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New data on morphological evolution and dietary adaptations of *Elephas recki* (Dietrich, 1915) from the Plio-Pleistocene Shungura Formation (Lower Omo Valley, Ethiopia)

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& Jean-Renaud BOISSERIE

GLIMPSES OF A PLIO-PLEISTOCENE AFRICAN ECOSYSTEM:
THE LOWER OMO VALLEY, ETHIOPIA

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ABSTRACT

The 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* (Dietrich, 1915) (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 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.

KEY WORDS
Elephas recki,
enamel thickness,
hypsodonty index,
mesowear,
Shungura Formation.

RÉSUMÉ

*Nouvelles données concernant l'évolution morphologique et les adaptations alimentaires d'*Elephas recki *(Dietrich, 1915) de la formation plio-pléistocène de Shungura (basse vallée de l'Omo, Éthiopie).*

Les proboscidiens, un groupe 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* (Dietrich, 1915) (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 complètes 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 évolutive.

MOTS CLÉS
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 Earth. Their evolutionary history is well-documented and fossils indicate an incredible diversity (Shoshani & Tassy 2005; Gheerbrant & Tassy 2009; Cantalapiedra *et al.* 2021). Most of their evolution occurred in Afro-Eurasia, with later dispersals to the Americas (Coppens 1978; Tassy 1988). The "true" elephants, i.e., the family Elephantidae (Gray, 1821), originated in Africa during the Late Miocene (Maglio 1973; Kalb & Mebrate 1993), and include three emblematic clades of extant and recently extinct crown elephantids (*Loxodonta* Anonymous, 1827, *Elephas* (Linnaeus, 1758), and *Mammuthus* Brookes, 1828). Following a steep decline during the last two million years (Cantalapiedra *et al.* 2021) and despite some successful diversifications (*Mammuthus*, *Palaeoloxodon* Matsumoto, 1924) in northern Eurasia, there are currently only three species of elephants in the world: the Asian elephant, *Elephas maximus* Linnaeus, 1758, and two species found in Africa, the savanna elephant *Loxodonta africana* (Blumenbach, 1797), and the forest elephant *Loxodonta cyclotis* (Matschie, 1900) (Owen-Smith 1988; Roca *et al.* 2001; Sukumar 2003; Sanders *et al.* 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) provided important proxies for biochronology and trends of environmental changes (Beden 1980, 1983, 1987; 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.* 1997, 2011, 2013; Strömberg 2011). Further attention was later brought to the ecology of African elephantids, notably to their isotopic ecology (e.g. Cerling *et al.* 1999, 2015; 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 & 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.

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 suitable for pursuing this objective. Our research focused on *Elephas recki* (Dietrich, 1915), 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 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., *c.* 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, five 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/39Ar 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 tracking the evolution, paleoecology and environmental context of various vertebrate groups at community level (Bobe & Eck 2001; Alemseged 2003; Bobe 2011).

In the Shungura stratigraphic sequence, elephantid fossils are abundant and constitute a significant proportion of the collected mammals (Coppens 1978; Beden 1980; Alemseged 2003; Alemseged *et al.* 2007). There are at least five species known from Shungura, including *Elephas ekorensis* (Maglio, 1970), *Loxodonta exoptata* (Dietrich, 1941), *Loxodonta adaurora* (Maglio, 1970), and *Loxodonta atlantica* (Pomel, 1979). 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 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* Garutt, 1957 and *Palaeoloxodon* Matsumoto, 1924, respectively. Based on cranial morphopology, Saegusa & Gilbert (2008) and Zhang (2020) advocated for relating *E. recki ileretensis* and *E. recki recki* within *Palaeoloxodon*. However, the implications of this result remain 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, for this paper, not intending to test conflicting taxonomic 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

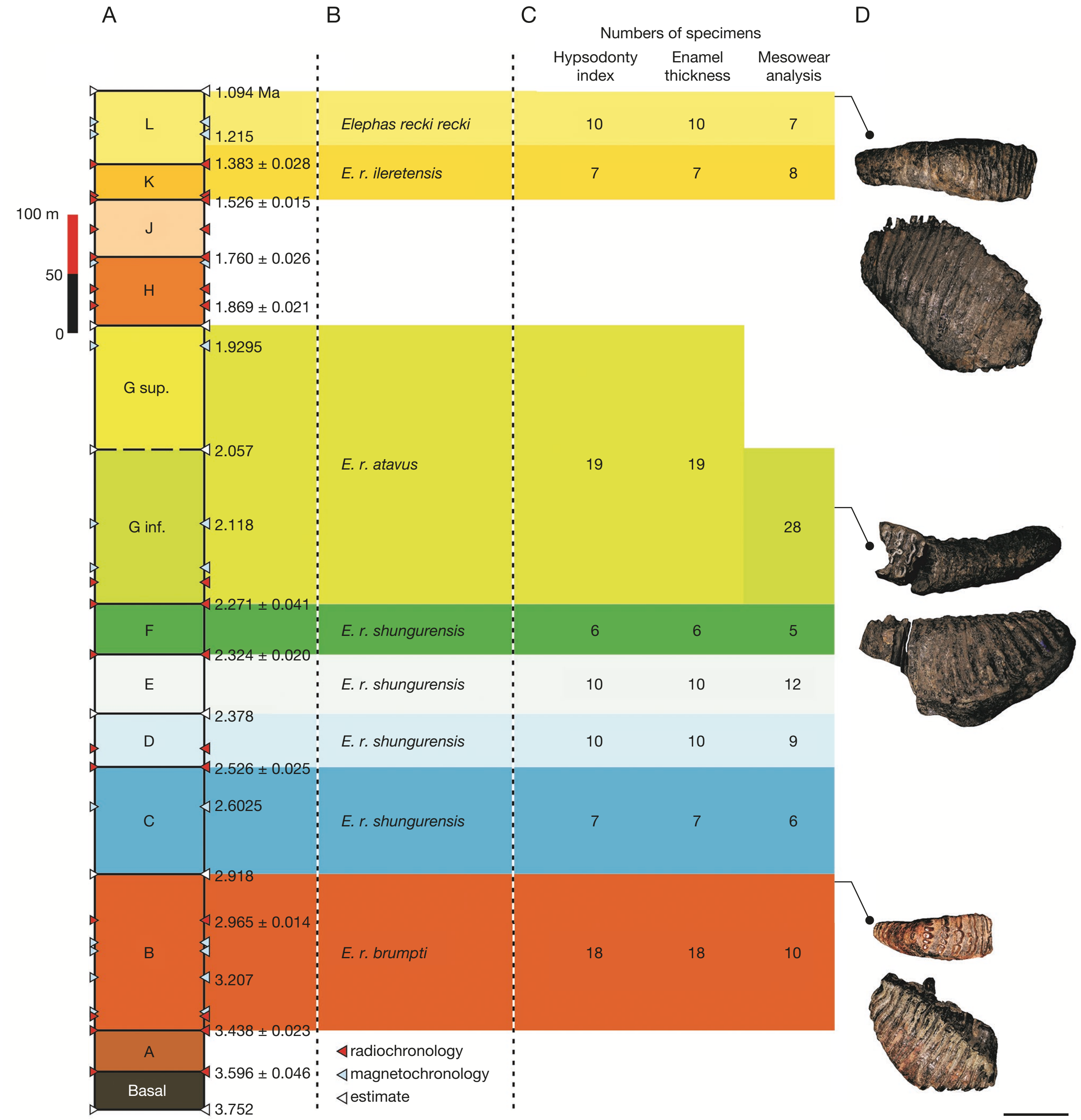

FIG. 1. — Summary of the stratigraphy, distribution, sample counts, and dental morphology of *Elephas recki* (Dietrich, 1915) from the Shungura Formation: **A**, chronostratigraphic composite column of the Shungura Formation following the stratigraphic and radiochronological work described by Heinzelin (1983) and with ages derived from (Feibel *et al.* 1989; Brown *et al.* 2006; McDougall & Brown 2008; McDougall *et al.* 2012; Kidane *et al.* 2014); **B**, distribution of the subspecies of the lineages of *Elephas 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, *Elephas recki brumpti* (OMO 3/01974961, M^3 from B-12), *E. recki atavus* (OMO 7519693196, M_3 from G-4 to G-13), and *E. recki recki* (OMO K 719693204, M3 from Unit L-9). Scale bar: 10 cm.

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 infor-

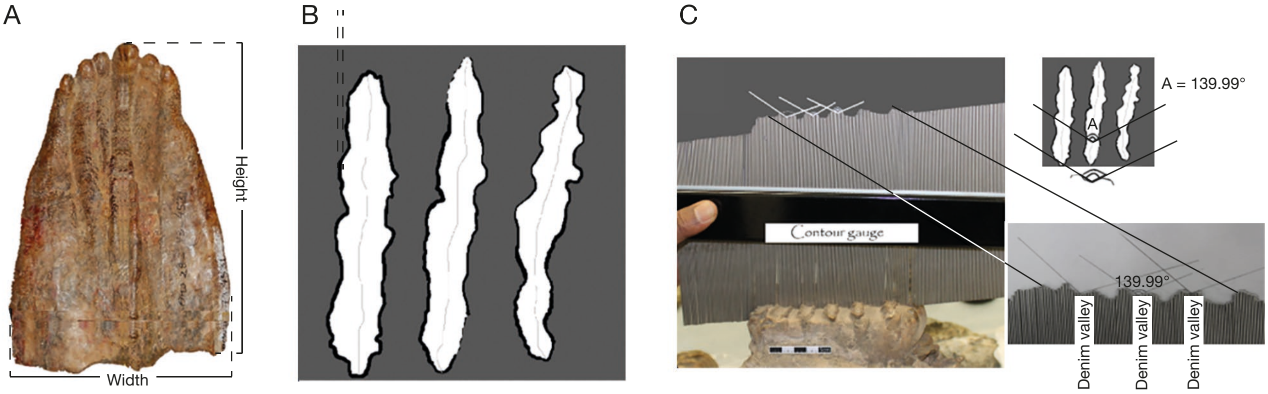

FIG. 2. — Measurements acquired from teeth of *Elephas recki* (Dietrich, 1915) from the Shungura Formation: **A**, measurements involved in the calculation of the hypsodonty index (HI); **B**, measurement of the enamel thickness (ET) on sketched occlusal surface of molar plates; **C**, measurements of mesowear angles (dentin valley angle, in **white** on the sketch) between ridge of enamel bands (in **black**) plates of a molar.

mation about morphology, past dietary habits, vegetation, environmental conditions, and climate (Maglio 1973; Beden 1980; Ungar 2010; Sanders *et al.* 2010; Saarinen *et al.* 2015; Saarinen & Lister 2023). 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 (Appendix 1). 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 (Appendices 2-4).

