Stable oxygen isotopes of crocodilian tooth enamel allow tracking Plio-Pleistocene evolution of freshwater environments and climate in the Shungura Formation (Turkana Depression, Ethiopia).

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Abstract.

15 This study adopts a new approach describing paleohydrology and paleoclimates based on the interpretation of stable oxygen isotopes ($\delta^{18}O_p$) recorded in fossil crocodilian teeth. They represent an archive of prime interest for tracking freshwater paleoenvironmental change, applicable for many paleontological localities in the world: crocodilian teeth are abundant in continental basins and widely distributed since their diversification during the Mesozoic; the enamel phosphate is resistant to diagenesis and retains its original isotopic composition over geological timescales; their $\delta^{18}O_p$ mainly relies on that of the

20 crocodilian's home water body ($\delta^{18}O_w$), which in turn reflects water body types, regional climate, and evaporation conditions. This study presents the first application of this interpretative model to the Shungura Formation (Lower Omo Valley, Ethiopia), a key witness of the important environmental changes in eastern Africa during the Plio-Pleistocene that impacted the evolution of regional faunas, including humans. In this complex and variable environmental context, the $\delta^{18}O_p$ of coexisting crocodilians allows for fingerprinting the diversity of aquatic environments they had access to at a local scale. Like previous geochemical

25 studies performed on paleosols and bivalves in this area, our data indicate a marked increase in $\delta^{18}O_w$ between 2.97 Ma and ca. 1.14 Ma, probably resulting from the joint effect of the migration of the air streams convergence zones between the West African and Indian Summer Monsoons and of the decrease in rainfall amounts above the Ethiopian Highlands. Contrary to some conclusions based on terrestrial proxies, the $\delta^{18}O_p$ of crocodilian teeth does highlight any major change affecting aquatic environments, rather pointing to stability of these environments between 2.97 Ma and ca. 2.57 Ma. By contrast, the diversity

30 of aquatic environments accessible to crocodilians seems to be restricted in most analysed stratigraphical units after ca. 2.32 Ma, a feature that may reflect more arid conditions in the Turkana Depression.

1 Introduction

Water availability is the main factor constraining the distribution of continental flora and fauna, in close connection to regional and local hydrography (climate, physiography of watersheds, geodynamics) (e.g., Bauder et al., 2005; Otero et al., 2011; Mushet et al., 2019; Smith and Boers, 2023). Freshwater environments, therefore, constitute vital components of regions that have yielded fossil hominid remains, but they are often overlooked and described in a more simplified way compared to terrestrial ones.

Over the last million years, in eastern Africa, the Turkana Depression experienced significant environmental changes, particularly in terms of hydrology (e.g., aridification, landscape opening, lake level fluctuation), however new studies have recently challenged the previous models (Nutz et al., 2017, 2020). This region may have hosted a great diversity of types of freshwater environments (hereafter also called water bodies, including channels, rivers, deltas, lakes, swamps, ponds, floodplains, etc., Fig. 1), whose spatial distribution and evolution across time remain to be studied (Haesaerts et al., 1983; Nutz et al., 2017, 2020). The Shungura Formation (Fm) in southwestern Ethiopia, located upstream of the delta of the Omo River flowing in Lake Turkana, indicates the continuous presence of water during the Plio-Pleistocene and is thus interpreted as a refuge area for wildlife (Bobe, 2006). However, so far, its freshwater environments have been only described by sedimentological studies and the analysis of invertebrate assemblages, despite their importance to capture the interactions between climate, geodynamics, and aquatic communities (Van Damme et Gautier 1972; Peypouquet et al. 1979, 1980; Heinzelin et al. 1983; Van Boxclaer et Van Damme 2009). Therefore, contextual studies on ecosystems' aquatic component often lack reliable and complete paleoenvironment reconstructions. In this context, the study of freshwater ectotherm vertebrates can provide original and valuable insights into the associated environmental conditions, such as hydrographic network connections, drainage characteristics, waterbody depth, salinity levels, temperatures, and seasonal climatic shifts (e.g., Otero et al., 2011). Such features differ from the environmental information gained through the study of terrestrial fauna, which is highly dependent on its ecology.

The present study focuses on the oxygen isotopic composition of crocodilian teeth enamel phosphate ($\delta^{18}O_p$) to track hydrological changes over time. Crocodilian enamel apatite is an ideal paleoenvironmental archive that can be used in multiple sites, as it is highly resistant to diagenetic and dissolution-precipitation
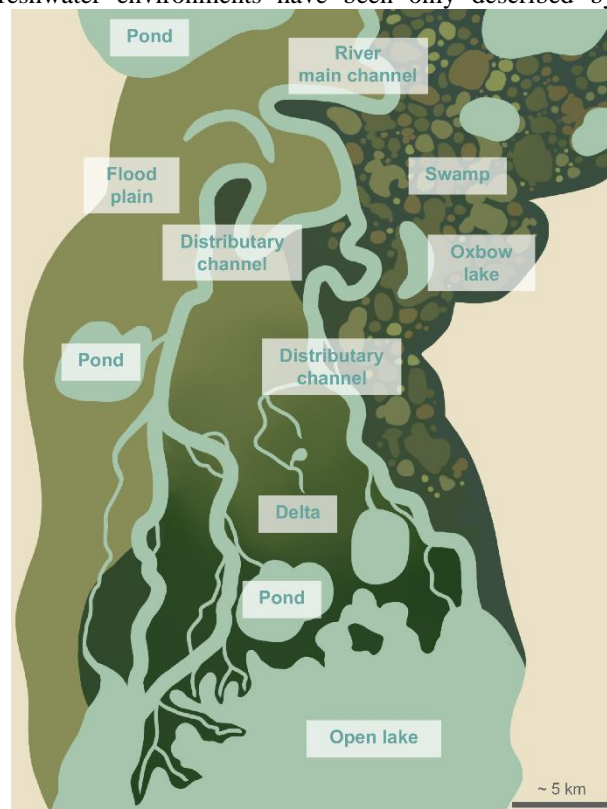
Figure 1. Schematic representation of the diversity the various freshwater environments or water bodies that could be expected at a local scale in a lacustrine delta context.

65   processes (Kolodny et al., 1983, 1996; Shemesh et al., 1983; Lécuyer et al., 1999) and found in abundance in continental sediments since the expansion of this clade in the Jurassic, especially in African continental series (e.g., Arambourg, 1967; Tchernov, 1976, 1986; Markwick, 1998; Brochu et al., 2022). As described hereafter, crocodilians have a low metabolism and are aquatic, this means that the interpretation of their $\delta^{18}O_p$ is much more constrained because it mainly reflects $\delta^{18}O_p$ of the water body ($\delta^{18}O_w$) they occupied during tooth formation (over several months). The linear relationship between $\delta^{18}O_p$ of

70   crocodilian apatite and $\delta^{18}O_w$ (Amiot et al., 2007) enables to estimate $\delta^{18}O_w$ from $\delta^{18}O_p$, thus providing valuable insights into aquatic environmental conditions. Previous analyses of $\delta^{18}O_p$ on crocodilians were systematically interpreted together with isotopic data from other sympatric vertebrates (fish, turtles, dinosaurs, mammals). This approach can help to infer the thermophysiology and ecology of taxa of interest (e.g., Amiot et al., 2010a), to estimate paleotemperatures (e.g., Amiot et al., 2008), aridity (Amiot et al., 2010b), to identify terrestrial or aquatic, freshwater or marine lifestyles (e.g., Goedert et al., 2020)

75   or to differentiate the water sources used by different co-existing taxa (Suarez et al. 2012).

This paper proposes a new interpretative model of the $\delta^{18}O_p$ of crocodilians by using the comprehensive knowledge of the physiology and ecology of crocodilians. This new approach is applied to fossil crocodilian teeth from the Shungura Fm, representing an ideal framework for the first application, due to the continuous sedimentary record from ca. 3.75 Ma and ca. 1.09 Ma (Boisserie et al., 2008; Table S1). The Shungura Fm reveals diverse aquatic environments, related to lake level

80   fluctuations, mainly fed by two monsoons, despite a complex, highly variable, and increasingly arid context (Haesaerts et al. 1983; Kebede and Travi, 2012; Nutz et al. 2020). The growing knowledge of the evolution of its environments, the continuity of the series over several million years, and its accurate dating allow for discussing the new isotopic data in a well-constrained framework. However, uncertainties persist about the timing of major environmental Plio-Pleistocene changes, reported in a disparate way according to the proxies, the factors that control them and their impact on the evolution of fauna, including

85   humans (e.g., Trauth et al., 2021).

