

## **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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### **Abstract**

 Although the Turkana Basin is one of the driest regions of the East African Rift, its Plio– Pleistocene sediments are rich in freshwater vertebrates and invertebrates, providing evidence 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 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 dating back to the Late Pliocene–Pleistocene. Freshwater conditions are reconstructed from river and lake sediments and the micro- and macofauna they contain. Data synthesis suggests that drinking water and freshwater foods prevailed in the western region of the Turkana Basin 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 from 1.27 to 0.75 Ma. Milestones in hominin evolution occurred in this context, such as the 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 *Homo* (2.33 Ma), *Paranthropus boisei* (2.25 Ma and 1.77–1.72 Ma) and *Homo ergaster*/*Homo erectus* (1.75 Ma, 1.47–1.42 Ma and 1.10–0.90 Ma). Developments in hominin behavior also 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 the emergence of bifacial shaping in eastern Africa (1.80 Ma), and the first known Acheulean site (1.76 Ma). Our synthesis suggests that, diachronic variation in hydroconnectivity played a role on the amount of drinking water and freshwater foods available in the western region of the Turkana Basin, despite regional aridity.

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

Omo Group deposits

### **1. Introduction**

 Over the past 25 years, numerous authors have linked climate change and hominin evolution based on the premise that resources essential to hominin development (e.g., brain 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, 1998, 2013; Bobe and Behrensmeyer, 2004; Wynn, 2000, 2004; Trauth et al., 2005, 2007, 2010, 2015; Behrensmeyer, 2006; Bobe, 2006; Bonnefille, 2010; Levin et al., 2011; Cerling et al., 2011; Maslin et al., 2014, 2015; Levin, 2015; Potts and Faith, 2015; Cuthbert et al., 2017; Blumenthal et al., 2017; Timmermann et al., 2022). An important related debate about the relationship between climate change, hominin diet and behavior concerns landscape aridification in the Turkana Basin (Kenya, Ethiopia) (Wynn, 2004; Sommerfeld et al., 2014; Fortelius et al., 2016; Blumenthal et al., 2017; Quinn and Lepre, 2020, 2021; Lepre and Quinn, 2022). During the Neogene, topographic uplift altered atmospheric moisture transport and distribution in the East African Rift, and the initiation of Northern Hemisphere glaciations at the end of the Pliocene intensified hydrological deficits in this region (Laporte and Zihlman, 1983; deMenocal, 2004; Sepulchre et al., 2006; Blumenthal et al., 2017; Trauth et al., 2021). 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 al., 2017). The debate on aridification and drinking water and food availability is especially relevant to hominin evolution, as some previous hypotheses, such as the savanna and the 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 key drivers of natural selection, adaptive divergence, and speciation in Plio–Pleistocene hominin evolution. Although the global climate changed during the Plio–Pleistocene transition, the responses of these changes on landscape, fauna and hominins are still debated in the East

 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 Lepre, 2020, 2021; Lepre and Quinn, 2022). The aims of this review are to examine the archeological and hominin records from the western region of the Turkana Basin (Kenya; Fig. 1) and the evidence for the existence of freshwater conditions and resources in the western region of Turkana Basin between 4.20 and 0.70 Ma. This specific region of the Turkana Basin provides evidence of hominin and archeological sites dating back to the Late Pliocene–Early Pleistocene, raising new questions about the role of climate and environmental change on water and food resources and hominin evolution.

 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 environment (Harmand et al., 2015; Lewis and Harmand, 2016; Quinn et al., 2021). Lomekwi 3 is at least 300 kyr older than the earliest known Oldowan assemblages discovered at other localities (i.e., Gona, Ledi-Geraru, and Nyayanga; Semaw, 2006; Braun et al., 2019; Plummer et al., 2023). Other important archeological sites have been discovered in the same region of 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; Roche et al., 1999; Delagnes et al., 2005; Harmand, 2009). The artifacts from Kokiselei 6 are the earliest known evidence for the emergence of bifacial shaping (Duke et al., 2021), and the archeological site of Kokiselei 4 has yielded the oldest Acheulean assemblage presently known (Lepre et al., 2011; Texier, 2018). These archeological sites provide some of the earliest 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, 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),

 *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 assigned to early *Homo* (Prat et al., 2005), *Homo ergaster* or *Homo erectus*, referred to here as *Homo ergaster/erectus* (Walker and Leakey, 1993; Prat et al., 2003; Wood and Leakey et al., 2011; Wood and Boyle, 2016), including the nearly complete skeleton of KNM-WT 15000 ('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., Walker and Leakey, 1993; Leakey et al., 2001; Ward et al., 2020). The western region of the Turkana Basin is also very rich in freshwater micro- and macrofauna demonstrating that 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; Martin and Trautwein, 2003; Storrs, 2003; Van Bocxlaer, 2011, 2020; Stewart and Rufolo, 2020).

 Similar, coeval records exist to the northern regions of the Turkana Basin in the Shungura, Mursi and Usno Formations (Ethiopia) along the Omo River and to the eastern 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, et al., 2005; Chapon et al., 2005, 2011; Van Bocxlaer et al., 2008; Braun et al., 2010; Barsky et al., 2011; Delagnes et al., 2011; Leakey et al., 2012; Maurin et al., 2017; Fig. 1). Reviews of the Turkana Basin generally combine data from these different fluvial and lacustrine formations (i.e., located in the northern, western, eastern and southern regions of the Turkana Basin). 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 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

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

 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  ${}^{40}Ar^{39}Ar$  ages of volcanic tuffs and/or lateral correlations by geochemical signatures specific to each tuff (e.g., Harris et al., 1988; Feibel et al., 1989; Brown and McDougall, 2011; McDougall et al., 2012). Plio–Pleistocene sediments and tuffs are outcropping in the Nachukui Formation, including Lothagam, Loruth Kaado, South Turkwel and in the Kanapoi Formation (Fig. 1; Table 2). The Nachukui and Kanapoi Formations offer ~700 m of strata with regularly intercalated tuffs that 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 that it is not possible at this time to provide accurate ages within the interval between 3.1 and 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 3.6 below on methods for controlling chronology). In what follows, ages in Ma with two 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 or were estimated.

 We begin by introducing the impact of global climate change on eastern Africa during 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 Turkana Basin and highlight the topoclimatic effects on the regional hydroclimate system. Subsequently, we present the datasets and criteria we used to reconstruct the paleohydrological 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 provided based on available datasets between 4.20 and 0.70 Ma and on field data verifications that were conducted between 2010 and 2023 in the western region of the Turkana Basin (Mission Préhistorique au Kenya; West Turkana Archaeological Project). We then relate our findings from this synthesis to the stratigraphic and spatiotemporal contexts of the archeological and paleoanthropological sites of the western region of the Turkana Basin. Along with the hypotheses linking increasing aridity to hominin evolution, we discuss the availability of drinking water and freshwater food resources for hominins occupying this arid region of the rift.

