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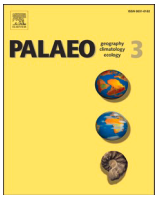

Stable Sr isotopes of fossil dental enamel reflect diet and digestive system differences among sympatric herbivores

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ABSTRACT

Reconstructing the trophic (paleo)ecology and associated physiological traits of both extinct and extant taxa is essential for understanding the functioning of (past) ecosystems. In this context, novel metal stable isotope proxies offer promising tools for investigating ancient diets and, to some extent, the digestive adaptations of animals. In this study, we analyzed the stable strontium isotope composition ($\delta^{88}Sr$), alongside $\delta^{13}C$, $\delta^{18}O$, and $^{87}Sr/^{86}Sr$ ratios, in fossil dental remains of herbivorous mammals from the Early Pleistocene site of Tighennif, Algeria (~1.2–1.0 Ma). Traditional carbon and oxygen isotope data indicate an environment dominated by C_3 vegetation, while the $^{87}Sr/^{86}Sr$ ratios suggest either a relatively homogeneous strontium baseline or limited geographic mobility of the animals. Our results demonstrate that $\delta^{88}Sr$ is sensitive to diagenetic alteration, with enamel samples retaining biogenic signatures comparable to those of modern mammals, whereas dentine exhibits $\delta^{88}Sr$ values shifted toward positive geogenic end-members. $\delta^{88}Sr$ patterns may reflect trophic niche differentiation among herbivores and potentially indicate distinct digestive physiologies, offering a novel alternative proxy for dietary and ecological reconstructions in the fossil record.

1. Introduction

Understanding how ancient ecosystems functioned requires detailed insights into the diets, behaviors, and ecological roles of extinct organisms. Among herbivorous taxa, even subtle differences in foraging strategies and habitat preferences can influence patterns of resource competition and ultimately shape community composition and structure (Carscadden et al., 2020). In recent years, advancements in geochemical methods have provided new avenues for reconstructing such aspects of paleoecology. Notably, the analysis of both radiogenic and stable strontium isotopes in fossil dental enamel has emerged as a powerful approach for inferring mobility, habitat use, and dietary preferences in extinct and extant taxa (Knudson et al., 2010; Guiserix et al., 2024; Griffith et al., 2025; Michailow et al., 2025; Weber et al., 2025).

Strontium (Sr) substitutes for calcium (Ca) in the hydroxyapatite of bones and teeth (Nielsen, 2004), preserving the isotopic signature of ingested food and water (see Bentley, 2006 for a review). The radiogenic strontium isotope ratio ($^{87}Sr/^{86}Sr$) reflects indeed the geological substrates of the environment animals inhabited and foraged in, thereby offering a geospatial signal that complements traditional stable isotope proxies such as $\delta^{13}C$ and $\delta^{18}O$ (see the review in Müller et al., 2024). This allows researchers to trace the movement of individuals across

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distinct geological zones and to infer residency or migration patterns in both modern and fossil faunas (e.g., Pellegrini et al., 2008; Britton et al., 2009; Radloff et al., 2010; Copeland et al., 2016; Lugli et al., 2017; Wooller et al., 2021; Koutamanis et al., 2023; Armaroli et al., 2024).

However, this geologically-driven signal represents only part of the isotopic record. Increasing attention has been given to the stable isotopes of strontium, particularly $^{88}Sr/^{86}Sr$ (reported as $\delta^{88}Sr$ in ‰ against NIST987), representing mass-dependent fractionation between isotopes during biological and geochemical processes (Wu et al., 2024). Studies showed that lighter metal isotopes (e.g., ^{86}Sr) are preferentially incorporated into bioapatite relative to heavier ones (e.g., ^{88}Sr), a phenomenon with important implications for interpreting dietary habits and physiological adaptations among taxa (Knudson et al., 2010). Akin to calcium isotope systematics, the mechanisms driving $\delta^{88}Sr$ variability in biological tissues are not yet fully understood, and it remains unclear to what extent dietary, metabolic, or digestive physiological factors influence these values in herbivores.

