

Aridity, availability of drinking water and freshwater foods, and hominin and archeological sites during the Late Pliocene–Early Pleistocene in the western region of the Turkana Basin (Kenya): A review.

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29 Abstract

Although the Turkana Basin is one of the driest regions of the East African Rift, its Plio-30 Pleistocene sediments are rich in freshwater vertebrates and invertebrates, providing evidence 31 32 that freshwater foods were available in this region during the Plio–Pleistocene (4.2–0.7 Ma). Here we provide an overview of the hydroconnectivity of the Turkana Basin. We then review 33 34 the period during which freshwater river and lake systems expanded into the western region of the Turkana Basin, where hominin and archeological sites have been discovered in sediments 35 dating back to the Late Pliocene-Pleistocene. Freshwater conditions are reconstructed from 36 river and lake sediments and the micro- and macofauna they contain. Data synthesis suggests 37 that drinking water and freshwater foods prevailed in the western region of the Turkana Basin 38 39 at 4.20–3.98 Ma, 3.70–3.10 Ma, 2.53–2.22 Ma, then between 2.10–1.30 Ma and intermittently 40 from 1.27 to 0.75 Ma. Milestones in hominin evolution occurred in this context, such as the 41 first occurrence of Australopithecus anamensis (4.20–4.10 Ma) and Kenyanthropus platyops (3.50 Ma and 3.30–3.20 Ma), the presence of *Paranthropus aethiopicus* (2.53–2.45 Ma), early 42 Homo (2.33 Ma), Paranthropus boisei (2.25 Ma and 1.77–1.72 Ma) and Homo ergaster/Homo 43 erectus (1.75 Ma, 1.47–1.42 Ma and 1.10–0.90 Ma). Developments in hominin behavior also 44 45 occurred during this timeframe, including the first known stone tools (3.30 Ma), the oldest Oldowan sites (2.34 Ma and 2.25 Ma) in the Turkana Basin, the earliest known evidence for 46 the emergence of bifacial shaping in eastern Africa (1.80 Ma), and the first known Acheulean 47 site (1.76 Ma). Our synthesis suggests that, diachronic variation in hydroconnectivity played a 48 role on the amount of drinking water and freshwater foods available in the western region of 49 50 the Turkana Basin, despite regional aridity.

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52 Keywords: Hominin evolution; Paleoclimatology; Paleoenvironment; Hydroconnectivity;

53 Omo Group deposits

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55 **1. Introduction**

56 Over the past 25 years, numerous authors have linked climate change and hominin 57 evolution based on the premise that resources essential to hominin development (e.g., brain 58 size, cognition and behavior), such as water and food availability, have fluctuated in tandem with climate in the East African Rift (deMenocal, 1995, 2004, 2011; Vrba et al., 1995; Potts, 59 1998, 2013; Bobe and Behrensmeyer, 2004; Wynn, 2000, 2004; Trauth et al., 2005, 2007, 2010, 60 2015; Behrensmeyer, 2006; Bobe, 2006; Bonnefille, 2010; Levin et al., 2011; Cerling et al., 61 2011; Maslin et al., 2014, 2015; Levin, 2015; Potts and Faith, 2015; Cuthbert et al., 2017; 62 Blumenthal et al., 2017; Timmermann et al., 2022). An important related debate about the 63 relationship between climate change, hominin diet and behavior concerns landscape 64 65 aridification in the Turkana Basin (Kenya, Ethiopia) (Wynn, 2004; Sommerfeld et al., 2014; 66 Fortelius et al., 2016; Blumenthal et al., 2017; Quinn and Lepre, 2020, 2021; Lepre and Quinn, 67 2022). During the Neogene, topographic uplift altered atmospheric moisture transport and 68 distribution in the East African Rift, and the initiation of Northern Hemisphere glaciations at 69 the end of the Pliocene intensified hydrological deficits in this region (Laporte and Zihlman, 70 1983; deMenocal, 2004; Sepulchre et al., 2006; Blumenthal et al., 2017; Trauth et al., 2021). 71 Along with hypotheses linking hominin adaptation to landscape aridification, the availability of water and food would also have been critical resources for their evolution (e.g., Cuthbert et 72 73 al., 2017). The debate on aridification and drinking water and food availability is especially 74 relevant to hominin evolution, as some previous hypotheses, such as the savanna and the 75 turnover pulse hypotheses (Vrba et al., 1995; deMenocal, 2004) or the pulsed climate variability hypothesis (Maslin and Trauth, 2009; Maslin et al., 2015), considered climate instability to be 76 key drivers of natural selection, adaptive divergence, and speciation in Plio-Pleistocene 77 78 hominin evolution. Although the global climate changed during the Plio–Pleistocene transition, 79 the responses of these changes on landscape, fauna and hominins are still debated in the East

80 African Rift and in the different regions of the Turkana Basin in particular (Blumenthal et al., 2017; Fortelius et al., 2016; Blumenthal et al., 2017; Villaseñor et al., 2020, 2023; Quinn and 81 Lepre, 2020, 2021; Lepre and Quinn, 2022). The aims of this review are to examine the 82 archeological and hominin records from the western region of the Turkana Basin (Kenya; Fig. 83 1) and the evidence for the existence of freshwater conditions and resources in the western 84 region of Turkana Basin between 4.20 and 0.70 Ma. This specific region of the Turkana Basin 85 provides evidence of hominin and archeological sites dating back to the Late Pliocene-Early 86 87 Pleistocene, raising new questions about the role of climate and environmental change on water and food resources and hominin evolution. 88

89 The western region of the Turkana Basin is unique, as the archeological site of Lomekwi 3 has yielded the first lithic assemblage associated with Late Pliocene sediments, climate, and 90 environment (Harmand et al., 2015; Lewis and Harmand, 2016; Quinn et al., 2021). Lomekwi 91 92 3 is at least 300 kyr older than the earliest known Oldowan assemblages discovered at other 93 localities (i.e., Gona, Ledi-Geraru, and Nyayanga; Semaw, 2006; Braun et al., 2019; Plummer 94 et al., 2023). Other important archeological sites have been discovered in the same region of 95 the basin over the past 30 years. For example, the Lokalalei 1A and 2C sites are among the oldest Oldowan assemblages known in Kenya and older than 2.2 Ma (Kibunjia et al., 1992; 96 Roche et al., 1999; Delagnes et al., 2005; Harmand, 2009). The artifacts from Kokiselei 6 are 97 98 the earliest known evidence for the emergence of bifacial shaping (Duke et al., 2021), and the archeological site of Kokiselei 4 has vielded the oldest Acheulean assemblage presently known 99 (Lepre et al., 2011; Texier, 2018). These archeological sites provide some of the earliest 100 101 evidence of hominin cognitive abilities in eastern Africa. As for the hominin record, the western region of the Turkana Basin has yielded some of the most important hominin fossils known, 102 103 including Australopithecus anamensis (Leakey et al., 1995; Leakey et al., 1998; Ward et al., 1999, 2001, 2013, 2020), Kenyanthropus platyops (Leakey et al., 2001; Spoor et al., 2016), 104

105 Paranthropus aethiopicus (Walker et al., 1986) and Paranthropus boisei (Leakey et Walker, 1988; Brown et al., 2001; Prat et al., 2003; Wood and Constantino, 2007), as well as specimens 106 assigned to early Homo (Prat et al., 2005), Homo ergaster or Homo erectus, referred to here as 107 Homo ergaster/erectus (Walker and Leakey, 1993; Prat et al., 2003; Wood and Leakey et al., 108 2011; Wood and Boyle, 2016), including the nearly complete skeleton of KNM-WT 15000 109 110 ('Nariokotome Boy'; Walker and Leakey, 1993). This fossil record highlights the importance of the western region of the Turkana Basin in terms of hominin taxonomy and phylogeny (e.g., 111 Walker and Leakey, 1993; Leakey et al., 2001; Ward et al., 2020). The western region of the 112 113 Turkana Basin is also very rich in freshwater micro- and macrofauna demonstrating that 114 freshwater conditions expanded into this arid region of the East African Rift during the Plio-Pleistocene (e.g., Williamson, 1981; Harris et al., 1988; Meylan et al., 1990; Stewart, 2003; 115 Martin and Trautwein, 2003; Storrs, 2003; Van Bocxlaer, 2011, 2020; Stewart and Rufolo, 116 117 2020).

118 Similar, coeval records exist to the northern regions of the Turkana Basin in the 119 Shungura, Mursi and Usno Formations (Ethiopia) along the Omo River and to the eastern 120 regions in the Koobi Fora Formation (Kenya) and at Fejej and Konso (Ethiopia) (Williamson, 1981; Howell et al., 1987; Stern et al., 1993; Isaac, 1997; Nagaoka et al., 2005; WoldeGabriel, 121 et al., 2005; Chapon et al., 2005, 2011; Van Bocxlaer et al., 2008; Braun et al., 2010; Barsky et 122 al., 2011; Delagnes et al., 2011; Leakey et al., 2012; Maurin et al., 2017; Fig. 1). Reviews of 123 the Turkana Basin generally combine data from these different fluvial and lacustrine formations 124 (i.e., located in the northern, western, eastern and southern regions of the Turkana Basin). 125 126 Howver, this review covers only the western region of the Turkana Basin (Nachukui and Kanapoi Formations) and does not include data from the northern and northeastern regions of 127 128 the basin (Shungura and Koobi Fora Formations). In these latter regions, freshwater conditions are more permanent, due to the presence of the Omo River delta. By contrast, in the western 129

130 and southern regions of the Turkana Basin, conditions have been more alkaline-saline since the 131 closure of the outlet to the Indian Ocean at around 2.2 Ma (Boës et al., 2019a). Given the 132 reorganization of the hydroconnectivity, it is important to consider the mosaic of landscapes with their own rhythms, hydoconnectivity and hydroclimatic influences from the northern, 133 southern, eastern and western regions of the Turkana Basin. Here, we focus on understanding 134 135 how landscapes changed regionally along the western region of the Turkana Basin, where the 136 hydrology and limnology is substantially different from that of the Omo delta region. Moreover, 137 in terms of hydroconnectivity, the upland river-lake systems in the western region of the 138 Turkana Basin are associated with the hydroclimate of the Kenyan Highlands, while in the 139 eastern region of the basin they are associated with the hydroclimate of the Ethiopian 140 Highlands.

141 The various sources of data from the western region of the Turkana Basin (see Tables 142 1–5) can be compiled in a reliable chronostratigraphic framework derived from ${}^{40}\text{Ar}/{}^{39}\text{Ar}$ ages 143 of volcanic tuffs and/or lateral correlations by geochemical signatures specific to each tuff (e.g., 144 Harris et al., 1988; Feibel et al., 1989; Brown and McDougall, 2011; McDougall et al., 2012). 145 Plio-Pleistocene sediments and tuffs are outcropping in the Nachukui Formation, including 146 Lothagam, Loruth Kaado, South Turkwel and in the Kanapoi Formation (Fig. 1; Table 2). The 147 Nachukui and Kanapoi Formations offer ~700 m of strata with regularly intercalated tuffs that 148 cover the period from 4.20 to 0.70 Ma without major chronostratigraphic gaps, although the interval between 3.1 and 2.7 Ma is represented by fewer outcrops. In this review, we consider 149 150 that it is not possible at this time to provide accurate ages within the interval between 3.1 and 151 2.7 Ma because there are no dated tuffs or paleomagnetic inversions, which considerably limits the reliability of sediment chronologies (and/or results in excessively large errors; see section 152 153 3.6 below on methods for controlling chronology). In what follows, ages in Ma with two 154 decimal places are argon-argon dated tuffs or ages that were directly interpolated from these

tuffs, whereas ages in Ma with one decimal place either were derived from paleomagnetism orwere estimated.

157 We begin by introducing the impact of global climate change on eastern Africa during 158 the Plio-Pleistocene and present our current understanding of the influence of regional climate on the Turkana Basin. We then provide an overview of the former hydroconnectivity of the 159 160 Turkana Basin and highlight the topoclimatic effects on the regional hydroclimate system. 161 Subsequently, we present the datasets and criteria we used to reconstruct the paleohydrological 162 evolution of the western region of the Turkana Basin and the development of freshwater systems accompanied by freshwater micro- and macrofauna in this region. A synthesis is 163 164 provided based on available datasets between 4.20 and 0.70 Ma and on field data verifications 165 that were conducted between 2010 and 2023 in the western region of the Turkana Basin 166 (Mission Préhistorique au Kenya; West Turkana Archaeological Project). We then relate our 167 findings from this synthesis to the stratigraphic and spatiotemporal contexts of the archeological 168 and paleoanthropological sites of the western region of the Turkana Basin. Along with the 169 hypotheses linking increasing aridity to hominin evolution, we discuss the availability of 170 drinking water and freshwater food resources for hominins occupying this arid region of the rift. 171

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173 2. Plio–Pleistocene climate change, aridity and hominin evolution in eastern Africa

Until recently, it was thought that major climate change in eastern Africa began ~2.7 Ma in response to the onset of Northern Hemisphere glaciations, and that the expansion of arid environments accompanied major developments in hominin evolution (deMenocal, 1995, 2004, 2011; Trauth et al., 2007; Maslin and Trauth, 2009; Potts and Faith, 2015). Recent data do not corroborate a consistent stepwise transition from ~2.7 Ma onward but suggest that glaciations

179 were initiated before ~ 2.7 Ma, as discussed by Trauth et al. (2021), partly in connection with tectonic, radiative forcing and feedback over oceans. These involved changes in the circulation 180 of the North Atlantic Ocean, due to the gradual closure of the Central American Seaway during 181 the uplift of the Central American Isthmus between 4 and 3 Ma (Bartoli et al., 2005; O'Dea et 182 183 al., 2016). Among the modifications of ocean circulation and air flow along the equator was the creation of the Gulf Stream, which initiated the storage of atmospheric humidity within the 184 Northern Hemisphere ice cap. This new ocean circulation system explains global differences in 185 the cyclicity of benthic δ^{18} O records related to changes in astronomical forcing on atmosphere-186 ocean circulation after 3.5 Ma (deMenocal, 2004; Lisiecki and Raymo, 2005), while orbital 187 parameters (Milankovitch cycles) were unaltered (Laskar et al., 2004). One of the earliest 188 glacial events occurred at 3.30 Ma, i.e., during MIS M2 (Lisiecki and Raymo, 2005; Raymo et 189 al., 2006; Tan et al., 2017). With the formation of the ice cap, a large amount of water was 190 removed from the oceans, resulting in global sea-level drops (Miller et al., 2005). This sea-level 191 192 fall would have expedited the tectonic closure of equatorial and tropical seaways (i.e., the Central American and Indonesian Seaways) and the associated alteration of ocean and 193 atmospheric circulation (Cane and Molnar, 2001; Yan et al., 2021). As tropical ocean 194 circulation declined, heat transfers reduced in the Indo-Pacific Ocean (Karas et al., 2009). The 195 196 resulting establishment of atmospheric circulation cells (i.e., the Walker and Hadley cells) 197 would have significantly weakened the East African monsoon (Yan et al., 2021) and thus 198 promoted the expansion of more seasonal and arid environments in eastern Africa, with implications for mammalian evolution, including hominins (e.g. Cohen et al., 2022; 199 200 Timmermann et al., 2022).

Multiple regional ecological indicators, such as the abundance of grazing bovids, C₄ plants, grass pollen, soil carbonate δ^{18} O and δ^{13} C values, leaf wax δ^{13} C values and phytoliths suggest a long-term trend toward aridification of eastern Africa during the Plio–Pleistocene

204 transition, including the Turkana Basin (e.g., Passey et al., 2010; Levin, 2015; Quinn and Lepre, 2020, 2021; Lepre and Quinn, 2022), rather than several arid punctuations as previously thought 205 (Wynn, 2004). Several studies have focused on climate change (mostly via temperature and 206 precipitation proxies) at the scale of the paleontological and archeological sites in the Turkana 207 Basin. For example, based on the distribution of ${}^{13}C{-}^{18}O$ bonds in soil carbonates, Passey et al. 208 209 (2010) suggested that the temperature in the Turkana Basin has remained stable (30–35 $^{\circ}$ C) over the last 4 Myr. Based on faunal ecometric methods, Fortelius et al. (2016) suggested that 210 211 the basin was already arid before 2.7 Ma and may have acted as a 'species factory', promoting 212 ecological adaptations to aridity prior to widespread aridification in eastern Africa. Based on 213 dietary changes of large herbivores, Cerling et al. (2015) suggested that C4-grazing taxa (savanna biome) increased after 2.35 Ma in the Turkana Basin. However, sampling of coeval 214 215 soil carbonate records from different regions in the basin shows that the distribution of C_3 and 216 C4 plants varied by region (Levin, 2015). For example, Uno et al. (2016) showed that C4-217 dominated ecosystems developed in the western region of the Turkana Basin only after 2.1 Ma. 218 Blumenthal et al. (2017) argued that changes in paleoaridity and herbivore paleodiets were decoupled in the basin during the Plio–Pleistocene. Using δ^{18} O values from tooth enamel, they 219 220 suggested that changes in the abundance of C₄ grass and grazing herbivores might reflect 221 rainfall seasonality rather than general aridity. Recent drill-core studies along the rift (Cohen et 222 al., 2022) do not extend beyond 700 ka, but drilling in the Turkana Basin at Kaitio (core WTK13) covers the interval between 1.9 and 1.4 Ma. Based on this drill-core, Lupien et al. 223 (2022) proposed that the Turkana Basin experienced a dramatic and abrupt increase in 224 precipitation (enrichment in δD_{wax} in WTK13 core in the western region of the Turkana Basin) 225 at 1.71 Ma and that rapid changes in aridity/humidity likely affected the basin. Finally, again 226 using soil carbonate δ^{18} O values, Lepre and Quinn (2022) suggested that aridity increased after 227

228 2.1 Ma in the Turkana Basin following the strengthening of the Indo-Pacific Walker circulation,

as seen in marine records (Van der Lubbe et al., 2021; Trauth et al., 2021).