By determining to what extent the $\delta^{18}O_p$ of crocodilians would allow tracking complex environmental changes in this region, this paper discusses (1) the diversity of aquatic environments occupied by crocodilians by interpreting the range of $\delta^{18}O_p$ values, and (2) the variation of the $\delta^{18}O_p$ values as an indicator of local evaporation and $\delta^{18}O$ values of meteoric waters. Building up on that discussion, guidelines are provided for further applications to other paleontological and archaeological sites.

90   **2 Material and method**

2.1 Study area and main information on the aquatic environments

The Omo Group, including the Shungura Fm, became a major reference for the Plio-Pleistocene biotic and environmental evolution thanks to the early work of the International Omo Research Expedition (IORE) from 1967 to 1976 (e.g., Howell, 1968; Coppens & Howell, 1976; Heinzelin, 1983). The present study takes place within the framework of renewed fieldwork
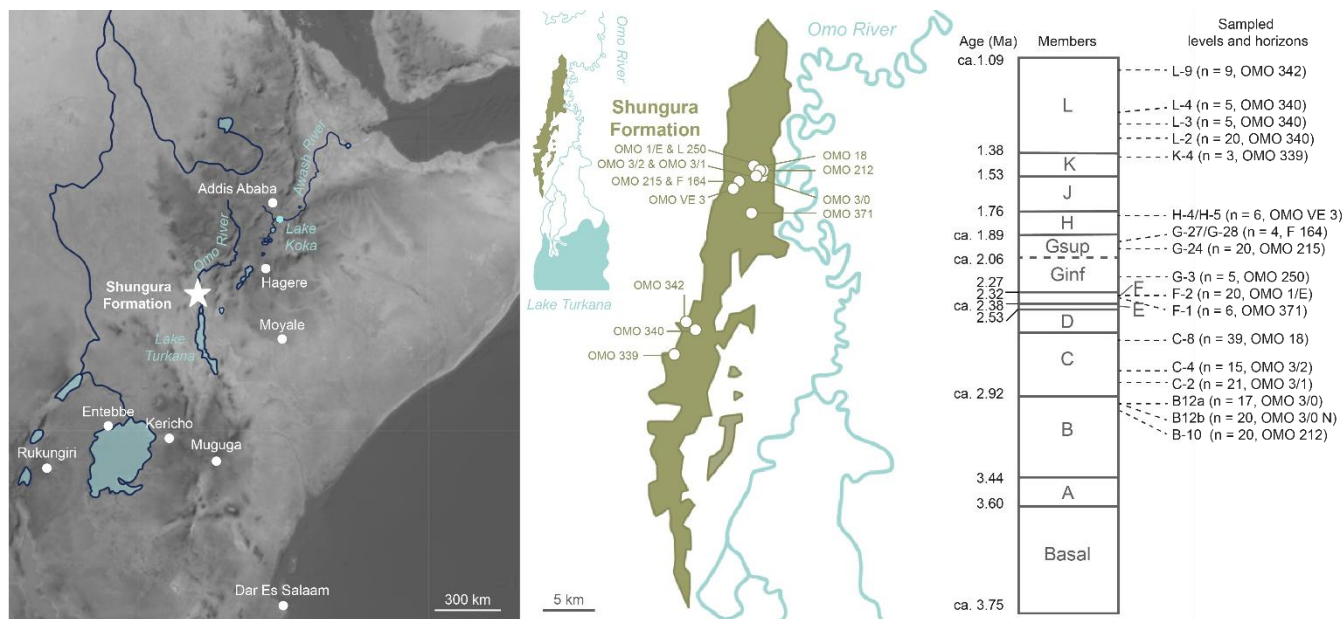
Figure 2. Geographic location and chronostratigraphic column of the Shungura Formation, Lower Omo Valley, Ethiopia and distribution in the map and the log of horizons where crocodilian teeth were sampled for this study. Geographic location of geochemical data from East-African GNIP stations and water samples of Ethiopian rivers and lakes (map ESRI 2022).

in the Shungura Fm and Usno Fm enabling new paleontological, archaeological, geological, and paleoenvironmental analyses developed by the Omo Group Research Expedition (OGRE) on both IORE and new data. This research program investigates biological evolution and its interactions with environmental factors at the local scale of the Lower Omo Valley (Boisserie et al., 2008). One approach favoured by the OGRE is to exploit paleoenvironmental proxies directly linked to the continental paleobiological record (e.g., Souron et al., 2012; the present study).

The Shungura Fm is exposed in the Lower Omo Valley (Fig. 2). With 800 m of alternating volcanic tuffs and fluvial, deltaic and lacustrine fossil-bearing sediments (more than 57,000 specimens to date), this continental sedimentary succession is one of the most extensive and best-dated, documenting the evolution of ecosystems of the Lower Omo between ca. 3.75 Ma and ca. 1.09 Ma (Fig. 2). The stratigraphic division into members and sub-members of the Shungura Formation defined by Heinzelin (1983) is used in this paper, while keeping in mind that it has its limits at the scale of the formation. A revised age model including the latest absolute ages is provided in Table S1. For the last 5 million years, the Omo River, which also feeds Lake Turkana, mainly received sediments and water from the Ethiopian Highlands. The Shungura Fm recorded hydrological change over time: although it was dominated by a river system most of the time, the lake level rose until covering the site in the middle of Member G (2.06-1.95 Ma, Lorenyang highstand) and again at the top of Member L (1.19-1.09 Ma) (Haesaerts et al., 1983; Nutz et al., 2020). New fieldwork observation by the OGRE suggests that the Shungura Fm was under lacustrine influence from the Basal Member to unit B-8, maybe until B-10 (3.75-2.98 Ma, Lokochot highstand). Currently, the course of the Omo River is more incised and constrained due to the rift narrowing that occurred after 1.2 Ma (Nutz et al., 2022). Before, the Omo River migrated onto the area occupied at present-day by the Shungura Fm.

This area underwent a general trend towards aridification in the Plio-Pleistocene, with the Lower Omo Valley becoming
115   increasingly dominated by grasslands (e.g., Levin et al., 2011; Negash et al., 2015, 2020; Blondel et al., 2018, 2022). This
trend was nevertheless locally buffered in the Lower Omo Valley, which maintained a more wooded environment than along
the lake shores (Nachukui Fm and Koobi Fora Fm), at least until the end of the Lorenyang highstand (Levin et al., 2011). This
was punctuated by periods of increased humidity and precipitation in the Ethiopian Highlands, which temporarily increased
the Omo woody cover (Nutz et al., 2020). This may have made the Omo Valley a refuge for forest and woodland flora and
120   fauna during this period of high climate variability (e.g., Bobe, 2006).

2.2 Plio-Pleistocene eastern African crocodilian diversity

The Shungura Fm yielded two distinct teeth morphologies: elongated and anteroposteriorly
curved teeth (hereafter referred to as pointed) and shorter and stouter, conical teeth (hereafter
referred to as rounded) (Fig. 3). This indicates the persistent presence of several crocodilian
125   taxa over time, despite the local environmental changes. Four main genera of crocodilians have
been identified in the Plio-Pleistocene outcrops of the Turkana Depression: the longirostrine
and piscivorous *Euthecodon* and *Mecistops*, the generalist *Crocodylus (C. niloticus* preys on all
kind of prey and *C. thorbjarnarsoni* is the largest known species in this genus and probably fed
on large mammals), and the brevirostrine *Rimasuchus* adapted to prey on large mammals
130   (Arambourg, 1967; Tchernov 1976, 1986; Storrs, 2003; Brochu et al., 2010; Brochu and Storrs,
2012; Brochu, 2020). The pointed crocodilian teeth correspond to a piscivorous crocodilian such
as *Euthecodon* and *Mecistops*, whereas the rounded crocodilian teeth could belong to
Crocodylus, *Rimasuchus* and possibly *Mecistops* too (molariform teeth at the back of the tooth
rows). The different diets reflected by these two dental morphologies could induce different
135   ecologies and therefore lead to a different oxygen isotopic signal as well, which was also tested
here.

