Seasonality and Paleoecology of the Late Cretaceous Multi-Taxa Vertebrate Assemblage of “Lo Hueco” (Central Eastern Spain)

Laura Domingo1,2,3*, Fernando Barroso-Barcenilla2,4, Oscar Cambra-Moo5

1 Departamento de Geología Sedimentaria y Cambio Medioambiental, Instituto de Geociencias IGEO-CSIC-UCM, Madrid, Spain, 2 Departamento de Paleontología, Universidad Complutense de Madrid, Madrid, Spain, 3 Earth and Planetary Sciences Department, University of California Santa Cruz, Santa Cruz, California, United States of America, 4 Grupo de Investigación IberCreta, Departamento de Geología y Geografía, Universidad de Alcalá de Henares, Alcalá de Henares, Spain, 5 Laboratorio de Poblaciones del Pasado, Departamento de Biología, Facultad de Ciencias, Universidad Autónoma de Madrid, Madrid, Spain

* laudomingo@gmail.com

Abstract

Isotopic studies of multi-taxa terrestrial vertebrate assemblages allow determination of palaeoclimatic and palaeoecological aspects on account of the different information supplied by each taxon. The late Campanian-early Maastrichtian “Lo Hueco” Fossil-Lagerstätte (central eastern Spain), located at a subtropical paleolatitude of ~31°N, constitutes an ideal setting to carry out this task due to its abundant and diverse vertebrate assemblage. Local δ18OPO4 values estimated from δ18OPO4 values of theropods, sauropods, crocodyliforms, and turtles are close to δ18OH2O values observed at modern subtropical latitudes. Theropod δ18OH2O values are lower than those shown by crocodyliforms and turtles, indicating that terrestrial endothermic taxa record δ18OH2O values throughout the year, whereas semiaquatic ectothermic taxa δ18OH2O values represent local meteoric waters over a shorter time period when conditions are favorable for bioapatite synthesis (warm season). Temperatures calculated by combining theropod, crocodyliform, and turtle δ18OPO4 values and gar δ18OPO4 have enabled us to estimate seasonal variability as the difference between mean annual temperature (MAT, yielded by theropods) and temperature of the warmest months (TWMs, provided by crocodyliforms and turtles). ΔTWMs-MAT value does not point to a significantly different seasonal thermal variability when compared to modern coastal subtropical meteorological stations and Late Cretaceous rudists from eastern Tethys. Bioapatite and bulk organic matter δ13C values point to a C3 environment in the “Lo Hueco” area. The estimated fractionation between sauropod enamel and diet is ~15‰. While waiting for paleoecological information yielded by the ongoing morphological study of the “Lo Hueco” crocodyliforms, δ13C and δ18OδCO3 results point to incorporation of food items with brackish influence, but preferential ingestion of freshwater. “Lo Hueco” turtles showed the lowest δ13C and
δ¹⁸O values of the vertebrate assemblage, likely indicating a diet based on a mixture of aquatic and terrestrial C₃ vegetation and/or invertebrates and ingestion of freshwater.

Introduction

The Mid-Cretaceous thermal maximum, which peaked in Turonian times and constituted the warmest climate warming of the last 144 Ma [1–2] was followed by a long-term cooling trend beginning at the early Campanian and detected in both the terrestrial and marine realms [3–8]. This trend was characterized by alternating cooling and warming episodes across the Campanian and Maastrichtian [9–11]. In spite of this cooling pattern, overall warmer conditions than today persisted until the end of the Cretaceous, as suggested by high atmospheric CO₂ concentrations and a lack of permanent ice at the poles [11–14]. During this time, enhanced ocean heat transport along with the maintenance of a low albedo at high latitudes, due to the presence of forests, contributed to a reduced latitudinal thermal gradient [15].

Although stable isotope studies on Cretaceous terrestrial vertebrate taxa can help to better understand continental climatic and environmental conditions, they are not as common as those performed on Cenozoic vertebrate taxa due to the scarcity of adequate sample sizes of fossil material, the destructive nature of the stable isotope technique, as well as pervasive diagenetic effects observed in fossils of this age. Some stable isotope studies on Cretaceous vertebrate assemblages have focused on the analysis of δ¹⁸O on the bioapatite with the aim of characterizing paleoclimate [16–18], faunal behavior and/or paleohydrology [18–20], and metabolism with special interest on dinosaurian body temperature [21–23]. δ¹³C values have been used to make inferences on paleoecology and to study the fractionation between diet (vegetation) and dinosaur enamel [24–26]. Domingo et al. [27] carried out a preliminary stable isotope study on the “Lo Hueco” vertebrate paleofauna (central eastern Spain) as a first approach to evaluate the potential, validity and degree of preservation of the bioapatite from this locality and as a first approach to characterize paleoclimatic (δ¹⁸OH₂O, temperature) and paleoecological/paleoenvironmental (diet, type of vegetation) variables existing during the late Campanian-early Maastrichtian in the southeastern area of the Iberian region. Albeit the Late Cretaceous Iberian geological record shows a good representation of vertebrate localities and outcrops, there are very scarce stable isotope studies on this area and time period [27–28]. Therefore, the isotopic investigation of the “Lo Hueco” vertebrate assemblage provide valuable data, which may shed light on climatic and environmental conditions that occurred in this subtropical setting located in the Tethys realm.