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

174 Until recently, it was thought that major climate change in eastern Africa began  $\sim$ 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 178 corroborate a consistent stepwise transition from  $\sim$  2.7 Ma onward but suggest that glaciations

 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 of the North Atlantic Ocean, due to the gradual closure of the Central American Seaway during the uplift of the Central American Isthmus between 4 and 3 Ma (Bartoli et al., 2005; O'Dea et 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 Northern Hemisphere ice cap. This new ocean circulation system explains global differences in the cyclicity of benthic  $\delta^{18}O$  records related to changes in astronomical forcing on atmosphere- ocean circulation after 3.5 Ma (deMenocal, 2004; Lisiecki and Raymo, 2005), while orbital parameters (Milankovitch cycles) were unaltered (Laskar et al., 2004). One of the earliest glacial events occurred at 3.30 Ma, i.e., during MIS M2 (Lisiecki and Raymo, 2005; Raymo et al., 2006; Tan et al., 2017). With the formation of the ice cap, a large amount of water was removed from the oceans, resulting in global sea-level drops (Miller et al., 2005). This sea-level 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 atmospheric circulation (Cane and Molnar, 2001; Yan et al., 2021). As tropical ocean circulation declined, heat transfers reduced in the Indo-Pacific Ocean (Karas et al., 2009). The resulting establishment of atmospheric circulation cells (i.e., the Walker and Hadley cells) would have significantly weakened the East African monsoon (Yan et al., 2021) and thus 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; Timmermann et al., 2022).

201 Multiple regional ecological indicators, such as the abundance of grazing bovids, C<sub>4</sub> 202 plants, grass pollen, soil carbonate  $\delta^{18}$ O and  $\delta^{13}$ C values, leaf wax  $\delta^{13}$ C values and phytoliths suggest a long-term trend toward aridification of eastern Africa during the Plio–Pleistocene

 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 (Wynn, 2004). Several studies have focused on climate change (mostly via temperature and precipitation proxies) at the scale of the paleontological and archeological sites in the Turkana 208 Basin. For example, based on the distribution of  ${}^{13}C-{}^{18}O$  bonds in soil carbonates, Passey et al.  $(2010)$  suggested that the temperature in the Turkana Basin has remained stable  $(30-35 \degree C)$  over the last 4 Myr. Based on faunal ecometric methods, Fortelius et al. (2016) suggested that the basin was already arid before 2.7 Ma and may have acted as a 'species factory', promoting ecological adaptations to aridity prior to widespread aridification in eastern Africa. Based on 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 215 soil carbonate records from different regions in the basin shows that the distribution of  $C_3$  and C4 plants varied by region (Levin, 2015). For example, Uno et al. (2016) showed that C4- dominated ecosystems developed in the western region of the Turkana Basin only after 2.1 Ma. Blumenthal et al. (2017) argued that changes in paleoaridity and herbivore paleodiets were 219 decoupled in the basin during the Plio–Pleistocene. Using  $\delta^{18}$ O values from tooth enamel, they suggested that changes in the abundance of C4 grass and grazing herbivores might reflect rainfall seasonality rather than general aridity. Recent drill-core studies along the rift (Cohen et 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. (2022) proposed that the Turkana Basin experienced a dramatic and abrupt increase in 225 precipitation (enrichment in  $\delta D_{\text{max}}$  in WTK13 core in the western region of the Turkana Basin) at 1.71 Ma and that rapid changes in aridity/humidity likely affected the basin. Finally, again 227 using soil carbonate  $\delta^{18}O$  values, Lepre and Quinn (2022) suggested that aridity increased after

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).

 Whereas soil temperature and moisture proxies suggest that the Turkana Basin has 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 inputs from the upper northern, northeastern and southwestern drainage basins as they connect, amplifying the hydroclimatic responses recorded in the Turkana Basin, especially when the 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 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 enabled freshwater fauna to colonize the Turkana Basin at certain periods despite the ambient aridity (Williamson, 1981; Harris et al. 1988; Meylan et al., 1990; Stewart, 2003; Martin and Trautwein, 2003; Storrs, 2003; Van Bocxlaer, 2011, 2020; Stewart and Rufolo, 2020). To gain deeper insight into the paleolandscapes of the Turkana Basin, it is important to integrate the 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 drainage basins may have fed freshwater into the different regions of the Turkana Basin, as suggested by the periodic occurrence of freshwater micro- and macrofauna in the basin (Williamson, 1981; Harris et al. 1988; Meylan et al., 1990; Stewart, 2003; Martin and Trautwein, 2003; Storrs, 2003; Van Bocxlaer, 2011, 2020; Stewart and Rufolo, 2020). Moreover, it is necessary to examine the effects of volcano-tectonic activity on basin topography and the reorganization of paleohydrographic networks and outlets during the Plio– Pleistocene (Bruhn et al, 2011; Salzburger et al., 2014; Boës et al., 2019a).

# **3. Hydroclimatic specifics and hydroconnectivity of the Turkana Basin within the East**

**African Rift system** 

### *3.1. Topoclimatic effects*

 In eastern Africa, precipitation is largely concentrated in a few uplifted mountain ranges (e.g., Nicholson, 2017). To the northeast and southwest of the Turkana Basin, the Ethiopian and Kenyan Highlands (Fig. 1) block atmospheric circulation and intercept most of the monsoon 259 rainfall in the region  $(>1500 \text{ m.a.s.}!)$ .  $>1500 \text{ mm}$  annual precipitation; 19 °C mean temperature=tropical monsoon climate). The isotopic composition of water suggests that the 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 moisture sources (Levin et al., 2009). To a large extent, the continental monsoon is driven by increased evapotranspiration rates in equatorial Africa during summer insolation maxima (Rossignol-Strick, 1985; Wang, 2009; Prömmel et al., 2013; Zhisheng et al., 2015; Kuechler et al., 2018; see also e.g., Ashley, 2007 and Verschuren et al., 2009 for lake responses in eastern Africa). For the Indian Ocean moisture source, it seems that when the Indian monsoon is strong, it causes rainfall deficits in eastern Africa, especially in northeast Kenya (Camberlin et al., 2010). Located between the Kenyan and Ethiopian Highlands, i.e., two topographic barriers that intercept most of the atmospheric moisture, the Turkana Basin is a rainfall-deficient 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 at the foot of the uplifted highlands (Nicholson, 2016). Because of this configuration, the 274 climate in the Turkana Basin remains warm and dry throughout the year  $(\sim 30$  °C mean temperature=hot desert climate). Isotope temperatures of paleosol carbonates from the Nachukui and Shungura Formations suggest that similar mean temperatures have prevailed in the basin since 4 Ma (Passey et al., 2010) and perhaps as early as the establishment of the