**Figure 3. Two morphotypes
of crocodilian teeth are
encountered in the Shungura
formation outcrops: A,
rounded (B-12-r-1); B,
pointed (B-12b-p-2).**

2. 3 Sample collection

Two hundred thirty-eight (238) crocodilian teeth were collected from 16 units of the Shungura Fm aged between ca. 2.97 Ma
and ca. 1.14 Ma (Tables 1 and S2, Fig. 2). The specimens were purposely collected for destructive analysis during the OGRE
140   field missions in 2013 and 2016. All teeth with a minimum size of 1 cm in height were exhaustively collected (rounded and
pointed) from a large part of the Shungura series, each sample corresponding to a single locality (or part of a locality). This
sampling strategy allows for exploring the signal yielded by crocodilian teeth in units documenting major environmental
transitions. Units K-4 and L-3 did not yield rounded teeth, and no pointed teeth were present in unit L-9. The analyses presented
were preferentially conducted on pointed teeth, to build a comparable dataset along the series, as they are most likely to be
145   from piscivorous crocodilians and are particularly linked to aquatic environments. Teeth with bright enamel and without white

alteration marks were selected for isotopic analyses. B-12a and B-12b are two spots in the same locality in lateral continuity, OMO 3/0 (ca. 2.94 Ma), separated by about 200 m. Some units are sometimes difficult to distinguish, and the elements collected on a surface can thus group two units (Tables 2 and S2, Fig. 2). On surface collections of this type, a little temporal mixing is therefore possible.

2. 4 Sample preparation and analysis

For each tooth, enamel was sampled from base to apex of the crown to average potential seasonal variation in $\delta^{18}O_p$ using a micro-milling Dremel device and was then crushed in an agate mortar and pestle.

To isolate the phosphate group of enamel apatite (O'Neil et al., 1994; Wenzel et al., 2000), dissolved apatite was converted in Ag_3PO_4 following a method adapted from Joachimski et al. (2009). About one mg of enamel powder was weighed into small polyethylene beakers and dissolved overnight in 33 µl 2M HNO_3. The solution was neutralized with 33 µl 2M KOH, and Ca^{2+} precipitated as CaF_2 by adding 33 µl of 2M HF. After centrifugation, the supernatant was transferred to a clean beaker and 0.5 ml of a silver amine solution was added in order to precipitate Ag_3PO_4 at 60°C for 8 hours. Silver phosphate crystals were rinsed several times with distilled water and dried at 40°C for 30-60 minutes, and ground into powder in an agate mortar and pestle.

Between 0.2 mg and 0.3 mg of Ag_3PO_4 were weighted into silver foil and analysed for part of the sample set at the GeoZentrum Nordbayern of the Friedrich-Alexander University Erlangen-Nürnberg using a TC-EA (high-temperature elemental analyser) coupled online to a Thermo Fisher Delta V IRMS and for the other part at the University of Burgundy (Dijon, France) using a High-Temperature Pyrolysis Analyzer (Elementar Pyrocube) connected online to an Elementar Isoprime mass spectrometer. Samples were all combusted at 1450 °C and the generated CO gas was transferred in a helium stream to the mass spectrometer. Samples as well as standards measured over the course of analyses were generally measured in triplicate. All values are reported in ‰ relative to V-SMOW. The average oxygen isotopic composition of NBS 120c standard was measured as 21.7 ‰ VSMOW. Accuracy was monitored by replicate analyses of NBS120c. Reproducibility was calculated based on triplicate sample and standard analyses and was generally < ±0.3 ‰.

Oxygen isotope analyses have additionally been performed on the carbonate group of some powdered enamel samples ($\delta^{18}O_c$) to control a possible effect of diagenesis on the sample isotopic composition. To this end, 0.10-0.13 mg of enamel powder were loaded in glass vials and reacted with a 102% H_3PO_4 solution at 70 °C for 20 min in a ThermoScientific™ Kiel VI carbonate preparation device coupled with a ThermoScientific™ Delta V Plus™ IRMS at the Biogéosciences Laboratory of the University of Burgundy. $\delta^{18}O_c$ data were reported in ‰ relative to V-PDB (Vienna Pee Dee Belemnite) using certified international standard NBS19 ($\delta^{18}O$ = −2.20 ‰). External reproducibility was assessed by replicate analyses of NBS19 over the course of the analyses and is better than ±0.07 ‰ (2σ).

2. 5 Statistical analyses

Means are presented with ±1- standard deviation. Significance is evaluated at α = 0.05. Analyses were performed in R Version
4.2.2 (R Core Team, 2022). The $\delta^{18}O_p$ difference between stratigraphical units was investigated with a two-way ANOVA and
Pairwise Wilcoxon Rank Sum Tests with Holm correction (non-parametric post-hoc tests). The trend over time was identified
180   using least-squares linear regression and reported as adjusted R^2.

3 Results

The isotopic composition of crocodilian enamel
phosphate and the resulting estimated $\delta^{18}O_w$ are
summarised in Table 1 (full dataset in Table S2) and
185   displayed in Figs. 4 and 8. $\delta^{18}O_p$ values range
between 15.1 ‰ and 22.9 ‰, while $\delta^{18}O_c$ values
range between −8.2 ‰ and 1.2 ‰. The $\delta^{18}O_p$ is not
statistically different between round and pointed
teeth (ANOVA: F = 1.136, df= 8, p = 0.342) (Fig. 4).
190   From B-10 to C-8, F-2, G-27/G-28, H-4/H-5, and K-

Figure 4. Oxygen isotopic composition (mean±1sd) of the crocodilian teeth of the Shungura Formation, relative to the tooth morphotypes.

4, the range of $\delta^{18}O_p$ values is greater than 2.3 ‰; while in the other units F-1, G-3 to G-24, and L-2 to L-9, the range of $\delta^{18}O_p$
values does not or barely exceeds this variation. Minimal $\delta^{18}O_p$ values increase from 15.3 ‰ in B-10 (2.97 Ma) to 18.6 ‰ in
L-9 (ca. 1.14 Ma) (R^2=0.49), corresponding to an increase in $\delta^{18}O_w$ values from −6.6 ‰ to −3.5 ‰. However, this trend is
nuanced when studying the isotopic signal between the stratigraphic units. The $\delta^{18}O_p$ values are particularly high in units F-2,
195   G-24, L-2, and L-9, while units C-2 and C-8 yielded low $\delta^{18}O_p$ values (Table S3). The $\delta^{18}O_p$ values are statistically homogenous
in the two sub-localities of unit B-12 (spatially close but with slightly different sedimentary facies, p = 0.12). After unit H-
4/H-5 (1.84 Ma), the $\delta^{18}O_p$ values strongly increase and remain high.

