New data on morphological evolution and dietary adaptations of *Elephas recki* from the Plio-Pleistocene Shungura Formation (Lower Omo Valley, Ethiopia)

Nouvelles données concernant l'évolution morphologique et les adaptations alimentaires d'*Elephas recki* de la formation plio-pléistocène de Shungura (basse vallée de l'Omo, Éthiopie)

Evolution of *Elephas recki* from the Shungura Formation

Tomas Getachew BEDANE
Ethiopian Heritage Authority (EHA), Ministry of Tourism, King George VI Street, PO BOX 13247 Addis Ababa, Ethiopia
and
Laboratoire Paléontologie Évolution Paléoécosystèmes Paléoprimatologie, UMR 7262 PALEVOPRIM, Université de Poitiers & CNRS, 6 rue Michel Brunet, 86073 Poitiers (France)
tomas.getachew.bedane@univ-poitiers.fr

Field Code Changed

Hassane Taïsso Mackaye
Université Polytechnique de Mongo
Rue de Am-Timan, Mondjino, B.P. 4377 Mongo – Tchad
and
Université de N'Djaména, faculté des sciences exactes et appliquées, département de paléontologie, B.P. 1117, N'Djaména, Tchad
mhtaisso@gmail.com

Formatted: French (France)

Field Code Changed

Jean-Renaud BOISSERIE
Centre Français des Études Éthiopiennes, CNRS & Ministère de l'Europe et des affaires étrangères, PO BOX 5554 Addis Ababa, Ethiopia
and
Laboratoire Paléontologie Évolution Paléoécosystèmes Paléoprimatologie, UMR 7262 PALEVOPRIM, CNRS & Université de Poitiers, 6 rue Michel Brunet, 86073 Poitiers (France)
jean.renaud.boisserie@univ-poitiers.fr

Field Code Changed

ABSTRACT

The ~~abundant and diverse~~ proboscideans, abundant and diverse throughout the Cenozoic, are essential terrestrial megaherbivores for studying morphological adaptations and reconstructing paleoenvironments in Africa. This new study of the lineage of *Elephas recki* (or "*Elephas recki* complex") from the Plio-Pleistocene deposits of the Shungura Formation aimed at investigating further the interplay between morphological and behavioral adaptations within proboscideans. For this, we used the most complete and well-preserved third molars of the series for characterizing morphological changes, while describing dietary behavior by applying mesowear angle analysis to all identifiable cheek teeth. Biometric character changes indicated that evolutionary change was not a gradual, progressive trend through the Shungura sequence deposition. Rather, we observed a complex trend involving sudden changes. The mesowear angle analysis suggested that *Elephas recki* from the Shungura Formation had consistently herbaceous monocot (such as grass and sedges) dominated ~~grazing~~ dietary habits throughout its evolution, except for some slight tendencies of mixed browse/graze diet in certain time intervals. We therefore did not observe any correlation between morphological change and feeding preferences over two million years. This delay between the acquisition of the observed diet and purportedly consequent morphological changes questions the classical interpretations of factors at play in this evolutionary sequence.

Keywords: *Elephas recki*, Enamel thickness, Hypsodonty index, Mesowear, Shungura Formation

Formatted: Font: Italic

Formatted: Font: Italic

RÉSUMÉ

Les proboscidiens, un groupe ~~abondant et diversifié~~ de mégaherbivores terrestres abondant et diversifié durant le Cénozoïque, revêtent une grande importance dans l'étude des adaptations morphologiques et dans la reconstruction des paléoenvironnements en Afrique. Cette nouvelle étude de la lignée *Elephas recki* (ou "complexe *Elephas recki*") des dépôts plio-pléistocènes de la Formation de Shungura a pour objectif d'investiguer plus avant les interrelations entre adaptations morphologiques et adaptations comportementales au sein des proboscidiens. Pour cela, nous utilisons les troisièmes molaires les plus completes et les mieux préservées de cette série pour caractériser les changements morphologiques, tout en décrivant le comportement alimentaire en appliquant l'analyse angulaire des méso-usures à toutes les dents identifiables. Les variations des caractères biométriques indiquent une évolution différant d'une tendance graduelle et progressive pendant le dépôt de la séquence de Shungura. Au lieu de cela, nous observons une tendance complexe impliquant des changements abrupts. L'analyse angulaire des méso-usures suggère qu'*Elephas recki* de la Formation de Shungura avait un comportement alimentaire invariable de paisseur (consommateur de monocotylédones herbacées telles que les graminées et les cypéracées), à l'exception de légères tendances à une alimentation mixte paisseur/brouteur à certains moments. Nous n'avons donc observé aucune corrélation entre changement morphologique et préférences alimentaires durant plus de deux millions d'années. Ce décalage entre l'acquisition du régime alimentaire observé et les changements morphologiques supposément résultants remet en question les interprétations classiques concernant les facteurs à l'œuvre dans cette séquence évolutionnaire.

Mots clefs : *Elephas recki*, Épaisseur de l'émail, Index d'hypsodontie, Méso-usures, Formation de Shungura

INTRODUCTION

Proboscidea Illiger, 1811 is an order of mammals that includes elephants, the largest extant land animals on extant Earth. Their evolutionary history is well-documented and fossils indicate an incredible diversity (Shoshani & Tassy 2005; Gheerbrant & Tassy 2009; Cantalapieadra *et al.* 2021). Most of their evolution occurred in Afro-Eurasia, with later ~~migrations~~ dispersals to the Americas (Coppens 1978; Tassy 1988). The "true" elephants, i.e. the family Elephantidae, originated in Africa during the Late Miocene (Maglio 1973; Kalb *et al.* 1993), and include three emblematic lineages of extant and recently extinct crown elephantids (*Loxodonta*, *Elephas*, and *Mammuthus*). Following a steep decline during the last two million years (Cantalapiedra *et al*. 2021) and despite some successful diversifications (*Mammuthus*, *Palaeoloxodon*) in northern Eurasia, there are currently only three species of elephants in the world: the Asian elephant, *Elephas maximus*, and two species found in Africa, the savanna elephant *Loxodonta africana* ~~living in the bush or savanna~~, and the forest elephant *Loxodonta cyclotis* ~~in the forest~~ (Owen-Smith 1988; Roca 2001; Sukumar 2003; Sanders 2010; Sanders 2024). Despite this relatively low diversity, these megaherbivores play particularly important roles in ecosystems (e.g., Owen-Smith 1988; Fritz *et al*. 2002).

In the past, the study of morphological changes in African elephant fossils (prominently in their dentition) ~~has been~~provided important proxies for ~~in~~ biochronology and trends of ~~used to approximate~~ environmental changes (Beden 1987, 1983, 1980; Saegusa & Gilbert 2008; Sanders & Haile-Selassie 2012). This contributed to the narrative of a late Neogene spread of drier environments and related biomes (prominently savanna) having a driving impact on faunal evolution, and notably on hominids (Bobe 2006; Cerling *et al*. 2013, 2011, 1997; Strömberg 2011). Further attention was latter brought to the ecology of African elephantids, notably to their isotopic ecology (e.g., Cerling *et al*. 2015, 1999; Uno *et al*. 2011) alongside with other taxa. Lister (2013) demonstrated a decoupling between these morphological trends and paleoecological signals at a regional scale (e.g., eastern Africa), suggesting a significant delay between environmental changes, dietary behaviors, and morphological responses. However, Saarinen and Lister (2023) recently observed a stepwise increase in crown height (hypsodonty) in true elephants happened rapidly but in distinct stage after 5 Ma, specifically corresponding to peaks in arid climatic phases.~~A decoupling between these morphological trends and paleoecological signals was~~

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font color: Custom Color(RGB(22,23,25)), Pattern: Clear (White)

~~demonstrated by Lister (2013) and Saarinen & Lister (2023) at regional scale (i.e., eastern Africa), suggesting substantial delay between environmental changes, dietary behavior, and morphological responses~~.

Our purpose is to further explore the modalities and factors of this decoupling, by investigating the evolutionary history of a well-documented, single lineage at a local scale. The rich fossil record of the chronostratigraphically well-controlled Shungura Formation (Lower Omo Valley, southwestern Ethiopia, Turkana Depression; Arambourg 1948; Howell & Coppens 1974; Boisserie *et al*. 2008) is particularly ~~adapted~~ suitable for~~to~~ pursuing~~e~~ this objective. Our research focused on *Elephas recki*, the most abundant proboscidean in the Shungura Formation, commonly found in the Plio-Pleistocene paleontological sites of eastern Africa (Maglio 1972, 1973; Gilbert & Asfaw 2008). The remains ~~of~~ attributed to *Elephas recki* (classically considered as a coherent evolutionary lineage, but for some authors may include different lineages; see below) from Shungura are considered as essential in establishing a reliable biochronological framework for the region as well as for paleoenvironmental reconstructions, given that they display considerable modifications of the craniodental apparatus seemingly in response to the spread of more open environments and greater competition for grazing resources (Maglio 1973; Cerling *et al*. 1999; Sanders & Haile-Selassie 2012; Zhang 2020; Sanders 2024).