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

### *3.2. Paleohydrographic network*

 Although the regional climate of the Turkana Basin is arid and decoupled from precipitation changes in the Kenyan and Ethiopian Highlands, the basin does receive water from these adjacent regions. Today, 80–90% of the permanent water inflow to the Turkana Basin 285 comes from the Omo River drainage catchment in the Ethiopian Highlands (140,000 km<sup>2</sup>;  $>500$  $\text{m}^3\text{/s}$ ; Kallqvist et al., 1988; Fig. 1). Most of the remaining 10–20% comes via inflow from the 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 regions of the Turkana Basin. Beyond the river systems that currently contribute water to the basin, several paleohydrographic connections may have been activated at certain periods during the Pliocene and Pleistocene.

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

 of the last lake in this cascade system, Lake Chew Bahir, would need to rise up by 45 m before 303 an outflow is established, expanding its surface area from to  $2100 \text{ km}^2$  (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).

 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 currently hydrographically separated from the Turkana watershed, this hydrographic network may be activated and overspill into the Turkana Basin when precipitation intensifies over the Kenyan Highlands. This cascading river-lake system consists of lakes Elmenteita (1790 312 m.a.s.l.; 18 km<sup>2</sup>), Nakuru (1758 m.a.s.l.; 45 km<sup>2</sup>), Bogoria (990 m.a.s.l.; 34 km<sup>2</sup>), Baringo (970 313 m.a.s.l.; 168 km<sup>2</sup>) and Logipi-Suguta (275 m.a.s.l.; 30 km<sup>2</sup>). When overfilled with water, these systems overspill into each other and finally into the Kerio River (Garcin et al., 2009; Olaka et al., 2010; Junginger, 2011; Melnick et al., 2012; Bloszies, 2014; Dommain et al., 2022; Figs. 2, 3d, f and 4c). Evidence for the activation of this cascading system comes from the presence of diatomite beds in the Baringo-Bogoria Basin (east of the Tugen Hills; Fig. 1), which indicate 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 last lake in this cascade system, Lake Logipi-Suguta, is a volcanic-dammed lake that formed 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 of Lake Logipi-Suguta could rise up by 300 m before overspilling, reaching a lake surface of 430 km<sup>2</sup> in contrast to the current 30 km<sup>2</sup> (=paleolake Suguta, with the outlet situated at 577 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

 precursors of Lake Turkana, which periodically were larger than the present-day lake (Figs. 3d, f and 4c). In other words, the redirection of the Suguta paleoriver into Lake Logipi-Suguta by 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 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 Hills). Sediments from the Kerio paleoriver formed the extensive Pliocene fossiliferous deltaic deposits at Kanapoi (Fig. 4b; Feibel, 2003a)

 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.

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

 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 345 from 6800 to 7200 km<sup>2</sup>; water volume of 200–240 km<sup>3</sup>). The current lake occupies the central axis of the volcano–tectonic basin and is on average only 30 m deep, with a maximum depth of 110 m in the central and southern basins (e.g., Dunkelman et al., 1989; Fig. 1). As a result of closed conditions, the lake water is saline (2500 ppm total dissolved solids [TDS]); Yuretich and Cerling, 1983) and alkaline (21–34 meq/L; Olago and Odada, 1996), except in the vicinity of the Omo River delta, where the conditions are fresher due to the continuous inflow of the

351 Omo River. The level of Lake Turkana is currently relatively stable  $(365 \pm 5 \text{ m.a.s.}!)$ , representing a balance between continuous inflow of the Omo River and high evaporation (2.5 353 to 3.5 m/year resulting in a volume of 20 km<sup>3</sup>/year; Kallqvist et al., 1988).

 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 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 358 present lake level (lake surface of nearly  $10,000 \text{ km}^2$ ; Garcin et al., 2012; Morrissey and Scholz, 2014). Over the last 4 Myr, the sediments in various regions of the Turkana Basin reveal a succession of fluvio-lacustrine systems that confirm the existence of large, deep paleolakes (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 caused by increased precipitation in the Kenyan and Ethiopian Highlands and by changes in the catchment size, due to the emergence of new connections extending to rivers and lakes in these two regions. The impact of tectonic subsidence on 'accommodation space' for sediment and water volume is limited for our time scale, considering the rate of basin extension (<500 cm/ka; 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 sedimentation and paleolake-level fluctuations in the basin. However, in our time interval, 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 et al., 2019a; Fig. 5b). These changes likely have influenced freshwater availablity and the colonization of the Turkana Basin by freshwater fauna.

 *3.4. Evidence of paleo-outlets and reorganization of the drainage of the Turkana Basin by 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 active, connected the Turkana Basin to the Turkana paleoriver, which flowed into the Indian 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 occurred in this area between 3 and 2 Ma, with the onset of explosive volcanism in the 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, 1989; Bosworth and Maurin, 1993; Haileab et al., 2004; Bruhn et al., 2011; Boës et al., 2019a). This volcanic activity initiated the closure of the Loiyangalani outlet, resulting in a shift of the 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 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 Nile River and the Mediterranean Sea (Figs. 3d and 4e). Unlike the Loiyangalani outlet, which was blocked by explosive volcanism (see below; Figs. 3f, 4e), the Ilemi outlet can still be 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 the current lake level (364 m). The longitudinal profile of the paleovalley connected to the Sobat

 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 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 region of the basin, river erosion may have affected the Ilemi outlet channel after its opening, 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 406 around 440 m.a.s.l. north of the basalt flows of Mount Kulal, which erupted  $\sim$ 3 Ma (Table 1). In other words, the outlet of the Turkana paleoriver to the Indian Ocean was lower than the outlet to the Nile River and the Mediterranean Sea. The activation of the Ilemi outlet in the Late Pleistocene has been demonstrated in numerous papers since the 1980s (Harvey and Grove, 1982; Dumont, 2009; Johnson and Malala, 2009; Stewart, 2009; Van Damme and Van Bocxlaer, 2009; Garcin et al., 2012; Morrissey and Scholz, 2014; Williams, 2019). Some studies suggest that this hydroconnectivity already existed in the Early Pleistocene (Cerling, 1979; Harris et al., 1988; Nyamweru, 1989; Haileab et al., 2004; Bruhn et al., 2011; Boës et al., 2019a). The presence of lake sediments east of Ilemi in the Shungura Formation (i.e., from 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 the basin was connected to the Nile as early as 1.7 Ma. However, ostracod data from the Shungura Formation indicate the presence of oligohaline conditions between 1.8 and 1.4 Ma and variable conditions after 1.4 Ma (i.e., appearance of *Limnocythere;* Carbonel and Peypouquet, 1979). This information suggests that if the basin opened to the Nile after 1.9 Ma, 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 freshwater in the northern and northeastern regions of the basin.

