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Body size histories of Shungura Formation reptiles in biotic and abiotic environmental context

Abigail K. PARKER, Jean-Renaud BOISSERIE, Johannes MÜLLER,
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GLIMPSES OF A PLIO-PLEISTOCENE AFRICAN ECOSYSTEM: THE LOWER OMO VALLEY, ETHIOPIA

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Body size histories of Shungura Formation reptiles in biotic and abiotic environmental context

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ABSTRACT

To investigate reptile body size as an ecological indicator and the relationships between size and environmental variables through time, we compared patterns of maximum size from the Plio-Pleistocene Shungura Formation of Ethiopia. For this previously-undescribed reptile fossil record, we provided estimates of body mass for pythonid snakes, aquatic pelomedusid and trionychid turtles, terrestrial testudinid turtles, whose carapace lengths reach over 1 m, and crocodylians including *Crocodylus* Laurenti, 1768*,* cf. *Mecistops* Gray, 1844, and the tubulirostrine *Euthecodon* Fourtau, 1920, which is the largest known crocodylian from the Early Pleistocene. Body size maxima in aquatic taxa correspond to lake level, with large body size observed in aquatic turtles, crocodylians, and hippopotamids during lake high stands on the north side of the Turkana Depression. However, these semi-aquatic groups display heterogenous trends over time and relationships to hydrologic proxies, indicating that their differential niches in these aquatic habitats were linked to different conditions and food resources. Terrestrial tortoises (Testudinidae Batsch, 1788) exceed 100 kg in mass in three members of the Shungura Formation, but are absent at large sizes between 2.3 and 2.1 Ma, during the main period of hominin stone tool production. We tested for correlation between reptile maximum sizes, mammal maximum sizes and faunal metrics, δ^{18}O and δ^{13}C records from paleosols and mammal tooth enamel, and paleotemperature estimates across members of the Shungura Formation. After correction for multiple comparisons, no correlation tests between reptile size and paleoenvironment or mammal metrics are significant. However, high correlation coefficients between size maxima and paleosol δ^{18}O values suggest temporal coincidence between size change and shifts in hydrological regimes and evaporation levels. These results suggest links between maximum size in reptiles and local environments that, if confirmed by trends in other settings, could be utilized in the future as paleoenvironmental proxies for terrestrial vegetation and aquatic habitats.

KEY WORDS
Reptile,
crocodylian,
turtle,
body size,
correlation.

RÉSUMÉ

Changements de taille corporelle chez les reptiles de la Formation de Shungura en contextes biotiques et abiotiques.

Afin d'envisager la taille corporelle des reptiles en tant que marqueur écologique et d'étudier les relations entre ce proxy et différentes variable environnementales au cours du temps, nous avons comparé les variations de taille maximale parmi des taxons non-squamates de la Formation plio-pléistocène de Shungura en Éthiopie. À partir de ce registre fossile herpétologique inédit, nous fournissons des estimations de la masse corporelle des serpents pythonids, des tortues aquatiques pélomedusidés et trionychidés, des testudinidés terrestres dont la longueur de la carapace atteint plus de 1 m, et des crocodiliens, notamment *Crocodylus* Laurenti, 1768*,* des formes apparentées à *Mecistops* Gray, 1844, et le genre tubulirostre *Euthecodon* Fourtau, 1920, le plus grand crocodilien connu du Pléistocène Ancien. Les tailles corporelles maximales chez les tortues aquatiques, les crocodiliens, et les hippopotamidés sont contemporaines des hauts niveaux lacustres enregistrés au nord de la Dépression Turkana. Cependant, ces taxons semi-aquatiques présentent des tendance hétérogènes au cours du temps et des relations avec des indicateurs hydrologiques, indiquant que leur niches différentielles dans ces habitats aquatiques étaient liées à des conditions et des ressources alimentaires différentes. Les grandes tortues terrestres (Testudinidae Batsch, 1788) dépassent les 100 kg dans trois membres de Shungura, mais sont absentes entre 2,3 et 2,1 Ma, de manière concomitante à la production importante d'outils lithiques. Nous avons testé la corrélation entre les tailles maximales des reptiles, les tailles maximales et les mensurations des mammifères, les données de δ^{18}O et δ^{13}C des paléosols et de l'émail dentaire des mammifères, et les estimations de paléotempérature pour les membres de la Formation de Shungura. Après correction pour plusieurs comparaisons, aucun test de corrélation entre les tailles des reptiles et les paramètres environnementaux ou mammifères n'est significatif. Néanmoins, des coefficients de corrélation élevés entre les tailles maximales et les valeurs de δ^{18}O des paléosols suggèrent une congruence temporelle entre les changements de taille corporelle et les changements de régime hydrologique et des niveaux d'évaporation. Nos résultats suggèrent des liens entre la taille maximale des reptiles et les milieux localement disponibles qui, s'ils sont confirmés par des tendances dans d'autres contextes, pourraient être utilisés à l'avenir comme marqueurs paléoenvironnementaux de la végétation terrestre et des habitats aquatiques.

MOTS CLÉS
Reptile,
crocodilien,
tortue,
taille corporelle,
corrélation.

INTRODUCTION

Body size is a key ecological trait reflecting diet, locomotion, and life history strategies (Peters 1983; Schmidt-Nielsen 1984). For poikilotherms including reptiles, body size plays an additional role in thermoregulation, specifically through its influence on the ratio of surface area to volume which governs heat exchange, and influences metabolic rates (Ashton & Feldman 2003; Makarieva *et al.* 2005; Rodrigues *et al.* 2018). Therefore, body size trends within poikilothermic groups such as reptiles provide insight into ecological niche availability over time and can potentially be used as paleoenvironmental proxies (Head *et al.* 2009, 2013; Godoy *et al.* 2019: Stockdale & Benton 2021; Parker *et al.* 2023;). Body size distributions within reptile communities may be useful indicators of paleohabitats, but they have rarely been measured in the fossil record because environment reconstructions based on the terrestrial vertebrate fossil record have relied mainly on mammalian faunal proxies (e.g. Hernández Fernández & Vrba 2006; Cerling *et al.* 2011; Liu *et al.* 2012; Bibi & Kiessling 2015; Plummer *et al.* 2015; Žliobaitė *et al.* 2016). The Shungura Formation of the Omo Group (Lower Omo River Valley, southwest Ethiopia) presents an excellent natural laboratory for using the reptile fossil record to characterize the abiotic and biotic conditions underpinning body mass changes in terrestrial and aquatic poikilotherms over time.

The Shungura Formation is a chronostratigraphically well-constrained and nearly continuous section of fluviolacustrine sedimentary sequences that preserves a rich, high-resolution record of faunal and environmental change during the Plio-Pleistocene (Arambourg 1948; Howell & Coppens 1974; Heinzelin 1983; Boisserie *et al.* 2008). The formation is divided into 12 members identified as Basal, then A to L (excluding I) from oldest to youngest. The depositional lithologies of these members represent changes in fluviolacustrine architecture on the paleolandscape, most notably expansion and reduction in lake extent (Heinzelin 1983). While mammalian evolution and diversity in the Shungura Formation have been described in detail, the only previous descriptions of the non-mammalian vertebrate faunas have been in taxonomic works on fishes, turtles, and crocodylians (Arambourg 1948; de Broin 1979; Tchernov 1986; Stewart & Murray 2008). Despite this limitation, the sedimentological interpretations and densely-sampled isotopic and mammalian faunal records of the Shungura Formation provide a unique opportunity to place changes in local reptile body size maxima in the context of environmental change, as informed by geochemical and mammalian fossil records. Here, we estimate the masses of the best-preserved reptile taxa from the Shungura Formation – crocodylians, turtles, and snakes – and investigate their potential relationships to biotic and abiotic factors in the environment of the Shungura Formation. We use the detailed time series of environmental and mammalian faunal changes in the Shungura sequence (Alemseged 2003; Bobe & Behrensmeyer 2004; Hernández Fernández & Vrba 2006; Cooke 2007; Boisserie *et al.* 2010; Passey *et al.* 2010; Levin 2015; Plummer *et al.* 2015; Blondel *et al.* 2018; Negash *et al.* 2020; Bibi 2023) to place body size histories of Shungura Formation reptiles within the context of local climate and community composition. We compare the maximum size time series for reptiles with mass estimates for various large mammal groups from Bibi & Cantalapiedra (2023) to test whether co-occurring reptiles and mammals exhibited common size trends, indicating shared environmental pressures, or inverse relationships, which could indicate competition or opposing habitat preferences.

Shungura Formation turtle body size histories at community scales were previously examined to estimate paleotemperature and paleoprecipitation using models relating modern turtle community body size to climate (Parker *et al.* 2023). These results indicated that, although climate variables are only loosely linked to size in modern communities, these models can provide information about relative environmental change through time based on the Shungura record. The tests for correlation with geochemical proxies and mammal faunas we present here expand on that study to identify factors influencing reptile size maxima, which can be evaluated in other contexts in the fossil record to better understand what conditions are necessary for the evolution of large body sizes.

MATERIAL AND METHODS

The Shungura Formation reptile fossil record

We examined reptile fossils derived from field expeditions, primarily the International Omo Research Expedition (IORE) (Howell & Coppens 1974) and Omo Group Research Expedition (OGRE) (Boisserie *et al.* 2008, 2010) housed in the National Museum of Ethiopia (NME)/Ethiopian Heritage Authority (EHA, ex-Authority for Research and Conservation of the Cultural Heritage) in Addis Ababa. Some of the largest turtle specimens discovered in the field were not collected due to resource constraints and were measured *in situ* during OGRE field campaigns.

Although mostly undescribed, the reptile fossil record of the Shungura Formation is composed of similar taxa to the more extensively studied records from more southern Neogene and Pleistocene localities in the Turkana Depression (Harris *et al.* 2003; Storrs 2003; Wood 2003; Brochu 2020; Head & Müller 2020). The fossil record of turtles consists of semi-aquatic trionychid taxa, including specimens referrable to *Cycloderma* Peters, 1854 (Fig. 1A) and *Trionyx* Saint-Hilaire, 1809 (Parker *et al.* 2023), pelomedusids, including specimens comparable to *Pelusios* Wagler, 1830 (Fig. 1B), and fully terrestrial testudinids (Fig. 1C), including giant specimens comparable to *Centrochelys* Gray, 1872 (Parker *et al.* 2023). Among examined squamates, *Python* Daudin, 1803 (Fig. 1D) is represented by precloacal vertebrae. Other squamates, including *Varanus* Merrem, 1820, and small-bodied snakes, are not included here due to their sparse record with prohibitively small sample sizes. Crocodylians from the Shungura include cranial remains referable to the extremely tubulirostrine genus *Euthecodon* Fourtau, 1920 (Fig. 1F) and members or close relatives of the extant longirostrine genus *Mecistops* Gray, 1844 (Fig. 1E). We refer to the latter as cf. *Mecistops* here, as some specimens were previously *Crocodylus cataphractus* Cuvier, 1824, a synonym of *Mecistops cataphractus* Cuvier, 1825, the extant African sharp-nosed or slender-snouted crocodile (McAliley *et al.* 2006), but note that they are morphologically distinct from modern *Mecistops* and their taxonomic assignment is tentative pending phylogenetic analysis (Brochu *et al.* personal communication). Additionally, numerous brevirostrine specimens (Fig. 1D) are similar to species of *Crocodylus* from other eastern African sequences (Brochu 2020). Species diagnoses within the genus *Crocodylus* of the Plio-Pleistocene are subject to ongoing revision (Brochu 2001, 2020; Storrs 2003; Brochu *et al.* 2010; Brochu & Storrs 2012). Cranial specimens that we identify as *Crocodylus* here include specimens comparable

