, S.A., Cerling, T.E., Smiley, T.M., Badgley, C.E., Plummer, T.W., 2019. Isotopic records of climate seasonality in equid teeth. Geochim. Cosmochim. Acta 260, 329-348.

Blumenthal, S.A., Levin, N.E., Brown, F.H., Brugal, J.-P., Chritz, K.L., Harris, J.M., Jehle, G.E., Cerling, T.E., 2017. Aridity and hominin environments. Proc. Natl. Acad. Sci. 114, 7331-7336.

Blumenthal, S.A., Rothman, J.M., Chritz, K.L., Cerling, T.E., 2016. Stable isotopic variation in tropical forest plants and applications in primatology. Am. J. Primatol. 78, 1041-1054.

Bobe, R., Behrensmeyer, A.K., 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. Palaeogeogr. Palaeoclimatol. Palaeoecol. 207, 399-420.

Bocherens, H., Koch, P.L., Mariotti, A., Geraads, D., Jaeger, J.-J., 1996. Isotopic biogeochemistry (^{13}C, ^{18}O) of mammal enamel from African Pleistocene hominid sites: implications for the preservation of paleoclimatic signals. Palaios 11, 306-318.

Boës, X., Prat, S., Arrighi, V., Feibel, C., Haileab, B., Lewis, J., Harmand, S., 2019. Lake-level changes and hominin occupations in the arid Turkana basin during volcanic closure of the Omo River outflows to the Indian Ocean. Quatern. Res. 91, 892-909.

Boesch, C., Boesch, H. 1990. Tool use and tool making in wild chimpanzees. Folia

Primatologica 54, 86–99.

Bond, W.J., 2008. What limits trees in C_4 grasslands and savannas? Annu. Rev. Ecol. Evol. Syst. 39, 641-59.

Bond, W.J., Midgley, G.F., Woodward, F.I., 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. Glob. Change Biol. 9, 973–82.

Brain, C.K., 1981. The evolution of man in Africa: was it a consequence of Cainozoic cooling? Alex L. du Toit Memorial Lectures 17. Trans. Geol. Soc. S. Afr. Ann. 84, 1-19.

Brain, C.K., 1985. Cultural and taphonomic comparisons of hominids from Swartkrans and Sterkfontein. In: Delson, E. (Ed.), Ancestors: The Hard Evidence. John Wiley & Sons, New York, pp. 72–75.

Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of *Homo*. Nature 432, 354-352.

Braun, D.R., Aldeias, V., Archer, W., Arrowsmith, J.R., Baraki, N., Campisano, C.J., Deino, A.L., DiMaggio, E.N., Dupont-Nivet, G., Engda, B., Feary, D.A., Garello, D., I., Kerfelew, Z., McPherron, S.P., Patterson, D.B., Reeves, J.S., Thompson, J.C., Reed, K.E., 2019. Earliest known Oldowan artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia, highlight technological diversity. Proc. Natl. Acad. Sci. 116, 11712-11717.

Braun, D.R., Harris, J.W.K., Levin, N.E., McCoy, J.T., Herries, A.I.R., Bamford, M.K., Bishop, L.C., Richmond, B.G., Kibunjia, M., 2010. Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. Proc. Natl. Acad. Sci. 107, 10002-10007.

Breecker, D.O., Sharp, Z.D., McFadden, L.D., 2009. Seasonal bias in the formation and stable isotopic composition of pedogenic carbonate in modern soils from central New Mexico, USA. GSA Bull. 121, 630–640.

Bromage, T.G., Schrenk, F., 1995. Biogeographic and climatic basis for a narrative of early hominid evolution. J. Hum. Evol. 28, 109-114.

Brown B, Brown FH, Walker A. 2001. New hominids from the Lake Turkana Basin, Kenya. J. Hum. Evol. 41, 29-44.

Brown, F.H., Feibel, C.S., 1986. Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya. J. Geol. Soc. London 143, 297-310.

Brown, F.H., Feibel, C.S., 1991. Stratigraphy, depositional environments and palaeogeography of the Koobi Fora Formation. In: Harris, J.M. (Ed.), Koobi For a Research Project. Stratigraphy, Artiodactyls and Palaeoenvironments, vol. 3. Clarendon

Press, Oxford, pp. 1-30.

Brown, F.H., McDougall, I., 2011. Geochronology of the Turkana Depression of Northern Kenya and Southern Ethiopia. Evol. Anthropol. 20, 217-227.

Bruhn, R.L., Brown, F.H., Gathogo, P.N., Haileab, B., 2011. Pliocene volcano-tectonics and paleogeography of the Turkana Basin, Kenya and Ethiopia. J. Afr. Earth Sci. 59, 295 312.

Brunet, M., Beauvilain, A., Coppens, Y., Heintz, E., Moutaye, A.H.E., Pilbeam, D., 1996. *Australopithecus bahrelghazali*, a new species of early hominid from Koro Toro region, Chad. C R Acad Sci Paris 322, 907–913.

Bryant, D., Froelich, P., 1995. A model of oxygen isotope fractionation in body water of large mammals. Geo. Cosmo. 59, 4523–4537

Bryant, D., Froelich, P., Showers, W., Genna, B., 1996. Biologic and climatic signals in the oxygen isotopic composition of Eocene–Oligocene equid enamel phosphate. Palaeogeog. Palaeoclim. Palaeoecol. 126, 75–89.

Bryant, J.D., Luz, B., Froelich, P.N., 1994. Oxygen isotopic composition of fossil horse tooth phosphate as a record of continental paleoclimate. Palaeogeog. Palaeoclim. Palaeoecol. 107, 303-316.

Bunn, H.T., 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. Nature 291, 547–577.

Bunn, H.T., 1994. Early Pleistocene hominid foraging strategies along the ancestral Omo River at Koobi Fora, Kenya. J. Hum. Evol. 27, 247–266.

Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio-Pleistocene hominids at Olduvai Gorge, Tanzania. Curr. Anthropol. 27, 431–452.

Burke, K.D., Williams, Chandler, M.A., Haywood, A.M., Lunt, D.J., Otto-Bliesner, B.L., 2018. Pliocene and Eocene provide best analogs for near-future climates. Proc. Natl. Acad. Sci. 115, 13288-13293.

Buschke, F.T., Brendonck, L., Vanschoenwinkel, B., 2015. Simple mechanistic models can partially explain local but not range-wide co-occurrence of African mammals. Glob. Ecol. Biogeogr. 24, 762.

Campisano, C.J.**,** Cohen, A.S., Arrowsmith, J.R., Asrat, A., Behrensmeyer, A.K., Brown, E.T., Deino, A.L., Deocampo, D.M., Feibel, C.S., Kingston, J.D., Lamb, H.F., Lowenstein, T.K., Noren, A., Olago, D.O., Owen, R.B., Pelletier, J.D., Potts, R., Reed, K.E., Renaut, R.W., Russell, J.M., Russell, J.L., Schabitz, F., Stone, J.R., Trauth, M.H., Wynn, J.G., 2017. The Hominin Sites and Paleolakes Drilling Project: High-resolution

paleoclimate records from the East African rift system and their implications for understanding the environmental context of hominin evolution. PaleoAnthropology, 1-43.

Carr, C.J., 1998. Patterns of vegetation along the Omo River in southwest Ethiopia. Plant Ecol. 135, 135-163.

Carter, M.L., Bradbury, M.W., 2016. Oxygen isotope ratios in primate bone carbonate reflect amount of leaves and vertical stratification in the diet. Am. J. Primatol. 78, 1086-1097.

Cerling, T.E., 1984. The stable isotopic composition of modern soil carbonate and its relationship to climate. Earth Planet. Sci. Lett. 71, 229-240.

Cerling, T.E., 1986. A Mass-balance approach to basin sedimentation: constraints on the recent history of the Turkana Basin. Palaeogeogr. Palaeoclimatol. Palaeoecol. 54, 63–86.

Cerling, T.E., 1992a. Development of grasslands and savannas in East Africa during the Neogene. Palaeogeog. Palaeoclim. Palaeoecol. 97, 241-247.

Cerling, T.E., 1992b. Use of carbon isotopes in paleosols as an indicator of the P(CO2) of the paleoatmosphere. Global Biogeochem. Cyc. 6, 307-314.

Cerling, T.E., Bowman, J.R., O'Neil, J.R., 1988. An isotopic study of a fluviolacustrine sequence: the Plio-Pleistocene Koobi Fora sequence, East Africa. Palaeogeog. Palaeoclim. Palaeoecol. 63, 335-356.

Cerling, T.E., Chritz, K.L., Jablonski, N.G., Leakey, M.G., Manthi, F.K., 2013a. Diet of *Theropithecus* from 4-1 Ma in Kenya. Proc. Natl. Acad. USA 110, 10507-10512.

Cerling, T.E., Harris, J.M., Leakey, M.G., 2003a. Isotope paleoecology of the Nawata and Apak Formations at Lothagam, Turkana Basin, Kenya. In: Leakey, M.G., Harris, J.M. (Eds.), Lothagam: the Dawn of Humanity in Africa. Columbia University Press, New York, pp. 605-624.

Cerling, T.E., Harris, J.M., Leakey, M.G., Mudida, N., 2003b. Stable isotope ecology of Northern Kenya, with emphasis on the Turkana Basin, Kenya. In: Leakey, M.G., Harris, J.M. (Eds.), Lothagam: the Dawn of Humanity in Africa. Columbia University Press, New York, pp. 583-603.

Cerling, T.E., Harris, J.M., Passey, B.H., 2003c. Diets of East African Bovidae based on stable isotope analysis. J. Mammal. 84, 456-470.

Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120, 347–363.