MATERIAL AND METHODS

FOSSIL SAMPLE

The fossils examined in this study were collected from the Shungura Formation by the International Omo Research Expedition (IORE, 1967-1976) and the Omo Group Research Expedition (OGRE, since 2006). The Plio-Pleistocene deposits of the Shungura Formation are well-known for their almost continuous stratigraphic sequence, i.e. ca. 800 m of sediments of fluvio-lacustrine and volcanic origins divided into 12 geological members (from the lowermost to the uppermost levels: Basal, A to H, and J to L) subdivided into variable numbers of units (e.g., 12 for Member B, 5 for Member F) corresponding generally to sedimentological cycles (Heinzelin, 1983). Each member was defined by a widespread volcanic ash at its base (except for the Basal Member), and many other volcanic layers are found within members. The chronology of this formation is one of the best known thanks to radiochronology (K/Ar and ^{40}Ar/^{39}Ar methods) and by magnetostratigraphy, indicating a time span from 3.75 Ma to 1.09 Ma (Fig. 1A; see recent age model in Gardin *et al.* 2024 and references herein). Thanks to these features, the Shungura record is particularly suitable for ~~studying~~ tracking the evolution, paleoecology and environmental context of various vertebrate groups~~, as well as their paleoecology and the contemporary environments~~ at community level (Bobe & Eck 2001; Alemseged 2003; Bobe 2011).

In the Shungura stratigraphic sequence, ~~fossil~~ elephantid fossils are abundant and constitute a significant proportion of the collected mammals (Coppens 1978; Beden 1980; Alemseged *et al.* 2003, 2007). There are at least five species known from Shungura, including *Elephas ekorensis*, *Loxodonta exoptata*, *Loxodonta adaurora*, and *Loxodonta atlantica*. The fifth one, *Elephas recki*, is the most common, comprising 98 % of elephantid specimens (Coppens 1978). Based notably on the Shungura record, Beden (1980) divided *E. recki* into five subgroups recorded throughout the stratigraphic sequence of the Shungura Formation (Fig. 1B,D) and were exclusively identified through changes in cheek tooth morphology (Beden 1980). The same author later refined their stratigraphic occurrences (Beden 1987): *E. recki brumpti* (members A and B), *E. recki shungurensis* (members C to F), *E. recki atavus* (members F and G), *E. recki ileretensis* (from Member K to lower Member L, til Unit L-4 included, and possibly also from Member J), and *E. recki recki* (upper Member L, from Unit L-5 to top).

There is an on-going debate about these systematic biology of~~s attributed within~~ the "*Elephas recki* complex" (Todd 2005; Zhang 2020; Sanders 2024). The disagreement is specifically about whether the earliest and youngest subspecies should be placed within the genus *Elephas* or, instead, within *Phanagoroloxodon* and *Palaeoloxodon*, respectively. Based on cranial morphopology, Saegusa & Gilbert (2008) and Zhang (2020) advocated for relating *E. recki ileretensis* and *E. recki recki* within *Palaeoloxodon* ~~(a subgenus of *Elephas* for the former authors, a genus on its own for the latter)~~. However, the implications of this ~~view~~ result~~this view~~ remain~~s~~ discussed in the literature (Sanders 2024). First, the inclusion of *Elephas recki brumpti* within Phanagoroloxodon is not universally approved (Sanders 2024). Second, *Palaeoloxodon* is considered as a subgenus of *Elephas* by various authors (e.g., Saegusa & Gilbert 2008) instead of a genus on its own as proposed by Zhang (2020). Third, recent paleogenetic work (Meyer *et al.* 2017; Palkopoulou *et al.* 2018) suggested that recent Eurasian specimens of *Palaeoloxodon* are nested within *Loxodonta*, which conflicts with phylogenetic results based on morphology (Zhang 2020). Consequently, f~~F~~or this paper, ~~which purpose is~~ not intending to test conflicting taxonomic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

hypotheses, we choose to retain the classical use of subspecific division within *Elephas recki* for two reasons: the vast majority of this material can still be interpreted as belonging to a single anagenetic lineage, and its subspecific subdivision retains a practical dimension. We note however that subspecies is a term more relevant to geographic variations within a species than to evolutionary stages, and that the subspecies of *E. recki* are more adequately viewed either as arbitrary, practical temporal stages displaying marked overlaps, or as substitutes for chronospecies (see Sanders 2024 for a more thorough discussion). Although we believe that further examinations of the Shungura record may eventually lead to the definition of chronospecies, this paper that does not consider all relevant data to perform a proper taxonomic revision is not the right place to take such decisions.

In our study, we also focused on analyzing only well-preserved molars of *Elephas recki*. Indeed, mammalian teeth are highly resistant to weathering, which makes them common skeletal remains found in the fossil record. They provide vital information about morphology, past dietary habits, vegetation, environmental conditions, and climate (Beden 1980; Maglio 1973; Saarinen *et al*. 2015; Sanders 2010; Ungar 2010; Saarinen & Lister 2024). As mammalian teeth are abundant, most research on mammalian dietary studies has relied mainly on the analysis of molar teeth.

For biometric and dental wear analyses, we utilized a total of 140 lower and upper molars, including five pairs of antimeres for which average values were used (Table ~~S4~~S5). We used a total of 89 lower and upper third molars for biometric analysis, and 86 diagnosable cheek teeth for dental wear analysis (Fig. 1C). Among these, 33 samples were analyzed in combination with both methods. Upper and lower molars display statistically similar values for biometric features and mesowear analysis, as stated in the supplementary information (Tables S1-S3).

The specimens for our study were selected based on the quality of preservation. We only chose molars that had good preservation quality for both methods. Molars were chosen from all members of the Shungura Formation, except for the Basal Member and Member A, as no well-preserved fossil evidence was available from these members. We also excluded molars from members H and J due to poor preservation quality of relatively few samples. This created a further gap of approximately 355 thousand years. A similar gap is present in our mesowear sample, with an additional lack of coverage for the approximately 170 thousand years represented by the upper part of Member G.

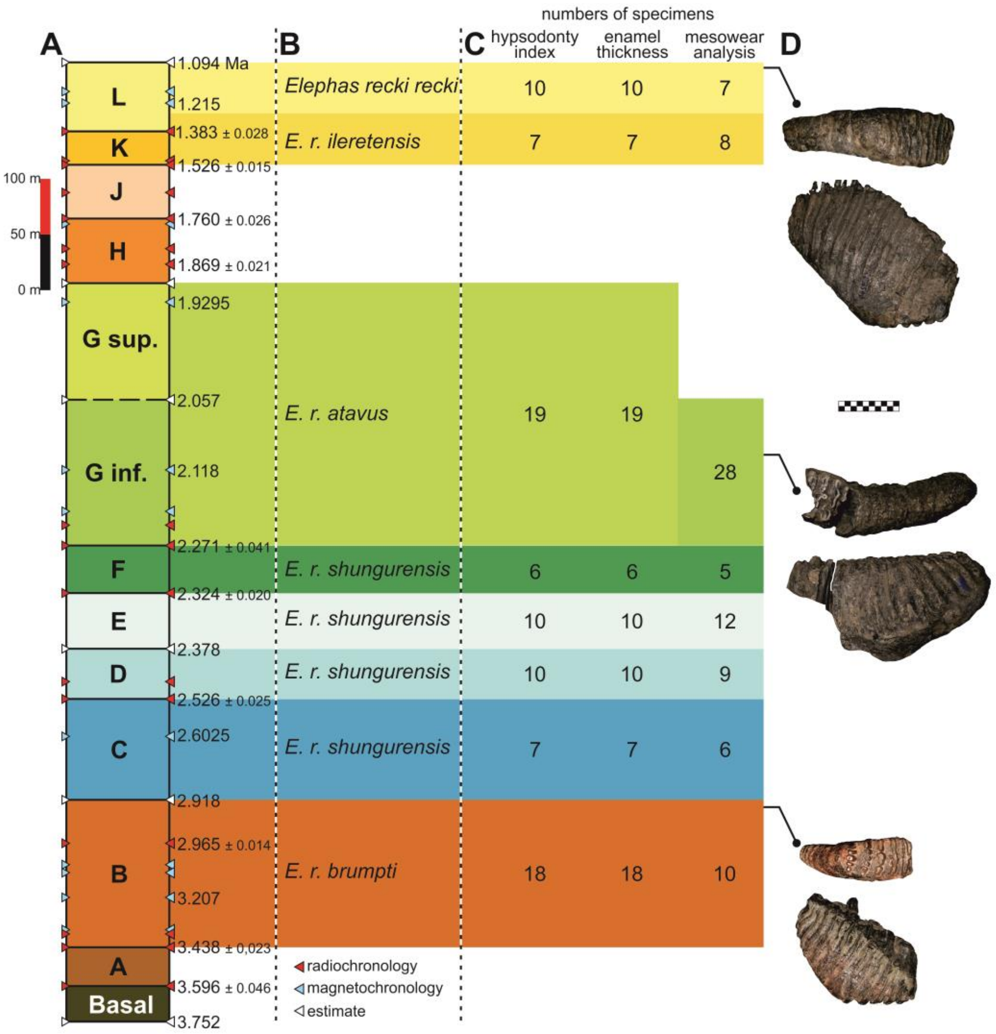


FIG. 1. – **A**, chronostratigraphic composite column of the Shungura Formation following the stratigraphic and radiochronological work described by Heinzelin (1983) and with ages derived from (Feibel *et al.* 1989; Brown *et al.* 2006; McDougall and Brown, 2008; McDougall *et al.* 2012; Kidane *et al.* 2014); **B**, distribution of the subspecies of the lineages of *E. recki* through the members of the Shungura Formation and corresponding numbers of analyzed specimens; **C**, sample sizes of analyzed molars from each member; **D**, morphological and biometric changes over time exemplified in lateral (bottom) and occlusal (top) views for, from top to bottom, *Elephas recki brumpti* (OMO 3/0-1974-961, M^3 from B-12), *E. recki atavus* (OMO 75-1969-3196, M_3 from G-4 to G-13), and *E. recki recki* (OMO K 7-1969-3204, M^3 from Unit L-9). Scale bar is 10 cm for all.