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

 In contrast to the saline–alkaline conditions that prevail in Lake Turkana today, various lines of evidence indicate that freshwater systems existed and/or expanded repeatedly in the Turkana Basin during the Plio–Pleistocene. These lines of evidence, among others, include sedimentology, water paleochemistry, isotope records and freshwater micro- and macrofauna and flora (Cerling, 1979; Feibel, 1993; Stewart, 2001, 2003, 2009; Wood, 2003; Van Bocxlaer 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 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 are essentially fresh, except for perhaps at the establishment of a lake outflow, when previously accumulated mineral salts are flushed. Given the aridity and high levels of evaporation within the Turkana Basin during the Plio–Pleistocene (Wynn, 2004; Passey et al., 2010; Blumenthal et al., 2017; Lepre and Quinn, 2022), the presence or absence of an outlet determines the 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 freshwater conditions develop or are maintained within it. For example, freshwater biota 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 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 accumulate within the basin and create saline–alkaline conditions. When a lake progressively becomes alkaline–saline, some freshwater organisms may persist for some time, or find refuge

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

 The development of enhanced hydroconnectivity and expansion of freshwater fauna into the Turkana Basin are evidenced by the occurrence of various freshwater vertebrates, invertebrates, microalgae and microbial structures in river and lake sediments. These include: the crocodile *Euthecodon*; turtles (Pelomedusidae and Trionychidae), fishes (*Sindacharax*, *Semlikiichthys*, *Polypterus*) and cartilaginous fish (*Dasyatis africana*); crabs of the family Potamonautidae, mollusks (such as various gastropod and bivalve species) and ostracods (*Stenocypris, Sclerocypris*); microalgae diatoms (*Stephanodiscus* spp*.* and *Aulacoseira* spp.) 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; Stewart, 2001, 2003, 2009; Harris et al., 2003; Martin and Trautwein, 2003; Storrs, 2003; Trauth et al., 2007; Van Bocxlaer et al., 2008; Tiercelin et al., 2010; Van Bocxlaer, 2011, 2020; Van Bocxlaer and Van Damme, 2009; Brochu, 2020; Stewart and Rufolo, 2020).

 Among the freshwater macrofauna, the aquatic mollusks found throughout the western region of the Turkana Basin belong exclusively to freshwater mollusk families, although some 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 conditions, some salt-tolerant 'freshwater' mollusks occur in Lake Turkana. The ostracods microfauna are likewise tolerant of various salinity/alkalinity levels and their ecological interpretations may be difficult without accurate species-level identification (Peypouquet et al., 1978; Carbonel and Peypouquet, 1979; Carbonel et al., 1988). Four ostracod assemblages have been identified in the Plio–Pleistocene sediments of the Turkana Basin (Cohen et al., 1983; Carbonel et al., 1988). Of these, the assemblage containing *Stenocypris and Hemicypris* (ostracods) reflects freshwater conditions with nutrient-rich water mixed by the wind, whereas

 the ostracod *Limnocythere* is tolerant to saline–alkaline waters. The ecological interpretations 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, 1993) and reptiles, i.e., crocodiles and turtles (Meylan et al., 1990; Harris et al., 2003; Wood, 2003; Brochu, 2020). With regard to microalgae, in closed systems within arid zones, changes in the diatom algal assemblage reflect the presence/absence of river inflow and/or the transition from an open to a closed lake basin (Gasse et al., 1997). Throughout the Plio–Pleistocene sediment series in the western region of the Turkana Basin, white diatomite beds occasionally occur and consist almost exclusively of diatom frustules (Trauth et al., 2007). This type of 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 blooms (e.g., Owen, 2002). However, the ecology of Plio–Pleistocene diatoms is still not well known, most notably the ecological tolerances of the various taxa, since freshwater and saline- tolerant diatom taxa may have occurred at times in the Turkana Basin as in other basins in 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.

 Finally, stromatolite microbial structures provide additional information on the paleohydrological conditions that existed in the western region of the Turkana Basin at certain times. The stromatolites (and oncolites) are formed by accretions of thermophilic blue-green 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 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 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

 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).

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

 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, 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) and crocodile (Harris et al., 1988; Brochu, 2020; Storrs, 2003). Freshwater microfauna (ostracods and diatoms) is also included in the definition of 'freshwater episode', despite some tolerance to alkaline and saline conditions and the absence of a biostratigraphy with accurate species-level identification for Plio–Pleistocene microfauna in the Turkana Basin (Peypouquet 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 expressed by the colonization of the region by freshwater macrofauna from upland river-lake systems via cascade hydroconnectivity. In the Turkana Basin, enhanced hydroconnectivity formed and disappeared from the Kenyan and Ethiopian Highlands and surrounding regions as 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., 2022). Finally, 'freshwater episodes' express enhanced hydroconnectivity and the occurrence

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

### *3.7. Methods to develop chronological control*

 In our review, it is important to revise the timing of various lines of evidence, and for 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 geological members to verify the ages that have been proposed in the different papers and available datasets (Tables 2–5). Tuff ages and interpolated ages between tuffs are therefore considered in the same framework and all published ages for fossils can be verified taking into 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) in relation to the presence of a tuff, or 2) as an age calculated from the sedimentation rate inferred from the thickness of the sediments accumulated in between tuffs. The Bayesian age model allowed us to verify the distribution of the published ages and uncertainties (Fig. 6). The 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 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 absence of tuffs (and paleomagnetic inversions). For this reason, as in most databases and papers on the western region of the Turkana Basin, the time interval between 3.1 and 2.7 Ma is not evaluated in this synthesis. For example, there is no soil carbonate nodules for the western 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 interval for the western region of the Turkana Basin (e.g., Levin, 2015; Nutz et al., 2020).