Cerling, T.E., Harris, J.M., Hart, J.A., Kaleme, P., Klingel, H., Leakey, M.G., Levin, N.E., Lewinson, R.L., Passey, B.H., 2008. Stable isotope ecology of the common hippopotamus. J. Zool. 276, 204–212.

Cerling, T.E., Hart, J.A., Hart, T.B., 2004. Stable isotope ecology in the Ituri Forest. Oecologia 138, 5-12.

Cerling, T.E., Levin, N.E., Passey, B.H., 2011a. Stable isotope ecology in the Omo Turkana basin. Evol. Anthropol. 20, 228–237.

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., 2011b. Woody cover and hominin environments in the past 6 million years. Nature 476, 51-56.

Cerling, T.E., Manthi, F.K., Mbua, E., Leakey, L.N., Leakey, M.G., Leakey, R.E., Brown, F.H., Grine, F.E., Hart, J.A., Kaleme, P., Roche, H., Uno, K.T., Wood, B.A., 2013b. Stable isotope-based diet reconstructions of Turkana Basin hominins. Proc. Natl. Acad. Sci. 110, 10501-10506.

Cerling, T.E., Andanje, S.A., Blumenthal, S.A., Brown, F.H., Chritz, K.L., Harris, J.M., Hart, J.A., Kirera, F.M., Kaleme, P., Leakey, L.N., Leakey, M.G., Levin, N.E., Manthi, F.K., Passey, B.H., Uno, K.T., 2015. Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. Proc. Natl. Acad. Sci. 112, 11467-11472.

Cerling, T.E., Quade, J., 1993, Stable carbon and oxygen isotopes in soil carbonate. In: Swart, P.K., Lohmann, K.C., McKenzie, J., and Savin, S. (Eds.), Climate Change in Continental Isotopic Records. AGU Monogr. 78, pp. 217–231.

Clark, J.D., 1960. Human ecology during Pleistocene and later times in Africa south of the Sahara. Curr. Anthropol. 1, 307-324.

Codron, D., Hull, J., Brink, J.S., Codron, J., Ward, D., Clauss, M., 2011. Influence of competition on niche dynamics of syntopic grazing ungulates: contrasting the predictions of habitat selection models using stable isotope analysis. Evol. Ecol. Res. 13, 217.

Cohen, A.S., Arrowsmith, J.R., Behrensmeyer, A.K., Campisano, C.J., Feibel, C.S., Fisseha, S., Bedaso, Z., Lockwood, C.A., Mbua, E., Olago, D., Potts, R., Reed, K., Renaut, R., Tiercelin, J.J, Umer, M., 2009. Understanding paleoclimate and human evolution through the Hominin Sites and Paleolakes Drilling Project. Scientific Drilling, 8, 60-65.

Cohen, A.**,** Campisano, C., Arrowsmith, R., Asrat, A., Behrensmeyer, A.K., Deino, A., Feibel, C., Hill, A., Johnson, R., Kingston, J., Lamb, H., Lowenstein, T., Noren, A., Olago, D., Owen, R.B., Potts, R., Reed, K., Renaut, R., Schabitz, F., Tiercelin, J.-J., Trauth, M.H., Wynn, J., Ivory, S., Brady, K., O'Grady, R., Rodysill, J., Githiri, J., Russell, J., Foerster, V., Dommain, R., Rucina, S., Deocampo, D., Russell, J., Billingsley,

A., Beck, C., Dorenbeck, G., Dullo, L., Feary, D., Garello, D., Gromig, R., Johnson, T., Junginger, A., Karanja, M., Kimburi, E., Mbuthia, A., McNulty, E., Muiruri, V., Nambiro, E., Negash, E.W., Njagi, D., Wilson, J.N., Rabideaux, N., Raub, T., Seir, M.J., Smith, P., Urban, J., Warren, M., Yadeta, M., Yost, C., Zinaye, B., 2016. The Hominin Sites and Paleolakes Drilling Project: inferring the environmental context of human evolution from eastern African rift lake deposits. Scientific Drilling 21, 1-16.

Cromsigt, J.P.G.M., Olff, H., 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. Ecology 87, 1532.

Dansgaard, W., 1964. Stable isotopes in precipitation, Tellus 16, 436-468.

Davis, N.E., Gordon, I.R., Coulson, G., 2017. The influence of evolutionary history and body size on partitioning of habitat resources by mammalian herbivores in southeastern Australia. Aust. J. Zool. 65, 226.

de Heinzelin, J., 1983. The Omo Group: Archives of the International Omo Research Expedition. In: Annales, Série in 8, Sciences Géologiques, vol. 85. Musée Royal de l'Afrique Centrale, Tervuren, Belgique.

de Heinzelin, J., Clark, D., White, T., Hart, W., Renne, P., WoldeGabriel, G., Beyene, Y., Vrba, E., 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. Science 284, 625-629.

Deino, A.L., Sier, M.J., Garello, D., Keller, B., Kingston, J., Scott, J., Dupont-Nivet, G., Cohen, A., 2019. Chronostratigraphy of the Baringo-Tugen-Barsemoi (HSPDP-BTB13-1A) core: $^{40}Ar/^{39}Ar$ dating, magnetostratigraphy, tephrostratigraphy, sequence stratigraphy and Bayesian age modeling. Palaeogeog. Palaeoclim. Palaeoecol. 532, 2

Delagnes, A., Roche, H. 2005. Late Pliocene hominid knapping skills: the case of Lokalalei 2C, West Turkana, Kenya. J. Hum. Evol. 48, 435–472.

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 Planet. Sci. Lett. 220, 3-24.

Dominguez-Rodrigo, M., Pickering, T.R., Semaw, S., Rogers, M.J., 2005. Cutmarked bones from Pliocene archaeological sites at Gona, afar, Ethiopia: Implications for the function of the world's oldest stone tools. J. Hum. Evol. 48, 109–121.

Dominguez-Rodrigo, M., Serrallonga, J., Jaun-Tresserras, J., Alcala, L., Luque, L., 2001. Woodworking activities by early humans: A plant residue analysis on Acheulean stone tools from Peninj (Tanzania). J. Hum. Evol. 40, 289–299.

Donges, J.F., Donner, R.V., Trauth, M.H., Marwan, N., Schellnhuber, H.-J., Kurths, J., 2011. Nonlinear detection of paleoclimate-variability transitions possibly related to human evolution. Proc. Natl. Acad. Sci. USA 108, 20422-20427.

Dowsett, H.J., Robinson, M., Haywood, A.M., Salzmann, U., Hill, D.J., Sohl, L., Chandler, M.A., Williams, M., Foley, K., Stoll, D., 2010. The PRISM3D paleoenvironmental reconstruction. Stratigraphy 7, 123-139.

Drapeau, M. S. M., Bobe, R., Wynn, J. G., Campisano, C. J., Dumouchel, L., Geraads, D., 2014. The Omo Mursi formation: A window into the east African Pliocene. J. Hum. Evol. 75, 64–79.

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.

du Toit, J.T., 2003. Large herbivores and savanna heterogeneity. In: du Toit, J.T., Rogers, K.H. Biggs, H.C. (Eds.), The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington.

Ebinger, C.J., Yemane, T., Harding, D.J., Tesfaye, S., Kelley, S., Rex, D.C., 2000. Rift deflection, migration, and propagation: linkage of the Ethiopian and Eastern rifts, Africa. GSA Bull. 112, 163-176.

Estes, R.D., 1991. The Behavior Guide to African Mammals. University of California Press, Los Angeles.

Fahy, G.E., Richards, M., Riedel, J., Hublin, J.-J., Boesch, C., 2013. Stable isotope evidence of meat eating and hunting specialization in adult male chimpanzees. Proc. Natl. Acad. Sci. USA 110, 5829-5833.

Faith, J.T., 2019. Paleodietary change and its implications for aridity indices derived from $\delta^{18}O$ of herbivore enamel. Palaeogeog. Palaeoclim. Palaeoecol. 490, 571-578.

Faith, J.T., Rowan, J., Du, A., Koch, P. L., 2018. Plio-Pleistocene decline of African megaherbivores: No evidence for ancient hominin impacts. Science, 362, 938–941.

Faurby, S., Silvestro, D., Werdelin, L., Antonelli, A., 2020. Brain expansion in early hominins predicts carnivore extinctions in East Africa. Ecol. Lett. 23, 537-544.

Fedorov, A., Brierley, C.M., Lawrence, K.T., Liu, Z., Dekens, P.S., Ravelo, A.C., 2013. Patterns and mechanisms of early Pliocene warmth. Nature 496, 43-49

Fedorov, A.V., Dekens, P.S., McCarthy, M., Ravelo, A.C., deMenocal, P.B., Barreiro, M., Pacanowski, R.C., Philander, S.G., 2006. The Pliocene paradox (mechanisms for a permanent El Niño). Science 312, 1485-1489.

Feibel, C.S., 1994. Freshwater stingrays from the Plio-Pleistocene of the Turkana Basin, Kenya and Ethiopia. Lethaia 26, 359-366.

Feibel, C.S., 1997. A terrestrial auxillary stratotype point and section for the Plio Pleistocene boundary in the Turkana Basin, East Africa. Quatern. Int. 40, 73-79.

Feibel, C. S., 2003a. Stratigraphy and depositional setting of the Pliocene Kanapoi formation, lower Kerio Valley, Kenya. In J. M. Harris & M. G. Leakey (Eds.), Geology and vertebrate paleontology of the early Pliocene site of Kanapoi, northern Kenya (pp. 9–20). Los Angeles, CA: Natural History Museum of Los Angeles County.