The main objectives of our study are three-fold: 1) to determine seasonal thermal variability in the Iberian Late Cretaceous, 2) to characterize the isotopic offset between δ¹³C values of dinosaur tooth enamel and their diet (Δ¹³Cenamel-diet), and 3) to unveil dietary and habitat affinities for “Lo Hueco” crocodyliforms and turtles. The richness and diversity of the Late Cretaceous “Lo Hueco” Fossil-Lagerstätte [29–30] have allowed us to approach the aforementioned questions by performing multi-taxa stable isotope analyses (δ¹⁸OPO₄, δ¹⁸OCO₃ and δ¹³C) on dinosaurs, crocodyliforms, turtles, gars and bulk organic matter. Most isotopic studies dealing with Mesozoic vertebrates focused on one or two groups [16–17, 19, 25–26, 31–32], so the advantage of considering co-existing taxa relies on the fact that they can shed light on differences in habitat and resource utilization, informing about climatic, environmental and ecological variables such as hydrology of the area, seasonality, type of vegetation, resource/habitat overlap and/or partitioning.
While different paleontological, geochemical and modelling studies offered a good characterization of long-term climatic variability for the Middle and Late Cretaceous (e.g., [1–3, 6, 16, 33], among others), the evaluation of seasonal thermal variability has proven challenging on account of the lack of proxies capable of recording intra-annual information. Controversy arises when discerning whether Middle and Late Cretaceous climate was more seasonally thermally equable (low mean annual range of temperatures) [34–39], although, there seems to be an agreement indicating a higher seasonal thermal variability (i.e., lower equability) during the colder Late Cretaceous in comparison to the warmer Middle Cretaceous [38].

\( \delta^{18}O \) values in the phosphate and carbonate fractions of vertebrate bioapatite record the \( \delta^{18}O \) value of their body water (\( \delta^{18}O_{bw} \)). In the case of terrestrial endothermic species, \( \delta^{18}O_{bw} \) is a reflection of oxygen uptake (inspired \( O_2 \) and water vapor, drinking water, dietary water, oxygen in food dry matter) and loss (excreted water and solids, expired \( CO_2 \), and water vapor). Dinosaur metabolism is a controversial issue that remains under debate [21, 40–45]. Fricke and Rogers [22] performed \( \delta^{18}O_{PO4} \) analyses on Late Cretaceous theropods and crocodilians from fossil sites located at different latitudes and found that the reconstructed theropod slope of the \( \delta^{18}O_{PO4} \)-latitude relationship was steeper than the one observed for crocodilians (ectotherms) and similar to that estimated for present-day endotherms such as mammals and birds. Amiot et al. [23] observed a widespread endothermy in different groups of Late Cretaceous dinosaurs and obtained body temperatures of 36–38°C for dinosaurs inhabiting high and low latitudes. Other authors such as O’Connor and Dodson [46] and Gillooly et al. [47] argued that dinosaur body temperature depended on body mass (inertial homeothermy), ranging from 25°C at 12 kg to 41°C at 13,000 kg [47]. However, Fricke and Rogers [22] observed similar metabolisms for Late Cretaceous theropods showing different body mass (e.g., Albertosaurus: 1.3–1.7 tons; Majungasaurus: 1.5 tons; Saurornitholestes: 10 kg). Amiot et al. [23] observed a widespread endothermy in different groups of Late Cretaceous dinosaurs (theropods, sauropods, ornithopods, and ceratopsians). Eagle et al. [48] performed clumped isotope analyses on sauropods and estimated body temperatures between 4 and 7°C lower (36 to 38°C) than those proposed by Gillooly et al. [47], arguing that sauropods were able to regulate their body temperatures, preventing overheating. Ectothermic semi-aquatic taxa, such as crocodiles and turtles, form their bioapatite within a narrow thermal window, and their bioapatite \( \delta^{18}O \) is a reflection of the \( \delta^{18}O_{H_2O} \) value of warm months when conditions are favorable for apatite synthesis [20, 49–50]. In the case of ectothermic aquatic taxa (gars), bioapatite forms in isotopic equilibrium with ambient water and since they do not thermoregulate, their bioapatite \( \delta^{18}O \) values record both \( \delta^{18}O_{H_2O} \) and ambient temperature independently of body temperature [51]. Therefore, it is possible to estimate temperature values from gars \( \delta^{18}O \) values if the \( \delta^{18}O_{H_2O} \) value is independently estimated [20, 51–52].