Formatted: Left, Space After: 8 pt, Line spacing: Multiple 1.08 li

METHODS

Given our interest for dental morphological evolution in response to dietary change, we selected two continuous features commonly used to depict dental evolution through time and which changes are interpreted as morphological adaptations to dietary changes (Maglio 1973; Beden 1987, 1980): hypsodonty index and enamel thickness (Fig. 2A-B). We compared them to mesowear angle analysis (Fig. 2C), a recently developed proxy of dietary behavior in proboscideans (Saarinen *et al.* 2015).

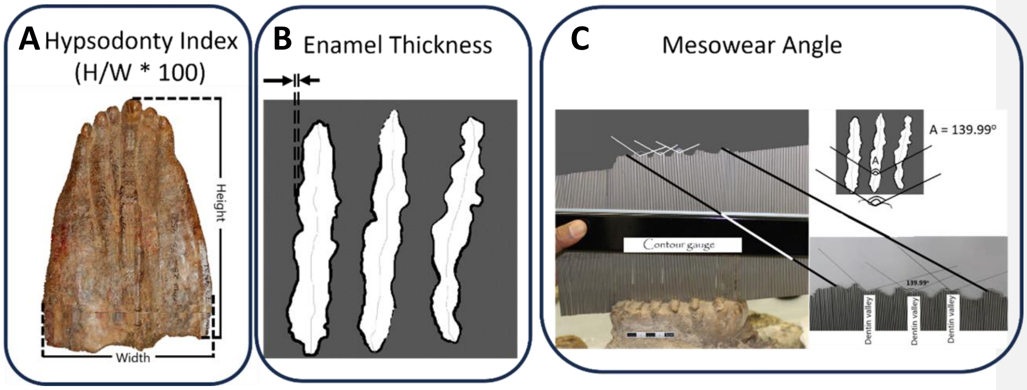


Fig. 2. – Measurements acquired from teeth of *Elephas recki* from the Shungura Formation. **A**, measurements involved in the calculation of the hypsodonty index (HI); **B**, measurement of the enamel thickness (ET) on sketched occlusal surface of molar plates; **C**, measurements of mesowear angles (dentin valley angle, in white on the sketch) between ridge of enamel bands (in black) plates of a molar.

Hypsodonty Index (HI)

This index (height/width of the crown ×100) is a measure of the relative crown height of elephantid molars, ~~which~~ the increase of which through time has been related to increasing abrasiveness of ingested food caused by a combined effect of plant phytoliths and exogenous mineral particles (Janis & Fortelius 1988; Damuth & Janis 2011). Using this ratio helps to eradicate the issues of individual size differences that would make it difficult to compare relative crown height in a~~ny~~ ~~acceptable~~ meaningful way (Maglio, 1973). According to Maglio (1973), Arambourg (1938) was the first to develop a method to quantify this biometric characteristic and then later Cooke (1947) modified this index by multiplying the height-to-width ratio by 100~~, as described in Maglio's~~

~~monograph (1973)~~. The height of a molar crown should be measured parallel to the vertical axis of the plate or loph(id), from the base of the enamel covering to the apex of the tallest pillar and the width of a molar should be measured across its widest plate or lophid, including cementum (see Fig. 2A).

Enamel Thickness (ET)

The thickness of molar enamel is a reliable biometric characteristic for studying the evolution of ~~E~~elephantid~~ae~~ molars, as noted by Beden (1980) and Maglio (1973). We followed the procedure suggested by Maglio (1973). This involves taking several measurements from different locations on the occlusal surface of a worn enamel band of multiple plates of a molar (series of worn enamel figures of plates along the molar). A minimum of three measurements is recommended on a single enamel band (see Fig. 2B), after which we calculate the average of those measurements.

Mesowear analyses

To investigate the dietary preferences within our elephantid sample, we used a relatively a new technique introduced by Saarinen *et al.* (2015). This technique consists in using the macroscopic relief and shape of worn molar surfaces, which, according to the seminal work by Fortelius & Solounias (2000), can serve as an indicator of the relative amount of abrasive plant material, primarily grass ~~material~~, consumed by herbivorous mammals. The ~~Mean~~ mean ~~Mesowear~~ mesowear ~~Angle~~ angle (MWA) has been calculated for each molar sample by taking the average angle from the dentine valleys of three ~~blades~~lamellae, following the method outlined by Saarinen *et al.* in 2015 (see Fig. 2C) and adapted by Saarinen & Lister (2023). However, we have also made a modification to the sampling method by measuring two lamellae ~~blades~~ from a single molar. A t-test was conducted on some of the representative individual measurements, but no significant difference was found between the series including three samples per individual and that including two samples only (see Supplemental materials Table ~~S3A~~S4A-C and associated information). This modification is useful for including smaller specimen fragments with well-preserved dental surfaces, which can help to increase the sample size.

Statistics

We used both parametric and non-parametric statistical tests to analyze our data. To analyze the variations in biometric and MWA values within *E. recki* across the Shungura sequence we conducted several statistical tests including the Mann-Whitney test to assess whether the differences in the median values of the biometric characters (HI and ET) across Shungura members are statistically significant. Secondly, we utilized One-way ANOVAs to examine the variation among the MWA values throughout the Shungura sequence. Additionally, to investigate the differences between lower and upper molars, we carried out a t-test on both biometric and MWA values, showing no significant differences (Tables S1-S3). Finally, we employed Ordinary Least Square (OSL) linear regression and Pearson's correlation analysis tests to evaluate the relationship between MWA and two important dental traits: HI and ET. The null hypotheses propose that there are correlations between paleoecological conditions and the resulting dental changes and among the different dental characteristics themselves. For this particular analysis, we examined 34 individuals that were sampled from the members of the Shungura Formation. ~~biometric evolution and dietary adaptation.~~

Formatted: Font color: Custom Color(RGB(22,23,25)), Pattern: Clear (White)

ABBREVIATIONS

ET	Enamel thickness
HI	Hypsodonty index
MWA	Mesowear Angle analysis
LG	lower part of Member G (units G-1 to G-13)
LL	lower part of Member L (units L-1 to L-4)
UG	upper part of Member G (units G-14 to G-29)
UL	upper part of Member L (units L-5 to L-9)

RESULTS

HYPSODONTY INDEX (HI)

Descriptive statistics for this variable are provided in Table 1 and distributions are illustrated by Fig. 3. The Kruskal-Wallis test showed a significant difference ($p << 0.001$) between HI median values of Shungura stratigraphic members, suggesting the assumption that HI values increased progressively through time is not accurate. Our results indicate a complex trend in the crown height of this group of elephantids, which contradicts the expected gradual change over time. Instead, we observe a change in the trend slope, with values for members K and L specimens much higher than expected if the rate of change observed from B to G remained constant through time (Fig. 3). We also conducted a Mann-Whitney multiple comparison test and found highly significant differences in HI median values notably between members K and L, and between these higher members and members lower in the sequence (Table 2). Other significant differences appeared between members B and F, B and LG, D and F, D and LG, F and K&LL.

TABLE 1. – Statistical summary of biometric characters by members/submembers.

Members		**B**	**C**	**D**	**E**	**F**	**G**	**K & LL**	**UL**
	N	17	7	9	9	7	19	7	10
HI	Min	100.8	123.8	102.4	117.5	121.4	102	154.8	183
	Max	151.3	159.6	142.5	143.1	167.4	169.5	188	239.9
	Mean	**122.2**	**134.8**	**118.9**	**129.8**	**145.1**	**135.5**	**173.2**	**202. 7**
	Median	**121.4**	**129.5**	**119**	**131.1**	**141**	**137.1**	**176**	**202**
	SD	14.50	12.18	13.73	8.91	18.72	17.95	11.86	16.23
ET	Min	3.8	2.6	2.8	3	2.6	2.7	2.4	2.3
	Max	4.5	3.5	3.5	3.6	3.6	4	3.6	3
	Mean	**4.12**	**3.15**	**3.27**	**3.19**	**3.24**	**3.37**	**3.01**	**2.60**
	Median	**4.22**	**3.20**	**3.35**	**3.18**	**3.21**	**3.40**	**2.99**	**2.60**
	SD	0.246	0.310	0.245	0.218	0.330	0.311	0.474	0.236

TABLE 2. – Mann-Whitney pairwise tests significant for HI and ET- values.

	B	**C**	**D**	**E**	**F**	**G**	**K & LL**	**UL**
B		**1.6E-04**	**3.7E-05**	**3.7E-05**	**1.6E-04**	**1.2E-06**	**1.6 E-04**	**2.0E-05**
C	0.057		0.3875	0.957	0.746	0.084	0.701	**0.005**
D	0.571	0.057		0.417	0.872	0.267	0.392	**8.5E-04**
E	0.118	0.525	0.064		0.592	0.065	0.483	**4.4E-04**
F	0.010	0.224	0.015	0.112		0.292	0.442	**0.003**
G	0.025	0.729	0.027	0.302	0.312		0.102	**4.4E-05**
K & LL	**1.8E-04**	**0.005**	**0.001**	**0.001**	0.021	**3.4E-04**		0.076
UL	**2.2E-05**	**7.6E-04**	**2.8E-04**	**2.8E-04**	**7.6E-04**	**1.5E-05**	**0.0011**	

Lower left values: test results for HI; upper right values: test results for ET; gray shaded, and bold face values are highlighting significant difference ($p<0.05$) and highly significant ($p<0.01$) between members, respectively.

