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

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1 Title: Influences of dietary niche expansion and Pliocene environmental changes on the  
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45

46 **Abstract**

47 The world's oldest known stone tools discovered at the Pliocene site of Lomekwi 3  
48 (LOM3) in the Nachukui Formation, northern Kenya, signals a prodigious behavioral  
49 change in the hominin lineage. LOM3, dated to 3.3 Ma, is significantly earlier than the  
50 first appearance of genus *Homo* and coincides with the onset of the Mid-Pliocene Warm  
51 Period, warranting new phylogenetic and environmental explanations for the origins of  
52 hominin stone tool making behaviors. Here we examined Pliocene paleoenvironments  
53 (4.3-3.0 Ma) within the Omo-Turkana Depression (OTD) with paleosol pedogenic  
54 carbonate (PC) and faunal enamel carbonate (EC)  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values. Amidst the  
55 gradual shift toward more grassy environments, intranodular  $\delta^{13}\text{C}_{\text{PC}}$  and  $\delta^{18}\text{O}_{\text{PC}}$  variation  
56 slightly increased through time. Three of fourteen ungulate herbivore taxa yielded  
57 statistically significant increases in  $\delta^{13}\text{C}_{\text{EC}}$  values. When all ungulate herbivore  $\delta^{13}\text{C}_{\text{EC}}$   
58 values are grouped by feeding categories ( $\text{C}_3$ -browsers,  $\text{C}_3$ - $\text{C}_4$ -mixed feeders,  $\text{C}_4$ -grazers)  
59 there is evidence that the  $\text{C}_3$ - $\text{C}_4$ -mixed feeding niche contracted and shifted toward the  
60  $\text{C}_4$ -grazing niche as hominins expanded their dietary breadth during the middle Pliocene.  
61 Only one of nine taxa showed a significant decrease in  $\delta^{18}\text{O}_{\text{EC}}$  values across the study  
62 interval. Abrupt, significant environmental perturbations are not evident during LOM3  
63 times in the OTD, casting doubt on variability selection or pulsed humidity as selective  
64 forces for middle Pliocene technological innovations. We propose that a long-term  
65 feedback system involving gradual environmental changes and biotic dietary competition  
66 influenced a suite of hominin adaptations to a broad dietary niche, culminating in the  
67 origins of stone tool making behaviors.

68 **1. Introduction**

69 *1.1 Repositioning the adaptive milestones of early African hominins*

70 Stone tool making is characterized as a critical adaptive threshold, which once  
71 crossed, paved the way toward language, complex social interactions and global dispersal  
72 (Ambrose, 2001). The ability to make stone tools was originally thought to be one of the  
73 defining characteristics of genus *Homo*; its earliest member, *Homo habilis* (“handy  
74 man”), was named for the adaptation (Leakey et al., 1964). The origin and evolution of  
75 stone tool technologies associated with genus *Homo* have been linked to environmental  
76 perturbations (Clark, 1960; Potts, 1996, 1998, 2012, 2013; Potts et al., 2017; Ziegler et  
77 al., 2013). Potts and Faith (2015) showed that early members of genus *Homo* were  
78 bombarded with near consecutive periods of environmental instability during the late  
79 Pliocene-early Pleistocene associated with global climatic forcing factors via  
80 teleconnections to the tropics. Global climatic and large-scale environmental changes  
81 emphasizing the increasing presence of open and variable (“mosaic”) landscapes were  
82 traditionally and continue to be evoked as primary selective pressures for hominin  
83 speciation events (Alemseged et al., 2020; Brain, 1981; Bromage and Schrenk, 1995;  
84 deMenocal, 1995, 2004; Stanley, 1992; Trauth et al., 2005, 2007, 2009; Vrba, 1985,  
85 1995, 1999) and influences of specific adaptations including thermoregulation (Ruff,  
86 1991, 1993; Ruff and Walker, 1993; Wheeler, 1991, 1992a, 1992b, 1994), energetic  
87 efficiency (Aiello and Wheeler, 1995; Aiello and Wells, 2002; Bramble and Leiberan,  
88 2004; Leonard and Robertson, 1997; Wheeler, 1993), and encephalization (Ash and  
89 Gallop, 2007; Bailey and Geary, 2009; Shultz and Maslin, 2013).

90 Published in 2015 (Harmand et al., 2015) the Lomekwi 3 archaeological site,  
91 (LOM3; Figure 1) located in the Nachukui Formation of the Omo-Turkana Depression  
92 (OTD; northern Kenya-southern Ethiopia; Figure 2) and dated to 3.3 Ma, revealed that  
93 Pliocene hominins made stone tools substantially earlier than previously thought. As  
94 compared to the evidence of stone tool *use* with the discovery of cutmarked bone at  
95 Dikika dated to 3.4 Ma (McPherron et al., 2010), LOM3 provided evidence of stone tool  
96 *manufacturing*. Prior to the discovery of LOM3, the earliest known stone tool making  
97 behaviors were preserved at Gona (Ethiopia) and dated to 2.6-2.5 Ma (Semaw et al.,  
98 1997). The LOM3 site and the surrounding paleontological collecting area are  
99 substantially older than the known origins of genus *Homo* dated to 2.8 Ma from Ledi-  
100 Geraru (Ethiopia) (Villmoare et al. 2015). Genus *Homo* identified as the first, and  
101 perhaps only, stone toolmaker in the earliest Pleistocene has been questioned for some  
102 time (e.g., Panger et al., 2002; Susman, 1991), but these finds likely place the tools in the  
103 hands of australopithecine-like hominins. In eastern and north-central Africa, hominin  
104 species that date to the middle Pliocene have been designated as *Australopithecus*  
105 *afarensis* (Kimbel and Delezene, 2009), *A. deyiremeda* (Haile-Selassie et al., 2015), *A.*  
106 *bahrelghazali* (Brunet et al., 1996) and *Kenyanthropus platyops* (Leakey et al., 2001).  
107 Although specimens were initially identified as *A. afarensis* (Brown et al., 2001; Kimbel,  
108 1988; Ward et al., 1999a), the majority of middle Pliocene hominin specimens found in  
109 the OTD has been designated as *K. platyops* (Wood and Leakey, 2011).

110 From excavations in 2011, 2012, and 2014, the West Turkana Archaeological  
111 Project (WTAP) recovered 165 surface and in situ artifacts at LOM3 (Harmand et al.,  
112 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<sub>4</sub> foods as revealed by stable carbon isotopic values of enamel  
124 carbonate (denoted here as  $\delta^{13}\text{C}_{\text{EC}}$ ) (Cerling et al., 2013b; Lee-Thorp et al., 1994;  
125 Sponheimer and Lee-Thorp, 1999a). Middle Pliocene hominin  $\delta^{13}\text{C}_{\text{EC}}$  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<sub>4</sub> foods, which may have included C<sub>4</sub> sedges  
128 and grass seeds, underground storage organs, termites and other arthropods, bird's eggs,  
129 as well as C<sub>3</sub>-C<sub>4</sub>-mixed- and C<sub>4</sub>-feeding vertebrates (Peters and Vogel, 2005; Sponheimer  
130 and Lee-Thorp, 2003; Yaekel et al., 2007). There is also an increase in  $\delta^{13}\text{C}_{\text{EC}}$  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<sub>3</sub>-C<sub>4</sub> feeding hominins with measured  $\delta^{13}\text{C}_{\text{EC}}$   
135 values and identified to species are *A. bahrelghazali* at 3.6 Ma (Lee-Thorp et al., 2012),

136 *A. afarensis* at 3.4 Ma (Wynn et al., 2013), and in the OTD, *K. platyops* at 3.4 Ma  
137 (Cerling et al., 2013b) (Figure 3). Consumption of C<sub>4</sub> food resources by hominins has  
138 been found as early as 3.7 Ma at Woranso-Mille (Ethiopia); these hominin specimens  
139 were not identified to species but are likely australopithecines (Levin et al., 2015).