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

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

*4.1. From 4.20 to 3.60 Ma* 

 The western region of the Turkana Basin is marked by the presence of river sediments 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 sequence (i.e., between the Upper Pumiceous and Kanapoi Tuffs=Lonyumun paleolake; Fig. 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 Lonyumun). Note that paleolake Lonyumun sediments are in the Lonyumun Member (e.g., Harris et al., 1988) and not in the Kataboi Member as indicated in Nutz et al. (2020; i.e., there 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 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 Nasechebun (Fig. 1; Harris et al., 1988). The end of paleolake Lonyumun is observed at 3.98 Ma in the sediments of the Nachukui Formation (i.e., 3 m below the Moiti Tuff that contains 564 pumice clasts). One brief lacustrine interval (lake muds and diatoms) is also present at  $\sim$ 3.7 Ma, i.e., 12 m above the Moiti Tuff (3.97 Ma) and below the Lokochot Tuff (3.60 Ma) in the middle 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).

 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

 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 of freshwater organisms are present in the Kanapoi Formation between 4.20 and 4.10 Ma, including ostracods such as *Sclerocypris* (Peypouquet, 1978); mollusks, such as *Bellamya* and *Etheria* (Feibel, 2003a; Van Bocxlaer, 2020); the fishes *Sindacharax* and *Semlikiichthys* (Stewart, 2001, 2003, 2009; Stewart and Rufolo, 2020); the crocodile *Euthecodon* (Harris et al., 2003; Brochu, 2020), and freshwater turtles of the families Pelomedusidae, Testudinidae and Trionychidae (Meylan et al., 1990; Harris et al., 2003; Wood, 2003). In the Kanapoi Formation, freshwater mollusks have only been observed from shell beds between 4.15 and 4.11 Ma (i.e., 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 Tuff (Fig. 7). *Etheria* is reported in a channel fill that cuts the Kanapoi Tuff (4.11 Ma). Freshwater ostracods (*Hemicypris*) occur between 4.20 and 3.98 Ma and freshwater mollusks are found at 3.99–3.98 Ma (i.e., from the Topernawi to the Moiti Tuffs; Fig. 7).

*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 588 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).

 The development of an open freshwater system is demonstrated by the occurrence of 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 Lomekwi, remains of *Euthecodon*, *Sindacharax*, mollusks and freshwater turtles are present in 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  $3.30$  Ma, in the same paleo-beach complex 23 m above the Tulu Bor  $\alpha$  Tuff. A similar sequence 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 the mollusk trace fossil *Lockeia* (Gathogo, 2017) and sponge spicules (Harris et al., 1988).

### *4.3. From 2.60 to 2.20 Ma*

 In the Lokalalei Member of the Nachukui Formation (Table 2), the development of river 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 2.53 and 2.44 Ma (Tiercelin et al., 2010; Table 3; Fig. 7). Then, lake sediments occur at 2.44 Ma (i.e., 3 m above the Kokiselei Tuff=paleolake Kokiselei; Fig. 7). In the lower Kalochoro 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 Nasura are separated by river sediments (2.33–2.25 Ma; Table 3; Fig. 7).

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

 mollusks occur between 2.34 and 2.32 Ma at Lokalalei. Other bioclastic facies with freshwater mollusks (lake-margin coquina) occur below and above the Ekalalei Tuff (undated), which 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 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 ratio) suggest alternating saline–alkaline conditions at 2.22 Ma (Boës et al., 2019a). In the transition from freshwater to saline–alkaline conditions, inhospitable conditions appear to have occurred briefly, as suggested by a fish kill event at 2.22 Ma (Boës et al., 2019a). This event is probably associated with a destabilization of the thermal stratification, low water inflows, high evaporation and substantial algae and microbial activities, such as cyanobacteria blooms (expansion and proliferation of cyanobacteria toxins; Olilo et al., 2023). The initiation of the volcanic blockage of the outlet of the Turkana Basin to the Indian Ocean may partly explain changing limnological conditions as early as 2.26 Ma (Boës et al., 2019a).

*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).

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

 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 Member, ostracods occur between 2.10 and 1.95 Ma (i.e., from 40 to 15 m below the KBS Tuff at 1.87 Ma). In the Kaitio Member of the Nachukui Formation (Table 2), freshwater mollusks and ostracods occur above the KBS Tuff. Ostracods have also been reported at the top of the Kaitio Member at Kokiselei (Table 3; Fig. 7). The expansion of freshwater environments at 1.8–1.7 Ma is supported by the presence of diverse freshwater mollusks including, for example, *Iridina* and *Chambardia* (Table 3; Fig. 7), and by the presence of *Euthecodon* and fossils of freshwater fish, including *Polypterus* (Brugal et al., 2003). Freshwater mollusks are also reported at 1.8 Ma near the archeological complex of Naiyena Engol, 16 m above the KBS Tuff (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 stromatolite beds occur at 1.6 Ma, in the upper Kaitio Member and the base of the Natoo Member of the Nachukui Formation (Tables 1 and 3; Fig. 7). However, it is difficult to differentiate the upper Kaitio Member from the overlying Natoo Member at this locality. Nutz 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 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 is one stromatolite bed at ~1.4 Ma, 15 m below the Lower Nariokotome Tuff (1.30 Ma; Table 3; Fig. 7). Note that in the stratigraphy of the Nachukui Formation, there are no stromatolite beds between 1.6 and 1.4 Ma in the Natoo Member as has been suggested by Nutz et al. (2020; i.e., there is a 440 kyr error in their publication in section 16, as the Malbe Tuff at 60 m is not dated at 1.40 Ma but at 1.84 Ma). Stomatolites occur at the transition between the Kaitio and Natoo Members and then at the top of the Natoo Member only (Harris et al., 1988). At

 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.

#### *4.5. From 1.30 to 0.70 Ma*

 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 Lower and Middle Nariokotome Tuffs), which are overlain by deposits enriched in shells of *Cleopatra* and *Melanoides,* at 1.27 Ma (Table 3; Fig. 7). Then ostracods and mollusks alternate with stromatolites in sediments of several river and lake systems between 1.20 and 0.75 Ma. Freshwater mollusks are common in sediments between these stromatolites. Notably, *Iridina* has been reported from the Nariokotome Member (Table 3), where the depositional 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 found within a stratigraphic interval extending from 9 m above the Upper Nariokotome Tuff at 1.23 Ma, up to 1 m below the Silbo Tuff at 0.75 Ma (Brown, unpublished data; Ward et al., 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 (=paleolake Nachukui; Table 3; Fig. 7). Four of the stromatolite beds occur from 23 m above the base of the member (Ward et al., 2014; Maddux et al., 2015). The stromatolites occur

 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 calcium carbonate around nuclei trapped in sediment when freshwater rivers and saline– alkaline lake waters mixed. Stromatolites developed near lakeshore and river channels, where 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 Tuff at Nadung'a (Delagnes et al., 2006; Maddux et al., 2015), these formed around rounded basalt cobbles, freshwater mollusks and even around a biface stone tool. The latest stromatolites of the Nariokotome Member found 1 m below the Silbo Tuff (0.75 Ma) can be very large (up 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 rivers with saline–alkaline lake waters played a role in stromatolite size, such as geothermal activity (Casanova, 1996).