Feibel, C. S., 2003b. Stratigraphy and depositional history of the Lothagam sequence. In: Leakey, M.G., Harris, J.M. (Eds.), Lothagam: The Dawn of humanity in eastern Africa. New York, NY, Columbia University Press, pp. 17–29.

Feibel, C.S., 2011. A geological history of the Turkana Basin. Evol. Anthropol. 20, 206-216.

Feibel, C. S., Brown, F. H., McDougall, I., 1989. Stratigraphic context of fossil hominids from the Omo Group deposits; northern Turkana Basin, Kenya and Ethiopia. Am. J. Phys. Anthropol. 78, 595 622.

Feibel, C. S., Harris, J. M., Brown, F. H., 1991. Palaeoenvironmental context for the late Neogene of the Turkana Basin. In: Harris, J.M. (Ed.), Koobi Fora research project, vol 3. Stratigraphy, artiodactyls and palaeoenvironments. Oxford, Clarendon Press, pp. 321–370.

Feranec, R.S., 2007. Stable carbon isotope values reveal evidence of resource partitioning among ungulates from modern C_3-dominated ecosystems in North America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 252, 575–585.

Ferretti, D.F., Pendall, E., Morgan, J.A., Nelson, J.A., LeCain, D., Mosier, A.R., 2003. Partitioning evapotranspiration fluxes from a Colorado grassland using stable isotopes: seasonal variations and ecosystem implications of elevated atmospheric CO_2. Plant Soil 254, 291–303.

Forman, S.L., Wright, D.K., Bloszies, C., 2014. Variations in water level for Lake Turkana in the past 8500 years near Mt. Porr, Kenya and the transition from the African humid period to holocene aridity Quat. Sci. Rev., 97, 84-101.

Fortelius, M., Zliobaite, I., Kaya, F., Bibi, F., Bobe, R., Leakey, L., Leakey, M., Patterson, D., Rannikko, J., Werdelin, L., 2016. An ecometric analysis of the fossil

mammal record of the Turkana Basin. Philos. Trans. Royal Soc. B, 371, 20150232.

Frostick, L.E., 1997. The East African Rift basins. In: Selley, R.C. (Ed.), Sedimentary Basins of the World 3: African Basins. Elsevier Science, Amsterdam, pp. 187-209.

Garcin, Y., Melnick, D., Strecker, M.R., Olago, D., Tiercelin, J.-J., 2012. East African mid-Holocene wet–dry transition recorded in palaeo-shorelines of Lake Turkana, northern Kenya Rift. Earth Planet. Sci. Lett., 331-332, 322-334.

Garrett, N.D., Fox, D.L., McNulty, K.P., Faith, J.T., Peppe, D.J., Van Plantinga, A., Tryon, C.A., 2015. Stable isotope paleoecology of late Pleistocene Middle Stone Age humans from equatorial East Africa, Lake Victoria basin, Kenya. J. Hum. Evol. 82, 1-14.

Gat, J.R., 1996. Oxygen and hydrogen isotopes in the hydrologic cycle. Ann. Rev. Earth Planet. Sci. 24, 225-262.

Gazis, C., Feng, X., 2004. A stable isotope study of soil water: evidence for mixing and preferential flow paths: Geoderma 119, 97–111.

Gebrechorkos, S.H., Hulsmann, S., Bernhofer, C., 2019. Long-term trends in rainfall and temperature using high-resolution climate datasets in East Africa. Sci. Rep. 9, 11376

Georgiadis, N.J., 2011. Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem. Smithsonian Contrib. Zool., 632.

Goren-Inbar, N., Sharon, G., Melamed, Y., Kislev, M., 2002. Nuts, nut cracking, and pitted stones at Gesher Benot Ya`aqov, Israel. Proc. Nat. Acad. Sci. USA 99, 2455-2460

Grine, F. E., Sponheimer, M., Ungar, P. S., Lee-Thorp, J., Teaford, M. F., 2012. Dental microwear and stable isotopes inform the paleoecology of extinct hominins. Am. J. Phys. Anthropol. 148, 285–317.

Grine, F.E., Ungar, P.S., Teaford, M.F., 2006. Was the early Pliocene hominin *'Australopithecus' anamensis* a hard object feeder? S. Afr. J. Sci. 102, 301–310.

Groenewald, P.A., Sealy, J., Stynder, D., Smith, K.M., 2020. Dietary resource partitioning among three coeval proboscidean taxa (Anacus capensis, Mammuthus subplanifrons, Loxodonta cookie) from the South African Early Pliocene locality of Langebaanweg E Quarry. Palaeogeog. Palaeoclim. Palaeoecol, 543, 109606.

Haile-Selassie, Y., Gibert, L., Melillo, S.M., Ryan, T.M., Alene, M., Deino, A., Levin, N.E., Scott, G., Saylor, B.Z., 2015. New species from Ethiopia further expands Middle Pliocene hominin diversity. Nature 521, 483–488

Halfman, J.D., Johnson, T.C., 1988. High-resolution record of cyclic climatic change during the past 4 ka from Lake Turkana, Kenya. Geology 16, 496–500.

Hardy, K., Brand-Miller, K., Brown, K.D., Thomas, M.G., Copeland, L., 2015. The importance of dietary carbohydrate in human evolution. Quart. Rev. Biol. 90, 251–268.

Harmand, S., 2007. Economic behaviors and cognitive capacities of early hominins between 2.34 Ma and 0.70 Ma in West Turkana, Kenya. Mitteilungen der Gesellschaft für Urgeschichte 16, 11-23.

Harmand, S., 2009a. Raw material and economic behaviours at Oldowan and Acheulean sites in the West Turkana region, Kenya. In: Adams, B., Blades, B. (Eds.), Lithic Materials and Paleolithic Societies. Wiley-Blackwell, New York, pp. 3-14.

Harmand, S., 2009b. Variability in raw material selectivity at the Late Pliocene sites of Lokalalei, West Turkana, Kenya. In: Hovers, E., Braun, D. (Eds.), Interdisciplinary Approaches to the Oldowan. Vertebrate Paleobiology and Paleoanthropology Book Series. Springer, New York, pp. 85-97.

Harmand, S., Lewis, J.E., Feibel, C.S., Lepre, C.J., Prat, S., Lenoble, A., Boës, X., Quinn, R.L., Brenet, M., Clément, S., Daver, G., Brugal, J.-P., Leakey, L., Kent, D.V., Mortlock, R.A., Wright, J.D., Roche, H., 2015. Before the Oldowan: 3.3 Ma Stone Tools from Lomekwi 3, West Turkana, Kenya. Nature 521, 310-315.

Harris, J.M., Brown, F.H., Leakey, M.G., 1988. Geology and paleontology of Plio-Pleistocene localities west of Lake Turkana, Kenya. Contributions in Science, 399, 1-128.

Harris, J.M., Cerling, T.E., Leakey, M.G., Passey, B.H., 2008. Stable isotope ecology of fossil hippopotamids from the Lake Turkana Basin of East Africa. J. Zool. 275, 323-331.

Haslam, M. 2014. On the tool use behavior of the bonobo-chimpanzee last common ancestor, and the origins of hominine stone tool use. Am. J. Primatol. 76, 910–918.

Haslam, M., A. Hernandez-Aguilar, V. Ling, S. Carvalho, I. de la Torre, A. DeStefano, A. Du, et al. 2009. Primate archaeology. Nature 460, 339–344.

Haywood, A.M., Dowsett, H.J., Ott-Bliesner, B., Chandler, M.A., Dolan, A.M., Hill, D.J., Lunt, D.J., Robinson, M.M., Rosenbloom, N., Salzmann, U., Sohl, L.E., 2010. Pliocene model intercomparison project (PlioMIP): experimental design and boundary conditions (Experment1). Geosci. Model Dev. 3, 227-242.

Haywood, A. M. et al. 2013. Large-scale features of Pliocene climate: results from the Pliocene Model Intercomparison Project. Clim. Past 9, 191–209.

Haywood, A.M., Dowsett, H.J., Dolan, A.M., 2016. Integrating geological archives and climate models for the mid-Pliocene warm period. Nat. Comm. 7, 10646.

Hempson, G.P., Archibald, S., Bond, W. J., 2015. A continent-wide assessment of the

form and intensity of large mammal herbivory in Africa. Science, 350, 1056-1061.

Hildebrand, E.A., Grillo, K.M., Sawchuk, E.A., Pfeiffer, S.K., Conyers, L.B., Goldstein, S.T., Hill, A.C., Janzen, A., Klehm, C.E., Helper, M., Kiura, P., Ndiema, E., Ngugi, C., Shea, J.J., Wang, J., 2018. A monumental cemetery built by eastern Africa's first herders near lake Turkana, Kenya. Proc. Natl. Acad. Sci. USA 115, 8942-8947.

Hillhouse, J.W., Cerling, T.E., Brown, F.H., 1986. Magnetostratigraphy of the Koobi Fora Formation, Lake Turkana, Kenya. J. Geophys. Res. 91, 11581-11595.

Illius, A.W., O'Connor, T.G., 2000. Resource heterogeneity and ungulate population dynamics. Oikos 89, 283.

Isaac, G.Ll (Ed.), 1997. Koobi Fora Research Project. Plio-Pleistocene Archaeology, vol. 5. Clarendon Press, Oxford.

Joordens, J.C.A., Vonhof, H.B., Feibel, C.S., Lourens, L.J., Dupont-Nivet, G., van der Lubbe, J.H.J.L., Sier, M.J., Davies, G.R., Kroon, D., 2011. An astronomically-tuned climate framework for hominins in the Turkana Basin. Earth Planet. Sci. Lett. 307, 1-8.