140

#### 141 *1.2 Searching for environmental forces of hominin evolution*

142 Finding evidence for stone tool making behaviors at 3.3 Ma potentially by  
143 australopithecine-like hominins complicates hypotheses of temporally discrete  
144 environmental perturbations as primary selective pressures for this adaptive milestone  
145 (Figure 4A-D). The formation of deep lakes forced by eccentricity-modulated precession  
146 has been proposed as a mechanism for environmental change influencing human  
147 evolution (Donges et al., 2011; Maslin et al., 2014; Trauth et al., 2005, 2007, 2009). Deep  
148 African lakes are interpreted to have occurred throughout the Pliocene (e.g., Trauth et al.,  
149 2005), but an identified lake phase in the OTD, Lake Lokochot (Feibel, 2011), ends  
150 approximately 200 Ka prior to the LOM3 site date (Figure 4D). Potts (1996, 1998) links  
151 high environmental variability to several hominin speciation events and technological  
152 innovations, but the middle Pliocene appears to encompass a long period of low climatic  
153 variability (Potts and Faith, 2015) (Figure 4C). Modeled global *p*CO<sub>2</sub> concentrations by  
154 Stap et al. (2016) (Figure 4A) suggests a steady decrease through time aligning with  
155 trends in sea level, temperature, and global ice volume (Figure 4B).

156 The LOM3 site is coincident with the start of the mid-Pliocene Warm Period  
157 (mPWP: 3.264–3.025 Ma: Dowsett et al., 2010; Haywood et al., 2010), which is  
158 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<sub>2</sub> 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  $\delta^{13}\text{C}$ -based paleo-shade proxy of Cerling et al. (2011) positioned the site in C<sub>3</sub>-dominated  
173 environments in the grassy woodland/bushland/shrubland category (fraction of woody  
174 canopy cover,  $f_{\text{WC}} = 60\text{-}40\%$ ) (Harmand et al., 2015).  $f_{\text{WC}}$  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  $\delta^{18}\text{O}_{\text{EC}}$ -based aridity



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

186         Additionally, through-time records show little evidence for substantial  
187 environmental shifts from the early to middle Pliocene, especially compared to the late  
188 Pliocene (Figure 5). From the compiled pedogenic carbonate (subscript PC)  $\delta^{13}\text{C}$  datasets  
189 of the OTD, there is a gradual increase in grassy environments from 4-1 Ma (Figure 5A);  
190 however the largest increase occurs after 2 Ma (Cerling et al., 2011a,b; Levin et al.,  
191 2011). The compiled herbivore ungulate OTD  $\delta^{13}\text{C}_{\text{EC}}$  database demonstrates a relatively  
192 steady increase in  $\text{C}_4$ -grazers from 4-1 Ma (Figure 5B); although sample sizes are not  
193 uniform and some time periods have small sample sizes, the trend appears gradual.  
194 Faunal abundance data of Bobe and Behrensmeyer (2004) from the Lower Omo Valley  
195 shows a major shift in grassland indicators after 3 Ma; the middle Pliocene appears stable  
196 (Figure 5C). Passey et al. (2010) estimated Plio-Pleistocene OTD soil temperatures with  
197 pedogenic carbonate clumped isotopes and found consistently high temperatures but no  
198 directional trend from 4-1 Ma (Figure 5D). Fortelius et al. (2016) estimated air  
199 temperatures in the OTD from 7-1 Ma via ecomorphic proxies and similarly found no  
200 directional shift through time. Blumenthal et al. (2017) found that aridity does not  
201 increase from 4-1 Ma, but rather variable water deficits are found throughout the OTD  
202 (Figure 5E). Fortelius et al. (2016) found a general decreasing trend in mean annual  
203 precipitation in the OTD based on ecometric analysis, but the largest decrease in rainfall  
204 was in the upper portion of the record from 3-1 Ma.

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

225

### 226 1.3. Approach of study

227 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  $\delta^{13}\text{C}$ -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  $\delta^{13}\text{C}_{\text{PC}}$  values provide spatially limited ( $\sim 1$   
241  $\text{m}^2$ ) and time averaged ( $\sim 10^1$ - $10^3$  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  $\delta^{13}\text{C}_{\text{EC}}$  values of fauna (Du et al., 2019). Here we  
244 contribute new  $\delta^{18}\text{O}_{\text{PC}}$  data of paleosols and faunal  $\delta^{13}\text{C}_{\text{EC}}$  and  $\delta^{18}\text{O}_{\text{EC}}$  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

251 not uniformly distributed, neither temporally nor spatially, primarily due to differential  
252 preservation of paleosols and fossil material suitable for isotopic analyses. Research  
253 focus has also impacted sample density. Much environmental research has historically  
254 focused on the rise and evolution of *Homo*. Early and middle Pliocene environments in  
255 eastern African hominin locales have been used as the “before” interval to emphasize the  
256 magnitude of directional shifts and changes in climatic variability in the “after” interval  
257 during the late Pliocene and early Pleistocene. We shifted the comparison to the early and  
258 middle Pliocene by examining isotopic proxy records in two 400-kyr intervals of time  
259 (4.3-3.9 Ma and 3.4-3.0 Ma). These relatively large temporal bins are comparable to  
260 those used by Cerling et al. (2015) and have considerable sample sizes of paleosols  
261 (Harmand et al., 2015; Levin et al., 2011; Quinn and Lepre, 2020; Wynn, 2000, 2004)  
262 and faunal enamel datasets (Blumenthal et al., 2017; Cerling et al., 2015; Manthi et al.,  
263 2020; Negash et al., 2020; this study), including those of hominins (Cerling et al., 2013b).  
264 *Australopithecus anamensis* occurs in the OTD during 4.3-3.9 Ma (Leakey et al., 1995,  
265 1998; Ward et al., 1999b, 2001), thus we use this species and time period as a comparison  
266 to gauge potentially new or different selective pressures on stone tool making behaviors  
267 preserved in the 3.4-3.0 Ma.

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

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

278 Taphonomic and collector biases are also concerns when reconstructing  
279 vegetation structures with isotopic analyses of faunal remains (e.g., Robinson et al.,  
280 2017). Moreover, considering modern mammalian speciosity in Kenya alone (309  
281 species, Musila et al., 2019) and herbivore ungulate population sizes (e.g.,  $10^2$ - $10^4$ ;  
282 Georgiadis, 2011), the number of enamel samples analyzed to date from eastern African  
283 fossil locales is miniscule. Due to preservation in and around the LOM3 site, we  
284 contribute a modest faunal enamel sample in order to make better comparisons to the  
285 early Pliocene OTD databases, but emphasize that larger sample sizes from many species  
286 are warranted to gauge the environmental context of Pliocene hominins.