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.

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).

Hypsodonty index (HI)

This index (height/width of the crown ×100) is a measure of the relative crown height of elephantid molars, 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 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. 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 elephantid 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, consumed by

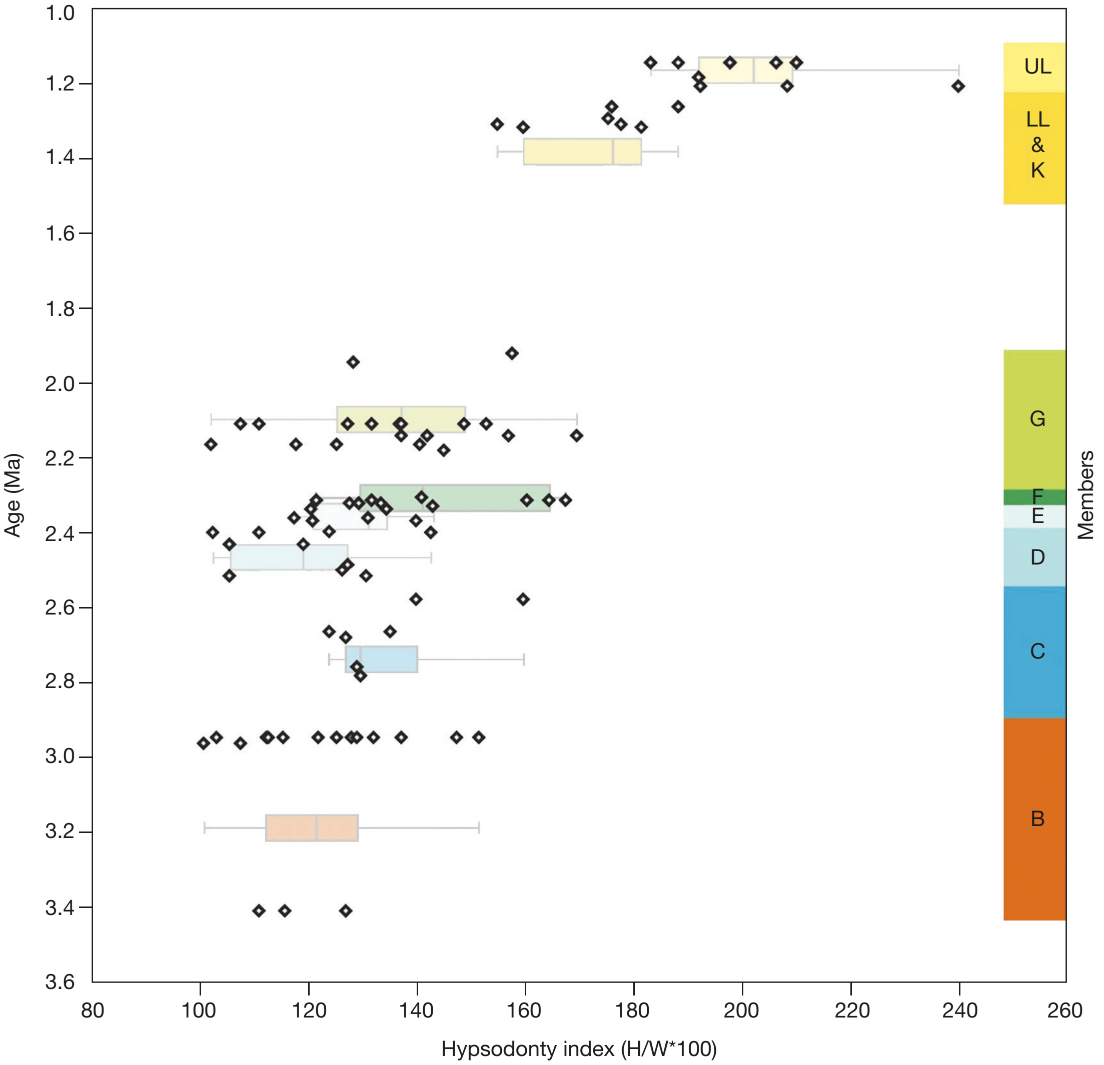

Fig. 3. — Box plots and individual values for hypsodonty index (HI) through time in *Elephas recki* (Dietrich, 1915) from different members of the Shungura Formation. Boxes represent the interquartile range, bar is median, and whiskers represent the lower and the upper 25% of the data.

Table 1. — Statistical summary of biometric characters by members/submembers. Abbreviations: **ET**, enamel thickness; **HI**, hypsodonty index.

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

herbivorous mammals. The mean mesowear angle (MWA) has been calculated for each molar sample by taking the average angle from the dentine valleys of three 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 from a single molar. A t-test was conducted on some of the representative individual

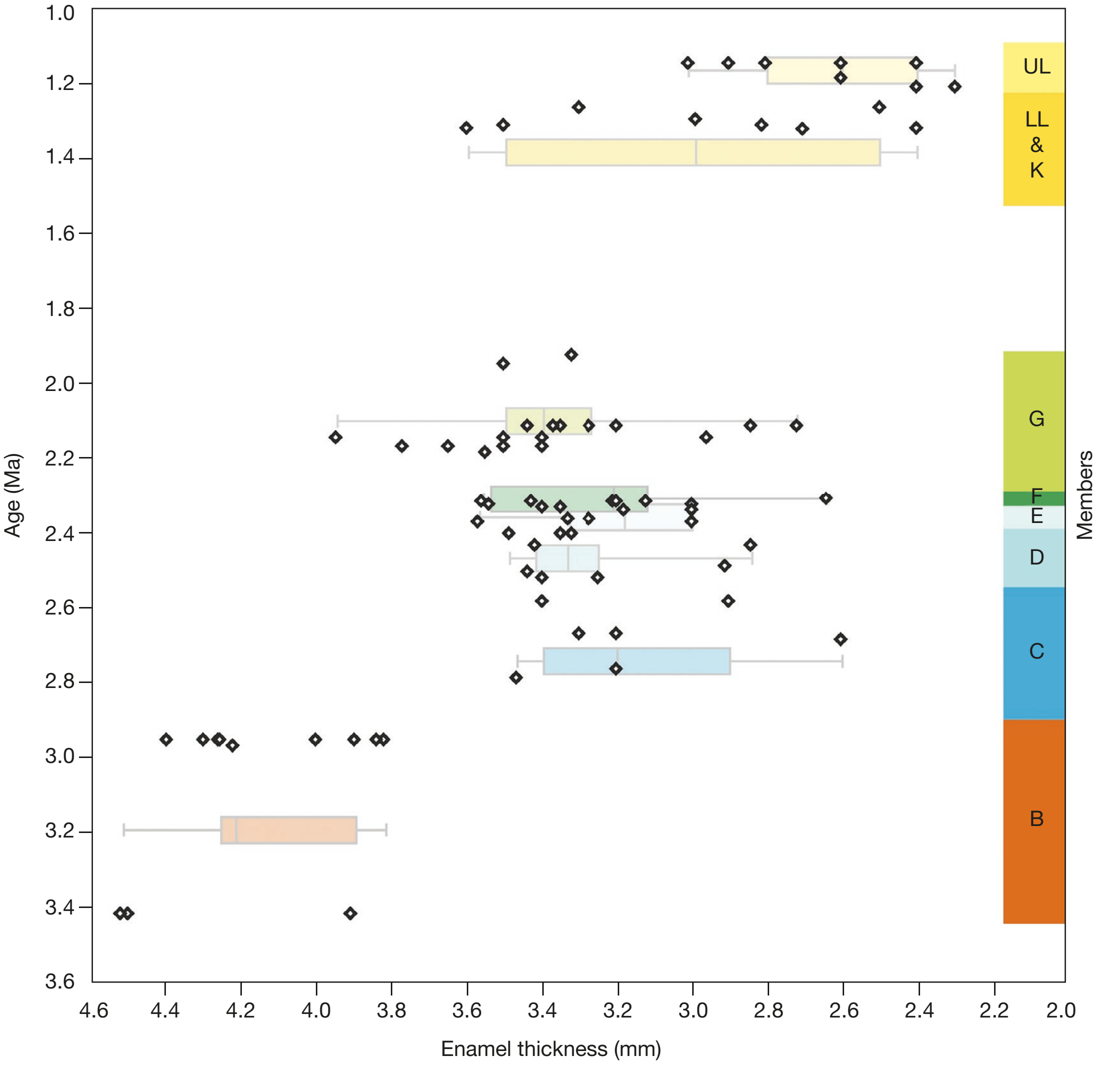

FIG. 4. — Box plots and individual values for enamel thickness (ET) through time in *Elephas recki* (Dietrich, 1915) from different members of the Shungura Formation. Boxes represent the interquartile range, bar is median, and whiskers represent the lower and the upper 25% of the data.

TABLE 2. — Mann-Whitney pairwise tests showing significant trends for hypsodonty index (HI) and enamel thickness (ET) values. 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.

	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	–

measurements, but no significant difference was found between the series including three samples per individual and that including two samples only (see Appendices 5-7). 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

Table 3. — Statistical summary of mesowear angle analysis 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 mesowear angle analysis 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

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 (Appendices 2-4). 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.