Junginger, A., Trauth, M.H., 2013. Hydrological constraints of paleo-Lake Suguta in the northern Kenya rift during the African humid period (15-5 ka BP). Glob. Planet. Change 111, 174-188.

Kartzinel, T.R., Chen, P.A., Coverdale, T.C., Erickson, D.L., Kress, W.J., Kuzmina, M.L., Rubenstein, D.I., Wang, W., Pringle, R.M., 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. Proc. Nat. Acad. Sci. 112, 8019.

Keeley, L.H., Toth, N., 1981. Microwear polishes on early stone tools from Koobi Fora, Kenya. Nature 293, 464-465.

Kim, S.-T., O'Neil, J.R., 1997. Equilibrium and nonequilibrium oxygen isotope effects in synthetic carbonates. Geochim. Cosmochim. Acta 61, 3461–3475.

Kimbel, W.H., 1988. Identification of a partial cranium of *Australopithecus afarensis*, from the Koobi Fora Formation, Kenya. J. Hum. Evol. 17, 647–656.

Kimbel, W.H., Delezene, L.K., 2009. "Lucy" redux: a review of research on *Australopithecus afarensis*. Yrbk. Phys. Anthropol. 52, 2-48.

Kimbel, W.H., Villmoare, B., 2016. From *Australopithecus* to *Homo*: the transition that wasn't. Philos. Trans. Royal Soc. B, 371, 1698.

Kingston, J.D., 2007. Shifting adaptive landscapes: progress and challenges in reconstructing early hominid environments. Yrbk. Phys. Anthropol. 134, 20-58.

Kingston, J.D., Harrison, T., 2007. Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: implications for early hominin paleoecology. Palaeogeog. Palaeoclim. Palaeoecol. 243, 272-306.

Knapp, E., Bendick, R., Ebinger, C., Birhanu, Y., Lewi, E., Floyd, M., King, R., Kianji, G., Mariita, N., Temtime, T., Waktola, B., Deresse, B., Musila, M., Kanoti, J., Perry, M., 2020. Accommodation of East African rifting across the Turkana Depression. J. Geophys. Res. Solid Earth 125, e2019JB018469.

Koch, P.L. 1998. Isotopic reconstruction of past continental environments. Ann. Rev. Earth Planet. Sci. 26, 573-613.

Koch, P.L., Fisher, D.C., Dettman, D., 1989. Oxygen isotope variation in the tusks of extinct proboscideans: a measure of season of death and seasonality. Geology 17, 515-519.

Koch, P.L., Tuross, N., Fogel, M.L., 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. J. Archaeol. Sci. 24, 417-429.

Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C_3 plants as indicators of (paleo)ecology and (paleo)climate. Proc. Nat. Acad. Sci. 107, 19691–19695.

Kohn, M.J., 1996. Predicting animal d18O: accounting for diet and physiological adaptation. Geochim. Cosmochim. Acta 60, 4811-4829.

Kohn, M.J., Cerling, T.E., 2002. Stable isotope compositions of biological apatites. In: Kohn, M.J., Rakovan, J., Hughes, J.M. (Eds.), Phosphates. Geochemical, geobiological and Materials Importance, Reviews in Mineralogy and Geochemistry, v. 48. Mineralogical Society of American, Washington, D.C., pp. 455-488.

Kohn, M.J., Schoeninger, M.J., Valley, J.W., 1996. Herbivore tooth oxygen isotope compositions: effects of diet and physiology. Geochim. Cosmochim. Acta 60, 3889-3896.

Krigbaum, J., Berger, M.H., Daegling, D.J, McGraw, W.S. 2016. Stable isotope canopy effects for sympatric monkeys at Tai Forest, Cote d'Ivoire. Biol. Lett. 9, 20130466.

Leakey, L.S.B., Tobias, P.V., Napier, J.R., 1964. A new species of the genus Homo from Olduvai Gorge. Nature 202, 7-9.

Leakey, R.E.F., 1973. Evidence for an advanced Plio-Pleistocene hominid from East Rudolf, Kenya. Nature 242, 447-450.

Leakey, M.G., Feibel, C.S., McDougall, I., Walker, A., 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. Nature 376, 565–571.

Leakey, M.G., Feibel, C.S., McDougall, I., Ward, C.V., Walker, A., 1998. New specimens and confirmation of an early age for Australopithecus anamensis. Nature 393, 62–66.

Leakey, M.G., Spoor, F., Brown, F.H., Gathogo, P.N., Kiare, C., Leakey, L.N., McDougall, I., 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. Nature 410, 433–440.

Lee-Thorp, J.A., 2011. The demise of "Nutcracker Man." Proc. Natl. Acad. Sci. 108, 9319-9320.

Lee-Thorp, J.A., Likius, A., Mackaye, H.T., Vignaud, P., Sponheimer, M., Brunet, M., 2012. Isotopic evidence for an early shift to C_4 resources by Pliocene hominins in Chad. Proc. Nat. Acad. Sci. 109, 20369–20372.

Lee-Thorp, J.A., Sealy, J.C., van der Merwe, N.J., 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. J. Arch. Sci. 16, 585–599.

Lee-Thorp, J.A., Sponheimer, M., Passey, B.H., de Ruiter, D.J., Cerling, T.E., 2010. Stable isotopes in fossil hominin tooth enamel suggest a fundamental dietary shift in the Pliocene. Philos Trans R Soc Lond B 365, 3389–3396.

Lee-Thorp, J.A., Sponheimer, M., van der Merwe, N.J., 2003. What do stable isotopes tell us about hominin dietary and ecological niches in the Pliocene? Int. J. Osteoarchaeol. 13, 104–113.

Lee-Thorp, J.A., van der Merwe, N.J., Brain, C.K., 1994. Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis. J. Hum. Evol. 27, 361-372.

Lehmann, S.B., Braun, D.R., Dennis, K.J., Patterson, D.B., Stynder, D.D., Bishop, L.C., Forrest, F., Levin, N.E., 2016. Stable isotopic composition of fossil mammal teeth and environmental change in southwestern South Africa during the Pliocene and Pleistocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 457, 396–408.

Leonard, W.R., Robertson, M.L., 1997. Comparative primate energetics and hominid evolution. Am. J. Phys. Anthropol. 102, 265–281.

Leonard, W.R., Robertson, M.L., Snodgrass, J.J., Kuzawa, C.W., 2003. Metabolic correlates of hominid brain expansion. Comp. Biochem. Physiol. 136A, 5–15.

Lepre, C.J., 2014. Early Pleistocene lake formation and hominin origins in the Turkana-Omo rift. Quatern. Sci. Rev. 102, 181-191.

Lepre, C.J., 2019. Constraints on Fe-oxide formation in monsoonal Vertisols of Pliocene Kenya using rock magnetism and spectroscopy. Geochem. Geophys. Geosys. 20, 4998-5013.

Lepre, C.J., Kent, D.V., 2010. New magnetostratigraphy for the Olduvai Subchron in the Koobi Fora Formation, northwest Kenya, with implications for early *Homo*. Earth Planet. Sci. Lett. 290, 362-374.

Lepre, C.J., Kent, D.V., 2015. Chronostratigraphy of KNM-ER 3733 and other Area 104 hominins from Koobi Fora. J. Hum. Evol. 86, 99-111.

Lepre, C.J., Quinn. R.L., Joordens, J., Swisher, C.C., Feibel, C.S., 2007. Plio-Pleistocene facies environments from the KBS Member, Koobi Fora Formation: implications for climate controls on the development of lake-margin hominin habitats in the northeast Turkana Basin (northwest Kenya). J. Hum. Evol. 53, 504-514.

Lepre, C.J., Roche, H., Kent, D., Harmand, S., Quinn, R.L., Brugal, J.-P., Texier, P.-J., Lenoble, A., Feibel, C.S., 2011. An earlier origin for the Acheulian. Nature 477, 82-85.

Levin, N.E., 2013. Compilation of East Africa soil carbonate stable isotope data, Integrated Earth Data Applications. doi: 10.1594/IEDA/100231

Levin, N.E., 2015. Environment and climate of early human evolution. Ann. Rev. Earth Planet. Sci. 43, 405-429.

Levin, N.E., Brown, F.H., Behrensmeyer, A.K., Bobe, R., Cerling, T.E., 2011. Paleosol carbonates from the Omo Group: isotopic records of local and regional environmental change in East Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 307, 75-89.

Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable isotope aridity index for terrestrial environments. Proc. Nat. Acad. Sci. 103, 11201–11205.

Levin, N.E., Haile-Selassie, Y., Frost, S. R., Saylor, B. Z., 2015. Dietary change among hominins and cercopithecids in Ethiopia during the early Pliocene. Proc. Nat. Acad. Sci. 112, 12304-12309.

Levin, N.E., Zipser, E.J., Cerling, T.E., 2009. Isotopic composition of waters from Ethiopia and Kenya: insights into moisture sources for eastern Africa. J. Geophys. Res. 114, D23306.

Lewis, J.E., Harmand, S., 2016. An earlier origin for stone tool making: implications for cognitive evolution and the transition to *Homo*. Phil. Trans. R. Soc. B 371: 20150233.

Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. Paleoceanography 20, PA1003.

Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? Geochim. Cosmochim. Acta 48, 385-390.

Loudon, J.E., Sandberg, P.A., Wrangham, R.W., Fahey, B., Sponheimer, M., 2016. The stable isotope ecology of Pan in Uganda and beyond. Am. J. Primatol. 78, 1070-1085.

Ludwig, F., de Kfroon, H., Berendse, F., Prins, H.H.T., 2004. The influence of savanna trees on nutrient, water and light availability and the understory vegetation. Plant Ecol. 170, 93–105.

