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Yohan Pochat-Cottilloux, Jeremy E Martin, Mathieu G Faure-Brac, Stéphane Jouve, Christian de Muizon, et al.. A multi-isotopic study reveals the palaeoecology of a sebecid from the Paleocene of Bolivia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2023, 625, pp.111667. 10.1016/j.palaeo.2023.111667 . hal-04133611

HAL Id: hal-04133611

<https://hal.science/hal-04133611v1>

Submitted on 20 Jun 2023

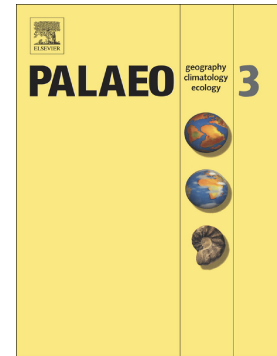
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Journal Pre-proof

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PII: S0031-0182(23)00285-7

DOI: <https://doi.org/10.1016/j.palaeo.2023.111667>

Reference: PALAEO 111667

To appear in: *Palaeogeography, Palaeoclimatology, Palaeoecology*

Received date: 4 February 2023

Revised date: 31 May 2023

Accepted date: 2 June 2023

Please cite this article as: Y. Pochat-Cottilloux, J.E. Martin, M.G. Faure-Brac, et al., A multi-isotopic study reveals the palaeoecology of a sebecid from the Paleocene of Bolivia, *Palaeogeography, Palaeoclimatology, Palaeoecology* (2023), <https://doi.org/10.1016/j.palaeo.2023.111667>

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A multi-isotopic study reveals the palaeoecology of a sebecid from the Paleocene of Bolivia

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Abstract

Sebecids constitute a family of notosuchian crocodylomorphs of probable terrestrial habits. They are notable for having survived the Cretaceous-Paleogene mass extinction and are known until the Miocene in South America. However, ecological traits that favoured their resilience in continental ecosystems remain unknown. Here, using a multi-isotopic approach, we infer several palaeoecological traits of a sebecid from the locality of Tiupampa (Bolivia), which contains a diverse vertebrate fauna of the Early Paleocene. After having constrained the effects of diagenesis, the study of the oxygen isotope compositions of apatite phosphate allows the identification of water resources for the various studied taxa and to infer an ectothermic thermoregulation strategy for the sebecids. A terrestrial lifestyle is also supported by different oxygen isotope compositions observed between sebecids and aquatic dyrosaurid crocodylomorphs. The radiogenic strontium isotope compositions confirm the continental affinities of this fauna, with no marine input in the palaeoenvironment frequented by the different faunal elements. The calcium and carbon isotope compositions show that the sebecids from Tiupampa were at the top of a C_3 -based food web. Finally, a local dry environment with tropical temperatures for those specimens is inferred both from oxygen and carbon isotope compositions of their hard tissues.

Keywords

Sebecidae; geochemistry; oxygen; carbon; calcium; strontium.

1. Introduction

Sebecidae is an extinct family of large supposedly terrestrial crocodylomorphs, known from the Maastrichtian to the Miocene (Langston, 1965; Paolillo & Linares, 2007; Pol & Powell, 2011; Sellés et al., 2020). They are the last survivors of the remarkably diverse group known as Notosuchia, Gasparini 1971. Sebecids were distributed in South America and Europe and were one of the major groups of terrestrial predators during the Early Cenozoic (Pol et al., 2012; Martin, 2016; Martin et al., 2023). They are inferred to be terrestrial based on numerous traits: the skull of sebecids is similar to those of terrestrial sauropsid carnivores (Busbey, 1986; Molnar, 2012); their postcranial anatomy (proportionately long limbs) implies an erect posture compatible with a terrestrial lifestyle (Pol et al., 2012; Martin et al., 2023) and their neuroanatomy displays several terrestrial characteristics (inner ear and pneumaticity of the skull; Pochat-Cottilloux et al., 2022). Through histological studies, they are further hypothesized to have been ectotherms (Cubo et al., 2020; 2022).

While this ecology was inferred thanks to the study of morpho-anatomical characters, the use of stable isotope geochemistry could bring other evidence to assess their palaeoecology and the numerous related issues. This has started to be applied recently, when Klock et al. (2022) assessed the diets of two South American notosuchians. The oxygen isotope compositions of apatite phosphate ($\delta^{18}\text{O}_p$) and carbonate ($\delta^{18}\text{O}_c$) from vertebrate bones, teeth and scales are linked to the animal body temperature and the oxygen isotope composition of body water, which is mainly derived from ingested ambient water (Kolodny et al., 1983; Longinelli, 1984; Luz et al., 1984; Faure-Brac et al., 2022). Physiological adaptations to a specific lifestyle (aquatic or terrestrial) affect the $\delta^{18}\text{O}$ of the body water by controlling the amount of input and output of oxygen, as well as the associated isotopic fractionations (Luz & Kolodny, 1985; Bryant & Froelich, 1995; Kohn, 1996). As a result, differences in $\delta^{18}\text{O}$ values between different vertebrate groups are linked to differences in either thermoregulation strategy, diet (e.g. herbivorous vs carnivorous) and/or living environment (Fricke & Rogers, 2000; Clementz & Koch, 2001; Clementz et al., 2003; Amiot et al., 2006, 2010).

The carbon isotope composition of vertebrate apatite constitutes a proxy of the animal diet. As the magnitude of ^{13}C -enrichments between vertebrate apatite and diet is known for several extant groups, it allows the estimation of the carbon isotope composition of the base of the food web for fossil specimens. Furthermore, there is a trophic ^{13}C isotope enrichment between meat consumers and their food (i.e., lower $\delta^{13}\text{C}$ values) of 0 to 2 ‰ (Bocherens & Drucker,

2003). There are different expected values between C₃ and C₄-based foodwebs (Lee-Thorp et al., 1989; Tieszen & Fagre, 1993; Sillen & Lee-Thorp, 1994; Koch, 1998; Cerling & Harris, 1999; Passey et al., 2005; Stanton, 2006). This is done while keeping in mind that C₄ plants did not appear before the Oligocene (Niklaus & Kelly, 2019). In aquatic environments, the relationship is more complex, as the primary producers that constitute organism diets have $\delta^{13}\text{C}$ values that can vary as a result of differences in productivity, dissolved CO₂ concentration or bicarbonate utilization (Clementz & Koch, 2001 and references therein).

Calcium isotope compositions ($\delta^{44/42}\text{Ca}$) are also of interest because calcium is almost exclusively derived from food in terrestrial vertebrates (Skuløn & DePaolo, 1999; Martin et al., 2018; Tacail et al., 2020). The observed change between the recorded isotopic value of their food relative to their mineralized tissues has allowed trophic levels to be inferred from continental food webs of the Cretaceous (Hassler et al., 2012; Martin et al., 2022).

Finally, the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of the mineralized tissue is a direct reflection of the geological substrate the animal lives on as it is not produced metabolically and is thus ingested through alimentation and water (Price et al., 2002; Uazzolini et al., 2021). It is hence possible to distinguish organisms living in different environments that are linked to different substrates (whether soils or waters).

Here, using a multi-isotopic approach involving those four isotopic systems, we discuss the impact of diagenetic processes on the preservation of the different geochemical proxies and infer several ecological traits of the sebecid from the locality of Tiupampa in terms of thermoregulation strategy, feeding habits and lifestyle, as well as a palaeoenvironmental reconstruction of this Pliocene locality.

2. Material & methods

2.1. Sample collection

Fifteen samples of fossil teeth enamel (and dentine when not enough material was available) of crocodylomorphs, fish and mammals and two samples of fish scale enameloid were analysed for their oxygen isotope composition of apatite phosphate ($\delta^{18}\text{O}_p$), oxygen ($\delta^{18}\text{O}_c$) and carbon ($\delta^{13}\text{C}$) isotope composition of apatite carbonate, calcium isotope composition ($\delta^{44/42}\text{Ca}$), radiogenic strontium isotope ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) and elemental concentrations. Crocodylomorphs samples most probably come from adult individuals as the teeth are longer than one centimetre (Supplementary File 1), compared with known fossil specimens (Buffetaut & Marshall, 1992; Paolillo & Linares, 2007; Jouve et al., 2021). Mammal samples

belong to the taxon *Alcidedorbignya inopinata* Muizon & Marshall 1987 which is inferred as agile, plantigrade, terrestrial and probably scansorial (Muizon et al., 2015). The sampled tooth type is unknown. The fish samples might either come from siluriforms (Gayet, 1988, 1990) or polypteriforms (Gayet & Meunier, 1992), but their referral is complex as the specimens described in previous studies from Tiupampa are not associated with teeth. Oxygen isotope compositions of phosphate ($\delta^{18}\text{O}_p$) of the samples have already been published in Faure-Brac et al., (2022), except for sebecid values. The details of the samples are given in Supplementary File 1.