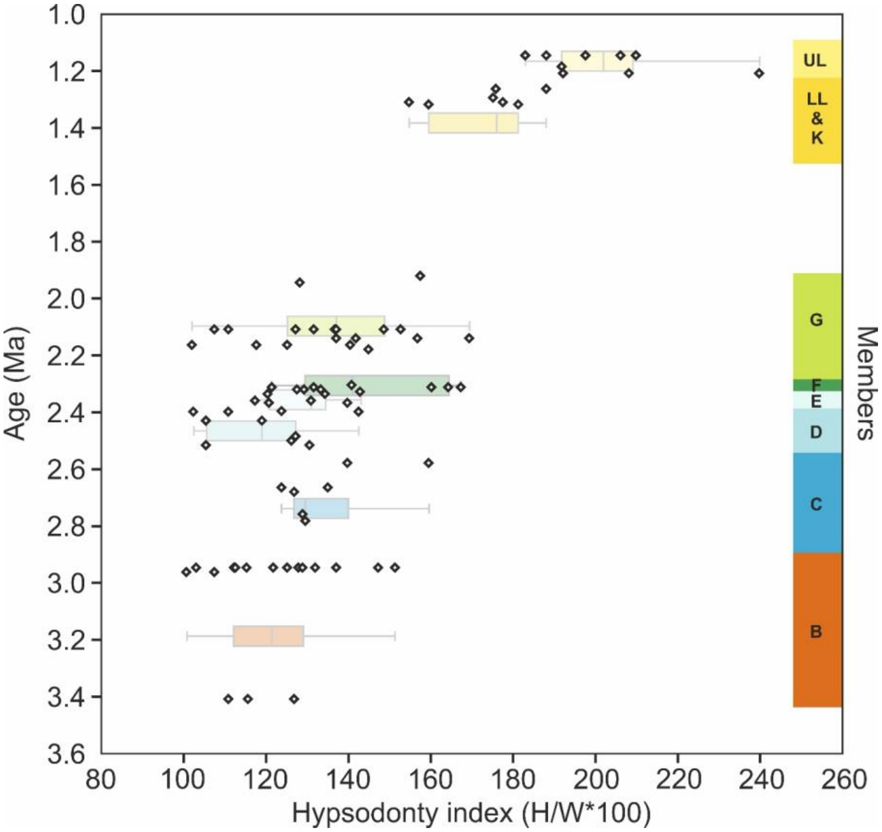


FIG. 3. – Box plots and individual values for hypsodonty index (HI) through time in *Elephas recki* from different members of the Shungura Formation. Boxes represent the interquartile range, bar is median, and whiskers represent the lower and the upper 25 % of the data.

ENAMEL THICKNESS (ET)

Descriptive statistics for this variable are provided in Table 1 and distributions are illustrated ~~by~~ in Fig. 4. The Kruskal-Wallis test indicates that there are statistically significant differences ($p < 0.05$) among ET values. Results of the Mann-Whitney pairwise test is reported in Table 2. Member B and upper part of Member L samples display mostly highly significant differences with all other samples. This is suggestive of two episodes of sudden changes in ET values, dropping from a mean value of 4.2 mm for Member B (*Elephas recki brumpti*, N=18) to a mean value of 3.25 mm for all samples from C to LL (N=61). There is no overlap between Member B sample and the rest of the samples, except a limited one with the larger LG sample (N=17; Fig. 4). For the upper part of Member L (N=10), again we observed a drop in ET to a mean value of 2.6 mm, however with a less significant difference with K and LL sample than with other samples. Despite the temporal gap between Member G and Member K samples, we did not observe significant differences between them (Table 2).

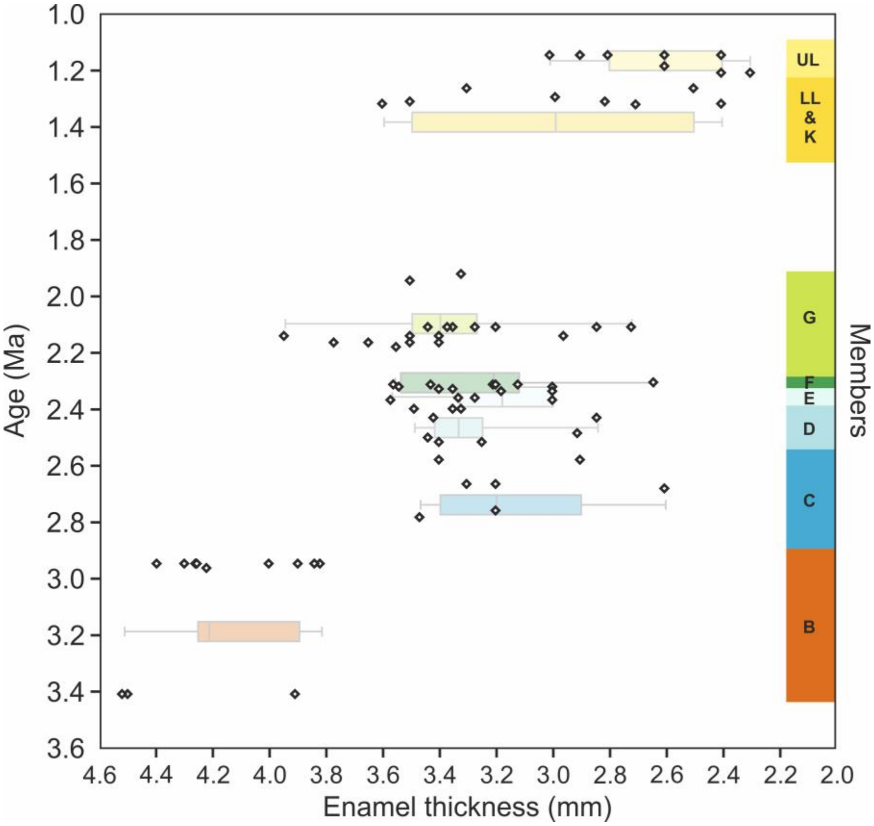


FIG. 4. – Box plots and individual values for enamel thickness (ET) through time in *Elephas recki* from different members of the Shungura Formation. Boxes represent the interquartile range, bar is median, and whiskers represent the lower and the upper 25 % of the data.

MESOWEAR ANGLE (MWA)

Descriptive statistics for MWA are provided in Tables 3 and 4. Mesowear distributions by members and subspecies are illustrated by Fig. 5A-B. The results of the ANOVA on MWA (F = 1.33, df = 7, and p = 0.250304) indicated that is no significant difference between members of the Shungura Formation for this variable. Following Saarinen ~~*et al.*~~ & Lister (2023~~15~~) who classified samples as browsers if their mean MWA is below ~~113~~106°, mixed feeders if their mean MWA is between ~~113~~106° and ~~124~~117°, and grazers if their mean MWA is above ~~124~~117°, we determined that *Elephas recki* from Shungura ~~tend to~~ displays a predominantly grazing diet, with a ~~tendency towards~~limited ~~more~~ occurrences of mixed diets for members B, D, F, K, and subspecies *E. r. brumpti* and *P. r. ileretensis* (Fig. 5; Tables 3 and 4).

Formatted: Font: Not Italic

TABLE 3. – Statistical summary of MWA measurements by members.

Members	B	C	D	E	F	LG	K	L
N	8	6	8	11	5	27	8	7
Min	113.5	116.3	109.2	108.7	109.7	112.0	115.0	120.7
Max	130.0	135.0	135.0	139.5	129.3	152.3	131.0	129.0
Mean	**122.30**	**125.66**	**118.61**	**128.78**	**122.34**	**127.98**	**122.90**	**124.30**
Median	**124.20**	**126.83**	**117.70**	**132.70**	**128.30**	**128.30**	**123.25**	**124.00**
SD	6.957	8.380	8.808	9.563	9.059	10.512	4.809	2.841

TABLE 4. – Statistical summary of MWA measurements by subspecies.

Subspecies	*brumpti*	*shungurensis*	*atavus*	*ileretensis*	*recki*
N	8	30	27	8	7
Min	113.5	108.7	112.0	115.0	120.7
Max	130.0	139.5	152.3	131.0	129.0
Mean	**122.30**	**124.37**	**127.98**	**122.90**	**124.30**
Median	**124.20**	**124.00**	**128.30**	**123.25**	**124.00**
SD	6.957	9.176	10.548	4.809	2.841