230 Whereas soil temperature and moisture proxies suggest that the Turkana Basin has 231 remained arid since the uplift of rift flanks, the interpretation of precipitation proxies recorded in the fluvio-lacustrine deposits seems to be more complex. Indeed, the basin sediments reflect 232 233 inputs from the upper northern, northeastern and southwestern drainage basins as they connect, 234 amplifying the hydroclimatic responses recorded in the Turkana Basin, especially when the 235 basin has no outlet (i.e., when it is a terminal basin). In other words, there was a 'decoupling' between basin aridity and the fluctuating/continuous presence of freshwater availability via 236 237 distantly sourced lakes and rivers (=hydroconnectivity), especially for regions of the basin that are further away from the direct influence of the Omo River delta. This hydroconnectivity has 238 239 enabled freshwater fauna to colonize the Turkana Basin at certain periods despite the ambient 240 aridity (Williamson, 1981; Harris et al. 1988; Meylan et al., 1990; Stewart, 2003; Martin and 241 Trautwein, 2003; Storrs, 2003; Van Bocxlaer, 2011, 2020; Stewart and Rufolo, 2020). To gain 242 deeper insight into the paleolandscapes of the Turkana Basin, it is important to integrate the 243 topoclimatic and hydroclimatic effects within the basin as well as adjacent regions of the East African Rift. Indeed, beyond the Omo River that supplies the region with freshwater, other 244 drainage basins may have fed freshwater into the different regions of the Turkana Basin, as 245 suggested by the periodic occurrence of freshwater micro- and macrofauna in the basin 246 (Williamson, 1981; Harris et al. 1988; Meylan et al., 1990; Stewart, 2003; Martin and 247 Trautwein, 2003; Storrs, 2003; Van Bocxlaer, 2011, 2020; Stewart and Rufolo, 2020). 248 Moreover, it is necessary to examine the effects of volcano-tectonic activity on basin 249 topography and the reorganization of paleohydrographic networks and outlets during the Plio-250 251 Pleistocene (Bruhn et al, 2011; Salzburger et al., 2014; Boës et al., 2019a).

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3. Hydroclimatic specifics and hydroconnectivity of the Turkana Basin within the East African Rift system

255 *3.1. Topoclimatic effects*

In eastern Africa, precipitation is largely concentrated in a few uplifted mountain ranges 256 257 (e.g., Nicholson, 2017). To the northeast and southwest of the Turkana Basin, the Ethiopian and 258 Kenyan Highlands (Fig. 1) block atmospheric circulation and intercept most of the monsoon rainfall in the region (>1500 m.a.s.l.; >1500 mm annual precipitation; 19 °C mean 259 temperature=tropical monsoon climate). The isotopic composition of water suggests that the 260 261 Indian Ocean is the moisture source for the Kenyan monsoon rainfall, whereas the source for Ethiopian monsoon rainfall has oscillated seasonally between continental and Indian Ocean 262 263 moisture sources (Levin et al., 2009). To a large extent, the continental monsoon is driven by 264 increased evapotranspiration rates in equatorial Africa during summer insolation maxima 265 (Rossignol-Strick, 1985; Wang, 2009; Prömmel et al., 2013; Zhisheng et al., 2015; Kuechler et 266 al., 2018; see also e.g., Ashley, 2007 and Verschuren et al., 2009 for lake responses in eastern 267 Africa). For the Indian Ocean moisture source, it seems that when the Indian monsoon is strong, 268 it causes rainfall deficits in eastern Africa, especially in northeast Kenya (Camberlin et al., 269 2010). Located between the Kenyan and Ethiopian Highlands, i.e., two topographic barriers 270 that intercept most of the atmospheric moisture, the Turkana Basin is a rainfall-deficient 271 depression (<500 m.a.s.l.; <300 mm annual precipitation). The Turkana Jet, a low-level jet stream channeled by the topography of the Turkana Basin, also reinforces the permanent aridity 272 at the foot of the uplifted highlands (Nicholson, 2016). Because of this configuration, the 273 climate in the Turkana Basin remains warm and dry throughout the year (~30 °C mean 274 275 temperature=hot desert climate). Isotope temperatures of paleosol carbonates from the Nachukui and Shungura Formations suggest that similar mean temperatures have prevailed in 276 the basin since 4 Ma (Passey et al., 2010) and perhaps as early as the establishment of the 277

topographic barriers in the Middle Miocene (Wichura et al., 2015; Sommerfeld et al., 2014;
Polissar et al., 2019).

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281 *3.2. Paleohydrographic network*

Although the regional climate of the Turkana Basin is arid and decoupled from 282 precipitation changes in the Kenyan and Ethiopian Highlands, the basin does receive water from 283 these adjacent regions. Today, 80–90% of the permanent water inflow to the Turkana Basin 284 comes from the Omo River drainage catchment in the Ethiopian Highlands (140,000 km²; >500 285 m^3/s ; Kallqvist et al., 1988; Fig. 1). Most of the remaining 10–20% comes via inflow from the 286 287 Turkwel and Kerio rivers (Fig. 1) that drain the southwestern side of the basin up to the Kenyan Highlands, supplemented by runoff from ephemeral streams along the western and eastern 288 regions of the Turkana Basin. Beyond the river systems that currently contribute water to the 289 290 basin, several paleohydrographic connections may have been activated at certain periods during 291 the Pliocene and Pleistocene.

292 In the northeastern region of the Turkana Basin, along the Ethiopian branch of the East 293 African Rift, a series of closed lake basins are currently separated from the Turkana watershed 294 (Figs. 2–4). However, if precipitation intensifies in the Ethiopian Highlands, a cascading riverlake system may form that ultimately would overflow into the Turkana Basin (Garcin et al., 295 296 2009; Junginger, 2011; Bloszies, 2014). This system includes current lakes Abaya (1175 m.a.s.l.; 1100 km²), Chamo (1110 m.a.s.l.; 310 km²) and Chew Bahir (498 m.a.s.l.; 120 km²). 297 When overfilled with water, these systems spill into each other and finally into the Il Bakate 298 paleoriver (Figs. 3d, f and 4d), which drains into the Turkana Basin in the paleodeltaic zone of 299 Koobi Fora along the eastern region of the Turkana Basin (Fig. 4d; see also Grove et al., 1975; 300 Cuthbert et al., 2017). When precipitation increases in the Ethiopian Highlands, the water level 301

of the last lake in this cascade system, Lake Chew Bahir, would need to rise up by 45 m before
an outflow is established, expanding its surface area from 120 to 2100 km² (the outlet is situated
at 543 m.a.s.l.; Fischer et al., 2020). The fluvio-lacustrine sediments along the Ethiopian branch
of the East African Rift are consistent with the activation of this system at several periods in
the Plio–Pleistocene (Trauth et al., 2005; Nagaoka et al., 2005).

307 In the southwestern region of the Turkana Basin, a similar series of currently closed lake basins exists along the Kenyan branch of the East African Rift (Figs. 2-4). Although these are 308 currently hydrographically separated from the Turkana watershed, this hydrographic network 309 may be activated and overspill into the Turkana Basin when precipitation intensifies over the 310 Kenvan Highlands. This cascading river-lake system consists of lakes Elmenteita (1790 311 312 m.a.s.l.; 18 km²), Nakuru (1758 m.a.s.l.; 45 km²), Bogoria (990 m.a.s.l.; 34 km²), Baringo (970 m.a.s.l.; 168 km²) and Logipi-Suguta (275 m.a.s.l.; 30 km²). When overfilled with water, these 313 314 systems overspill into each other and finally into the Kerio River (Garcin et al., 2009; Olaka et 315 al., 2010; Junginger, 2011; Melnick et al., 2012; Bloszies, 2014; Dommain et al., 2022; Figs. 2, 316 3d, f and 4c). Evidence for the activation of this cascading system comes from the presence of 317 diatomite beds in the Baringo-Bogoria Basin (east of the Tugen Hills; Fig. 1), which indicate 318 that deep lakes existed along the Kenyan branch of the East African Rift during the Plio-Pleistocene (Trauth et al., 2005; Kingston et al., 2007; Westover et al., 2021). In addition, the 319 last lake in this cascade system, Lake Logipi-Suguta, is a volcanic-dammed lake that formed 320 321 with the eruption of 'the Barrier' from 1.44–1.37 to 0.69 Ma (Fig. 4c; Dunkley et al., 1993; McDougall et al., 2012). When precipitation increased in the Kenyan Highlands, the water level 322 of Lake Logipi-Suguta could rise up by 300 m before overspilling, reaching a lake surface of 323 430 km² in contrast to the current 30 km² (=paleolake Suguta, with the outlet situated at 577 324 325 m.a.s.l.; Fig. 4c; Garcin et al., 2009; Junginger, 2011; Bloszies, 2014). Before deposition of the Barrier, Lake Logipi-Suguta did not exist; instead, the Suguta paleoriver flowed directly into 326

327 precursors of Lake Turkana, which periodically were larger than the present-day lake (Figs. 3d, 328 f and 4c). In other words, the redirection of the Suguta paleoriver into Lake Logipi-Suguta by 329 volcanism drastically reduced the excess water input from the Kenyan Highlands to the Turkana Basin after 1.37 Ma (with the overflow of Lake Suguta reoriented towards the Kerio River and 330 331 then into the Turkana Basin; Fig. 3d, f). Located next to the Suguta paleovalley, the Kerio River is today a major river system that drains the Kenyan Highlands (Kerio Basin, west of Tugen 332 Hills). Sediments from the Kerio paleoriver formed the extensive Pliocene fossiliferous deltaic 333 deposits at Kanapoi (Fig. 4b; Feibel, 2003a) 334

Activation of these cascading river-lake systems at various periods in the Plio– Pleistocene and the resulting enhanced hydroconnectivity would likely also have promoted dispersal of freshwater fauna into the Turkana Basin (Fig. 5a). This hydroconnectivity amplified the volume of water flowing into the Turkana Basin and would have caused the periodic formation of large, deep freshwater paleolakes, depending on the configuration of the basin outlet.

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342 *3.3. Evidence for large, deep paleolakes in the Turkana Basin*

343 Today, the continuous water inflow of the Omo River into the Turkana Basin renders Lake Turkana the largest permanent 'desert lake' in a closed drainage system (lake surface area 344 from 6800 to 7200 km²; water volume of 200–240 km³). The current lake occupies the central 345 axis of the volcano-tectonic basin and is on average only 30 m deep, with a maximum depth of 346 110 m in the central and southern basins (e.g., Dunkelman et al., 1989; Fig. 1). As a result of 347 closed conditions, the lake water is saline (2500 ppm total dissolved solids [TDS]); Yuretich 348 and Cerling, 1983) and alkaline (21–34 meq/L; Olago and Odada, 1996), except in the vicinity 349 of the Omo River delta, where the conditions are fresher due to the continuous inflow of the 350

351 Omo River. The level of Lake Turkana is currently relatively stable (365 ± 5 m.a.s.l.), representing a balance between continuous inflow of the Omo River and high evaporation (2.5 352 to 3.5 m/year resulting in a volume of 20 km³/year; Kallqvist et al., 1988). 353 354 Over the past 150 years the water level of Lake Turkana has fluctuated, reaching levels 15 m above the present lake level when precipitation intensity increased in the adjacent Kenyan 355 356 and Ethiopian Highlands (Bloszies and Forman, 2015; Bloszies et al., 2015). Reconstructions over the last 25 kyr suggest even larger fluctuations, with levels having reached 95 m above the 357 present lake level (lake surface of nearly 10,000 km²; Garcin et al., 2012; Morrissey and Scholz, 358 2014). Over the last 4 Myr, the sediments in various regions of the Turkana Basin reveal a 359 succession of fluvio-lacustrine systems that confirm the existence of large, deep paleolakes 360 361 (Feibel et al., 1993; Trauth et al., 2005, 2007; Feibel, 2011; Joordens et al., 2011; Lepre, 2014; Gathogo, 2017; Boës et al., 2019a; Nutz et al., 2020). Such changes in water volume may be 362 363 caused by increased precipitation in the Kenyan and Ethiopian Highlands and by changes in the 364 catchment size, due to the emergence of new connections extending to rivers and lakes in these 365 two regions. The impact of tectonic subsidence on 'accommodation space' for sediment and 366 water volume is limited for our time scale, considering the rate of basin extension (<500 cm/ka; 367 Knappe et al., 2020) and the highest sedimentation supply during the Plio–Pleistocene (<55 cm/ka). Thus, hydroconnectivity and water supply were the primary drivers of fluvio-lacustrine 368 369 sedimentation and paleolake-level fluctuations in the basin. However, in our time interval, 370 explosive volcanoes (Mount Kulal and the Barrier; Table 1) reorganized outlets and inlets across the southern region of the Turkana Basin (Dunkley et al., 1993; Bruhn et al., 2011; Boës 371

et al., 2019a; Fig. 5b). These changes likely have influenced freshwater availablity and thecolonization of the Turkana Basin by freshwater fauna.

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375 3.4. Evidence of paleo-outlets and reorganization of the drainage of the Turkana Basin by
376 volcanism

During the Plio–Pleistocene, water outflowed from the Turkana Basin, first to the Indian Ocean and subsequently to the Mediterranean Sea, through the Loiyangalani and Ilemi outlets respectively (Figs. 2, 3c, e, 4e, f and 5b; Nyamweru, 1986, 1989; Feibel, 1993; Bruhn et al., 2011; Salzburger et al., 2014; Lepre, 2014; Boës et al., 2019a).

Situated on the southeastern region of the Turkana Basin, the Loiyangalani outlet, when 381 active, connected the Turkana Basin to the Turkana paleoriver, which flowed into the Indian 382 383 Ocean (Figs. 3f and 4e; Feibel, 1993; Van Damme and Van Bocxlaer, 2009; Bruhn et al., 2011; Feibel, 2011; Salzburger et al., 2014; Boës et al., 2019a). Major paleohydrographic changes 384 385 occurred in this area between 3 and 2 Ma, with the onset of explosive volcanism in the 386 southeastern region of the Turkana Basin and the damming of the Loiyangalani outlet by the Mount Kulal volcano and the Lenderit Basalt (Figs. 4e and 5b; Table 1; Frostick and Reid, 387 388 1989; Bosworth and Maurin, 1993; Haileab et al., 2004; Bruhn et al., 2011; Boës et al., 2019a). 389 This volcanic activity initiated the closure of the Loiyangalani outlet, resulting in a shift of the 390 basin outflow sill towards the Ilemi outlet (Fig. 3d, f and 5b).

391 The Ilemi outlet is located in the northwestern region of the Turkana Basin, ~300 km 392 distant from the Loiyangalani sill (Nyamweru, 1989; Bruhn et al., 2011; Feibel, 2011; Lepre, 2014; Boës et al., 2019a; Figs. 1, 2 and 3d, f). The Ilemi outlet channel connected to the White 393 394 Nile River and the Mediterranean Sea (Figs. 3d and 4e). Unlike the Loiyangalani outlet, which 395 was blocked by explosive volcanism (see below; Figs. 3f, 4e), the Ilemi outlet can still be 396 reactivated if the lake level rises by 100 m, as during the 'African Humid Period' (Bloszies, 2014; Bloszies and Forman, 2015; Bloszies et al., 2015). The Ilemi outlet is located 95 m above 397 the current lake level (364 m). The longitudinal profile of the paleovalley connected to the Sobat 398

399 River and then the White Nile River shows elevations from 455 to 440 m.a.s.l., respectively, through the Ilemi sill (Fig. 4f). However, these are modern altitudes, and the elevations may 400 401 have been different in the past due to volcano-tectonic influences on topography and erosion, notably in the eastern and southeastern regions of the Turkana Basins. In the northwestern 402 403 region of the basin, river erosion may have affected the Ilemi outlet channel after its opening, 404 so this outlet was probably initially situated in a higher position (possibly ~465 m.a.s.l.). In comparison, the longitudinal profile of the Turkana paleoriver (Fig. 4e) shows elevations 405 around 440 m.a.s.l. north of the basalt flows of Mount Kulal, which erupted \sim 3 Ma (Table 1). 406 407 In other words, the outlet of the Turkana paleoriver to the Indian Ocean was lower than the 408 outlet to the Nile River and the Mediterranean Sea. The activation of the Ilemi outlet in the Late 409 Pleistocene has been demonstrated in numerous papers since the 1980s (Harvey and Grove, 410 1982; Dumont, 2009; Johnson and Malala, 2009; Stewart, 2009; Van Damme and Van 411 Bocxlaer, 2009; Garcin et al., 2012; Morrissey and Scholz, 2014; Williams, 2019). Some 412 studies suggest that this hydroconnectivity already existed in the Early Pleistocene (Cerling, 413 1979; Harris et al., 1988; Nyamweru, 1989; Haileab et al., 2004; Bruhn et al., 2011; Boës et al., 414 2019a). The presence of lake sediments east of Ilemi in the Shungura Formation (i.e., from 415 submember G-14 to G-27; Feibel et al., 1989; Bobe and Eck, 2001) indicates that paleolake levels came close to the Ilemi outlet channel at 2.00–1.95 Ma. Harris et al. (1988) proposed that 416 the basin was connected to the Nile as early as 1.7 Ma. However, ostracod data from the 417 Shungura Formation indicate the presence of oligohaline conditions between 1.8 and 1.4 Ma 418 and variable conditions after 1.4 Ma (i.e., appearance of Limnocythere; Carbonel and 419 Peypouquet, 1979). This information suggests that if the basin opened to the Nile after 1.9 Ma, 420 421 it must have been in alternation with closed alkaline-saline conditions in the Turkana Basin (see Boës et al., 2019a), although the Omo River and potentially the Il Bakate River provided 422 423 freshwater in the northern and northeastern regions of the basin.