All the samples come from the locality of Tiupampa in the Santa Lucia Formation near the Vila Vila village about 90 km southeast of Cochabamba in the Mizque Province (southcentral Bolivia; Supplementary File 2). This fauna dates back to the Early Paleocene (Early Danian, palaeomagnetic Chron 28r, ca. 65 Mya; Muizon & Ladevèze, 2020, fig. 4; Muizon & Billet, 2022) and has yielded a rich and diverse fauna including diapsids (Muizon et al., 1983; Buffetaut & Marshall, 1992; Rage, 1992; Jouve et al., 2021; Pochat-Cottilloux et al., 2022), fishes (Gayet, 1988, 1990; Gayet & Meunier, 1992), amphibians (Rage, 1991), turtles (de Lapparent de Broin, 1992) and mammals which constitute a large part of the relative abundance of the fossils (Marshall et al., 1983, 1995; Marshall & Muizon, 1988; Muizon & Marshall, 1991, 1992; Muizon, 1992, 1994, 1998; Muizon & Cifelli, 2000; Muizon et al., 1998, 2015, 2018, 2019; Muizon & Ladevèze, 2020, 2022; Muizon & Billet, 2022).

2.2. Analytical techniques

2.2.1. Oxygen isotope analysis of biogenic apatite phosphate

The vertebrate apatite powders were treated following the protocol described in Crowson et al., 1991 and Lécuyer et al., 1993 (see also Supplementary File 3). Oxygen isotope compositions were measured using a vario PYRO cube™ elemental analyser coupled with an Isoprime™ isotopic ratio mass spectrometer (Elementar UK) in continuous flow mode at the Plateforme d'Ecologie Isotopique du Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés (LEHNA, UMR5023, Université Lyon 1). For each sample (whenever possible), five replicates of 300 µg of Ag_3PO_4 were mixed with pure graphite powder in excess and loaded in silver foil capsules. Pyrolysis was performed at 1450°C. Measurements have been calibrated against silver phosphate prepared from the NIST 120c ($\delta^{18}\text{O}_p = 21.7$ ‰ V-SMOW; Lécuyer et al., 1993) and NIST 8557 (9.3 ‰ V-SMOW; Hut, 1987; Halas & Szaran, 2001). Isotopic compositions are reported in the δ notation relative to V-SMOW.

2.2.2. Oxygen and carbon isotope analysis of biogenic apatite carbonate

Potential organic contaminants as well as secondarily precipitated calcite were removed from the vertebrate apatite powder following the protocol of Koch et al. (1997; see also Supplementary File 3 for more details). Stable isotope compositions were measured using an iso-FLOW system connected on-line in continuous flow mode to a precision mass spectrometer (Elementar UK). For each sample, three aliquots of 2 mg of pre-treated vertebrate apatite powder were loaded in LABCO Exetainer 3.7 mL soda glass vials, round bottomed with Exetainer caps (LABCO UK) and reacted with anhydrous phosphoric acid at 90°C. The CO₂ gas generated during the acid digestion was then transferred to the mass spectrometer via the centrION interface. The materials used for calibration were Carrara marble ($\delta^{18}\text{O}_{\text{c V-PDB}} = -1.95 \text{ ‰}$, $\delta^{13}\text{C}_{\text{V-PDB}} = 1.96 \text{ ‰}$; Fourlet et al., 2016), NIST 8543 ($\delta^{18}\text{O}_{\text{c V-PDB}} = -23 \text{ ‰}$, $\delta^{13}\text{C}_{\text{V-PDB}} = -5.01 \text{ ‰}$) and NIST 120c ($\delta^{18}\text{O}_{\text{c V-PDB}} = -1.13 \text{ ‰}$, $\delta^{13}\text{C}_{\text{V-PDB}} = -6.27 \text{ ‰}$; Passey et al., 2007). Isotopic compositions are reported in the δ notation relative to V-SMOW for oxygen and V-PDB for carbon.

2.2.3. Calcium and strontium isotope analysis of vertebrate apatite

For these two elements, 11 samples were duplicated and placed in Teflon beakers. The first duplicate was submitted to a leaching procedure following the protocol described in Balter et al. (2002; see also Supplementary File 2), to remove potential secondary calcite. The second one was left without leaching. All samples were then digested using ultrapure, concentrated nitric acid (15N) at 130°C for one hour, before being evaporated and re-dissolved in a dilute solution of ultrapure nitric acid (0.5N). Calcium and strontium from samples was chemically purified following previously described protocols (Tacail et al., 2014; see also Supplementary File 3). The reliability of elutions has been controlled by also processing and analysing the standard material NIST-SRM1486 (mean $\delta^{44/42}\text{Ca}_{\text{ICP Ca Lyon}} = -1.03 \pm 0.04 \text{ ‰}$, 2 s.e.; Martin et al., 2015; Hassler et al., 2018, 2021a,b and references therein; Dodat et al., 2021; Martin et al., 2022; mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.709292 \pm 3.98 \cdot 10^{-5}$, 2 s.e.; Galler et al., 2007; De Muynck et al., 2009; Weber et al., 2017; Brazier et al., 2019; Guiserix et al., 2022). Calcium and radiogenic strontium isotope abundance ratio ($^{44}\text{Ca}/^{42}\text{Ca}$ and $^{87}\text{Sr}/^{86}\text{Sr}$) were measured using a Neptune Plus multi-collector ICP-MS (MC-ICP-MS) following previously described methods (Tacail et al., 2014, 2016). All calcium isotope compositions are expressed using the ‘ δ ’ notation defined as follows:

$$(1) \delta^{44/42}Ca = \left(\left(\frac{\left(\frac{^{44}Ca}{^{42}Ca} \right)_{sample}}{\left(\frac{^{44}Ca}{^{42}Ca} \right)_{ICP\ Ca\ Lyon}} \right) - 1 \right) * 1000$$

where $(^{44}Ca/^{42}Ca)_{sample}$ and $(^{44}Ca/^{42}Ca)_{ICP\ Ca\ Lyon}$ are the calcium isotope abundance ratios measured in sample and ICP Ca Lyon reference standard, respectively. The ICP Ca Lyon, which is used as a bracketing standard, is a Specpure calcium plasma standard solution (Alfa Aesar; Tacail et al., 2014, 2016, 2017; Martin et al., 2015, 2017a). To assess the accuracy of the strontium isotope abundance ratios, the standard NIST-SRM987 was monitored (mean $^{87}Sr/^{86}Sr = 0.710256 \pm 5.18.10^{-5}$; Clemens et al., 1993; McArthur et al., 2001; Faure & Mensing, 2005; Galler et al., 2007; De Muynck et al., 2009; Weber et al., 2017; Brazier et al., 2019; Guiserix et al., 2022).

2.2.4. Elemental concentrations

Concentrations of major and trace elements were measured respectively on an inductively coupled plasma atomic emission spectrometer (ICP-AES; ICAP 7400 Series, Thermo Scientific) and on an inductively coupled plasma mass spectrometer (ICP-MS, ICAP-Q, Thermo Scientific). The reliability of measurements has been controlled through a set of blanks and the reference material NIST SRM1400.

2.3. Thermophysiological inferences

The calculation of seabed body temperatures was performed as follows:

The apatite phosphate $\delta^{18}O_p$ value is linked to the mineralization temperature (here body temperature T_b) and the $\delta^{18}O$ value of the body water ($\delta^{18}O_{bw}$) by the following equation adapted from the phosphate-water temperature scale (Lécuyer et al., 2013):

$$(2) T_b = 117.4 - 4.5 * (\delta^{18}O_p - \delta^{18}O_{bw})$$

Furthermore, the $\delta^{18}O$ of body water is linked to the $\delta^{18}O$ of ambient water and an enrichment value as follows:

$$(3) \delta^{18}O_{bw} = \delta^{18}O_{aw} + E$$

where $\delta^{18}O_{aw}$: $\delta^{18}O$ of ambient water and E: enrichment value.