287

## 288 **2. The Omo-Turkana Depression**

289 The OTD, also known as the Turkana Depression and the Turkana-Omo rift,  
290 extends across northern Kenya and southern Ethiopia (Figure 2) and lies within the  
291 eastern branch of the East African Rift System (EARS) between the Kenyan and  
292 Ethiopian domes (Ebinger et al., 2000; Knapp et al., 2020). The OTD is composed of  
293 several structural sub-basins within the tectonic complex associated with the development  
294 of the EARS (Feibel, 2011). The OTD presently contains one of the largest rift lakes,  
295 Lake Turkana, with an area of  $7000\text{ km}^2$  and a catchment surface of  $130,800\text{ km}^2$  (UNEP,  
296 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

320 (Brown and McDougall, 2011; Bruhn et al., 2011). Omo Group Plio-Pleistocene  
321 environmental proxy records include those from the Kanapoi and Lothagam formations  
322 in the southwestern portion of the Turkana Basin, the Mursi Formation located in the  
323 Omo River Valley, the Koobi Fora Formation exposed along the northeast and southeast  
324 side of the Turkana Basin, and the Nachukui Formation along the northwest and  
325 southwest basin (Feibel et al., 1991; Feibel, 2003a, 2003b; Harris et al., 1988). Pliocene  
326 mudstones, sandstones, and conglomerates comprise the bulk of the Nachukui  
327 Formation's Lomekwi Member, which preserves the LOM3 site (Harmand et al., 2015).  
328 The Omo Group formations have been dated and correlated through a combination of  
329 tephrostratigraphy, radioisotopic ages, and paleomagnetic stratigraphy (Brown and  
330 Feibel, 1986, 1991; Feibel et al., 1989; Hillhouse et al., 1986; Lepre, 2014; Lepre and  
331 Kent, 2010, 2015; Lepre et al., 2011; McDougall, 1985; McDougall and Brown, 2006,  
332 2008; McDougall et al., 2012), which has afforded a high degree of temporal resolution  
333 for several long records of terrestrial environments (Figure 5).

334         Late Pliocene and early to middle Pleistocene sedimentary records indicate the  
335 presence of large lakes. The longest in duration is Lake Lorenyang (Feibel, 1997)  
336 beginning at 2.14 Ma (Lepre, 2014) and extending to ~1.5 Ma (Feibel, 2011) and likely  
337 caused by the damming of the basin with the eruption of Mt. Kulal during the early  
338 Pleistocene (Bruhn et al., 2011). Fluctuations in lake levels during the early Pleistocene  
339 may have been influenced by orbitally-paced variations in water delivery to the Omo  
340 River source region in the Ethiopian Highlands (Boës et al., 2019; Joordens et al., 2011;  
341 Lepre et al., 2007; Nutz et al., 2017). The increasing abundance of C<sub>4</sub> grasslands in the  
342 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<sup>2</sup> 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 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analyses*

374 For nearly forty years, African terrestrial vegetation communities have been  
375 reconstructed with measurements of  $\delta^{13}\text{C}_{\text{PC}}$  and  $\delta^{18}\text{O}_{\text{PC}}$  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  $\text{C}_3$  and  $\text{C}_4$  plants show normal and non-overlapping distributions (Sage  
380 and Monson, 1999).  $\text{C}_3$  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,  $^{13}\text{C}$ .  $\text{C}_4$  plants (most sedges and  
383 warm season growing grasses) utilize the Hatch-Slack four carbon photosynthetic  
384 pathway and allow some incorporation of  $^{13}\text{C}$ . In eastern Africa,  $\text{C}_3$  dicots from closed  
385 and open canopy forests have lower  $\delta^{13}\text{C}$  values ( $-31.4 \pm 0.5 \text{‰}$ ,  $-27.8 \pm 0.3 \text{‰}$ ,  
386 respectively) than those of savanna and bushlands ( $-27.0 \pm 0.2 \text{‰}$ ; Cerling et al., 2003c).  
387 Mesic  $\text{C}_4$  grasses (NADP subpathway) have an average  $\delta^{13}\text{C}$  value of  $-11.8 \pm 0.2\text{‰}$ ; xeric  
388  $\text{C}_4$  grasses utilizing the NAD and PCK subpathways have average  $\delta^{13}\text{C}$  values of  $-13.1 \pm$

389 0.3‰ and  $-12.9 \pm 0.1$ ‰, respectively (Cerling et al., 2003c) in eastern African savanna  
390 environments. Vegetation  $\delta^{13}\text{C}$  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  $\text{CO}_2$  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  $\delta^{13}\text{C}_{\text{PC}}$  values preserved in  
396 paleosols are used to quantitatively measure the relative amounts of  $\text{C}_3$  and  $\text{C}_4$  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  $\text{C}_4$   
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 ( $f_{\text{WC}}$ ) from paleosol  
401 carbonate  $\delta^{13}\text{C}_{\text{PC}}$  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:  $f_{\text{WC}} = 0\text{-}10\%$ , 2) open wooded grassland:  $f_{\text{WC}} = 10\text{-}20\%$ , 3)  
404 wooded grassland:  $f_{\text{WC}} = 20\text{-}40\%$ , 4) grassy woodland/bushland/shrubland:  $f_{\text{WC}} = 40\text{-}$   
405  $60\%$ , 5) woodland/bushland/shrubland:  $f_{\text{WC}} = 60\text{-}80\%$ , 6) forest/closed forest:  $f_{\text{WC}} = 80\text{-}$   
406  $100\%$ .

407  $\delta^{18}\text{O}_{\text{PC}}$  values are controlled by soil pore water  $\delta^{18}\text{O}$  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  $\delta^{18}\text{O}$  values track those of meteoric water (Amundson and Wang, 1996; Cerling,  
411 1984; Cerling and Quade, 1993). Soil pore water  $\delta^{18}\text{O}$  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  $\delta^{18}\text{O}_{\text{MW}}$  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  $\delta^{13}\text{C}_{\text{PC}}$  and  $\delta^{18}\text{O}_{\text{PC}}$  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  $\delta^{13}\text{C}_{\text{PC}}$  and  $\delta^{18}\text{O}_{\text{PC}}$  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 $\delta^{13}\text{C}_{\text{EC}}$ and $\delta^{18}\text{O}_{\text{EC}}$ analyses*

429 Faunal enamel carbonate  $\delta^{13}\text{C}_{\text{EC}}$  and  $\delta^{18}\text{O}_{\text{EC}}$  values record  $\delta^{13}\text{C}$  values of whole  
430 diet and  $\delta^{18}\text{O}$  values of body water, respectively, and thus have been used for some time  
431 to reconstruct continental paleoenvironments (e.g., Koch, 1998). Fossil faunal  $\delta^{13}\text{C}_{\text{EC}}$   
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  $\delta^{13}\text{C}_{\text{EC}}$  values of herbivorous ungulate taxa,  
436 specimens are assigned to one of three dietary groups: C<sub>3</sub>-browsers, C<sub>3</sub>-C<sub>4</sub>-mixed feeders,  
437 and C<sub>4</sub>-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).  $\delta^{13}\text{C}_{\text{EC}}$  values of carnivores reflect the feeding category(ies) of  
440 their prey, and of omnivores, a mixture of plant and prey  $\delta^{13}\text{C}$  values (Lee-Thorp et al.,  
441 1989).

442  $\delta^{13}\text{C}_{\text{EC}}$ -based dietary reconstructions and by extension environmental  
443 reconstructions are not without methodological assumptions. Cerling et al. (2015)  
444 proposed the following  $\delta^{13}\text{C}_{\text{EC}}$  values to delineate the three feeding categories of the  
445 Artiodactyla, Perissodactyla and Proboscidea (APP) orders: C<sub>3</sub>-browsers,  $\delta^{13}\text{C}_{\text{EC}} < -8\text{‰}$ ;  
446 C<sub>4</sub> grazers,  $\delta^{13}\text{C}_{\text{EC}} > -1\text{‰}$ ; C<sub>3</sub>-C<sub>4</sub>-mixed feeders,  $\delta^{13}\text{C}_{\text{EC}}$  between -8 and -1‰, which were  
447 based on the large modern  $\delta^{13}\text{C}_{\text{EC}}$  database of APP taxa, a pre-industrial CO<sub>2</sub>  $\delta^{13}\text{C}$  offset  
448 of 1.5‰, a  $\epsilon^*_{\text{enamel-diet}}$  value of 14‰. In fossil organisms, the  $\epsilon^*_{\text{enamel-diet}}$  value is based on  
449 modern analogs. The use the  $\epsilon^*_{\text{enamel-diet}}$  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  $\epsilon^*_{\text{enamel-diet}}$  value for a non-fermenting-gut  
453 omnivore is +10‰; however, this  $\epsilon^*_{\text{enamel-diet}}$  value may be more applicable to members  
454 of genus *Homo* than Pliocene hominins (Schoeninger, 2014). An  $\epsilon^*_{\text{enamel-diet}}$  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  $\epsilon^*_{\text{enamel-diet}}$  value of mammalian herbivores is predicted by body mass and

458 gut physiology, producing  $\epsilon^*_{\text{enamel-diet}}$  values ranges between +9 and +16‰. The use of  
459 specific  $\epsilon^*_{\text{enamel-diet}}$  values can impact dietary reconstructions (Quinn, 2019).