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

*5.1. From 4.20 to 3.60 Ma* 

 The KNM-LT 329 mandibular fragment from the lowermost Apak Member is older than 4.20 Ma and thus represents the earliest known hominin from the Turkana Basin (Leakey and 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 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 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-



#### *5.2. From 3.60 to 3.1 Ma*

 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 et al., 2001). The remains of *K. platyops* have been described only from the Kataboi and Lomekwi Members in the Lomekwi region (Leakey et al., 2001). The holotype (KNM-WT 40000 cranium; Table 4; Fig. 8) of this species occurs at 3.50 Ma, whereas the paratype (KNM- WT 38350 maxilla) dates to 3.30 Ma (Leakey et al., 2001). The oldest fossils of *K. platyops*, including the holotype cranium, were found in nearshore lake deposits at 3.50 Ma in the Kataboi 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 Lomekwi (Skinner et al., 2020), and at 3.5 Ma at Lothagam (KNM-LT 23181, 23182, 23183; Table 4; Fig. 8) and south of the Turkwel River (KNM-WT 22936 and KNM-WT 22944; Table 4; Fig. 8). The hominin remains at South Turkwel have been found in the same spatiotemporal 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 Lomekwi Member at 3.30 Ma and 3.30–3.2 Ma (e.g., KNM-WT 16003, 08556, 08557, 38343,

 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 collection), which has yielded the oldest known artifacts dated at 3.30 Ma (Table 4; Fig. 8). The 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 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 3.30 Ma are the earliest evidence of hominin cognitive abilities for tool making (Harmand et al., 2015; Lewis and Harmand, 2016). The LOM3 site and the *K. platyops* paratype were found 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). The paleo-beach and sand dune complex, the latter containing fossilized calcified roots and termite nests, lie a few meters above the Toroto Tuff at 3.31 Ma (Harmand et al., 2015). Nearshore river and alluvial fan deposits exclusively mark the periods at 3.60 Ma and 3.30– 3.20 Ma.

*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 761 (undated) at LA1 $\alpha$  (Prat et al., 2005), i.e., a paleoanthropological site located in the same

 stratigraphic context as the Oldowan sites of Lokalalei (Prat et al., 2005). KNM-WT 42718 was subsequently dated at 2.33 Ma based on the fact that the Ekalalei Tuff is slightly younger than 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) 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 assumptions, KNM-WT 42718 is probably slightly younger than 2.33 Ma. The lithic material excavated at the archeological site of Lokalalei 1A and 2C demonstrates a level of technical and manual skill that is exceptional for the early Oldowan, with high productivity flaking between 2.33 and 2.25 Ma (Delagnes and Roche, 2005; Harmand, 2009; Arroyo et al., 2020). Another archeological complex of early Oldowan sites named Nasura (Roche et al., 2018) contains in situ artifacts at 2.33–2.25 Ma (NAS2, 1, 3; Table 5; Fig. 8). The remains of one hominin allocated to *Paranthropus* (probably *P. boisei*, KNM-WT 64910) is also reported within the archeological complex of Nasura (Table 4; Fig. 8). There are currently no remains of *P. aethiopicus* associated with an archeological site in the western region of the Turkana Basin.

### *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;

 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 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 Ma is marked by the presence of *H. ergaster/erectus*, of which the most complete skeleton 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 Nariokotome drainage, is dated at 1.44 Ma by McDougall et al. (2012). A metacarpal (KNM- WT 51260) has been discovered at 1.42 Ma in the Natoo Member (i.e., at the level of the Lokapetamoi Tuff) at Kaitio, and allocated to the genus *Homo* and probably to *H. erectus* sensu lato (i.e., *H. ergaster/erectus*; Ward et al., 2014).

 The following chronostratigraphic interval between 1.8 and 1.7 Ma yielded many Oldowan sites at Kokiselei and Naiyena Engol (KS3, KS2, KS5, KS1; Table 5; Fig. 8). At 1.80 Ma, the archeological site of Kokiselei 6 (KS6) provides the earliest known evidence for the emergence of bifacial shaping in eastern Africa (Duke et al., 2021). At 1.76 Ma, the archeological site of Kokiselei 4 (KS4) contains the oldest known Acheulean industry (Lepre 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 by shaping smaller detached products. Kokiselei 4 includes picks with trihedral or square sections, unifacial or roughly shaped handaxes, as well as pieces left as rough outs (Roche et al., 2003; Texier, 2018). The chronostratigraphy of the upper Kaitio Member requires further investigation, especially at Naiyena Engol, an archeological complex currently under study (NY1, NY2; Table 5; Fig. 8).

*5.5. From 1.30 to 0.70 Ma* 



### **6. Discussion**

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

 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

 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; 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 *K. Platyops* exploited resources from both C3 and C4 environments and was no longer a 841 primarily  $C_3$  or dense forest/shrubland inhabitant. Stewart (2014) has suggested that climate variability is associated with early *Homo* and perhaps *P. boisei* broadening their diet to familiar but less preferred foods: vertebrates and invertebrates. These foods consistently provided early *Homo* with essential nutrients, which reduced selection pressures and allowed for increases in 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 C4/C<sub>3</sub> wetland resources. Broadly, the availability of water in arid regions of eastern Africa is a major limiting factor for vegetation growth and the development of terrestrial ecosystems in which hominins lived. The landscape of the Turkana Basin is currently arid due to the presence of topographic barriers that block atmospheric moisture. However, during the Plio–Pleistocene, former rivers and lakes that connected and disconnected in the Kenyan and Ethiopian Highlands 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 the balance between water influx and evaporation. The paleohydrology of the Turkana Basin 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 Kenyan and Ethiopian Highlands and surrounding regions, except near the Omo River delta 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
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 paleoriver, among others, has increased the water retention capacity of the Turkana Basin after 2.0 Ma, while the redirection of the Suguta paleoriver into Lake Logipi-Suguta drastically reduced the excess water input from the Kenyan Highlands to the basin after 1.4 Ma. The period between 2.0 and 1.4 Ma was thus favorable to large, deep lake formation, while the period after 1.4 Ma was not (Fig. 7). These paleohydrographic and paleogeographic changes should be taken into consideration in paleoclimate and paleoenvironmental reconstructions for the Turkana Basin, as they certainly amplified or reduced water and freshwater food availability in the 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 regions, is a complex issue and cannot be isolated from the specifics of each region (e.g., evolution of the Omo River delta in the northern region; volcanic closure of the Suguta and Turkana paleorivers in the south and southeastern regions; relocation of the basin outlet 300 km to the north; evolution of the Il Bakate River in the northeastern region; etc.).