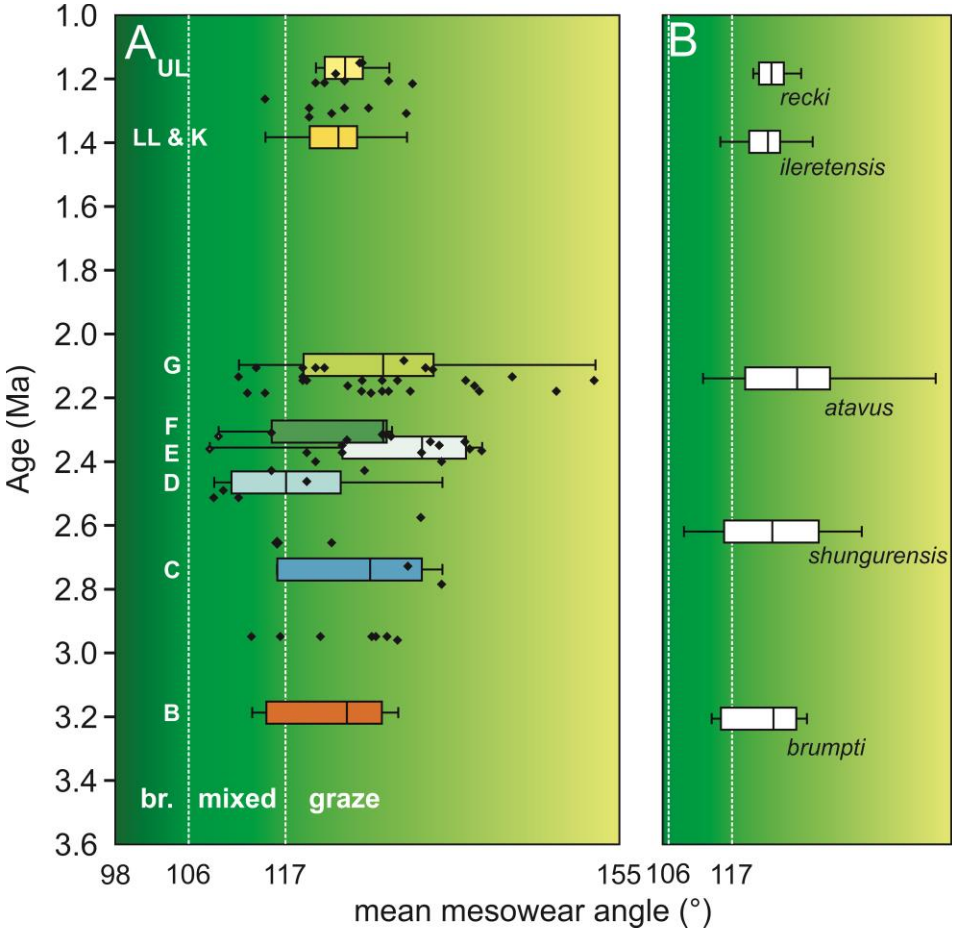


FIG. 5. – Box plots and individual values for mesowear angles (MWA) through time in *Elephas recki* from the Shungura Formation. **A**, by members; **B**, by subspecies. Boxes represent the interquartile range, bar is median, whiskers represent the lower and the upper 25 % of the data. Limits for dietary categories browse (br.)-mixed and mixed-graze at ~~113~~ 106 and ~~124~~ 117, respectively, were ~~obtained~~ revised by Saarinen & Lister (~~Saarinen *et al.*~~ 2023~~15~~).

RELATIONS BETWEEN MORPHOLOGICAL AND PALEOECOLOGICAL PROXIES

As initially suggested by Maglio (1973) for elephantid molar morphology, a HI increase should be correlated with a decrease in ET in relation to an increasing proportion of abrasive food in diet, mainly grass. To verify these assumptions, after conducting a linear regression test, we evaluated

Formatted: Space After: 10 pt

the functional relationship of variables of the two functions for the subset of specimens for which HI, ET and MWA data were available. We then assessed the correlation by comparing the HI and ET for specimens. The results ($R^2 = 0.42$) showed significant links between the biometric characters (Fig. 6B). Regarding correlation between the two independent biometric characters (HI and ET) and behavior (MWA), the results showed $R^2 = 0.008$**,** $t = 0.51$, $p = 0.62$ and $R^2 = 0.044$, $t = 1.21$, $p = 0.23$, respectively, hence no significant correlation between the HI and MWA (Fig. 6A), nor between ET and MWA values (see Fig. S1).

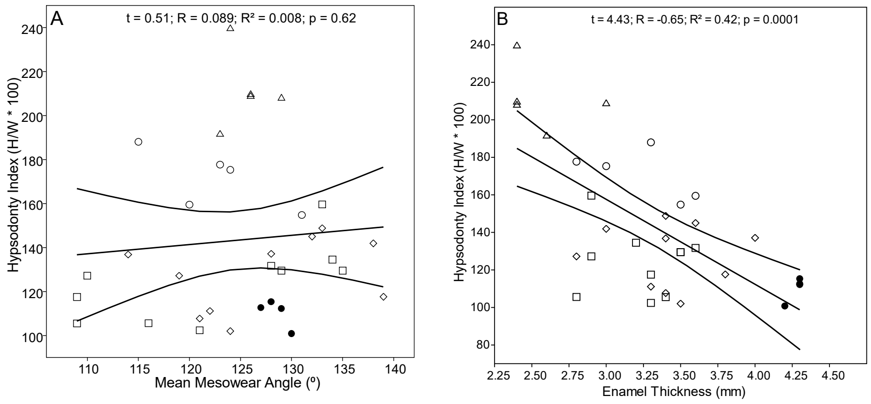


FIG. 6. – Linear regressions (Ordinary Least Squares Regression): **A**, MWA versus HI; **B**, ET versus HI in the lineage of *Elephas recki* throughout members of the Shungura Formation. Symbols correspond to members: filled circles, Member B; open squares, members C to F; open diamonds, Member G; open circles, Member K and lower Member L; open triangles, upper Member L.

DISCUSSION

The evolution of hypsodonty in herbivorous mammals has long been believed as one of the best examples of a sustained macroevolution drive~~d~~ caused by abrasive diets (Damuth & Janis 2011; Kaiser *et al*. 2013). This trend has well recognized in the evolutionary history of different mammalian groups (Simpson, 1945). It is also an indication of convergent evolution in various clades since, considered evidence of an adaptation for an abrasive herbivorous diet generally and mainly consisting of grasses (Williams and Kay 2001; Cerling *et al.* 2011).

~~As proposed by~~According to Maglio (1973)~~ in his monograph~~, ~~the~~ in African representatives of the genus *Elephas*~~;~~, the rate of change in molar structure, mainly for the HI and ET, was extremely rapid. He also ~~outlined~~ highlighted that the functional ~~meaning~~ implications of the enamel thinning is less ~~obvious~~salient, however, for Plio-Pleistocene elephantid lineages that had a reduced enamel thickness while being subjected to a highly abrasive diet linked to grass feeding preference.

Concerning the hypothesis of continuous increase in HI and reduction in ET, our results generally do not support it. In both biometric characters, which display a significant correlation (Fig. 6B), no apparent progressive, continuous evolutionary changes were observed in the lineage of *E. recki* from the Shungura Formation. Instead, a significant decrease in enamel thickness was observed between members B and C, followed by little to no change from Member C to upper Member G, then again going through a rapid, significant decrease in the top members (K, L). Statistically, little significant changes between members were perceived in the values of hypsodonty from members B to G, until values display significant increases in K-LL then in UL. These patterns fit better the description of "incremental changes" suggested by Lister (2013), and of stepwise evolution by Saarinen & Lister (2023), to mark a difference with gradual evolution through "infinitesimal gradations" accumulated in a continuous process. Temporal gaps in our sample do not impact this interpretation of successive sudden changes and stasis, but it is expected that future collections in Shungura deposits within non-documented time intervals will help identifying more precisely tipping ages, especially between the lower sequence of Shungura and members K and L.

One way to interpret these results is that they would correspond to the lumping of multiple lineages within the "*Elephas recki* Complex" (see Zhang 2020). However, similar stepwise

Formatted: Font: Italic

changes in evolutionary rates can be observed in single lineages (Saarinen & Lister 2023) and should not necessarily seen as evidence for taxonomic comingling. As indicated above, the debate on the taxonomic status of *Elephas recki* has still not reached a conclusion (e.g., Sanders 2024). We considered here that the studied material is more parsimoniously interpreted as belonging to a single lineage (following Beden 1980 among many others). We acknowledge that subspecies were used as a practical rank for chronological stages, and that alternatively at least some of them could be reconsidered as chronospecies, notably *Elephas recki brumpti* in agreement with Sanders (2024). Yet we are convinced that further work is required for finalizing the taxonomic revision of the Shungura material attributed to *Elephas recki*.

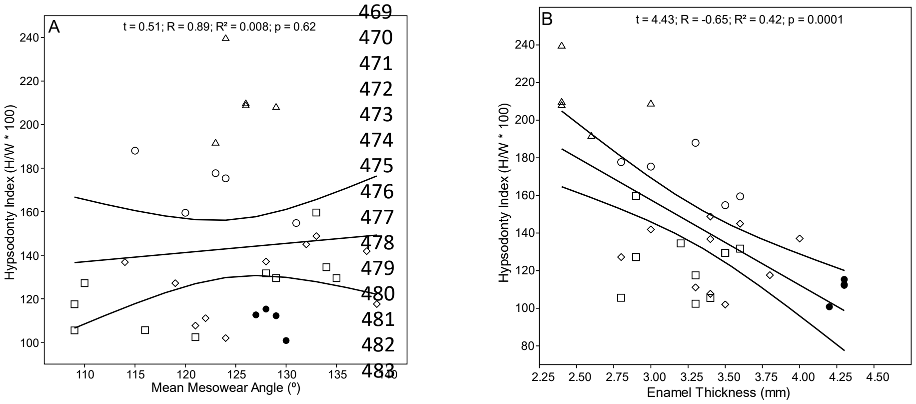
Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

In the meantime, we compared our results with those recently obtained by Saarinen & Lister (2023) on the '*Elephas recki* complex' from sites contemporaneous to the Shungura Formation (notably from eastern and western Turkana, see Supplementary Comparative Data Fig. S2). Their results for HI ~~very well fit~~are congruent with the trend and values we observed, and to some extent fill the temporal gap between upper G and K, suggesting that the main shift occurred sharply just after 1.5 Ma. However, compared to ours, their ET results display lower values for pre-3.0 Ma specimens (equivalent to Member B in age), no change between these and values for the interval 3.0 Ma - 2.5 Ma (Member C age), then again lower values after 2.0 Ma. It remains to be determined if these differences reflect real regional differences, if discrepancies in measurements acquired by different operators could be sufficient to explain these trend and absolute value differences, or if the way of defining the temporal range of specimens could impact the observed distributions.