Lupien, R.L.**,** Russell, J.M., Feibel, C., Becj, C., Castañeda, I., Deino, A., Cohen, A.S., 2018. A leaf wax biomarker record of early Pleistocene hydroclimate from West Turkana, Kenya. Quatern. Sci. Res. 186, 225-235.

Lupien, R., Russell, J., Yost, C., Kingston, J., Deino, A., Logan, J., Schuh, A., Cohen, A., 2019. Vegetation change in the Baringo Basin, East Africa across the onset of Northern Hemisphere glaciation 3.3-2.6 Ma. Palaeogeog. Palaeoclim. Palaeoecol.

Luz, B., Kolodny, Y., Horowitz, M., 1984. Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. Geochim. Cosmochim. Acta 48, 1689-1693.

Macho, G.A., 2014. An ecological and behavioural approach to hominin evolution during the Pliocene. Quat. Sci. Rev. 96, 23-31.

Macho, G.A., Leakey, M.G., Williamson, D.K., Jiang, Y., 2003. Palaeoenvironmental reconstruction: evidence for seasonality at Allia Bay, Kenya, at 3.9 million years. Palaeogeog. Palaeoclim. Palaeoecol. 199, 17-30.

Macho, G.A., Shimizu, D., Jiang, Y., Spears, L.R., 2005. *Australopithecus anamensis*: A finite element approach to studying the functional adaptations of extinct hominins. Anat. Rec. 283A, 310-318.

Malindie, S., Buschke, F.T., Codron, D., 2020. Carbon isotope differences between grassland and savanna herbivores reveal environmentally driven rather than phylogenetically conserved niches. J. Zool. doi:10.1111/jzo.12762

Mana, S., Hemming, S., Kent, D.V., Lepre, C.J., 2019. Temporal and stratigraphic framework for paleoanthropology site within East-Central Area 130, Koobi Fora, Kenya. Front. Earth Sci. 7, 230.

Manthi, F.K., Cerling, T.E., Chritz, K.L., Blumenthal, S.A., 2020. Diets of mammalian fossil fauna from Kanapoi, northwestern Kenya. J. Hum. Evol. https://doi.org/10.1016/j.jhevol.2017.05.005.

Marchant, L.F., McGrew, W.C., 2005. Percussive technology: chimpanzee baobab smashing and the evolutionary modeling of hominid knapping. In: Stone knapping the necessary conditions for an uniquely hominin behaviour. Blandine Bril and Valentine Roux, eds. Pp. 341–350. McDonald Institute Monograph Series. Cambridge: McDonald Institute for Archaeological Research.

Marchant, R., Mumbi, C., Behera, S., Yamagata, T., 2007. The Indian Ocean dipole? The unsung driver of climatic variability in East Africa. African J. Ecol. 45, 4–16.

Maslin, M.A., Brierly, C.M., Milner, A.M., Shultz, S., Trauth, M.H., Wilson, K.E., 2014. East African climate pulses and early human evolution. Quatern. Sci. Rev. 101, 1-17.

Maslin, M.A., Li, X.S., Loutre, M.-F., Berger, A., 1998. The contribution of orbital forcing to the progressive intensification of Northern Hemisphere glaciation. Quaternary Science Reviews 17, 411-426.

Mbaluka, J.K., Brown, F.H., 2016. Vegetation of the Koobi Fora region northeast of Lake Turkana, Marsabit County, Northern Kenya. J. E. Afr. Nat. Hist. 105, 21-50.

McDougall, I., 1985. K–Ar and $^{40}Ar/^{39}Ar$ dating of the hominid-bearing Pliocene–Pleistocene sequence at Koobi Fora, Lake Turkana, northern Kenya. Geol. Soc. Am. Bull. 96, 159-175.

McDougall, I., Brown, F.H., 2006. Precise $^{40}Ar/^{39}Ar$ geochronology for the upper Koobi Fora Formation, Turkana Basin, northern Kenya. J. Geol. Soc. London 163, 205-220.

McDougall, I., Brown, F.H., 2008. Geochronology of the pre-KBS Tuff sequence, Omo Group, Turkana Basin. J. Geol. Soc. London 165, 549-562.

McDougall, I., Brown, F.H., Vasconcelos, P.M., Cohen, B.E., Thiede, D.S., Buchanan, M.J., 2012. New single crystal $^{40}Ar/^{39}Ar$ ages improve time scale for deposition of the Omo Group, Omo-Turkana Basin, East Africa. J. Geol. Soc. London 169, 213-226.

McHenry, H.M., Coffing, K., 2000. Australopithecus to Homo: transformations in body and mind. Ann. Rev. Anthropol. 29, 125-146.

McPherron, S.P., Alemseged, Z., Marean, C., Wynn, J.G., Reed, D., Geraads, D., Bobe, R., Béarat, H., 2011. Tool-marked bones from before the Oldowan change the paradigm. Proc. Nat. Acad. Sci. 108, E116.

McPherron, S.P., Alemseged, Z., Marean, C., Wynn, J.G., Reed, D., Geraads, D., Bobe, R., Béarat, H.A., 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. Nature 466, 857–860.

Mirazón Lahr, M., Rivera, F., Power, R.K., Mounier, A., Copsey, B., Crivellaro, F., Edung, J.E., Maillo Fernandez, J.M., Kiarie, C., Lawrence, J., Leakey, A., Mbua, E., Miller, H., Muigai, A., Mukhongo, D.M., Van Baelen, A., Wood, R., Schwenninger, J.L., Grün, R., Achyuthan, H., Wilshaw, A., Foley, R.A., 2016. Inter-group violence among early Holocene hunter-gatherers of West Turkana, Kenya. Nature, 529, 394-398.

Molnar, P., Cane, M.A., 2002. El Niño's tropical climate and teleconnections as a blueprint for pre-Ice Age climates Paleoceanog.17, 11-1.

Morrissey, A., Scholz, C.A., 2014. Paleohydrology of Lake Turkana and its influence on the Nile River System. Palaeogeogr. Palaeoclimatol. Palaeoecol. 403, 88–100.

Morrissey, A., Scholz, C.A., Russell, J.M., 2018. Late Quaternary TEX_{86} paleotemperatures from the world's largest desert lake, Lake Turkana, Kenya. J. Paleolimnol 59, 103-117.

Mudelsee, M., Raymo, M.E., 2005. Slow dynamics of the Northern Hemisphere glaciation. Paleooceanogr. 20, PA4022

Musila, S., Monadjem, A., Webala, P.W., Patterson, B.D., Hutterer, R., DeJong, Y.A., Butynski, T.M., Mwangi, G., Chen, Z.-Z., Jiang, X.-L., 2019. An annotated checklist of mammals of Kenya. Zoolog. Res. 40, 3-52.

Negash, E.W., Alemseged, Z., Bobe, R., Grine, F., Sponheimer, M., Wynn, J.G., 2020. Dietary trends in herbivores from the Shungura Formation, southwestern Ethiopia. PNAS doi/10.1073/pnas.2006982117.

Nelson, S.V., 2013. Chimpanzee fauna isotopes provide new interpretations of fossil ape and hominin ecologies. Proc. Roy. Soc. B 280, 20132324.

Nicholson, S.E., 1996. A review of climate dynamics and climate variability in Eastern Africa. In: Johnson, T.C., Odada, E.O. (Eds.), The Limnology, Climatology and Paleoclimatology of the East African Lakes. Gordon and Breach, Amsterdam, pp. 25-56.

Nutz, A., Schuster, M., 2016. Stepwise drying of Lake Turkana at the end of the African humid period: a forced regression modulated by solar activity variations? Solid Earth 7, 1609-1618.

Nutz, A., Schuster, M., Boes, X., Rubino, J.-L., 2017. Orbitally-driven evolution of Lake Turkana (Turkana Depression, Kenya, EARS) between 1.95 and 1.72 Ma: a sequence stratigraphy perspective. J. Afr. Earth Sci. 125, 230-243.

Oelze, V.M., Fuller, B., Richards, M.P., Fruth, B., Surbeck, M., Hublin, J.-J., Gottfried, H., 2011. Exploring the contribution and significance of animal protein in the diet of bonobos by stable isotope ratio analysis of hair. Proc. Nat. Acad. Sci. 108, 9792-9797.

Oelze, V.M., Head, J.S., Robbins, M.M., Richards, M., Boesch, C., 2014. Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis. J. Hum. Evol. 66, 95–106.

Owen, R.B., Barthelme, J.W., Renaut, R.W., Vincens, A., 1982. Palaeolimnology and archaeology of Holocene deposits north-east of Lake Turkana, Kenya. Nature 298, 523–529.

Owen-Smith, N., 1997. Distinctive features of the nutritional ecology of browsing versus grazing ruminants. Z. Saugetierkunde 62, 176.

Pagani, M., Liu, Z., LaRiviere, J., Ravelo, A. C., 2010. High Earth-system climate sensitivity determined from Pliocene carbon dioxide concentrations. Nat. Geosci. 3, 27-30.

Panger, M. A., Brooks, A.S., Richmond, B.G., Wood, B., 2002. Older than the Oldowan? rethinking the emergence of hominin tool use. Evol. Anthropol. 11, 235-245.

Passey, B.H, Levin, N.E., Cerling, T.E., Brown, F.H., Eiler, J.M., 2010. High-temperature environments of human evolution in East Africa based on bond ordering in paleosol carbonates. Proc. Nat. Acad. Sci. 107, 11245–11249.

Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dering, M.D., Roeder, B.L., Ehleringer, J.R., 2005. Carbon isotopic fractionation between diet, breath, and bioapatite in different mammals. J. Arch. Sci. 32, 1459-1470.