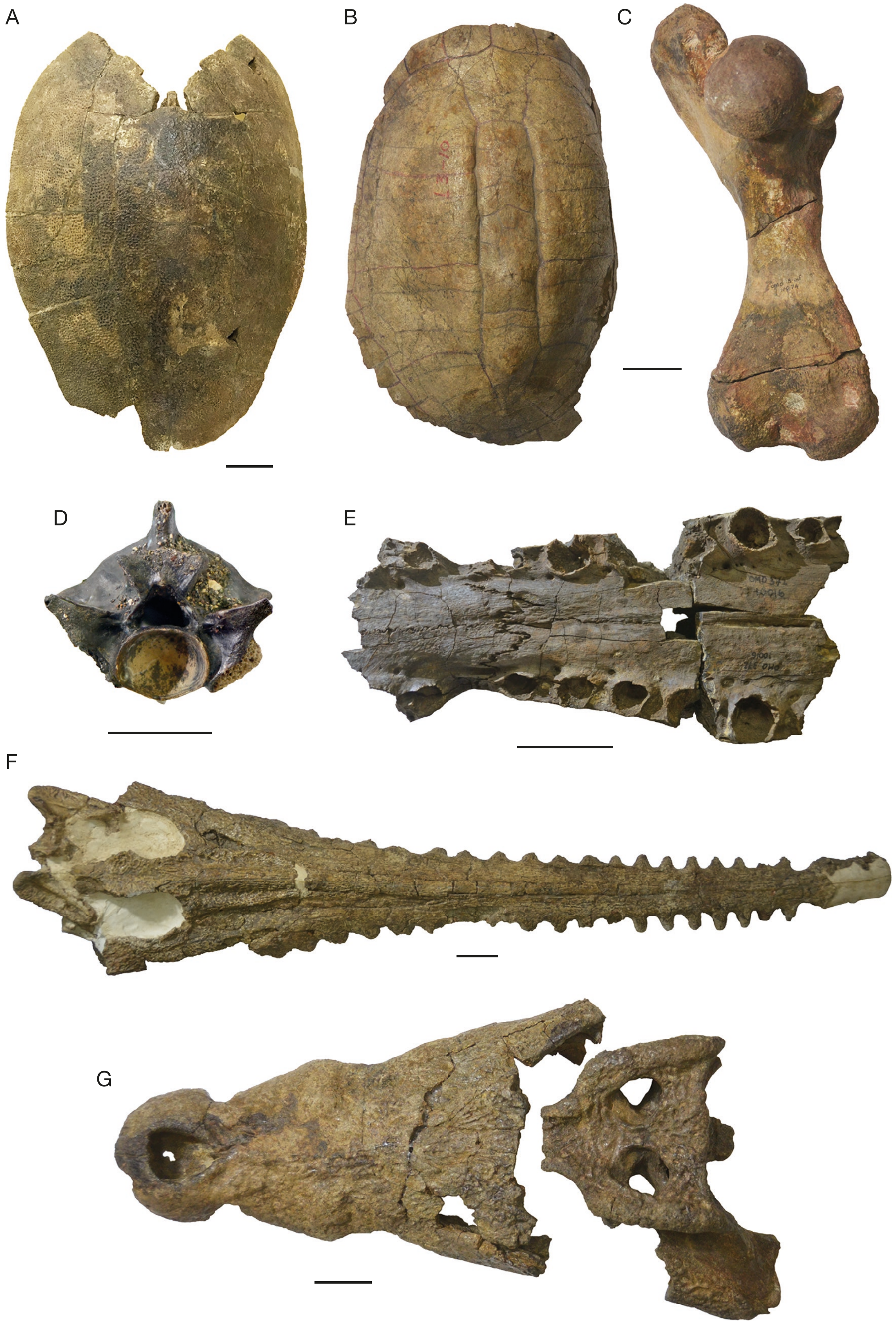

Fig. 1. — Representative specimens of examined reptile taxa from the Shungura Formation: **A**, *Cycloderma* sp. (OMO 229) carapace in dorsal view; **B**, *Pelusios* sp. (L 3-10, F-3, *c.* 2.31 Ma) carapace in dorsal view; **C**, Testudinidae indet. (OMO 18/inf-10074, C-4-8, *c.* 2.57-2.76 Ma) right humerus in dorsal/capitular view; **D**, *Python* sp. (OMO 340-10193, L-2, *c.* 1.34 Ma) precloacal vertebra in anterior view; **E**, cf. *Mecistops* Gray, 1844 (OMO 372-10016, upper G, *c.* 2.057-1.911 Ma) partial rostrum in palatal view; **F**, *Euthecodon brumpti* (Joleaud, 1920) (IORE collections unnumbered) skull in dorsal view; **G**, *Crocodylus* sp. (L 875-1, F-3, *c.* 2.32 Ma) partial skull in dorsal view. Scale bars: A-C, E-G, 5 cm; D, 1 cm.

TABLE 1. — Regression equations used to estimate body mass (in kg, unless noted otherwise) from body lengths for turtles and crocodylians.

Taxon	Measurement, x (cm)	Regression to body mass	Regression source
Testudinidae	Carapace length	BM = 2.751*log10(x) -3.424	Regression derived from data in Regis & Meik (2017)
Trionychidae	Carapace length	log10(BM) = 1.344*log10(x) -1.049	Regression derived from data in Regis & Meik (2017)
Pelomedusidae	Carapace length	log10(BM) = -3.814 + 2.861*log10(x)	Regression derived from data in Regis & Meik (2017)
Crocodylia	Total length	log10(BM) = -4.67 + 2.79*log10(x)	Slavenko *et al.* (2016)
Python	Total length	log10(BM) = -5.131 + 2.611*log10(x) [mass unit: g]	Feldman & Meiri (2013)

to the robust species *C. thorbjarnarsoni*, but further taxonomic study is required to determine whether other species from the genus are also present in the Shungura Formation.

Occurrences and abundances of reptile taxa are not uniformly distributed throughout the members of the Shungura Formation. Member G, spanning 2.27 to 1.91 Ma, is divided into "lower G" and "upper G", which have yielded distinct fossil assemblages, likely due to the lacustrine system present during the deposition of upper G. Therefore, we have considered these two levels separately alongside the other members. Including all specimens cataloged from 1967-1976 (IORE) and 2006-2018 (OGRE), the highest sampling is from Member E (2.39-2.33 Ma), with 699 reptile specimens in total (nearly 12 % of the total fossil record for this member). Over 100 specimens have also been collected from members C (2.94-2.54 Ma), F (2.32-2.29 Ma), and lower G (2.27-2.06 Ma). Sampling of turtles is also sufficient for the oldest members A (3.60-3.44 Ma) and B (3.44-2.94 Ma), with pelomedusid specimens recovered from every member from B through upper G (2.06-1.91 Ma). However, trionychid fossils complete enough for body size estimation have only been collected from four of those members, B, E, F and upper G. Only 1-2 turtle specimens are known from each member from H (1.91-1.78 Ma) through L (1.38-1.09 Ma). Abundances of crocodylians collected vary greatly across members, with 572 specimens from Member E, but zero from A and under 10 for B, D (2.53-2.39 Ma), H, and J (1.76-1.56 Ma). No occurrences of *Euthecodon* are recorded from members A and D, while *Crocodylus* is absent from members A, B, and H. Cf. *Mecistops* specimens are known from members C, F through J, and L.

BODY SIZE ESTIMATION

We estimated body length and body mass for each specimen and determined the maximum reconstructed body mass for turtle and crocodylian groups in each member of the Shungura Formation. For turtles, we used carapace length as the metric for body length. For incomplete specimens, we estimated carapace length using linear regressions from other element measurements based on complete specimens (Appendix 1). We used clade-specific linear regressions to estimate body mass from these carapace lengths. These linear regressions (Table 1) are derived from the data in Regis & Meik (2017).

For *Python*, we used the regression for total body length from the width between the prezygapophyses from McCartney *et al.* (2018); this regression is based on a sample of extant snakes, and the equation is ln(Total Body Length) = 1.095*ln(x) + 4.528, where x is the trans-prezygapophyseal width in mm. Then, we used the regression for body mass from total length for Pythonidae Fitzinger, 1826 from Feldman & Meiri (2013).

For crocodylians, we used regressions relating skull length to total body length or body mass for extant taxa (Webb & Messel 1978; Hutton 1987; Thorbjarnarson 1988; Verdade 2000; Sereno *et al.* 2001; Iijima *et al.* 2016). For incomplete specimens, we estimated skull length using regressions from postcranial or mandibular measurements (Appendix 2), or, in the case of vertebral specimens, estimated total length using the regressions from vertebral centrum length of Iijima & Kubo (2020; Appendix 2).

For cf. *Mecistops*, identifiable cranial fragments most frequently comprise the anterior premaxilla and maxilla or the mandibular symphysis of the dentary. We relate the measurement of the narrowest width of the premaxilla, across the diastema between the premaxillary and maxillary alveoli, to the total skull length, based on the ratio observed in the complete specimen NME L 398 2508A (Appendix 2). Similarly for mandible specimens, we estimate skull length using the ratio between the length of the mandibular symphysis and skull length observed in NME L 398 2508A and 2508B (Appendix 2). Because Shungura specimens identified here as cf. *Mecistops* have broader snouts relative to skull length than either of the two extant species of *Mecistops* (*M. cataphractus* and *M. leptorhynchus*; Brochu *et al.* personal communication), this method for total skull length measurement is better practice than estimating from a regression on modern specimens (for reference, the equation SL = 10.719*x + 10.225 relates the narrowest premaxilla width of five specimens of *Mecistops* housed at the Natural History Museum, London to total skull length).

For *Euthecodon*, most specimens from the Shungura Formation are rostral fragments. We developed an equation relating the spacing between maxillary or mandibular tooth alveoli to total skull length (Fig. 2). We excluded measurements between the anteriormost two alveoli because those teeth are spaced further apart than those along the rest of the snout, which may be due to ontogenetic exclusion of the second premaxillary tooth by the large third tooth, which occurs early in ontogeny, leaving four premaxillary teeth (Brochu 2021). We then estimated total body length for *Euthecodon* based on the relationship between dorsal cranial length (DCL) and total body length (TL) for the extant tubulirostrine crocodylian *Gavialis gangeticus*, TL = –69.369 + 7.4*(DCL) (Sereno *et al.* 2001).

Crocodylus cranial specimens from the Shungura Formation have intermediate snout lengths, with similar snout to skull length ratios to the extant saltwater crocodile *C. porosus*, so

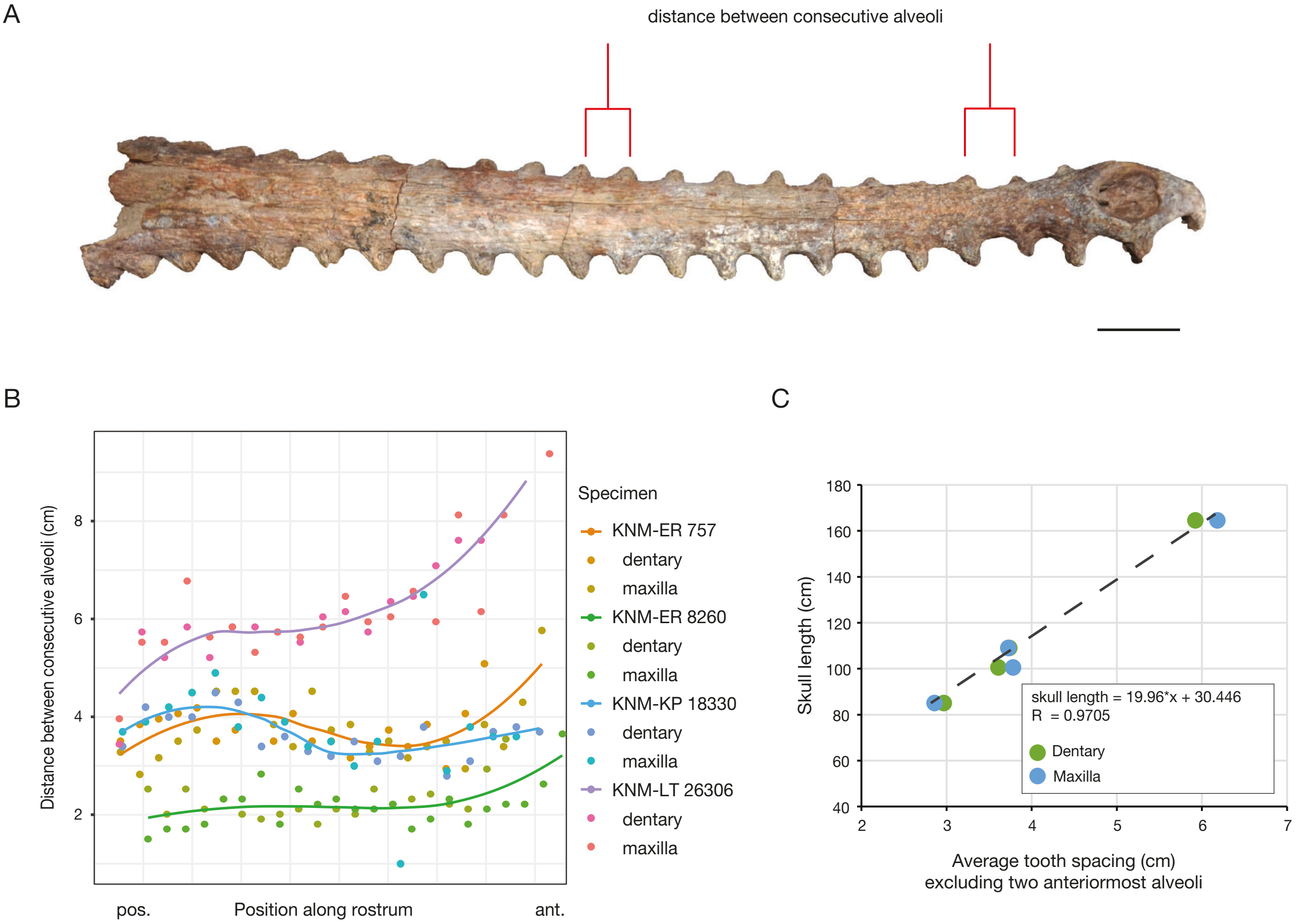

FIG. 2. — Estimation of skull length for fragmentary specimens of *Euthecodon* Fourtau, 1920: **A**, partial mandible of *E.* cf. *brumpti* (L 32-203, C 5-7, *c.* 2.6-2.7 Ma) in dorsal view; **B**, tooth spacing along the rostra of four complete skulls used to train the regression, plotted as points, with smoothed curves showing how alveolar spacing changes along each snout, with the anteriormost alveoli the greatest distances apart; **C**, the linear regression equation used to relate that average tooth spacing value (excluding the anteriormost two alveoli) to dorsal skull length, based on the best-fit line through points representing the average tooth spacing of each dentary and maxilla in the four complete skulls. Abbreviations: **Ant**, anterior; **ER**, East Rudolf; **KNM**, National Museums of Kenya; **KP**, Kanapoi; **LT**, Lothagam; **Pos**, posterior. Scale bar: A, 5 cm.

we used the equation trained on that extant species from Sereno *et al.* (2001): TL = –20.224 + 7.717*(DCL). Using these two different equations to estimate total body length takes into account the difference in the proportion of body length made up by the skull in crocodylians with varying snout morphologies. We used a single regression equation (Table 1) to estimate body mass from body length (Slavenko *et al.* 2016). No species-specific body mass regressions have been published for extant tubulirostrine crocodylians, but the mass regression for general Crocodylia performed consistently and conservatively in estimating crocodylian mass in comparison to species-specific regressions (Webb & Messel 1978; Chabreck & Joanen 1979; Hutton 1987; Thorbjarnarson 1996).

MAMMAL AND ENVIRONMENT DATA SOURCES

We compiled mammal body size and environmental proxy datasets from the literature to compare with the trends of Shungura Formation maximum reptile size, including maximum size for mammalian taxa, reconstructed lake level in the Turkana Depression, paleosol carbon and oxygen isotopes, faunal composition of mammalian herbivores, and herbivore carbon and oxygen isotopes. We used member-level stratigraphic resolution for all data.