In this study, we analyze fossil dental enamel from multiple herbivore families, recovered at the Early Pleistocene archaeological site of Tighennif (Algeria, ~1.2–1.0 Ma). Our goal is to reconstruct aspects of the paleoecology of these herbivores using a multi-isotope approach, with a particular focus on $\delta^{88}Sr$, an emerging proxy that holds potential for distinguishing trophic niches and digestive physiology of sympatric herbivores. Specifically, we measured first the classical isotopic systematics of $\delta^{13}C$ and $\delta^{18}O$ to assess the habitat and the occupied trophic niche, $^{87}Sr/^{86}Sr$ to evaluate provenance and landscape use, and finally $\delta^{88}Sr$ to explore potential differences in Sr isotope fractionation across taxa. In particular, we investigate whether $\delta^{88}Sr$ values vary systematically according to diet and/or digestive physiology, by comparing animals categorized as monogastric versus polygastric herbivores. This approach aims to test whether differences in digestive system anatomy and physiology may influence Sr isotope incorporation and thus reflect rooted ecological or physiological variability among extinct herbivore communities.

1.1. Premises on C-O-Sr isotope composition of bioapatite

Carbon isotope analysis of the carbonate moiety of dental enamel hydroxyapatite is a powerful tool for distinguishing between consumers of C_3 and C_4 plants. This distinction arises from the contrasting $\delta^{13}C$ signatures associated with C_3 and C_4 photosynthetic pathways (O'Leary, 1981), which are passed on to herbivores through their diet. C_3 plants – including most trees, shrubs, and cool-season grasses – typically exhibit more negative $\delta^{13}C$ values (around −30 ‰ to −22 ‰), whereas C_4 plants – mainly warm-season tropical grasses and sedges – have higher $\delta^{13}C$ values (around −14 ‰ to −10 ‰) (Cerling et al., 1997). These isotopic signals are incorporated into the herbivore enamel via the diet, with a relatively well-characterized enrichment factor of ~12–14 ‰ (Cerling et al., 1997). As enamel mineralizes during tooth development, it registers the isotopic signal of the diet during that period, enabling reconstructions of dietary preferences and infer habitat use over time. In African environments, $\delta^{13}C$ is traditionally used to classify herbivores as C_3-browsers, C_4-grazers or mixed-feeders (Cerling et al., 2015).

Oxygen isotopes in mammal enamel are in equilibrium with blood bicarbonate and are mainly controlled by the $\delta^{18}O$ composition of body water (Pederzani and Britton, 2019). This latter is, in turn, governed by the mass balance and isotopic fractionation of oxygen as it enters and exits the body. Oxygen is introduced through ingested water, inhaled O_2, and diet. Internally, metabolic processes generate H_2O and CO_2 as byproducts. Oxygen is lost via excretions – such as urine, sweat, and feces – as well as through water vapor and CO_2 in exhaled air. Under steady-state conditions, a predictable relationship exists between ingested water and body water $\delta^{18}O$ values (Luz et al., 1984). Herbivores obtain ingested water primarily from two sources: drinking water and the water contained in plants (Pederzani and Britton, 2019). While the $\delta^{18}O$ value of drinking water reflects that of meteoric precipitation, which itself is correlated with mean annual temperature (D'Angela and Longinelli, 1990), plant water is typically enriched in ^{18}O relative to groundwater due to isotope fractionation during evapotranspiration. This, in turn, suggests that herbivore's behavioral ecology may also impact the $\delta^{18}O$ value of their tissues. For example, obligate drinkers tend to exhibit lower $\delta^{18}O$ values in their tissues compared to non-obligate drinkers (see e.g. Levin et al., 2006).