460 Notably, global  $\text{CO}_2$   $\delta^{13}\text{C}$  values have changed through time (Tipple et al., 2010),  
461 and thus through-time analyses of faunal  $\delta^{13}\text{C}_{\text{EC}}$  values must consider specific  $\text{CO}_2$   $\delta^{13}\text{C}$   
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  $\text{C}_3$  and  $\text{C}_4$  diets (Garrett et al., 2015). Moreover, Robinson et al. (2017) have  
465 suggested that the methods of Cerling et al. (2015) artificially skew  $\delta^{13}\text{C}_{\text{EC}}$ -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  $\delta^{18}\text{O}$  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  $\delta^{18}\text{O}_{\text{EP/EC}}$  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  $\delta^{18}\text{O}_{\text{EC}}$   
475 values are derived primarily from drinking water, atmospheric  $\text{O}_2$ , 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  $\delta^{18}\text{O}_{\text{EP/EC}}$  values than non-obligate drinkers (Bocherens et al.,  
480 1996; Cerling et al., 2003b). Eastern African  $\text{C}_3$ -browsing and  $\text{C}_3$ - $\text{C}_4$ -mixed-feeding

481 herbivore ungulates were found to have lower bone phosphate  $\delta^{18}\text{O}$  values than  $\text{C}_4$ -  
482 grazing ungulates (Kohn et al., 1996). As recently reviewed by Faith (2019),  $\text{C}_3$ -browsers  
483 obtain substantial amounts of water from  $\text{C}_3$  vegetation.  $\text{C}_4$  grasses offer little water  
484 content and therefore  $\text{C}_4$ -grazers typically obtain water from surface water sources, which  
485 generally have lower  $\delta^{18}\text{O}$  values than that of  $\text{C}_3$  vegetation.

486 Sponheimer and Lee-Thorp (1999b, 2001) suggested that trophic level is  
487 correlated with  $\delta^{18}\text{O}_{\text{EC}}$  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  $\delta^{18}\text{O}_{\text{EC}}$  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  $\delta^{18}\text{O}_{\text{EC}}$   
493 values than the one isotopically analyzed jackal. At Tsavo, lions ( $n=9$ ) yielded lower  
494  $\delta^{18}\text{O}_{\text{EC}}$  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  $\delta^{18}\text{O}_{\text{EC}}$  values  
497 of forest-living fauna vary with canopy height. For example, high canopy primates  
498 achieve higher  $\delta^{18}\text{O}_{\text{EC}}$  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  $\delta^{18}\text{O}$  values are  
502 transferred to consumers (Carter and Bradbury, 2016; Nelson, 2013). Additionally,  
503 woodland- and grassland-dwellers achieve higher  $\delta^{18}\text{O}_{\text{EC}}$  values than those living in

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

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

515       Several studies from eastern African hominin sites have shown that analyzing  
516  $\delta^{13}\text{C}_{\text{EC}}$  and  $\delta^{18}\text{O}_{\text{EC}}$  values of mammalian taxa from discrete stratigraphic intervals  
517 captures a large range of available resources via different dietary behaviors practiced by  
518 various species (Du et al., 2019; Kingston and Harrison, 2007; Lehmann et al., 2016;  
519 Patterson et al., 2019; Robinson et al., 2016; Wynn et al., 2016). If diagenetic alteration  
520 of tooth enamel is negligible,  $\delta^{13}\text{C}_{\text{EC}}$  and  $\delta^{18}\text{O}_{\text{EC}}$  analyses of individual specimens record  
521 diet and water intake over the duration of enamel formation ( $10^0$ - $10^1$  years), which  
522 represents a small amount of time in contrast to the formation times of pedogenic  
523 carbonates ( $10^1$ - $10^3$  years). Spatially, however, faunal  $\delta^{13}\text{C}_{\text{EC}}$  and  $\delta^{18}\text{O}_{\text{EC}}$  values record  
524 information from across the range of animal movements, which vary by species and span  
525  $10^1$ - $10^2$  km<sup>2</sup> (Estes, 1991). In a similar approach to measuring intranodular variability,  
526 faunal isotopic variation measured in several specimens from individual taxonomic

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

531

## 532 **4. Materials and Methods**

### 533 *4.1. Pliocene OTD $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ analyses*

534 We present new  $\delta^{18}O_{PC}$  values (nodules=23, analyses=47) from LOM3 (see  
535 sampling described in Harmand et al., 2015; Supplementary Table 1). We combine  
536  $\delta^{13}C_{PC}$  and  $\delta^{18}O_{PC}$  data and compare across two 400-kyr intervals, 4.3-3.9 Ma (n=70) and  
537 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  
538 Kanapoi Formation (data from Quinn and Lepre, 2020; Wynn, 2000), the Koobi Fora  
539 Formation (data from Cerling et al., 1988; Levin et al., 2011), and the Nachukui  
540 Formation (data from Harmand et al., 2015; Levin et al., 2011; Wynn, 2004). OTD  
541  $\delta^{13}C_{PC}$  and  $\delta^{18}O_{PC}$  data used in this study have been compiled into a publicly available  
542 database (Levin, 2015).  $f_{WC}$  values were estimated after methods of Cerling et al. (2011).  
543 We utilized standard variation of intranodular  $\delta^{13}C_{PC}$  and  $\delta^{18}O_{PC}$  values from these two  
544 intervals, 4.3-3.9 Ma (n=38) and 3.4-3.0 Ma (n=33), to represent environmental  
545 variability (data from Harmand et al., 2015; Levin et al., 2011; Quinn and Lepre, 2020;  
546 this study).

547

### 548 *4.2. Pliocene OTD faunal $\delta^{13}C_{EC}$ and $\delta^{18}O_{EC}$ analyses*



549 We add faunal  $\delta^{13}\text{C}_{\text{EC}}$  and  $\delta^{18}\text{O}_{\text{EC}}$  values (taxa =8, n =28) from LOM3 to  
550 published OTD faunal  $\delta^{13}\text{C}_{\text{EC}}$  and  $\delta^{18}\text{O}_{\text{EC}}$  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  $\delta^{18}\text{O}_{\text{EC}}$  values to proxy meteoric water  $\delta^{18}\text{O}$  values (e.g.,  
553 Amiot et al., 2007). We combine  $\delta^{13}\text{C}_{\text{EC}}$  and  $\delta^{18}\text{O}_{\text{EC}}$  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  $\delta^{13}\text{C}_{\text{EC}}$  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  $\delta^{18}\text{O}_{\text{EC}}$  values (Table 1). After Cerling et  
564 al. (2015) we distinguish two Rhinocerotidae taxa based on bimodal  $\delta^{13}\text{C}_{\text{EC}}$  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  $\delta^{13}\text{C}_{\text{EC}}$   
570 and  $\delta^{18}\text{O}_{\text{EC}}$  values grouped by taxon present in both time intervals. We assess variability  
571 in food and water inputs by comparing interquartile ranges of  $\delta^{13}\text{C}_{\text{EC}}$  and  $\delta^{18}\text{O}_{\text{EC}}$  values