We took estimates of maximum mammalian body masses for each Shungura member using the methods and data in Bibi & Cantalapiedra (2023), which use loglinear regressions between tooth length and body mass trained on extant species with masses in the Pantheria database (Jones *et al.* 2009). We applied regressions specific to each order of mammals and each tooth position (Bibi & Cantalapiedra 2023). We applied these regressions to obtain mass estimates for all of the Shungura specimens in the Mammal Dental Metrics Database (Bibi 2023). Because this database includes no proboscidean specimens from the Shungura Formation, we avoided the issues with order-specific regressions for Proboscidea noted by Bibi & Cantalapiedra (2023). We also followed their method for removing duplicates by averaging mass estimates for individual specimens for which multiple teeth were measured. From the dataset, we removed specimens that were not attributable to a specific Shungura member, and subsequently took the maximum mass from each group in each member. For Equidae Gray, 1821, most specimens were described prior to the differentiation of Member G into upper/lower units (Hooijer 1975); we assigned these specimens to lower G, to which the majority of the terrestrial mammal specimens in Member G date (Bibi 2023). The bovid tribe Tragelaphini was well-sampled across members, unlike other tribes, so we also tested for correlation with its maximum sizes. We excluded Rhinocerotidae Gray, 1821 due to low sampling in this dataset. For Hippopotamidae Gray, 1821, we instead used unpublished mass estimates based on astragali measurements (522 specimens measured by JRB) using Martinez & Sudre (1995)'s equation for terrestrial cetartiodactyls. They belong to three distinct lineages: aff. *Hippopotamus protamphibius* (Arambourg, 1944) and its likely successor aff. *Hippopotamus karumensis* (Coryndon, 1977) (see Harris 1991), the dominant hippopotamus lineage in the Shungura Formation, which is endemic to the Turkana Depression; aff. *Hippopotamus aethiopicus* Coryndon & Coppens, 1975, a pygmy hippopotamid (Coryndon & Coppens 1975) possibly related to aff. *Hip. protamphibius/karumensis* but of much smaller size, known only in the upper part of the sequence (from Member G to Member L); and *Hippopotamus* sp., less frequent that the other hippopotamids in the Omo Valley during the Plio-Pleistocene and distinguished by particular massive and wide astragali differing from the more slender build of the postcranials belonging to the other lineages. Today *Hippopotamus* shares semi-aquatic habitats with crocodylians and turtles. The largest Shungura specimens belong to *Hippopotamus* sp. and to aff. *Hippopotamus karumensis*, which also displays morphological features (high orbits) and a geochemical signature (δ^{18}O; Harris *et al.* 2008) indicating semiaquatic behavior.

We used the reconstruction of lake levels in the Turkana Depression by Nutz *et al.* (2020), which is based on study of the sedimentary formations of the Nachukui Formation, south of the Shungura Formation on the western bank of Lake Turkana. This lake level record is suited for comparison to ecological and environmental changes in the region, although lake level change is at least partially diachronous between the Shungura and Nachukui Formations (Lepre 2014). We used member average lake level values on a relative scale based on the curve presented in figure 15 of Nutz *et al.* (2020). Differential patterns of lake extent between the west and north shores of paleo-lakes in Turkana are minimal relative to the temporal durations included in these averaged member ages. For an additional metric of Shungura Formation-specific lake extent, we quantified the depositional environments of each member using the coding provided by Heinzelin (1983), which scored each unit's facies in the following scheme: 0 for ephemeral streams, 1-4 for fluviatile facies (from channel to levee, floodplains, and swamps), 5 for mudflats, 6 for deltaic, and 7-8 for lacustrine (nearshore to deeper water). For each member, we used the maximum score in this scheme across units as a metric for the presence of lake conditions in the member.

Paleosol isotope data for both carbon and oxygen comes from the measurements of pedogenic carbonates compiled by Levin *et al.* (2011). This dataset includes 49 samples of Shungura paleosols dated between 3.2-1.18 Ma. We calculated the average δ^{18}O and δ^{13}C values for each member. We additionally drew on published data for mammalian tooth enamel δ^{18}O and δ^{13}C, based on isotopic ratios measured for over 1,000 dental specimens from nine herbivore families by Negash *et al.* (2020). We use member-average values for all specimens as a metric for the dietary composition of all mammalian herbivores, derived from a subsample of this dataset only including stable carbon isotopic values of specimens for which element identification is documented in the Omo Database, and attributed to a M2 or M3 tooth.

We used two Shungura Formation mammalian faunal composition datasets. Bobe & Behrensmeyer (2004) defined a subset of mammals that they took to be grassland indicators, including bovids in the families Alcelaphini Simpson,1945 and Antilopini Gray, 1821, the suid *Metridiochoerus* Hopwood, 1926, *Equus* Linnaeus, 1758, and *Theropithecus oswaldi* (Andrews, 1916). We used the proportion of mammal fossils from each member falling in this group as a metric for grassland habitat, although these raw fossil abundances may not accurately represent the relative abundances of taxa in the true paleocommunity due to filtering in taphonomy and collection biases (Bobe & Behrensmeyer 2004). However, with relatively constant taphonomic conditions and collections procedures, changes in abundance values across time bins represent shifts in the relative proportion of taxa, regardless of their absolute abundances. The second dataset (Bobe *et al.* 2007) provided an alternative faunal proxy for the presence of grasslands, measuring separately the percentage of mammal fossils from each member belonging to reduncin bovids and bovids in the clades Antilopini, Alcelaphini, and Hippotragini ("AAH bovids"). Reduncin bovids indicate open but moist habitats with fresh grass, while the AAH bovids today live only in at least seasonally dry grasslands or bushlands (Levin 2015).

Finally, we used two numeric estimates of paleoenvironmental variables sampled across Shungura members. Passey *et al.* (2010) provided estimates of soil temperatures based on measurements of clumped isotopes in pedogenic carbonates. Hernández Fernández & Vrba (2006) reconstructed mean annual precipitation at sites including individual Shungura members based on models of mammal community structures trained on modern sites. Figure 3 summarizes all data series used as paleoenvironmental proxies to which we compared the maximum body size time series.

CORRELATION ANALYSES

To test for coordinated patterns of maximum size change over time between groups and with environmental variables, we used correlation tests. For all body mass variables, we used $\log_{10}$ transformation of mass estimates in kilograms. We employed standard Pearson product-moment correlation tests (rcorr function from the R package Hmisc). We also ran Spearman's rank correlation tests, appropriate for non-normal data, for comparisons including data series whose values were not

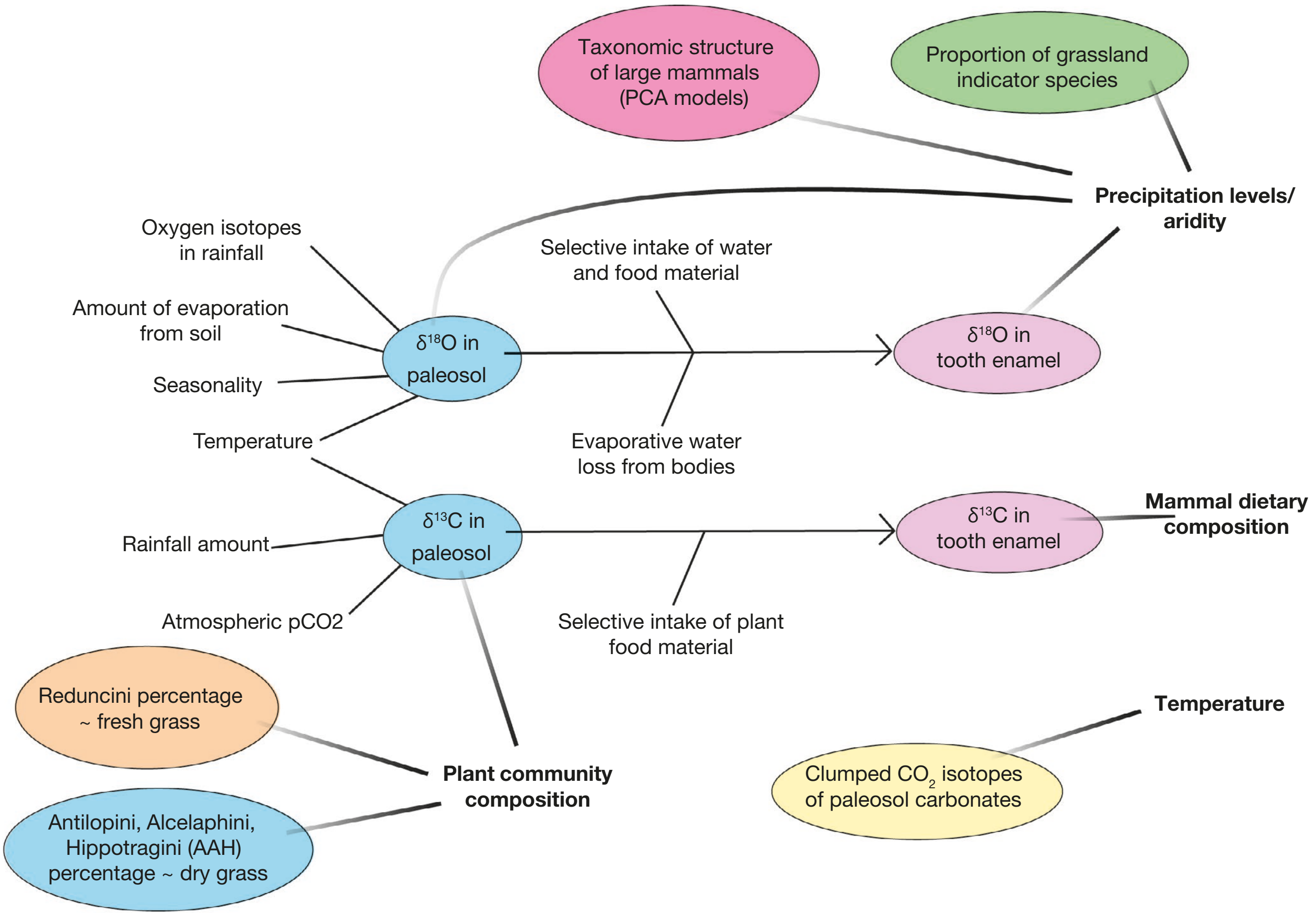

FIG. 3. — Schematic summarizing all paleoenvironmental variables used in analyses of correlation with reptile body sizes (colored ovals), excluding paleo-lake level (Nutz *et al.* 2020) and depositional lake scores (Heinzelin 1983), which were estimated independently through sedimentological synthesis. The data series are color-coded by their sources: **blue**, Levin 2015; **green**, Bobe & Behrensmeyer 2004; **pink**, Hernández Fernández & Vrba 2006; **orange**, Bobe *et al.* 2007; **purple**, Negash *et al.* 2020; **yellow**, Passey et al. 2010. **Faded lines** run from each variable (colored ovals) to the concept for which it acts as a proxy. Components influencing the paleosol isotopic ratios are linked to them by **solid lines**, as are the processes which filter those isotopic ratios in fossil material relative to paleosol values.

normally distributed. We also tested for correlation between maximum size in each reptile group and fossil abundance by member for all reptiles and for only turtles or crocodylians. Abundance counts came from the catalog of specimens identified to these groups collected in the Shungura Formation between 1967 and 2023. These correlation tests reveal whether maximum size is higher in members where reptiles are more frequently preserved or more intensely sampled.

Because we ran many tests for pairwise correlation between the same set of data series, it was necessary to correct for multiple comparisons (Wright 1992). For each set of correlation tests whose results are presented in Tables 2-6, we used sequential Bonferroni correction to adjust the significance cutoff for the resulting p-values. This correction takes into account that some of a large set of pairwise statistical tests will have p-values under 0.05 by chance, rather than due to true significance. It adjusts the significance level for the pairwise test with the lowest p-value by dividing it by the number of tests, then adjusts the significance level for the next lowest p-value to (0.05 / n(comparisons) –1), and so on, until the next lowest p-value does not fall under the adjusted significance level (Holm 1979).

It is important to note that correlation tests do not take into account the order of the data points and, therefore, cannot test hypotheses of causal effects of one variable on another over time. Tests differentiating correlative and causal relationships between time series require more data points than are available from sampling at the member level within the Shungura Formation (Sugihara *et al.* 2012; Reitan & Liow 2019). However, we were able to test whether two time series change together between members using correlation tests between the first differences of the series' values. These tests use the value of a variable in one member subtracted from its value in the next member, calculated iteratively for each data series. Correlation between first differences shows that the magnitude and direction of change between bins for two series is coordinated across the time series. The results for first difference correlation are more informative than the correlation tests on raw values because first differencing detrends the data series; if independent directional trends exist in two series over time, significant correlation in raw variable values is likely even without any causal relationship between the variables.

TABLE 2. — Correlation tests between the maximum sizes of Shungura Formation reptiles and sampling (overall reptile or order-specific) or member age. Each cell contains the Pearson correlation coefficient and the p-value for the test. For the sampling comparisons (data series with non-normal distributions), each cell also shows the Spearman rank correlation coefficient and corresponding p-value. Significant results after sequential Bonferroni correction are marked with **. P-values under 0.05 which are not significant after Bonferroni correction are marked with *, and correlation coefficients over 0.75 are marked in **bold**.

Taxon	Reptile sampling	Turtle sampling	Crocodylian sampling	Squamate sampling	Time
Aquatic turtles	0.217, p = 0.605 0.071, p = 0.867	0.24, p = 0.567 0.171, p = 0.686	–	–	–0.229, p = 0.586
Trionychidae	**–0.933**, p = 0.067 –0.8, p = 0.2	**–0.907**, p = 0.093 –0.738, p = 0.262	–	–	–0.578, p = 0.422
Pelomedusidae	0.132, p = 0.755 0.548, p = 0.16	0.109, p = 0.798 0.366, p = 0.373	–	–	0.284, p = 0.495
Testudinidae	0.595, p = 0.159 0.45, p = 0.31	0.697, p = 0.082 0.414, p = 0.355	–	–	0.024, p = 0.96
Euthecodon	–0.406, p = 0.215 –0.073, p = 0.831	–	–0.448, p = 0.167 –0.087, p = 0.8	–	0.336, p = 0.313
Crocodylus	0.574, p = 0.065 0.45, p = 0.165	–	0.552, p = 0.078 0.626, p = 0.04*	–	0.238, p = 0.48
cf. *Mecistops*	0.4, p = 0.433 0.543, p = 0.266	–	0.426, p = 0.399 0.429, p = 0.397	–	0.189, p = 0.719
Python	0.003, p = 0.994 0.25, p = 0.516	–	–	0.227, p = 0.558	0.141, p = 0.718

ABBREVIATIONS

AAH bovids	Antilopini, Alcelaphini, and Hippotragini;
DCL	dorsal cranial length;
IORE	International Omo Research Expedition;
NME/EHA	National Museum of Ethiopia/Ethiopian Heritage Authority (ex-Authority for Research and Conservation of Cultural Heritage);
OGRE	Omo Group Research Expedition;
TL	total body length.