In semi-aquatic to aquatic crocodylians, the $\delta^{18}O$ measured in the phosphate is linked to the $\delta^{18}O$ of ambient water by the following equation (Amiot et al., 2007):

$$(4) \delta^{18}\text{O}_{\text{aw}} = 0.82 * \delta^{18}\text{O}_{\text{p}} - 19.13$$

In mammals, it is the following equation (Amiot et al., 2004):

$$(5) \delta^{18}\text{O}_{\text{aw}} = 1.11 * \delta^{18}\text{O}_{\text{p}} - 26.44$$

The enrichment of sebecid body water relative to ambient water would be ~ 2 ‰ if this taxon was semi-aquatic to aquatic (as in extant crocodylians; Amiot et al., 2007) or ~ 5.1 ‰ if this taxon was terrestrial (value for terrestrial tortoises; Barrick et al., 1999).

3. Results

3.1. Oxygen isotope compositions of apatite phosphate

The phosphate oxygen isotope compositions of all samples are reported in Supplementary File 4. Sebecid teeth have $\delta^{18}\text{O}_{\text{p}}$ values ranging from 20.1 to 21.5 ‰ (mean 2 s.d. = 0.3, n = 4), which are the highest values measured compared to dyrosaurids (17.5 to 20.4 ‰, mean 2 s.d. = 0.5, n = 4), fishes (15.0 to 20.0 ‰, mean 2 s.d. = 0.4, n = 3) and mammals (18.5 to 19.3 ‰, mean 2 s.d. = 0.3, n = 4; see also Fig. 1 & 2).

3.2. Oxygen and carbon isotope compositions of apatite carbonate

The isotopic compositions of all samples are reported in Supplementary File 4. Analysed samples have $\delta^{18}\text{O}_{\text{c}}$ values ranging from 22.4 to 29 ‰ (mean 2 s.d. = 0.5, n = 13) and $\delta^{13}\text{C}$ values ranging from -12.6 to -9.5 ‰ (mean 2 s.d. = 0.1, n = 13). Sebecid teeth have $\delta^{18}\text{O}_{\text{c}}$ values that are significantly higher than those of the other sampled organisms (Wilcoxon test, p-value = 0.01; Fig. 1) and mammal teeth have $\delta^{13}\text{C}$ values that are significantly lower than those of other sampled organisms (Wilcoxon test, p-value = 0.02; Fig. 3).

3.3. Calcium isotope compositions of vertebrate apatite

Blanks realized during purification protocols have been analysed with the MC-ICP-MS. All blanks contained less than 120 ng of calcium. Thus, considering our measurement precision, our isotopic measurements are not affected by this nano-pollution. The mass dependency curve of the isotopic measurements follows the expected relation for calcium (Fig. 4): the slope value is 0.504 ± 0.020 (2 s.e., n = 36), which agrees with the 0.5067 slope predicted by the linear approximation of exponential mass-dependent fractionation and is in line with previously published values (Tacail et al., 2014, 2016, 2017; Martin et al., 2015, 2017a, b, 2022; Hassler et al., 2018, 2021a, b), supporting the accuracy of the measurements. The composition of all samples is reported in Supplementary File 4. The standard NIST-SRM1486

has a $\delta^{44/42}\text{Ca}$ mean value of $-0.98 \pm 0.05 \text{ ‰}$ (2s.e., $n = 26$), which is also in line with previously published values (see Material & Methods). The $\delta^{44/42}\text{Ca}$ values of the vertebrates sampled from Tiupampa range from -1.32 to -0.35 ‰ (mean 2 s.d. = 0.10 ‰ , $n = 31$; Fig. 3). Mammals teeth have the highest values (mean value = $-0.51 \pm 0.24 \text{ ‰}$, 2 s.d., $n = 9$) and differ significantly from the other organisms (Wilcoxon test, $p\text{-value} = 5.64 \cdot 10^{-5}$) whereas sebecid teeth display the lower values (mean value = $-1.24 \pm 0.15 \text{ ‰}$, 2 s.e., $n = 8$) and also differ significantly from the other organisms (Wilcoxon test, $p\text{-value} = 3.58 \cdot 10^{-5}$).

3.4. Strontium isotope compositions of vertebrate apatite

The composition of all samples is reported in Supplementary File 4. The standard NIST-SRM1486 has a mean $^{87}\text{Sr}/^{86}\text{Sr}$ value of $0.709225 \pm 3.73 \cdot 10^{-4}$ (2 s.e., $n = 1$), and the standard NIST-SRM987 has a mean $^{87}\text{Sr}/^{86}\text{Sr}$ value of $0.710201 \pm 2.63 \cdot 10^{-4}$ (2 s.e., $n = 37$) which in line with previously published values (see Material & Methods). The $^{87}\text{Sr}/^{86}\text{Sr}$ values of the different organisms sampled range from 0.715554 to 0.717602 (mean 2 s.d. = $5.12 \cdot 10^{-4}$, $n = 29$), and none of the groups of sampled organisms statistically differ from one another (Fig. 2).

3.5. Elemental concentrations

The full dataset compiling all the elemental and rare earth element concentrations measured in this study is reported in Supplementary File 4 and Figure 4 & 5. An important result is that the mean ratio of calcium versus phosphorus is 2.12 ± 0.20 2 s.d., $n = 17$ (molar ratio = 1.64 ± 0.14 2 s.d., $n = 17$), suggesting that the stoichiometry of bioapatite is preserved.

4. Discussion

4.1. Assessing the impact of diagenesis on the isotope compositions

First, we assess the state of isotopic preservation of the fossil samples studied as a prerequisite to interpret isotopic data in terms of palaeocological inferences. Although biotic and abiotic processes during taphonomy always have an impact on the measured compositions of fossil samples (secondary precipitation, ion adsorption, dissolution-recrystallization; Kolodny et al., 1996; Blake et al., 1997; Lécuyer et al., 2003; Trueman et al., 2003; Zazzo et al., 2004a, b), there are several ways to assess their impact on the original preservation of the isotope compositions of the sample.

In the skeletal tissues of vertebrates, carbonate and phosphate precipitate in equilibrium with body water, such that $\delta^{18}\text{O}_p$ and $\delta^{18}\text{O}_c$ values are correlated. As exchanges rates between

phosphate-water and carbonate-water are different, re-equilibration (and thus diagenetic alteration) of both systems is unexpected and altered samples should show an isotopic shift from the expected correlation in at least one of the two complexes. On the other hand, minimally altered samples should have $\delta^{18}\text{O}_p$ and $\delta^{18}\text{O}_c$ values that are correlated and display a slope close to unity, as established in other studies (Bryant et al., 1996; Iacumin et al., 1996; Zazzo et al., 2004b; Lécuyer et al., 2010; Chenery et al., 2012). Here, the correlation between the $\delta^{18}\text{O}_p$ and $\delta^{18}\text{O}_c$ values is significant ($R^2 = 0.73$, $p\text{-value} = 4.79 \cdot 10^{-3}$; Fig. 1) so the isotope compositions measured are preserved to a certain degree. One sample (GA1, fish scale enamel) greatly diverges from the theoretical slope. As it may have undergone some diagenetic processes modifying its oxygen and carbon isotope compositions, it will not be considered in those interpretations.

Furthermore, using the elemental concentrations measured on each sample (Supplementary File 4), we obtain a calcium/phosphorus ratio of 2.17 ± 0.20 (2 s.d., $n = 17$) which is in line with those measured in modern animals (2.15 ± 0.06 , 2 s.d.; Balter et al., 2001) and other studies on fossil dinosaurs (2.3 ± 0.2 , 2 s.d.; Haskin et al., 2018; 2.3 ± 0.12 , 2 s.d.; Martin et al., 2022), bringing a further argument supporting the preservation of the fossils sampled here. Rare earth elements content (REE) can also indicate the state of preservation of our samples: as those elements are almost absent from a living organism, they can only be incorporated in reasonable quantity after its death, making it a marker of early or late diagenetic conditions as well as burial conditions (Reynard et al., 1999; Kocsis et al., 2009; Hinz & Kohn, 2010; Suarez & Kohn, 2020). Among fossils from Tiupampa, REE enrichment profiles (normalized to NASC, Haskin & Frey, 1955 and Gromet et al., 1984; Fig. 5A) are similar for each sample, meaning that those fossils can be considered as autochthonous (Trueman, 2013). Furthermore, none of those patterns are bell-shaped, indicating that the recrystallization processes were limited (Reynard et al., 1999; Lécuyer et al., 2004; Reynard & Balter, 2014). Strontium concentrations are not correlated with lead, uranium, iron, manganese, or the sum of REE (Fig. 5B-F), meaning that this element was not preferentially incorporated after the death of the organisms: the radiogenic strontium isotope compositions can thus be considered as reflecting those of the substrates or waters where the organisms lived. Finally, lanthanum/ytterbium (La/Yb) and lanthanum/samarium (La/Sm) ratios for all samples fall within the range of modern freshwater samples (Fig. 6), indicating a moderate intensity of adsorption and substitutions processes (Reynard et al., 1999; Reynard & Balter, 2014).