424

3.5. Criteria and evidence for the expansion of freshwater systems into the western region of the Turkana Basin during the Plio–Pleistocene

427 In contrast to the saline–alkaline conditions that prevail in Lake Turkana today, various 428 lines of evidence indicate that freshwater systems existed and/or expanded repeatedly in the 429 Turkana Basin during the Plio–Pleistocene. These lines of evidence, among others, include sedimentology, water paleochemistry, isotope records and freshwater micro- and macrofauna 430 and flora (Cerling, 1979; Feibel, 1993; Stewart, 2001, 2003, 2009; Wood, 2003; Van Bocxlaer 431 432 et al., 2008; Van Bocxlaer, 2011, 2020; Dumont, 2009; Vonhof et al., 2013; Boës et al., 2019a). These records indicate the existence of enhanced hydroconnectivity, and at least the periodic 433 434 occurrence of freshwater conditions in the western region of the Turkana Basin despite persistent ambient aridity. As rivers transport water, they do not accumulate mineral salts and 435 are essentially fresh, except for perhaps at the establishment of a lake outflow, when previously 436 437 accumulated mineral salts are flushed. Given the aridity and high levels of evaporation within 438 the Turkana Basin during the Plio-Pleistocene (Wynn, 2004; Passey et al., 2010; Blumenthal 439 et al., 2017; Lepre and Quinn, 2022), the presence or absence of an outlet determines the 440 physicochemical properties of water bodies (freshwater versus saline-alkaline). When an outlet exists (open drainage=exorheic basin), mineral salts are flushed from the Turkana Basin and 441 442 freshwater conditions develop or are maintained within it. For example, freshwater biota 443 colonize the basin when new rivers connect to the Turkana Basin and/or when the lake level develops an outlet; thus, shell beds and other micro- and macrofaunal assemblages could be an 444 445 indicator of the existence of enhanced hydroconnectivity with upland river-lake systems and/or an outflow. In the absence of an outlet (closed drainage=endorheic basin), mineral salts 446 accumulate within the basin and create saline-alkaline conditions. When a lake progressively 447 becomes alkaline-saline, some freshwater organisms may persist for some time, or find refuge 448

in rivers, in this particular case near the Omo River delta, despite increasing alkalinity–salinityin the rest of the basin.

451 The development of enhanced hydroconnectivity and expansion of freshwater fauna into 452 the Turkana Basin are evidenced by the occurrence of various freshwater vertebrates, invertebrates, microalgae and microbial structures in river and lake sediments. These include: 453 454 the crocodile *Euthecodon*; turtles (Pelomedusidae and Trionychidae), fishes (Sindacharax, Semlikiichthys, Polypterus) and cartilaginous fish (Dasyatis africana); crabs of the family 455 Potamonautidae, mollusks (such as various gastropod and bivalve species) and ostracods 456 (Stenocypris, Sclerocypris); microalgae diatoms (Stephanodiscus spp. and Aulacoseira spp.) 457 458 and sponge spicules; and stromatolite microbial structures (Wood, 1979, 2003; Williamson, 1981; Schwartz, 1983; Harris et al., 1988; Meylan et al., 1990; Feibel, 1993; Brugal et al., 2003; 459 Stewart, 2001, 2003, 2009; Harris et al., 2003; Martin and Trautwein, 2003; Storrs, 2003; 460 Trauth et al., 2007; Van Bocxlaer et al., 2008; Tiercelin et al., 2010; Van Bocxlaer, 2011, 2020; 461 462 Van Bocxlaer and Van Damme, 2009; Brochu, 2020; Stewart and Rufolo, 2020).

463 Among the freshwater macrofauna, the aquatic mollusks found throughout the western 464 region of the Turkana Basin belong exclusively to freshwater mollusk families, although some 465 taxa like *Melanoides* can tolerate enhanced salinity/alkalinity (see Mandahl-Barth, 1988; Brown, 1994; Van Bocxlaer, 2020; Graf and Cummings, 2021). Note that even under current 466 467 conditions, some salt-tolerant 'freshwater' mollusks occur in Lake Turkana. The ostracods microfauna are likewise tolerant of various salinity/alkalinity levels and their ecological 468 interpretations may be difficult without accurate species-level identification (Peypouquet et al., 469 1978; Carbonel and Peypouquet, 1979; Carbonel et al., 1988). Four ostracod assemblages have 470 been identified in the Plio-Pleistocene sediments of the Turkana Basin (Cohen et al., 1983; 471 Carbonel et al., 1988). Of these, the assemblage containing Stenocypris and Hemicypris 472 (ostracods) reflects freshwater conditions with nutrient-rich water mixed by the wind, whereas 473

474 the ostracod *Limnocythere* is tolerant to saline–alkaline waters. The ecological interpretations 475 of freshwater conditions based on ostracods are congruent with those based on some mollusks (Cohen et al., 1983), various fish taxa (Stewart et al., 2003) including cartilaginous fish (Feibel, 476 1993) and reptiles, i.e., crocodiles and turtles (Meylan et al., 1990; Harris et al., 2003; Wood, 477 2003; Brochu, 2020). With regard to microalgae, in closed systems within arid zones, changes 478 in the diatom algal assemblage reflect the presence/absence of river inflow and/or the transition 479 from an open to a closed lake basin (Gasse et al., 1997). Throughout the Plio-Pleistocene 480 sediment series in the western region of the Turkana Basin, white diatomite beds occasionally 481 482 occur and consist almost exclusively of diatom frustules (Trauth et al., 2007). This type of 483 biogenic sediment only forms when a lake is sufficiently large and deep to be thermally stratified with seasonal nutrient upwelling caused by wind-driven mixing, resulting in diatom 484 485 blooms (e.g., Owen, 2002). However, the ecology of Plio–Pleistocene diatoms is still not well 486 known, most notably the ecological tolerances of the various taxa, since freshwater and saline-487 tolerant diatom taxa may have occurred at times in the Turkana Basin as in other basins in 488 eastern Africa (Gasse, 1980; Gasse et al., 1997). As such, the diatom record of the western region of the Turkana is incomplete and requires further study. 489

Finally, stromatolite microbial structures provide additional information on the 490 491 paleohydrological conditions that existed in the western region of the Turkana Basin at certain 492 times. The stromatolites (and oncolites) are formed by accretions of thermophilic blue-green 493 algae (fresh/brackish water cyanobacteria) and trapped sediment around nuclei (Abell et al., 1982). Blue-green algae may have enhanced CO₃ evasion and caused the direct precipitation of 494 495 CaCO₃ onto their filaments (Riding, 1991). The association of stromatolites with saline-alkaline or freshwater environments is a complex issue. As a clue to stromatolite growth, mixing 496 497 freshwater rivers with saline-alkaline lake waters results in carbonate dissolution. In other words, as the water is supersaturated with carbonate in the mixing zone, it is reprecipitated by 498

the microbial activity of carbonate reduction in stromatolites. The stromatolite beds therefore
suggest the possibility that a freshwater river mixed with saline–alkaline lake waters. In some
cases, stromatolites may also be related to thermal circulations channeled by faults (Casanova,
1996).

503

504 3.6 Definition of 'freshwater episodes' and enhanced hydroconnectivity in the western region
505 of the Turkana Basin

506 From the fossil record of the western region of the Turkana Basin, 'freshwater episodes' can be defined by the presence of river and lake sediments and the freshwater macrofauna they contain, 507 508 such as: mollusks (Van Bocxlaer, 2011, 2020; Van Bocxlaer and Van Damme, 2009), fish (Stewart, 2001, 2003, 2009; Stewart and Rufolo, 2020), cartilaginous fish (Feibel et al., 1993) 509 and crocodile (Harris et al., 1988; Brochu, 2020; Storrs, 2003). Freshwater microfauna 510 511 (ostracods and diatoms) is also included in the definition of 'freshwater episode', despite some 512 tolerance to alkaline and saline conditions and the absence of a biostratigraphy with accurate 513 species-level identification for Plio-Pleistocene microfauna in the Turkana Basin (Peypouquet 514 et al., 1978; Carbonel and Peypouquet, 1979; Carbonel et al., 1988; Harris et al., 1988; Trauth et al., 2007). As such, 'freshwater episodes' in the western region of the Turkana Basin can be 515 expressed by the colonization of the region by freshwater macrofauna from upland river-lake 516 systems via cascade hydroconnectivity. In the Turkana Basin, enhanced hydroconnectivity 517 518 formed and disappeared from the Kenyan and Ethiopian Highlands and surrounding regions as 519 observed in the Pleistocene records (Grove et al., 1975; Garcin et al., 2009; Olaka et al., 2010; Junginger, 2011; Melnick et al., 2012; Bloszies, 2014; Cuthbert et al., 2017; Dommain et al., 520 2022). Finally, 'freshwater episodes' express enhanced hydroconnectivity and the occurrence 521

of freshwater food chain with drinking water while there is a decoupling between the ambientaridity and the type of biota that colonized the region via distantly sourced lakes and rivers.

524

525 *3.7. Methods to develop chronological control*

526 In our review, it is important to revise the timing of various lines of evidence, and for 527 this purpose, we created a Bayesian age model using ChronoModel v. 2.0. (Lanos and Dufresne, 2019; Fig. 6). All of the argon-argon ages of the tuffs were plotted against the different 528 529 geological members to verify the ages that have been proposed in the different papers and 530 available datasets (Tables 2-5). Tuff ages and interpolated ages between tuffs are therefore 531 considered in the same framework and all published ages for fossils can be verified taking into 532 account uncertainty via error bars. In the published literature (Tables 2–5), the age of vertebrate and invertebrate fossils, microalgae, hominin remains and archeological sites is given either 1) 533 534 in relation to the presence of a tuff, or 2) as an age calculated from the sedimentation rate 535 inferred from the thickness of the sediments accumulated in between tuffs. The Bayesian age 536 model allowed us to verify the distribution of the published ages and uncertainties (Fig. 6). The 537 age modeling between 4.20 and 0.70 Ma shows that it is currently not possible to obtain an individual date with an accuracy of less than 50 ka for the chronostratigraphic interval between 538 3.2 and 2.6 Ma. The error bars extend to 300 ka between 3.1 and 2.7 Ma (Fig. 6), due to the 539 absence of tuffs (and paleomagnetic inversions). For this reason, as in most databases and 540 541 papers on the western region of the Turkana Basin, the time interval between 3.1 and 2.7 Ma is 542 not evaluated in this synthesis. For example, there is no soil carbonate nodules for the western 543 region of the Turkana Basin (Nachukui Formation) between 3.1 and 2.7 Ma in the recent paper published by Lepre and Quinn (2022). However, note some soil carbonate datasets cover this 544 interval for the western region of the Turkana Basin (e.g., Levin, 2015; Nutz et al., 2020). 545

Finally, note that the new ages recently proposed by Phillips et al. (2023) for the Chari andMalbe tuffs correspond to the ages obtained here with the Bayesian age model (Fig. 6).

548

549 4. Evolution of freshwater ecosystems in the western region of the Turkana Basin

550 *4.1. From 4.20 to 3.60 Ma*

The western region of the Turkana Basin is marked by the presence of river sediments 551 552 between 4.17 and 4.12 Ma and around 4.07 Ma at Lothagam (Tables 2 and 3). In the Kanapoi Formation, lake sediments at 4.15–4.11 Ma are intercalated between a lower and upper fluvial 553 554 sequence (i.e., between the Upper Pumiceous and Kanapoi Tuffs=Lonyumun paleolake; Fig. 555 7). In the Lonyumun Member of the Nachukui Formation (Table 2), lake sediments occur between <4.20 and 3.98 Ma (i.e., from the basalts to above the Topernawi Tuff=paleolake 556 Lonyumun). Note that paleolake Lonyumun sediments are in the Lonyumun Member (e.g., 557 Harris et al., 1988) and not in the Kataboi Member as indicated in Nutz et al. (2020; i.e., there 558 559 is an error of 400 kyr in their section 3, as the Naibar Tuff at 40 m is not dated at 3.60 Ma but 560 at 4.02 Ma). Diatomites occur in the Lonyumun Member, below the Naibar Tuff (Table 3; Fig. 7). Diatomite beds occur in the same temporal context at Loruth Kaado, Lomekwi, and 561 Nasechebun (Fig. 1; Harris et al., 1988). The end of paleolake Lonyumun is observed at 3.98 562 Ma in the sediments of the Nachukui Formation (i.e., 3 m below the Moiti Tuff that contains 563 564 pumice clasts). One brief lacustrine interval (lake muds and diatoms) is also present at \sim 3.7 Ma, 565 i.e., 12 m above the Moiti Tuff (3.97 Ma) and below the Lokochot Tuff (3.60 Ma) in the middle 566 of the Kataboi Member of the Nachukui Formation at Lomekwi (Tables 2 and 3; Fig. 7). Diatomites are also present at this level at South Turkwel (Tables 2 and 3; Fig. 7). 567

The development of an open freshwater system is demonstrated by the occurrence of freshwater crabs of the family Potamonautidae at 4.2 Ma (Martin and Trautwein, 2003) and

570 freshwater crocodile Euthecodon (Storrs, 2003) at Lothagam (Fig. 1; Tables 2 and 3). Sindacharax is also reported at 4.15–4.11 Ma at Lothagam (Table 3; Fig. 7). In addition, fossils 571 of freshwater organisms are present in the Kanapoi Formation between 4.20 and 4.10 Ma, 572 including ostracods such as *Sclerocypris* (Peypouquet, 1978); mollusks, such as *Bellamya* and 573 Etheria (Feibel, 2003a; Van Bocxlaer, 2020); the fishes Sindacharax and Semlikiichthys 574 (Stewart, 2001, 2003, 2009; Stewart and Rufolo, 2020); the crocodile Euthecodon (Harris et al., 575 2003; Brochu, 2020), and freshwater turtles of the families Pelomedusidae, Testudinidae and 576 577 Trionychidae (Meylan et al., 1990; Harris et al., 2003; Wood, 2003). In the Kanapoi Formation, 578 freshwater mollusks have only been observed from shell beds between 4.15 and 4.11 Ma (i.e., 579 between the Upper Pumiceous and the Kanapoi Tuffs; Fig. 7). Some mollusks derive from river deposits, but most are from paleolake Lonyumun and in stratigraphic proximity to the Kanapoi 580 581 Tuff (Fig. 7). Etheria is reported in a channel fill that cuts the Kanapoi Tuff (4.11 Ma). 582 Freshwater ostracods (Hemicypris) occur between 4.20 and 3.98 Ma and freshwater mollusks 583 are found at 3.99–3.98 Ma (i.e., from the Topernawi to the Moiti Tuffs; Fig. 7).

584

585 *4.2. From 3.60 to 3.1 Ma*

The western region of the Turkana Basin is marked by the presence of river sediments in association with the Lokochot Tuff (3.60 Ma; Table 3; Fig. 7), succeeded by lake sediments at 3.58 Ma (i.e., 3 m below the burrowed fine-sandstone marker bed=paleolake Lokochot; Fig. 7). This paleolake phase is marked by the presence of diatomites between 3.58 and 3.44 Ma (i.e., between the Lokochot and Tulu Bor α Tuffs). Diatomites are well exposed at Loruth Kaado, South Turkwel, Lomekwi and Nasechebun (Fig. 1; Harris et al., 1988; Ward et al., 1999). An alluvial system developed between 3.30 and 3.2 Ma (Table 3; Fig. 7). Then, lake

sediments with diatoms occurred at about 3.2–3.1 Ma, in association with the Waru Tuff
(=paleolake Waru; Table 3; Fig. 7).

595 The development of an open freshwater system is demonstrated by the occurrence of 596 freshwater sponge spicules within the upper 12 m of the Kataboi Member (i.e., <3.60-3.44 Ma). Freshwater mollusks such as *Bellamya*, *Cleopatra* and *Melanoides* are present at 3.5 Ma. At 597 Lomekwi, remains of Euthecodon, Sindacharax, mollusks and freshwater turtles are present in 598 599 a paleo-beach complex at 3.30 Ma (LO-5 and LO-4w localities of fossil collection in Leakey et al., 2001; Table 3; Fig. 7). Harris et al. (1988) have already reported the presence of *Etheria* at 600 3.30 Ma, in the same paleo-beach complex 23 m above the Tulu Bor α Tuff. A similar sequence 601 602 of freshwater biota including *Etheria* is observed at 3.30 Ma at Loruth Kaado in sediments of the lower Lomekwi Member (Tables 2 and 3; Fig. 7). The sediments of paleolake Waru include 603 604 the mollusk trace fossil *Lockeia* (Gathogo, 2017) and sponge spicules (Harris et al., 1988).