Patterson, D.B., Braun, D.R., Behrensmeyer, A.K., Merritt, S., Zliobaite, I., Reeves, J.S., Wood, B.A., Fortelius, M., Bobe, R., 2017. Ecosystem evolution and hominin paleobiology at East Turkana, northern Kenya between 2.0 and 1.4 Ma. Palaeogeogr. Palaeoclimatol. Palaeoecol. 481, 1-13.

Patterson, D.B., Braun, D.R., Allen, K., Barr, W.A., Behrensmeyer, A.K., Biernat, M., Lehmann, S.B., Maddox, T., Manthi, F.K., Merritt, S.R., Morris, S.E., O'Brien, K., Reeves, J.S., Wood, B.A., Bobe, R., 2019. Comparative isotopic evidence from East Turkana supports a dietary shift within the genus *Homo*. Nat. Ecol. Evol. doi.org/10.1038/s41559-019-0916-0

Peters, C.R., Vogel, J.C., 2005. Africa's wild C_4 plant foods and possible early hominid diets. J. Hum. Evol. 48, 219-36.

Plummer, T.W., Ditchfield, P.W., Bishop, L.C., Kingston, J.D., Ferraro, J.V., Braun, D., Hertel, F., Potts, R.B., 2009. Oldest evidence of toolmaking hominins in a grassland-dominated ecosystem. Plos One 4, e7199.

Pobiner, B.L., Rogers, M.J., Monahan, C.M., Harris, J.W.K., 2008. New evidence for hominin carcass processing strategies at 1.5Ma, Koobi Fora, Kenya. J. Hum. Evol. 55, 103-130

Podlesak, D.W., Torregrossa, A.-M., Ehleringer, J.R., Dearing, M.D., Passey, B.H., Cerling, T.E., 2008. Turnover of oxygen and hydrogen isotopes in the body water, CO_2, hair, and enamel of a small mammal. Geochim. Cosmochim. Acta 72, 19-35.

Polissar, P.J., Rose, C., Uno, K.T., Phelps, S.R., deMenocal, P., 2019. Synchronous rise of African C_4 ecosystems 10 million years ago in the absence of aridification. Nat. Geosci. 12, 657-660.

Potts, R., 1996. Evolution and climate variability. Science 273, 922-923.

Potts R. 1998. Variability selection and hominid evolution. Evol Anthropol 7, 81-96.

Potts, R., 2012. Environmental and behavioral evidence pertaining to the evolution of early *Homo*. Curr. Anthropol 53, 299-317.

Potts, R., 2013. Hominin evolution in settings of strong environmental variability. Quatern. Sci. Rev. 73, 1-13.

Potts, R., Behrensmeyer, A.K., Faith, J.T., Tryon, C.A., Brooks, A.S., Yellen, J.E., Deino, A.L., Kinyanjui, R., Clark, J.B., Haradon, C.M., Levin, N.E., Meijer, H.J.M., Veatch, E.G., Owen, R.B., Renaut, R.W., 2017. Environmental dynamics during the onset of the Middle Stone Age in eastern Africa. Science 360, 86-90.

Potts, R., Faith, J.T., 2015. Alternating high and low climate variability: the context of natural selection and speciation in Plio-Pleistocene hominin evolution. J. Hum. Evol. 87, 5-20.

Potts, R., Shipman, P., 1981. Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. Nature 291, 577–580.

Prat, S., Brugal, J.-P., Tiercelin, J.-J., Barrat, J.-A., Bohn, M., Delagnes, A., Harmand, S., Kimeu, K., Kibunjia, M., Texier, P.-J., Roche, H., 2005. First occurrence of early Homo in the Nachukui Formation (West Turkana, Kenya) at 2.3-2.4 Myr. J. Hum. Evol. 49, 230-240.

Prendergast, M.E., Beyin, A., 2018. Fishing in a fluctuating landscapes: terminal Pleistocene and early Holocene subsistence strategies in the Lake Turkana Basin, Kenya. Quatern. Internat. 471, 203-218.

Quade, J., Cerling, T.E., Bowman, J.R., 1989. Systematic variations in the carbon and oxygen isotopic composition of pedogenic carbonate along elevation transects in the southern Great Basin, United States. GSA Bull. 101, 464-475.

Quinn, R.L., 2015. Influence of Plio-Pleistocene basin hydrology on the Turkana hominin enamel carbonate $\delta^{18}O$ values. J. Hum. Evol. 86, 13-31.

Quinn, R.L., 2019. Isotopic equifinality and rethinking the diet of *Australopithecus anamensis.* Am. J. Phys. Anthropol. 169, 403-421.

Quinn, R.L., Lepre, C.J., 2020. Revisiting the pedogenic carbonate isotopes and paleoenvironmental interpretation of Kanapoi. J. Hum. Evol. 140, 102549.

Quinn, R.L., Lepre, C.J., Wright, J.D., Feibel, C.S., 2007. Paleogeographic variations of pedogenic carbonate $\delta^{13}C$ values from Koobi Fora, Kenya: Implications for floral compositions of Plio-Pleistocene hominin environments. J. Hum. Evol. 53, 560-573.

Raymo, M., Grant, B., Horowitz, M., Rau, G., 1996. Mid-Pliocene warmth: stronger greenhouse and stronger conveyor. Mar. Micropaleontol. 27, 313-326.

Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. J. Hum. Evol. 32, 289-322.

Retallack, G.J., 2005. Pedogenic carbonate proxies for amount and seasonality of precipitation in paleosols. Geology 33, 333-336.

Robinson, J.R., Rowan, J., Faith, J.T., Fleagle, J.G., 2016. Paleoenvironmental change in late Middle Pleistocene-Holocene Kibish Formation, southern Ethiopia: evidence from ungulate isotopic ecology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 450, 50–59.

Robinson, J.R., Rowan, J., Campisano, C.J., Wynn, J.G., Reed, K.E., 2017. Late Pliocene environmental change during the transition from *Australopithecus* to *Homo*. Nat. Ecol. Evol. 1, 0159.

Roche, H., Delagnes, A., Brugal, J.P., Feibel, C., Kibunjia, M., Mourre, V., Texier, P.-J., 1999. Early hominid stone tool production and technical skill 2.34 myr ago in West Turkana, Kenya. Nature 399, 57-60.

Roche, H., Brugal, J.-P., Delagnes, A., Feibel, C., Harmand, S., Kibunjia, M., Prat, S., Texier, P.-J., 2003. Les sites archéologiques plio-pléistocènes de la formation de Nachukui, Ouest-Turkana, Kenya: bilan synthétique 1997-2001. C.R. Palevol 2, 663-673.

Ruff, C.B.,1991. Climate and body shape in hominid evolution. J. Hum. Evol. 21, 81 105.

Ruff, C.B., 1993. Climatic adaptation and hominid evolution: the thermoregulatory imperative. Evol. Anthropol. 2, 53-60.

Ruff, C.B., Walker, A., 1993. Body size and body shape. In: Walker, A., Leakey, R.E. (Eds.), The Nariokotome Homo erectus Skeleton. Harvard University Press, Harvard, pp.

234-265.

Sage, R.F., Monson, R.K., 1999. C_4 plant biology. San Diego, CA: Academic.

Salzmann, U., Williams, M., Haywood, A.M., Johnson, A.L.A., Kender, S., Zalasiewicz, J., 2011. Climate and environment of a Pliocene warm world. Palaeogeogr. Palaeoclimatol. Palaeoecol. 309, 1-8.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H., Ringrose, S., Sea, W., Tews, J., Worden, J., Zambatis, N., 2005. Determinants of woody cover in African savannas. Nature 438, 846–849.

Schick, K.D., Toth, N., 1993. Making Silent Stones Speak. Simon and Schuster, New York.

Schoeninger, M.J., 2014. Stable isotope analyses and the evolution of human diets. Ann. Rev. Anthropol. 43, 413–430.

Schoeninger, M.J., Kohn, M.J., Valley, J.W., 2000. Tooth oxygen isotope ratios as paleoclimate monitors in arid ecosystems. In: Ambrose, S.H., Katzenberg, M.A. (Eds.), Biogeochemical Approaches To Paleodietary Analysis in Archaeology, Advances in Archaeological and Museum Science Plenum Press, Vol. 5, pp. 117-140.

Schoeninger, M. J., Reeser, H., Hallin, K., 2003. Paleoenvironment of *Australopithecus anamensis* at Allia bay, East Turkana, Kenya: Evidence from mammalian herbivore enamel stable isotopes. J. Anthropol. Arch. 22, 200–207.

Sealy, J., Naidoo, N., Hare, V.J., Brunton, S., Faith, J.T., 2020. Climate and ecology of the palaeo-Agulhas Plain from stable carbon and oxygen isotopes in bovid tooth enamel from Nelson Bay Cave, South Africa. Quat. Sci. Rev. 235, 105974.

Ségalen, L., Lee-Thorp, J. A., Cerling, T., 2007. Timing of C_4 grass expansion across sub-Saharan Africa. J. Hum. Evol. 53, 549–559.

Semaw, S., Renne, P., Harris, J.W.K., Feibel, C.S., Bernor, R.L., Fesseha, N., 1997. 2.5-million-year-old stone tools from Gona. Ethiopia. Nature 385, 333–336.

Sept, J.M., 1986. Plant foods and early hominids at site FxJj 50, Koobi Fora, Kenya. J. Hum. Evol. 15, 751-770.

Sept, J.M., 1994. Beyond bones: archaeological sites, early hominid subsistence, and the costs and benefits of exploiting wild plant foods in east African riverine landscapes. J. Hum. Evol. 27, 295-320.