RESULTS

SIZE ESTIMATES

While some body size estimates reported here fall within the range of local extant faunas, there are extraordinary size maxima present in the Shungura Formation. For crocodylians (*Euthecodon*) and tortoises, the Turkana Depression is home to the largest representatives of those groups anywhere in the world during the Early Pleistocene. Notably, the estimated mass of *Euthecodon* sp. from Shungura Member L of 2 300 kg makes it the largest Early Pleistocene reptile globally. The large body size of *Euthecodon* in the Turkana Depression contributes to a global trend of increased mean crocodylian body size during the Plio-Pleistocene (Godoy *et al.* 2019; Godoy & Turner 2020). The high diversity of crocodylians occurring in Turkana during this period indicates the availability of multiple distinct niches, including macro-predatory ones, for these semi-aquatic carnivores within a large lake system (Scheyer *et al.* 2013; Drumheller & Wilberg 2020). Of the specimens we attribute to *Crocodylus*, the largest has an estimated mass just over 1 000 kg (Member F), while the largest cf. *Mecistops* measured is slightly smaller, at an estimated 860 kg (Member L).

The *in situ* tortoises from Shungura Members E and H, with preserved carapace lengths of 110 and 100 cm, respectively, are the largest known testudinids from the Early Pleistocene of Africa. Tortoises from 1-1.7 m in length are present continuously in eastern Africa from the Early Miocene through the Middle Pleistocene (de Lapparent de Broin 2000). Thereafter, these massive tortoises survived only in Madagascar into the Holocene (Bour 1984). Freshwater turtles in Africa have maintained a maximum body size of 40-60 cm since the Oligocene (Meylan *et al.* 1990; Pérez-García 2019). Most soft-shelled turtle specimens (Trionychidae Gray, 1825) from the Shungura Formation fall within this range, but the largest partial specimen, from Member B, is larger, with an estimated carapace length of 71 cm. Modern species of *Pelusios* range in size from 12-55 cm carapace length (Itescu *et al.* 2014), so the Shungura Formation pelomedusids, whose maximum sizes center around 30 cm, fall around the middle of this range. Similar to *Euthecodon* and cf. *Mecistops*, the largest pelomedusid specimen is from Member L, with a carapace length of 42 cm.

Size estimates for *Python* are consistent with maxima of extant African *P. sebae* (Gmelin, 1789) and *P. natalensis* Smith, 1840 (e.g. Pitman 1974; Alexander 2018). A single vertebra from Member F (OMO 33-3613), with trans-prezygapophyseal width 52.1 mm, represents an estimated body length of 7 m, larger than reliable estimates for modern African pythons and equivalent to the largest verifiable lengths of any extant snake species (Murphy & Henderson 1997).

SIZE PATTERNS THROUGH TIME

The three crocodylian groups measured (Appendix 4) have relatively similar body length estimates in the early Members of the Shungura Formation (452 cm for cf. *Mecistops*, Member C, 300-500 cm for *Crocodylus* from members A-D, and *c.* 600 cm for *Euthecodon* from Members B-F). All three groups increase in size in Member F, where the largest *Crocodylus* specimen, a robust partial skull (OMO 221-1973-2716) was found. From 2-1 Ma, the maximum size pattern for *Crocodylus* diverges from that of *Euthecodon*, as *Euthecodon* increases in size into Member L, while *Crocodylus* body length decreases to under 5 m in members K and L. In the final member, cf. *Mecistops*

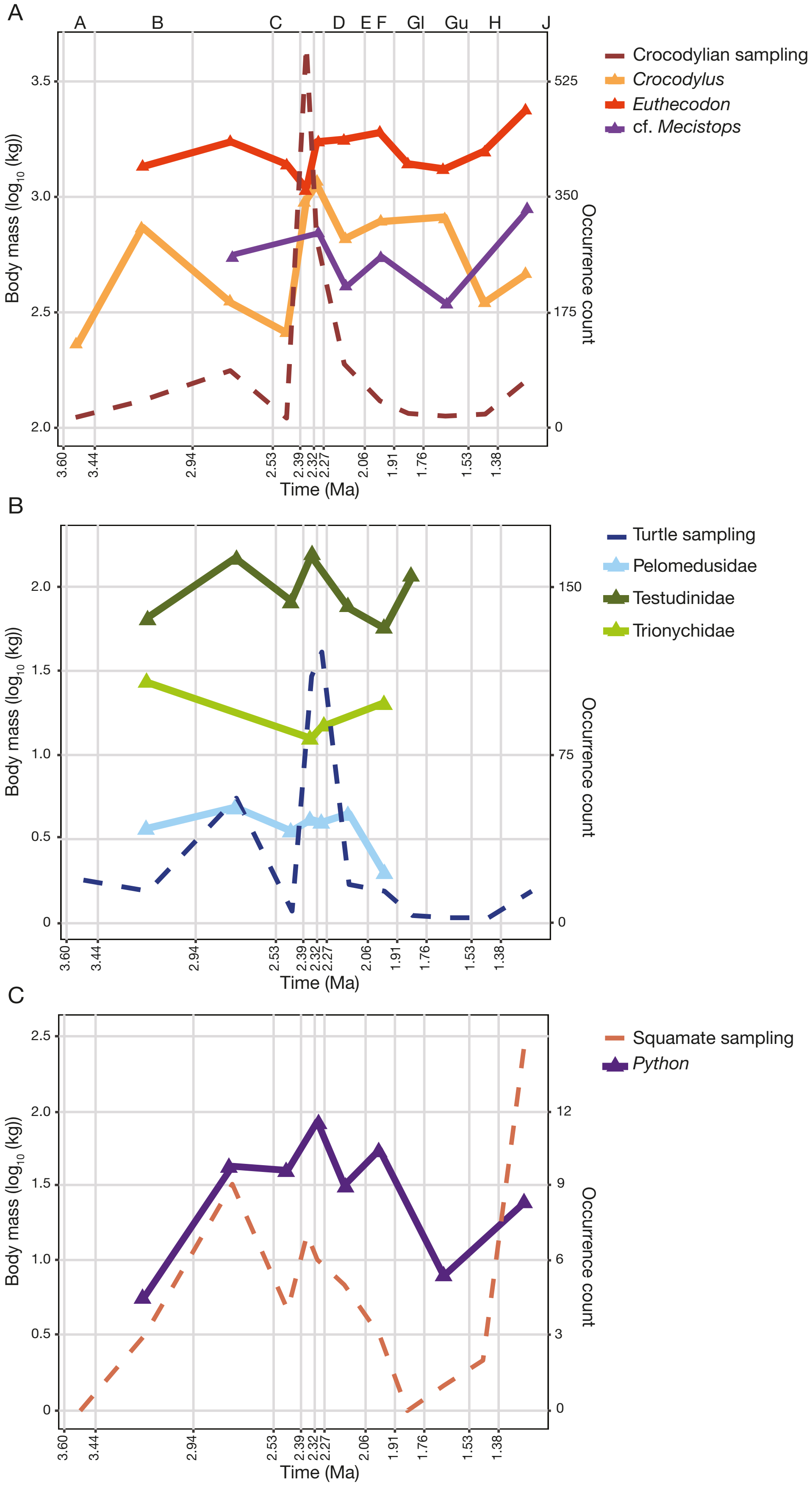

FIG. 4. — Maximum body size of crocodylians (**A**), turtles (**B**), and *Python* (**C**) by member in the Shungura Formation in comparison with sampling based on specimen counts by member from Omo collections.

Table 3. — Correlation between maximum size of reptile groups sampled in the Shungura Formation across the members of the formation. Each cell contains the Pearson correlation coefficient and the p-value for the test. **A** shows results for pairwise correlation tests between log$_{10}$ mass values and **B** shows results for pairwise correlation tests for the first differences in those values between members, not including results for Trionychidae because the sampled specimens come from too few consecutive members to calculate correlation in their first differences. **NA** indicates comparison with too few observations of change between bins in common between the two series to run correlation test. P-values under 0.05 which are not significant after Bonferroni correction are marked with *, and correlation coefficients over 0.75 are marked in **bold**.

		Crocodylus	**cf. *Mecistops***	**Pelomedusidae**	**Testudinidae**	**Trionychidae**	***Python***
A	*Euthecodon*	–0.276 p = 0.44	0.513 p = 0.298	0.25 p = 0.551	–0.464 p = 0.295	0.555 p = 0.445	0.38 p = 0.313
	Crocodylus	–	–0.209 p = 0.691	–0.257 p = 0.538	–0.139 p = 0.793	**–0.85** p = 0.15	–0.22 p = 0.569
	cf. *Mecistops*	–	–	0.41 p = 0.492	0.283 p = 0.817	NA	0.547 p = 0.262
	Pelomedusidae	–	–	–	0.674 p = 0.142	–0.401 p = 0.599	–0.172 p = 0.684
	Testudinidae	–	–	–	–	**–0.88** p = 0.315	–0.12 p = 0.82
	Trionychidae	–	–	–	–	–	–0.286 p = 0.714
B	*Euthecodon*	–0.239 p = 0.568	NA	0.238 p = 0.65	0.102 p = 0.87	NA	0.086 p = 0.914
	Crocodylus	–	NA	–0.079 p = 0.881	0.141 p = 0.859	NA	–0.216 p = 0.784
	Pelomedusidae	–	–	–	**0.826** p = 0.174	NA	0.165 p = 0.835
	Testudinidae	–	–	–	–	NA	**0.997** p = 0.051

(OMO 341-10040) exceeds the *Crocodylus* in size, which is not observed outside of Member L. Differences in postcranial morphologies, which could indicate how mass per body length varies between groups, have not been studied in these fossil taxa; therefore, we applied the same length to mass regressions for all three groups. Such unknown variation in mass per length between crocodylians makes trends within each of these groups over time more reliable than absolute differences between groups (Fig. 4).

Testudinids have estimated size maxima over 50 kg in all members where they are recorded: B, C, D, E, G, and H (Appendix 3). Tortoises are figured as absent in Member F because no specimens complete enough for size estimation have been collected; the only tortoise material known from F is small fragmentary material from an excavation in unit F-0 (2.34-2.321 Ma). In lower G, the only known tortoise specimen comes from unit G-13 (2.062-2.072 Ma), so there is an apparent *c.* 200 000 year gap in the presence of large terrestrial turtles during that interval, despite high sampling of reptiles in members F and G (Fig. 4).

Aquatic turtle maximum size is greatest in the members where trionychids occur – B, E, F, and upper G – with the overall largest aquatic turtle estimated at 28 kg in Member B. Pelomedusid maximum size remains approximately constant across the Formation, with its minimum occurring at around 2 kg in upper G and its maximum of 6.8 kg in Member L.

The largest estimated body masses for *Python* come from the middle of the Shungura sequence, in Member F and upper G (Appendix 5). Python maximum size is lowest, under 3 m in length (or 10 kg in mass), in Members B, E, and J. In the remaining members, typical *Python* maximum length is between 4-5.5 m.

Correlation with sampling

Maximum body size across the Shungura Formation is not correlated to reptile sampling across members (Fig. 4). Table 2 lists correlation coefficients testing for relationships between maximum size in each group and the number of occurrences per member of all reptiles, crocodylians, and turtle specimens, as well as correlation between maximum size and member age. No significant correlation is observed with time; maximum size in all groups both increases and decrease across the sequence. *Crocodylus* has near-significant positive correlation with crocodylian sampling. However, there is a highly negative correlation coefficient for the relationship between trionychid maximum size and turtle sampling.

Correlation between groups and with paleoenvironmental variables

No tests for pairwise correlation between reptile groups' sizes show result in significant correlation after correction for multiple comparisons (Table 3). The observed correlation coefficient between the maximum sizes of terrestrial tortoises and *Python* (0.997) is the highest. High negative correlation coefficients are observed between trionychid turtle size and the size of both *Crocodylus* and terrestrial tortoises.

After correction for multiple comparisons, none of the relationships between reptile size and paleoenvironmental or mammalian faunal variables are significant. The sequential Bonferroni correction reduces the significance cutoff for correlation tests within Table 4 (comparing reptile and mammal sizes) to 0.0009; none of the observed p-values are below this threshold which applies to the pairwise test with the highest significance. Therefore, the correlations denoted with * in Tables 4-6 do not exceed the number that are expected to

TABLE 4. — Correlation statistics for reptile masses vs mammal masses by taxon. **A** shows results for pairwise correlation tests between $\log_{10}$ mass values and **B** shows results for pairwise correlation tests for the first differences in those values between members. The columns marked **S** have non-normally-distributed data, so the correlation test results shown in **A** are the Spearman rank correlation coefficient and corresponding p-value. The cercopithecid, aff. *Hip. aethiopicus*, *Hippopotamus* sp., and trionychid data series are excluded from **B** because they include too few consecutive members sampled. **NA** indicates other comparisons with too few observations of change between bins in common between the two series to run correlation test. P-values under 0.05 which are not significant after Bonferroni correction are marked with *****, and correlation coefficients over 0.75 are marked in **bold**. Mammal data from Bibi (2023), Bibi & Cantalapiedra (2023), except for Hippopotamidae (this study). Abbreviations: ***aHa***, aff. *Hip. aethiopicus*; ***aHpk***, aff. *Hip. protamphibius/karumensis*; **Cerco**, cercopithecids; ***Hsp.***, *Hippopotamus* sp.; **Trag**, tragelaphins.