605

606 *4.3. From 2.60 to 2.20 Ma*

607 In the Lokalalei Member of the Nachukui Formation (Table 2), the development of river 608 systems is reported at 2.53 Ma (Table 3; Fig. 7); this environment is replaced by a lagoonal/embayment environment that develops between the Lokalalei and Kokiselei Tuffs at 609 2.53 and 2.44 Ma (Tiercelin et al., 2010; Table 3; Fig. 7). Then, lake sediments occur at 2.44 610 611 Ma (i.e., 3 m above the Kokiselei Tuff=paleolake Kokiselei; Fig. 7). In the lower Kalochoro 612 Member of the Nachukui Formation (Table 2), lake sediments occur between 2.25 and 2.22 Ma (i.e., a few meters above Tuff G=paleolake Nasura; Fig. 7). The paleolakes Kokiselei and 613 Nasura are separated by river sediments (2.33–2.25 Ma; Table 3; Fig. 7). 614

615 The development of an open freshwater system is demonstrated by the occurrence of 616 *Etheria* deposited in channels with the Lokalalei Tuff at 2.53 Ma (Table 3; Fig. 7). Freshwater

617 mollusks occur between 2.34 and 2.32 Ma at Lokalalei. Other bioclastic facies with freshwater 618 mollusks (lake-margin coquina) occur below and above the Ekalalei Tuff (undated), which 619 contain, among others, Melanoides shell beds. At 2.25 Ma, the aquatic environment was inhabited by the freshwater mollusks Melanoides and Potadoma, which suggest malacofaunal 620 621 continuity between 2.34 and 2.25 Ma. Siltstones and claystones in the Kokiselei drainage dated between 2.27 and 2.20 Ma contain ostracods (Table 3; Fig. 7). Geochemical studies (Sr/Ba 622 623 ratio) suggest alternating saline-alkaline conditions at 2.22 Ma (Boës et al., 2019a). In the 624 transition from freshwater to saline–alkaline conditions, inhospitable conditions appear to have 625 occurred briefly, as suggested by a fish kill event at 2.22 Ma (Boës et al., 2019a). This event is 626 probably associated with a destabilization of the thermal stratification, low water inflows, high evaporation and substantial algae and microbial activities, such as cyanobacteria blooms 627 (expansion and proliferation of cyanobacteria toxins; Olilo et al., 2023). The initiation of the 628 volcanic blockage of the outlet of the Turkana Basin to the Indian Ocean may partly explain 629 630 changing limnological conditions as early as 2.26 Ma (Boës et al., 2019a).

631

632 *4.4. From 2.20 to 1.30 Ma*

In the Kalochoro Member, lake sediments occur from 2.19 Ma onwards (i.e., 15 m above Tuff G=paleolake Lorenyang; Fig. 7). Diatomites occur above the KBS Tuff in the Kaitio Member of the Nachukui Formation (Table 2). Diatomites are also reported at 1.48–1.38 Ma within the Natoo Member of the Nachukui Formation (Table 2) and river sediments are present in the upper Natoo Member (Table 3; Fig.7), sometimes called the 'Chari floodplain' (Feibel, 2011).

639 The development of an open freshwater system is demonstrated by the occurrence of640 the freshwater stingray *D. africana* (spine fragments), with fossils reported in the Kalochoro,

641 Natoo and basal Nariokotome Members of the Nachukui Formation (i.e., from below the KBS Tuff at 1.87 Ma up to the Chari Tuff at 1.38 Ma; Table 3; Fig. 7). In the upper Kalochoro 642 Member, ostracods occur between 2.10 and 1.95 Ma (i.e., from 40 to 15 m below the KBS Tuff 643 at 1.87 Ma). In the Kaitio Member of the Nachukui Formation (Table 2), freshwater mollusks 644 and ostracods occur above the KBS Tuff. Ostracods have also been reported at the top of the 645 Kaitio Member at Kokiselei (Table 3; Fig. 7). The expansion of freshwater environments at 646 1.8–1.7 Ma is supported by the presence of diverse freshwater mollusks including, for example, 647 648 Iridina and Chambardia (Table 3; Fig. 7), and by the presence of Euthecodon and fossils of 649 freshwater fish, including *Polypterus* (Brugal et al., 2003). Freshwater mollusks are also 650 reported at 1.8 Ma near the archeological complex of Naiyena Engol, 16 m above the KBS Tuff 651 (Table 3; Fig. 7). The earliest stromatolite beds of the Nachukui Formation occur between the Malbe Tuff (1.84 Ma) and the Orange Tuff (1.76 Ma). At Kokiselei and Kalochoro, other 652 653 stromatolite beds occur at 1.6 Ma, in the upper Kaitio Member and the base of the Natoo 654 Member of the Nachukui Formation (Tables 1 and 3; Fig. 7). However, it is difficult to 655 differentiate the upper Kaitio Member from the overlying Natoo Member at this locality. Nutz 656 et al. (2017) reported the presence of stromatolite beds at Kokiselei, but their dating seems to be erroneous due to the presence of erosional/chronological gaps in the upper Kaitio Member 657 658 that have not been taken into consideration (Boës et al., 2019b). A stromatolite bed is also present at the base of the Natoo Member (Table 2) at Lowarengak (Harris et al., 1988) and there 659 is one stromatolite bed at ~1.4 Ma, 15 m below the Lower Nariokotome Tuff (1.30 Ma; Table 660 3; Fig. 7). Note that in the stratigraphy of the Nachukui Formation, there are no stromatolite 661 beds between 1.6 and 1.4 Ma in the Natoo Member as has been suggested by Nutz et al. (2020; 662 i.e., there is a 440 kyr error in their publication in section 16, as the Malbe Tuff at 60 m is not 663 dated at 1.40 Ma but at 1.84 Ma). Stomatolites occur at the transition between the Kaitio and 664 Natoo Members and then at the top of the Natoo Member only (Harris et al., 1988). At 665

Kokiselei, the period between 1.7 and 1.6 Ma (upper Kaitio Member) is characterized by
mollusk coquina, including *Celopatra* and *Melanoides* with the preserved trace fossil *Pelecypodichnus* (bivalve burrows) at the base of the coquina (Table 3; Fig. 7). Ostracods occur
in a tuff 9 m above the base of the Natoo Member (=Ebei Tuff at 1.48 Ma) and the freshwater
gastropod *Pila* occurs at 1.47 Ma. Mollusks are also present at 1.47 Ma at Loruth Kaado (Harris
et al. 1988). Fossils of freshwater fishes (*Sindacharax*) are abundant between 1.47 and 1.42 Ma
in the Natoo Member.

673

674 4.5. From 1.30 to 0.70 Ma

675 The Nariokotome Member of the Nachukui Formation (Table 2) is marked by the presence of river and lake sediments. Sediments contain ostracods at 1.29 Ma (i.e., between the 676 Lower and Middle Nariokotome Tuffs), which are overlain by deposits enriched in shells of 677 678 Cleopatra and Melanoides, at 1.27 Ma (Table 3; Fig. 7). Then ostracods and mollusks alternate 679 with stromatolites in sediments of several river and lake systems between 1.20 and 0.75 Ma. 680 Freshwater mollusks are common in sediments between these stromatolites. Notably, Iridina 681 has been reported from the Nariokotome Member (Table 3), where the depositional 682 environments evolved from river to lake systems (Fig. 7). Etheria is occasionally found associated with stromatolites (Harris et al., 1988). Mollusks and stromatolites are commonly 683 found within a stratigraphic interval extending from 9 m above the Upper Nariokotome Tuff at 684 685 1.23 Ma, up to 1 m below the Silbo Tuff at 0.75 Ma (Brown, unpublished data; Ward et al., 686 2014; Maddux et al., 2015). The biostratigraphy of the Nariokotome Member suggests that freshwater and saline-alkaline conditions fluctuated, notably between 1.27 and 0.75 Ma 687 (=paleolake Nachukui; Table 3; Fig. 7). Four of the stromatolite beds occur from 23 m above 688 the base of the member (Ward et al., 2014; Maddux et al., 2015). The stromatolites occur 689

690 between the Upper Nariokotome and Silbo Tuffs (1.23 and 0.75 Ma, respectively). As previously discussed, these stromatolites may have formed by the precipitation of 691 calcium carbonate around nuclei trapped in sediment when freshwater rivers and saline-692 alkaline lake waters mixed. Stromatolites developed near lakeshore and river channels, where 693 694 mollusks or rounded basalt cobbles frequently served as hard nucleating surfaces (Ekdale et al., 1989; Hargave et al., 2014). For the stromatolites observed 9 m above the Upper Nariokotome 695 Tuff at Nadung'a (Delagnes et al., 2006; Maddux et al., 2015), these formed around rounded 696 697 basalt cobbles, freshwater mollusks and even around a biface stone tool. The latest stromatolites 698 of the Nariokotome Member found 1 m below the Silbo Tuff (0.75 Ma) can be very large (up 699 to 1.5 m) immediately east of the fault at the Nariokotome Mission, or very small (<5 cm) west of the fault at Nadung'a. This variation suggests that factors other than the mixing of freshwater 700 701 rivers with saline-alkaline lake waters played a role in stromatolite size, such as geothermal 702 activity (Casanova, 1996).

703

5. Archeological and hominin sites in the western region of the Turkana Basin

705 5.1. From 4.20 to 3.60 Ma

The KNM-LT 329 mandibular fragment from the lowermost Apak Member is older than 706 4.20 Ma and thus represents the earliest known hominin from the Turkana Basin (Leakey and 707 708 Walker, 2003; Wood and Leakey, 2011; Kissel and Hawks, 2015). Hominin fossils attributed to the species A. anamensis (e.g., KNM-KP 29281, 29283, 29285, 29286, 29287; KNM-WT 709 710 30498, 31712, 34725, 53160, 58759; Table 4; Fig. 8) have been found in the Kanapoi Formation (Leakey et al., 1995, 1998), from the Lower Pumiceous Tuff and in the unit above the Kanapoi 711 712 Tuff, i.e., between 4.20 and 4.10 Ma (Table 4; Figs. 7 and 8; Feibel, 2003a). Note that in the original publication by Leakey et al. (1998), the Lower Pumiceous and Kanapoi Tuffs were re-713

dated at 4.17 Ma and 4.07 Ma, respectively, but were later dated to between 4.20 and 4.11 Ma
by McDougall et al. (2012). Thus far, the discoveries at Kanapoi represent the first occurrence
of *A. anamensis* and likewise of the genus *Australopithecus*. However, remains found in the
Koobi Fora region at Ileret may be 100,000 years older (Ward et al., 2023). The hominin fossils
from Kanapoi are almost contemporaneous with the material of *A. anamensis* from Fejej, 4.18–
4.0 Ma (Ward, 2014), and slightly older than the remains of *A. anamensis* from Allia Bay in the
Koobi Fora Formation, 3.90 Ma (Leakey et al., 1995; Ward et al., 2001).

721

722 5.2. From 3.60 to 3.1 Ma

723 The period between 3.60 and 3.10 Ma coincides with the appearance of a new hominin genus and species, Kenyanthropus platyops, in the western region of the Turkana Basin (Leakey 724 725 et al., 2001). The remains of K. platyops have been described only from the Kataboi and 726 Lomekwi Members in the Lomekwi region (Leakey et al., 2001). The holotype (KNM-WT 727 40000 cranium; Table 4; Fig. 8) of this species occurs at 3.50 Ma, whereas the paratype (KNM-728 WT 38350 maxilla) dates to 3.30 Ma (Leakey et al., 2001). The oldest fossils of K. platyops, 729 including the holotype cranium, were found in nearshore lake deposits at 3.50 Ma in the Kataboi 730 Member at Lomekwi (e.g., KNM-WT 38339, 38341; Table 4; Fig. 8). Other hominin remains, mentioned here as Pliocene hominins, have been discovered between 3.50 and 3.20 Ma at 731 Lomekwi (Skinner et al., 2020), and at 3.5 Ma at Lothagam (KNM-LT 23181, 23182, 23183; 732 733 Table 4; Fig. 8) and south of the Turkwel River (KNM-WT 22936 and KNM-WT 22944; Table 734 4; Fig. 8). The hominin remains at South Turkwel have been found in the same spatiotemporal 735 and depositional contexts as those at Lomekwi (see Ward et al., 1999 and Leakey et al., 2001). At Lomekwi, most of the remains of K. platyops and Pliocene hominins were found in the 736 Lomekwi Member at 3.30 Ma and 3.30-3.2 Ma (e.g., KNM-WT 16003, 08556, 08557, 38343, 737

738 38344, 38345, 38346, 38356, 38357; see Leakey et al., 2001) and in the same spatiotemporal context as the archeological bed ('LOM3 bed') excavated at Lomekwi 3 (LO-5 locality of fossil 739 collection), which has yielded the oldest known artifacts dated at 3.30 Ma (Table 4; Fig. 8). The 740 741 stone artifacts at the archeological site of Lomekwi 3 (LOM3) are mainly large cores, some reaching more than 20 cm in length, as well as flakes, hammerstones and anvils (Harmand et 742 743 al., 2015). Some specimens are multipurpose and were used both as cores to produce flakes and as anvils or percussors (Harmand et al., 2015). At present, the lithic artifacts from LOM3 at 744 745 3.30 Ma are the earliest evidence of hominin cognitive abilities for tool making (Harmand et 746 al., 2015; Lewis and Harmand, 2016). The LOM3 site and the K. platyops paratype were found 747 in sediments of the same age, just above a paleo-beach complex topped by sand dunes, and only about 650 m apart (LO-5 locality of fossil collection; Harmand et al., 2015; Leakey et al., 2001). 748 749 The paleo-beach and sand dune complex, the latter containing fossilized calcified roots and 750 termite nests, lie a few meters above the Toroto Tuff at 3.31 Ma (Harmand et al., 2015). 751 Nearshore river and alluvial fan deposits exclusively mark the periods at 3.60 Ma and 3.30-752 3.20 Ma.

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754 5.3. From 2.60 to 2.20 Ma

Two specimens of *P. aethiopicus* have been found in the Lokalalei Member: the KNM-WT 17000 cranium at 2.53 Ma and the KNM-WT 16005 mandible at 2.45 Ma (Table 4; Fig. 8). The chronostratigraphic position of these fossils is constrained by the Lokalalei Tuff at 2.53 Ma. KNM-WT 17000 lies within river sediments a few meters below this tuff and KNM-WT 16005 is positioned around 20 m above in river sediments (Walker et al., 1986). A tooth attributed to early *Homo* (KNM-WT 42718) was discovered 2.2 m above the Ekalalei Tuff (undated) at LA1 α (Prat et al., 2005), i.e., a paleoanthropological site located in the same

762 stratigraphic context as the Oldowan sites of Lokalalei (Prat et al., 2005). KNM-WT 42718 was 763 subsequently dated at 2.33 Ma based on the fact that the Ekalalei Tuff is slightly younger than 764 Tuff F (Shungura Formation) dated at 2.34 Ma. It was then shown that the Ekalalei Tuff lies four meters above the Kalochoro Tuff at Loakalalei (Tiercelin et al., 2010). Harris et al. (1988) 765 766 correlated the Kalochoro Tuff with Tuff F dated at 2.33 Ma, but McDougall and Brown (2008) suggested that they are two different eruptions very closely spaced in time. Based on these 767 assumptions, KNM-WT 42718 is probably slightly younger than 2.33 Ma. The lithic material 768 excavated at the archeological site of Lokalalei 1A and 2C demonstrates a level of technical 769 770 and manual skill that is exceptional for the early Oldowan, with high productivity flaking 771 between 2.33 and 2.25 Ma (Delagnes and Roche, 2005; Harmand, 2009; Arroyo et al., 2020). 772 Another archeological complex of early Oldowan sites named Nasura (Roche et al., 2018) 773 contains in situ artifacts at 2.33–2.25 Ma (NAS2, 1, 3; Table 5; Fig. 8). The remains of one 774 hominin allocated to Paranthropus (probably P. boisei, KNM-WT 64910) is also reported 775 within the archeological complex of Nasura (Table 4; Fig. 8). There are currently no remains 776 of *P. aethiopicus* associated with an archeological site in the western region of the Turkana 777 Basin.

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779 5.4. From 2.20 to 1.30 Ma

No hominins or archeological sites have been discovered thus far from the period between 2.2 and 1.9 Ma, but more archeological surveys are needed for the upperpart of the Kalochoro Member. Note that the hominin cranium (KNM-WT 15001) previously identified as *Homo habilis* at Kangaki is from the Holocene (Harris et al., 1994). Remains of *P. boisei* (KNM-WT 37100, 37744, 37747, 37748; Table 4; Fig. 8) have been found from coeval sediments during the excavation of the Oldowan material at Kokiselei 1, dated at 1.79 Ma (KS1;

786 Tables 4 and 5; Fig. 8). Other remains of *P. boisei* at 1.77–1.72 Ma (KNM-WT 17400, 17396, 18600) have been discovered in the same spatiotemporal context as the Kokiselei archeological 787 788 complex. A tooth at 1.75 Ma attributed to Homo sp. aff. H. ergaster (KNM-WT 37745) was uncovered at the Oldowan site of Naiyena Engol 1 (NY1; Table 5; Fig. 8). The period after 1.7 789 790 Ma is marked by the presence of *H. ergaster/erectus*, of which the most complete skeleton 791 known (KNM-WT 15000) was unearthed at the Nariokotome III site at 1.47 Ma (Walker et Leakey, 1993). Another cranium of H. ergaster/erectus (KNM-WT 16001), discovered in the 792 793 Nariokotome drainage, is dated at 1.44 Ma by McDougall et al. (2012). A metacarpal (KNM-794 WT 51260) has been discovered at 1.42 Ma in the Natoo Member (i.e., at the level of the 795 Lokapetamoi Tuff) at Kaitio, and allocated to the genus Homo and probably to H. erectus sensu 796 lato (i.e., *H. ergaster/erectus*; Ward et al., 2014).