Finally, the fact that we have mainly sampled enamel rather than dentine (whenever possible), hints to isotopic compositions less subject to diagenesis, because this tissue is highly mineralized and exhibit a lower porosity than dentine or bone (Wang & Cerling, 1994; Heuser et al., 2011; Martin et al., 2017a, b; Dodat et al., 2023). Furthermore, in the four isotopic systems studied here, there is no clear differences between enamel samples and enamel + dentine samples in the different group of organisms, bringing further evidence to the low impact of diagenetic processes on the primary preservation of stable isotope compositions. Given the high quantity of calcium in vertebrates samples (at least 15% of mass here, see Supplementary File 4), it is unlikely that the measured calcium isotopic compositions have been entirely overprinted by diagenetic processes, even if those were important. Also, leached and non-leached samples display the same values in calcium and radiogenic strontium isotope compositions (Wilcoxon test, p -value = 0.57, $n = 14$ and p -value = 0.98, $n = 13$ respectively), which is another argument for the weak impact of diagenesis on our samples.

In summary, there is no evidence for important diagenetic alteration of the elemental compositions of the samples analysed here, in all the different isotopic systems used. As a result, associated isotope compositions reported here are interpreted in terms of palaeotrophic networks, palaeoenvironments and thermophysiological abilities.

4.2. Palaeobiological inferences

4.2.1. Thermophysiology

Using equations (2) to (5), Faure-Brac et al. (2022) calculated that mammals have ingested ambient waters having an average $\delta^{18}\text{O}_{\text{aw}}$ value of $-5.4 \pm 0.9 \text{ ‰}$ (2 s.e.). In the present study, we add that dyrosaurids have ingested an ambient water having a $\delta^{18}\text{O}_{\text{aw}}$ value of $-3.5 \pm 2.2 \text{ ‰}$ (2 s.e., $n = 4$), which is in line with the other source of drinking water previously identified in Faure-Brac et al. (2022) (turtle sample: -2.1 ‰). As a result, it is a reasonable assumption that sebecids either consumed the same drinking water as dyrosaurids (and turtles and fishes) or as mammals, and that they either have a semi-aquatic (with an enrichment value of around 2 ‰) or terrestrial lifestyle (with an enrichment value of around 5.1 ‰). Those hypotheses are summarized in Figure 7. In the first case (Fig. 7A; semi-aquatic lifestyle), we obtain a mean body temperature ranging from 5 to 12°C with the $\delta^{18}\text{O}_{\text{aw}}$ value of mammals (Fig. 7A, green dot; mean value = $8 \pm 6^\circ\text{C}$, 2 s.e., $n = 4$), or a mean body temperature ranging from 14 to 20°C with the $\delta^{18}\text{O}_{\text{aw}}$ value of dyrosaurids (Fig. 7A, red dot; mean value = $16 \pm 6^\circ\text{C}$, 2 s.e., $n = 4$). Those values are both too low to be realistic. In the second case (Fig. 7B; terrestrial

lifestyle), we obtain a mean body temperature ranging from 19 to 26°C with the $\delta^{18}\text{O}_{\text{aw}}$ value of mammals (Fig. 7B, green dot; mean value = $22 \pm 6^\circ\text{C}$, 2 s.e., $n = 4$) or a mean body temperature ranging from 28 to 34°C with the $\delta^{18}\text{O}_{\text{aw}}$ value of dyrosaurids (Fig. 7B, red dot; mean value = $30 \pm 6^\circ\text{C}$, 2 s.e., $n = 4$), which is in both cases much more realistic and implies an ectothermic thermoregulation strategy for the sebecids. Although, the source of drinking water for sebecids cannot be directly identified so far, we confirm here the interpretations obtained from an independent histological approach performed on notosuchians (Cubo et al., 2020, 2022), which also estimated ectothermic thermoregulation strategies in representatives of this clade.

4.2.2. Lifestyle

The oxygen isotope composition of the samples studied here is mainly controlled by the body temperature and the drinking water. As we have assessed that the sebecids from Tiupampa were most probably ectotherms, which would put them in the same temperature range as the dyrosaurids sampled (25-38°C; Faure-Brac et al., 2022), the almost significant difference between the $\delta^{18}\text{O}_p$ of these two groups (mean $\delta^{18}\text{O}_p$ for dyrosaurids: $19 \pm 2.7\text{‰}$, 2 s.d., $n = 4$; mean $\delta^{18}\text{O}_p$ for sebecids: $20.9 \pm 1.3\text{‰}$, 2 s.d., $n = 4$; p-value = 0.06 under a Wilcoxon test) could be interpreted as a difference in lifestyle, especially if those two groups had the same drinking water, i.e. $\delta^{18}\text{O}_{\text{aw}}$ value of -2.5‰ . Indeed, the difference between these two groups is due to higher water turnover and lower transcutaneous water evaporation in aquatic forms compared to terrestrial ones, which in turn translates to lower $\delta^{18}\text{O}_p$ values for aquatic forms compared to terrestrial ones with an equivalent body temperature. Furthermore, those differences are similar to those observed in Mesozoic and modern ecosystems (Cerling et al., 2008; Amiot et al., 2019). Unfortunately, this hypothesis cannot be confirmed by another independent proxy: strontium isotope compositions could have highlighted different substrates between the two groups, however the $^{87}\text{Sr}/^{86}\text{Sr}$ values are not significantly different from one another. Nonetheless, the strontium isotope compositions bring an interesting information about the global environment of Tiupampa: the $^{87}\text{Sr}/^{86}\text{Sr}$ value of seawater just after the end of the Cretaceous was $0.7079 \pm 4.83 \cdot 10^{-5}$ (2 s.e., $n = 10$; Martin & Macdougall, 1991), which is much less than the values obtained for the Tiupampa fauna. Thus, as highlighted in Faure-Brac et al. (2022), Tiupampa can be considered as a strictly continental deposit and the dyrosaurids sampled here were not marine: they either belong to a yet unknown species or they represent marine individuals that had been living in the fluvial system for at least a dental generation. The freshwater origin for the Tiupampa sediments was

previously suggested (Gayet et al., 1993; Muizon et al., 2015; Jouve et al., 2021) based on the sedimentology and fauna. The present work provides new arguments in this way, as well as evidence of a freshwater lifestyle for the dyrosaurids of Tiupampa.

4.2.3. Diet

Sebecids show depleted Ca isotope compositions in contrast to dyrosaurids and fish and especially mammals which have the highest $\delta^{44/42}\text{Ca}$ values (Fig. 3). This is in line with the fractionation that occurs within the body resulting in tissues being depleted in ^{44}Ca compared with the food source (Skulan & DePaolo, 1999; Chu et al., 2006; Tacail et al., 2014), indicating that sebecids were at the top of the food chain in this environment. The trophic pyramid would thus have been supported both by fishes and mammals, these last ones probably being herbivores given both their high $\delta^{44/42}\text{Ca}$ and $\delta^{13}\text{C}$ values. Those two groups would have thus represented two potential primary sources of calcium for predators. Considering a carnivore-herbivore offset of 0.3 to 0.5 ‰ as reported in other studies (Martin et al., 2018, 2022; Tacail et al., 2020), dyrosaurids ($\delta^{44/42}\text{Ca}$ values ranging from -0.68 to -1.06 ‰, mean 2 s.d. = 0.08, n = 8) would have preferentially fed on fishes ($\delta^{44/42}\text{Ca}$ values ranging from -0.64 to -0.96 ‰, mean 2 s.d. = 0.09, n = 6) or mammals ($\delta^{44/42}\text{Ca}$ values ranging from -0.35 to -0.75 ‰, mean 2 s.d. = 0.11, n = 9). However, given their long rostrum with sharp teeth, they were more likely adapted for piscivory (Jouve et al., 2021). However, data obtained on sebecids are more difficult to interpret: applying a 0.3 to 0.5 ‰ offset corresponds to the values obtained for the dyrosaurids and fishes, however this does not necessarily fit with a terrestrial lifestyle, as inferred from other independent proxies (Pol et al., 2012; Pochat-Cottilloux et al., 2022). Thus, either sebecids did feed on dyrosaurids and fishes, possibly making them more semi-aquatic than previously thought and contradicting our results on oxygen isotope composition, or there is another explanation for the observed distribution of $\delta^{44/42}\text{Ca}$ values. First, $\delta^{44/42}\text{Ca}$ values of prey mammals (-0.51 ± 0.24 , 2 s.e., n = 9) could be modified by lactation and/or gestation processes with an offset of up to -0.3 ‰ (Hassler et al., 2021b), which would in turn make them suitable preys for sebecids. Though this is only applicable to female individuals, this could fit with the mortality profile observed in Tiupampa, which may indicate a breeding ground (Muizon et al., 2022) and be in line with a 0 to 2 ‰ trophic enrichment when looking at $\delta^{13}\text{C}$ values between sebecids and mammals (Bocherens & Drucker, 2003). Second, the preferred prey of sebecids could simply not have been sampled during our study, among the diverse fauna of the Tiupampa locality. Third, sebecids being at the top of the trophic network, could have possibly ingested a significant