Abbreviations

Dental analyses

ET	enamel thickness;
HI	hypsodonty index;
MWA	mesowear angle analysis.

Stratigraphic references

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.

Enamel thickness (ET)

Descriptive statistics for this variable are provided in Table 1 and distributions are illustrated 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).

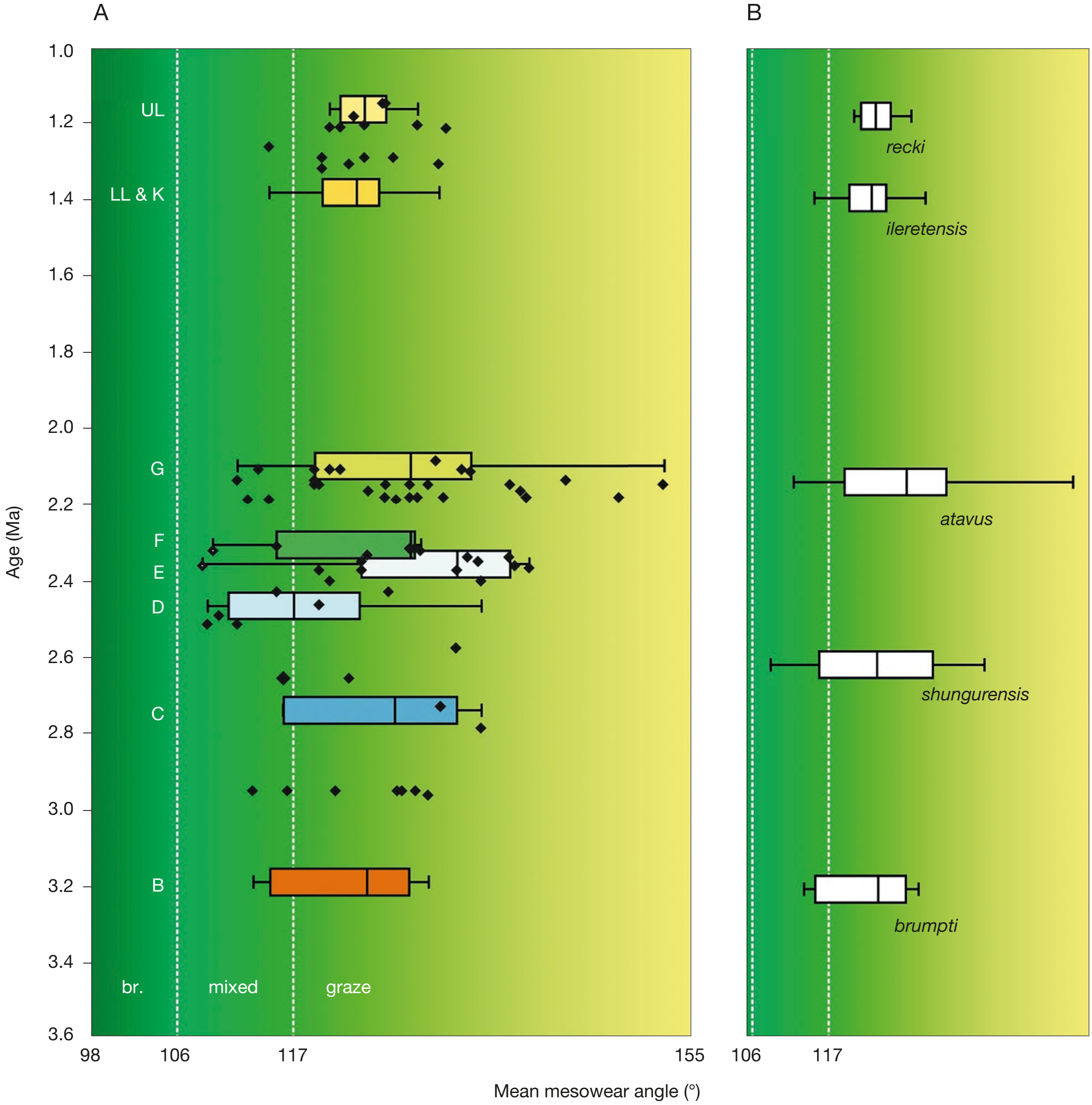

FIG. 5. — Box plots and individual values of mesowear angles (MWA) in *Elephas recki* (Dietrich, 1915) from the Shungura Formation, shown: **A**, by members (testing temporal trends vs stochastic variation); **B**, by subspecies (testing dietary differences), with dietary thresholds for browsers (br.), mixed feeders, and grazers at 106° and 117° revised after Saarinen & Lister (2023).

MESOWEAR ANGLE (MWA)

Descriptive statistics for MWA are provided in Tables 3 and 4. Mesowear distributions by members and subspecies are illustrated by Figure 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 & Lister (2023) who classified samples as browsers if their mean MWA is below 106°, mixed feeders if their mean MWA is between 106° and 117°, and grazers if their mean MWA is above 117°, we determined that *Elephas recki* from Shungura displays a predominantly grazing diet, with a limited occurrences of mixed diets for members B, D, F, K, and subspecies *E. r. brumpti* and *P. r. ileretensis* (Fig. 5; Tables 3; 4).

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 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 R2 = 0.008, t = 0.51, p = 0.62 and R2 = 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 Appendix 9).

DISCUSSION

The evolution of hypsodonty in herbivorous mammals has long been believed as one of the best examples of a sustained macroevolution drive 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 & Kay 2001; Cerling *et al.* 2011).

According to Maglio (1973), 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 highlighted that the functional implications of the enamel thinning is less 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 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*.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 Appendix 10). Their results for HI 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 3.0-2.5 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.

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 Appendix 10C, 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, 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

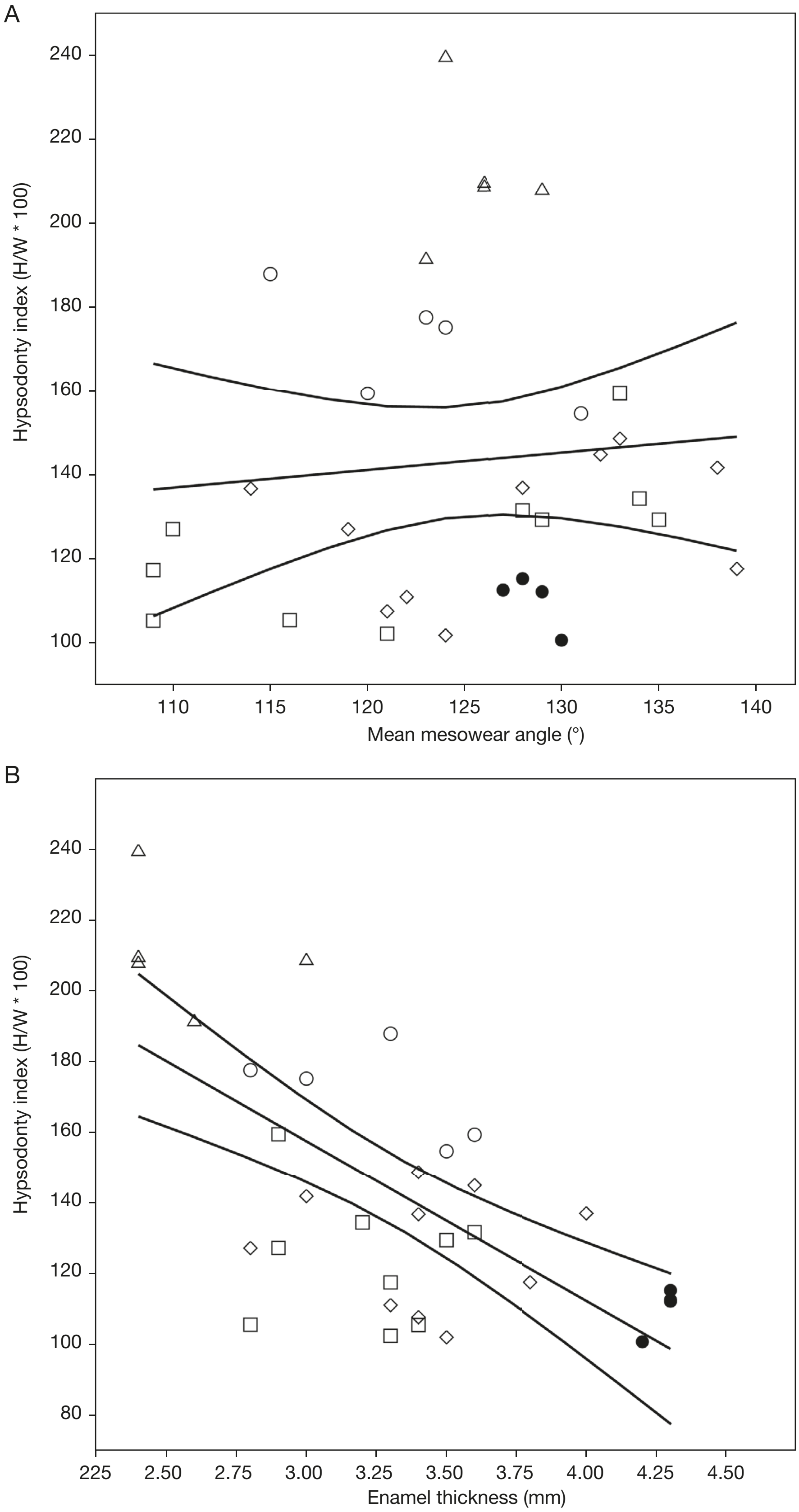

FIG. 6. — Regressions testing whether increasing hypsodonty in *Elephas recki* (Dietrich, 1915) from the Shungura Formation is associated with: **A**, mesowear angles; or **B**, enamel thickness, showing a weak correlation for **A** (t = 0.51, $R^2 = 0.008$, p = 0.62) and a strong positive correlation for **B** (t = 4.43, $R^2 = 0.42$, p = 0.0001); symbols indicate 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.