~~As initially suggested by Maglio (1973) for elephantid molar morphology, a HI increase should be correlated with a decrease in ET in relation to an increasing proportion of abrasive food in diet, mainly grass. To verify these assumptions, after conducting a linear regression test, we evaluated the functional relationship of variables of the two functions for the subset of specimens for which HI, ET and MWA data were available. We then assessed the correlation by comparing the HI and ET for specimens. The results ($R^2 = 0.42$) showed significant links between the biometric characters (Fig. 6B). Regarding correlation between the two independent biometric characters (HI and ET) and behavior (MWA), the results showed $R^2 = 0.008$, $t = 0.51$, $p = 0.62$ and $R^2 = 0.044$, $t = 1.21$, $p = 0.23$, respectively, hence no significant correlation between the HI and MWA (Fig. 6A), nor between ET and MWA values (see Fig. S1).~~



~~FIG. 6. — Linear regressions (Ordinary Least Squares Regression): **A**, MWA versus HI; **B**, ET versus HI in the lineage of *Elephas recki* throughout members of the Shungura Formation. Symbols correspond to members: filled circles, Member B; open squares, members C to F; open diamonds, Member G; open circles, Member K and lower Member L; open triangles, upper Member L.~~

Our MWA results indicated a constantly abrasive diet (i.e., consumption incorporating a significant amount of grasses) showing little variation through time, and no correlation with morphological (HI) changes (Fig. 6A). This is consistent with results obtained by Saarinen *et al.* (2015) for *Elephas recki* from the Koobi Fora Formation (also belonging the Omo Group of the Turkana Depression). Carbon isotope contents in dental enamel of *Elephas* obtained by Cerling *et al.* (2015) between 3.5 Ma and 1.0 Ma for Kenyan formations of the Omo Group display a signal that can be interpreted as more dominated by grazing but similarly with no trend through time. Saarinen & Lister (2023) obtained also a range of variation in their MWA results constant through time (see Supplementary Comparative Data Fig. S2 C), however these are systematically lower than ours (with a mean difference of 11°). They suggest a diet dominated by low abrasion to mixed contents, and a third of individuals (N = 24 out of 68) exhibiting a grazing signal. This is at odd with our findings showing a clear majority of individuals (N = 63 out of 80) fall in the grazing range~~few individuals with a fully grazing signal (4.3 %). This is at odd with our results (55.0 % of individual in grazing range, Fig. 5)~~, with above mentioned isotopic data and with data indicating that the Turkana sites from Kenya sampled landscapes consistently more arid and open than the Omo (see, e.g., Levin *et al*. 2011). We suggest that these differences could be linked to different ways of acquiring MWA values, which stresses the need of building comparisons based on measurements performed by a single operator at this stage of methodological development.

At the local scale of the Shungura Formation, our results on biometric character changes of *Elephas recki* are decoupled from the tooth mesowear proxy indicating a constantly abrasive diet (i.e., consumption of grasses). This decoupling is congruent with results obtained by Lister (2013) and Saarinen & Lister (2023) using stable isotope data and MWA, respectively, at broader temporal, geographical and taxonomical scales. This suggests that behavioral adaptation, such as diet or feeding preferences, preceded by far what has been depicted as morphological adaptations to these preferences (Maglio 1973). Indeed, enamel isotopic contents of eastern African elephantids displayed C_4 signals interpreted as a dietary behavior dominated by graze from the Late Miocene until 0.2 Ma (Cerling *et al.* 2011; Uno *et al.* 2011). However, Saarinen & Lister (2023) observed that, over long timescales, major proboscidean dental adaptations aligned with periods of aridification, suggesting that increasing aridity and not just grazing was a key driver of these evolutionary changes due to shifts toward tougher, dry-adapted vegetation.

Isotopic results obtained by Negash *et al.* (2020) for elephantids from the Shungura Formation are not fully congruent with this view. As for our MWA results, they indicate a graze-dominated mixed diet to strictly grazing diet, as previously for bovids and suids from the same formation (Bibi *et al.* 2013), but also display significant differences between Member B and Member C values (matching an increase in our MWA results between these two members, although non-significant) and an increase in C_4 plants between the lower and the upper part of the sequence. These results could be more in line with the stepwise morphological changes we observed. Yet, these isotopic contents at family level cannot be attributed with certainty to *Elephas recki* and may include different dental positions, and as such are not fully comparable with the dataset used in the present study. In addition, the interpretation of a shift toward a more C_4 signal may not necessarily reflect a significant change of dietary category (see discussion by Blondel *et al.* 2018). Future work on Shungura isotopic ecology will be required to test these results specifically for *E. recki*.

Formatted: Subscript

Formatted: Font: Italic

~~The usual~~A common assumption in evolutionary ecology is that behavior and morphology are tightly connected and that permanent changes in the former would be quickly followed by morphological adaptations. On these premises, many studies suggested that global climatic changes drove vegetation changes resulting in behavioral and/or morphological innovations of African fauna (e.g., Coppens 1975; Vrba 1988, 1995; Bobe & Eck 2001; Negash *et al.* 2015, 2020).

The decoupling between dietary behavior and morphological changes in elephantids raises the possibility of alternate hypotheses for explaining morphological changes through dietary adaptations.

The 'evolutionary lag' (Lister 2013) between the acquisition of the grass-dominated diets and the morphological changes seen in proboscideans and other taxa could be related to intrinsic evolutionary constraints, such as the slow reproduction rate of K-strategist elephantids (but not explaining for relatively sudden changes in their tooth morphology) or the need to acquire first craniomandibular morphologies that allow accommodating higher-crown teeth with more enamel plates. We checked the r~~R~~ecent work by Zhang (2020) focusing on cranio-mandibular morphology for taxonomic and phylogenetic purpose, in order to see if some of the character changes listed in this comprehensive study ~~did not suggest~~ documented particular changes that could have played a role in relaxing constraints on teeth between *E. r. brumpti*, *E. r. shungurensis-atavus*, and *E. r. ileretensis-recki*. Our search was not successful, and this question remains open to future advances.

External, alternative factors may also have contributed to the observed morphological changes. For instance, exogenous grit could have increased as the eastern African landscapes dried up during the Plio-Pleistocene time interval. This could have resulted in a higher rate of abrasion of elephantid teeth, even after they transitioned to a grazing diet. Debates about the role of exogenous grits in herbivore tooth wear versus abrasive plant materials are not new (e.g., Strömberg *et al.* 2013; Merceron *et al.* 2016). Grits significantly influenced the selective adaptation of a mammal's tooth with hypsodonty, as noted by Ungar (2015). Janis and Fortelius (1988) suggested that ungulates that live in open, dry habitats and feed on ground level often grow hypsodont molars. However, in contrast, mammals that feed aboveground in wet, closed-canopy forests tend to have brachydont (low-crowned molars).

Studying the amount of grit and dust in the eastern African rift system can help testing the hypothesis that there is a link between external grit and the rate of morphological evolution. Volcanic ash contains glassy materials that make it highly abrasive (Strömberg *et al.* 2013; Madden 2015). Madden (2015) suggested that the ideal place to test this hypothesis would be the fossiliferous sites in the Plio-Pleistocene geologic sequences of the eastern African rift system such as in Ethiopia and Kenya, where two lineages of suids, australopithecines, and *Theropithecus* all responded similarly to changes in the concentration of external grit. The lineage of *Elephas recki* from the Shungura Formation could have responded the same way as the above referred taxa.

Saarinen & Lister (2023) reached this conclusion after observing tight correlations between changes in dental feature ~~changes~~ (including HI and ET) and ~~picks~~ periods of increased~~of~~ aridity (based on dust in marine sediments as a proxy of general aridification and dustiness in eastern Africa). According to them, episodes of increased airborne dust may have resulted in rapid morphological responses preserved during following milder time intervals, explaining the observed stepwise evolution through this ratchet effect.

This requires considering that increased hypsodonty mostly responded to exogenous particles and that mesowear mostly responded to abrasion by plant silica contents. Sanson *et al.* (2017) concluded, among others, that dental wear in general results from interaction between exogenous and endogenous (plant-embedded) abrasives. If some studies reported that exogenous particles (dust, silt, sand) has little influence on mesowear (Kaiser *et al.* 2013), others demonstrated that it may not be necessarily the case depending on environmental conditions (e.g., Wronski & Schulz-Kornas 2015) or on the considered taxa (e.g., Martin *et al.* 2021). Experimental works and hypotheses based on medium-sized ungulates – prominently ruminants – may not so readily apply to proboscideans, i.e. hindgut fermenters of particularly large size. The apparent lack of impact of Early Pleistocene grit abundance trends on mesowear analyses in proboscideans therefore calls for caution.

Formatted: Pattern: Clear

Formatted: Font: Italic, Pattern: Clear

Formatted: Pattern: Clear

Formatted: Font: Italic, Pattern: Clear

Formatted: Pattern: Clear

Formatted: Not Highlight

Formatted: Font: Italic

~~And yet, the apparent lack of impact of Early Pleistocene grit abundance trends on mesowear analysis results calls for caution, and for i~~Investigating additional ecological and morphological data from *Elephas* in well-documented, local contexts such as the Shungura Formation should provide relevant tests of single-factor explanations.

CONCLUSION

The decoupling we observed between morphology and diet aligned with that observed by Lister (~~Lister~~ 2013) at family level, this time at the local scale of the Lower Omo Valley, with a different dietary proxy and an expanded dataset for what has been described as a single lineage. At the core of this decoupling are stepwise changes in dental morphology for which there seem to be no fully satisfying explanations for the time being. Could the abrupt change in HI and ET trends between Member G and Member K be linked to a cladogenesis resulting in a diversification of what has been named the '*Elephas recki* complex' (Sanders 2024)? Or can it be explained through changes in evolutionary rates within an anagenetic framework in response to environmental factors? Answering to ~~this~~ these questions should require additional work on Shungura elephantid taxonomy, multiproxy paleoecological data focusing at specific level, and an integration of these megaherbivores within the more general picture of local community dynamics. This work is currently in progress and should help taking a better account of Plio-Pleistocene megaherbivores within our explanations of eastern African ecosystem evolution.