		Equidae	**Bovidae**	**Trag (S)**	**Cerco**	**a*Hpk* (S)**	**a*Ha***	***H*sp.**
A	*Euthecodon*	–0.42 p = 0.349	–0.559 p = 0.074	–0.37 p = 0.293	0.215 p = 0.683	0.027 p = 0.937	–0.143 p = 0.819	–0.227 p = 0.714
	Crocodylus	–0.575 p = 0.177	0.407 p = 0.214	0.541 p = 0.106	0.473 p = 0.421	0.36 p = 0.277	**–0.965** p = 0.035*	–0.158 p = 0.8
	cf. *Mecistops*	0.427 p = 0.573	–0.557 p = 0.251	0.1 p = 0.873	0.587 p = 0.413	0.143 p = 0.787	**0.809** p = 0.4	–0.074 p = 0.906
	Aquatic turtles	–0.292 p = 0.526	0.238 p = 0.57	–0.536 p = 0.215	0.487 p = 0.406	0.119 p = 0.779	NA	–0.489 p = 0.511
	Trionychidae	0.16 p = 0.84	0.208 p = 0.792	–0.6 p = 0.4	NA	–0.2 p = 0.8	NA	NA
	Pelomedusidae	0.522 p = 0.229	–0.262 p = 0.532	0.357 p = 0.432	0.326 p = 0.593	0.119 p = 0.779	NA	**0.949** p = 0.051
	Testudinidae	0.392 p = 0.443	–0.31 p = 0.498	0.179 p = 0.702	–0.255 p = 0.745	–0.071 p = 0.879	NA	NA
	Python	–0.222 p = 0.632	–0.114 p = 0.771	0.095 p = 0.823	–0.151 p = 0.809	0.083 p = 0.831	**0.914** p = 0.267	–0.722 p = 0.168
B	*Euthecodon*	0.127 p = 0.81	–0.468 p = 0.172	–0.073 p = 0.852	–	0.048 p = 0.895	–	–
	Crocodylus	–0.558 p = 0.25	0.326 p = 0.392	0.42 p = 0.301	–	0.274 p = 0.476	–	–
	Aquatic turtle	–0.373 p = 0.466	0.061 p = 0.908	0.112 p = 0.833	–	0.719 p = 0.108	–	–
	Pelomedusidae	–0.132 p = 0.803	0.296 p = 0.569	0.122 p = 0.819	–	–0.629 p = 0.181	–	–
	Testudinidae	–0.323 p = 0.677	–0.006 p = 0.993	0.035 p = 0.955	–	–0.498 p = 0.393	–	–
	Python	0.642 p = 0.358	–0.644 p = 0.356	0.696 p = 0.304	–	0.472 p = 0.528	–	–

exhibit that level of correlation by chance alone. However, they do identify which reptile and mammal taxa show the relatively strongest covariance in maximum size over time. The highest correlation coefficient in Table 4A is for a negative relationship between maximum size of *Crocodylus* and aff. *Hippopotamus aethiopicus* (the pygmy hippos), while both cf. *Mecistops* and *Python* maximum size are positively related to aff. *Hip. aethiopicus*. The next strongest relationship is positive, between size in pelomedusid turtles and *Hippopotamus* sp.

No significant correlation is observed between change between members in maximum size of reptiles and mammals (Table 4B). The highest positive correlation coefficient there is between aquatic turtles and aff. *Hippopotamus protamphibius/karumensis*.

Among the comparisons with paleoenvironmental variables (Table 5), there is one correlation test that is significant after sequential Bonferroni correction: a positive relationship between the maximum size of aff. *Hippopotamus protamphibius/karumensis* and paleosol δ^{18}O. Among the other correlation tests with high correlation coefficients, paleosol δ^{18}O displays a positive relationship to size in both Pelomedusidae Cope, 1868 and *Hippopotamus* sp. Pelomedusid size is negatively related to paleosol δ^{13}C. Three groups display high negative correlation coefficients with lake level in Table 5A: pelomedusids, *Hippopotamus* sp., and Equidae. Equid size is also negatively related to the depositional environment lake scores of Heinzelin (1983). Finally in Table 5A, soil temperature estimates (Passey *et al.* 2010) are negatively related to the size of *Crocodylus* and aquatic turtles and positively related to tragelaphin bovid size.

Table 5B shows correlation in change between consecutive members in size series and environmental proxies. There, the highest observed positive correlation coefficients are between size in *Python* and paleosol δ^{18}O, and between aquatic turtle size and lake level (Fig. 8). The greatest negative correlation coefficient is between pelomedusid size and δ^{13}C.

There are several groups whose maximum size is nearly correlated with mammalian faunal environmental proxies (Table 5A), though not after Bonferroni correction. Mammalian herbivore δ^{18}O is positively related to body size in Cercopithecidae Gray, 1821, Pelomedusidae, and *Hippopotamus* sp. aff. *Hippopotamus protamphibius/karumensis* size is higher when the AAH % indicating open-habitat bovids is also high. Also, aff. *Hip. protamphibius/karumensis* size is strongly positively related to the grassland indicator proportion of Bobe & Behrensmeyer (2004). Mean annual precipitation from Hernández Fernández & Vrba (2006) is negatively related to size in Cercopithecidae.

TABLE 5. — Correlation statistics of reptile and mammal maximum sizes with a) environmental variables across members of the Shungura Formation. **A** shows results for pairwise correlation tests between $\log_{10}$ mass values and **B** shows results for pairwise correlation tests for the first differences in those values between members, not including results for Trionychidae, Cercopithecidae, or soil temperature because those series have too few consecutive members sampled to calculate correlation in their first differences. Each cell contains the Pearson correlation coefficient and p-value for the correlation test. The row marked **S** has non-normally-distributed data, so the correlation test results shown are the Spearman rank correlation coefficient and corresponding p-value. The cercopithecids, *Hippopotamus* sp., and soil temperature data series are excluded from **B** because they include too few consecutive members sampled. **NA** indicates other comparisons with too few observations of change between bins in common between the two series to run correlation test. P-values under 0.05 which are not significant after Bonferroni correction are marked with *, p-values which are significant after Bonferroni correction are marked with **, and correlation coefficients over 0.75 are marked in **bold**. Data from Heinzelin (1983), Passey *et al.* (2010), Levin (2015) and Nutz *et al.* (2020).

		Paleosol δ^{13}C	**Paleosol δ^{18}O**	**Lake level**	**Soil temperature**	**Depositional lake score**
A	*Euthecodon*	–0.082 p = 0.822	0.373 p = 0.289	0.224 p = 0.533	0.202 p = 0.745	0.685 p = 0.02*
	Crocodylus	–0.129 p = 0.742	–0.05 p = 0.898	0.192 p = 0.594	**–0.824** p = 0.176	0.378 p = 0.252
	cf. *Mecistops*	–0.302 p = 0.621	0.307 p = 0.615	0.028 p = 0.964	NA	0.053 p = 0.921
	Testudinidae	0.019 p = 0.968	0.252 p = 0.63	–0.721 p = 0.067	–0.142 p = 0.82	–0.542 p = 0.208
	Aquatic Turtles	0.028 p = 0.952	–0.108 p = 0.818	0.654 p = 0.111	**–0.834** p = 0.166	0.098 p = 0.818
	Trionychidae	–0.232 p = 0.768	–0.667 p = 0.535	0.476 p = 0.524	NA	0.587 p = 0.413
	Pelomedusidae	**–0.751** p = 0.052	**0.832** p = 0.02*	**–0.762** p = 0.047*	–0.207 p = 0.793	0.063 p = 0.883
	Python	0.106 p = 0.803	0.005 p = 0.99	0.052 p = 0.903	0.76 p = 0.24	0.003 p = 0.995
	aff. *Hip. protamphibius-karumensis* (S)	0.588 p = 0.08	**0.952** p<0.0001**	0.172 p = 0.614	0.2 p = 0.783	0.33 p = 0.294
	aff. *Hip. aethiopicus*	0.292 p = 0.708	–0.229 p = 0.711	0.133 p = 0.867	NA	–0.224 p = 0.718
	Hippopotamus sp.	0.323 p = 0.677	**0.815** p = 0.185	**–0.901** p = 0.099	NA	–0.002 p = 0.997
	Equidae	–0.297 p = 0.518	–0.522 p = 0.288	**–0.825** p = 0.022*	0.186 p = 0.814	**–0.805** p = 0.029*
	Cercopithecidae	–0.455 p = 0.441	0.629 p = 0.181	0.637 p = 0.248	0.537 p = 0.639	0.232 p = 0.658
	Bovidae	–0.6 p = 0.067	–0.471 p = 0.17	–0.108 p = 0.752	0.168 p = 0.787	–0.411 p = 0.185
	Tragelaphini (S)	–0.273 p = 0.448	0.167 p = 0.678	–0.418 p = 0.203	**0.9** p = 0.083	0.005 p = 0.989
B	*Euthecodon*	–0.096 p = 0.807	0.032 p = 0.941	0.017 p = 0.965	–	0.671 p = 0.034*
	Crocodylus	–0.092 p = 0.845	0.272 p = 0.555	0.127 p = 0.765	–	0.387 p = 0.303
	Aquatic turtles	0.255 p = 0.625	0.323 p = 0.596	**0.813** p = 0.049*	–	0.024 p = 0.964
	Pelomedusidae	**–0.79** p = 0.061	–0.201 p = 0.746	–0.704 p = 0.119	–	–0.049 p = 0.926
	Python	0.488 p = 0.512	**0.803** p = 0.406	–0.65 p = 0.35	–	–0.707 p = 0.293
	Testudinidae	–0.582 p = 0.304	0.322 p = 0.791	–0.737 p = 0.155	–	–0.31 p = 0.611
	aff. *Hip. protamphibius-karumensis*	0.237 p = 0.54	**0.895** p = 0.003*	0.495 p = 0.145	–	–0.034 p = 0.92
	aff. *Hip. aethiopicus*	NA	NA	NA	–	–0.436 p = 0.713
	Equidae	0.575 p = 0.233	0.633 p = 0.252	–0.365 p = 0.477	–	–0.518 p = 0.292
	Bovidae	–0.455 p = 0.219	0.319 p = 0.442	0.003 p = 0.993	–	–0.325 p = 0.33
	Tragelaphini	0.054 p = 0.89	**0.927** p = 0.003*	–0.107 p = 0.768	–	0.182 p = 0.615

As for correlation in change between members (Table 6B), we observed high negative correlation coefficients between mammalian herbivore δ^{13}C and size in aquatic turtles and aff. *Hip. protamphibius/karumensis.* The relationship to herbivore δ^{13}C was positive for size in aff. *Hip. aethiopicus*. Pelomedusid size increased when herbivore δ^{18}O increased (Fig. 8). Changes in percentage of AAH bovids were negatively related to size change in Pelomedusidae, positively related to size change

TABLE 6. — Correlation statistics of reptile and mammal maximum sizes with faunal variables across members of the Shungura Formation. **A** shows results for pairwise correlation tests between log$_{10}$ mass values and **B** shows results for pairwise correlation tests for the first differences in those values between members, not including results for Trionychidae and Cercopithecidae because the sampled specimens come from too few consecutive members to calculate correlation in their first differences. Each cell contains the Pearson correlation coefficient and p-value for the correlation test. The row and column marked **S** have non-normally-distributed data, so the correlation test results shown are the Spearman rank correlation coefficient and corresponding p-value. P-values under 0.05 which are not significant after Bonferroni correction are marked with *****, p-values which are significant after Bonferroni correction are marked with ******, and correlation coefficients over 0.75 are marked in **bold**. Data from Bobe & Behrensmeyer (2004), Hernández Fernández & Vrba (2006), Levin *et al.* (2011), and Negash *et al.* (2020) and *Homo* Linnaeus, 1758 in the late Pliocene, as constituents of broader pulses of faunal turnover synchronized by episodes of global climatic change. A more recent concept, the variability selection hypothesis, emphasizes the importance of fluctuating climates and environments, rather than any single trend, in shaping human adaptation and evolution. Here we evaluate these ideas for the Plio-Pleistocene in light of new analyses of fossil mammals from the Turkana Basin of Kenya and Ethiopia. Our results show that between 4 and 1 Ma (million years ago).

		Herbivore δ^{13}C (S)	**Herbivore δ^{18}O**	**AAH % (S)**	**Reduncin %**	**Grassland indicator proportion**	**Faunal mean annual precipitation**
A	*Euthecodon*	0.591 p = 0.061	–0.054 p = 0.875	0.1 p = 0.769	0.238 p = 0.482	0.157 p = 0.645	0.258 p = 0.622
	Crocodylus	–0.077 p = 0.821	0.048 p = 0.889	0.061 p = 0.867	0.036 p = 0.921	–0.038 p = 0.916	–0.179 p = 0.734
	cf. *Mecistops*	0.029 p = 1	0.191 p = 0.717	0.086 p = 0.919	–0.186 p = 0.724	–0.137 p = 0.796	0.375 p = 0.755
	Aquatic turtles	–0.619 p = 0.115	–0.392 p = 0.337	0.539 p = 0.168	0.043 p = 0.919	0.123 p = 0.772	0.324 p = 0.531
	Trionychidae	–0.4 p = 0.75	–0.645 p = 0.355	0.4 p = 0.75	**0.915** p = 0.085	–0.021 p = 0.979	**1** p = 0.006*
	Pelomedusidae	0.31 p = 0.462	**0.857** p = 0.007*	–0.395 p = 0.332	0.37 p = 0.367	–0.027 p = 0.949	0.206 p = 0.695
	Python	0.05 p = 0.912	–0.194 p = 0.617	0.05 p = 0.898	–0.38 p = 0.313	–0.044 p = 0.911	–0.23 p = 0.66
	Testudinidae	NA	0.55 p = 0.201	–0.649 p = 0.115	–0.104 p = 0.824	–0.433 p = 0.332	0.085 p = 0.891
	aff. *Hip. protamphibius-karumensis* (S)	0.462 p = 0.134	0.35 p =0.266	0.743 p = 0.0089*	0.533 p = 0.091	**0.882** p = 0.0006*	–0.543 p = 0.297
	aff. *Hip. aethiopicus*	0.7 p = 0.233	–0.492 p = 0.4	0.2 p = 0.783	0.31 p = 0.611	–0.297 p = 0.627	NA
	Hippopotamus sp.	–0.1 p = 0.95	**0.769** p = 0.128	–0.1 p = 0.95	0.696 p = 0.192	0.561 p = 0.326	NA
	Equidae	–0.286 p = 0.556	0.305 p = 0.507	–0.342 p = 0.452	–0.656 p = 0.109	**–0.78** p = 0.038*	0.575 p = 0.232
	Cercopithecidae	–0.029 p = 1	**0.971** p = 0.001*	0.628 p = 0.173	–0.045 p = 0.933	0.553 p = 0.255	**–0.864** p = 0.136
	Bovidae	–0.431 p = 0.162	–0.092 p = 0.777	–0.237 p = 0.482	–0.456 p = 0.158	–0.247 p = 0.465	0.138 p = 0.794
	Tragelaphini (S)	–0.064 p = 0.86	0.6 p = 0.056	–0.334 p = 0.345	–0.286 p = 0.424	–0.103 p = 0.785	–0.543 p = 0.297
B	*Euthecodon*	0.098 p = 0.787	–0.056 p = 0.878	0.356 p = 0.312	–0.303 p = 0.394	0.371 p = 0.291	0.465 p = 0.43
	Crocodylus	–0.258 p = 0.502	0.109 p = 0.781	0.342 p = 0.406	–0.47 p = 0.24	0.372 p = 0.364	0.247 p = 0.689
	Testudinidae	0.638 p = 0.247	0.506 p = 0.385	–0.532 p = 0.356	0.628 p = 0.257	–0.611 p = 0.273	**0.999** p = 0.035*
	Aquatic turtles	**–0.825** p = 0.043*	–0.432 p = 0.393	0.648 p = 0.164	–0.517 p = 0.293	0.624 p = 0.185	0.079 p = 0.9
	Pelomedusidae	0.505 p = 0.306	**0.796** p = 0.058	**–0.845** p = 0.034*	0.693 p = 0.127	**–0.856** p = 0.029*	**0.766** p = 0.131
	Python	0.553 p = 0.447	–0.084 p = 0.916	0.227 p = 0.773	–0.373 p = 0.627	0.211 p = 0.789	0.559 p = 0.622
	aff. *Hip. protamphibius-karumensis*	**–0.791** p = 0.004*	–0.478 p = 0.137	**0.86** p = 0.001*	**–0.79** p = 0.007**	0.742 p = 0.014*	0.363 p = 0.548
	aff. *Hip. aethiopicus*	**0.755** p = 0.455	–0.555 p = 0.626	**–0.988** p = 0.097	**0.941** p = 0.219	**–0.954** p = 0.193	NA
	Equidae	0.175 p = 0.741	0.011 p = 0.983	0.045 p = 0.933	–0.591 p = 0.217	0.231 p = 0.66	–0.158 p = 0.799
	Bovidae	–0.382 p = 0.247	–0.116 p = 0.734	–0.012 p = 0.973	–0.072 p = 0.843	0.012 p = 0.975	0.18 p = 0.772
	Tragelaphini	–0.514 p = 0.129	0.194 p = 0.591	0.482 p = 0.189	–0.643 p = 0.062	0.654 p = 0.056	0.333 p = 0.584