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 C4 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 C4 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*.

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 recent 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 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 & 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* I.Geoffroy Saint-Hilaire, 1843 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 (including HI and ET) and periods of increased 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.* 2022). 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.

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 (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 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.

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Author contributions

TGB, JRB, and MHT designed the study. JRB provided supervision. TGB and JRB were responsible for data curation. JRB supervised fieldwork, curated collections, and managed the specimen database. TGB was responsible for data collection, formal analysis, and visualization. TGB wrote the article with contributions from all the co-authors.

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APPENDICES

APPENDIX 1. — List of specimens with their measured biometric values. Abbreviations: **H**, height of a molar; **L**, length of a molar; **LF**, lamellar frequency; **P**, number of plates of a molar; **W**, width of a molar. The **gray shaded** dataset was adopted from Saarinen & Lister 2024.

Inventory	Molar type	Subspecies	Stratigraphic interval	Estimated interval age	Member	Member codes	P	L	W	H	LF	ET	HI	MWA
L 1-33	L M/3	*E. r. brumpti*	B-9 to C-0	2.965	B	1-B	11	222.52	82.76	83.45	5	4.22	100.83	130
L 1-57	M3/	*E. r. brumpti*	B-9 to C-0	2.965	B	1-B	7x	158.97	92.3	99.33	5	4.22	107.62	–
L 2-3	M/3	*E. r. brumpti*	B-10	2.965	B	1-B	x5	120+	75.5	94.6	4	4.3	125.3	–
L 2-4	R M/3	*E. r. brumpti*	B-10	2.965	B	1-B	x5	89+	80	82.37	5	3.9	102.96	–
L 2-6	M1/	*E. r. brumpti*	B-10	2.965	B	1-B	–	–	–	–	–	–	–	116.7
L 2-8	L M2/	*E. r. brumpti*	B-10	2.965	B	1-B	–	–	–	–	–	–	–	113.5
L 2-10	M2/	*E. r. brumpti*	B-10	2.965	B	1-B	–	–	–	–	–	–	–	121.3
L 2-11	M/3	*E. r. brumpti*	B-10	2.965	B	1-B	x2x	49+	83	100.77	?	3.84	121.41	–
L 2-12	M/3	*E. r. brumpti*	B-10	2.965	B	1-B	x5	115.5+	80	105.7	4.5	4.4	132.13	–
L 2-14	L M/3	*E. r. brumpti*	B-10	2.965	B	1-B	x5x	98+	66	97.36	5	3.9	147.52	–
OMO 20/3-1967-1039	L M3/	*E. r. brumpti*	B-0	3.412	B	1-B	x7	129+	83	105.5	5	4.52	127.11	–
OMO 20/3-1967-1041	R M3/	*E. r. brumpti*	B-0	3.412	B	1-B	X6	146.65+	76.46	88.53	4.5	4.5	115.79	–
OMO 20/3-1968- 3094	L M3/	*E. r. brumpti*	B-0	3.412	B	1-B	11	220	99	110	5	3.91	111.11	–
OMO 28-1967-476	M1/	*E. r. brumpti*	B-10	2.965	B	1-B	–	–	–	–	–	–	–	113.5
OMO 28-1968-204	M/3	*E. r. brumpti*	B-10	2.965	B	1-B	X4	89+	77	98.45	4.5	3.82	127.86	–
OMO 28-1969-3197	M/3	*E. r. brumpti*	B-10	2.965	B	1-B	x10x	192+	76.42	104.74	4.5	4	137.06	–
OMO 3/0-1968-213	M/3	*E. r. brumpti*	B-12	2.965	B	1-B	x3x	66+	72	92.91	4	3.9	129.04	–
OMO 3/0-1974-572	L M/3	*E. r. brumpti*	B-12	2.965	B	1-B	11	229	72	83	5	4.26	115.28	127.5
OMO 3/0-1974-959	R&L M3/	*E. r. brumpti*	B-12	2.965	B	1-B	11	214	75.5	113.2815714	5	4.255	112.59	127.1
OMO 3/0-1974-960	R M/3	*E. r. brumpti*	B-12	2.965	B	1-B	11	229	74	83	5	4.26	112.16	128.8
OMO 3/0-1974-961	L M3/	*E. r. brumpti*	B-12	2.965	B	1-B	14	219	70	105.93	4.5	3.9	151.33	–
L 32-59	R M/3	*E. r. shungurensis*	C-5 to C-7	2.670	C	C	x3x	69+	79	106.65	?	3.3	135	–
L 32-60	L M/3	*E. r. shungurensis*	C-5 to C-7	2.670	C	C	x5	108+	80	99	?	3.2	123.75	–
L 42-21 & L 42-22	M3/	*E. r. shungurensis*	C-4 to C-5	2.760	C	C	x12x	224+	80	103.13	5.5	3.2	128.91	–
OMO 3/2-1967-920	R M/3	*E. r. shungurensis*	C-4	2.790	C	C	13	194.5	66.5	86.14	5	3.47	129.53	135
OMO 18/inf-10043	M/3	*E. r. shungurensis*	C-4 to C-8	2.680	C	C	x7	145+	80	101.45	5	2.6	126.81	–
OMO 18-1967-1046	M/3	*E. r. shungurensis*	C-8	2.580	C	C	7x	117.96	65.59	104.7	5	2.9	159.63	132.67
OMO 18-10030	M/3	*E. r. shungurensis*	C-7	2.580	C	C	7+	144+	70	98	6	3.4	140	–
OMO 40-1968-171	M2/	*E. r. shungurensis*	C-5 to C-8	2.654	C	C	–	–	–	–	–	–	–	116.3
OMO 40-1968-3029	L M/3	*E. r. shungurensis*	C-5 to C-8	2.654	C	C	–	–	–	–	–	–	–	116.33
OMO 40-1968-3030	R M/2	*E. r. shungurensis*	C-5 to C-8	2.654	C	C	–	–	–	–	–	–	–	122.5
OMO 160-1973-2571	R&L M/2	*E. r. shungurensis*	C-5	2.729	C	C	–	–	–	–	–	–	–	131
L 19-2	M2/	*E. r. shungurensis*	D-4	2.432	D	D	–	–	–	–	–	–	–	126.3
L 21-1	R M2/	*E. r. shungurensis*	D-1	2.516	D	D	–	–	–	–	–	–	–	112
L 22-1	L M/3	*E. r. shungurensis*	D-3	2.465	D	D	–	–	–	–	–	–	–	119.7
L 76-1	L M/3	*E. r. shungurensis*	D-4	2.432	D	D	x9	163.5	69	72.88	5	2.84	105.62	115.7
L 113-1	M1/	*E. r. shungurensis*	D-5	2.404	D	D	–	–	–	–	–	–	–	135
L 170-2	L M3/	*E. r. shungurensis*	D-5	2.404	D	D	11	242	102	113.34	5.5	3.49	111.12	–
L 231-1	R&L M3/	*E. r. shungurensis*	D-5	2.404	D	D	x7	162+	82.51	117.57	5.5	3.35	142.53	–
L 348-1c	R M/3	*E. r. shungurensis*	D-1	2.516	D	D	11	217.5	87.5	92.28	5.5	3.4	105.46	109.2
L 570-3	L M3/	*E. r. shungurensis*	D-5	2.404	D	D	7	131+	82	84	4.5	3.32	102.44	120.7
L 788-1b	L M3/	*E. r. shungurensis*	D-1	2.516	D	D	x7x	120	85	111	5	3.25	130.59	–
OMO 10/A-1967-736	M3/	*E. r. shungurensis*	D-3 to D-5	2.435	D	D	5	85.51+	79	94	5.5	3.42	118.99	–
OMO 54-1974-463	R M3/	*E. r. shungurensis*	D-2	2.499	D	D	11	190	74	93.47	5.5	3.44	126.31	–

Appendix 1. — Continuation.