amount of bone material (Baquedano et al., 2012), modifying the measured calcium isotope compositions (Dodat et al., 2021). Interestingly, we notice an offset of ~ 0.1 ‰ between the $\delta^{44/42}\text{Ca}$ values of dyrosaurid samples composed exclusively of enamel (D1 & D3) and those composed of enamel and dentine (D2 & D4). This would seem to confirm the observation by Heuser et al. (2011) of an offset of ~ 0.14 - 0.18 ‰ in $\delta^{44/42}\text{Ca}$ values between reptile samples made out exclusively of enamel and those made out exclusively of dentine. However, this trend is not retrieved in the sebecid samples (S1, S3 & S4 vs S2 respectively), so the mechanisms at play here might be more complex.

Sebecids and dyrosaurids display respectively mean $\delta^{13}\text{C}$ values of -11.3 ± 1.8 ‰ (2 s.e., $n = 4$) and -12.5 ± 0.4 ‰ (2 s.e., $n = 2$), which, using an isotope fractionation of 9 ‰ between crocodile apatite and diet (Lee-Thorp et al., 1989; Tieszen & Fagre, 1993; Stanton, 2006), indicate a diet with a $\delta^{13}\text{C}$ value of -20.7 ± 1.8 ‰ (2 s.e., $n = 6$). Furthermore, using the data from Passey et al. (2005), we estimate a $\delta^{13}\text{C}$ apatite-diet offset of 12.3 ± 4.2 ‰ (2 s.e.) in mammals. Mammal samples thus display a $\delta^{13}\text{C}$ diet value of -22 ± 0.5 ‰ (2 s.e., $n = 4$). We then must estimate the $\delta^{13}\text{C}$ value of atmospheric CO_2 in the early Paleocene, as it has a direct effect on the stable carbon isotope composition of plants (Fricke, 2007). Through carbon and oxygen isotope compositions of benthic foraminifera in the literature (Cramer et al., 2009), we estimate the $\delta^{13}\text{C}_{\text{CO}_2}$ during the Early Paleocene at -5.7 ± 0.8 ‰ (2 s.e., $n = 83$; see also Supplementary File 5, equation 3 to 7) in contrast with modern $\delta^{13}\text{C}_{\text{CO}_2}$ of -7 ‰ (Gröcke, 2002). Thus, C_3 plants $\delta^{13}\text{C}$ range during this period should shift towards values 1.3 ‰ higher, i.e., -35.7 to -18.7 ‰ (Oleary, 1988; Kohn, 2010). The values calculated here for the Tiupampa fauna correspond, although they belong to the higher part of the $\delta^{13}\text{C}$ range of plants, which would indicate an arid environment, as assessed in the Bauru Group (Upper Cretaceous of Brazil; Klock et al., 2022). The $\delta^{13}\text{C}$ values measured in Tiupampa vertebrates cluster in two groups: one with $\delta^{13}\text{C}$ values lower than -11.0 ‰ and one with $\delta^{13}\text{C}$ values higher than -10.5 ‰ (Fig. 3). Although this difference is significant (p -value = 0.005 under a Wilcoxon test), it is difficult to interpret as both clusters include samples belonging to the same taxonomic group (fishes and sebecids). More analyses would be needed to assess the potential ecological consequences of this clustering. Finally, it is interesting to observe that the $\delta^{44/42}\text{Ca}$ and $\delta^{13}\text{C}$ values of sebecids and dyrosaurids do not overlap (Fig. 3). This could either be due to a different source of alimentation (as hypothesized above) or a different digestive physiology leading to a different apatite-diet ^{13}C enrichment.

4.3 Palaeoenvironmental reconstruction

$\delta^{18}\text{O}_{\text{aw}}$ values calculated from $\delta^{18}\text{O}_{\text{p}}$ values measured from different group of organisms using equations (4) and (5) range from -2.4 to -5.8 ‰ (mean value: -4.4 ± 2.5 ‰, 2 s.e., $n = 8$), which corresponds to continental surface water values measured today at tropical to equatorial latitudes (IAEA/WMO, 2022). As fish body water is not fractionated from the ambient water, their body temperature reflects the water temperature of their living environment. Using equation (2) and the $\delta^{18}\text{O}_{\text{aw}}$ values calculated from turtles and crocodilians, those temperatures range from 12 to 22°C (mean value: 17 ± 10 °C, 2 s.d., $n = 2$), which would be expected of a freshwater tropical environment and further indicates that those fish were also autochthonous. The measured $\delta^{18}\text{O}_{\text{p}}$ values in Tiupampa fauna are high and comparable to those measured in the terrestrial ecosystems of the Songliao basin (mean $\delta^{18}\text{O} = 22.20 \pm 1.65$ ‰, 2 s.d., $n = 57$; Huang et al., 2013; Gao et al., 2015; Zhang et al., 2018) and Nanxiong basin (mean $\delta^{18}\text{O} = 24.53 \pm 1.92$ ‰, 2 s.d., $n = 6$; Yin et al., 2023, but not as high as those measured in desertic environments (Lécuyer et al., 1999; Schoeninger et al., 2000), therefore being more in line with a dry environment. The $\delta^{18}\text{O}_{\text{p}}$ values are also in accordance with climatic conditions measured nowadays in Palaeo or South China, with a mean annual temperature around 20°C and a mean precipitation of a few hundred millimeters per year (IAEA, 2022). Finally, this is also confirmed when looking at $\delta^{13}\text{C}$ values measured here: those correspond to C_3 plants with mean $\delta^{13}\text{C}$ values ranging from -20.7 to -22 ‰. These values indicate dry ecosystems today with annual precipitation of less than 200 mm/year (Kohn, 2010, see also Supplementary File 5). It would thus appear from two independent elements that the specimens sampled here were living in a dry environment, albeit with the presence of freshwater, contrary to what was hypothesized in other studies (Woodburne et al., 2014 and references therein). This is further confirmed by large scale studies that infer a global warming at the beginning of the Paleogene (Sewall & Sloan, 2001; Sewall, 2004; Quillévéré et al., 2008; Gilabert et al., 2022), and some regional scale studies in China (Gao et al., 2021) or France (Cojan & Moreau, 2006). However, there are also differing results when looking at other parts of the world (Krassilov, 1975; Adatte et al., 2002; Hao et al., 2010). In any case, those interpretations must thus be taken with caution as the data we use here is merely a local snapshot rather than a long-term interpretation.

5. Conclusions

Using a multi-isotopic proxy approach, we highlight several ecological traits of the sebecids from Tiupampa, as well as a palaeoenvironmental reconstruction of this locality. After assessing the impact of diagenesis on our samples from numerous methods, we reconstruct a

local dry environment with tropical temperatures for the specimens sampled here, inferred both from oxygen and carbon isotope compositions.

The calcium and carbon isotope compositions of vertebrate apatite indicate that the sebecids were at the top of the C₃-based food web, although their main source of alimentation remains elusive. The dominance of those terrestrial organisms in post-Cretaceous ecosystems is here ascertained, probably as a result of the disappearance of competitors, such as dinosaurs. Using the oxygen isotope compositions of apatite phosphate, their inferred body temperature is consistent to those of extant ectotherms, such as crocodylians, as were also the dyrosaurids living in the same locality. We thus imply that the difference measured in $\delta^{18}\text{O}_p$ values between the two groups most probably reflects a difference in lifestyle, with aquatic dyrosaurids and terrestrial sebecids.