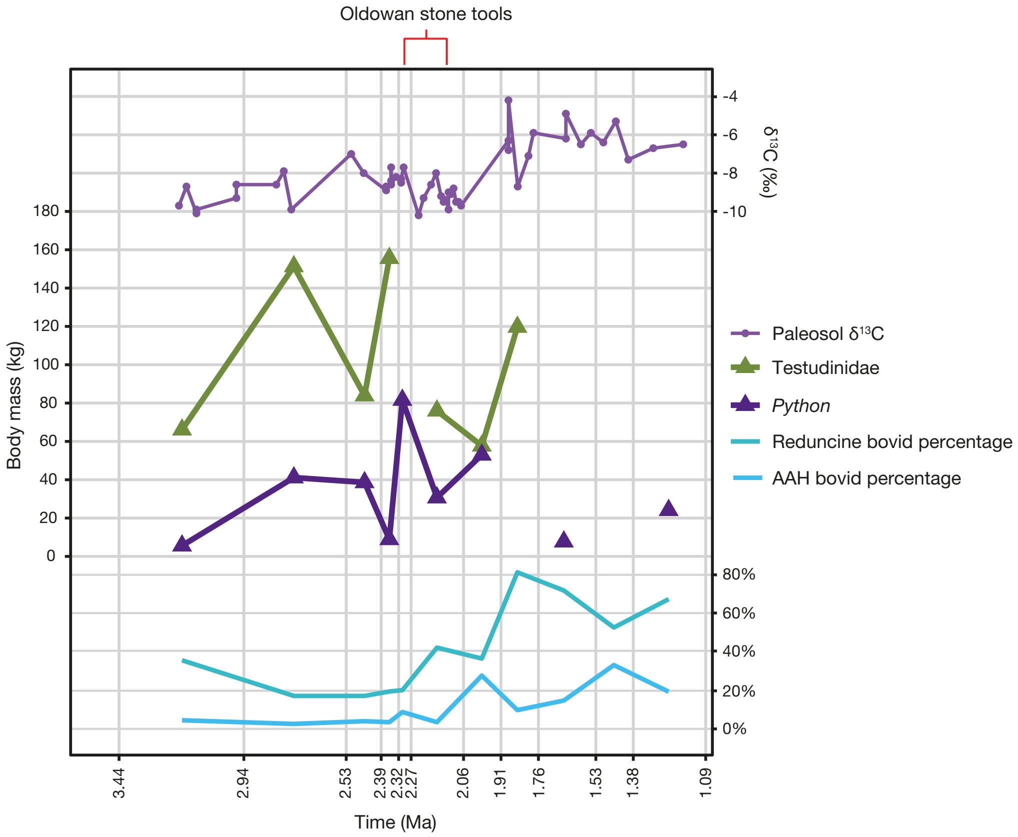

FIG. 5. — Maximum testudinid and *Python* Daudin, 1803 body mass by member in the Shungura Formation vs paleosol $\delta^{13}C$ sample values (Levin *et al.* 2011) and the percentage of Reduncini and Antilopini, Alcelaphini, and Hippotragini (AAH) bovids in each member's mammal fauna (Bobe *et al.* 2007).

in aff. *Hip. protamphibius/karumensis*, and negatively related to size change in aff. *Hip. aethiopicus*. The latter two relationships were reversed with respect to the Reducine bovid proportion; the smaller aff. *Hip. aethiopicus* increased in size as the moist/open-habitat-specialist reduncins became more numerous, while the larger endemic hippopotamid lineage increased in size as the more dry-adapted AAH bovids came to predominate. Aff. *Hip. aethiopicus* size change had a highly negative correlation coefficient vs. the proportion of grassland indicator mammals, as did size change in Pelomedusidae. Size change in testudinid tortoises had a correlation coefficient of 0.999 with change in the mean annual precipitation estimates. Pelomedusid size change was also positively related to those precipitation changes. Although none of these relationships are significant, each instance of high correlation indicates where two series change over time in a coordinated manner, possibly due to similar environmental factors affecting both.

DISCUSSION

Body size maxima for these groups are not artefacts of uneven sampling across members because there are no cases of significant positive correlation between size and member-specific occurrence counts of reptile specimens. The negative correlation between trionychid size and sampling increases our confidence that the absence of this taxon from some members is not due to insufficient sampling of turtles in those intervals. However, positive correlation between *Crocodylus* size and crocodylian sampling indicates that maximum size in this group, which includes size estimates based on post-crania that may have been inconsistently collected, may be partially related to sampling effort. Apart from this case, low correlation with sampling metrics suggests that sampling throughout the formation, while very uneven for reptiles, is not driving the size trends observed across members. Collection bias against reptiles does not appear to be size-selective. If anything, larger reptiles are generally more likely to be collected due to ease of identification relative to, for example, small squamate specimens (although we note that the very largest specimens, such as intact tortoise carapaces and one cranium of *Euthecodon*, are left *in situ* due to resource constraints). However, the very low sample counts, particularly in the most recent members, mean that the maximum sizes reconstructed there may not accurately reflect the actual maximum sizes in the paleocommunities of every member.

Maximum size trends in the crocodylians and turtles of the Shungura Formation point to local-scale environmental influences on body size in these reptiles. The two dominantly terrestrial reptile taxa, Testudinidae and *Python*, have high (though non-significant) correlation in change in size maxima between members (Table 3B). Figure 5 plots these size changes against paleosol carbon isotopes and mammalian herbivore faunal metrics, both providing information about

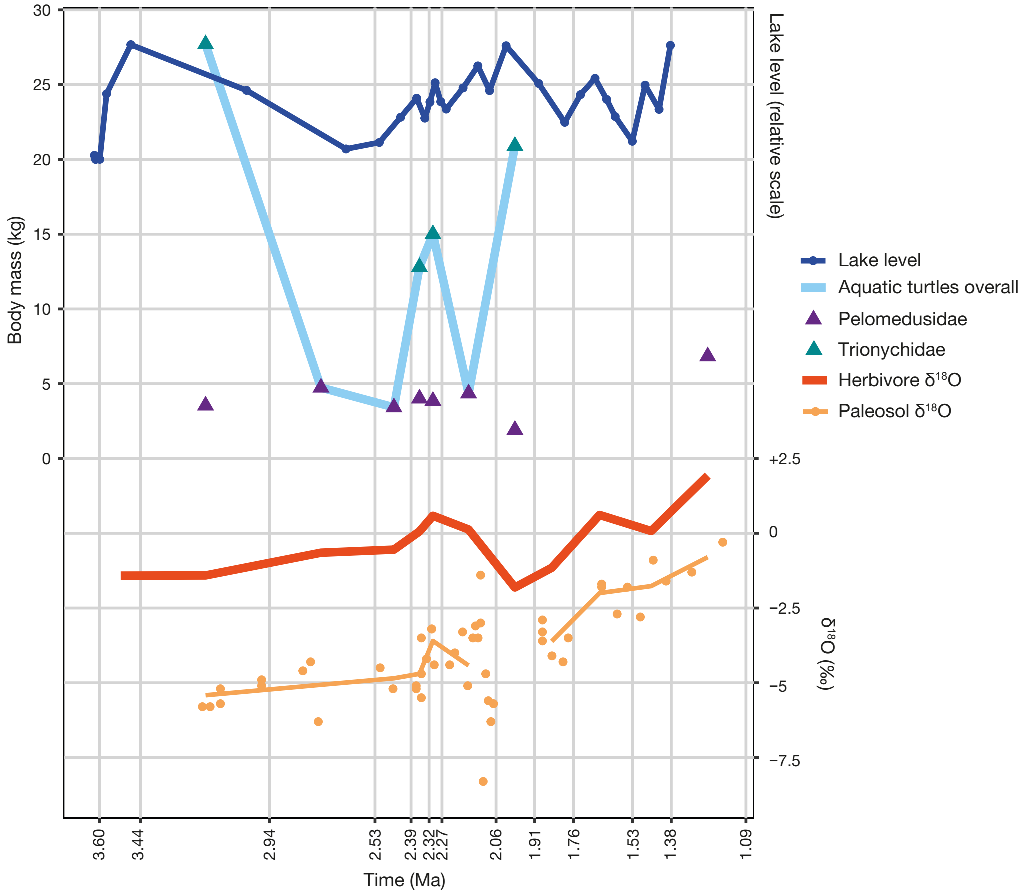

FIG. 6. — Maximum body size of aquatic turtles (trionychid or pelomedusid specimens indicated by color) by member in the Shungura Formation vs reconstructed relative lake level in the Turkana Depression (Nutz *et al.* 2020), $\delta^{18}O$ values from paleosol samples (Levin *et al.* 2011), and $\delta^{18}O$ values from mammal herbivore dental samples (Negash *et al.* 2020).

the openness of vegetation over time. With respect to habitat preferences, extant tortoises are frequently found in open areas within tropical forest or savannas (Brattstrom 1961). Modern giant tortoises, which survive only on oceanic islands, have a grazing diet and help to maintain open habitats known as "tortoise turf" (Hansen & Galetti 2009; Falcón & Hansen 2018). However, it is unknown whether their ecologies shifted after colonization of those islands from continental mainlands (Hansen *et al.* 2010). The presence of large tortoises in Member C of the Shungura Formation, which is reconstructed as having a relatively higher tree cover compared to later members, suggests that these testudinids were not restricted to open habitats in the Pleistocene. However, their maximum size increased into Member H coincident with increasing paleosol $\delta^{13}C$ values and the proportion of grazing mammals, which suggests that newly open environments were also then suitable for giant terrestrial tortoises, as they are today. Maximum size change in tortoises is positively correlated with change in the faunally-derived estimates of paleoprecipitation by member (Hernández Fernández & Vrba 2006; Table 6B). Across the sequence, tortoise size increased as mammalian herbivore faunas shifted away from being arid-adapted, a result which undermines the putative open-habitat association of tortoises, although increased evaporative water loss indicated by $\delta^{18}O$ records may have maintained open habitats during intervals with higher estimated paleoprecipitation. Modern African testudinids require at least somewhat open habitats because they use basking behavior for thermoregulation, so we interpret this pattern as indicating that, in the Shungura sequence, tortoise size most likely increased during intervals with higher rainfall but also some open environments available.

Python is a habitat generalist within African ecosystems, and the relationship between size and environment is not well understood for its largest species. Here, the strongest environmental correlate for size change in *Python* is a positive relationship with pedogenic $\delta^{18}O$ (Table 5B). Pedogenic $\delta^{18}O$ is influenced by the isotopic composition of rainwater and increases to less negative values with more evaporative water loss from soils. $\delta^{18}O$ changes over time with different sources of water input to the Omo River, including direct precipitation (low $\delta^{18}O$), and high levels of evapotranspiration increase $\delta^{18}O$. Therefore, this result represents a contrast between precipitation histories reconstructed by faunal proxies, which we observed to change with the tortoise and snake body size series, and isotopic proxies, which indicate *Python* size increase concurrent with shifts to more evaporative water loss from the landscape. Tests of association between tortoise and snake size and isotopic values at other eastern African sites could confirm whether the largest representatives of these groups preferentially inhabited wetter or drier environments.