Inventory	Molar type	Subspecies	Stratigraphic interval	Estimated interval age	Member	Member codes	P	L	W	H	LF	ET	HI	MWA
OMO 148-1972-7	M3/	*E. r. shungurensis*	D-1 to D-3	2.490	D	D	x10	191	84.99	108.11	4.5	2.91	127.2	110.3
L 26-45	L M/3	*E. r. shungurensis*	E-2	2.361	E	E	14	219	65	76.39	6	3.33	117.52	108.7
L 26-47A	R&L M/3	*E. r. shungurensis*	E-2	2.361	E	E	x11	142+	69	90.28	6	3.27	131.06	–
L 26-49	M/2	*E. r. shungurensis*	E-2	2.361	E	E	–	–	–	–	–	–	–	138.2
L 114-11	R M3/	*E. r. shungurensis*	E-3 to E-5	2.341	E	E	x7	119	83.92	101.22	5.5	3	120.61	–
L 267-1	R M3/	*E. r. shungurensis*	E-1	2.372	E	E	x9	137+	71	99.24	6	3.57	139.77	–
OMO 57-1969-3203	LM/2	*E. r. shungurensis*	E-3 to F-1	2.336	E	E	–	–	–	–	–	–	–	124.3
OMO 57/4-1971-2002	R M3/	*E. r. shungurensis*	E-4	2.341	E	E	14	277	103	138.49	4	3.18	134.46	133.7
OMO 57/5-1972-367	R M3/	*E. r. shungurensis*	E-5	2.331	E	E	5	86.3+	68	97.31	6	3.4	143.1	–
OMO 57/4-10010	R&L M1/	*E. r. shungurensis*	E-4	2.341	E	E	–	–	–	–	–	–	–	136.5
OMO 58-124	R M3/	*E. r. shungurensis*	E-5 to F-1	2.326	E	E	x6x	112+	89.5	119.51	5.5	3	133.53	–
OMO 58-134	R M3/	*E. r. shungurensis*	E-5 to F-1	2.326	E	E	10	215	92	117.44	5.5	3	127.65	–
OMO 71-1969-3079	M1/	*E. r. shungurensis*	E-1	2.372	E	E	–	–	–	–	–	–	–	123.7
OMO 71-1969-3030	L M/2	*E. r. shungurensis*	E-1	2.372	E	E	–	–	–	–	–	–	–	132.7
OMO 73-1969-3179	M/2	*E. r. shungurensis*	E-1	2.372	E	E	–	–	–	–	–	–	–	119.7
OMO 73-1969-3179	M/3	*E. r. shungurensis*	E-1	2.372	E	E	9x	185+	73	88.19	4.5	3	120.81	–
OMO 151-1973-184	R M1/	*E. r. shungurensis*	E-3	2.351	E	E	–	–	–	–	–	–	–	134.7
OMO 151-1973-185	L M1/	*E. r. shungurensis*	E-3	2.351	E	E	–	–	–	–	–	–	–	123.7
OMO K 2-1969-3199	M/3	*E. r. shungurensis*	E	2.366	E	E	–	–	–	–	–	–	–	139.5
L 3-7b	L M/3	*E. r. shungurensis*	F-3	2.311	F	F	x7x	153+	79	111.42	5	2.64	141.04	–
L 204-5	L M3/	*E. r. shungurensis*	F-1	2.322	F	F	12	216	89	115.24	5.5	3.54	129.48	129.3
L 465-60	R M/3	*E. r. shungurensis*	F-1 to F-3	2.316	F	F	x6	100+	54	86.56	6	3.2	160.3	–
L 467-49	R M/3	*E. r. shungurensis*	F-1 to F-3	2.316	F	F	x5	83+	68	82.52	5.5	3.21	121.35	–
L 874-1	R M2/	*E. r. shungurensis*	F-3	2.321	F	F	–	–	–	–	–	–	–	109.7
OMO 1/E-1967-712	R M3/	*E. r. shungurensis*	F-1 to F-3	2.316	F	F	x8	142+	78	130.54	5.5	3.12	167.36	–
OMO 1/E-10007	L M3/	*E. r. shungurensis*	F-1 to F-3	2.316	F	F	x4	105.86	90.27	118.91	5	3.56	131.73	128.3
OMO 72-1969-3000	L M3/	*E. r. shungurensis*	F-3	2.31	F	F	–	–	–	–	–	–	–	115.7
OMO 76-1969-3028	M/3	*E. r. shungurensis*	F-1 to F-3	2.316	F	F	8	138+	47	77.28	6	3.43	164.43	–
OMO 76-1969-3049	L M1/	*E. r. shungurensis*	F-1 to F-3	2.316	F	F	–	–	–	–	–	–	–	128.7
L 7-109	M3/	*E. r. atavus*	G-5	2.135	G	G	–	–	–	–	–	–	–	112
L 7-112	R M3/	*E. r. atavus*	G-5	2.135	G	G	–	–	–	–	–	–	–	143
L 16-169	M/3	*E. r. atavus*	G-4	2.146	G	G	x7	125+	74	116.13	5.5	3.4	156.93	–
L 16-170	R M/3	*E. r. atavus*	G-4	2.146	G	G	X12	208+	66	111.84	6	3.5	169.45	–
L 74-20	M3/	*E. r. atavus*	G-4	2.146	G	G	–	–	–	–	–	–	–	119.7
L 74-23	R M3/	*E. r. atavus*	G-4	2.146	G	G	–	–	–	–	–	–	–	126
L 577-1b	M/1	*E. r. atavus*	G-12	2.087	G	G	–	–	–	–	–	–	–	130.7
L 776-1a	M1/	*E. r. atavus*	G-5	2.135	G	G	–	–	–	–	–	–	–	119.3
OMO 6-1967-398	L M/3	*E. r. atavus*	G-4	2.146	G	G	12	224	76	107.84	5.5	2.96	141.89	137.7
OMO 6-1967-399	M3/	*E. r. atavus*	G-4	2.146	G	G	–	–	–	–	–	–	–	152.3
OMO 6-1967-400	L M/3	*E. r. atavus*	G-4	2.146	G	G	10	226	67.46	92.5	4.5	3.95	137.12	128.3
OMO 29-1968-187	L M3/	*E. r. atavus*	G-1 to G-9	2.182	G	G	11	193.75	80	116	5	3.55	145	131.5
OMO 29-1970-1382	M/2	*E. r. atavus*	G-1 to G-9	2.182	G	G	–	–	–	–	–	–	–	129
OMO 29-1968-3075	L M/2	*E. r. atavus*	G-1 to G-9	2.182	G	G	–	–	–	–	–	–	–	148
OMO 29-1969-3189	M3/	*E. r. atavus*	G-1 to G-9	2.182	G	G	–	–	–	–	–	–	–	139.3
OMO 29-1970-1164	M/2	*E. r. atavus*	G-1 to G-9	2.182	G	G	–	–	–	–	–	–	–	128.3
OMO 47-1970-1737	R M/3	*E. r. atavus*	G-8	2.114	G	G	x6	121+	79.5	104.73	5.5	3.37	131.74	–
OMO 47-1970-2014	M/2	*E. r. atavus*	G-8	2.114	G	G	–	–	–	–	–	–	–	134
OMO 72-1969-3150	M3/	*E. r. atavus*	G-3	2.188	G	G	–	–	–	–	–	–	–	115
OMO 75/i-1970-1122	M/2	*E. r. atavus*	G-3	2.188	G	G	–	–	–	–	–	–	–	113

Appendix 1. — Continuation.

Inventory	Molar type	Subspecies	Stratigraphic interval	Estimated interval age	Member	Member codes	P	L	W	H	LF	ET	HI	MWA
OMO 75/i-1970-2158	M/1	*E. r. atavus*	G-3	2.188	G	G	–	–	–	–	–	–	–	127
OMO 75/Sb-1970-562	M/2	*E. r. atavus*	G-4	2.146	G	G	–	–	–	–	–	–	–	130
OMO 75/s-1969-3144	L M/3	*E. r. atavus*	G-1 to G-13	2.164	G	G	x4x	74+	91.84	115	?	3.4	125.22	–
OMO 75/s-1970-1279	L M/3	*E. r. atavus*	G-1 to G-13	2.164	G	G	11	195	85	99.96	5	3.77	117.6	138.7
OMO 75/s-1971-2005	L M/3	*E. r. atavus*	G-1 to G-13	2.164	G	G	11	250	98	100	4.5	3.5	102.04	124.33
OMO 75-1969-3051	R M3/	*E. r. atavus*	G-4 to G-13	2.11	G	G	12	210	91	98	6.5	3.35	107.69	120.7
OMO 75-1969-3052	L M3/	*E. r. atavus*	G-4 to G-13	2.11	G	G	14	245	84	106.87	5	2.84	127.23	119.3
OMO 75-1969-3063	L M/3	*E. r. atavus*	G-4 to G-13	2.11	G	G	12	176.32	70	95.97	6.5	2.72	137.1	–
OMO 75-1969-3065	L M/3	*E. r. atavus*	G-4 to G-13	2.11	G	G	14	224	77	85.53	6	3.27	111.08	121.7
OMO 75-1969-3066	L M/3	*E. r. atavus*	G-4 to G-13	2.11	G	G	8x	140+	77.88	106.55	6	3.35	136.81	114
OMO 75-1969-3067	L M/3	*E. r. atavus*	G-4 to G-13	2.11	G	G	x4x	70+	72.37	110.52	?	3.2	152.72	–
OMO 75-1969-3150	L M/3	*E. r. atavus*	G-4 to G-13	2.164	G	G	x6	141+	70.46	99.1	5.5	3.65	140.65	–
OMO 75-1969-3196	L M/3	*E. r. atavus*	G-4 to G-13	2.11	G	G	4x	73.6+	77.6	115.48	5.5	3.44	148.81	133.2
OMO 75-1970-826	R&L M/2	*E. r. atavus*	G-4	2.146	G	G	–	–	–	–	–	–	–	119
OMO 100-1970-1932	R M3/	*E. r. atavus*	G-28 to G-29	1.923	G	G	x6x	109.04	73	115.12	5.5	3.32	157.7	–
OMO 256-10002	R M/3	*E. r. atavus*	G-27	1.951	G	G	14	250	78	100	6	3.5	128.21	–
F 8-6	R M/2	*E. r. ileretensis/ P.r. ileretentsis*	L-1 to L-5	1.295	K & L	LLK	–	–	–	–	–	–	–	120
OMO 378-10004	L M/3	*E. r. ileretensis/ P. r. ileretentsis*	K-4	1.310	K & L	LLK	x14	275+	77.44	137.64	6	2.81	177.74	122.5
OMO 266-1974-140	M1/	*E. r. ileretensis/ P. r. ileretentsis*	L-1 to L-5	1.295	K & L	LLK	–	–	–	–	–	–	–	124
OMO 266-1974-141a	M2/	*E. r. ileretensis/ P. r. ileretentsis*	L-1 to L-5	1.295	K & L	LLK	–	–	–	–	–	–	–	126.7
OMO 340-10106	L M/3	*E. r. ileretensis/ P. r. ileretentsis*	L-3	1.320	K & L	LLK	7+	141+	80	145	6	2.4	181.25	–
OMO 340-10110	L M/3	*E. r. ileretensis/ P. r. ileretentsis*	L-3	1.320	K & L	LLK	7+	133+	84	134	5.5	3.6	159.52	120
OMO 383-10011	L M/3	*E. r. ileretensis/ P. r. ileretentsis*	L-4	1.266	K & L	LLK	11+	160+	69.58	130.84	6.5	3.3	188.04	115
OMO 391-10058	L M/3	*E. r. ileretensis/ P. r. ileretentsis*	K-4	1.310	K & L	LLK	14	285	80	123.83	6	3.5	154.79	131
OMO K 1-1968-111	L M3/	*E. r. ileretensis/ P. r. ileretentsis*	L-1 to L-9	1.263	K & L	LLK	11	185+	78	137.31	6	2.5	176.04	–
P 997-1b	R M3/	*E. r. ileretensis/ P. r. ileretentsis*	L-1 to L-5	1.295	K & L	LLK	13	264	87	152.52	5.5	2.99	175.31	124
OMO 377-10146	R M/3	*E. r. recki/P. r. recki*	L-6	1.210	UL	UL	9+	170+	71.7	172	6	2.4	239.89	124
OMO 383-10044	L M/3	*E. r. recki/P. r. recki*	L-5	1.215	UL	UL	11+	243	90	173.16	6	2.3	192.4	
OMO 386-10028	R M/3	*E. r. recki/P. r. recki*	L-5 to L-6	1.212	UL	UL	10+	185+	60	125	6	2.4	208.33	129
OMO 395-10237	L M/3	*E. r. recki/P. r. recki*	L-7	1.188	UL	UL	10+	193+	86	165	6	2.6	191.86	123
OMO K 7-1969-3001	LM3/	*E. r. recki/P. r. recki*	L-5	1.215	UL	UL								121.7
OMO K 7-1969-3009	L M/3	*E. r. recki/P. r. recki*	L-9	1.150	UL	UL	13	230	68.83	129.44	6.5	2.9	188.06	–
OMO K 7-1969-3012	L M3/	*E. r. recki/P. r. recki*	L-9	1.150	UL	UL	x3	??	66.57	137.32	??	2.8	206.28	–
OMO K 7-1969-3013	M/3	*E. r. recki/P. r. recki*	L-5	1.215	UL	UL								120.7
OMO K 7-1969-3014	R M3/	*E. r. recki/P. r. recki*	L-9	1.15	UL	UL	x3	??	69.26	136.91	??	2.6	197.68	–
OMO K 7-1969-3015	L M/3	*E. r. recki/P. r. recki*	L-9	1.15	UL	UL	x6x	84+	68.84	126	6	2.6	183.03	–
OMO K 7-1969-3204	R M3/	*E. r. recki/P. r. recki*	L-9	1.15	UL	UL	17	305	91	191.1	6	2.4	210	125.7
OMO K 7-1969-3205	L M3/	*E. r. recki/P. r. recki*	L-9	1.15	UL	UL	18	322	91	190.31	6	3.01	209.13	126