572 of each taxonomic group separated into the two temporal bins. After Cerling et al. (2015),  
573 we place the taxonomic and temporal groups along the spectrum of  $\delta^{13}\text{C}_{\text{EC}}$  values  
574 designated as separate feeding categories. However, we also consider canopy effects on  
575 vegetation  $\delta^{13}\text{C}$  values (Kohn, 2010) and separate the  $\text{C}_3$  browser category into “forest”  
576  $\text{C}_3$  browsers and “woodland”  $\text{C}_3$  browsers. We define forest  $\text{C}_3$ -browsers when  $\delta^{13}\text{C}_{\text{EC}}$   
577 values drop below  $-14\text{‰}$ . This is based on the average plant  $\delta^{13}\text{C}$  value of five lowland  
578 tropical closed canopy forests in Africa ( $-30.6\text{‰}$ ) (data from: Loango National Park, Côte  
579 d’Ivoire,  $-30.5\pm 3.5\text{‰}$ , Oelze et al., 2014; Tai Natural Park, Côte d’Ivoire,  $-30.8\pm 4.1\text{‰}$ ,  
580 Fahy et al., 2013; Ituri Forest, DRC,  $-31.2\pm 2.8\text{‰}$ , Cerling et al., 2004; Salonga National  
581 Park, DRC,  $-29\pm 2.7\text{‰}$ , Oelze et al., 2011; Kakamega Forest, Kenya,  $-31.4\pm 0.5\text{‰}$ ,  
582 Cerling et al, 2003c) and a correction for the Pliocene atmospheric  $\text{CO}_2$   $\delta^{13}\text{C}$  offset of  
583  $2.3\text{‰}$  (Tippie et al., 2010). We use the term “woodland” for  $\text{C}_3$ -feeders exploiting the  
584 more open  $\text{C}_3$  biome resources;  $\delta^{13}\text{C}_{\text{EC}}$  values range from  $-8\text{‰}$  to  $-14\text{‰}$ . Based on Tippie  
585 et al. (2010), the time periods compared in this study vary only by  $0.2\text{‰}$  and therefore we  
586 do not change our feeding category demarcations through time. We also compare feeding  
587 categories through time by combining  $\delta^{13}\text{C}_{\text{EC}}$  values and gauge change in mean  $\delta^{13}\text{C}_{\text{EC}}$   
588 values and variance (similar to methods of Sealy et al., 2020).

589

#### 590 *4.3. Mass Spectrometry*

591 Pedogenic nodules were cross-sectioned and sampled for microcrystalline calcite  
592 with a 0.5 mm carbide drill bit (Foredom Series), avoiding surface and sparry calcite. We  
593 subsampled nodules twice and averaged the subsample values. Enamel samples from  
594 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  $\delta^{18}\text{O}_{\text{PC}}$  are reported in delta notation (per mil, ‰) versus V-PDB through  
602 analysis of NBS-19; error for  $\delta^{18}\text{O}_{\text{PC}}$  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 $\delta^{13}\text{C}_{\text{PC}}$ and $\delta^{18}\text{O}_{\text{PC}}$ values*

608 Summary data for the compiled Pliocene OTD  $\delta^{13}\text{C}_{\text{PC}}$  and  $\delta^{18}\text{O}_{\text{PC}}$  values for the  
609 two time intervals are shown in Figures 6-8.  $\delta^{13}\text{C}_{\text{PC}}$  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  $\delta^{13}\text{C}_{\text{PC}}$  increase of  
612 0.9‰ equates to an 8% decrease in  $f_{\text{WC}}$ . The dominant vegetation structural category is  
613 reconstructed as grassy woodlands/ bushland/shrubland in both time periods.  $\delta^{18}\text{O}_{\text{PC}}$   
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  $\delta^{13}\text{C}_{\text{PC}}$  and  $\delta^{18}\text{O}_{\text{PC}}$  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 $\delta^{13}\text{C}_{\text{EC}}$ and $\delta^{18}\text{O}_{\text{EC}}$ values

621 Pliocene OTD faunal  $\delta^{13}\text{C}_{\text{EC}}$  and  $\delta^{18}\text{O}_{\text{EC}}$  values are listed in Table 1, and box plots  
622 are illustrated in figures 9 and 10. Pairwise comparisons of  $\delta^{13}\text{C}_{\text{EC}}$  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<sub>3</sub>-C<sub>4</sub> mixed feeding category toward  
626 more C<sub>4</sub>-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  $\delta^{13}\text{C}_{\text{EC}}$  values separated into the three  
629 feeding categories (C<sub>3</sub>-browsers, C<sub>3</sub>-C<sub>4</sub>-mixed feeders, C<sub>4</sub>-grazers). The position and  
630 shape of the plots illustrate a slight directional shift toward more C<sub>4</sub> consumption  
631 especially within the C<sub>3</sub>-C<sub>4</sub>-mixed-feeding category. C<sub>3</sub>-C<sub>4</sub>-mixed feeders show  
632 significant changes in mean and median  $\delta^{13}\text{C}_{\text{EC}}$  values (t test,  $p < 0.000$ ; Mann-Whitney U,  
633  $p < 0.01$ ) and variance (f test,  $p = 0.04$ ).

634 Pairwise comparisons of  $\delta^{18}\text{O}_{\text{EC}}$  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  $\delta^{18}\text{O}_{\text{EC}}$  values (Mann-Whitney U,  $p < 0.01$ ). Giraffidae  
638 and Aepycerotini yielded lower  $\delta^{18}\text{O}_{\text{EC}}$  mean values, but do not achieve statistical

639 significance (Mann-Whitney U,  $p < 0.08$ ). Pairwise  $\delta^{18}\text{O}_{\text{EC}}$  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  $\text{C}_4$  vegetation through time. Average  $f_{\text{WC}}$   
646 decreased by 8%, and three herbivore ungulate taxa showed increases in  $\text{C}_4$  consumption.  
647 Modern species opportunistically shift their diets in response to resource availability  
648 (e.g., Cromsigt and Olf, 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  $\text{C}_4$  plants may indicate a higher abundance of  $\text{C}_4$   
651 grasslands during the 3.4-3.0 Ma interval in general agreement with  $f_{\text{WC}}$  estimates.  
652 However, faunal  $\delta^{13}\text{C}_{\text{EC}}$  values are also a reflection of species interactions (Buschke et  
653 al., 2015) and resource partitioning of  $\text{C}_3$  and  $\text{C}_4$  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  $\text{C}_4$  grass abundance with faunal  $\delta^{13}\text{C}_{\text{EC}}$  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  $\text{C}_4$  consumption were highly variable in tempo and mode. Moreover, through-  
659 time faunal  $\delta^{13}\text{C}_{\text{EC}}$  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  $\text{C}_4$  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  $\delta^{13}\text{C}_{\text{EC}}$  values, it appears that the  $\text{C}_3$ - $\text{C}_4$  mixed feeding niche contracted over  
666 this study interval (Figure 11), which may have been due to reductions in  $\text{C}_3$  resource  
667 availability and/or increased competition.