Tortoises over one meter in length were present in the Turkana Depression from the Late Miocene (at Lothagam, Wood 2003) until the Middle Pleistocene (personal observations in West Turkana, Turkana Basin Institute Turkwel collections). However, no tortoises of this size are documented between 2.3 Ma and 2.1 Ma; this age range is well-sampled for turtles in the Shungura Formation, yet no large tortoises at all have been discovered in Member F or lower G below unit G-13 (though lower G has nearly 16 000 vertebrate remains collected, making it the richest sequence of the formation). The NME/EHA collections include very fragmentary material likely attributable to Testudinidae collected during a 1971-1973 excavation in unit F-0; while too fragmentary for use in any body size regression, these specimens appear to be of tortoises much less than 1 m in length. This temporal gap in the record of giant tortoises aligns with the timing of the Shungura Formation's archaeological record, which is concentrated in Member F and lower G (noted in Fig. 5; Delagnes *et al.* 2011; Maurin *et al.* 2014). These stone tools indicate hominin occupations at several locations in the vicinity of the Omo River. The earliest presence of archeological lithic remains is in F-1, after which no tortoises have been recovered from Member F. The next tortoise in age appears in unit G-12. In situ lithics are known from unit G-13, but not thereafter, when tortoise size rebounds to over 1 m/100 kg (Member H, Fig. 5). In the Early Pleistocene and thereafter, there is evidence of consumption of tortoise meat by hominins (Stiner *et al.* 2000; Blasco *et al.* 2011; Klein & Cruz-Uribe 2016), with reduction in tortoise body sizes observed globally coincident with the spread of Pleistocene humans (Joos *et al.* 2022). Large tortoises are easy hunting for humans, and individually contain plentiful meat, so may have been preferentially butchered by humans, who display preferences toward catching larger prey (Ben-Dor & Barkai 2021). However, without any direct evidence of tortoise butchery in eastern Africa from this time period, we cannot currently determine whether the gap in the record of large tortoises in F and (most of) lower G relates to hominin occupation. Testudinid fossils from diverse localities await further study, from which a high-resolution regional time series could then be assembled to reveal what environmental conditions and interactions restrict tortoise size.

Among aquatic turtles, trionychids are consistently larger than pelomedusids (Fig. 6). Both trionychid and pelomedusid turtles today inhabit permanent bodies of water and derive their diets primarily from aquatic animals and plants (Akani *et al.* 2001), though the pelomedusid species *Pelusios niger*, with a maximum carapace length of around 35 cm, comparable to many of the Shungura Formation pelomedusid specimens, incorporates a higher proportion of terrestrial vertebrate prey items than smaller-bodied species of *Pelusios* (Luiselli *et al.* 2021). Extant *Trionyx triunguis* has also been observed scavenging carcasses of herbivorous mammals, though fish and frog meat are much larger components of their omnivorous diets (Akani *et al.* 2001). With functional links to terrestrial and freshwater habitats, trait structure observed in terrestrial and aquatic turtles can inform environmental conditions where fossil communities lived (Conley & Samuels 2022; Parker *et al.* 2023).

Across the Turkana Depression, trionychid specimens of around half a meter in length have been collected at many Plio-Pleistocene sites. Extant *Trionyx triunguis* which inhabits the Omo and Lake Turkana can reach over 100 cm in carapace length (Taskavak & Akcinar 2009), but body sizes in the 40-60 cm range reported here from the Shungura Formation would also be common in extant populations. To understand whether maximum body size in this species, or size distributions within populations, have changed over time, more comprehensive collection of trionychid fossil material is necessary. Past field collections have had a strong bias against collection of fragmentary turtle material, although it is relatively abundant. If the gaps in the trionychid record from all members except for Basal, B, E, F, and upper G are true absences, and not due to collection bias, then the lack of large trionychids could provide information about the depositional environments preserved from those ages.

The positive correlation coefficients between overall aquatic turtle maximum size and lake level (Table 5B; Figs 6; 8) suggest that large size in these turtles is dependent on habitat availability. Aquatic turtle size maxima are driven by the presence of trionychids in members B, E, F, and lower G, all of which sample lake high stands. Where lacustrine environments in the Lower Omo Valley had smaller volumes, large-bodied trionychids may have avoided those areas in favor of other areas of the Turkana Depression where lake volume or food resources were higher. In contrast, pelomedusid body size displays negative correlation with lake level, potentially suggesting that the smaller-bodied aquatic turtle group was more successful in smaller water bodies (Table 5A). Trionychid body size is also negatively related to the size of terrestrial tortoises and *Crocodylus*, the latter of which is a possible predator of turtles. Pelomedusid size change, while not dramatic across the sequence, also shows links to terrestrial environmental proxies. It is negatively correlated with paleosol $\delta^{13}C$ (Table 5B) and shows positive correlation with herbivore $\delta^{18}O$ and the faunal precipitation estimates (Table 6B). Again, these non-significant correlation results present mixed signals as to whether reptile size maxima relate to more open/arid environments and mammal faunas, or the opposite. However, the relationship between $\delta^{18}O$ and pelomedusid size (Figs 6; 8) indicates that this trait is responding to changes in regional hydrology. The changes in sources of water input reflected in soil $\delta^{18}O$ could correspond to differences in nutrient availability or water temperature relevant to these aquatic turtles' niches. Overall aquatic turtle size is higher in members where Passey *et al.* (2010)'s soil temperature estimates are lower.

The hippopotamid lineage aff. *Hip. protamphibius-karumensis* has size maxima significantly correlated to paleosol $\delta^{18}O$ (Table 5), providing evidence that these semi-aquatic mammals were responding to regional hydrologic changes. Additionally, this hippopotamid lineage' size maxima occurred concurrently with higher AAH percentage in mammal communities,

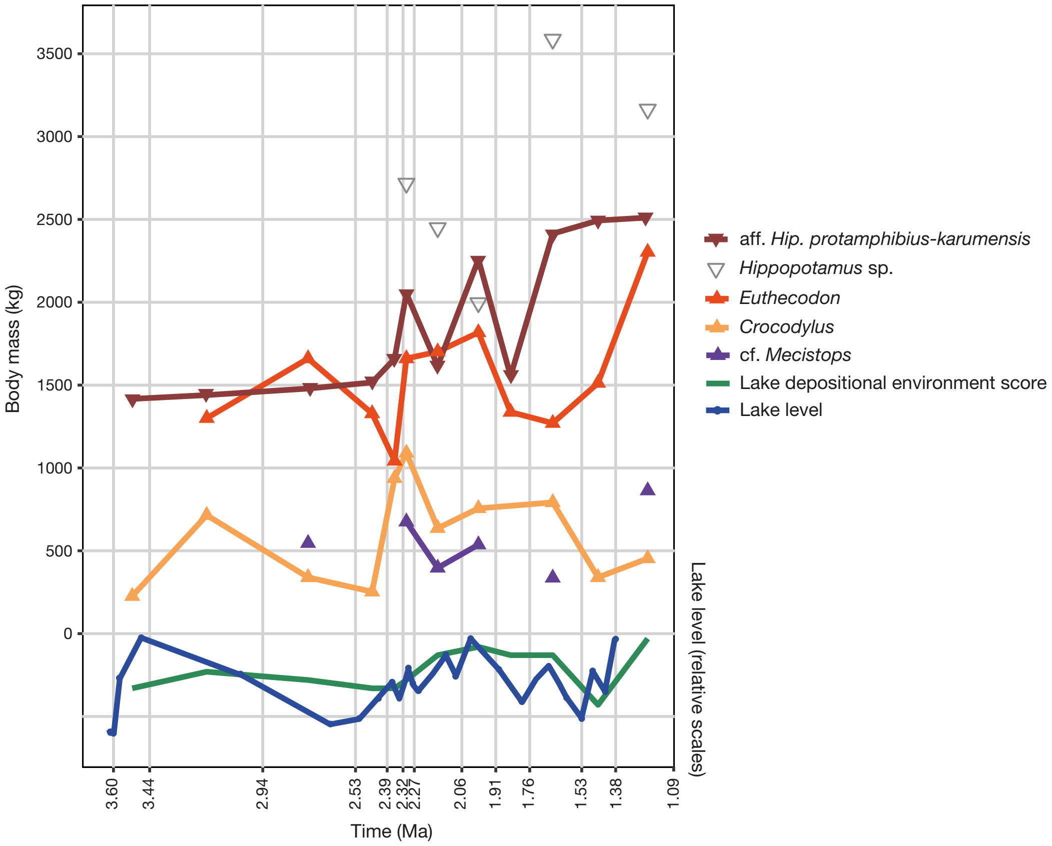

FIG. 7. — Maximum body size of crocodylians (*Euthecodon* Fourtau, 1920, *Crocodylus* Laurenti, 1768, and cf. *Mecistops* Gray, 1844) and hippopotamids (**brown line** series for the local *protamphibius-karumensis* lineage) by member in the Shungura Formation vs reconstructed relative lake level in the Turkana Depression (Nutz *et al.* 2020), and the maximum lacustrine facies score by member from Heinzelin (1983).

which reflects the abundance of dry grass-adapted bovids (Table 6). This indicates that these hippopotamids increased in size during intervals with higher evaporative water loss and coincident with the spread of grassier habitats. This echoes the proposed relation between C4 grassland developments and the success of hippopotamines (Boisserie *et al.* 2011), and the dental enamel δ^{13}C results from Harris *et al.* (2008) indicating a nearly pure C4 diet for this lineage. However, with respect to δ^{13}C, the lineage aff. *Hip. protamphibius-karumensis* has a negative correlation coefficient in our results, while the smaller aff. *Hip. aethiopicus* has high size maxima in more C4-enriched members (Table 6B). Such opposite relationships for these two hippopotamid groups are also seen in correlation with overall mammal herbivore δ^{18}O (Table 6B), suggestive of niche partitioning between the hippopotamids. *Hippopotamus* sp. is not consistently present in the Shungura sequence, but where it is, size maxima are negatively related to lake level and positively related to paleosol δ^{18}O (Table 5A). This result suggests that the third group of hippopotamids, who are generally present in the region during lake high stands, seem to decrease in size when lake area expands and evaporation decreases.

Another semi-aquatic group whose evolution to large size is of interest in the Shungura Formation are the otters, a very large (*c.* 200 kg) species of which was present in members B and C and which may have competed with crocodylians for aquatic or terrestrial prey (Grohé *et al.* 2022). The gigantism observed in both *Euthecodon* and this otter suggests the presences of high resource and habitat availability for aquatic vertebrate carnivores in the Omo Valley during several intervals of the Shungura Formation's deposition. In particular for *Euthecodon*, large aquatic range sizes would be necessary to support a population of these extremely large carnivores (Scheyer *et al.* 2013). We propose that these body size increases are due to indeterminate growth exhibited by these reptiles; in permissive habitats with abundant food and/or limited mortality, individuals reached larger sizes.

The three crocodylian morphotypes considered, the extremely tubulirostine *Euthecodon*, *Crocodylus*, and cf. *Mecistops*, have both similarities and differences in their maximum size changes over time (Fig. 7). Both *Euthecodon* and cf. *Mecistops* attain their overall size maxima in the most recent Shungura member. Both *Crocodylus* and *Euthecodon* increase in size from members E-F. From Member F onwards, there is an apparent decrease in *Crocodylus* size. Specimens from members B, D, and F (OMO 28-1968-3213, L 40-29, and OMO 221-1973-2716) are all extremely robust cranial fragments, likely comparable to *C. thorbjarnarsoni* (Brochu & Storrs 2012), while specimens from later members have unresolved taxonomy and attain smaller size maxima. Looking at high-resolution temporal sequences like this with multiple crocodylians present can help untangle dynamics of their niche partitioning

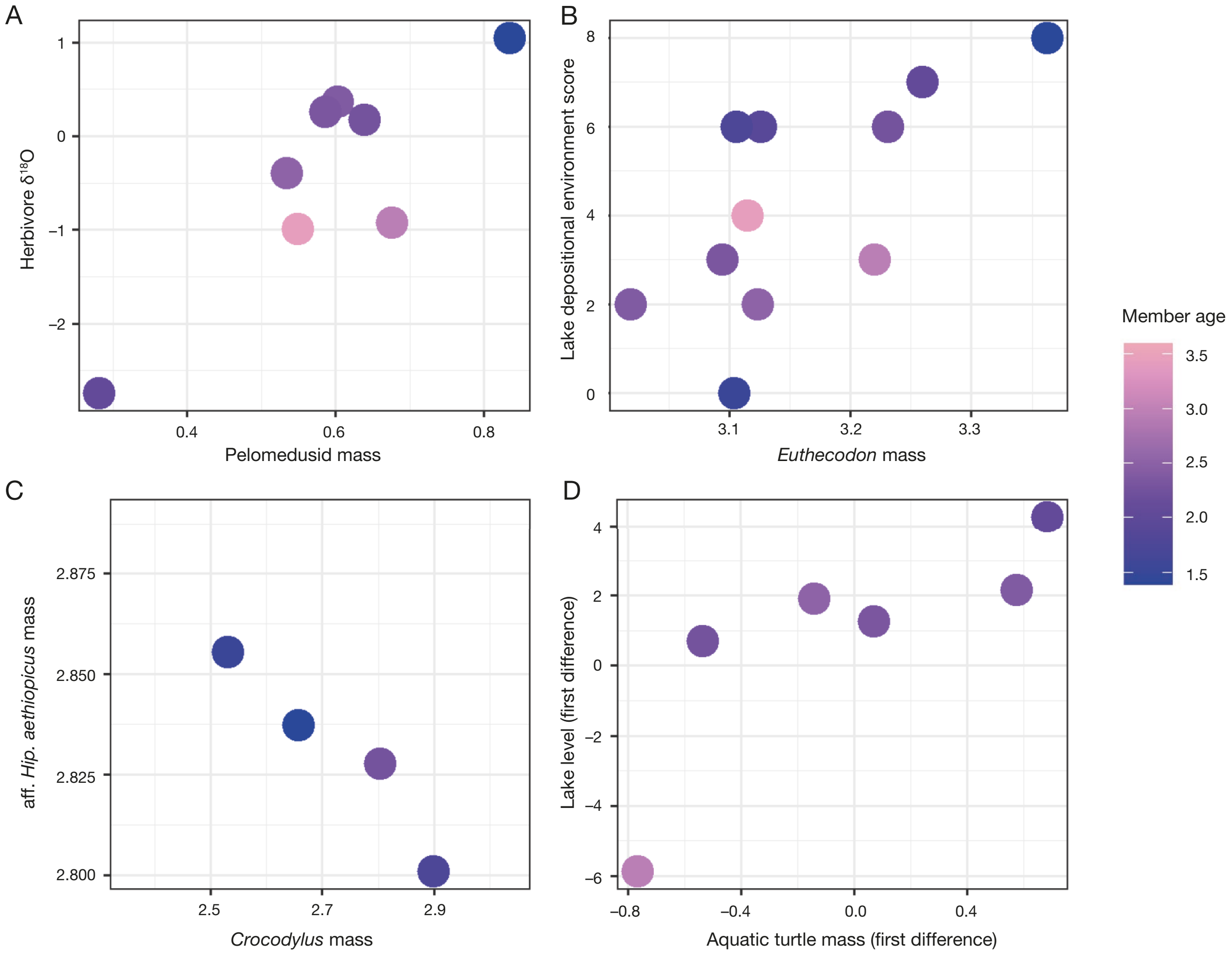

FIG. 8. — Alternative visualizations of correlation tests, with the two data series compared on the two axes. The color of the points indicates the age of the member for each observation. All mass data are shown with units log$_{10}$(kg).

and faunal turnover in the context of paleoenvironments and prey species presence (Gardin *et al.* 2024). In our tests, there were few instances where high correlation coefficients were observed between crocodylian size maxima and environmental proxies. *Crocodylus* size showed negative correlation with the size of terrestrial tortoises and aff. *Hip. aethiopicus* (Fig. 8), as well as negative correlation with estimated soil temperatures. The latter is of interest in light of the theoretical expectation that ectothermic reptiles can attain the largest body sizes only at high temperatures (Head *et al.* 2009; Parker *et al.* 2023).