The $^{87}Sr/^{86}Sr$ ratio is a well-known geochemical tracer used to investigate the geographic origin and mobility of organisms, rooted in the field of human paleoecology (Ericson, 1985). This isotopic ratio reflects the local geology because radiogenic ^{87}Sr is produced by the radioactive decay of ^{87}Rb, while ^{86}Sr is stable. Since both Sr and Rb are ubiquitously present as trace elements within the Earth's crust, crustal rocks and mantle-derived materials acquire different $^{87}Sr/^{86}Sr$ ratios in relation to their age and to their initial Sr—Rb contents. As strontium ions enter ecosystems through weathering and are taken up by plants and animals, the $^{87}Sr/^{86}Sr$ signature of a geological region becomes imprinted in biological tissues, particularly into the bioapatite of teeth and bones (Faure and Mensing, 2005). By comparing the $^{87}Sr/^{86}Sr$ values of vertebrate bioapatite with local geological baselines (e.g. Armaroli et al., 2024), one can assess whether an organism was local to a given place or originated from a different area. This approach is especially powerful in paleoecology for reconstructing patterns of animal migration and habitat use (e.g., Balter et al., 2008; Lugli et al., 2017; Wooller et al., 2021; Kowalik et al., 2023). Although fractionation along the trophic chain is expected, any eventual isotope effect is corrected during mass spectrometry analyses, due to mass bias normalization against a constant $^{88}Sr/^{86}Sr$ ratio.

Yet, this latter is known to be variable in the environment. By analysing this ratio ($\delta^{88}Sr$), using external mass bias correction (e.g. through double-spike or Zr-doping), it is possible to explore Sr isotope fractionation across different reservoirs and trophic niches (Knudson et al., 2010; Hajj et al., 2017). $\delta^{88}Sr$ can thus provide insights into physiological and dietary habits. Since Sr mainly enters the body through diet and drinking water, and is mostly extracted via the kidneys, only a small portion (10–30 %) is absorbed in the small intestine of monogastric mammals (and both small intestine and rumen for ruminants; Hyde et al., 2019), through mechanisms that passively follow Ca^{2+} metabolism. This generates an overall decrease of Sr/Ca ratios along the trophic chain (Burton et al., 1999). Most of the absorbed Sr is deposited in bone bioapatite, where lighter isotopes are preferentially fixed over heavier ones, thus resulting in a $\delta^{88}Sr$ lighter than that of the diet. This was confirmed experimentally with controlled-feeding studies, showing a $\delta^{88}Sr$ trophic shift of about −0.20 ‰ (Lewis et al., 2017; Weber et al., 2025). Still, the exact mechanisms that produce the observed isotope variability among humans and animals (see e.g. Knudson et al., 2010) remain incompletely understood. Similar isotope effects are observed for calcium (Skulan and DePaolo, 1999; Reynard et al., 2010; Heuser et al., 2011; Martin et al., 2018). The $\delta^{44/42}Ca$ values have been shown to vary between grazer and browser herbivores in modern trophic chains, suggesting that isotope differences in consumed plant tissues are retained in consumer tissues (Martin et al., 2018). Notably, other physiological mechanisms – such as e.g. digestive system features – are often invoked to explain element partitioning (Balter and Simon, 2006) and isotope ratio fractionation (Martin et al., 2018), but yet relatively unexplored.

1.2. Geoarcheological setting

The hominin site of Tighennif was discovered in 1872 during sand quarry exploitation. Subsequent explorations of the site unearthed further fossils (Balout, 1955). Large scale excavations conducted in the 1950s have led to the discovery of the oldest *Homo erectus* fossil remains in North Africa named *Atlanthropus mauritanicus*, associated with large and small mammal fossils and Acheulian stone tools (Arambourg and Hoffstetter, 1963). Tighennif is located on the High Plateaus of northwestern Algeria (35° 24′57.30" N; 0° 19′21.30″ E) in the province of

Mascara (Fig. 1). The site is formed near the northern edge of the plain of Ghriss. The plain of Ghriss consists of a depression that extends from north-east to south-west between the Jurassic Mountains of Saida in the south, which have undergone intense tectonic activities, and the Beni Chougrane folded mountains in the north of Cretaceous-Tertiary age. The sedimentary deposits around Tighennif include clays, sandy clays, sands, and sandstones dated to Miocene, Pliocene and Quaternary (Bekkoussa et al., 2008, 2013) (Fig. 1).