797 The following chronostratigraphic interval between 1.8 and 1.7 Ma yielded many 798 Oldowan sites at Kokiselei and Naiyena Engol (KS3, KS2, KS5, KS1; Table 5; Fig. 8). At 1.80 799 Ma, the archeological site of Kokiselei 6 (KS6) provides the earliest known evidence for the 800 emergence of bifacial shaping in eastern Africa (Duke et al., 2021). At 1.76 Ma, the 801 archeological site of Kokiselei 4 (KS4) contains the oldest known Acheulean industry (Lepre 802 et al., 2011; Texier, 2018). The lithic material is characterized by large flakes and heavy tools obtained by splitting large cobbles, direct shaping (unifacially or bifacially) of flat cobbles, and 803 by shaping smaller detached products. Kokiselei 4 includes picks with trihedral or square 804 sections, unifacial or roughly shaped handaxes, as well as pieces left as rough outs (Roche et 805 al., 2003; Texier, 2018). The chronostratigraphy of the upper Kaitio Member requires further 806 investigation, especially at Naiyena Engol, an archeological complex currently under study 807 (NY1, NY2; Table 5; Fig. 8). 808

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810 5.5. From 1.30 to 0.70 Ma

811	Currently under study, the Acheulean site of Nachukui 6 at 1.27 Ma (NK6; Table 5; Fig.
812	7) is located a few meters above the Middle Nariokotome Tuff (1.28 Ma) and intercalated
813	between conglomerates and channels. It is for the moment the only archeological site at the
814	base of the Nariokotome Member. Higher in this member, a left proximal tibia attributed to H.
815	erectus (KNM-WT 19700; Table 4; Fig. 8) is dated approximately to 1 Ma (i.e., 45 m above
816	the Lower Nariokotome Tuff and 8-8.5 m below stromatolite horizon S3; NC1 locality in
817	Brown et al., 2001). A hominin molar (KNM-WT 51261) was uncovered in marginal lake
818	deposits within the Acheulean complex of Nadung'a at 0.75 Ma (i.e., at the level of the Silbo
819	Tuff) and was attributed to the genus Homo (African Middle Pleistocene Homo; Maddux et al.,
820	2015). The Acheulean sites of Nadung'a 1, 2 and 3 (NAD1, 2, 3; Table 5; Fig. 8) were excavated
821	just below the pumices of the Silbo Tuff at 0.75 Ma and Nadung'a 4 (NAD4; Fig. 7) lies just
822	above the tuff (Delagnes et al., 2006; Maddux et al., 2015). As the Silbo Tuff is not a continuous
823	bed, it is very difficult to find pumice clasts at Nadung'a; they were found in situ at NAD2
824	(Brown, unpublished data, and fieldwork done by the WTAP in 2022).

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826 6. Discussion

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6.1. A complex hominin habitat in the western region of the Turkana Basin, with interaction
between hydroclimate, hydroconnectivity and ambient aridity

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Most of the known hominin genera (*Australopithecus, Kenyanthropus, Paranthropus, Homo*) appear approximately between 4.3 and 1.7 Ma in eastern Africa, notably in the western region of the Turkana Basin (Walker et al., 1986; Leakey and Walker, 1988; Walker and Leakey 1988, 1993; Leakey et al., 1995, 1998, 2001; Ward et al., 1999, 2001, 2013, 2014, 2020; Brown et al., 2001; Prat et al., 2003, 2005; Wood and Leakey, 2011; Maddux et al., 2015; Skinner et

836 al., 2020; Table 4; Fig. 7). Explanations of these speciation events have focused on adaptations to climatic and environmental changes, with effects on landscape aridification (Wynn, 2004; 837 838 Stewart, 2014; Levin, 2015; Blumenthal et al., 2017; Villaseñor et al., 2020; Quinn and Lepre, 2020, 2021; Lepre and Quinn, 2022). For example, Villaseñor et al. (2020) has suggested that 839 K. Platyops exploited resources from both C_3 and C_4 environments and was no longer a 840 primarily C₃ or dense forest/shrubland inhabitant. Stewart (2014) has suggested that climate 841 variability is associated with early Homo and perhaps P. boisei broadening their diet to familiar 842 843 but less preferred foods: vertebrates and invertebrates. These foods consistently provided early 844 Homo with essential nutrients, which reduced selection pressures and allowed for increases in 845 brain size (Stewart, 2014). This author suggested that in response to environmental fluctuations 846 hominins adopted ecological and dietary patterns based on predictable terrestrial and C_4/C_3 847 wetland resources. Broadly, the availability of water in arid regions of eastern Africa is a major 848 limiting factor for vegetation growth and the development of terrestrial ecosystems in which 849 hominins lived. The landscape of the Turkana Basin is currently arid due to the presence of 850 topographic barriers that block atmospheric moisture. However, during the Plio-Pleistocene, 851 former rivers and lakes that connected and disconnected in the Kenyan and Ethiopian Highlands 852 created a mosaic of habitats with sufficient resources to sustain hominins. When connected, these hydrosystems modified the landscapes in certain regions of the Turkana Basin and altered 853 the balance between water influx and evaporation. The paleohydrology of the Turkana Basin 854 855 and the colonization of the different regions of the basin by freshwater fauna thus resulted from a complex interplay of cascading hydroconnectivity that formed and disappeared from the 856 Kenyan and Ethiopian Highlands and surrounding regions, except near the Omo River delta 857 858 where freshwater conditions are more permanent.

In addition to the climate decoupling and hydroconnectivity, inflows to the Turkana Basin and the outflow to the Indian Ocean and later to the Mediterranean Sea appear to have

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861 been reorganized by volcano-tectonic activity and the deposition of various major basalts throughout the basin between 4.2 and 1.3 Ma (Table 1; Fig. 7). The closure of the Turkana 862 paleoriver, among others, has increased the water retention capacity of the Turkana Basin after 863 2.0 Ma, while the redirection of the Suguta paleoriver into Lake Logipi-Suguta drastically 864 reduced the excess water input from the Kenyan Highlands to the basin after 1.4 Ma. The period 865 between 2.0 and 1.4 Ma was thus favorable to large, deep lake formation, while the period after 866 1.4 Ma was not (Fig. 7). These paleohydrographic and paleogeographic changes should be taken 867 into consideration in paleoclimate and paleoenvironmental reconstructions for the Turkana 868 869 Basin, as they certainly amplified or reduced water and freshwater food availability in the 870 different regions around the basin. Thus, the influence of climate on the hominin environment, drinking water and food resources, in the western region of the Turkana Basin and the other 871 872 regions, is a complex issue and cannot be isolated from the specifics of each region (e.g., 873 evolution of the Omo River delta in the northern region; volcanic closure of the Suguta and 874 Turkana paleorivers in the south and southeastern regions; relocation of the basin outlet 300 km 875 to the north; evolution of the Il Bakate River in the northeastern region; etc.).

In terms of climate and vegetation, published δ^{13} C values from soil carbonate nodules 876 877 sampled in the East African Rift system have been interpreted as a long-term C4 vegetation trend in different publications (Wynn, 2000, 2004; Cerling et al., 2003, 2011; Levin et al., 878 2011,; Quinn et al., 2013; Quinn and Lepre, 2021; Fig. 8). However, recent studies (Polissar et 879 al., 2019; Faith et al., 2019) have proposed that the long-term C₄ vegetation trend was likely 880 responding to changing atmospheric CO^2 rather than aridity. Compared to $\delta^{13}C_{soil carbonate}$ values, 881 δ^{18} O_{soil carbonate} values reflect local rainfall source and amount, evaporation and temperature 882 (Lepre and Quinn, 2022). The δ^{18} O_{soil carbonate} values from the Turkana Basin (Fig. 8) suggest 883 that evaporation and temperature (or the amount of water available for evaporation, see Fig. 8) 884 increased after 2.1 Ma (Lepre and Quinn, 2022). Our synthesis on the western region of the 885

886 Turkana Basin suggests that hydrological conditions have developed repeatedly from 4.20 to 887 2.22 Ma, then more permanently from 2.10 to 1.30 Ma and more intermittently from 1.27 to 888 0.70 Ma (Fig. 7). New freshwater vertebrates and invertebrates (e.g., Euthecodon and Potadoma) arrived in the western region of the Turkana Basin when new hydrographic 889 890 connections were made to the basin. Various biota, including ostracods and diatoms, among others, indicate the presence of freshwater conditions for the Late Pliocene, although ecological 891 tolerance of Plio-Pleistocene diatoms and ostracods is still not well known and requires further 892 893 study. The freshwater micro- and macrofauna suggest that paleolake Lonyumun was fresh and 894 connected to the Indian Ocean, as perhaps were paleolakes Lokochot and Waru. It seems that 895 paleolake Lorenyang expanded after the eruption of the Lenderit basalt, which closed the 896 outflow of the Omo River and Turkana Basin to the Indian Ocean after 2 Ma (Fig. 7). In the 897 western region of the Turkana Basin, the freshwater stingray D. africana is present between 898 1.90 and 1.38 Ma, but in the Koobi Fora and Shungura Formations D. africana is known to 899 occur at around 2 Ma and persisted until its extinction around 1.3 Ma (Feibel et al., 1993; 900 Joordens et al., 2013). With the volcanic closure of the Turkana paleoriver, stingrays could no 901 longer migrate to the Indian Ocean, and it appears that D. africana became endemic to the 902 Turkana Basin. It is possible that the Omo River delta offered more perennial freshwater 903 conditions and a refugium, even when conditions were alkaline-saline in the rest of the Turkana Basin. Paleolake Lorenyang potentially overspilled to the Nile outlet at 1.8-1.7 Ma, as 904 suggested by the presence of Euthecodon and freshwater mollusks (Fig. 7). In the western 905 region of the Turkana Basin, paleolake Lorenyang appears to have experienced fluctuating 906 paleolimnological conditions from 1.9 to 1.3 Ma, resulting in the enrichment of sediments by 907 908 various aquatic fossils, including stromatolites (Table 3; Fig. 7). After 1.4 Ma and the formation of the Barrier volcanoes, the southern drainage basin partially closed and it appears that the 909 910 Turkana Basin became more unstable with alternating freshwater to saline-alkaline conditions,

as suggested by the extinction of *D. africana* and by the alternation of mollusks, ostracods and

stomatolite beds between 1.27 and 0.70 Ma (Fig. 7).

913 With regard to the hominin environment, most A. anamensis remains were deposited in lakeshore and nearshore river environments between 4.20 and 4.11 Ma, when drinking water 914 915 and freshwater foods were available in the western region of the Turkana Basin due to enhanced hydroconnectivity (Figs. 7 and 8), but no hominin remains have been found in the freshwater 916 environment at 3.99–3.98 Ma (Fig. 8). The majority of K. platyops and Pliocene hominin 917 remains occur when drinking water and freshwater foods were available at both \sim 3.50 Ma and 918 919 3.30–3.2 Ma (Table 4; Figs. 7 and 8). Moreover, the lithic artifacts excavated at LOM3 occur 920 when drinking water and freshwater foods were available at 3.30 Ma (Fig. 8), but no lithic 921 artifacts have been unearthed in the freshwater environments at <3.60-3.44 Ma. Most P. 922 aethiopicus, P. boisei and Homo sp. have also been found when drinking water and freshwater 923 foods were available at 2.53, 2.33 and 2.25 Ma (Fig. 8). However, no lithic artifacts have been 924 found at 2.53 Ma. The Oldowan complexes of Lokalalei (LA1A and LA2C; 2.34–2.25 Ma) and 925 Nasura (NAS 2, 1, and 3; 2.33, 2.27 and 2.25 Ma, respectively) occur when drinking water and freshwater foods were available at 2.34-2.32 Ma and 2.25 Ma. NAS 3, dated at 2.25 Ma, 926 927 appears to be positioned on the last beach with freshwater mollusks associated with a lake level whose outlet was still connected to the Indian Ocean (Boës et al., 2019a). At 2.19 Ma, the 928 archaeological site of NAS 4 does not seem to be in an environment where freshwater was 929 abundant (Fig. 8). Thereafter, there are no archaeological and hominin sites up to 1.8 Ma found 930 931 to date; all the sites belonging to the archaeological complex of Kokiselei lie above a major paleo-beach complex dating from around 1.8 Ma (Lepre et al., 2011; Duke et al., 2021). 932 933 Remains of H. ergaster/erectus and P. boisei and Oldowan and Acheulean sites occur when drinking water and freshwater foods were available between 1.8 and 1.7 Ma, with freshwater 934 935 conditions that seem to have begun to alternate with saline–alkaline conditions as suggested by

936 the formation of stromatolite beds (Table 3; Figs. 7 and 8). The in situ skeleton of H. ergaster/erectus (KNM-WT 15000) excavated in sediments dated at 1.47 Ma occurs within the 937 938 same stratigraphic context as the remains of the freshwater gastropod *Pila* (Table 3; Figs 6 and 7). The Acheulean complex of Nadung'a is closely associated with environments where 939 940 drinking water and freshwater foods are available sporadically, mostly with beach and sand 941 dune deposits with fossilized calcified roots, except for NAD4, which is embedded in a paleosol at the top of a paleo-beach complex (Delagnes et al., 2006). African Middle Pleistocene Homo 942 943 is present at the level of the Silbo Tuff, within the spatiotemporal context of the Nadung'a 944 archeological complex (KNM-WT 51261; Table 5; Fig. 8).

945 Our synthesis suggests that hominins were mainly present in the western region of the Turkana Basin when drinking water and freshwater foods were available, despite the ambient 946 aridity. However, as discussed below, several caveats complicate the assessment of an 947 948 association between drinking water, freshwater foods and hominin occupation, and in 949 particular, the existence of a preference for freshwater foods in the hominin diet and various 950 adaptations to a decoupled landscape, i.e., occupation of the western region of the Turkana 951 Basin by hominins when freshwater macrofauna that could supply their needs colonized this 952 arid zone during episodes of enhanced hydroconnectivity.

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954 6.2. *Caveats and limitations*

More quantitative explorations fall beyond the scope of this review paper. Rather, we focus on building the framework to develop future quantitative explorations and on caveats to consider upon undertaking such endeavors. A first caveat relates to how hominin and archeological sites are preserved. Does the recovery of hominin fossils from certain sediments imply hominins occupied the associated depositional environment? First, we need to consider that the location of freshly exposed fossils may be different from the area of primary occupation.

961 Postmortem transport may have occurred, and chances of preservation mainly exist in depositional centers, where the natural burial of remains occurs. Therefore, archeological, 962 paleontological and paleoanthropological sites may be mainly found near aquatic environments 963 because water effectively transports sediments (and biotic remains) toward areas of deposition. 964 Whereas the Turkana Basin arguably represents a Plio-Pleistocene depocenter within 965 the East African Rift system, our synthesis indicates that the conditions of burial and 966 preservation of fossil remains were not uniform throughout the period considered in the western 967 region of the Turkana Basin. Two important factors toward preservation potential are 968 969 physicochemical conditions at the depocenter and sedimentation rates, which affect the chance 970 of preservation over time and the rate of burial, respectively. Biomineralized remains preserve better under neutral/alkaline conditions (less chance for demineralization) and in calmer 971 972 depositional environments (less chance for fragmentation/abrasion; Kendall et al., 2018). In 973 addition, environments where bone and water interactions remain static preserve bones better 974 than do environments where cyclic wetting and drying occurs; increased temperatures also negatively affect collagen survival (Kendall et al., 2018). Therefore, we would expect a 975 976 somewhat higher degree of bone preservation potential in alkaline than freshwater 977 environments and in low energy depositional environments. Substantial variation in rates of 978 deposition between 4.20 and 0.70 Ma primarily relates to hydroconnectivity and sediment influx into an open or closed basin. Interestingly, many hominin remains and archeological sites 979 were found between 1.8 and 1.4 Ma (e.g., the archeological complex of Kokiselei; Figs. 7 and 980 981 8), when sedimentation rates were very high (55 cm/kyr; Fig. 9). However, during the formation of the archeological complex of Nadung'a, between 0.8 and 0.7 Ma, the sedimentation rate was 982 983 much lower (15 cm/kyr). Sedimentation rates were also lower between 2.4 and 2.2 Ma (10 cm/kyr), when the sites of the archeological complex of Nasura were buried. Therefore, it 984 985 appears that as long as deposition occurred through time, there was a potential to preserve

hominin remains and archeological sites, as well as freshwater vertebrates, invertebrates, and
microalgae, although the formation and preservation of archeological sites may follow different
depositional processes from those of fossil remains (see Fig. 9).