The assembly of high-resolution time series datasets for vertebrate traits through particular stratigraphic sections like this one enables the testing of hypotheses of differential responses to environmental change. The use of regressions like those deployed here (see Appendices) based on isolated skeletal elements makes estimating body mass tractable for large sample sizes of reptile specimens. In thoroughly-studied depositional contexts like the Turkana Depression, comparison of time series data from vertebrate, invertebrate, plant, and geochemical metrics can identify processes influencing evolution in both community composition and individual taxa's traits. Beyond correlation tests, future studies with only a small increase in the number of time steps used for sampling can test for causal relationships between such variables (Sugihara *et al.* 2012; Reitan & Liow 2019). Such analyses have previously been carried out mainly in marine settings, but their application to temporal sequences in the terrestrial fossil record has high potential to reveal how co-evolution and trait-based responses to environmental change have occurred in the past (Liow *et al.* 2015; Hannisdal & Liow 2018; Reitan & Liow 2019; Lidgard *et al.* 2021). Identifying such trait changes within faunas can, in this case, provide information about habitat shifts that occurred where early humans lived, and more broadly, allow us to build predictive models of faunal responses to future climate changes (Polly *et al.* 2011; Parker *et al.* 2023).

CONCLUSION

We situated reptile body size histories in their environmental context through time in the Shungura Formation in order to characterize the abiotic and biotic conditions underpinning body mass changes in these groups. The observed patterns of maximum body size through time in relation to environmental proxy data demonstrate how local environmental shifts can drive body size evolution. While correlation tests were non-significant, we identify several reptile size-environment relationships, both matching and challenging previous expectations, that can be developed as proxies through testing in other contexts.

Several of the reptile groups studied display relationships between their body size and estimates of paleo-temperature, paleo-precipitation, and vegetation openness, all of which could be clarified through comparison to other sequences in the Turkana Depression. The presence and size of aquatic trionychid turtles is positively related to lacustrine conditions. Both crocodylians and hippopotamids also attain size maxima during lake high stands. The associations between body size in these reptile groups and habitat that we identify here can serve in future to assist in reconstructing climate and vegetation patterns in the eastern African record, if they prove generalizable to other sedimentary sequences. Reptile size is simple to measure and the previously-understudied fossil record of turtles, snakes, and crocodylians can be tapped into as a proxy to inform habitat availability in both terrestrial and aquatic habitats.

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Data Availability

All data and code used are available at: https://doi.org/10.5281/zenodo.18403027

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APPENDICES

Appendix 1. — Linear regression equations used to estimate straight line carapace length for turtle specimens. Abbreviations: **CL**, carapace length; **EHA**, National Museum of Ethiopia/Ethiopian Heritage Authority; **KNM**, National Museums of Kenya; **NHML**, Natural History Museum (London); **PPHM**, Panhandle Plain Historical Museum; **UMZC**, Cambridge University Museum of Zoology.

Taxon	Measurement, x (cm)	Regression to CL (in cm)	Regression trained on N =	Sources for regression data
Trionychidae	Skull length	CL = 3.5595*x - 5.3869	3	UMZC
	Hyohypoplastron maximum length	CL = 2.25*x	2	KNM-LT 28483, EHA OMO 229
	Costal width at midline (average)	CL = 10.051*x -2.9827	10	NHML, KNM, & EHA collections
Pelomedusidae	Plastron length	CL = 0.985*x	1	KNM-WS 14376
	Midline length of posterior lobe of plastron	CL = 4.2047*x -54.557	5	OMO 57/5-1972-324, OMO 38-1968-3640, L 3-10, F 164-10079, F 256-10009, L 182-100002
Testudinidae	Humerus length	CL = 1.7523*x + 49.703	3	NHML & Hay 1908
	Maximum width of acetabulum	CL = 13.32*x	2	NHM 3097, PPHM 1534
	Midline length of neural	CL = 5.234*x	1	KNM-FM 21225

Appendix 2. — Linear regression equations used to estimate skull length for crocodylian specimens; total body length for vertebral regressions from Iijima & Kubo (2020). * measurement for final two rows, vertebral centrum length, is in mm. Abbreviations: **KNM**, National Museums of Kenya; **N**, number of specimens; **NHML**, Natural History Museum (London); **SL**, skull length; **TBI**, Turkana Basin Insitute; **TL**, total body length.

Taxon	Measurement, x (cm*)	Regression to SL (in cm) and TL (in mm)	Regression trained on N =	Sources for regression data
Euthecodon	Mandible length	SL = 0.8754*x + 1.2113	4	KNM-ER 757, KNM-KP 18330, KNM-ER 8260, KNM-LT 26306
	Mandible length to posterior of dentary articulation	SL = 0.8754*x + 1.2113	5	NMK-ER 757, KNM-KP 18330, KNM-ER 8260, KNM-LT 26306, KNM-KP 66227
	Average tooth spacing (excluding two anteriormost tooth sockets)	SL = 19.966*x + 30.446	4	KNM-ER 757, KNM-LT 26306, KNM-ER 8260, KNM-ER 18330
cf. *Mecistops*	Narrowest width of premaxilla	SL = 9.97*x	1	NME L 398 2508A
	Length of mandibular symphysis	SL = 3.8706*x	1	NME L 398 2508A
Crocodylus	Mandible length	SL = 0.6829*x +6.4381	23	NHML collections
	Mandible length to posterior of dentary articulation	SL = 0.8206*x + 4.5791	19	NHML collections
	Length of mandibular symphysis	SL = 3.1846*x + 17.789	20	NHML collections
	Height of dentary at posterior end of mandibular symphysis	SL = 13.158*x	2	NME AL 126-11, L.449-4 (Hadar, Shungura *Crocodylus*)
	Length between centers of d9-d12 alveoli	SL = 5.1384*x + 8.318	18	NHML collections
	Femur circumference	SL = 4.8793*x + 1.2857	4	NHML collections
	D3-D10 vertebral centrum length	log(TL) = 1.906 + 0.993*log(x)	5	Iijima & Kubo 2020
	C8-D2 vertebral centrum length	log(TL) = 2.015 + 0.956*log(x)	2	Iijima & Kubo 2020

Appendix 3. — Specimen data of Testudines by taxa for specimens with maximum body mass estimates for each member of the Shungura Formation.

Taxon	Shungura Member	Midpoint Age (Ma)	Specimen number	Measurement	Dimension (cm)	Carapace length (cm)	Mass reconstruction (kg)
Trionychidae	Basal	3.672	OMO 80-1974-903	Costal width	4.7	44.3	14.6
	B	3.188	L 729-10005	Costal width	7.4	71.4	27.7
	E	2.356	OMO 57/5-10025	Costal width	4.3	40.2	12.8
	F	2.305	OMO 306-1976-386	Costal width	4.8	45.3	15.0
	upper G	1.986	F 164-NC3	Carapace length	58	58	20.9
Pelomedusidae	B	3.188	OMO 28-1967-960	Carapace length	33.5	33.5	3.54
	C	2.734	OMO 3/1-10038	Length of posterior lobe of plastron	21.8	37.1	4.74
	D	2.457	L 824-13	Carapace length	33.1	33.1	3.42
	E	2.356	OMO 38-1968-3640	Carapace length	35	35	4.01
	F	2.305	L 182-10002	Carapace length	34.5	34.5	3.85
	lower G	2.167	OMO 257-1973-5315	Carapace length	36	36	4.35
	upper G	1.986	F164-10079	Carapace length	27	27	1.91
	L	1.239	OMO 346-10082	Length of posterior lobe of plastron	23	42.2	6.83
Testudinidae	B	3.188	OMO 28-1967-958	Neural length	15.4	80.6	66.1
	C	2.734	L 823-3	Plastron length	103	108.9	151.3
	D	2.457	[measured in field]	Maximum width of acetabulum	6.6	87.9	83.9
	E	2.356	OMO 70-NC1	Carapace length	110	110	155.6
	lower G	2.167	L 626-105	Neural length	16.2	84.8	76.0
	upper G	1.986	F 164-10068	Humerus length	15.4	76.7	57.7
	H	1.84	OMO VE 3-NC1	Carapace length	100	100	119.7

Appendix 4. — Specimen data of Crocodylidae by taxa for specimens with maximum body mass estimates for each member of the Shungura Formation. For *Crocodylus* Laurenti, 1768, measurement type “Dentary height” refers to the height of the mandible at the posteriormost level of the mandibular symphysis. For cf. *Mecistops*, “narrowest width” refers to the width of the narrowest part of the premaxilla, posterior to the premaxillary alveoli. For *Euthecodon* Fourtau, 1920, the measurement “Tooth spacing” is the average distance between the center of alveoli (dentary or maxilla) for all alveoli present in each specimen, excluding the anteriormost two.

Taxon	Shungura Formation Member	Age (Ma)	Specimen number	Measurement	Dimension (cm)	Estimated skull length	Length reconstruction (cm)	Mass reconstruction (kg)
Crocodylus	A	3.517	OMO 127-1973-4466	Length between d9-d12 alveoli	7.2	45.3	329.4	226.1
	B	3.188	OMO 28-1968-3213	Dentary height	5.1	67.1	497.6	714.9
	C	2.734	L 449-4	Skull length	52	–	381.1	339.6
	D	2.457	OMO 5/2-1967-617	D3-D10 vertebral centrum length	4.3	–	342.8	252.8
	E	2.356	L 40-29	Dentary height	5.6	73.7	548.4	937.7
	F	2.305	OMO 221-1973-2716	Dentary height	5.9	77.6	578.9	1080.4
	lower G	2.167	OMO 310-1976-549	C8-D2 vertebral centrum length	5.5	–	477.3	636.5
	upper G	1.986	OMO 2-1967-209	Length between d9-d12 alveoli	11.7	68.4	507.6	755.9
	J	1.658	OMO 358-10043	D3-D10 vertebral centrum length	6.6	–	516.2	792
	K	1.458	P 995-1a	Skull length	53	–	381.1	339.6
	L	1.239	OMO 393-10133	Femur circumference	11.5	57.4	422.7	453.6
	C	2.734	OMO 3-1967-910	Length of mandibular symphysis	15.8	61.1	451.7	545.8
cf. *Mecistops*	F	2.305	L 398-2508A	Skull length	65.8	–	487.6	675.4
	lower G	2.167	OMO 150-1972-1	Width of narrowest part of snout	5.5	54.8	402.9	396.8
	upper G	1.986	OMO 372-10016	Narrowest width	6.1	60.8	449.1	537.1
	J	1.658	OMO 358-10041	Narrowest width	5.3	51.8	379.9	336.6
	L	1.239	OMO 341-10040	Length of mandibular symphysis	18.5	71.6	532.3	863.2
Euthecodon	B	3.188	L1-151	Tooth spacing	3.12	92.7	616.9	1302.3
	C	2.735	OMO 18-1968-3215	Tooth spacing	3.5	103.1	673	1660.6
	D	2.547	L 64-34	Tooth spacing	3.15	93.3	621.3	1328.6
	E	2.356	OMO 38-1973-4629	Tooth spacing	2.8	89.6	569.6	1042.6
	F	2.305	OMO 129/a-1972-4	Tooth spacing	3.05	94.4	606.5	1242.3
	lower G	2.167	OMO 6-1967-381	Tooth spacing	3.54	103.9	679	1701.6
	upper G	1.986	F 164-10102	Tooth spacing	3.65	106	695.2	1817.6
	H	1.84	F 161-22	Tooth spacing	3.16	96.5	622.8	1337.4
	J	1.658	OMO 394-10046	Tooth spacing	3.09	95.2	612.5	1276.4
	K	1.458	OMO 339-NC1	Skull length	92	–	611.4	1270.3
	L	1.239	OMO K 7-1969-4410	Tooth spacing	4.07	111.6	756.8	2303.1

Appendix 5. — Specimen data of *Python* Daudin, 1803 for specimens with maximum body mass estimates for each member of the Shungura Formation.

Taxon	Shungura Member	Midpoint Age (Ma)	Specimen number	Measurement	Dimension (mm)	Total length (cm)	Mass reconstruction (kg)
Python	B	3.188	L1-32b	Prezygapophyseal width	20.4	251	5.59
	C	2.735	L 47-67	Prezygapophyseal width	41	540	41.13
	D	2.547	L 824-12	Prezygapophyseal width	40.1	527	38.6
	E	2.356	L 82-30	Prezygapophyseal width	24	300	8.9
	F	2.305	OMO 33-3613	Prezygapophyseal width	52.1	702	81.6
	lower G	2.167	OO 75-1971-2862	Prezygapophyseal width	37	483	30.67
	upper G	1.986	F 163-11	Prezygapophyseal width	44.8	595	52.99
	J	1.658	OMO 379-10008	Prezygapophyseal width	22.9	284	7.68
	L	1.239	OMO 389-10055	Prezygapophyseal width	34	440	24.08