New multidisciplinary studies involving stratigraphy, dating, and archaeological excavations are conducted at four loci (namely A, B, D, and E) within the Tighennif site. Our work focuses on Locus A that showed a great abundance of archaeological and fossil remains. The predominantly sandy stratigraphic sequence at this locus is of fluvial origin or associated with floodplain environments. It includes three major sedimentary deposits: 1) varicolored clays with patches and $CaCO_3$ nodules; 2) in erosive discordance, a thick deposit of sand, resting on the varicolored clays, includes three parts of stratigraphic layers: lower, middle and upper. The lower part includes a layer of sandy gray clay containing stone tools and fossil bones, a deposit of fine and medium sands with carbonate clasts, and a layer of medium-size sands with clay. The middle layers, rich in archaeological remains, are sandy of medium to fine particles and mostly massive with very low clay content and $CaCO_3$ nodules. The upper layers consist of fine and very fine sands with oxidation lines; and 3) the top of the section entails a thick layer of sandstones of fine to medium sands resting on a disconformity. A caliche soil seals the stratigraphic sequence. As of the dating, comprehensive studies of clays and quartz-rich samples are underway involving paleomagnetism, Electron Spin Resonance (ESR), Optically Stimulated Luminescence (OSL), and cosmogenic nuclide ^{10}Be and ^{26}Al dating techniques. Based on faunal taxa of biostratigraphic interest, Locus A is estimated to ~1.2–1.0 Ma in age (Sahnouni and van der Made, 2009).

The lithic industry is typical of Acheulian tradition. In addition to Oldowan-type of artifacts, it is characterized primarily by the presence of Large Cutting Tools (LCT) (trihedrons, bifaces, and cleavers). It includes cores, LCTs, whole flakes, retouched pieces, various fragments, hammerstones, and unmodified cobbles. In terms of raw materials, the stone artifacts are made of sandstone, flint, quartzite, and limestone.

Taphonomic evidence clearly shows a causal association between the fossil bones and the stone artifacts. Bone surface preservation is generally good, allowing the recognition of anthropogenic modifications. The Tighennif Locus A archaeofauna record includes several bones with cut marks evidence (Chelli Cheheb, 2018). These are slicing marks occurring primarily on appendicular and axial bone elements. The majority of the cut marks are found on the lower limbs, followed by intermediate limbs and upper limbs. The activities involved in hominin butchery processes include skinning, defleshing, and evisceration. In addition, hammerstone percussed bones are documented in the form of conchoidal percussion scars, notches and impact flakes, mainly of large and very large animals suggesting intentional bone marrow extraction.

2. Materials and methods

Fossil herbivore teeth were sampled from the Locus A faunal assemblage (Saidani, 2023) of the Early Pleistocene archeological site of Tighennif (Algeria). Sampled families include: Bovidae (*Parmularius ambiguous*, *Tragelaphus algericus*, *Connochaetes taurinus progun*), Camelidae (*Camelus thomasi*), Elephantidae (*Loxodonta atlantica*), Equidae (*Equus mauritanicus*), Hippopotamidae (*Hippopotamus sirensis*), Rhinocerotidae (*Ceratotherium mauritanicum*), and Suidae (*Metridiochoerus compactus*) (Suppl. Table 1).

Enamel powder (ca. 10 mg) was drilled from $n = 49$ fossil dental specimens, along the full length of the crown. In addition, $n = 7$ dentine specimens (one sample per family) were collected as well to test the Sr isotope composition of a tissue easily altered diagenetically.