876 In terms of climate and vegetation, published  $\delta^{13}$ C values from soil carbonate nodules 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., 2011,; Quinn et al., 2013; Quinn and Lepre, 2021; Fig. 8). However, recent studies (Polissar et 880 al., 2019; Faith et al., 2019) have proposed that the long-term C<sub>4</sub> vegetation trend was likely 881 responding to changing atmospheric  $CO^2$  rather than aridity. Compared to  $\delta^{13}C_{\text{sol carbonate}}$  values,  $\delta^{18}$ Osoil carbonate values reflect local rainfall source and amount, evaporation and temperature 883 (Lepre and Quinn, 2022). The  $\delta^{18}O_{\text{solid carbonate}}$  values from the Turkana Basin (Fig. 8) suggest 884 that evaporation and temperature (or the amount of water available for evaporation, see Fig. 8) increased after 2.1 Ma (Lepre and Quinn, 2022). Our synthesis on the western region of the

 Turkana Basin suggests that hydrological conditions have developed repeatedly from 4.20 to 2.22 Ma, then more permanently from 2.10 to 1.30 Ma and more intermittently from 1.27 to 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 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 tolerance of Plio–Pleistocene diatoms and ostracods is still not well known and requires further study. The freshwater micro- and macrofauna suggest that paleolake Lonyumun was fresh and connected to the Indian Ocean, as perhaps were paleolakes Lokochot and Waru. It seems that paleolake Lorenyang expanded after the eruption of the Lenderit basalt, which closed the outflow of the Omo River and Turkana Basin to the Indian Ocean after 2 Ma (Fig. 7). In the western region of the Turkana Basin, the freshwater stingray *D. africana* is present between 1.90 and 1.38 Ma, but in the Koobi Fora and Shungura Formations *D. africana* is known to occur at around 2 Ma and persisted until its extinction around 1.3 Ma (Feibel et al., 1993; Joordens et al., 2013). With the volcanic closure of the Turkana paleoriver, stingrays could no longer migrate to the Indian Ocean, and it appears that *D. africana* became endemic to the Turkana Basin. It is possible that the Omo River delta offered more perennial freshwater 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 suggested by the presence of *Euthecodon* and freshwater mollusks (Fig. 7)*.* In the western region of the Turkana Basin, paleolake Lorenyang appears to have experienced fluctuating paleolimnological conditions from 1.9 to 1.3 Ma, resulting in the enrichment of sediments by 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 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).

 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 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 environment at 3.99–3.98 Ma (Fig. 8). The majority of *K. platyops* and Pliocene hominin remains occur when drinking water and freshwater foods were available at both ~3.50 Ma and 3.30–3.2 Ma (Table 4; Figs. 7 and 8). Moreover, the lithic artifacts excavated at LOM3 occur when drinking water and freshwater foods were available at 3.30 Ma (Fig. 8), but no lithic artifacts have been unearthed in the freshwater environments at <3.60–3.44 Ma. Most *P. aethiopicus*, *P. boisei* and *Homo* sp. have also been found when drinking water and freshwater foods were available at 2.53, 2.33 and 2.25 Ma (Fig. 8). However, no lithic artifacts have been found at 2.53 Ma. The Oldowan complexes of Lokalalei (LA1A and LA2C; 2.34–2.25 Ma) and 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, 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 archaeological site of NAS 4 does not seem to be in an environment where freshwater was abundant (Fig. 8). Thereafter, there are no archaeological and hominin sites up to 1.8 Ma found 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). 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 conditions that seem to have begun to alternate with saline–alkaline conditions as suggested by

 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 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 drinking water and freshwater foods are available sporadically, mostly with beach and sand 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*  is present at the level of the Silbo Tuff, within the spatiotemporal context of the Nadung'a archeological complex (KNM-WT 51261; Table 5; Fig. 8).

 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 aridity. However, as discussed below, several caveats complicate the assessment of an association between drinking water, freshwater foods and hominin occupation, and in particular, the existence of a preference for freshwater foods in the hominin diet and various adaptations to a decoupled landscape, i.e., occupation of the western region of the Turkana Basin by hominins when freshwater macrofauna that could supply their needs colonized this arid zone during episodes of enhanced hydroconnectivity.

#### *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.

 Postmortem transport may have occurred, and chances of preservation mainly exist in depositional centers, where the natural burial of remains occurs. Therefore, archeological, paleontological and paleoanthropological sites may be mainly found near aquatic environments because water effectively transports sediments (and biotic remains) toward areas of deposition. Whereas the Turkana Basin arguably represents a Plio–Pleistocene depocenter within the East African Rift system, our synthesis indicates that the conditions of burial and preservation of fossil remains were not uniform throughout the period considered in the western region of the Turkana Basin. Two important factors toward preservation potential are physicochemical conditions at the depocenter and sedimentation rates, which affect the chance 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 depositional environments (less chance for fragmentation/abrasion; Kendall et al., 2018). In addition, environments where bone and water interactions remain static preserve bones better 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 somewhat higher degree of bone preservation potential in alkaline than freshwater environments and in low energy depositional environments. Substantial variation in rates of 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 were found between 1.8 and 1.4 Ma (e.g., the archeological complex of Kokiselei; Figs. 7 and 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 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 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 dating uncertainty. First, if the confidence intervals for dates are large, existing associations may be blurred by noise derived from dating uncertainty. Second, age determinations of hominin fossils and archeological sites, as well as vertebrates, invertebrates, and microalgae, can be problematic when volcanic ash beds are too widely spaced. However, we consider the effect of geochronological constraints on our observations to be minimal for two reasons: 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 from 4.20 to 0.70 Ma and, secondly, geochronological uncertainty would obfuscate existing associations rather than create false associations (dating uncertainties <50 kyr; Fig. 6). That being said, there are two periods in the western region of the Turkana Basin, from 3.1 to 2.6 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 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 yet been discovered between 3.1 and 2.6 Ma. By contrast, there are a substantial number of correlated outcrops to consider in the period between 1.2 and 0.8 Ma, as geological work has been carried out on hominin and archeological sites found in this chronostratigraphic interval (Delagnes et al., 2006; Maddux et al., 2015, and Brown, unpublished data).