Acknowledgments

We are grateful to the National Museum of Ethiopia/Ethiopian Heritage Authority (ex-ARCCH, Ministry of Tourism) for allowing to access collections and perform research. We deeply thank the NME/EHA staff Getahun Tekle and Sahle-Selassie Melaku for guidance and support with collection study. We thank Gildas Merceron for his comments that greatly improved this manuscript. This work was funded by the Ministry of Europe and foreign affairs and conducted within the framework of the Omo Group Research Expedition (OGRE). We are deeply indebted to the hundreds of people who participated to the fieldwork missions of the IORE and of the OGRE, who managed collections and databases, who prepared specimens, who contributed to their study, who provided financial support, who helped with administrative processes, and who provided advice and moral support. The OGRE is a joint program of PALEVOPRIM, the CFEE and the EHA principally funded by the Ministry of Europe and Foreign Affairs, the National Research Agency, the Région Nouvelle-Aquitaine, CNRS INEE, PALEVOPRIM, and the Fyssen Foundation. The OGRE is extremely grateful to the EHA, the SNNPR, the South Omo Zone, the Nyangatom and Dassanetch Weredas and their people for their help and reception.

REFERENCES

ALEMSEGED Z. 2003. — An integrated approach to taphonomy and faunal change in the Shungura Formation (Ethiopia) and its implication for hominid evolution. *Journal of Human Evolution* 44: 451–478.

Alemseged Z., Bobe R. & Geraads D. 2007. — Comparability of fossil data and its significance for the interpretation of hominin environments: a case study in the lower Omo Valley, Ethiopia, *in* Bobe R., Alemseged Z. & Behrensmeyer A. K. (eds), *Hominin Environments in the East African Pliocene*. Springer, Dordrecht: 159–181.

Arambourg C. 1938. — Mammiferes fossiles du Maroc. *Verlag nicht ermittelbar* 46: 1–74.

Arambourg C. 1948. — Contribution à l'étude géologique et paléontologique du bassin du lac Rodolphe et de la basse vallée de l'Omo. Deuxième partie : paléontologie, *in* Arambourg C. (ed.), *Mission Scientifique de l'Omo, 1932-1933. Tome 1 : géologie - anthropologie.* Vol. Fascicule 3 Editions du Muséum, Paris: 231–562.

Beden M. 1980. — *Elephas recki* Dietrich, 1915 (Proboscidea, Elephantidae). Evolution au cours du Plio-Pléistocène en Afrique orientale. *Géobios* 13 (6): 891-901.

Beden M. 1983. — Family Elephantidae, *in* Harris J. M. (ed.), *Koobi Fora Research Project. Volume 2. The fossil ungulates: Proboscidea, Perissodactyla, and Suidae*. Clarendon Press, Oxford: 40-129.

Beden M. 1987. — Les éléphantidés (Mammalia-Proboscidea), *in* Coppens Y. & Howell F. C. (eds), *Les faunes plio-pléistocènes de la basse vallée de l'Omo (Ethiopie), tome 2*. Vol. Cahiers de Paléontologie. Editions du Centre National de la Recherche Scientifique, Paris: 162 p.

Bibi F., Souron A., Bocherens H., Uno K. & Boisserie J.-R. 2013. — Ecological change in the lower Omo Valley around 2.8 Ma. *Biology Letters* 9 (1): 1–4.

Blondel C., Rowan J., Merceron G., Bibi F., Negash E., Barr W. A. & Boisserie J. R. (2018). Feeding ecology of Tragelaphini (Bovidae) from the Shungura Formation, Omo Valley, Ethiopia: contribution of dental wear analyses. *Palaeogeography, Palaeoclimatology, Palaeoecology* 496: 103-120.

Bobe R. 2006. — The evolution of arid ecosystems in eastern Africa. *Journal of Arid Environments* 66: 564–584.

Bobe R. & Eck G. G. 2001. — Responses of African bovids to Pliocene climatic change. *Paleobiology memoirs* suppl. 27 (Memoir 2): 1–47.

Boisserie J.-R., Guy F., Delagnes A., Hlusko L. J., Bibi F., Beyene Y. & Guillemot C. 2008. — New palaeoanthropological research in the Plio-Pleistocene Omo Group, Lower Omo

Formatted: Not Small caps

Formatted: Font: Italic, Not Small caps

Formatted: Not Small caps

Formatted: Not Small caps

Valley, SNNPR (Southern Nations, Nationalities and People Regions), Ethiopia. *Comptes Rendus Palevol* 7: 429–439.

BROWN F. H., HAILEAB B. & MCDOUGALL I. 2006. — Sequence of tuffs between the KBS tuff and the Chari tuff in the Turkana Basin, Kenya and Ethiopia. *Journal of the Geological Society* 163: 185–204.

DAMUTH J. & JANIS C. M. 2011. — On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. *Biological Reviews* 86 (3): 733-758.

CANTALAPIEDRA J. L., SANISIDRO Ó., ZHANG H., ALBERDI M. T., PRADO J. L., BLANCO F. & SAARINEN J. 2021. — The rise and fall of proboscidean ecological diversity. *Nature Ecology & Evolution* 5 (9): 1266-1272.

CERLING T. E., HARRIS J. M., MACFADDEN B. J., LEAKEY M. G., QUADE J., EISENMANN V. & EHLERINGER J. R. 1997. — Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389: 153–158.

CERLING T. E., HARRIS J. M. & LEAKEY M. G. 1999. — Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. *Oecologia* 120: 364–374.

CERLING T. E., LEVIN N. E. & PASSEY B. H. 2011. — Stable isotope ecology in the Omo-Turkana Basin. *Evolutionary Anthropology* 20: 228–237.

CERLING T. E., MANTHI F. K., MBUA E. N., LEAKEY L. N., LEAKEY M. G., LEAKEY R. E., BROWN F. H., GRINE F. E., HART J. A., KALEME P., ROCHE H., UNO K. T. & WOOD B. A. 2013. — Stable isotope-based diet reconstructions of Turkana Basin hominins. *Proceedings of the National Academy of Sciences of the United States of America* 110 (26): 10501–10506.

CERLING T. E., ANDANJE S. A., BLUMENTHAL S. A., BROWN F. H., CHRITZ K. L., HARRIS J. M., HART J. A., KIRERA F. M., KALEME P., LEAKEY L. N., LEAKEY M. G., LEVIN N. E., MANTHI F. K., PASSEY B. H. & UNO K. T. 2015. — Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. *Proceedings of the National Academy of Sciences of the United States of America* 112 (37): 11467–11472.

COOKE, H. B. S. (1947). *"Variation in the Molars of the Living African Elephant and a Critical Revision of the Fossil Proboscidea of Southern Africa*. 434–457; 492–517.

Formatted: Small caps

Formatted: Small caps

Formatted: Font: Italic

COPPENS Y. 1975. — Évolution des mammifères, de leurs fréquences et de leurs associations, au cours du Plio-Pléistocène dans la basse vallée de l'Omo en Éthiopie. *Comptes Rendus de l'Académie des Sciences* 281: 1571-1574.

COPPENS Y. 1978. — Evolution of the hominids and of their environment during the Plio-Pleistocene in the lower Omo Valley, Ethiopia. *Geological Society, London, Special Publications* 6(1): 499–506.

FEIBEL C. S., BROWN F. H. & MCDOUGALL I. 1989. — Stratigraphic context of fossil hominids from the Omo group deposits: Northern Turkana Basin, Kenya and Ethiopia. *American Journal of Physical Anthropology* 78 (4): 595–622.

FORTELIUS M. & SOLOUNIAS N. 2000. — Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *American Museum novitates* 3301: 1–36.

FRITZ H., DUNCAN P., GORDON I. J. & ILLIUS A. W. 2002. — Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia* 131: 620–625.

GHEERBRANT E. & TASSY P. 2009. — L'origine et l'évolution des éléphants. *Comptes Rendus Palevol* 8: 281–294.

GILBERT W. H. & ASFAW B. 2008. — *Homo erectus. Pleistocene Evidence from the Middle Awash, Ethiopia*. University of California Press, Berkeley, The Middle Awash Series, 458 p.

HEINZELIN J. de 1983. — *The Omo Group. Archives of the International Omo Research Expedition*. Musée Royal de l'Afrique Centrale, Tervuren, Annales, Sciences Géologiques, 365 p.

HOWELL F. C. & COPPENS Y. 1974. — Inventory of remains of Hominidae from Pliocene/Pleistocene formations of the lower Omo basin, Ethiopia (1967-1972). *American Journal of Physical Anthropology* 40: 1–16.

JANIS C. M. & FORTELIUS M. 1988. — On the means whereby mammals achieve increased functional durability of their dentition, with special reference to limiting factors. *Biological Reviews* 63: 197–230.

KAISER T. M., MÜLLER D. W. H., FORTELIUS M., SCHULZ E., CODRON D. & CLAUSS M. 2013. — Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: Implications for understanding tooth wear: Hypsodonty, mesowear, tooth wear. *Mammal Review* 43(1): 34–46.

Kalb J. E. & Mebrate A. 1993. — Fossil elephantoids: from the hominid-bearing Awash Group, Middle Awash Valley, Afar Depression, Ethiopia. *Transactions of the American Philosophical Society* 83 (1): 1–114.

Kidane T., Brown F. H. & Kidney C. 2014. — Magnetostratigraphy of the fossil-rich Shungura Formation, southwest Ethiopia. *Journal of African Earth Sciences* 97: 207–223.

Levin N. E., Brown F. H., Behrensmeyer A. K., Bobe R. & Cerling T. E. 2011. — Paleosol carbonates from the Omo Group: isotopic records of local and regional environmental change in East Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 307: 75–89.

Lister A. M. 2013. — The role of behaviour in adaptive morphological evolution of African proboscideans. *Nature* 500: 331-334.