Table 1. Mean, SD, minimal and maximal values of $\delta^{18}O_p$ values for each sampled locality of the Shungura Formation.
200   **Abbreviations: n number of analysed teeth.**

				$\delta^{18}O_p$ of crocodilian teeth (‰ V-SMOW)				Estimated $\delta^{18}O_w$ (‰ V-SMOW)	
Unit	Locality	Age (Ma)	n	Mean	SD	Min	Max	Min	Max
L-9	OMO 342	ca. 1.14	9	19.84	0.77	18.55	20.95	−3.92	−3.44
L-4	OMO 340	ca. 1.24	5	19.89	0.72	19.28	21.00	−3.32	−1.91
L-3	OMO 340	ca. 1.30	5	19.49	0.41	19.07	20.13	−3.49	−2.62
L-2	OMO 340	ca. 1.34	20	20.12	0.48	18.99	20.78	−3.56	−2.09
K-4	OMO 339	ca. 1.39	3	20.74	2.47	18.06	22.93	−4.32	−0.34
H-4/H-5	OMO VE 3	1.84	6	17.96	1.66	16.29	20.99	−5.77	−1.92

G-27/G-28	F 164	ca. 1.95	4	17.97	1.20	16.01	20.48	−6.00	−2.34
G-24	OMO 215	ca. 1.98	20	20.28	0.58	19.40	21.28	−3.22	−1.68
G-3	L 250	2.19	5	16.75	0.80	16.07	18.04	−5.95	−4.34
F-2	OMO 1/E	ca. 2.32	20	19.45	1.10	16.57	20.87	−5.54	−2.01
F-1	OMO 371	ca. 2.32	3	17.88	1.28	16.46	18.97	−5.63	−3.57
C-8	OMO 18	ca. 2.57	39	17.86	1.43	15.11	21.08	−6.74	−1.84
C-4	OMO 3/2	ca. 2.76	15	18.57	1.43	15.87	20.26	−6.12	−2.52
C-2	OMO 3/1	ca. 2.86	21	17.96	1.00	15.84	19.70	−6.14	−2.98
B-12a	OMO 3/0	ca. 2.94	17	19.11	0.86	17.92	20.89	−4.45	−2.00
B-12b	OMO 3/0 N	ca. 2.94	20	18.14	0.58	16.85	18.96	−5.31	−3.59
B-10	OMO 212	2.97	20	18.53	2.02	15.32	22.22	−6.56	−0.91

4 Discussion

4.1 Preservation of the original oxygen isotopic composition
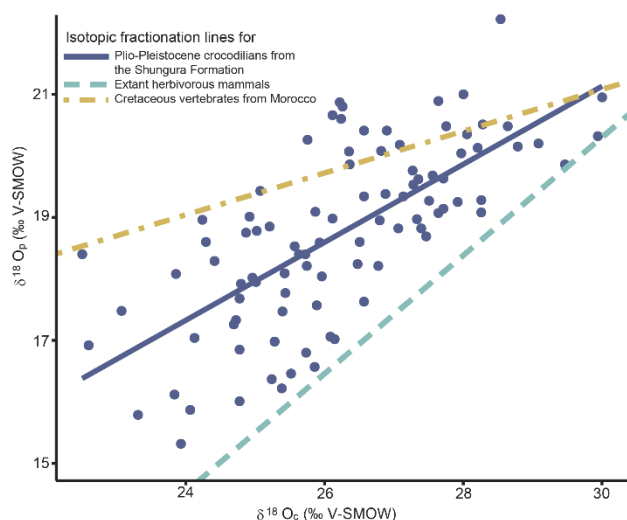
Figure 5. Oxygen isotope compositions of enamel phosphate ($\delta^{18}O_p$) from the studied crocodilians from the Shungura Formation plotted against their corresponding oxygen isotope composition of carbonate ($\delta^{18}O_c$), along with the phosphate–carbonate isotopic fractionation line established for Cretaceous vertebrates from Morocco (Amiot et al., 2010b) and extant herbivorous mammals (Iacumin et al., 1996).

Tooth enamel has densely packed large apatite crystallites, which should best retain the primary $\delta^{18}O_p$ (Kolodny et al., 1983; Shemesh et al., 1983; Pucéat et al., 2004). However, alterations due to secondary apatite precipitation and diagenesis can still occur and the preservation of the original isotopic signal must be ensured before proceeding to paleoenvironmental interpretations (Blake et al., 1997; Zazzo et al., 2004a). Although no reliable method exists to definitively attest the preservation of the original isotopic signal, combined phosphate and carbonate $\delta^{18}O$ of enamel has been used to evaluate potential impact of post-mortem processes on apatite $\delta^{18}O$. Indeed, in modern mammal and fossil vertebrates, phosphate and carbonate $\delta^{18}O$ of apatite defines a linear relationship, from which samples that have been modified by post-mortem diagenetic processes depart (Iacumin et al., 1996, Amiot et al., 2010b).

The samples analyzed in this study lay on the linear relationship

220   established for mammals and various northern African Cretaceous vertebrates (Iacumin et al., 1996; Amiot et al., 2010b) (adjusted R² = 0.50; Spearman's correlation coefficient = 0.74) (Fig. 5), suggesting preservation of their original oxygen isotope composition. This is also supported by the maximal difference of 10.8 ‰ between $\delta^{18}O_p$ and $\delta^{18}O_c$ (V-SMOW), which lays below the value of 14.7 ‰ expected for altered samples (Vennemann et al., 2001; Zazzo et al., 2004b). In addition, the lack of homogeneity (<1 ‰ range) of $\delta^{18}O_p$ values within each unit (except L-3) further supports this view, reflecting the

225   diversity of the life history of individuals and the good match of values to other geochemical studies dealing with modern and ancient crocodilians. We hence argue that the $\delta^{18}O_p$ values of the teeth analyzed in this work can be interpreted as a function of the evolution of the local aquatic environments and regional climate during the Plio-Pleistocene in the Turkana Depression.

4.2 Construction of the interpretation model of the $\delta^{18}O_p$ of a fossil crocodilian enamel in the Shungura Fm

4.2.1 How representative is the $\delta^{18}O_p$ of a fossil crocodilian tooth of the water body it used to live in?

230   To use the $\delta^{18}O_p$ of crocodilian enamel as a paleoenvironmental proxy, it is first necessary to understand how the isotopic signal is constructed. The $\delta^{18}O_p$ of crocodilian enamel depends on the body temperature in the jaw where the enamel mineralizes, which controls the amplitude of the isotopic fractionation between phosphate and body water, and on the isotopic composition of the body water, which is dependent on the balance between oxygen inputs and output fluxes (Kohn, 1996; Bryant and Froelich, 1995; Amiot et al., 2007) (Fig. 6).

235   Crocodilians have various sources of oxygen, including drinking water, water from food, oxygen from dry food, and inhaled O_2. Oxygen outputs include liquid water losses (urine) and vapour water losses (cutaneous, oral, and nasal) as well as exhaled CO_2 (Bryant and Froelich, 1995; Kohn, 1996). Rough estimates of the relative contribution of these oxygen fluxes can be made based on the existing literature on crocodilian physiology and ecology (Cott, 1960; Cloudsley-Thompson, 1968; Altman & Dittmer, 1972; Grigg, 1978; Glass & Johansen, 1979; Seymour et al., 1985, 2013; Davis et al., 1980; Mazzotti & Duson, 1989;

240   Christian et al., 1996). Based on these studies, at 25 °C, 85 % of oxygen input comes from environmental water and most of the water output is vapour water losses (up to 75 %) (Fig. 6). Hence, the crocodilian body water $\delta^{18}O$ is mainly determined by their drinking water, which corresponds to the water in which crocodilians live ($\delta^{18}O_w$), and by body water evaporation (Fig. 6).
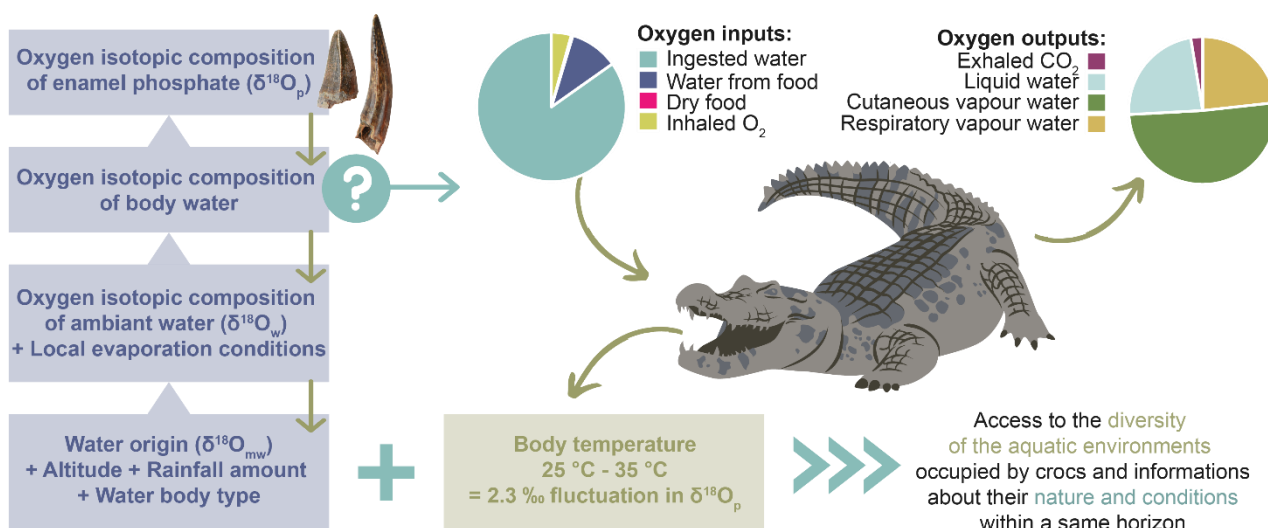
Figure 6. Summary of the extrinsic (water origin, altitude, rainfall amount, evaporation) and intrinsic (oxygen outputs, body temperature) factors influencing the oxygen isotopic composition of the crocodilian enamel, including the main oxygen fluxes controlling the oxygen isotope composition of crocodilian body water.