668         Unchanging  $\delta^{18}\text{O}_{\text{EC}}$  values in taxa whose modern descendants tend to be water  
669 dependent (e.g., Hippopotamidae, Crocodylia, Deinotheriidae, Elephantidae) suggests  
670 that meteoric water  $\delta^{18}\text{O}$  values did not significantly change over the two time intervals.  
671 Hippopotamidae  $\delta^{18}\text{O}_{\text{EC}}$  values reflect the  $\delta^{18}\text{O}$  values of the water in which they swim  
672 and thus have been suggested as faithful records of meteoric water  $\delta^{18}\text{O}$  values (Cerling  
673 et al., 2008; Levin et al., 2006). Crocodylia  $\delta^{18}\text{O}_{\text{EC}}$  values, which also mirror meteoric  
674 water  $\delta^{18}\text{O}$  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  $\delta^{18}\text{O}_{\text{EC}}$  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  $\delta^{18}\text{O}_{\text{EC}}$  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  $\delta^{18}\text{O}_{\text{EC}}$ -based aridity index of Levin et al. (2006) and refined by  
684 Blumenthal et al. (2017). But notably, the decrease in Giraffidae  $\delta^{18}\text{O}_{\text{EC}}$  values was not

685 statistically significant. As mentioned, Faith (2019) cautions that  $\delta^{18}\text{O}_{\text{EC}}$ -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  $\text{C}_4$ -grazing triggers more  
688 surface water drinking. The relatively lower  $\delta^{18}\text{O}_{\text{EC}}$  values of *Aepycerotini* may have  
689 been a by-product of higher  $\text{C}_4$  consumption (e.g., Faith, 2019). The drop in  $\delta^{18}\text{O}_{\text{EC}}$   
690 values in *Alcelaphini* is accompanied by a slight decrease in  $\delta^{13}\text{C}_{\text{EC}}$  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  $\text{C}_4$ -grazer, OTD *Alcelaphini* likely obtained their  
696 water from surface sources due to the low water content in grasses. Reduced  $\delta^{18}\text{O}_{\text{EC}}$   
697 values imply that surface drinking water sources shifted to lower  $\delta^{18}\text{O}$  values.  
698 *Alcelaphini*  $\delta^{18}\text{O}_{\text{EC}}$  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,  $1315 \pm 994$  mm/year), Allia Bay  
706 (3.9 Ma,  $500 \pm 1315$  mm/year) and the Lomekwi member (3.4 Ma,  $1 \pm 892$  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  $\delta^{18}\text{O}_{\text{EC}}$  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  $\delta^{18}\text{O}_{\text{EC}}$  values appear to track changes in humidity that  
718 were not recorded in  $\delta^{18}\text{O}_{\text{PC}}$  values, which may indicate that changes in humidity were  
719 minor. However,  $\delta^{18}\text{O}_{\text{PC}}$  values have several influences, which may have acted in concert  
720 to blur environmental signals. Koch (1998) suggested that increased  $\delta^{18}\text{O}_{\text{PC}}$  values can be  
721 a by-product of grassland expansion. Relatively more  $\text{C}_4$  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  $\delta^{18}\text{O}_{\text{PC}}$  values during the middle Pliocene.

725         Increasing standard deviations of  $\delta^{13}\text{C}_{\text{PC}}$  and  $\delta^{18}\text{O}_{\text{PC}}$  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  $\leq 0.3\%$  for both isotopic systems, which is negligible with respect  
735 to significant changes in OTD environments. For example, variations in  $\delta^{13}\text{C}_{\text{PC}}$  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  $\text{C}_4$  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  $\text{C}_4$  grassland spread (e.g.,  
746 Blumenthal et al., 2017; Levin, 2015; Polissar et al., 2019). The increasing trend of  
747 eastern African  $\text{C}_4$  vegetation appears related to the long-term decrease in atmospheric  
748  $p\text{CO}_2$  (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<sub>4</sub>  
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<sub>3</sub>-C<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> consumption signals behavioral changes rather than the tracking of C<sub>4</sub> resource  
773 abundances per se. The increasing database of OTD faunal  $\delta^{13}\text{C}_{\text{EC}}$  values supports the  
774 hypothesis that hominins experienced a "protracted" adaptation to the widespread  
775 presence of C<sub>4</sub> resources available by the late Miocene and early Pliocene (Ségalen et al.,  
776 2007).

777           Biotic competition for the broad C<sub>3</sub>-C<sub>4</sub> feeding niche may have been one of the  
778 selective pressures for stone tool making behaviors. As viewed in the temporal bins, *K.*  
779 *platyops* shared its general diet shift toward a greater reliance on C<sub>4</sub> plants with three  
780 ungulate herbivore C<sub>3</sub>-C<sub>4</sub> mixed feeders in the OTD (Figure 9). Several ungulate  
781 herbivores and *Theropithecus*, the large-bodied baboon, had occupied the C<sub>4</sub> biome for  
782 some time (Cerling et al., 2013a; Uno et al., 2011). As many researchers have suggested,  
783 stone tools may have offered enhanced efficiency for processing vegetation (e.g., Brain,  
784 1985; Dominguez-Rodrigo et al., 2001; Goren-Inbar et al., 2002; Hardy et al., 2015;  
785 Keeley and Toth, 1981; Panger et al., 2002; Schick and Toth, 1993; Sept, 1986, 1994).  
786 Notably, the combined ungulate herbivore  $\delta^{13}\text{C}_{\text{EC}}$  data show evidence for dietary niche  
787 contraction within the C<sub>3</sub>-C<sub>4</sub> mixed feeding niche in the 3.4-3.0 Ma interval. In contrast,  
788 hominins expand dietary breadth from a woodland C<sub>3</sub>-browser to a broad C<sub>3</sub>-C<sub>4</sub>-mixed  
789 feeder, possibly filling the dietary niche left vacated by some of the C<sub>3</sub>-C<sub>4</sub>-mixed feeders,  
790 especially Antilopini, Aepycerotini, and *Notochoerus* (Figures 9 and 11).

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

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

807 Dietary changes could have lowered *K. platyops*'  $\delta^{18}\text{O}_{\text{EC}}$  values such as feeding  
808 on ground level food resources in closed woodland settings (e.g., Nelson, 2013) or on  
809 wetland sedges and underground storage organs (e.g., Lee-Thorp, 2011). Changes in  
810 feeding and activity times could have also impacted *K. platyops*'  $\delta^{18}\text{O}_{\text{EC}}$  values (e.g.,  
811 Kohn, 1996; Schoeninger et al., 2000). Additionally, lower  $\delta^{18}\text{O}_{\text{EC}}$  values indicate that *K.*  
812 *platyops* may have increased its water dependency by drinking a higher proportion of  
813 surface waters than ingesting water contained in vegetation. The relationship between  
814 lower  $\delta^{18}\text{O}_{\text{EC}}$  values and increasing C<sub>4</sub> grass consumption as shown for Tragelaphini by  
815 Faith (2019) and here with Aepycerotini aligns with the dietary increase of C<sub>4</sub> resources  
816 by hominins.

817 Prior to the LOM3 publication (Harmand et al. 2015), Macho (2014) proposed  
818 that the increase in C<sub>4</sub> food consumption by Pliocene hominins was in part selected by an  
819 increase in predation as evident by an increasing speciosity of members of the Order  
820 Carnivora in the OTD and other eastern African hominin locales circa 3.6 Ma (data from  
821 Werdelin and Lewis; 2005, 2013). More frequent terrestriality practiced by habitual  
822 bipeds in the context of increased predation risk was thought to have been a prime mover

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

837 Tool-related activities by *Homo* (Blumenshine and Selvaggio, 1988; Braun et al.,  
838 2010; Bunn, 1981, 1994; Bunn and Kroll, 1986; Dominguez-Rodrigo et al., 2005;  
839 Pobiner et al., 2008; Potts and Shipman, 1981) and *Australopithecus* (de Heinzelin et al.,  
840 1999; McPherron et al., 2010) have been associated with animal carcass nutrient  
841 acquisition. Thompson et al. (2019) proposed that the Human Predatory Pattern (HPP)  
842 involving the scavenging of animals of equal or greater body size arose in Pliocene  
843 hominins with percussion-based marrow extraction of animal carcasses, rather than flake-  
844 tool assisted meat procurement like that interpreted for early *Homo*. The timing in the  
845 decrease of carnivore speciosity in the OTD is suggestive of direct competition between

846 carcass-scavenging hominins and sympatric predators beginning with *A. anamensis* and  
847 increasing throughout the Plio-Pleistocene (Faurby et al., 2020). Recent  $^{44}\text{Ca}/^{42}\text{Ca}$   
848 analysis, typically a proxy used to distinguish herbivory from carnivory, did not  
849 distinguish *A. anamensis* from *K. platyops*, and both species have  $^{44}\text{Ca}/^{42}\text{Ca}$  values  
850 overlapping those of *Homo* sp., *Theropithecus*, and some eastern African carnivores  
851 (Martin et al., 2020). Indeed, discerning different dietary components of omnivorous  
852 primates requires multiple lines of evidence; we suggest that an increase in faunivory by  
853 *K. platyops* is consistent with the decrease of  $\delta^{18}\text{O}_{\text{EC}}$  values relative to those of *A.*  
854 *anamensis* (e.g., Sponheimer and Lee-Thorp, 1999b, 2001). Although many variables  
855 could have influenced Pliocene hominin  $\delta^{18}\text{O}_{\text{EC}}$  values (Faith, 2019; Lee-Thorp et al.,  
856 2010; Quinn, 2015), we cannot discount the possibility that faunivory via scavenging  
857 behaviors was one of several potential  $\delta^{18}\text{O}_{\text{EC}}$ -lowering factors.