Another aspect to consider when examining association patterns is geochronology and 989 dating uncertainty. First, if the confidence intervals for dates are large, existing associations 990 may be blurred by noise derived from dating uncertainty. Second, age determinations of 991 hominin fossils and archeological sites, as well as vertebrates, invertebrates, and microalgae, 992 993 can be problematic when volcanic ash beds are too widely spaced. However, we consider the 994 effect of geochronological constraints on our observations to be minimal for two reasons: 995 firstly, because the presence of various tuff layers in the Turkana Basin, and the western region of the Turkana Basin in particular, provide unique opportunities to build a robust geochronology 996 997 from 4.20 to 0.70 Ma and, secondly, geochronological uncertainty would obfuscate existing 998 associations rather than create false associations (dating uncertainties <50 kyr; Fig. 6). That 999 being said, there are two periods in the western region of the Turkana Basin, from 3.1 to 2.6 1000 Ma and from 1.2 to 0.8 Ma, where fewer tuffs occur in the sedimentary series (Figs. 7–9). As mentioned in the introduction, the chronostratigraphic interval between 3.1 and 2.6 Ma is not 1001 1002 well dated (and is represented by few outcrops) in the western region of the Turkana Basin and was thus not evaluated in this synthesis. Furthermore, no hominin and archeological sites have 1003 yet been discovered between 3.1 and 2.6 Ma. By contrast, there are a substantial number of 1004 correlated outcrops to consider in the period between 1.2 and 0.8 Ma, as geological work has 1005 been carried out on hominin and archeological sites found in this chronostratigraphic interval 1006 (Delagnes et al., 2006; Maddux et al., 2015, and Brown, unpublished data). 1007

Despite the abovementioned considerations and caveats, the presence of different types of fossils (microbial structures, diatom silica, bones, shell carbonate) throughout the Plio– Pleistocene suggests that the conditions were quite favorable for their preservation. In the

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1011 context of the quasi-continuous potential for fossil preservation, we consider our qualitative 1012 observation of a possible association between hominin and archeological sites and the 1013 development of drinking water and freshwater food resources for mammals, including hominins 1014 across the western region of the Turkana Basin, as noteworthy.

Considering our synthesis, we are tempted to provide a possible paleobiological 1015 explanation, namely, that most hominin and archeological sites occur when drinking water 1016 expanded into the arid zone and freshwater macrofauna colonized the region. The recurring 1017 presence of freshwater micro- and macrofauna in the western region of the Turkana Basin 1018 necessarily modified the food chain and the terrestrial environment in which hominins lived. 1019 1020 The presence of rivers and a large lake with an outflow has affected this arid landscape, enabling colonization by new species adapted to freshwater and providing additional natural resources 1021 (water, plants, fauna) that resulted in iterative occupation of the western region of the Turkana 1022 1023 Basin by various hominins. We highlight periods when freshwater was available, as well as 1024 freshwater resources, indicated by the presence of river and lake deposits with freshwater 1025 micro-and macrofauna they contain, during the following periods: 4.20–3.98 Ma, 3.70–3.10 Ma, 2.53–2.22 Ma, 2.10–1.30 Ma, then more intermittently after 1.27 Ma, as indicated by the 1026 1027 presence of stromatolite beds, which increase in number between 1.27 and 0.75 Ma (Figs. 7 and 8). Enhanced hydrological activity into the arid zone of the western region of the Turkana Basin 1028 may have promoted 1) the growth of C₄ grasses and sedges, which are found on lake margins, 1029 deltas, marshes, or floodplain, 2) the dispersal of freshwater foods and 3) the increased 1030 accessibility of drinking water and food resources for mammals, including hominins. Thus, in 1031 association with the arid environment, these hydrological conditions may have played a role in 1032 1033 driving hominin dietary and behavioral changes, as well as techno-cultural developments in this region, as already suggested in the western region of the Turkana Basin by Stewart (2014) and 1034 in the eastern region of the basin as well (Braun et al., 2010b; Archer et al., 2014). 1035

1036 We do not have yet in-depth studies regarding the consumption of freshwater animals in the western region of the Turkana Basin. However, with regard to the abundance of drinking 1037 water, the regional isotopic studies from Lomekwi suggest that K. platyops shifted from 1038 acquiring liquids directly from food toward drinking more water at 3.30 Ma (Quinn et al., 2021); 1039 this could be a reflection of enhanced hydroconnectivity in this region associated with the 1040 colonization of freshwater biota, which could have supplied the food needs of hominins in the 1041 arid zone. In addition, isotopic study at Lokalalei 1A and 2C indicates that 1042 woodland/bushland/shrubland was the dominant vegetation structural category. Notably, the 1043 wooded grassland category was also present in abundance. Riparian woodlands near a large, 1044 1045 perennial river system may have provided shade, protection, floral food resources and drinkable water to hominins at 2.34–2.32 Ma (Quinn et al., 2013). At Kokiselei 1–6, isotopic study 1046 suggests the presence of wooded grasslands near a lake margin (Quinn et al., 2013), which may 1047 1048 have favored hominin resource use and tool-making behavior between 1.8 and 1.6 Ma. 1049 According to these authors, it is possible that Kenyanthropus, Paranthropus and/or Homo used 1050 tools for the extraction of freshwater invertebrate fauna and the processing of vertebrate carcasses. However, to date, no taphonomic studies have found percussion or extraction marks 1051 1052 on invertebrate remains in the western region of the Turkana Basin.

Along the eastern region of the basin, the consumption of aquatic foods has been argued 1053 at Koobi Fora, for the archeological site of FwJj 20 at 1.95 Ma, based on taphonomic evidence 1054 and the association of aquatic fauna with lithic assemblages (Braun et al., 2010b; Archer et al., 1055 2014). These authors suggest that hominins predating Homo ergaster/erectus may have 1056 incorporated aquatic resources such as crocodiles and catfish into their diet, and that these 1057 1058 aquatic foods may have had a beneficial effect on brain development and function. Broadly, several authors have suggested a potential link between the exploitation of aquatic resources 1059 (vertebrates and invertebrates) and the evolution of hominin brain size and cognition 1060

1061 (Wrangham et al., 2009; Archer et al., 2014; Joordens et al., 2014; Russon et al., 2014;
1062 Hohmann et al., 2019; de Chevalier et al., 2022). In this context, our synthesis suggests that
1063 diachronic variation in hydroconnectivity in the western region of the Turkana Basin explains
1064 the occurrence of drinking water and freshwater macrofauna that could have supplied the food
1065 needs of hominins despite the ambient aridity.

1066

1067 7. Conclusions

In summary, our synthesis shows that there is a complex interaction between 1068 topographic barriers along the Turkana Basin and changes in hydroconnectivity that result over 1069 1070 time in changes to how drinking water has been provided from the Ethiopian and Kenyan Highlands to the arid Turkana Basin. The development of enhanced hydroconnectivity with 1071 upland rivers and lakes, as well as the temporary establishment of outflows toward other 1072 1073 drainages, promoted the colonization of the western region of the Turkana Basin by freshwater 1074 macrofauna, such as crocodiles, fish and mollusks. In the northern basin, freshwater conditions 1075 are more persistent due to the presence of the Omo River delta, but in the rest of the basin, conditions have at times been alkaline and saline, except when the lake had an outlet. The 1076 paleogeography of basin outlets has been modified after 2 Ma by the volcanic closure of the 1077 Turkana paleoriver that connected the southern region of the Turkana Basin to the Indian Ocean 1078 (Bruhn et al., 2011; Boës et al., 2019), and by the opening of a new outlet connected to the Nile, 1079 possibly from 1.9 Ma, as well as the obstruction of the Suguta paleoriver after 1.4 Ma. These 1080 aspects are fundamental to understanding how freshwater conditions interacted with ambient 1081 aridity in the Turkana Basin in relation to hominin occupation and faunal succession within a 1082 1083 constrained chronological framework. As such, periods of enhanced hydroconnectivity with freshwater foods available to hominins may be assessed by the presence of macrofauna, such 1084

as freshwater mollusks, fish and crocodiles (the freshwater crocodile *Euthecodon*, with its
elongated jaw, fed exclusively on fish and could not be a predator for hominins).

Our synthesis of these data in the western region of the Turkana Basin suggests that 1087 river-induced hydrological changes and high-amplitude paleolake-level fluctuations may be 1088 explained without 'extreme and abrupt climate pulses', but rather through the interactions of 1089 various regional factors. These include a dormant cascading river-lake system and the 1090 reorganization of the hydrographic network and outflows by volcanism. Secondly, our synthesis 1091 suggests that hominin and archeological sites exist in the western region of the Turkana Basin 1092 1093 within this context of hydrological variability. In light of these insights, we consider that there 1094 may be a direct causality between the variation and availability of drinking water and freshwater foods and hominin occurrences through the increased total biomass productivity in freshwater 1095 environments compared to periods of water stress in an arid environment with high evaporation 1096 1097 rates. However, several caveats are to be considered because the effective use of these data is 1098 precluded by limitations of pattern-matching strategies to infer causal relationships between 1099 ecological and evolutionary change (see e.g., Faith et al., 2021).

The consumption of C_4 and aquatic resources by homining has been hypothesized in the 1100 1101 western (Stewart, 2014) and eastern (Braun et al., 2010b; Archer et al., 2014) regions of the Turkana Basin and a search for more direct evidence of interactions among hominins and 1102 aquatic organisms may be warranted in the western region of the Turkana Basin. To what extent 1103 such interactions affected the anatomical, cognitive and behavioral evolution of hominins in the 1104 Turkana Basin remains an important question. Beyond a search for direct interactions, an 1105 association between freshwater availability and hominin occupation in the western region of 1106 1107 the Turkana Basin requires in-depth quantitative comparisons, which should focus on compiling independent datasets on fossil occurrences of freshwater biota and hominins for 1108 subsequent correlative analyses. Such analyses could be undertaken at the scale of the western 1109

region of the Turkana Basin or of the Turkana Basin, but taking into account the mosaic of landscapes and numerous paleohydrographic and paleogeographic parameters which interfere with paleoclimatic interpretations of proxies. This new framework offers exciting prospects to the study of the interrelationship between multifactorial paleoenvironmental changes and the anatomical and cognitive evolution of hominins in the Turkana Basin.

1115

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1813

1814 **Figure legends**

1815

Figure 1. a) Digital elevation model of eastern Africa. b) Map of the present-day Lake Turkana 1816 watershed (dotted line), with the main Omo River watershed in the North and the Kerio and 1817 Turkwel River watersheds in the South. c) Digital elevation model of the entire Turkana Basin 1818 and Lake Turkana with the limit of the East African Rift and the extensional rift basin (white 1819 dotted line. Sources: Shuttle Radar Topography Mission (SRTM-90 m) and bathymetric map 1820 1821 from Garcin et al. (2012). Locations: A=Gombe Group basalts; B=Loiyangalani sill (former outlet channel to the Indian Ocean); C=Kulal Volcano and Lenderit basalts; D=Chalbi Basin; 1822 E=Tirr Tirr; F=the Barrier and Suguta; G=Lothagam and Kerio; H=Nasechebun and Kataboi; 1823 I=Ilemi sill (former outlet channel to the White Nile River); J=Lapur Range; K=Chew Bahir; 1824 L=Abaya-Chamo lakes; M=Awash River Basin; N=Baringo-Bogoria Basin; O=Tugen Hills; 1825 P=Elgevo Escarpment and Kerio Basin. Plio-Pleistocene Formations affiliated with the Omo 1826 1827 Group: 1=Nachukui; 2=Shungura; 3=Koobi Fora and Allia Bay region; 4=Kanapoi; 5=Kibish; 1828 6=Usno; 7=Mursi and Nkalabong; 8=Fejej—other localities affiliated with the Nachukui 1829 Formation: 9=Lothagam, 10=South Turkwel, and 11=Loruth Kaado. The Konso Formation (12) is considered separate from the Turkana Basin. 1830

1831

Figure 2. Schematic map of the Plio–Pleistocene drainage system of the entire Turkana Basin with indication of cascading hydroconnectivity with upland rivers and lakes from the Ethiopian and Kenyan Highlands. See text for explanations. Plio–Pleistocene formations affiliated with the Omo Group: 1=Nachukui (4.2–0.7 Ma; McDougall et al., 2012); 2=Shungura (3.7–1.1 Ma; McDougall et al., 2012); 3=Koobi Fora (4.4–0.70 Ma; McDougall et al., 2012) and Allia Bay region (4.1–3.9 Ma; Wynn, 2000); 4=Kanapoi (4.3–3.9 Ma; McDougall et al., 2012); 5=Kibish

(196–8 ka; McDougall et al., 2012); 6=Usno (3.4–3.1 Ma; Drapeau et al. 2022; Jolly and Bonnefille, 203); 7=Mursi (>4.0 Ma; Drapeau et al. 2022) and Nkalabong (4.0–1.7 Ma; Drapeau et al. 2022); 8=Fejej (4.3–1.8 Ma; Brown and McDougall, 2011)—other localities affiliated with the Nachukui Formation: 9=Lothagam (>3.9 Ma; Feibel, 2003b), 10=South Turkwel (>4.1–3.6 Ma; Ward, 1999), and 11=Loruth Kaado (3.6–3.2 Ma; Harris et al., 1988).
The Konso Formation=12 (1.9–1.4 Ma; Katoh et al., 2000) is considered separate from the Turkana Basin.

1845

Figure 3. Digital terrain model of the Omo-Turkana-Nile region (from the Shuttle Radar 1846 Topography Mission, SRTM-90 m). Paleo-drainage system of the Turkana Basin (see Fig. 4 1847 for the longitudinal profiles of the paleorivers). a and b) Present-day (Holocene) closed drainage 1848 system with no outlet to the ocean, the sea, or other lakes (=endorheic and saline-alkaline 1849 1850 conditions); c and d) Early Pleistocene open drainage system with an outlet channel connected 1851 to the Mediterranean Sea (=freshwater-exorheic conditions); e and f) Late Pliocene open 1852 drainage system with an outlet channel connected to the Indian Ocean (=freshwater-exorheic conditions). 1853

1854

Figure 4. Longitudinal profiles of elevation changes along major rivers and paleorivers of the entire Turkana Basin (from the Shuttle Radar Topography Mission, SRTM-90 m). a) Omo River; b) Kerio River and cascading connections from the Kerio Basin (West of Tugen Hills); c) Suguta paleoriver and cascading connections from the Baringo-Bogoria Basin (east of Tugen Hills); d) II Bakate paleoriver and cascading connections between lakes Chamo, Abaya, and Chew Bahir; e) Turkana paleoriver, i.e., Loiyangalani outlet connected to the Indian Ocean; f)

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the paleo-tributary to the White Nile and the Nile rivers, i.e., Ilemi outlet connected to theMediterranean Sea. (m.a.s.l.).

1863

1864	Figure 5. a) Map showing the maximum extension of Plio–Pleistocene paleolakes (shaded in
1865	blue) when the size of the entire Turkana drainage basin is connected/disconnected (dotted
1866	red/blue lines) from the watersheds of lakes in the Ethiopian and Kenyan branches of the East
1867	African Rift (Abaya, Chamo, and Chew Bahir/Elmenteita, Nakuru, Borgoria, Baringo, and
1868	Logipi-Suguta). Arrows show major inflows. b) Location of the volcanic eruptions of Gombe
1869	$(4.22 \pm 0.09 - 3.95 \pm 0.10 \text{ Ma}; \text{Haileab et al., 2004}; \text{Erbello and Kidane, 2018})$ and Kulal (3.01
1870	\pm 0.55–1.91 \pm 0.21 Ma; Rundle, 1985; Dunkley et al., 1993; Gathogo et al., 2008;) near the
1871	Loiyangalani outlet, connected to the Indian Ocean and influencing the evolution of the
1872	drainage basin.

1873

Figure 6. Bayesian Age model of the Nachukui Formation based on argon-argon dating of tuffs
and stratigraphy (after Harris et al., 1988; Brown and McDougall, 2011; McDougall et al.,
2012). Age model and error ranges calculated using Chronomodel v. 2.0 (software developed
by Lanos and Dufresne, 2019).

1878

Figure 7. Compilation of geochronological data from the western region of the Turkana Basin
(Turkana Basin, Kenya). From left to right: Magnetostratigraphy (McDougall et al., 1992;
Lepre et al., 2011; Lepre, 2014; Harmand et al., 2015; Sier et al., 2017); volcano-tectonic
activity in the basin (Baker et al., 1971; Brotzu et al., 1984; Rundle, 1985; Nyamweru, 1986;
Key et al., 1987; Bosworth and Maurin, 1993; Dunkley et al., 1993; Haileab et al., 2004; Furman
et al., 2006; Kaeser, 2006; Gathogo et al., 2008; McDougall et al., 2012); tephrostratigraphy

1885 (Brown and McDougall, 2011; McDougall et al., 2012); geologic members (Harris et al., 1988; Feibel et al., 1989; Feibel, 2003a; McDougall and Brown, 2008; Brown and McDougall, 2011; 1886 McDougall et al., 2012); major Plio-Pleistocene river and lake systems in the entire Turkana 1887 Basin (Harris et al., 1988; Feibel, 2011; Gathogo, 2017; Lepre, 2014; Boës et al., 2019a); 1888 evolution of the aquatic fauna, including freshwater vertebrates, invertebrates and microalgae 1889 (Wood, 1979; Williamson, 1981; Meylan et al., 1990; Feibel, 1993; Harris et al., 1988, 2003; 1890 Stewart, 2001, 2003, 2009; Brugal et al., 2003; Martin and Trautwein, 2003; Storrs, 2003; Van 1891 Bocxlaer et al., 2008; Tiercelin et al., 2010; Van Bocxlaer, 2011, 2020; Joordens et al., 2013; 1892 Gathogo, 2017; Boës et al., 2019a; Brochu, 2020; Stewart and Rufolo, 2020). For the 1893 1894 tephrostratigraphy: U=upper; M=middle; L=lower.