Crocodilians are ectothermic vertebrates, meaning their body temperature fluctuates with environmental conditions, which has
245 an impact on the amplitude of the oxygen isotopic fractionation between body water and enamel apatite. However, they can
somewhat regulate their body temperature by land-water movements for heat-seeking or -avoidance and physiological
adjustments (Smith, 1979; Lang, 1987a, 1987b). The activity range for many extant species is 25-35 °C, but they tend to prefer
a thermal gradient near the upper limit (35-37 °C) in tropical regions (Lang, 1987b; Markwick, 1998). Existing studies suggest
that crocodilians have a high degree of thermoregulation, and their body temperature is relatively independent of water
250 temperature, especially for large individuals (Smith, 1979; Lang, 1987b; Grigg et al., 1998; Seebacher et al., 1999). This is
due to the convective transfer of heat decreasing and the metabolic production of heat increasing with body size. In this study,
most of the sampled material consists of large fossil teeth, allowing to assume that they may have belonged to large individuals
with relatively stable and high body temperatures. Given their capacity for thermoregulation, crocodilians occupying the same
environment probably do not always have the same body temperature. Therefore, several individuals living in the same
255 environmental context are expected to present a range of variation in body temperature up to 10 °C, approximately
corresponding to a maximal shift of 2.3 ‰ in $\delta^{18}O_p$ (Longinelli and Nuti, 1973; Kolodny et al., 1983; Pucéat et al., 2010) (Fig.
6). Amiot et al. (2007) did not identify any interspecific variation of $\delta^{18}O_p$ in captive crocodilians reared in the same water,
but it may be due to the artificial environment they were in, which may not have allowed them to display the same diversity
of behaviour as in the wild.

260 Crocodilians are relatively sedentary, they only migrate over short distances seasonally or to mate (a few tens of kilometres)
(Lang, 1987a; Tucker et al., 1997; Swanepoel, 1999; Campbell et al., 2010; Beauchamp et al., 2018). Their fast-growing teeth
thus record the oxygen isotopic composition of the water body or watershed they occupied. Despite the significant Plio-
Pleistocene hydrological changes, several crocodilian species have persisted for millions of years in the Shungura Fm, likely
due to their ability to adapt to a wide range of aquatic habitats. These include rivers, swamps, lakes, estuaries, and freshwater
265 and saline waters (e.g., Isberg et al., 2019). The diversity of water bodies occupied by past crocodilians thus likely reflects a
significant part of the types of aquatic environments available at a local scale (Figs. 1 and 6).

4.2.2 Determinants of $\delta^{18}O$ of Ethiopian waters

Rainfall amount, topography, distance from coastlines, temperature and moisture source are usually invoked to explain the
isotopic composition of meteoric waters ($\delta^{18}O_{mw}$) in intertropical regions (Dansgaard, 1964; Rozanski et al., 1996; Levin et
270 al., 2009). Moisture supply in the Ethiopian Highlands is determined by the seasonal migration of the Intertropical
Convergence Zone (ITCZ) and the Congo Air Boundary (CAB) and comes from the Atlantic and Indian Oceans, recycled
continental moisture from the Congo Basin and possibly from southern lakes (Levin et al., 2009; Kebede and Travi, 2012).
Table 2 shows that the oxygen isotopic composition of rainfalls in eastern Africa at similar altitudes is not correlated to the
amount of precipitation. This indicates that other factors, such as the source of the moisture, are dominant.

275 Currently, the Turkana Depression is a region with a hot and semi-arid climate, with less than 500 mm of annual precipitation
and an annual average temperature of 29-30 °C (Merkel, 2023), a climate that does not explain the relatively large water

availability in the basin. Lake Turkana is mainly fed by the Omo River, which originates in the Ethiopian Highlands, southwest of Addis Ababa (Schuster et al. 2022). The $\delta^{18}O_w$ of the Omo River is influenced by the climate of this region, where moisture is brought at 75 % by the Western African Monsoon, coming from the Atlantic Ocean and crossing the Congo basin (June-

280 September, $\delta^{18}O_{mw}$ of −2.59 to −1.99 ‰ at Entebbe, west to Addis Ababa), and the rest by the Indian Summer Monsoon from the equatorial Indian Ocean ($\delta^{18}O_{mw}$ of −4.65 to −3.81 ‰ at Muguga, east to Addis Ababa) (Camberlin, 1997; Kebede and Travi, 2012). In regions with high levels of evapotranspiration, the $\delta^{18}O_{mw}$ values are generally similar or greater than the $\delta^{18}O$ values of ocean source water due to the wholesale return of transpired water consumed by plants to the atmosphere (Levin et al., 2009). Therefore, the water vapour in the Congo basin results in rainfall with $\delta^{18}O_{mw}$ equal to or greater than that of the

285 Atlantic Ocean. This ^{18}O-enriched rainfall is the main contributing factor to the higher $\delta^{18}O_{mw}$ values recorded in Addis Ababa compared to other parts of eastern Africa (Table 1, Rozanski et al., 1996; Levin et al., 2009; Kebede and Travi, 2012). The Ethiopian and eastern-African Dome form channels or obstacles for these low-level air streams, preventing the Indian Summer Monsoon to get further west in the Ethiopian Highlands and the Atlantic and Congo moisture to get further north and east (Levin et al., 2009). The elevation of the Ethiopian Dome up to 4500 m has mainly taken place well before the Plio-Pleistocene,

290 so a change in topography seems unlikely to result in significant variation in $\delta^{18}O_{mw}$ in the context of the Shungura series (Abbate et al., 2015). Moreover, Passey et al. (2010) concluded that air temperature has not changed or only slightly decreased in the Turkana Depression over the past 3 million years, and thus cannot explain the $\delta^{18}O_{mw}$ variation observed in this region.

Table 2. Present-day geographic, meteorological, and geochemical data recorded from eastern African GNIP stations and surface water samples of Ethiopian rivers and lakes, placed on the map in Fig. 2. Additional data from the Goma station is provided for the
295 **Discussion section.**

Locality	Country	Altitude (m)	Mean annual precipitation (mm)	Mean annual $\delta^{18}O$ (‰, V-SMOW)	References
Surface waters					
Omo Delta	Ethiopia	395	226	−1.2 to −0.1	Vonhof et al., 2013
Lake Turkana	Kenya	360	437	4.44 to 7.21	
Awash River	Ethiopia	1590	371	−2.41	Hailemichael et al., 2002
Lake Koka	Ethiopia	1590	371	1.55	
Meteoric waters from eastern Africa					
Addis Ababa	Ethiopia	2355	1179	−1.31	
Dar Es Salaam	Tanzania	55	1123	−2.83	
Entebbe	Uganda	1140	1628	−2.78	
Hagere Selam	Ethiopia	2625	1138*	−3.34 to −0.67	IAEA, 2023 except *Merkel, 2023
Kericho	Kenya	2144	1958*	−2.77	
Moyale	Ethiopia	1090	619*	−4.04 to −3.82	
Muguga	Kenya	2102	674*	−6.18 to −1.09	
Rukungiri	Uganda	1640	1509*	−4.78 to −0.11	
Meteoric waters from central Africa					
Goma (Biraro)	Democratic Republic of the Congo	1540	1916	−3.55	