Those results would be especially interesting to compare to future multi-isotopic studies with a focus on similar communities living before the K/Pg crisis, as has already been done on dinosaurs using calcium isotope compositions (Martin et al., 2022) and to a lesser extent on other notosuchians using carbon and oxygen isotope compositions (Klock et al., 2022). Finally, the study of the strontium isotope compositions allows to clearly discard the marine influence from the environment sampled in this study, which is especially interesting due to the presence of dyrosaurids in the sampled organisms, which have until now mainly been inferred as a marine group.

Acknowledgments

This work was supported by the Agence Nationale de la Recherche (SEBEK project no. ANR-19-CE31-0006-01 to Jeremy E. Martin). The authors would like to thank Auguste Hassler (University of Aberdeen and University of Ottawa) for discussion about calcium isotopes; Pierre-Jean Dodat, Samuel Le Goff, Florent Arnaud-Godet and Philippe Telouk (ENS Lyon) for technical expertise on the spectrometers; Erika Schumacher and Julián Bayona for helping us to illustrate our study by having transferred their work to the public domain or under a creative commons licence.

Authors contributions

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Data availability statement

All data used for this study are made available in the supplementary files.

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Figure captions

Figure 1: Oxygen isotope compositions of apatite phosphate reported against their corresponding oxygen isotope compositions of apatite carbonate. 2 s.d. for each sample are represented by bars. Black circles correspond to sebecids, blue squares to mammals, green triangles to fishes and red diamonds to dyrosaurids. Dashed line as a theoretical slope of 1. The shapes of the organisms are from phylopic.org.

Figure 2: Oxygen isotope compositions of apatite phosphate reported against their corresponding strontium isotope compositions of vertebrate apatite. 2 s. d. for each sample are represented by bars. Black circles correspond to sebecids, blue squares to mammals, green triangles to fishes and red diamonds to dyrosaurids. Filled shapes and plain bars are leached samples, whereas empty shapes and dotted bars are unleached samples. The shapes of the organisms are from phylopic.org.

Figure 3: Calcium isotope compositions of vertebrate apatite reported against their corresponding carbon isotope compositions of apatite carbonate. 2 s. d. for each sample are represented by bars. Black circles correspond to sebecids, blue squares to mammals, green triangles to fishes and red diamonds to dyrosaurids. Filled shapes and plain bars are leached samples, whereas empty shapes and dotted bars are unleached samples. The shapes of the organisms are from phylopic.org.

Figure 4: $\delta^{43/42}\text{Ca}$ values plotted against $\delta^{44/42}\text{Ca}$ values for all samples (black circles) and standards (white circles) studied.

Figure 5: Diverse graphs highlighting the negligible impact of diagenesis on the samples. A: NASC normalized REE profiles of each sample from Tiupampa. Concentrations are plotted on a logarithmic scale. Black: sebecids, blue: mammals, green: fishes, red: dyrosaurids. Strontium concentration plotted against lead (B), uranium (C), iron (D), manganese (E) and sum of REE (F) concentrations. Black circles: sebecids, blue squares: mammals, green triangles: fishes, red diamonds: dyrosaurids.

Figure 6: La/Sm_N plotted against La/Yb_N values (normalized to NASC; Haskin & Frey, 1966; Gromet et al., 1984) for multiple fossil and extant apatite samples, as well as modern waters (Reynard & Balter, 2014, and references therein). Squares: conodonts, crosses: fishes, triangles: waters, circles: fossil faunas. Brown: Devonian, light green: Silurian, blue: Mesozoic-Cenozoic, yellow: Quarternary, dark purple: freshwaters, purple: estuarine and coastal waters, pink: ocean waters, red: Gadoufaoua fauna (Niger, middle Cretaceous; Hassler et al., 2018), beige: Kem Kem fauna (Morocco, middle Cretaceous; Hassler et al., 2018), grey: dinosaur communities (USA, late Cretaceous; Martin et al., 2022), black: Tiupampa.

Figure 7: Sebecids' oxygen isotope compositions of apatite phosphate are plotted against their possible ambient water values ($\delta^{18}\text{O}_{aw}$) within a frame showing expected vertebrates $\delta^{18}\text{O}_p - \delta^{18}\text{O}_{aw}$ relationships for a range of body temperatures (black lines). The blue area represents the expected body temperatures range for ectotherm modern crocodylians, whereas the red area represents the expected body temperatures range for modern endotherms. Green dots: considering the $\delta^{18}\text{O}_{aw}$ value of mammals; red dots: considering the $\delta^{18}\text{O}_{aw}$ value of dyrosaurids. A: considering a semi-aquatic lifestyle, i.e., an enrichment value of 2 ‰, B: considering a terrestrial lifestyle, i.e., an enrichment value of 5.1 ‰.

Supplementary Files

Supplementary File 1: Samples used in this study.

Supplementary File 2: Geographical and stratigraphical situation of Tiupampa. Red dot is the locality of Tiupampa. Maps is from Google Maps (2023) and Jouve et al., (2021; fig. 1), scale bar is 10 km. Stratigraphic scale is modified from Jouve et al., 2021; fig. 2).

Supplementary File 3: Detailed protocols and analytical techniques.

Supplementary File 4: Detailed values obtained for all samples in the different isotopic systems, as well as elemental and rare earth concentrations recorded.

Supplementary File 5: Estimation of mean annual precipitation (MAP)

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Highlights

- Palaeoecological traits of a sebecid from Tiupampa (Paleocene, Bolivia) are inferred.
- Oxygen isotope compositions indicate terrestriality and ectothermy.
- Strontium isotope compositions indicate continentality.
- Calcium and carbon isotope compositions indicate a predator diet on a C₃-based food web.
- Diagenesis effects are deemed negligible.