Shackleton, N.J., Opdyke, N.D., 1977. Oxygen isotope and palaeomagnetic evidence for early Northern Hemisphere glaciation, Nature, 270, 216–219.

Shea, J.J., 2017. Occasional, obligatory, and habitual stone tool use in hominin evolution. Evol. Anthropol. 26, 200–217.

Shipman, P., Walker, A., 1989. The costs of becoming a predator. J. Hum. Evol. 18, 373-392.

Shultz, S., Maslin, M., 2013. Early human speciation, brain expansion and dispersal influenced by African climate pulses. PLoS ONE 8, e76750.

Sier, M.J.**,** Langereis, C.G., Dupont-Nivet, G., Feibel, C.S., Joordens, J.C.A, van der Lubbe, J.H.J.L. Beck, C.C., Olago, D., Cohen, A.S., 2017. The top of the Olduvai Subchron in a high-resolution magnetostratigraphy from the West Turkana core WTK13, hominin sites and Paleolakes Drilling Project (HSPDP). Quat. Geochron. 42, 117-129.

Sikes, N.E., 1994. Early hominid habitat preferences in East Africa: paleosol carbon isotopic evidence. J. Hum. Evol. 27, 25-45.

Sikes, N.E., Potts, R., Behrensmeyer, A.K., 1999. Early Pleistocene habitat in Member 1 Olorgesailie based on paleosol stable isotopes. J. Hum. Evol. 37, 721-746.

Sparks, J.P., Ehleringer, J.R., 1997. Leaf carbon isotope discrimination and nitrogen content for riparian trees along elevational transects. Oecologia 109, 362-367.

Sponheimer, M., Lee-Thorp, J.A., 1999a. Isotopic evidence for the diet of an early hominid, Australopithecus africanus. Science, 283, 368–370.

Sponheimer, M., Lee-Thorp, J.A., 1999b. Oxygen isotopes in enamel carbonate and their ecological significance. J. Arch. Sci. 26, 723–728.

Sponheimer, M., Lee-Thorp, J.A. 2001. The oxygen isotope composition of mammalian enamel carbonate: a case study from Morea Estate, Mpumalanga Province, South Africa. Oecologia 126, 153–157.

Sponheimer, M., Lee-Thorp, J.A., 2003. Differential resource utilization by extant great apes and Australopithecines: towards solving the C4 conundrum. Comp. Biochem. Physiol.: Part A, Molec. Integr. Physiol. 136, 27-34.

Sponheimer, M., Alemseged, Z., Cerling, T.E., Grine, F.E., Kimbel, W.H., Leakey, M.G., Lee-Thorp, J.A., Manthi, F.K., Reed, K.E., Wood, B.A., Wynn, J.G., 2013. Isotopic evidence of early hominin diets. Proc. Nat. Acad. Sci. 110, 10513–10518.

Spoor, F., Leakey, M.G., Gathogo, P.N., Brown, F.H., Anton, S.C., McDougall, I.,

Kiarie, C., Manthi, F.K., Leakey, L.N., 2007. Implications of new early Homo fossils from Ileret, east of Lake Turkana, Kenya. Nature 448, 688-691.

Srivastava, P., 2001. Paleoclimatic implications of pedogenic carbonates in Holocene soils of the Gangetic Plains, India. Palaeogeogr. Palaeoclimatol. Palaeoecol. 172, 207-222.

Stanley, S., 1992. An ecological theory for the origin of *Homo*. Paleobiology 18, 237-257.

Stap, L.B., de Boer, B., Ziegler, M., Bintanja, R., Lourens, L.L., van de Wal, R.S.W., 2016. CO2 over the past 5 million years: continuous simulation and new d11B-based proxy data. Earth and Planetary Science Letters 439: 1-10.

Sternberg, L.S.L., Mulkey, S.S., Wright, S.J., 1989. Oxygen isotope ratio stratification in a tropical moist forest. Oecologia 81, 51–56.

Stout, D., Semaw, S., Rogers, M.J., Cauche, D., 2010. Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. J. Hum. Evol. 58, 474-491.

Susman, R.L., 1991. Who made the Oldowan tools? Fossil evidence for tool behavior in Plio-Pleistocene hominids. J. Anthropol. Res. 47, 129-152.

Tejada-Lara, J.V., MacFadden, B.J., Bermudez, L., Rojas, G., Salas-Gismondi, R., Flynn, J.J., 2018. Body mass predicts isotope enrichment in herbivorous mammals. Proc. Roy. Soc. Ser. B, Biol. Sci. 285, 20181020.

Thompson, J.C., Carvalho, S., Marean, C.W., Alemseged, Z., 2019. Origins of the human predatory pattern. Curr. Anthropol. 60, 1-23.

Tieszen, L.L., 1991. Natural variation in the carbon isotope values of plants: Implications for archaeology, ecology, and paleoecology. J. Arch. Sci. 18, 227-248.

Tipple, B. J., Meyers, S., Pagani, M., 2010. Carbon isotope ratio of Cenozoic CO_2: A comparative evaluation of available geochemical proxies. Paleoceanography, 25, PA3202.

Toth, N., Schick, K., 2009. The Oldowan: the tool making of early hominins and chimpanzees compared. Ann. Rev. Anthropol. 38, 289-305.

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 African climate and human evolution. J. Hum. Evol. 53, 475-486.

Trauth, M.H., Larrasoan, J.C., Mudelsee, M., 2009. Trends, rhythms and events in Plio Pleistocene African climate. Quatern. Sci. Rev. 28, 399-411.

UNEP, 2004. East African Rift Valley lakes, GIWA Regional assessment 47. University of Kalmar, Kalmar

Ungar, P. S., Scott, R. S., Grine, F. E., Teaford, M. F., 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. Proc. Roy. Soc. Lond. B, Biol. Sci. 365, 3345-3354.

Uno, K. T., Cerling, T. E., Harris, J. M., Kunimatsu, Y., Leakey, M. G., Nakatsukasa, M., Nakaya, H., 2011. Late Miocene to Pliocene carbon isotope record of differential diet change among east African herbivores. Proc. Nat. Acad. Sci. 108, 6509-6514.

van der Merwe, N.J., Thackeray, J.F., Lee-Thorp, J.A., Luyt, J., 2003. The carbon isotope ecology and diet of Australopithecus africanus at Sterkfontein, South Africa. J. Hum. Evol. 44, 581– 597.

Villmoare, B., Kimbel, W.H., Seyoum, C., Campisano, C.J., DiMaggio, E.N., Rowan, J., Braun, D.R., Arrowsmith, J.R., Reed, K.E., 2015. Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. Science 347, 1352–1355.

Vrba, E.S., 1985. Ecological and adaptive changes associated with early hominid evolution. In: Delson, E. (Ed.), Ancestors: The Hard Evidence. John Wiley & Sons, New York, pp. 63-71.

Vrba, E.S., 1995. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, pp. 385-424.

Vrba, E.S., 1999. Habitat theory in relation to the evolution in African Neogene biota and hominids. In: Bromage, T.G., Schrenk, F. (Eds.), African Biogeography, Climate Change, and Human Evolution. Oxford University Press, Oxford, pp. 19-34.

Wang, Y., Cerling, T.E., 1994. A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. Palaeogeog, Palaeoclim, Palaeoecol. 107, 281–289.

Wang, Y., Deng, T., 2005. A 25 m.y. isotopic record of paleodiet and environmental change from fossil mammals and paleosols from the NE margin of the Tibetan Plateau. Earth Planet. Sci. Lett. 236, 322-338.

Wang, Y., Kromhout, E., Zhang, C., Xu, Y., Parker, W., Deng, T., Qiu, Z., 2007. Stable isotopic variations in modern herbivore tooth enamel, plants and water on the Tibetan

Plateau: implication for paleoclimate and paleoelevation reconstructions. Palaeogeog, Palaeoclim, Palaeoecol. 260, 359-374.

Wara, M.W., Ravelo, A.C., Delaney, M.L., 2005. Permanent El Nino-like conditions during the Pliocene warm period. Science 309, 758-761.

Ward, C.V., Leakey, M.G., Brown, B., Brown, F., Harris, J., Walker, A., 1999a. South Turkwel: A new Pliocene hominid site in Kenya. J. Hum. Evol. 36, 69-96.

Ward, C.V., Leakey, M.G., Walker, A.C., 1999b. The new hominid species, *Australopithecus anamensis*. Evol. Anthropol. 7, 197–205.

Ward, C.V., Leakey, M.G., Walker, A. 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. J. Hum. Evol. 41, 255–368.

Werdelin, L., Lewis, M.E., 2005. Plio-Pleistocene Carnivora of eastern Africa: species richness and turnover patterns. Zool. J. Linnean Soc. 144, 121–144.

Werdelin, L., Lewis, M.E., 2013. Temporal change in functional richness and evenness in the eastern African Plio-Pleistocene carnivoran guild. PLoS ONE 8, e57944.

Westover, K**.,** Stone, J.R., Yost, C.L., Scott, J.J., Cohen, A.S., Rabideaux, N.M., Stockhecke, M., Kingston, J.D., 2019. Diatom paleolimnology of late Pliocene Baringo Basin (Kenya) paleolakes. Palaeogeog, Palaeoclim, Palaeoecol.

Wheeler, P.E., 1991. The thermoregulatory advantages of hominid bipedalism in open equatorial environments: the contribution of increased convective heat loss and cutaneous evaporative cooling. J. Hum. Evol. 21, 107-115.

Wheeler, P.E., 1992a. The influence of the loss of functional body hair on the energy and water budgets of the early hominids. J. Hum. Evol. 23, 379-388.

Wheeler, P.E., 1992b. The thermoregulatory advantages of large body size for hominids foraging in savannah environments. J. Hum. Evol. 23, 351-362.