Today, the average $\delta^{18}O_w$ value at the Omo River Delta is between −1.2 ‰ and −0.1 ‰, while the value at Lake Turkana (endorheic) is between 4.4 ‰ and 7.2 ‰, with an ^{18}O-enrichment between 4.3 ‰ and 8.4 ‰ (Table 1) (Kebede and Travi, 2012; Vonhof et al., 2013) (Table 1). Lake Koka is an artificial and exoreic lake ($\delta^{18}O_w = 1.55$ ‰) with a minor ^{18}O-enrichment

300   of 4.0 ‰ compared to its tributary, the Awash River ($\delta^{18}O_w = −2.4$ ‰) (Table 1) (Hailemichael et al., 2002). The surface area, evaporation and drainage can be determining factors for the isotopic composition of lakes (Kebede et al., 2009; Kebede and Travi, 2012). From the data of Lake Koka and the Awash River, one could expect an exoreic lake fed by the Omo River to have a $\delta^{18}O_w$ in the order of 2 ‰ to 4 ‰. These values will be compared to the Plio-Pleistocene $\delta^{18}O_w$ values estimated from the $\delta^{18}O_p$ of Shungura crocodilian enamel. Calculation of $\delta^{18}O_w$ values from $\delta^{18}O_p$ of Shungura fossil crocodilian enamel is

305   based on the fractionation equation of Amiot et al. (2007). Note that this fractionation equation mainly relies on isotopic data from extant modern captive crocodilians, which form their teeth in humid greenhouse contexts, potentially overestimating the inferred values. In their natural environment, large cutaneous and respiratory evaporation may lead to an ^{18}O enrichment of crocodilians' body water relative to their environmental water, which is not considered in the equation (Amiot et al., 2007).

4.2.3 Interpretative model of the $\delta^{18}O_p$ of crocodilian enamel

310   The interpretative model proposed in this paper is adapted to the context of the Shungura Fm (Fig. 7). In the first part of the model, once the small variation in $\delta^{18}O_p$ due to the fluctuating body temperature of crocodilians (2.3 ‰) is excluded, the
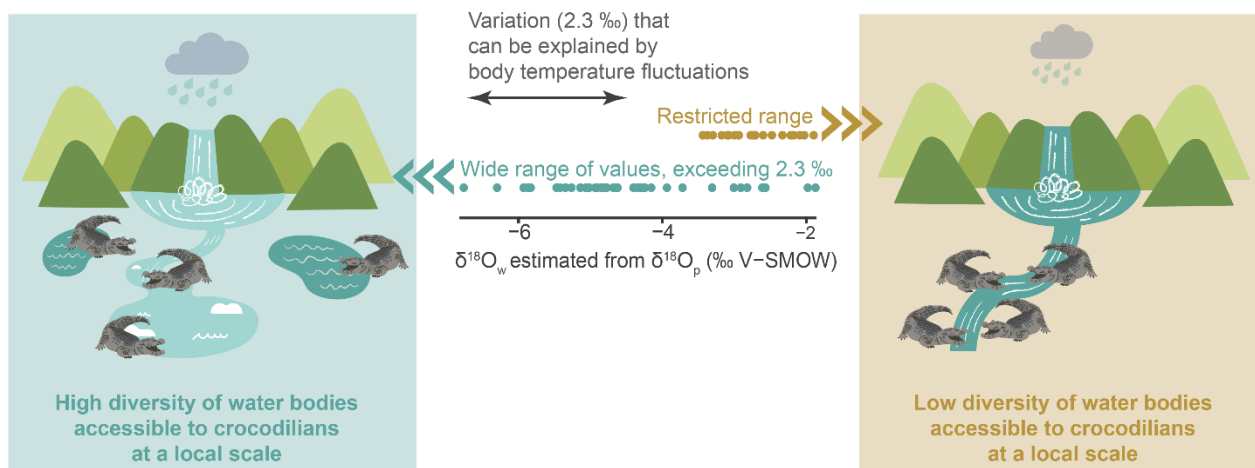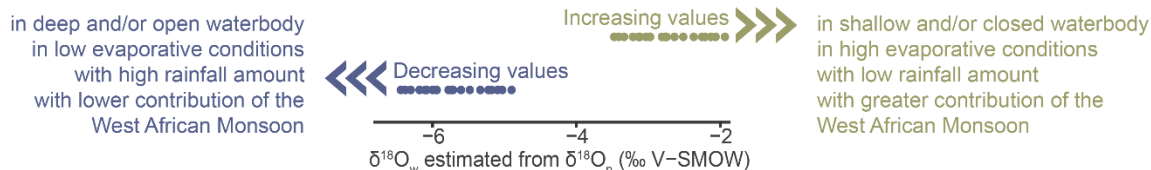
Figure 7. Interpretative model of the $\delta^{18}O_w$ estimated from $\delta^{18}O_p$ of crocodilian teeth in the context of the Shungura Fm.

remaining range of $\delta^{18}O_p$ values within the same unit should reflect the local variety of water body types (with different $\delta^{18}O_w$) occupied by these animals. In other words, only one type of aquatic environment was available for crocodilians in a unit where the data distribution does not exceed 2.3 ‰. On the contrary, if the distribution exceeds 2.3 ‰, then different aquatic

315 environments were occupied by these animals, characterised by different evaporation conditions and/or different water sources. This part of the model opens a window into the hydrological dynamics of the basin.

Concerning the second part of the model, interpreting past $\delta^{18}O_w$ in the Omo Valley context should mainly consider the variability of the evaporative state of water (aridity, drainage, and depth of water bodies) and rainfall (especially the water supply on the Ethiopian Dome), low-level air streams and the migration of the convergence zone. In other words, decreasing

320 $\delta^{18}O_w$ values might be mainly linked to an increased rainfall supply on the Ethiopian Dome, a northward penetration of the Indian Summer Monsoon (consistent with low relief and a decrease in its intensity), and/or a more open/deep water body (Otero et al., 2011; Kebede and Travi, 2012). On the contrary, increasing $\delta^{18}O_w$ values are expected to result from drier regional conditions enhanced, an increase in the intensity of the Indian Summer Monsoon and a relatively greater contribution of the recycled moisture from the Congo Basin to the water supply, and/or to a close/shallow water system (Otero et al., 2011;

325 Kebbede and Travi, 2012).

4.3 Interpretation of the $\delta^{18}O_p$ of fossil crocodilian enamel

The large range of $\delta^{18}O_p$ values in units B-10 to C-8 indicates that crocodilians occupied different water body types. Low $\delta^{18}O_p$ values suggest an open water body or an ^{18}O-depleted water source (e.g., unevaporated meteoric water from rivers or underground water); while the high values reflect shallow, isolated water bodies subject to evaporation (e.g., pond, shallow

330 closed lake, swamp) or an ^{18}O-enriched water source. If the Shungura Fm was under lacustrine influence in unit B-10, it could explain the great diversity of waterbodies present in the area (Fig. 8). In Member C, the environment is predominantly fluvial, but the present isotopic data suggest that it was probably connected to other nearby water bodies making them accessible to local crocodilians. These $\delta^{18}O_p$ values do not indicate aridification affecting freshwater environments between 2.8 Ma and 2.5 Ma (Members B and C). This contrasts with changes observed in the aquatic and terrestrial ecosystems of the eastern African

335 Rift: such as lake level drop, landscape opening, and aridification (e.g., Maslin and Trauth, 2009; Trauth et al., 2009, 2021; Levin et al., 2011; Negash et al., 2015, 2020; Blondel et al., 2018, 2022; Nutz et al., 2020) (Fig. 8). Interestingly, $\delta^{13}C$ of soil carbonates indicates aridification in the Shungura Fm but not in the Nachukui Fm in the West Turkana area (Levin et al., 2011; Levin, 2013; Nutz et al., 2020) (Fig. 8). Considering that the Shungura Fm records the climate signal from the Ethiopian Dome and that the Nachukui Fm records a more local or regional signal (Nutz et al., 2020), these data also point to stable