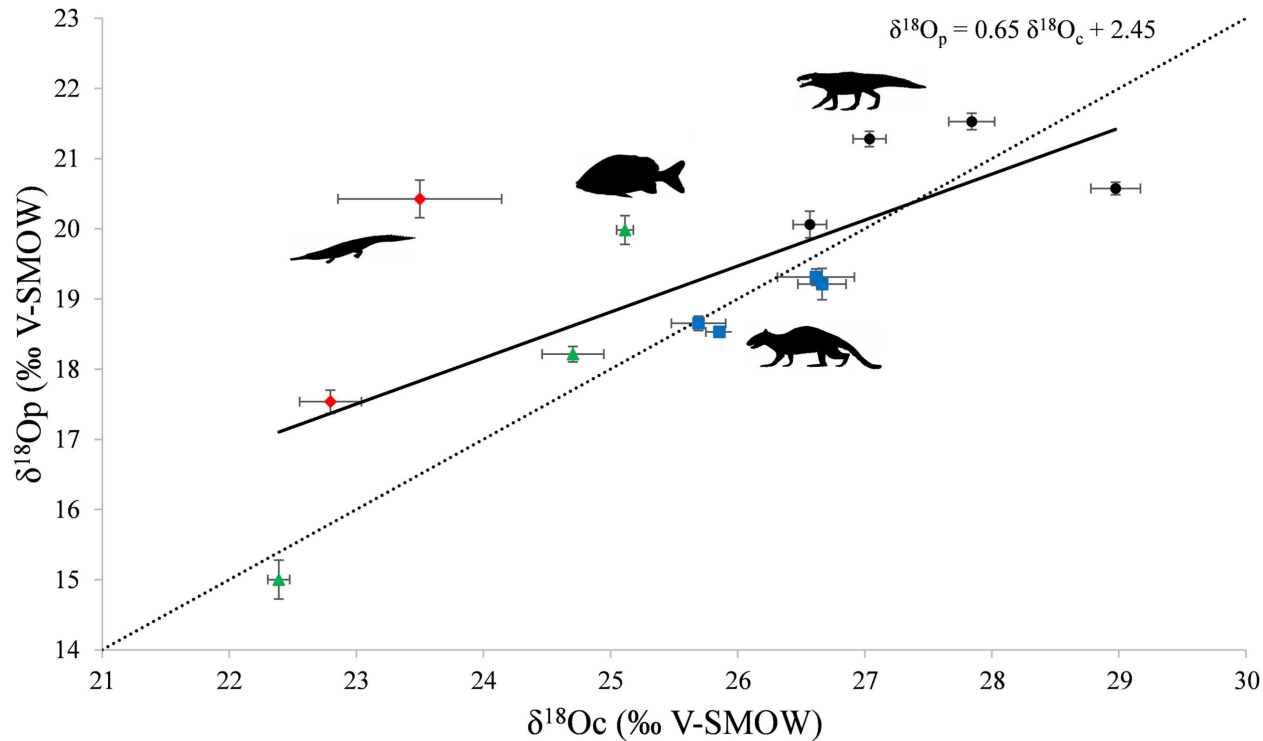


Figure 1

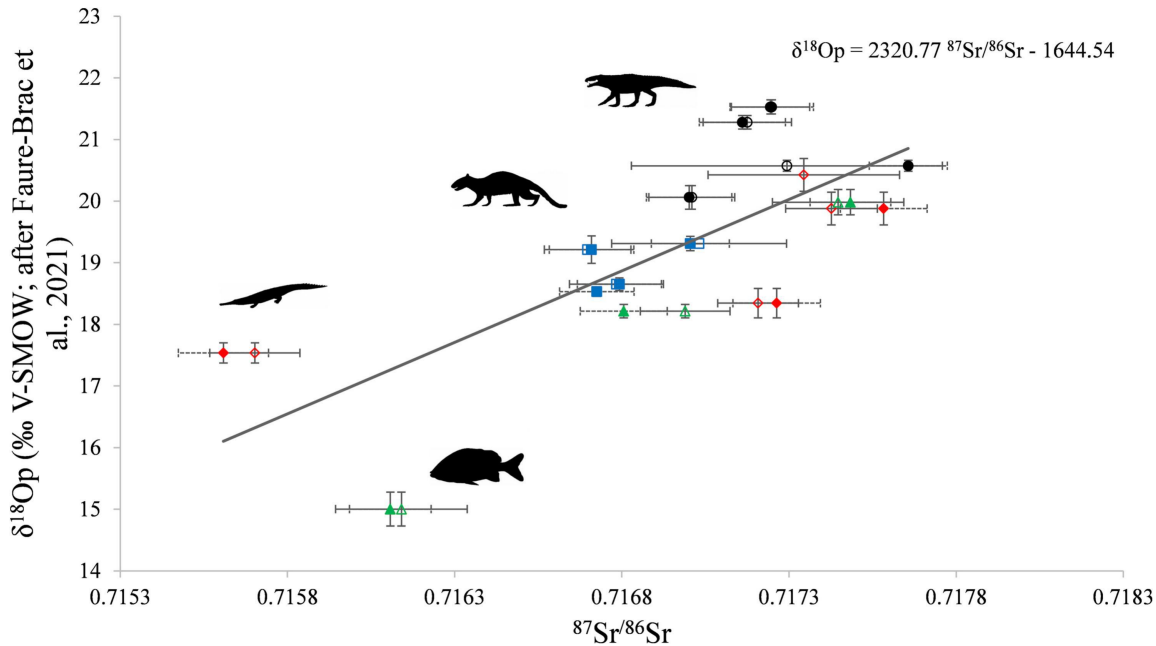


Figure 2

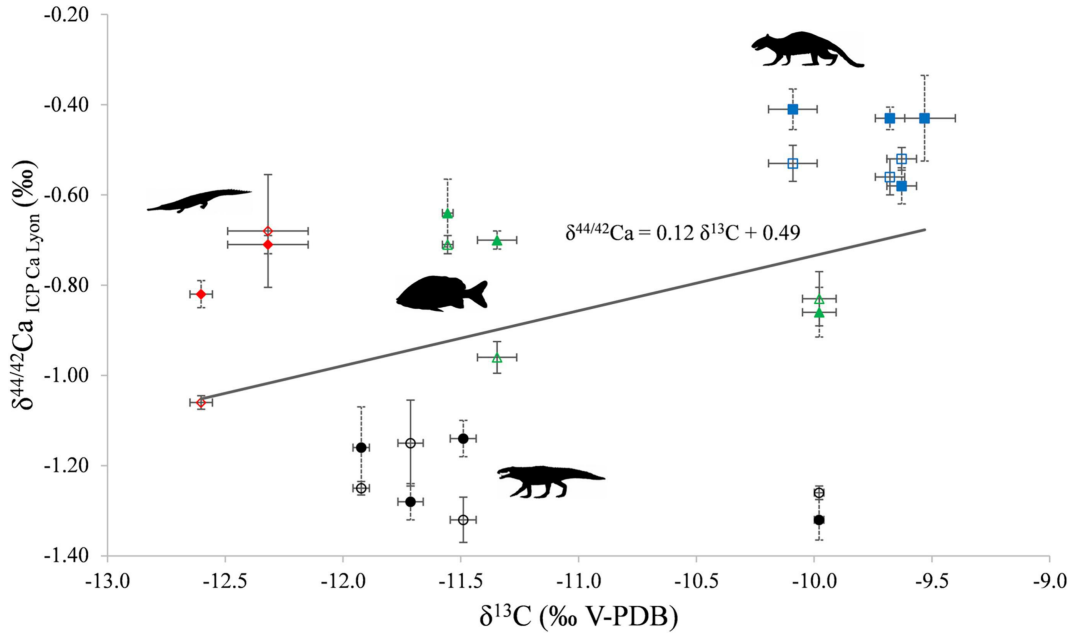


Figure 3

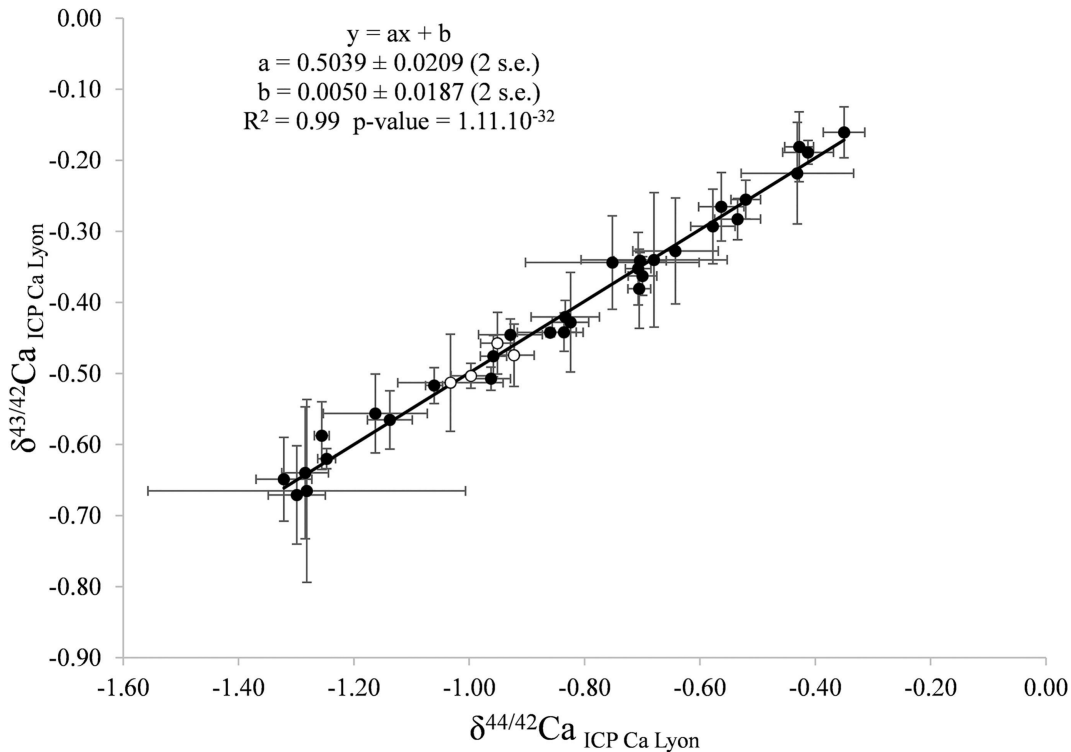