Wheeler, P.E., 1993. The influence of stature and body form on hominid energy and water budgets: a comparison of *Australopithecus* and early *Homo* physiques. J. Hum. Evol. 24, 13-28.

Wheeler, P.E., 1994. The thermoregulatory advantages of heat storage and shadeseeking behaviour to hominids foraging in equatorial savannah environments. J. Hum. Evol. 26, 339-350.

White, T.D., WoldeGabriel, G., Asfaw, B., Ambrose, S., Beyene, Y., Bernor, R.L., Suwa, G., 2006. Asa Issie, Aramis and the origin of *Australopithecus*. Nature 440, 883–889.

Wieder, M., Yaalon, D.H., 1982. Micromorphological fabrics and developmental stages of carbonate nodular forms related to soil characteristics. Geoderma 28, 203-220.

Willeit, M., Ganopolski, A., Calov, R., Robinson, A., Maslin, M., 2015. The role of CO_2 decline for the onset of Northern Hemisphere glaciation. Quaternary Science Reviews 119, 22-34.

Wood, B., 1991. Koobi Fora Research Project Volume 4: Hominid Cranial Remains. Clarendon Press, Oxford.

Wood, B., Leakey, M., 2011. The Omo-Turkana Basin fossil hominins and their contribution to our understanding of human evolution in Africa. Evol. Anthropol. 20, 264-292.

Wright, D.K., Forman, S.L., Kiura, P., Bloszies, C., Beyin, A., 2015. Lakeside view: sociocultural responses to changing water levels of Lake Turkana, Kenya Afr. Archaeol. Rev. 32, 335-367.

Wynn, J.G., 2000. Paleosols, stable carbon isotopes and paleoenvironmental interpretation of Kanapoi, Northern Kenya. J. Hum. Evol. 39, 411-432.

Wynn, J.G., 2004. Influence of Plio-Pleistocene aridification on human evolution: evidence from paleosols from the Turkana Basin, Kenya. Am. J. Phys. Anthropol. 123, 106-118.

Wynn, J.G., Alemseged, Z., Bobe, R., Grine, F.E., Negash, E.W., Sponheimer, M., 2020. Isotopic evidence for the timing of the dietary shift toward C_4 foods in eastern African *Paranthropus*. PNAS doi/10.1073/pnas.2006221117.

Wynn, J.G., Reed, K.E., Sponheimer, M., Kimbel, W.H., Alemseged, Z., Bedaso, Z.K., Campisano, C.J., 2016. Dietary flexibility of *Australopithecus afarensis* in the face of paleoecological change during the middle Pliocene: Faunal evidence from Hadar, Ethiopia. J. Hum. Evol. 99, 93-106.

Wynn, J.G., Sponheimer, M., Kimbel, W.H., Alemseged, Z., Reed, K., Bedaso, Z.K., Wilson, J.W., 2013. Diet of *Australopithecus afarensis* from the Pliocene Hadar Formation, Ethiopia. Proc. Nat. Acad. Sci. 110, 10495-10500.

Yaekel, J.D., Bennett, N.C., Koch, P.L., Dominy, N.J., 2007. The isotopic ecology of African mole rats informs hypotheses on the evolution of human diet. Proc. R. Soc. B 274, 1723-1730.

Yakir, D., DeNiro, M.J., Gat, J.R., 1990. Natural deuterium and oxygen-18 enrichment in leaf water of cotton plants grown under wet and dry conditions: evidence for water compartmentation and its dynamics. Plant Cell Envir. 13, 49-56.

Yuretich, R.F., 1979. Modern sediments and sedimentary processes in Lake Rudolf (Lake Turkana), eastern Rift Valley, Kenya. Sedimentol. 26, 313-330.

Ziegler, M., Simon, M.H., Hall, I.R., Barker, S., Stronger, C., Zahn, R., 2013. Development of Middle Stone Age innovation linked to rapid climate change. Nat. Comm. 4, 1905.

Table and Figure Captions

Table 1. OTD fossil mammalian mean $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ values $\pm\sigma$ (‰) and interquartile ranges (data from Blumenthal et al., 2017; Cerling et al., 2013b, 2015; Drapeau et al., 2014; Manthi et al., 2020; Negash et al., 2020; this study).

Figure 1. The LOM3 archaeological site and artifacts Photos courtesy of the Mission Préhistorique au Kenya (MPK)/West Turkana Archaeological Project (WTAP).

Figure 2. A: regional map with location of OTD (after Harmand et al., 2015); B: OTD map with locations of the Omo Group Formations mentioned in this study (after Feibel, 2011).

Figure 3. A: Generalized eastern African Plio-Pleistocene hominin phylogeny characterized with three main lineages and representative fossil specimens from the OTD. *denotes debate of specimen designation in the OTD. No complete cranial specimens of *A. afarensis* or *A. anamensis* are preserved in the OTD (Kimbel, 1988; Ward et al., 1999); those pictured are from Ethiopia. Permissions of hominin fossil photos: courtesy of Human Origins Program, Smithsonian Institution (*Homo*, *Paranthropus*, *A. afarensis*); *A. anamensis* by Dale Omori courtesy of Cleveland Museum of Natural History; *K. platyops* by Fred Spoor copyright National Museums of Kenya. B: OTD hominin $\delta^{13}C_{EC}$ values (data from Cerling et al., 2013b; Wynn et al., 2020). C: Early Stone Age record in the OTD represented by single artifacts from assemblage; first appearance (gray box) and known duration (gray arrow); ^denotes older Oldowan site occurrences in Ethiopia; artifact photos courtesy of the Mission Préhistorique au Kenya (MPK)/West Turkana Archaeological Project (WTAP).

Figure 4. Global records of environmental change: A: pCO_2 (Stap et al., 2016), B: marine benthic $\delta^{18}O$ values (L04 stack: Lisiecki and Raymo, 2005), C: African dust flux from ODP 721/722 (deMenocal, 1995, 2004); shaded bars are proposed intervals of high climatic variability (Potts and Faith, 2015); D: Curve depicts ~100-kyr eccentricity cycle and hence a proxy of Plio-Pleistocene tropical insolation and monsoonal rainfall intensity; shaded bars indicate eastern African lake phases that correlate to the peaks in the 405-kyr cycle (Trauth et al., 2005).

Figure 5. Plio-Pleistocene OTD environmental records: A: Exponentially-smoothed (alpha = 0.1) $\delta^{13}C_{PC}$ values (‰) estimates (data from Cerling et al., 1988; Harmand et al., 2015; Levin et al., 2011; Quinn et al., 2007, 2013; Quinn and Lepre, 2020; Patterson et al., 2019; Wynn, 2000, 2004); B: relative abundance of APP taxa (methods after Cerling et al., 2015; data from Blumenthal et al., 2017 and references therein; Cerling et al., 2015 and references therein; Negash et al., 2020; Patterson et al., 2019); C: faunal abundances of arid-adapted taxa (Bobe and Behrensmeyer, 2004); D: pedogenic carbonate clumped isotope temperatures (°C) (Passey et al., 2010); E: $\delta^{18}O_{EC}$-based water deficit estimates (mm/year) (Blumenthal et al., 2017).

Figure 6. A: Individual data points; B: box and whisker plots of two time intervals (4.3-3.9 Ma and 3.4-3.0 Ma) and all $\delta^{13}C_{PC}$ values from the OTD (‰). Large black box denotes 25th and 75th percentiles; black line shows median value; gray line equals mean value; whiskers denote 1.5* interquartile range.

Figure 7. A: Individual data points; B: box and whisker plots of two time intervals (4.3-3.9 Ma and 3.4-3.0 Ma) and all $\delta^{18}O_{PC}$ values from the OTD (‰). Large black box denotes 25th and 75th percentiles; black line shows median value; gray line equals mean value; whiskers denote 1.5* interquartile range.

Figure 8. Box and whisker plots of two time intervals (A: 4.3-3.9 Ma and B: 3.4-3.0 Ma) superimposed on all intranodular $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ standard deviations from the OTD (‰). Large black box denotes 25th and 75th percentiles; black line shows median value; gray line equals mean value; whiskers denote 1.5* interquartile range.

Figure 9. Box and whisker plots separated in two time intervals (4.3-3.9 Ma=orange, 3.4-3.0 Ma=blue) of $\delta^{13}C_{EC}$ values of ungulate herbivore taxonomic groups and hominins from the OTD (‰). Large black box denotes 25th and 75th percentiles; black line shows median value; gray line equals mean value; whiskers denote 1.5* interquartile range. Asterisk denotes significant differences in pairwise comparisons (Mann-Whitney U, $p<0.05$).

Figure 10. Box and whisker plots separated in two time intervals (4.3-3.9 Ma=orange, 3.4-3.0 Ma=blue) of $\delta^{18}O_{EC}$ of ungulate herbivore taxonomic groups, Crocodylia and hominins from the OTD (‰). Large black box denotes 25th and 75th percentiles; black line shows median value; gray line equals mean value; whiskers denote 1.5* interquartile range. Asterisk denotes significant differences in pairwise comparisons (Mann-Whitney U, $p<0.05$).

Figure 11. Probably density function of all ungulate herbivore $\delta^{13}C_{EC}$ values separated into C_3-browsers, C_3-C_4 mixed feeders, C_4-grazers (methods described in text). A: 4.3-3.9 Ma, B: 3.4-3.0 Ma. Hominin $\delta^{13}C_{EC}$ ranges are shown with bar.

Figure 12. Hypothesized feedback relationships between gradual environmental shifts, dietary niche expansion, morphological adaptations and stone tool making behaviors.