 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

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

 Considering our synthesis, we are tempted to provide a possible paleobiological explanation, namely, that most hominin and archeological sites occur when drinking water expanded into the arid zone and freshwater macrofauna colonized the region. The recurring presence of freshwater micro- and macrofauna in the western region of the Turkana Basin necessarily modified the food chain and the terrestrial environment in which hominins lived. 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 (water, plants, fauna) that resulted in iterative occupation of the western region of the Turkana Basin by various hominins. We highlight periods when freshwater was available, as well as freshwater resources, indicated by the presence of river and lake deposits with freshwater 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 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 1029 may have promoted 1) the growth of  $C_4$  grasses and sedges, which are found on lake margins, deltas, marshes, or floodplain, 2) the dispersal of freshwater foods and 3) the increased accessibility of drinking water and food resources for mammals, including hominins. Thus, in association with the arid environment, these hydrological conditions may have played a role in 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 in the eastern region of the basin as well (Braun et al., 2010b; Archer et al., 2014).

 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 water, the regional isotopic studies from Lomekwi suggest that *K. platyops* shifted from acquiring liquids directly from food toward drinking more water at 3.30 Ma (Quinn et al., 2021); this could be a reflection of enhanced hydroconnectivity in this region associated with the colonization of freshwater biota, which could have supplied the food needs of hominins in the arid zone. In addition, isotopic study at Lokalalei 1A and 2C indicates that woodland/bushland/shrubland was the dominant vegetation structural category. Notably, the wooded grassland category was also present in abundance. Riparian woodlands near a large, 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 suggests the presence of wooded grasslands near a lake margin (Quinn et al., 2013), which may have favored hominin resource use and tool-making behavior between 1.8 and 1.6 Ma. According to these authors, it is possible that *Kenyanthropus*, *Paranthropus* and/or *Homo* used 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 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 at Koobi Fora, for the archeological site of FwJj 20 at 1.95 Ma, based on taphonomic evidence and the association of aquatic fauna with lithic assemblages (Braun et al., 2010b; Archer et al., 2014). These authors suggest that hominins predating *Homo ergaster*/*erectus* may have incorporated aquatic resources such as crocodiles and catfish into their diet, and that these 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 (vertebrates and invertebrates) and the evolution of hominin brain size and cognition

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

#### **7. Conclusions**

 In summary, our synthesis shows that there is a complex interaction between topographic barriers along the Turkana Basin and changes in hydroconnectivity that result over 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 upland rivers and lakes, as well as the temporary establishment of outflows toward other drainages, promoted the colonization of the western region of the Turkana Basin by freshwater macrofauna, such as crocodiles, fish and mollusks. In the northern basin, freshwater conditions 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 paleogeography of basin outlets has been modified after 2 Ma by the volcanic closure of the Turkana paleoriver that connected the southern region of the Turkana Basin to the Indian Ocean (Bruhn et al., 2011; Boës et al., 2019), and by the opening of a new outlet connected to the Nile, possibly from 1.9 Ma, as well as the obstruction of the Suguta paleoriver after 1.4 Ma. These aspects are fundamental to understanding how freshwater conditions interacted with ambient aridity in the Turkana Basin in relation to hominin occupation and faunal succession within a constrained chronological framework. As such, periods of enhanced hydroconnectivity with freshwater foods available to hominins may be assessed by the presence of macrofauna, such

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

1100 The consumption of  $C_4$  and aquatic resources by hominins has been hypothesized in the 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 aquatic organisms may be warranted in the western region of the Turkana Basin. To what extent such interactions affected the anatomical, cognitive and behavioral evolution of hominins in the Turkana Basin remains an important question. Beyond a search for direct interactions, an association between freshwater availability and hominin occupation in the western region of the Turkana Basin requires in-depth quantitative comparisons, which should focus on compiling independent datasets on fossil occurrences of freshwater biota and hominins for subsequent correlative analyses. Such analyses could be undertaken at the scale of the western

 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.

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### **Figure legends**



 **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.

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

 **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) Il 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)

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

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

 **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).

 **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

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

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



 **Figure 9.** Long-term variation in sedimentation rates in the western region of the Turkana Basin (Nachukui Formation) and its influence on archeological site formation and preservation. 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 (<20 cm/kyr), as at Nasura (NS) and Lokalalei (LA). These results suggest that, as long as deposition occurred through time, there was a potential to preserve hominin remains and archeological sites in the Western region of the Turkana Basin. Sedimentation rates have been calculated using Chronomodel v. 2.0 (software developed by Lanos and Dufresne, 2019).









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







#### 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.



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)







 $0.80 - 0.70$ Lakeshore environment, nearshore river deposits and beaches; Nariokotome Mb

tes and invertebrates, including freshwater fauna, between 4.20 Ma and 1.20 Ma and 1.20 Ma and 1.20 Ma and 1.20

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)	<b>Hominins</b>
$\frac{1}{4.9-4.2}$	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	<b>KNM-KP 29287</b>
$3.53 \pm 0.01$	<b>KNM-WT 38341</b>
$\sim$ 3.5 env	KNM-LT 23181,23182,23183
3.5	KNM-WT 22936, 22944
3.5	KNM-WT 40000 (Holotype), 38339
$3.35 \pm 0.05$	<b>KNM-WT 16006</b>
$3.3 \pm 0.1$	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
$3.26 \pm 0.01$	<b>KNM-WT 16003</b>
$3.26 \pm 0.01$	KNM-WT 08556, 08557
$3.2 \pm 0.1$	KNM-WT 38356, 38357
$2.53 \pm 0.02$	<b>KNM-WT 17000</b>
$2.45 \pm 0.05$	KNM-WT 16005
$2.33 \pm 0.02$	<b>KNM-WT 42718</b>
$2.25 \pm 0.02$	<b>KNM-WT 64910</b>
$1.79 \pm 0.02$	KNM-WT 37100, 37744, 37747, 37748
$1.77 \pm 0.1$	<b>KNM-WT 17400</b>
$1.75 \pm 0.05$	<b>KNM-WT 37745</b>
$1.72 \pm 0.07$	<b>KNM-WT 18600</b>
$1.72 \pm 0.07$	<b>KNM-WT 17396</b>
$1.47 \pm 0.03$	<b>KNM-WT 15000</b>
$1.42 \pm 0.01$	<b>KNM-WT 51260</b>
$1.44 \pm 0.03$	<b>KNM-WT 16001</b>
$1 \pm 0.15$	<b>KNM-WT 19700</b>
0.75	<b>KNM-WT 51261</b>

Data from West Turkana on hominins between 4.20 Ma and 0.70 Ma. See text for explana

tions. **References** 

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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.