$\delta^{13}C$ and $\delta^{18}O$ isotope analyses were performed on the carbonate moiety of tooth enamel ($n = 46$) at the Centro Interdipartimentale Grandi Strumenti of the University of Modena and Reggio Emilia. Sample powders (2 mg) were reacted for 2 h at 50 °C with +100 % phosphoric acid. Isotope ratios were determined on liberated CO_2 by continuous flow IRMS (Elementar precisION) coupled to an equilibration system (Elementar isoFLOW). Repeated analyses of NBS18 and NBS19 reference materials showed a precision (1SD) of ±0.1 ‰ for $\delta^{13}C$ and ± 0.2 ‰ for $\delta^{18}O$. C—O data are expressed in ‰ against VPDB.

Sr isotope analysis was performed at the MeGic Lab of the Department of Chemical and Geological Sciences (University of Modena and Reggio Emilia). Samples (n = 49 enamel + n = 7 dentine) were cleaned with MilliQ in an ultrasonic bath and digested with concentrated nitric acid. After Sr purification (Argentino et al., 2021), samples were diluted to 4 % vol. nitric acid and measured with the Neptune MC-ICPMS housed at the Centro Interdipartimentale Grandi Strumenti of the University of Modena and Reggio Emilia. $\delta^{88}Sr$ and $^{87}Sr/^{86}Sr$ were collected simultaneously following Argentino et al. (2021). Data were reported to a NIST SRM 987 value of 0.710248 (McArthur et al., 2001). Repeated analysis of SRM 987 yielded an average $^{87}Sr/^{86}Sr$ of 0.710251 ± 0.000016 (2SD, $n = 21$) and a reproducibility of ±0.05 ‰ (1SD, n = 21) for $\delta^{88}Sr$. A NIST SRM 1400 (Bone Ash) processed along with the samples yielded an $^{87}Sr/^{86}Sr$ ratio of 0.71310 ± 0.00001 (2SE) and a $\delta^{88}Sr$ of −0.37 ‰ ± 0.02 (2SE), in agreement with literature data (Romaniello et al., 2015; Guiserix et al., 2022; Weber et al., 2018, 2025). $\delta^{88}Sr$ data are expressed in ‰ against NIST RMS 987. All data generated during this study are included in this manuscript and its supplementary materials.

Statistical analyses were conducted in R (version 4.0.5). Individual samples were analyzed after grouping by taxonomic family and digestive system type (monogastric vs. polygastric). Among polygastric

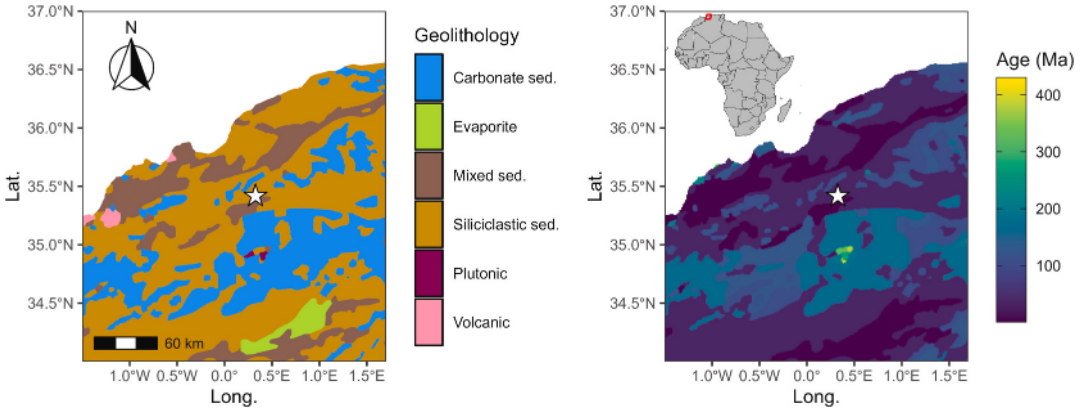

Fig. 1. Geolithological map from GLiM (Hartmann and Moosdorf, 2012) of the area surrounding Tigheniff (white star). The age of the rocks from GLiM is also reported.