340 local/regional conditions during this time interval. This could be explained by less evaporation or less precipitation in the lower Omo Valley during the 2.8-2.5 Ma period but there was less water coming from the Ethiopian Dome. Instead of increasing and showing a restricted range of $\delta^{18}O_p$ values, as expected for an aridification context, the distribution of $\delta^{18}O_p$ values in Members B to C remains relatively stable, suggesting that crocodilians had access to the same range of water bodies, which remained nearby or interconnected. It implies that the $\delta^{18}O$ of the water sources remained relatively the same, or if evaporation
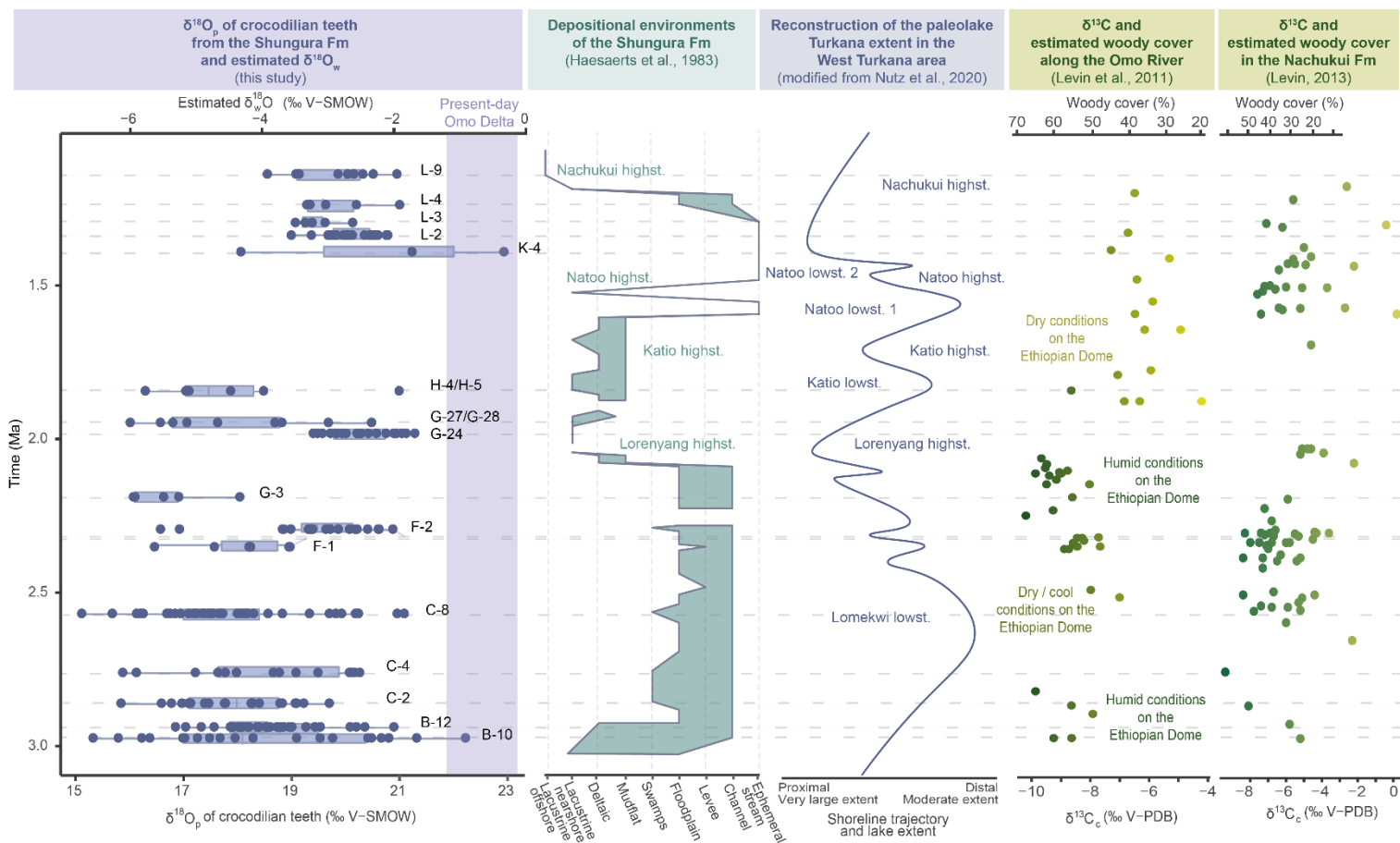
Figure 8. Comparison of oxygen isotopic composition of crocodilian teeth ($\delta^{18}O_p$) and estimated for surface water ($\delta^{18}O_w$) fluctuations with data on the evolution of sedimentary systems of the Shungura Formation, Lake Turkana level and woody cover in the Shungura Fm.

345   increased, the $\delta^{18}O$ of the source decreased in balance (resulting then from a greater contribution of the Indian Summer Monsoon) (Kebede and Travi, 2012) (Fig. 8).

The $\delta^{18}O$ values are more homogeneous in unit F-1, indicating that crocodilians probably had access to only one type of water body at the local scale (Fig. 8). The minimal values are higher than in the older units, while the maximal values are lower, indicating that if the most evaporated water bodies present in Members B and C still existed, they were no longer accessible

350   to crocodilians. In unit F-2, the values are mostly higher than those of F-1 except for two teeth. This range would reflect at least two distinct water body types (Fig. 8). This is coherent with the formation of this unit during a period of lake transgression and increased water supply over the Ethiopian Dome (Levin et al., 2011; Nutz et al., 2020) (Fig. 8). By contrast, in unit G-3, crocodilian teeth yielded a restricted range of low $\delta^{18}O_p$ values, reflecting a single accessible environment, probably the river according to sedimentological studies and to the increasingly humid conditions (Haesaerts et al., 1983; Levin et al., 2011; Nutz

355   et al., 2020) (Fig. 8). The G-24 unit shows a restricted range of high $\delta^{18}O_p$ values, indicating a highly evaporated water body. This interpretation is consistent with sedimentological and paleontological observations, pointing to a dominance of a very

saline lake, probably shallow, with evaporitic facies, initiating the beginning of the regression following the Lorenyang lake highstand and recorded fish kill event (cichlids and *Sindacharax*) (Van Damme and Gautier, 1972; Haesaerts et al., 1983).

360 The G-27/G-28 and H-4/H-5 units show the same pattern of isotopic compositions with a wide range, covering more negative values, and some values as positive as in G-24 (Fig. 8). Therefore, crocodilians likely had access to at least two different types of water bodies: an evaporated shallow lake and its tributary. The difference between the two is 4 ‰, as expected for a present-day Ethiopian exoreic lake and its tributary (Hailemichael et al., 2002, Table 2). This change in isotopic pattern illustrates the progressing regression of the lake (Katio lowstand) and the establishment of a deltaic environment, consistent with previous sedimentological studies (Nutz et al., 2020) (Fig. 8). The present-day vast Omo Delta shows a great diversity of sub-

365 environments (e.g., active or abandoned distributary channels, interior lakes not connected to the open lake), giving a glimpse of what it might have looked like in the Pleistocene (Schuster et al. 2022). The three teeth analysed in unit K-4 show divergent values, reflecting the presence of at least two different water bodies accessible to crocodilians. Units L-2 to L-4 show particularly high minimal $\delta^{18}O_p$ values, indicating that the crocodilians only had access to one type of water body, evaporated and/or that the $\delta^{18}O$ of precipitation increased. The depositional environments in these units are described as ephemeral streams

370 by Haesaerts et al. (1983), therefore at least seasonally evaporating waterbodies could have existed (Fig. 8). The L-9 unit does not appear to be different from the other units analysed in the Member L in terms of the oxygen isotopic composition of crocodilian enamel. Nevertheless, sedimentary studies demonstrate that it was deposited in a lacustrine context (Haesaerts et al., 1983). The difference in $\delta^{18}O_w$ of ephemeral streams and the lake may not be striking in case the evaporation states of the water bodies, ephemeral stream, and offshore lake waters, are similar or if it is compensated by a change in the $\delta^{18}O$ of

375 precipitation.