Appendix 1. — Continuation.

Inventory	Molar type	Subspecies	Stratigraphic interval	Estimated interval age	Member	Member codes	P	L	W	H	LF	ET	HI	MWA
ER 1300	M3	*E. r. shungurensis*	Koobi Fora, Upper Burgi	2.62	Upper Burgi	CUB	–	–	–	–	–	–	138.0	–
ER 1301	M3	*E. r. shungurensis*	Koobi Fora, Upper Burgi	2.62	Upper Burgi	CUB	–	–	–	–	–	–	138.0	–
ER 1616	M3	*E. r. shungurensis*	Koobi Fora, Upper Burgi	2.62	Upper Burgi	CUB	–	–	–	–	–	–	120.0	–
ER 75 FS 1449	M3	*E. r. shungurensis*	Koobi Fora, Upper Burgi	2.62	Upper Burgi	CUB	–	–	–	–	–	–	134.0	–
KNM-BC 30	M3 (dext.) + M2-M3 (dext.)	*E. r. shungurensis*	Chemeron (Tugen Hills)	2.625	Chemeron	CUB	–	–	80	87	–	–	107.6	111.3
KNM-ER 1302 A & B	M3 (sin.) m3 (sin.) + M3 (dext.)	*E. r. ileretensis/ P. r. ileretentsis*	Koobi Fora (KBS)	1.7	KBS	KBS	–	–	92	127	5	2.0	138.2	120.8
KNM-ER 1304	M3 (sin.) m3 (sin.)	*E. r. ileretensis/ P. r. ileretentsis*	Koobi Fora (KBS)	1.7	KBS	KBS	–	–	–	–	–	–	–	120.6
KNM-ER 1305	m3 (sin.)	*E. r. atavus*	Koobi Fora (Upper Burgi)	1.7	–	KUS	–	258.5	83	–	5	2.1	–	108.8
KNM-ER 1313	m3 (dext.) fragment with 2 anterior lamellae in dentary	*E. r. recki/P. r. recki*	Koobi Fora (Okote)	1.46	Okote	OK	–	–	95	176	–	1.8	185.3	116.6
KNM-ER 1583	M3 (dext.)	*E. r. recki/P. r. recki*	Koobi Fora (Okote)	1.46	Okote	OK	–	[244]	76	137	5	1.9	180.5	126.3
KNM-ER 1587	m1 (dext.) in dentary	*E. r. ileretensis/P. r. ileretentsis*	Koobi Fora (KBS)	1.7	KBS	KBS	–	–	–	–	–	–	–	116.4
KNM-ER 1690	M1 (dext.)	*P. r. recki*	Koobi Fora (Okote)	1.46	Okote	OK	–	–	–	–	–	–	–	118.9
KNM-ER 17180	m3 (sin.)	*E. r. brumpti*	Koobi Fora, Lokochot/Tulu Bor	3.12	Lokochot/Tulu Bor	1-BKL	–	293	96	104	5	3.7	108.5	–
KNM-ER 2137	m3 (dext.)	*E. r. atavus*	Koobi Fora (Upper Burgi)	1.91	Upper Burgi	GKUB	–	[255,5]	88	–	4	2.2	–	118.3
KNM-ER 2270	m2 (dext.)	*E. r. atavus*	Koobi Fora (Upper Burgi)	1.91	Upper Burgi	GKUB	–	–	–	–	–	–	–	117.6
KNM-ER 2729	m1 (sin.) posterior part	*E. r. atavus*	Koobi Fora (Upper Burgi)	1.91	Upper Burgi	GKUB	–	–	–	–	–	–	–	114.9
KNM-ER 2890	m2? (sin.) fragm. with 5 lamellae	*E. r. brumpti*	Koobi Fora (Lokochot/Tulu Bor)	3.12	Lokochot/Tulu Bor	1-BKL	–	–	–	–	–	–	–	120.7
KNM-ER 2893	m3 (sin.) fragment with 3 unworn central lamellae	*E. r. brumpti*	Koobi Fora (Lokochot/Tulu Bor)	3.12	Lokochot/Tulu Bor	1-BKL	–	–	88	97	–	–	109.9	–
KNM-ER 2894	M3 (sin.) M3 (sin.)	*E. r. brumpti*	Koobi Fora (Lokochot/Tulu Bor)	3.12	Lokochot/Tulu Bor	1-BKL	–	–	113	115	3	3.6	102.1	105.4
KNM-ER 299	M3 (dext.)	*E. r. ileretensis/ P. r. ileretentsis*	Koobi Fora (KBS)	1.7	KBS	KBS	–	–	92	137	5	2.0	148.6	117.0
KNM-ER 300	m3 (dext.)	*E. r. recki/P. r. recki*	Koobi Fora (Okote)	1.46	–	OK	–	–	86	–	6	1.8	–	116.5

Appendix 1. — Continuation.

Inventory	Molar type	Subspecies	Stratigraphic interval	Estimated interval age	Member	Member codes	P	L	W	H	LF	ET	HI	MWA
KNM-ER 3190 A & B	m3 sin.) m3 (dext.)	*E. r. brumpti*	Koobi Fora (Lokochot)	3.12	Lokochot	1-BKL		279?	81	83	4.5	2.5	103.4	116.1
KNM-ER 341	m3 (dext.) in mandible + m2-m3 (dext.) in mandible	*E. r. ileretensis* / *P. r. ileretentsis*	Koobi Fora (KBS)	1.7	KBS	KBS	–	–	69	–	6	2.3	–	115.0
KNM-ER 342 A	m3 (sin.)	*E. r. shungurensis*	Koobi Fora (Upper Burgi)	1.91	–	GKUB	–	–	–	–	–	–	–	123.0
KNM-ER 343	M3 (sin.) M3 (dext.)	*E. r. ileretensis*/ *P. r. ileretentsis*	Koobi Fora (KBS)	1.7	KBS	KBS	–	300	84	123	6	1.8	146.8	117.1
KNM-ER 349 B	M3 (sin.)	*E. r. ileretensis*/ *P. r. ileretentsis*	Koobi Fora (KBS)	1.7	KBS	KBS	–	–	–	–	–	–	–	112.1
KNM-ER 351	m3 (dext.), posterior part	*E. r.shungurensis*	Koobi Fora (Upper Burgi)	1.91	–	GKUB	–	–	–	–	–	–	–	104.3
KNM-ER 352 B	m3 (sin.)	*E. r. brumpti*	Koobi Fora (Lokochot)	3.43	Lokochot	0-BKL	–	–	81	98	4	2.6	121.0	110.8
KNM-ER 4102 A	M2 (dext.)	*E. r. shungurensis*	Koobi Fora (Upper Burgi)	1.91	–	GKUB	–	–	–	–	–	–	–	124.2
KNM-ER 4109	M3 (dext.)	*E. r. brumpti*	Koobi Fora (Lokochot/Tulu Bor	3.12	Lokochot/Tulu Bor	1-BKL	–	–	96	103	5	3.4	107.6	–
KNM-ER 4110	m3 (sin.)	*E. r. shungurensis*	Koobi Fora, Upper Burgi	2.62	Upper Burgi	CUB	–	–	89	112	6	–	126.2	–
KNM-ER 4115 A	m3 (sin.), fragmentary	*E. r. shungurensis*	Koobi Fora (Upper Burgi)	2.62	Upper Burgi	CUB	–	–	–	–	4	3.1	–	114.0
KNM-ER 4305	M3 (sin.) m3 (sin.), central fragment with 5 lamellae	*E. r. atavus*	Koobi Fora (Upper Burgi)	1.94	Upper Burgi	GKUB	–	260	113	–	6	2.3	–	111.3
KNM-ER 4306	M3 (sin.)	*E. r. atavus*	Koobi Fora Upper Burgi	1.94	Upper Burgi	GKUB	–	252	86	121	6	2.8	141.0	–
KNM-ER 4309 A	M3 (dext.)	*E. r.brumpti*	Koobi Fora (Lokochot)	3.12	Lokochot	1-BKL	–	[187,6]	98	102	4	2.3	103.7	115.2
KNM-ER 4564 A	m3 (sin.)	*E. r. shungurensis*	Koobi Fora (Upper Burgi)	1.91	Upper Burgi	GKUB	–	–	–	–	–	–	–	123.4
KNM-ER 4906 A & B	M3 (sin.) M3 (dext.)	*E. r. shungurensis*	Koobi Fora (Upper Burgi)	1.91	Upper Burgi	GKUB	–	–	94	95	6	2.6	100.7	105.2
KNM-ER 5255	m3 (sin.) in mandible	*E. r. shungurensis*	Koobi Fora, Upper Burgi	2.62	Upper Burgi	CUB	–	256	73	83	6	–	113.0	–
KNM-ER 5711	M2 (sin.) + M3 M2 (dext.)	*E. r. atavus*	Koobi Fora (Upper Burgi)	1.94	Upper Burgi	GKUB	–	321.5	113	162	6	2.7	143.7	118.9
KNM-ER 5810	m3 (sin.) posterior fragm.	*E. r.brumpti*	Koobi Fora, Lokochot/Tulu Bor	3.12	Lokochot/Tulu Bor	1-BKL	–	–	96	95	5	–	99.8	–
KNM-ER 6096	M3 (dext.) in skull	*E. r.brumpti*	Koobi Fora (Lokochot/Tulu Bor)	3.12	Lokochot/Tulu Bor	1-BKL	–	225	91	–	4	3.6	–	106.5
KNM-ER 719	M2 (dext.) in palate M2 (sin.) in palate	*E. r. shungurensis*	Koobi Fora (Upper Burgi)	1.91	Upper Burgi	GKUB	–	–	–	–	–	–	–	101.6