animals, we included both true ruminants (Bovidae, four-chambered stomach) and non-ruminant foregut fermenters with a three-chambered stomach, such as Camelidae (Niehaus and Mora, 2022) and Hippopotamidae (Clauss et al., 2004). Due to the small sample sizes of some families and the lack of homogeneity of variances, normality assumptions could not be met. Therefore, differences among groups were assessed using the non-parametric Kruskal-Wallis test. Post hoc pairwise comparisons were performed using Dunn's test with Holm correction for multiple testing. Isotopic differences between monogastric and polygastric groups were evaluated using the Wilcoxon rank-sum test, while paired Wilcoxon rank-sum tests were applied to compare dentine-enamel pairs. Statistical significance was set at $p < 0.05$.

3. Results

Our dataset is composed of four isotope ratios, namely $\delta^{13}C_{VPDB}$, $\delta^{18}O_{VPDB}$, $\delta^{88}Sr_{NIST987}$ and $^{87}Sr/^{86}Sr$ measured on tooth enamel (Suppl. Table 1). $\delta^{88}Sr$ and $^{87}Sr/^{86}Sr$ were measured on a subset of dentine samples, to help interpret the diagenetic pathways of Sr in teeth. Enamel $\delta^{13}C_{VPDB}$ showed an average value of −10.2 ‰ ± 0.93 ‰ (1SD, $n = 46$), ranging between −11.7 ‰ and − 7.3 ‰; while $\delta^{18}O$ showed an average value of −3.6 ‰ ± 1.1 ‰ (1SD, n = 46), ranging between −6.4 ‰ and − 2.0 ‰ (Fig. 2). $\delta^{88}Sr$ showed an average value of −0.28 ‰ ± 0.11 ‰ (1SD, $n = 49$, min = −0.53 ‰, max = −0.10 ‰) for enamel and − 0.05 ‰ ± 0.07 ‰ (1SD, $n = 7$, min = −0.19 ‰, max = 0.02 ‰) for dentine specimens (Fig. 3). $^{87}Sr/^{86}Sr$ showed an average value of 0.70918 ± 0.00013 (1SD, n = 49, min = 0.70893, max = 0.70950) for enamel and 0.70916 ± 0.00010 (1SD, n = 7, min = 0.70897, max = 0.70930) for dentine specimens (Fig. 3). For each tooth where both dentine and enamel were measured, a difference ($\Delta_{dentine\text{-}enamel}$) between the two tissues was calculated. The average $\Delta_{dentine\text{-}enamel}$ values are 0.24 ‰ ± 0.11 ‰ (1SD, n = 7) for $\delta^{88}Sr$ and 0.00003 ± 0.00007 (1SD, n = 7) for $^{87}Sr/^{86}Sr$. The difference between the enamel and dentine datasets was evaluated with a paired Wilcoxon rank sum test, resulting in a significant difference for $\delta^{88}Sr$ ($p = 0.016$), but not for $^{87}Sr/^{86}Sr$ ($p = 0.22$). Summary statistics for each taxonomic family group are reported in Table 1.