The minimum estimated values of $\delta^{18}O_w$ display an evolution through time, increasing from -6.5 ± 2 ‰ at 2.97 Ma to -3.9 ± 2 ‰ at ca. 1.14 Ma. In general, estimated $\delta^{18}O_w$ values do not, or barely, reach (considering the 2 ‰ error on the estimate) the moderb $\delta^{18}O_w$ values of Omo River waters at the delta (between -1.2 ‰ and -0.1 ‰), and of the Ethiopian lakes (between 1.5

380 ‰ and 7.2 ‰) (Table 2). Considering minimum $\delta^{18}O_w$ value at 2.97 Ma and comparing it to present-day values, our reconstructed $\delta^{18}O_w$ data show an increase between 5.3 ± 2 ‰ to 6.4 ± 2 ‰ (compared to the Omo River) (Table 2). Again, it should be kept in mind that these values represent a maximum estimate of the ancient $\delta^{18}O_w$ values. Therefore, the difference between the ancient and the present values may be greater because the rainwater probably suffered from evaporation before its uptake crocodilian body water. This increase in $\delta^{18}O_w$ is similar to that evidenced by the oxygen isotopic composition of

385 paleosols and fossil molluscs in other Plio-Pleistocene eastern African deposits (Hailemichael et al., 2002; Levin et al., 2004) and thus requires a regional explanation.

The increase in $\delta^{18}O_w$ cannot be explained by major changes in the topography in the Ethiopian and Kenyan domes and the eastern African Rift (Abbate et al., 2005; Nutz et al., 2017; Ragon et al., 2019), but could be due a rarefaction of rainfalls. The xtent of this remains difficult to estimate, as the oxygen isotopic composition of meteoric water ($\delta^{18}O_{mw}$) in eastern Africa is

390 currently not highly correlated with rainfall intensity. Levin et al. (2004) suggest that a 1 ‰ increase in $\delta^{18}O_{mw}$ would reflect

a 32 mm decrease in precipitation, based on GNIP stations in East Central Africa. The data from Table 2 shows a relatively weak correlation between $\delta^{18}O_{mw}$ and the amount of precipitation ($R^2 = 0.21$), suggesting that a 1 ‰ increase in $\delta^{18}O_{mw}$ could be associated with a 160 mm decrease in precipitation. In the case of the Ethiopian Dome, with $\delta^{18}O_{mw}$ values at least 5.3 ‰ lower than today's, Addis Ababa would then have received 870 mm more precipitation in the late Pliocene, thus reaching

395 about 2050 mm/year of precipitation. This amount is close to that recorded now in the equatorial forest of Congo (ex. Goma GNIP station, IAEA, 2023, Table 2). If the Pliocene climatic regime were similar to the present day's one, then higher sea surface temperatures in the Indian Ocean could have led to increased precipitation in eastern Africa at that time. This hypothesis is consistent with the progressive global cooling observed in the last million years (Zachos et al., 2001).

On the other hand, the sources and trajectories of precipitation play a major role in the variation of $\delta^{18}O_{mw}$ in eastern Africa.

400 Changes in the location of the Intertropical Convergence Zone (ITCZ) or Congo Air Boundary (CAB) are more likely to strongly impact the variation of the isotopic composition of the eastern African meteoric water, potentially exceeding 3 ‰ (Kebede and Travi, 2012). With a warmer Indian Ocean, the ITCZ would have been expected to move northward, and the Ethiopian Dome would have received a larger proportion of Indian Summer Monsoon rains, which have lower $\delta^{18}O_{mw}$ values than the West African Monsoon. Alternatively, a more westerly location of the Congo Air Boundary in Ethiopia during the

405 Plio-Pleistocene could have lowered the $\delta^{18}O_{mw}$ values up to the extent recorded 2.97 Ma in the Lower Omo Valley (Kebede and Travi, 2012; Levin et al., 2009).

Conclusions

Given their low metabolism and aquatic ecology, crocodilians stand out as excellent recorders of environmental conditions, with their $\delta^{18}O_p$ values closely linked to that of the water they live in during teeth formation. Combining knowledge of the

410 physiology and ecology of crocodilians is of crucial importance to further interpret their oxygen isotopic signal: it allows to gain insights into the local diversity of aquatic environments, local evaporation and $\delta^{18}O$ values of meteoric waters. This approach opens a new understanding of past freshwater environments and is complementary to sedimentological studies and terrestrial proxies. It is noteworthy that this variability in the paleohydrology, revealed by a single stratigraphic unit-based study, corresponding to or within a given locality, could not have been highlighted by a study based on mean values performed

415 at the stratigraphic member-based scale of the Shungura Formation.

The new data set suggests that between 2.97 Ma and ca. 2.57 Ma, the Lower Omo Valley hosted a great diversity of water body types, with different water sources or evaporative states. From ca. 2.32 Ma, the diversity of freshwater environments decreased drastically to only one or two types of water bodies at each stratigraphic unit, probably due to aridification that caused some water bodies to either disappear or to become further separated and isolated, making them inaccessible to local

420 crocodilians. This freshwater environment restriction prevailed in the rest of the Shungura Fm, except at ca. 1.95 Ma and 1.84 Ma: the lake level decreased giving way to a deltaic environment in the Shungura Fm with a high diversity of water bodies.
The $\delta^{18}O_p$ of crocodilian teeth also carries valuable information about regional paleoenvironments but cannot help identifying the exact cause between different potential factors (origin of water, rainfall amount, topography, temperature, etc.). This new dataset highlights a large increase in $\delta^{18}O_w$ values, between 5.3 ‰ and 6.4 ‰, from the Pliocene to the present, consistent with

425   other studies in eastern Africa (Hailemichael et al., 2002; Levin et al., 2004). This increase is likely to have resulted from the migration of convergence zones of low air streams affecting the distribution of the monsoons affecting the $\delta^{18}O_w$ in addition to the resulting scarcity of rainfalls over the Ethiopian Dome. The data point to a main shift in $\delta^{18}O_w$ between 1.84 Ma and ca. 1.34 Ma, slightly later than suggested by studies on paleosols (Levin et al., 2011). Contrary to some conclusions based on terrestrial proxies, the $\delta^{18}O_p$ of crocodilian teeth does highlight any major change affecting aquatic environments, rather

430   pointing to the stability of these environments between 2.97 Ma and ca. 2.57 Ma.

Crocodilian teeth are also abundant in continental series and widely distributed across the globe, notably in the Neogene strata of Africa. Although adapted in the context of the Shungura Fm, the proposed interpretation model can be generalized to comparable paleontological and archaeological sites, especially in other sites in the Turkana Depression but will require sampling as detailed as that done by OGRE in the Shungura Fm. For optimal use of this approach, particularly along a

435   stratigraphic sequence, it is necessary to ensure that temperature changes are limited and do not significantly affect the body temperature of crocodilians. For the same purpose, it is necessary to compare the same taxa throughout the sequence to avoid interspecific variation. Better control of the potential phylogeny-dependent variation of $\delta^{18}O_p$ in the present dataset would benefit from a study on the systematics and temporal distribution of the different crocodilian taxa in the Shungura Fm. Once the preservation of the original isotopic signal of the crocodilian fossil tooth enamel is ensured and the physiological,

440   ecological, and environmental parts of the signal identified, then the $\delta^{18}O_p$ could be used to characterize the aquatic environments and their diversity over time in many other continental intertropical contexts.

Supplement

The supplement related to this article is available online at: (*to be provided later*).

Author contributions

445   AG, EP, GG, JRB, and OO designed the study. EP, GG, and OO provided supervision. JRB supervised fieldwork and specimen sampling, involving AN, MS, and OO. AG and EP performed enamel sampling and preparation in the lab. EP and MMJ performed the stable isotope analysis and data treatment. AE, AG, and JRB built the age model for the Shungura Fm. AG was responsible for statistical analysis, data curation, and visualisation, and wrote the paper with contributions from all the co-authors.

Competing interests

The contact author has declared that none of the authors has any competing interests.

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