1895

Figure 8. From left to right: Woody canopy cover (%): combined published percentages of 1896 woody canopy cover from the East African Rift (calculated from $\delta^{13}C_{soil carbonate}$ values are 1897 reported relative to Vienna Pee Dee Belemnite and are derived from Cerling et al. (2003), Wynn 1898 (2000, 2004), Levin et al. (2011), Quinn et al. (2013), Levin (2015), and Quinn and Lepre 2021). 1899 Soil carbonate δ^{18} O values from the western region of the Turkana Basin (Lepre and Quinn, 1900 2022). Hydrological changes: major hydrological changes induced by lake and river activity 1901 and freshwater episodes with freshwater vertebrates, invertebrates and microalgae (based on 1902 this synthesis). Lithic industries: archeological sites with lithic industries excavated by the 1903 Mission Préhistorique au Kenya (Kibunjia et al., 1992; Roche et al., 1999, 2003, 2018; Brugal 1904 et al., 2003; Prat et al., 2003, 2005; Delagnes and Roche, 2005; Delagnes et al., 2006; Harmand, 1905 2009; Tiercelin et al., 2010; Harmand et al., 2015; Lewis and Harmand, 2016; Texier, 2018; 1906 Boës et al., 2019a; Arroyo et al., 2020; Duke et al., 2021). Major hominin remains from (black) 1907 work conducted by the Mission Préhistorique au Kenya (Prat et al., 2003, 2005) and from (gray) 1908 major work conducted in the region by other teams (Walker et al., 1986; Walker and Leakey 1909

1910	1988, 1993; Leakey and Walker, 1988; Leakey et al., 1995, 1998, 2001; Ward et al., 1999,
1911	2001, 2013, 2014, 2020; Brown et al., 2001; Wood and Leakey, 2011; Maddux et al., 2015;
1912	Skinner et al., 2020). For the hominins, the color gradient within each box takes into account
1913	the estimated error range of the age estimates for the hominin remains and archeological sites.
1914	Mission Préhistorique au Kenya/WTAP archeological sites: LOM3=Lomekwi 3 (Harmand et
1915	al., 2015); LA1A=Lokalalei 1A and LA2C=Lokalalei 2C (Roche et al., 1999; Delagnes et al.,
1916	2005; Harmand, 2009; Tiercelin et al., 2010); NAS1, 2, 3, 4=Nasura 1, 2, 3, 4 (Boës et al.,
1917	2019a); KS1, 2, 3, 5, 6=Kokiselei 1, 2, 3, 5, 6 (Brugal et al., 2003; Roche et al., 2003;
1918	KS4=Kokiselei 4 (Lepre et al., 2011; Texier, 2018); NY1, 2=Naiyena Engol 1, 2 (Brugal et al.,
1919	2003; Prat et al., 2003; Roche et al., 2003, 2018); NAD4=Nadung'a 4 (Delagnes et al., 2006).

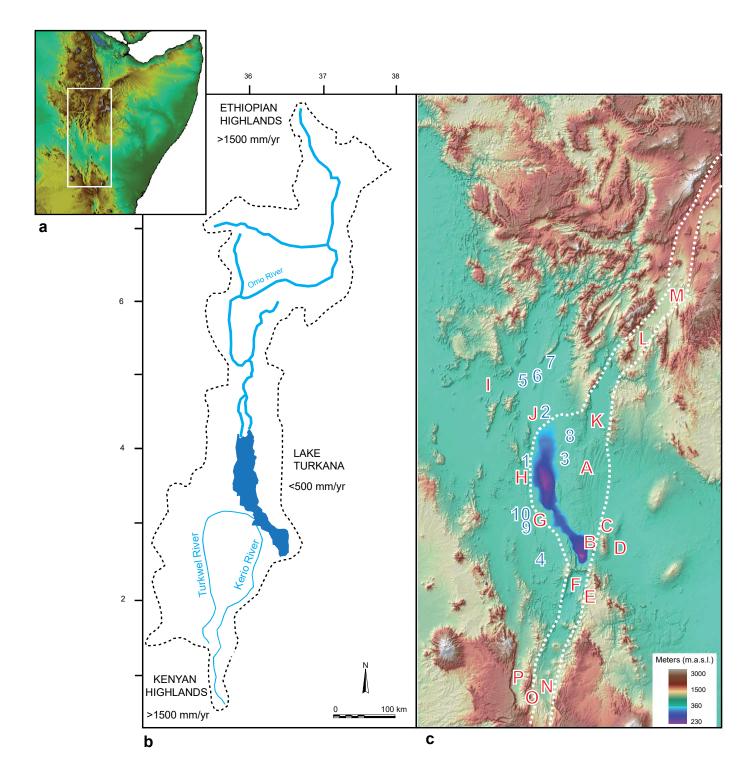
1920

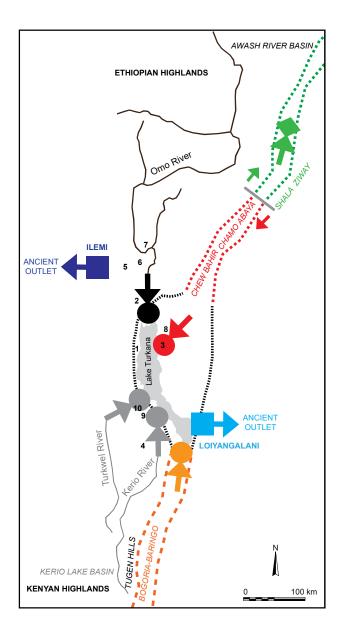
1921 Figure 9. Long-term variation in sedimentation rates in the western region of the Turkana Basin 1922 (Nachukui Formation) and its influence on archeological site formation and preservation. 1923 Archaeological and hominin sites are present where the sedimentation rate is high (>40 cm/kyr), as at Kokiselei (KS) and Naiyena Engol (NY), but also where the sedimentation rate is lower 1924 (<20 cm/kyr), as at Nasura (NS) and Lokalalei (LA). These results suggest that, as long as 1925 deposition occurred through time, there was a potential to preserve hominin remains and 1926 archeological sites in the Western region of the Turkana Basin. Sedimentation rates have been 1927 calculated using Chronomodel v. 2.0 (software developed by Lanos and Dufresne, 2019). 1928

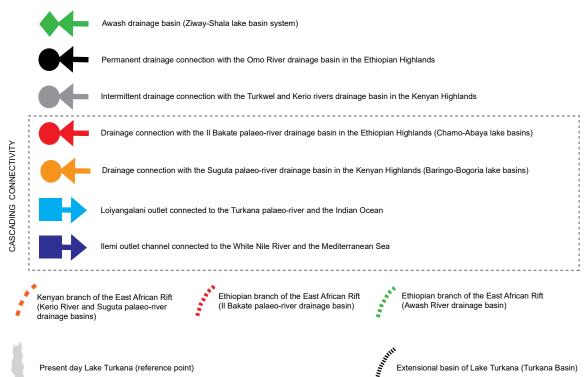
1929

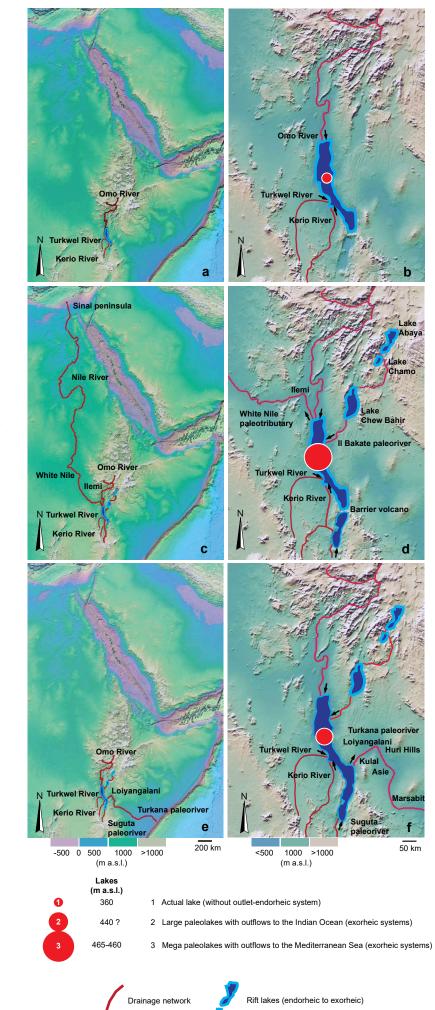
1930

1931





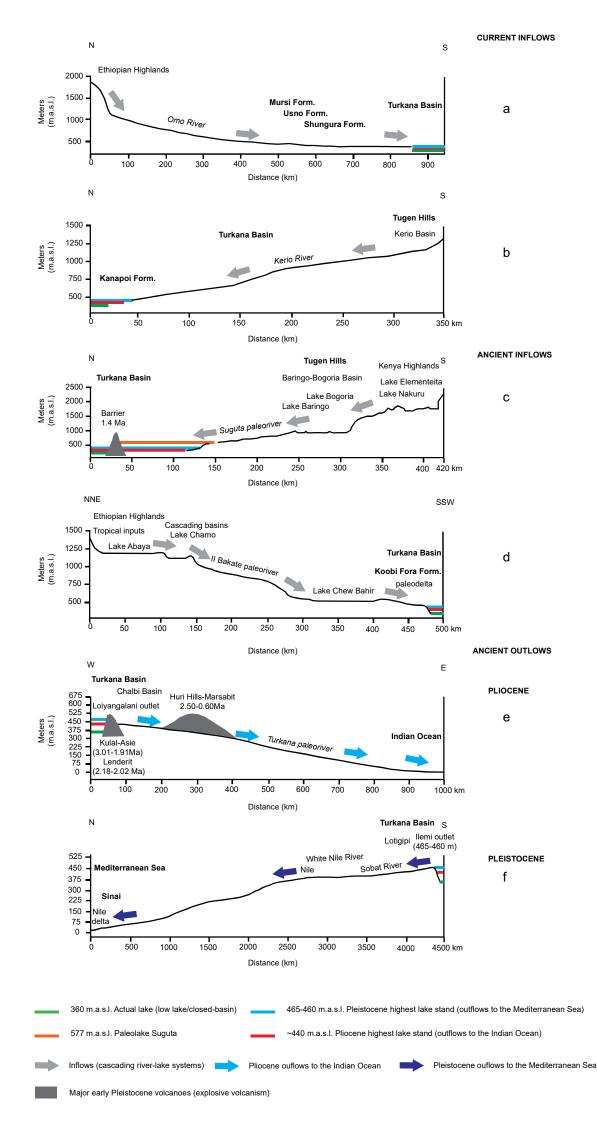


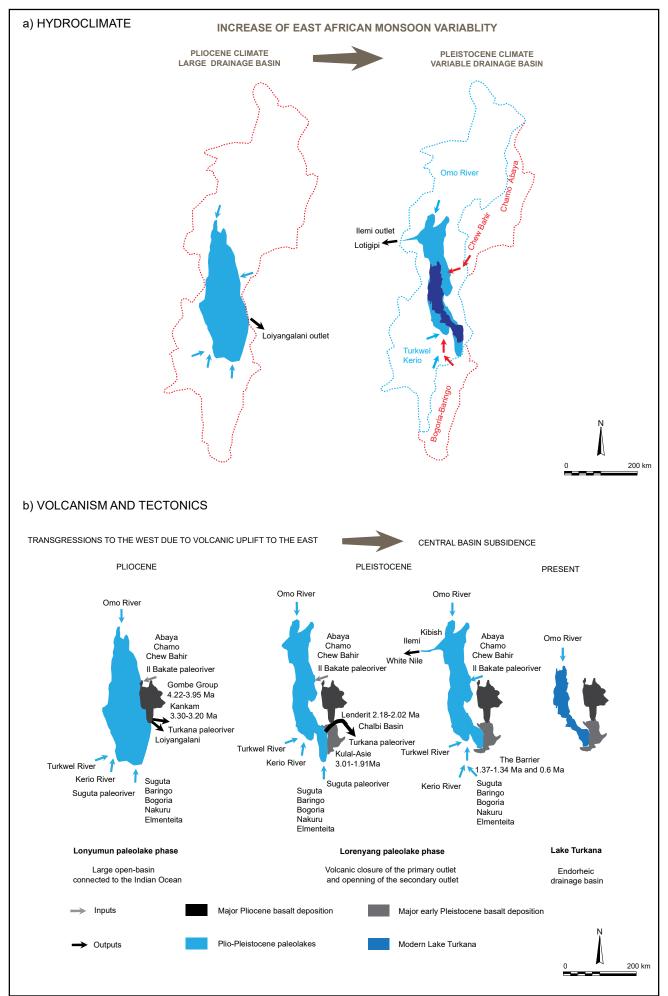


HOLOCENE

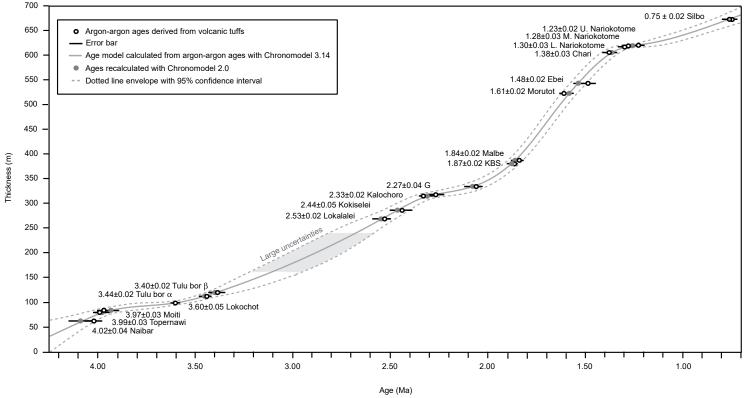
PLEISTOCENE

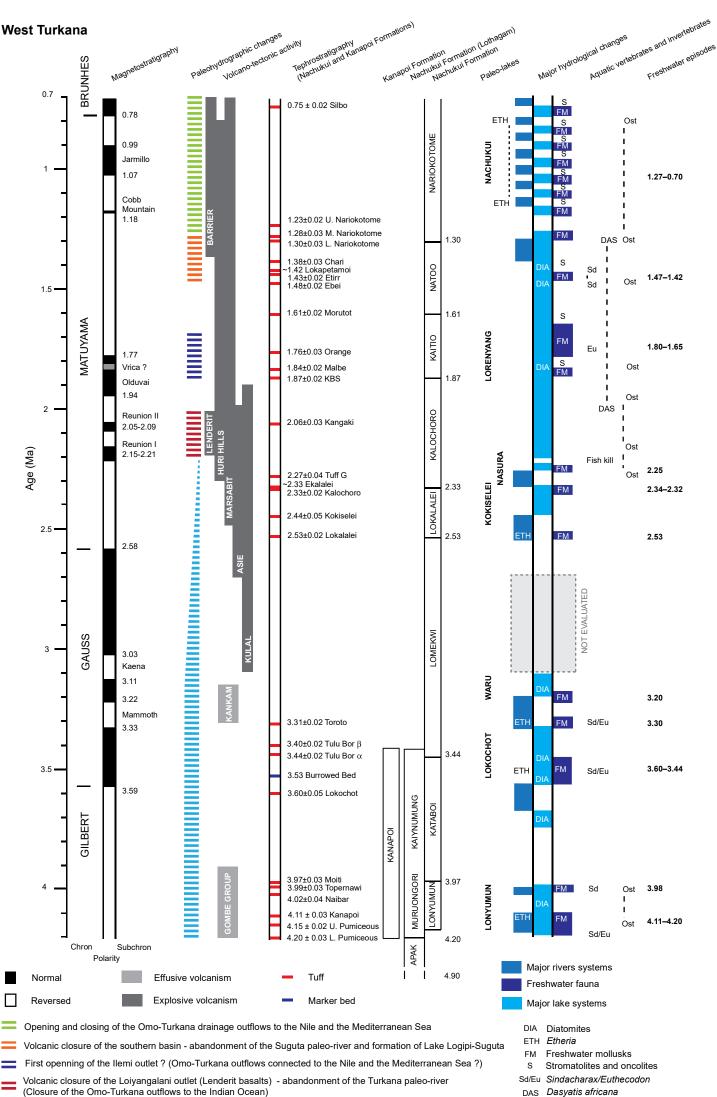
PLIOCENE





EVOLUTION OF THE TURKANA DRAINAGE BASIN

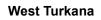


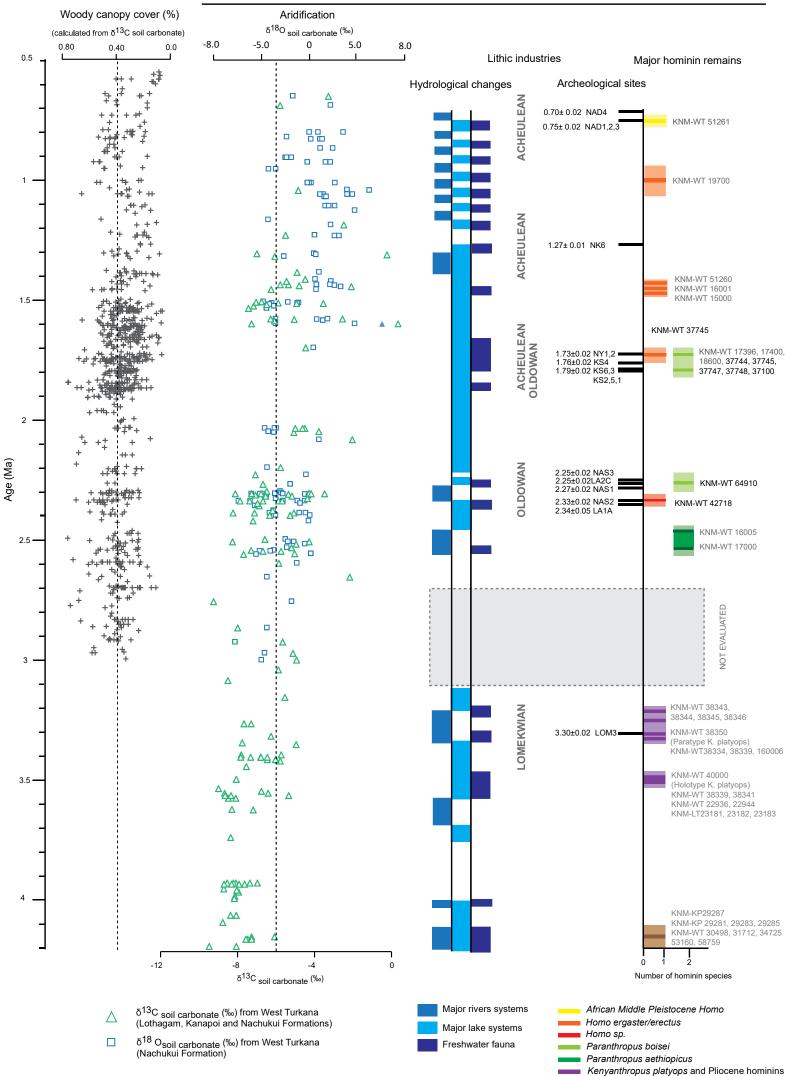


Omo-Turkana drainage outflows connected to the Turkana paleo-river and the Indian Ocean