The non-parametric Kruskal-Wallis test was used to compare the data among families. The test showed statistically significant differences for $\delta^{88}Sr$ and $\delta^{18}O$ ratios (p = 8e-04, $p = 0.001$ respectively), but not for $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ ($p = 0.54$, $p = 0.37$ respectively). $\delta^{88}Sr$ and $\delta^{18}O$ post hoc Dunn tests are reported in Table 2 for family-pairs. When grouped by digestive system, both $\delta^{88}Sr$ and $^{87}Sr/^{86}Sr$ ratios differed significantly between monogastric (hindgut fermenters) and polygastric (foregut fermenters) vertebrates (Wilcoxon rank sum test, p = 2.5e-05 and p = 0.04 respectively), whereas no significant differences were observed for $\delta^{13}C$ or $\delta^{18}O$ ($p = 0.62$ and $p = 0.11$ respectively). It should be noted that, due to the low number of individuals in some families, much of the observed variance is likely driven by Equidae and Bovidae. Caution is therefore warranted when interpreting patterns for families represented by few specimens.

4. Discussion

4.1. Diagenetic alteration of Sr in bioapatite: inferences from the $\delta^{88}Sr$ ratio

Understanding the diagenetic alteration of Sr in fossil bioapatite dental and bone specimens is key to unravel the origin of the observed isotope signal, i.e. if it is of post-depositional or biogenic origin. Enamel is nowadays considered a robust proxy for metal isotope analyses, due to its intrinsic resistance to diagenetic alteration, driven by its compact and low-organic structure. Yet, especially for deep-time, Sr isotope signals can be found altered by post-depositional uptake of Sr (see e.g. Michailow et al., 2025).

Many proxies are currently used for diagenetic assessment of

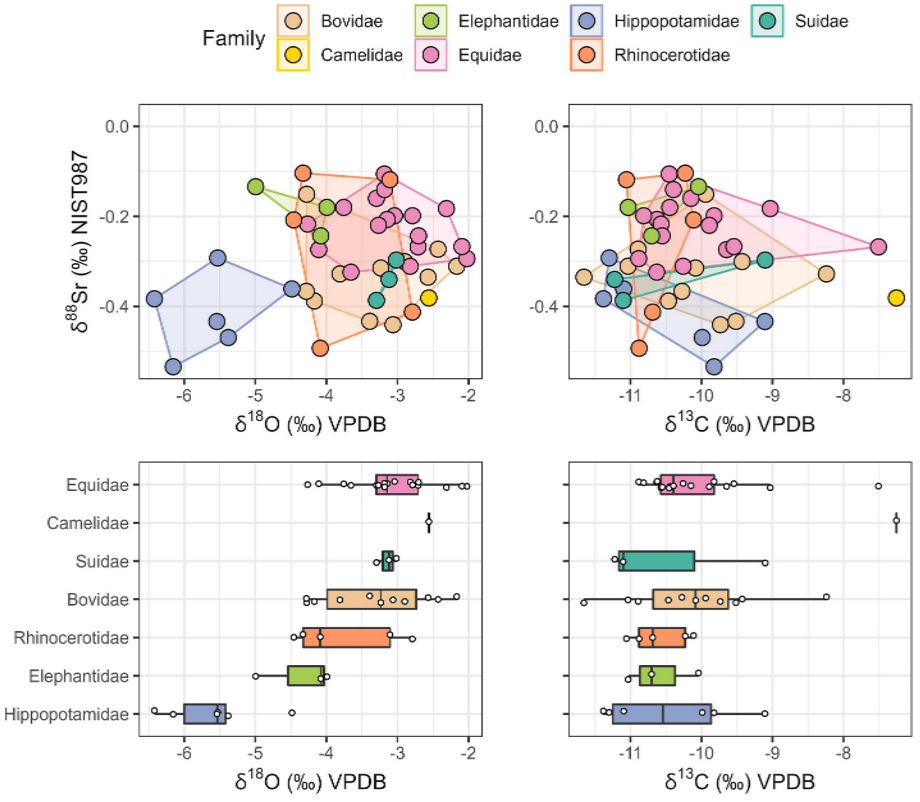

Fig. 2. $\delta^{88}Sr$ data are compared with $\delta^{18}O$ and $\delta^{13}C$ for the different families. Boxplots represent data distribution of individual families; these are reordered based on the family $\delta^{18}O$ average value.