858         Temporally discrete and sizable environmental events between 3-2 Ma are well  
859 documented in eastern Africa (Alemseged et al., 2020; Levin et al., 2011; Robinson et al.,  
860 2017; Wynn et al., 2016), but the adaptive morphological transitions from genus  
861 *Australopithecus* to *Homo* during this time appear less punctuated (Antón et al., 2014;  
862 Kimbel and Villmoare, 2016) than once characterized (McHenry and Coffing, 2000).  
863 Brain size and hand morphology did not cross a significant grade-level threshold with the  
864 first appearance of genus *Homo*, rather these adaptations were rooted in *Australopithecus*  
865 (Kimbel and Villmoare, 2016). Dietary niche expansion may have also occurred as a  
866 gradual increase in  $\text{C}_4$  food consumption beginning with *A. anamensis*. The initial dietary  
867 interpretations of *A. anamensis* concluded that the earliest biped consumed 0-10% of  $\text{C}_4$   
868 foods (Cerling et al., 2013b), similar to that of modern savanna chimps (Loudon et al.,

869 2016). However, unlike savanna chimps, *A. anamensis*' dentognathic morphology was  
870 adapted for processing hard/tough foods (Grine et al., 2012; Macho et al., 2005; Ward et  
871 al., 1999b, 2001; White et al., 2006). Although microwear data contrast those of  
872 dentognathic morphology and imply soft foods were regularly consumed (Grine et al.,  
873 2012), *A. anamensis*' dental microwear patterns are similar to those of the C<sub>3</sub>-C<sub>4</sub> mixed  
874 feeding *A. afarensis* (Grine et al., 2006; Ungar et al., 2010). Quinn (2019) reanalyzed the  
875  $\delta^{13}\text{C}_{\text{EC}}$ -based C<sub>4</sub> consumption percentage of *A. anamensis* in the OTD informed by  
876 Pliocene CO<sub>2</sub>  $\delta^{13}\text{C}$  values and vegetation structural categories and suggested that C<sub>4</sub>  
877 resources may have been more regular components in the earliest habitual biped (i.e.,  
878 ~20% C<sub>4</sub> diet), constituting an stepwise increase from a purely C<sub>3</sub> diet to a C<sub>3</sub>-C<sub>4</sub> mixed  
879 diet. Moreover, Blumenthal et al. (2020) has found high intra- and inter-annual  $\delta^{13}\text{C}_{\text{EC}}$   
880 values with laser ablation techniques in specimens of *A. anamensis* and *K. platyops*,  
881 suggesting seasonal fluctuations in resource use. Thus hominins' dietary forays into the  
882 C<sub>3</sub>-C<sub>4</sub> biome may be characterized as incremental increases in dietary breadth throughout  
883 the early Pliocene, reaching the broad C<sub>3</sub>-C<sub>4</sub> mixed diet in the middle Pliocene.

884 In a common thread, we suggest a gradual and stepwise but not necessarily abrupt  
885 behavioral shift underpins the earliest known stone tool making behaviors as represented  
886 by LOM3. Tools are used by extant chimpanzees to forage (Boesch and Boesch, 1990;  
887 Haslam, 2014; Haslam et al., 2009; Marchant and McGrew, 2005); thus tool-assisted  
888 foraging may be a shared ape-human behavioral trait also present in the earliest hominins  
889 (Toth and Schick, 2009). As Thompson et al. (2019) proposed, the use of unmodified  
890 stone for carcass marrow extraction might have been practiced throughout the early  
891 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<sub>4</sub> 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<sub>3</sub>-C<sub>4</sub>-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<sub>3</sub>-C<sub>4</sub> 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



915 include foraging C<sub>3</sub>-C<sub>4</sub> plants and carcass scavenging. Incremental changes in foraging  
916 across habitats with different and more variable food properties (e.g., hardness, caloric  
917 and macronutrient contents) and procurement requirements (e.g., stone percussion)  
918 influenced a mosaic suite of morphological changes to the body and brain including but  
919 not limited to habitual bipedal locomotion, a masticatory apparatus for hard, tough, and  
920 abrasive foods, hand morphology for object manipulation, and an increased brain size.  
921 (Un)modified stone-assisted percussion-based, food-getting behaviors were also  
922 influenced by food properties and procurement requirements. Moreover, changes in  
923 morphology and stone tool making behaviors, in turn, enhanced foraging efficiency and  
924 continued to increase hominins' capacity for dietary niche expansion. Gradual  
925 environmental changes in the early Pliocene and occurring throughout the middle  
926 Pliocene did not necessarily evoke abrupt changes to hominin morphology and diet, but  
927 provided consistent changes to resource abundances, shaping biotic competition.  
928 Likewise, stone tool-making behaviors involving rudimentary but deliberate core and  
929 flake technology do not represent the start of a new dietary niche, but the result of a long-  
930 term and stepwise adaptive zone throughout the Pliocene.

931

## 932 **7. Conclusions**

933 OTD environments shifted incrementally toward more open biomes but with  
934 slightly more humid conditions across the early and middle Pliocene. Some aspects of the  
935 environment became marginally more variable as indicated by intranodular  $\delta^{13}\text{C}_{\text{PC}}$  and  
936  $\delta^{18}\text{O}_{\text{PC}}$  values, but these changes are modest. Three herbivore ungulate taxa accompanied  
937 hominins in their increasing consumption of C<sub>4</sub> resources over the study interval.

938 Notably, the C<sub>3</sub>-C<sub>4</sub> feeding niche contracted through time, which was then occupied by  
939 broad C<sub>3</sub>-C<sub>4</sub>-mixed feeding hominins. No climatic changes are indicated with  $\delta^{18}\text{O}_{\text{PC}}$   
940 values from the early to middle Pliocene, but faunal  $\delta^{18}\text{O}_{\text{EC}}$  values signal a slight increase  
941 in humidity. The drop in hominin  $\delta^{18}\text{O}_{\text{EC}}$  values suggests an increase in water  
942 dependency as a function of increasing C<sub>4</sub> consumption, but also may have tracked the  
943 vegetation  $\delta^{18}\text{O}$  decrease and/or the consumption of animal products. The gradual  
944 increase in C<sub>4</sub> vegetation detected across this time interval is consistent with the long-  
945 term decrease in  $p\text{CO}_2$ ; however, the evidence for a slight uptick in humidity suggests  
946 that C<sub>4</sub> grassland spread was not accompanied by aridification. To date, OTD proxy  
947 records do not indicate the types of habitat changes predicted by variability or pulsed  
948 selection hypotheses per se (e.g., Maslin et al., 2014; Potts and Faith, 2015; Schultz and  
949 Maslin, 2013), but rather point to gradual, long-term environmental shifts. Making stone  
950 tools to more efficiently and effectively access foods provided the earliest knappers with  
951 a competitive edge relative to the established C<sub>3</sub>-C<sub>4</sub> feeding guild members including  
952 carnivores. We assert that hominin dietary niche expansion in the Pliocene, involving a  
953 wide range of plant foods and possibly carcass scavenging, was not a punctuated event  
954 but rather a series of incremental steps as hominins became increasingly more reliant on  
955 tool-assisted foraging, which culminated in stone tool making origins.