Appendix 1. — Continuation.

Inventory	Molar type	Subspecies	Stratigraphic interval	Estimated interval age	Member	Member codes	P	L	W	H	LF	ET	HI	MWA
KNM-ER 767 A & B	m3 (sin.) m3 (dext.)	*E. r. recki/P. r. recki*	Koobi Fora (Okote)	1.46	Okote	OK	–	–	–	–	–	–	–	121.5
KNM-ER 927 A & B (1 & 2)	m3 (dext.) m3 (sin.) m3 (sin.)	*E. r. ileretensis/ P. r. ileretentsis*	Koobi Fora (KBS)	1.7	KBS	KBS	–	–	–	–	–	–	–	120.4
KNM-ER 972 B	M3 (sin.)	*E. r. ileretensis/ P. r. ileretentsis*	Koobi Fora KBS	1.7	KBS	KBS	–	272	85	148	5	2.0	174.4	–
KNM-TH 19311	M2 (sin.), posterior frag. with 4x lamellae	*E. r. shungurensis*	Chemeron (Tugen Hills)	2.625	Chemeron	CTH	–	–	–	–	–	–	–	–
KNM-TH 19314	M3 (dext.)	*E. r. shungurensis*	Chemeron (Tugen Hills)	2.625	Chemeron	CTH	–	224	92	–	5	2.6	–	116.8
KNM-TH 19316	m1? (sin.) fragm.	*E. r. shungurensis*	Chemeron (Tugen Hills)	2.625	Chemeron	CTH	–	–	–	–	–	–	–	113.0
KNM-TH 32834	m3 (dext.)	*E. r. shungurensis*	Chemeron (Tugen Hills)	2.625	Chemeron	CTH	–	–	83	–	5	2.5	–	111.1
KNM-TH 48375	m2 (dext.) in dentary	*E. r. shungurensis*	Chemeron (Tugen Hills)	2.625	Chemeron	CTH	–	–	–	–	–	–	–	116.6
KNM-TH 48405	m2 (dext.) posterior fragm. with 5 lamellae	*E. r. shungurensis*	Chemeron (Tugen Hills)	2.625	Chemeron	CTH	–	–	–	–	–	–	–	116.4
KNM-TH 48408	M3 (dext.)	*E. r. shungurensis*	Chemeron	2.625	Chemeron	CTH	–	–	92	101	5	–	110.3	–
KNM-TH 48414	M3 (sin.)	*E. r. shungurensis*	Chemeron	2.625	Chemeron	CTH	–	238.5	87	106	4	3.6	120.7	–
KNM-WT 14503	m2-m3 (sin.) in mandible	*E. r. recki/P. r. recki*	Nariokotome MB, Nachukui FM, West Turkana	1	Nariokotome	WTN	–	–	80	144	6	–	180.1	119.8
KNM-WT 14538	m2 (dext.) posterior fragm. with 5 lamellae	*E. r. recki/P. r. recki*	Nariokotome MB, Nachukui FM, West Turkana	1	Nariokotome	WTN	–	–	–	–	–	–	–	112.0
KNM-WT 16008	M2 (sin.)	*E. r.brumpti*	Lomekwi 4, West Turkana	3.22	Lomekwi 4	1-LWT	–	–	–	–	–	–	–	114.3
KNM-WT 16009	m3 (sin.)	*E. r.brumpti*	Lomekwi 5, West Turkana	3.22	Lomekwi 5	1-LWT	–	–	–	–	5	3.0	–	108.2
KNM-WT 16169	m3 (dext.) in mandible	*E. r. shungurensis*	Upper Lomekwi	2.5	Upper Lomekwi	CUL	–	211.7	66	73	5	–	110.8	–
KNM-WT 16230	m3 (sin.)	*E. r. shungurensis*	Upper Lomekwi	2.5	Upper Lomekwi	CUL	–	–	76	110	5	–	145.8	–
KNM-WT 16234	m3 (dext.)	*E. r. shungurensis*	Lomekwi 2, West Turkana	2.5	Lomekwi 2	CUL	–	–	–	–	5	2.8	–	106.5
KNM-WT 16387	M3 (sin.) in palate	*E. r.brumpti*	Lomekwi 9, West Turkana	2.8	Lomekwi 9	2-LWT	–	–	94	–	4	2.9	–	112.5
KNM-WT 16457	M3 (dext.) M3 (sin.)	*E. r.brumpti*	Lomekwi 10, West Turkana	2.8	Lomekwi 10	2-LWT	–	–	87	98	4	3.1	113.0	118.9
KNM-WT 16679	M3 (dext.)	*E. r. shungurensis*	Kangatukuseo 2, West Turkana	2.5	Kangatukuseo 2	DKWT	–	241.4	91	119	5	2.8	131.5	106.2
KNM-WT 16687	M3 (sin.)	*E. r. shungurensis*	Upper Lomekwi	2.5	Upper Lomekwi	CUL	–	–	92	130	–	2.9	142.3	–

Appendix 1. — Continuation.

Inventory	Molar type	Subspecies	Stratigraphic interval	Estimated interval age	Member	Member codes	P	L	W	H	LF	ET	HI	MWA
KNM-WT 38865	M3 (dext.)	*E. r.brumpti*	Lomekwi 4, West Turkana	3.1	Lomekwi 4	1-LWT	–	217.6	84	–	4	3.2	–	103.8
KNM-WT 38952	M3 (dext). M3 (sin). m3 (sin.)	*E. r. recki/P. r. recki*	Nariokotome MB, Nachukui FM, West Turkana	1	Nariokotome	WTN	–	250.5	72	152	6	1.7	208.9	118.1
KNM-WT 38953	m3 (sin.)	*E. r.brumpti*	Lomekwi 5, West Turkana	3.22	Lomekwi 5	1-LWT	–	291.1	72	83	6	3.0	115.0	110.6
KNM-WT 38956	M3 (sin.)	*E. r. shungurensis*	Lomekwi 3, West Turkana	2.43	Lomekwi, 3	DLWT	–	245.3	84	117	5	2.9	138.9	106.2
KNM-WT 39243	M3 (dext.)	*E. r. shungurensis*	Upper Lomekwi	2.5	Upper Lomekwi	CUL	–	–	99	125	4	3.1	126.1	–
KNM-WT 39246	M3 (dext.)	*E. r. shungurensis*	Upper Lomekwi	2.5	Upper Lomekwi	CUL	–	–	96	116	5	3.1	121.8	–
KNM-WT 39248	M3 (dext.)	*E. r. recki/P. r. recki*	Nariokotome MB, Nachukui FM, West Turkana	1	Nariokotome	WTN	–	[216,9]	82	155	6	1.7	189.7	122.7
KNM-WT 39249	M3? (dext.) fragm. with 8 anterior lamellae	*E. r. recki/P. r. recki*	Nariokotome MB, Nachukui FM, West Turkana	1	Nariokotome	WTN	–	–	–	–	–	–	–	117.8
KNM-WT 39252	m2? (sin.) fragm. with 5 lamellae	*E. r. shungurensis*	Kangatukuseo 2, West Turkana	2.57	Kangatukuseo 2	CKWT	–	–	–	–	–	–	–	116.4
KNM-WT 69449	m3 (dext.) in dentary	*E. r.brumpti*	Lomekwi 5, West Turkana	3.1	Lomekwi 5	1-LWT	–	–	85	–	5	3.2	–	108.5
NHMUK PV M 14691	M1 (sin.) M1 (dext.)	*E. r. atavus*	Olduvai Bed I	1.775	Bed I	LB I	–	–	–	–	–	–	–	113.6
NHMUK PV M 14693	m3 (sin.) m3 (dext.)	*E. r. atavus*	Olduvai Bed II	1.425	Bed II	OB II	–	–	–	–	–	–	–	100.4
NHMUK PV M 14700	m1 (sin.)	*E. r. atavus*	Olduvai Bed I	1.775	Bed I	LB I	–	–	–	–	–	–	–	120.5
NHMUK PV M 21652	m2 (5 posterior lamellae left) and m3 (starting to erupt, not worn)	*E. r. atavus*	Olduvai Bed I	1.775	Bed I	LB I	–	–	–	–	–	–	–	113.6
no nr. (in exhibition)	M3 (dext.)	*E. r. atavus*	Nyabusosi FM	1.5	Nyabusosi FM	NFM	–	320	123	171	5	2.9	138.9	–
OLD/41 F. 3046	M3 (dext.)	*E. r. atavus*	Olduvai Bed II	1.425	Bed II	OB II	–	–	89	136	6	2.3	153.5	–
OLD/41 F. 3660	m3 (sin.)	*E. r. atavus*	Olduvai Bed II	1.425	Bed II	OB II	–	[270]	96	138	4	2.5	144.1	–
OLD/57 F. 1294	M3 (dext.)	*E. r. atavus*	Olduvai Bed II	1.425	Bed II	OB II	–	–	99	–	5	2.9	–	114.2
OLD/57 F. 346	m3 (sin.)	*E. r. atavus*	Olduvai Bed II	1.425	Bed II	OB II	–	–	83	110	6	2.9	131.9	111.4
OLD/59 HWK 4776	m2 (sin.) in dentary fragment	*E. r. atavus*	Olduvai Bed II	1.425	Bed II	OB II	–	–	–	–	–	–	–	105.7
OLD/60 F. 90	m3 (sin.) fragment with 3 lamellae	*E. r. atavus*	Olduvai Bed II	1.425	Bed II	OB II	–	–	81	115	–	–	141.4	–
OLD/62 F. 10292	m1 and m2 (dext.) in dentary m1 and m2 (sin.) in dentary	*E. r. atavus*	Olduvai Bed I	1.775	Bed I	LB I	–	–	–	–	–	–	–	125.8
OLD/62 F. 10381	M1 (sin.) M1 (dext.)	*E. r. atavus*	Olduvai Bed I	1.775		LB I	–	–	–	–	–	–	–	120.6
OLD/62 F. 3785	M1 (sin.)	*E. r. atavus*	Olduvai Bed II	1.425	Bed II	OB II	–	–	–	–	–	–	–	102.2