Figure 4

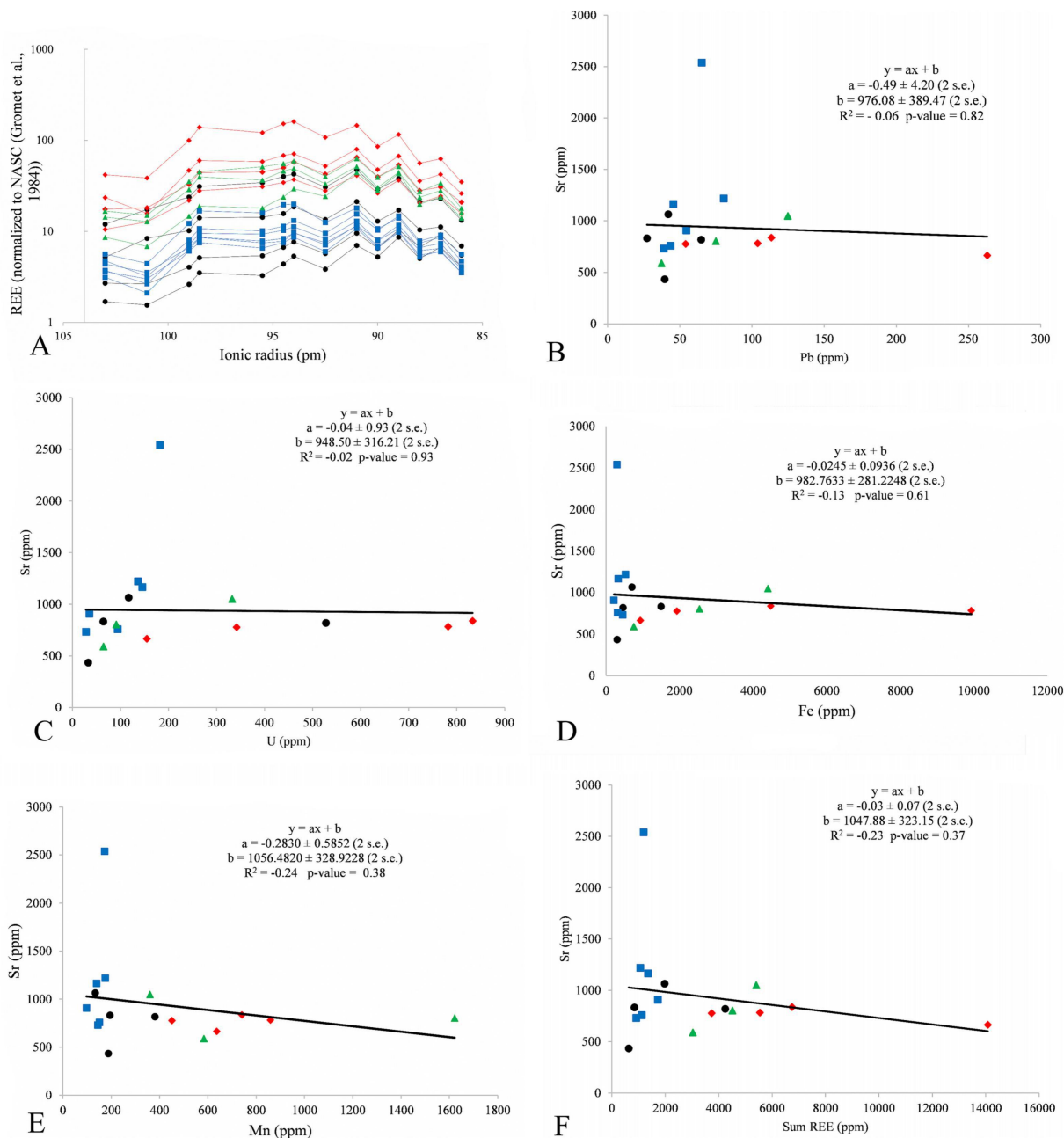


Figure 5

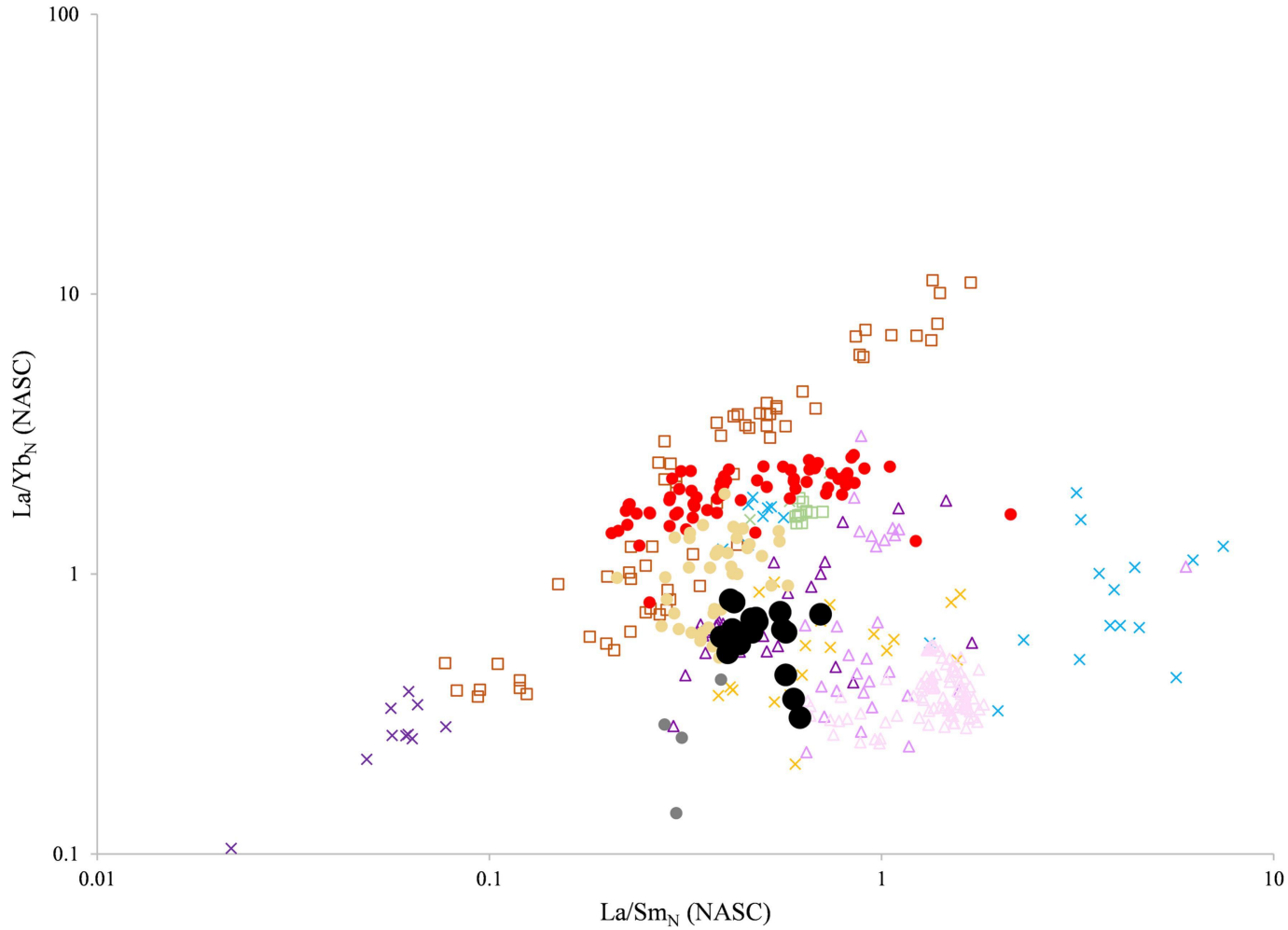


Figure 6

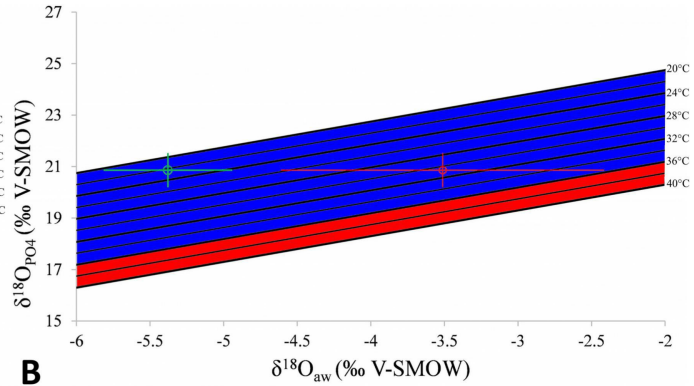
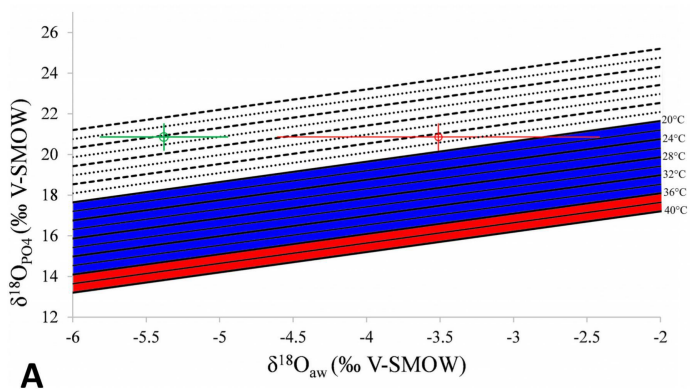


Figure 7