956

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974  
975

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2212 **Table and Figure Captions**

2213

2214 Table 1. OTD fossil mammalian mean  $\delta^{13}\text{C}_{\text{EC}}$  and  $\delta^{18}\text{O}_{\text{EC}}$  values  $\pm\sigma$  (‰) and interquartile  
2215 ranges (data from Blumenthal et al., 2017; Cerling et al., 2013b, 2015; Drapeau et al.,  
2216 2014; Manthi et al., 2020; Negash et al., 2020; this study).

2217

2218 Figure 1. The LOM3 archaeological site and artifacts Photos courtesy of the Mission  
2219 Préhistorique au Kenya (MPK)/West Turkana Archaeological Project (WTAP).

2220

2221 Figure 2. A: regional map with location of OTD (after Harmand et al., 2015); B: OTD  
2222 map with locations of the Omo Group Formations mentioned in this study (after Feibel,  
2223 2011).

2224

2225 Figure 3. A: Generalized eastern African Plio-Pleistocene hominin phylogeny  
2226 characterized with three main lineages and representative fossil specimens from the OTD.  
2227 \*denotes debate of specimen designation in the OTD. No complete cranial specimens of  
2228 *A. afarensis* or *A. anamensis* are preserved in the OTD (Kimbel, 1988; Ward et al., 1999);  
2229 those pictured are from Ethiopia. Permissions of hominin fossil photos: courtesy of  
2230 Human Origins Program, Smithsonian Institution (*Homo*, *Paranthropus*, *A. afarensis*); *A.*  
2231 *anamensis* by Dale Omori courtesy of Cleveland Museum of Natural History; *K. platyops*  
2232 by Fred Spoor copyright National Museums of Kenya. B: OTD hominin  $\delta^{13}\text{C}_{\text{EC}}$  values  
2233 (data from Cerling et al., 2013b; Wynn et al., 2020). C: Early Stone Age record in the  
2234 OTD represented by single artifacts from assemblage; first appearance (gray box) and  
2235 known duration (gray arrow); ^denotes older Oldowan site occurrences in Ethiopia;  
2236 artifact photos courtesy of the Mission Préhistorique au Kenya (MPK)/West Turkana  
2237 Archaeological Project (WTAP).

2238

2239 Figure 4. Global records of environmental change: A:  $p\text{CO}_2$  (Stap et al., 2016), B: marine  
2240 benthic  $\delta^{18}\text{O}$  values (L04 stack: Lisiecki and Raymo, 2005), C: African dust flux from  
2241 ODP 721/722 (deMenocal, 1995, 2004); shaded bars are proposed intervals of high  
2242 climatic variability (Potts and Faith, 2015); D: Curve depicts ~100-kyr eccentricity cycle  
2243 and hence a proxy of Plio-Pleistocene tropical insolation and monsoonal rainfall  
2244 intensity; shaded bars indicate eastern African lake phases that correlate to the peaks in  
2245 the 405-kyr cycle (Trauth et al., 2005).

2246

2247 Figure 5. Plio-Pleistocene OTD environmental records: A: Exponentially-smoothed  
2248 ( $\alpha = 0.1$ )  $\delta^{13}\text{C}_{\text{PC}}$  values (‰) estimates (data from Cerling et al., 1988; Harmand et al.,  
2249 2015; Levin et al., 2011; Quinn et al., 2007, 2013; Quinn and Lepre, 2020; Patterson et  
2250 al., 2019; Wynn, 2000, 2004); B: relative abundance of APP taxa (methods after Cerling  
2251 et al., 2015; data from Blumenthal et al., 2017 and references therein; Cerling et al., 2015  
2252 and references therein; Negash et al., 2020; Patterson et al., 2019); C: faunal abundances  
2253 of arid-adapted taxa (Bobe and Behrensmeyer, 2004); D: pedogenic carbonate clumped  
2254 isotope temperatures ( $^{\circ}\text{C}$ ) (Passey et al., 2010); E:  $\delta^{18}\text{O}_{\text{EC}}$ -based water deficit estimates  
2255 (mm/year) (Blumenthal et al., 2017).

2256



2257 Figure 6. A: Individual data points; B: box and whisker plots of two time intervals (4.3-  
2258 3.9 Ma and 3.4-3.0 Ma) and all  $\delta^{13}\text{C}_{\text{PC}}$  values from the OTD (‰). Large black box  
2259 denotes 25<sup>th</sup> and 75<sup>th</sup> percentiles; black line shows median value; gray line equals mean  
2260 value; whiskers denote 1.5\* interquartile range.

2261  
2262 Figure 7. A: Individual data points; B: box and whisker plots of two time intervals (4.3-  
2263 3.9 Ma and 3.4-3.0 Ma) and all  $\delta^{18}\text{O}_{\text{PC}}$  values from the OTD (‰). Large black box  
2264 denotes 25<sup>th</sup> and 75<sup>th</sup> percentiles; black line shows median value; gray line equals mean  
2265 value; whiskers denote 1.5\* interquartile range.

2266  
2267 Figure 8. Box and whisker plots of two time intervals (A: 4.3-3.9 Ma and B: 3.4-3.0 Ma)  
2268 superimposed on all intranodular  $\delta^{13}\text{C}_{\text{PC}}$  and  $\delta^{18}\text{O}_{\text{PC}}$  standard deviations from the OTD  
2269 (‰). Large black box denotes 25<sup>th</sup> and 75<sup>th</sup> percentiles; black line shows median value;  
2270 gray line equals mean value; whiskers denote 1.5\* interquartile range.

2271  
2272 Figure 9. Box and whisker plots separated in two time intervals (4.3-3.9 Ma=orange, 3.4-  
2273 3.0 Ma=blue) of  $\delta^{13}\text{C}_{\text{EC}}$  values of ungulate herbivore taxonomic groups and hominins  
2274 from the OTD (‰). Large black box denotes 25<sup>th</sup> and 75<sup>th</sup> percentiles; black line shows  
2275 median value; gray line equals mean value; whiskers denote 1.5\* interquartile range.  
2276 Asterisk denotes significant differences in pairwise comparisons (Mann-Whitney U,  
2277  $p < 0.05$ ).

2278  
2279 Figure 10. Box and whisker plots separated in two time intervals (4.3-3.9 Ma=orange,  
2280 3.4-3.0 Ma=blue) of  $\delta^{18}\text{O}_{\text{EC}}$  of ungulate herbivore taxonomic groups, Crocodylia and  
2281 hominins from the OTD (‰). Large black box denotes 25<sup>th</sup> and 75<sup>th</sup> percentiles; black  
2282 line shows median value; gray line equals mean value; whiskers denote 1.5\* interquartile  
2283 range. Asterisk denotes significant differences in pairwise comparisons (Mann-Whitney  
2284 U,  $p < 0.05$ ).

2285  
2286 Figure 11. Probably density function of all ungulate herbivore  $\delta^{13}\text{C}_{\text{EC}}$  values separated  
2287 into C<sub>3</sub>-browsers, C<sub>3</sub>-C<sub>4</sub> mixed feeders, C<sub>4</sub>-grazers (methods described in text). A: 4.3-3.9  
2288 Ma, B: 3.4-3.0 Ma. Hominin  $\delta^{13}\text{C}_{\text{EC}}$  ranges are shown with bar.

2289  
2290 Figure 12. Hypothesized feedback relationships between gradual environmental shifts,  
2291 dietary niche expansion, morphological adaptations and stone tool making behaviors.

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