Appendix 1. — Continuation.

Inventory	**Molar type**	**Subspecies**	**Stratigraphic interval**	**Estimated interval age**	**Member**	**Member codes**	**P**	**L**	**W**	**H**	**LF**	**ET**	**HI**	**MWA**
OLD/62 F. 861	m2 or m3 (dext.)	*E. r. atavus*	Olduvai Bed II	1.425	Bed II	OB II	–	–	–	–	–	–	–	114.4
OLD/63 F. 156	M3 (dext.) anterior part with 6 lamellae	*E. r. atavus*	Olduvai Bed II	1.425	Bed II	OB II	–	–	81	–	5	1.8	–	111.0
OLD/63 F. 2037	m2 (sin.), anterior part with 8 lamellae	*E. r. atavus*	Olduvai Bed II	1.425	Bed II	OB II	–	–	–	–	–	–	–	120.7

APPENDIX 2. — The Kruskal-Wallis test is utilized to compare the degree of variation in median values of Hypsodonty Index (HI), particularly between lower and upper molars. Kruskal-Wallis test for equal medians; H (chi2) = 0.0004509; P = 0.9831. There is no signifficant difference between sample medians.

	M3/	**M/3**
N	33	30
Min	107.62	100.83
Max	240	210
Mean	141.76	142.37
SD	29.766	29.542
Median	136.95	131.73

APPENDIX 3. — T-test to compare the degree of variation in mean values of enamel thickness (ET) between the lower and upper molars. Tests for equal means; M/3 M3/; N = 56; N = 33; Mean: 3.3432; Mean: 3.3742; t = 0.26693; p = 0.79015.

	M/3	**M3/**
N	56	33
Min	2.3	2.4
Max	4.4	4.52
Mean	3.343214	3.374242
SD	0.51915	0.5473061
Median	3.385	3.32

APPENDIX 4. — T-test to compare the degree of variation in mean values of mean mesowear angle (MWA) between the lower and upper molars. t-test for equal means; L_MWA U_MWA; N: 23; N: 14; Mean: 125.3; Mean: 125.07; t = 0.089786; p = 0.92.

	MWA (M/3)	**MWA (M3/)**
N	23	14
Min	109	110
Max	139	134
Mean	125.3	125.1
SD	1.769	1.598
Median	128	126

APPENDIX 5. — T-test to compare mean mesowear angle (MWA) between band A1 (a measured angle of an anterior enamel band) and A2 (a measured angle of an intermediate enamel band) vs total Av-mean. T-test for equal means; Av (Band A1 & Band A2), N = 18 and Av Total; N = 18; Mean = 124.74; Mean = 126.12; t = 0.52366; p = 0.60391.

	Av (Band A1 & Band A2)	**Total Av**
N	18	18
Min	100.5	108.7
Max	139.5	138.7
Sum	2245.25	2270.2
Mean	124.7361	126.1222
Variance	72.26818	53.84654
Median	123.75	126

APPENDIX 6. — . t-test to compare mean mesowear angle between band A1 (a measured angle of an anterior enamel band) and A2 (a measured angle of an intermediate enamel band) vs total Av-mean. T-test for equal means; Av (Band A1 & Band A3), N = 18 and Av Total; N = 18; Mean = 126.99; Mean = 126.12; t = 0.34955; p = 0.72883.

	Av (Band A1 & Band A3)	**Total Av**
N	18	18
Min	114	108.7
Max	143	138.7
Sum	2285.75	2270.2
Mean	126.9861	126.1222
Variance	56.09906	53.84654
Median	127.875	126

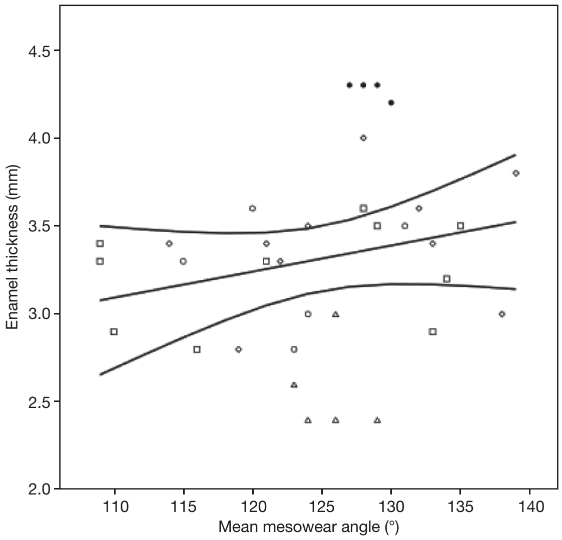
APPENDIX 7. — T-test to compare mean mesowear angle between band A1 (a measured angle of an anterior enamel band) and A2 (a measured angle of an intermediate enamel band) vs total Av-mean. T-test for equal means; Av (Band A2 & Band A3), N = 18 and Av Total; N = 18; Mean = 126.61; Mean = 126.12; t = 0.34955; p = 0.72883.

	Av (Band A2 & Band A3)	**Total Av**
N	18	18
Min	110	108.7
Max	147.5	138.7
Sum	2279	2270.2
Mean	126.6111	126.1222
Variance	88.65605	53.84654
Median	126.75	126

APPENDIX 8. — Mann-Whitney pairwise tests significant for hypsodonty index (HI) and enamel thickness (ET) values for the members of Koobi Fora and Shungura Formations. 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. Abbreviations: **KBS**, KBS member of the Koobi Fora Formation; **Oko**, Okote member of the Koobi Fora Formation; **UBu**, Upper Burgi member of the Koobi Fora Formation.

	B	**C**	**UBu**	**D**	**E**	**F**	**LG**	**KBS**	**Oko**	**K & LL**	**UL**
B		0.04261	**3E-04**	**3.7E-05**	**3.7E-05**	**2E-04**	**1.2E-06**	**7E-05**	**7E-03**	**1.E-04**	**2E-05**
C	0.043		0.0264	0.3875	0.9572	0.7459	0.08411	**1.3E-03**	0.0218	0.7005	**4E-03**
UBu	0.7	0.34		**5E-03**	**7E-03**	**0.02172**	**1.3E-03**	**2.6E-03**	0.027	0.195	0.621
D	0.89	0.12	0.84		0.417	0.8717	0.2666	**5.4E-04**	0.01406	0.3915	**8E-04**
E	0.08	0.41	0.54	0.21		0.592	0.0653	**5E-04**	0.01406	0.4833	**4E-04**
F	**0.009**	0.25	0.09	0.022	0.11		0.2921	**1.E-03**	0.0218	0.4418	**3E-03**
LG	0.019	0.7287	0.1537	0.04847	0.3019	0.3257		**5.35E-05**	6.E-03	0.1024	**4.4E-05**
KBS	**0.007**	0.051	0.023	0.009	0.012	0.63	0.16		0.045	**1E-03**	**5E-04**
Oko	0.0275	0.057	0.045	0.041	0.041	0.057	0.027	0.081		0.0223	0.0131
K & LL	**7E-05**	**2.2E-03**	**6.4E-04**	**4.5E-04**	**4.5E-04**	0.02403	**2E-04**	0.01572	0.24		0.076
UL	**8E-04**	**3E-04**	**2E-04**	**2E-04**	**8E-04**	**1.45E-05**	**0.0027**	0.06784	**6E-04**		

APPENDIX 9. — Linear regressions (ordinary least squares regression) mean mesowear angle (MWA) vs enamel thickness (ET). t = 1.21; R = 0.21; R^2 = 0.444; p = 0.23.



APPENDIX 10. — Box plots for *Elephas recki* (Dietrich, 1915) from different members of the Koobi Fora and Shungura Formation, and Bed I & II of the Olduvia George. Boxes represent the interquartile range, bar is median, and whiskers represent the lower and the upper 25% of the data: **A**, hypsodonty index (HI); **B**, enamel thickness (ET); **C**, mesowear angle (MWA). Rerefe Appendix 1 for member codes used in the above figures.