Madden R. H. 2015. — *Hypsodonty in mammals*. Cambridge University Press, 423 p.

Maglio V. J. 1972. — Evolution of mastication in the Elephantidae. *Evolution* 26 (4): 638-658.

Maglio V. J. 1973. — Origin and evolution of the Elephantidae. *Transactions of the American Philosophical Society* 63 (3): 1-149.

Martin L. F., Ackermans N. L., Richter H., Kircher P., Hummel J., Codron D., Clauss M. & Hatt J. M. 2022. — Macrowear effects of external quartz abrasives of different size and concentration in rabbits (*Oryctolagus cuniculus*). *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 338 (8): 586-597.

Mcdougall I. & Brown F. H. 2008. — Geochronology of the pre-KBS Tuff sequence, Omo Group, Turkana Basin. *Journal of the Geological Society* 165: 549–562.

Mcdougall I., Brown F. H., Vasconcelos P. M., Cohen B. E., Thiede D. S. & Buchanan M. J. 2012. — New single crystal ^{40}Ar/^{39}Ar ages improve time scale for deposition of the Omo Group, Omo–Turkana Basin, East Africa. *Journal of the Geological Society* 169: 213–226.

Merceron G., Ramdarshan A., Blondel C., Boisserie J.-R., Brunetiere N., Francisco A., Gautier D., Milhet X., Novello A. & Pret D. 2016. — Untangling the environmental from the dietary: dust does not matter. *Proceedings of the Royal Society B* 283 (20161032): 1-8.

Meyer M., Palkopoulou E., Baleka S., Stiller M., Penkman K. E., Alt K. W., Ishida Y., Mania D., Mallick S., Meijer T., Meller H., Nagel S., Nickel B., Ostritz S., Rohland N., Schauer K., Schüler T., Roca A. L., Reich D., Shapiro B. & Hofreiter M. 2017. — Palaeogenomes of Eurasian straight-tusked elephants challenge the current view of elephant evolution. *Elife* 6: e25413.

Formatted: Small caps

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: (Default) Times New Roman, 12 pt, Small caps, Ligatures: Standard + Contextual

Formatted: Font: (Default) Times New Roman, 12 pt, Ligatures: Standard + Contextual

Formatted: Font: (Default) Times New Roman, 12 pt, Small caps, Ligatures: Standard + Contextual

Formatted: Font: (Default) Times New Roman, 12 pt, Ligatures: Standard + Contextual

Formatted: Font: (Default) Times New Roman, 12 pt, Small caps, Ligatures: Standard + Contextual

Formatted: Small caps

Formatted: Left, Indent: Left: 0", Hanging: 0.2", Don't adjust space between Latin and Asian text, Don't adjust space between Asian text and numbers, Pattern: Clear

Formatted: Font: (Default) Times New Roman, 12 pt, Small caps, Ligatures: Standard + Contextual

Formatted: Font: (Default) Times New Roman, 12 pt, Ligatures: Standard + Contextual

Formatted: Font: (Default) Times New Roman, 12 pt, Ligatures: Standard + Contextual

Formatted: Font: (Default) Times New Roman, 12 pt, Not Italic, Ligatures: Standard + Contextual

Formatted: Font: (Default) Times New Roman, 12 pt, Ligatures: Standard + Contextual

Negash E. W., Alemseged Z., Bobe R., Grine F., Sponheimer M. & Wynn J. G. 2020. — Dietary trends in herbivores from the Shungura Formation, southwestern Ethiopia. *Proceedings of the National Academy of Sciences of the United States of America* 117 (36): 21921-21927.

Negash E. W., Alemseged Z., Wynn J. G. & Bedaso Z. K. 2015. — Paleodietary reconstruction using stable isotopes and abundance analysis of bovids from the Shungura Formation of South Omo, Ethiopia. *Journal of Human Evolution* 88: 127-136.

Owen-Smith R. N. 1988. — *Megaherbivores. The influence of very large body size on ecology*. Cambridge University Press, 369 p.

Palkopoulou, E., Lipson, M., Mallick, S., Nielsen, S., Rohland, N., Baleka, S., Karpinski E., Ivancevic A. M., To T.-H., Kortschak R. D., Raison J. M., Qu Z., Chin T.-J., W. Alt K. W., Claesson S., Dalén L., MacPhee R. D. E., Meller H., Roca A. L., Ryder O. A., Heiman D., Young S., Breen M., Williams C., Aken B. L., Ruffier M., Karlsson E., Johnson J., Di Palma F., Alfoldi J., Adelson D. L., Mailund T., Munch K., Lindblad-Toh K., Hofreiter M., Poinar H. & Reich D. 2018. — A comprehensive genomic history of extinct and living elephants. *Proceedings of the National Academy of Sciences*, 115 (11): E2566-E2574.

Roca A. L., Georgiadis N., Pecon-Slattery J. & O'brien S. J. 2001. — Genetic evidence for two species of Elephant in Africa. *Science* 293: 1473–1477.

Saarinen J., Karme A., Cerling T., Uno K., Säilä, Kasiki S., Ngene S., Obari T., Mbua E., Manthi F. K. & Fortelius M. 2015. — A new tooth wear-based dietary analysis method for Proboscidea (Mammalia). *Journal of Vertebrate Paleontology* 35 (3): 1-8.

Saarinen J. & Lister A. M. 2023. — Fluctuating climate and dietary innovation drove ratcheted evolution of proboscidean dental traits. *Nature Ecology & Evolution* 7(9): 1490–1502.

Saegusa H. & Gilbert W. H. 2008. — Elephantidae, *in* Gilbert W. H. & Asfaw B. (eds), *Homo erectus. Pleistocene Evidence from the Middle Awash, Ethiopia*. University of California Press, Berkeley: 193–226.

Sanders W. J. 2024. — *Evolution and fossil record of African* ~~*p*~~ *Proboscidea* (First edition). CRC Press, 346 p.

SANDERS W. J. & HAILE-SELASSIE Y. 2012. — A new assemblage of mid-Pliocene proboscideans from the Woranso-Mille area, Afar region, Ethiopia: taxonomic, evolutionary, and paleoecological considerations. *Journal of Mammalian Evolution* 19: 105-128.

SANDERS W. J., GHEERBRANT E., HARRIS J. M., SAEGUSA H. & DELMER C. 2010. — Proboscidea, *in* WERDELIN L. & SANDERS W. J. (eds), *Cenozoic Mammals of Africa*. University of California Press, Berkeley: 161–251.

SANSON G. D., KERR S. & READ J. 2017. — Dietary exogenous and endogenous abrasives and tooth wear in African buffalo. *Biosurface and Biotribology* 3 (4): 211-223.

SHOSHANI J. & TASSY P. 2005. — Advances in proboscidean taxonomy & classification, anatomy & physiology, and ecology & behavior. *Quaternary International* 126-128: 5–20.

SIMPSON G. G. 1945. — The principles of classification and a classification of the mammals. *Bulletin of the American Museum of Natural History* 85: 1–350.

STRÖMBERG C. A. E. 2011. — Evolution of Grasses and Grassland Ecosystems. *Annual Review of Earth and Planetary Sciences* 39(1): 517–544.

STRÖMBERG C. A. E., DUNN R. E., MADDEN R. H., KOHN M. J. & CARLINI A. A. 2013. — Decoupling the spread of grasslands from the evolution of grazer-type herbivores in South America. *Nature Communications* 4: 1-8.

SUKUMAR R. (2003). — *The living elephants: Evolutionary ecology, behavior, and conservation.* Oxford University Press, 478 p.

TASSY P. (1988). — The classification of Proboscidea: how many cladistic classifications? *Cladistics* 4(1): 43–57.

TODD N. E. (2005). — Reanalysis of African *Elephas recki*: Implications for time, space and taxonomy. *Quaternary International* 126-128: 65–72.

UNGAR P. S. (2010). — *Mammal Teeth: Origin, Evolution, and Diversity*. The John Hopkins University Press, 320 p.

UNGAR P. S. (2015). Mammalian dental function and wear: A review. *Biosurface and Biotribology* 1(1): 25–41.

UNO K. T., CERLING T. E., HARRIS J. M., KUNIMATSU Y., LEAKEY M. G., NAKATSUKASA M. & NAKAYA H. 2011. — Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. *Proceedings of the National Academy of Sciences of the United States of America* 108 (16): 6509–6514.

Formatted: Not Small caps

Formatted: Font: Italic, Not Small caps

Formatted: Not Small caps

Formatted: Not Small caps

Formatted: Not Small caps

VRBA E. S. 1988. — Late Pliocene climatic events and hominid evolution, *in* GRINE F. (ed.), *Evolutionary History of the Robust Australopithecines*. De Gruyter, New York: 405–426.

VRBA E. S. 1995. — The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolutions and paleoclimate, *in* VRBA E. S., DENTON G. H., PARTRIDGE T. C. & BURCKLE L. H. (eds), *Paleoclimate and evolution with emphasis on human origins*. Yale University Press, New Haven: 385–424.

WILLIAMS S. H. & KAY R. F. 2001. — A comparative test of adaptive explanations for hypsodonty in ungulates and rodents. *Journal of Mammalian Evolution* 8 (3): 207–229.

WRONSKI T. & SCHULZ-KORNAS E. 2015. — The Farasan gazelle—A frugivorous browser in an arid environment? *Mammalian Biology* 80: 87-95.

ZHANG H. 2020. — Evolution and systematics of the Elephantidae (Mammalia, Proboscidea) from the Late Miocene to Recent [Ph. D. dissertation: University of Bristol, 319 p.

Formatted: Not Small caps

Formatted: Font: Italic, Not Small caps

Formatted: Not Small caps

Formatted: Not Small caps