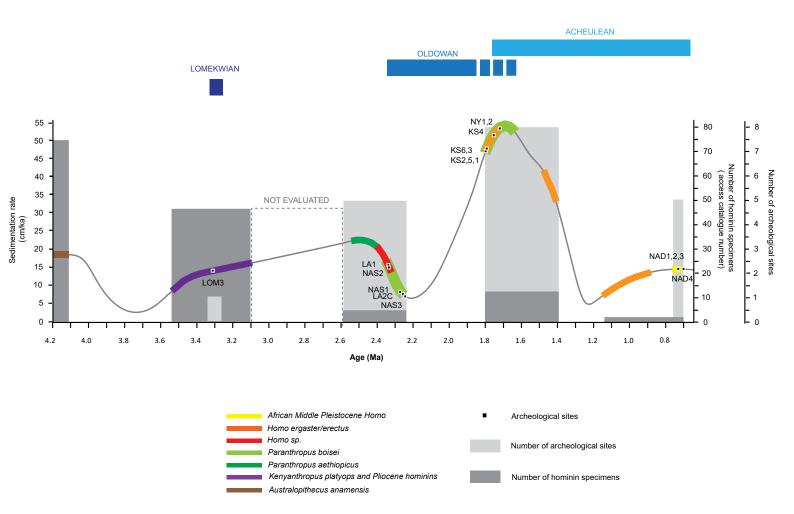
Ost Ostracods

East African Rift





Australopithecus anamensis



Volcanism	Туре	Radiometric dating	
Gombe Group	Effusive	4.22 ± 0.09–3.95 ± 0.10 Ma	
Tirr Tirr	Effusive	3.90 ± 0.4 Ma; 3.60 ± 0.4 Ma	
Lothagam	Effusive	$3.71\pm0.23~\mathrm{Ma}$	
Longipi	Explosive	$3.50 \pm 0.27 1.50 \pm 0.19 \text{ Ma}$	
Kankam	Effusive	3.30–3.20 Ma	
Kulal	Explosive	$3.01 \pm 0.55 2.60 \pm 0.02$ Ma; $2.40 \pm 0.03 2.04 \pm 0.02$ Ma; 1.91 ± 0.21 Ma	
Asie	Explosive	$2.70 \pm 0.35 2.07 \pm 0.13 \text{ Ma}$	
Marsabit	Explosive	$2.50 \pm 0.3 0.60 \pm 0.2 \text{ Ma}$	
Huri Hills	Effusive	$2.30 \pm 0.17 0.8 \pm 0.3 \text{ Ma}$	
Lenderit	Effusive	2.18 ± 0.02 Ma; 2.02 ± 0.02 Ma	
Balo	Effusive	$1.79\pm0.02~\mathrm{Ma}$	
The Barrier	Explosive	$1.37 \pm 0.02 - 1.34 \pm 0.01$ Ma (Likayu East); 0.69 ± 0.05 Ma (Likayu West)	

Geochronology of	volcano-tectonic activity in th	ne Turkana Basin during the Plio-Pleistocene.

References

Haileab et al., 2004 Baker et al., 1971; Bosworth and Maurin, 1993 Baker et al., 1971 Furman et al., 2006 Gathogo et al., 2008 Rundle, 1985; Gathogo et al., 2008; Dunkley et al., 1993 Key et al., 1987 Nyamweru, 1986; Brotzu et al., 1984; Kaeser, 2006 Brotzu et al., 1984 Gathogo et al., 2008 Gathogo et al., 2008 Dunkley et al., 1993; McDougall et al., 2012

Geochronology of the Kanapoi Formation (Feibel, 2003a; Leakey et al., 1995; McDougall et al., 2012) and the Nachukui Formation (Harris et al., 1988; McDougall et al., 2012) in West Turkana.

Kanapoi Formation (southwestern basin)	4.2–3.4 Ma		
Members of the Nachukui Formation (western basin)			
Apak*	4.9–4.2 Ma		
Muruongori*	4.2–3.9 Ma		
Kaiyumung*	3.9–3.4 Ma		
Lonyumun	<4.2–3.97 ± 0.03 Ma		
Kataboi	$3.97 \pm 0.03 3.44 \pm 0.02 \ \text{Ma}$		
Lomekwi	3.44 ± 0.02 – 2.53 ± 0.02 Ma		
Lokalalei	$2.53 \pm 0.02 2.33 \pm 0.02 \text{ Ma}$		
Kalochoro	$2.33 \pm 0.02 1.87 \pm 0.02 \ \text{Ma}$		
Kaitio	$1.87 \pm 0.02 1.61 \pm 0.02 \ \text{Ma}$		
Natoo	$1.61 \pm 0.02 - 1.30 \pm 0.03$ Ma		
Nariokotome	$1.30 \pm 0.03 0.70 \pm 0.02 \text{ Ma}$		
Loruth Kaado	3.9–3.3 Ma		
South Turkwel	4.1–3.3 Ma		

Members found only at Lothagam (McDougall and Feibel, 2003; Schofield et al., 2021)

Notably, Loruth Kaado (northwestern basin) is attached to the Lomekwi Member

and South Turkwel (south of Nachukui and northwest of Lothagam) to the Lonyumun, Kataboi, and lower Lomekwi Members (Harris et al., 1988; Ward et al., 1999)

Age (Ma)	Environment
4.20-4.15	River deposits; Lothagam
4.15-4.11	Lakeshore environment and nearshore river deposits; Kanapoi Fm

4 20 2 00	Laka andimonta Lammun Mh
4.20-3.98	Lake sediments; Lonyumun Mb
4.17-4.12	River sediments; Lower fluvial sequence; Lothagam
4.15-4.11	Lake sediments; Kanapoi Fm
4.11	River deposits, Kanapoi Fm
4.10-4.00	Lake sediments; Lonyumun Mb
4.07	River sediments; upper fluvial sequence; Lothagam
3.99–3.98	Lake sediments; Lonyumun Mb
4.02-3.98	Lake sediments; Lonyumun Mb
~3.7	Lake sediments; Kataboi Mb
3.65-3.60	River deposits; Kataboi Mb
3.58-3.44	Lake sediments; Kataboi Mb
3.50	Lake sediments; Kataboi Mb
3.30	Lakeshore environment, beach, sand dune, and river deposits;
	Lomekwi Mb
3.30-3.20	Alluvial deposits; Lomekwi Mb
3.20-3.10	Lake sediments; Lomekwi Mb
2.53	River deposits; Lomekwi/Lokalalei Mb
2.44	Lake sediments; Lokalalei Mb
2.34-2.32	Lakeshore environment and nearshore river deposits; Lokalalei Mb
	and Kalochoro Mb
2.25-2.22	Lake sediments; Kalochoro Mb
2.25	Lakeshore environment and nearshore river deposits; Kalochoro Mb
2.27-2.17	Lake sediments; lower Kalochoro Mb
2.22	Lakeshore environment; Kalochoro Mb
2.10-1.95	Lake sediments; upper Kalochoro Mb
1.85	Lakeshore environment; Kaitio Mb
1.8	Lakeshore environment; Kaitio Mb
1.80-1.70	Lakeshore environment and nearshore river deposits; Kaitio Mb
1.7-1.65	Lakeshore environment; Kaitio Mb
1.6	Lakeshore environment; Natoo Mb
1.48	Lake sediments; Natoo Mb
1.48-1.38	Lake sediments; Natoo Mb
1.47-1.42	Lakeshore environment and nearshore river deposits; Natoo Mb
1.4	Lakeshore environment; Natoo Mb
1.29-0.80	Lakeshore environment; Nariokotome Mb
1.27-0.75	Lakeshore environment and nearshore river deposits; Nariokotome Mb

0.80–0.70 Lakeshore environment, nearshore river deposits and beaches; Nariokotome Mb tes and invertebrates, including freshwater fauna, bet

Aquatic fauna

Potamonautidae, Euthecodon Euthecodon; Pelomedusidae, Testudinidae, and Trionychidae; Sindacharax, Semlikiichthys; Bellamya, Etheria; Sclerocypris Hemicypris

Freshwater mollusks *Etheria* Diatomites

Freshwater mollusks Pure diatomites and mollusks at 3.99–3.98 Ma Diatoms

Pure diatomites; sponge spicules Bellamya, Cleopatra, and Melanoides Etheria; Euthecodon; Sindacharax; turtles; mollusks

Mollusks, Lockeia, sponge spicules and diatoms Etheria

Melanoides

Melanoides and Potadoma Ostracods Fish kill Ostracods Mollusks overlain by ostracods and diatomites Stromatolites Iridina, Chambardia; Euthecodon; Polypterus Celopatra and Melanoides Stromatolites Ostracods Diatoms Pila; Sindacharax Stromatolites Ostracods Cleopatra and Melanoides at 1.27 Ma;ostracods and mollusks (Iridina) interfinger with stromatolites in sediments of several river and lake systems between 1.27 and 0.70 Ma Mollusks; small stromatolites (<5 cm) 1 m below the Silbo Tuff

ween 4.20 Ma and 0.70 Ma. See text for explanations.

References Martin and Trautwein, 2003; Storrs, 2003 Peypouquet, 1978; Meylan et al., 1990; Harris et al., 2003; Wood, 2003; Feibel, 2003a; Stewart, 2001, 2003, 2009; Stewart and Rufolo, 2020; Brochu, 2020; Van Bocxlaer, 2020 Harris et al., 1988 Harris et al., 2003; Feibel, 2003b; Stewart 2003 Wynn, 2000; Feibel, 2003a Feibel, 2003a Harris et al., 1988 Harris and Leakey, 2003 this study Harris et al., 1988; this study Ward et al. 1999; this study Gathogo, 2017; this study Harris et al., 1988 this study Harris et al., 1988; Harmand et al., 2015; this study Harris et al., 1988 Harris et al., 1988; Ward et al., 1999; Gathogo, 2017 Harris et al., 1988 Harris et al., 1988; Roche et al., 1999 Harris et al., 1988; Prat et al., 2005; Tiercelin et al., 2010; this study Boës et al., 2019a Boës et al., 2019a; this study Harris et al., 1988; Boës et al., 2019a; this study Boës et al., 2019a Harris et al., 1988 Harris et al., 1988 Brown, unpublished Van Bocxlaer and Van Damme, 2009, 2011; Brugal et al., 2003 Harris et al., 1988, this study Harris et al., 1988, this study Harris et al., 1988; Mcdougall et al., 2012 Brindle et al., 2018 Harris et al., 1988; Walker and Leakey, 1993 Brown, unpublished Harris et al., 1988 Harris et al., 1988; Lamond and Tapanilla, 2003; Delagnes et al., 2006; Van Bocxlaer and Van Damme, 2009; Ward et al., 2014; Maddux et al., 2015; Brown, unpublished; this study

this study

Data from West Turkana on hominins between 4.20 Ma and 0.70 Ma. See text for explana			
Age (Ma)	Hominins		
4.9-4.2	KNM-LT 329		
4.2-4.11	e.g. KNM-KP 29281, 29283, 29285, 29286 ; KNM-WT 30498, 30500, 31712,		
	34725, 47951, 47952, 47953, 53160, 58759		
4.1	KNM-KP 29287		
3.53±0.01	KNM-WT 38341		
~3.5 env	KNM-LT 23181,23182,23183		
3.5	KNM-WT 22936, 22944		
3.5	KNM-WT 40000 (Holotype), 38339		
$3.35 {\pm} 0.05$	KNM-WT 16006		
3.3±0.1	KNM-WT 38350 (Paratype)		
3.3-3.2	e.g. KNM-WT 38332, 38334, 38335, 38337, 38338, 38345, 38342, 38343, 38344,		
	38345, 38346, 38347, 38348, 38349, 38352, 38358, 38359, 38360, 38361, 38362,		
	39949, 39950, 39951, 39952, 39953, 39954, 39955, 40001, 66289, 66290, 66291		
3.26 ± 0.01	KNM-WT 16003		
3.26 ± 0.01	KNM-WT 08556, 08557		
3.2 ± 0.1	KNM-WT 38356, 38357		
2.53 ± 0.02	KNM-WT 17000		
2.45 ± 0.05	KNM-WT 16005		
2.33 ± 0.02	KNM-WT 42718		
2.25 ± 0.02	KNM-WT 64910		
$1.79{\pm}0.02$	KNM-WT 37100, 37744, 37747, 37748		
1.77 ± 0.1	KNM-WT 17400		
1.75 ± 0.05	KNM-WT 37745		
1.72 ± 0.07	KNM-WT 18600		
1.72 ± 0.07	KNM-WT 17396		
1.47 ± 0.03	KNM-WT 15000		
1.42 ± 0.01	KNM-WT 51260		
$1.44{\pm}0.03$	KNM-WT 16001		
1±0.15	KNM-WT 19700		
0.75	KNM-WT 51261		

Data from West Turkana on hominins between 4 20 Ma and 0 70 Ma. See text for explana

tions. **References**

Leakey et Walker 2003 Leakey et al., 1995, 1998; Ward et al., 2001, 2013, 2020; Manthi et al., 2012 Leakey et al., 1995, 1998; Ward et al., 2001, 2013, 2020; Manthi et al., 2012 Leakey et al., 2001; Skinner et al., 2020 Leakey et Walker 2003 Ward et al., 1999 Leakey et al., 2001 Leakey et al., 2001 Leakey et al., 2001 Leakey et al., 2001

Brown et al., 2001 Brown et al., 2001 Skinner et al., 2020 Walker et al., 1986 Walker et al., 1986 Prat et al., 2005, this paper unpublished Prat et al., 2003; this paper Leakey et Walker, 1988 Prat et al., 2003; this paper Brown et al., 2001 Leakey et Walker, 1988 Walker et Leakey, 1993 Ward et al., 2013 Brown et al., 2001 Brown et al., 2001 Maddux et al. 2015

Data from	West Turkana archaeologic	al sites between 3.30 Ma and 0.
Age (Ma)	Archaeological site	Culture

Age (Ma)	Archaeological site	Culture
3.30±0.02	Lomekwi 3 (LOM3)	Lomekwian
$2.34{\pm}0.05$	Lokalalei 1A (LA1A)	Oldowan
2.33 ± 0.02	Nasura 2 (NAS2)	Oldowan
2.27 ± 0.02	Nasura 1 (NAS1)	Oldowan
2.25 ± 0.02	Lokalalei 2C (LA2C); Nasura 3 (NAS3)	Oldowan
1.79 ± 0.03	Kokiselei 6,3,2,5,1 (KS6,3,2,5,1)	Oldowan
1.76 ± 0.02	Kokiselei 4 (KS4)	Acheulean
1.75 ± 0.05	Naiyena Engol 1 (NY1)	Oldowan
1.73 ± 0.02	Naiyena Engol 2 (NY2)	Oldowan
1.27 ± 0.01	Nachukui 6 (NK6)	Acheulean
$0.75 {\pm} 0.02$	Nadung'a 1,2,3 (NAD1,2,3)	Acheulean
$0.70{\pm}0.02$	Nadung'a 4 (NAD4)	Acheulean

.70 Ma. See text for explanations. **References**

Harmand et al., 2015 Kibunjia et al., 1992; Roche et al., 1999; Harmand, 2009 this paper this paper Delagnes and Roche, 2005; Harmand, 2009; Arroyo et al., 2020 Kibunjia et al., 1992; Arroyo et al., 2020; Duke et al., 2021 Lepre et al. 2011; Texier, 2018; Arroyo et al., 2020 Kibunjia et al., 1992; Prat et al., 2003 Kibunjia et al., 1992; Roche et al., 2018 this paper Kibunjia et al., 1992; this paper Delagnes et al., 2006

Comparison of number of hominins versus total number of mammalian fossils and collected surface area (where available, from information in Harris et al., 1988) (from the Turkana Database) for members of the Nachukui formations from West Turkana. See Table 1 for the geochronology.

Geology	Hominins	Fauna	Hom %	Sq. km
Kanapoi	75	958	7.83	-
Apak	1	225	0.44	-
Muruongori	0	0	0.00	-
Kaiyumung	4	124	3.23	-
Lonyumun	0	0	0.00	-
Kataboi	6	134	4.48	0.85
Lomekwi	40	1174	3.41	10.93
Lokalalei	2	70	2.86	0.59
Kalochoro	3	185	1.62	1.31
Kaitio	8	189	4.23	2.33
Natoo	4	185	2.16	2.34
Nariokotome	2	83	2.41	0.77