Studies dealing with dinosaur \( \delta^{13}C \) values have mainly focused on herbivore taxa (e.g., [24–26, 53]). These authors obtained relatively high \( \delta^{13}C \) values for hadrosaurian and ceratopians dinosaurs for a typical C3 environment (C3 plant expansion took place in the late Miocene–Pliocene). Plants following the C3 or Calvin-Benson photosynthetic pathway (trees, shrubs, forbs, and cool-season grasses) strongly discriminate against \( ^{13}C \) during fixation of \( CO_2 \), yielding tissues with \( \delta^{13}C \) values averaging ~ -27.5‰ (VPDB) (ranging from -36‰ to -22‰). The most negative \( \delta^{13}C \) values of this range (-36‰ to -30‰) reflect closed canopy conditions due to recycling of \( ^{13}C \)-depleted \( CO_2 \) and low irradiance. The highest values (-25‰ to -22‰) correspond to C3 plants from high insolated, arid, or water stressed environments [54–56]. When considering fossil taxa, it is necessary to account for shifts in the \( \delta^{13}C \) value of atmospheric \( CO_2 \) (\( \delta^{13}C_{atmCO_2} \), the source of plant carbon, including anthropogenic modification due to fossil fuel burning, which has decreased the \( \delta^{13}C \) value of atmospheric \( CO_2 \) from a value of ~-6.0‰ in the Late Cretaceous [57] to a modern value of ~-8.0‰ [58–59]. Accounting for these
shifts in baseline and assuming the modern fractionation of $\sim -19.5\%$ between $\delta^{13}C_{\text{atm}}$ and $C_3$ vegetation $\delta^{13}C$ values [60]. Late Cretaceous mean $\delta^{13}C$ value for $C_3$ plants would be $\sim -25.5\%$ (ranging from $-34\%$ to $-20\%$), with the most negative $\delta^{13}C$ values ($-34\%$ to $-28\%$) reflecting closed canopy conditions and the highest values ($-23\%$ to $-20\%$) reflecting high insolated, arid, or water stressed environments. Studies of $\delta^{13}C$ offsets between terrestrial vertebrate enamel and diet ($\Delta\delta^{13}C_{\text{enamel-diet}}$) have been mainly carried out on modern mammalian taxa, which allows for extrapolation on paleontological studies dealing with mammals, so that a consistent $\Delta\delta^{13}C_{\text{enamel-diet}}$ of $+12$ to $+14\%$ has been observed between herbivore mammalian tooth enamel and vegetation $\delta^{13}C$ values [61–63], while the difference between mammalian carnivore and herbivore tooth enamel $\delta^{13}C$ values ($\Delta\delta^{13}C_{\text{carnivore-herbivore}}$) has been proposed to be $\sim -1.3\%$ [64]. Johnson et al. [65] and Angst et al. [66] also investigated this tissue-diet fractionation on modern birds by analyzing ostrich eggshells and diet, obtaining a $\Delta\delta^{13}C_{\text{eggshell-diet}}$ value of $+16\%$ and $+13.4\%$, respectively. The lack of modern counterparts in the case of dinosaurs makes it difficult to assess this offset and we can just rely on the fossil record geochemical imprint to determine tissue-diet fractionation values. In this vein, analyzing herbivore dinosaur bioapatite and bulk organic matter $\delta^{13}C$ values, Fricke and Pearson [25] and Fricke et al. [26] argued that $\Delta\delta^{13}C_{\text{enamel-diet}}$ for ornithischian dinosaurs was $\sim +18\%$, whereas Tütken [32] estimated a $\Delta\delta^{13}C_{\text{enamel-diet}}$ value of $\sim +16\%$ for sauropods.

Geographic and geological setting

The Late Cretaceous "Lo Hueco" Fossil-Lagerstätte is located in the province of Cuenca (central eastern Spain: 2° 02'50"W, 39° 57'15"N) (Fig. 1). It was fortuitously discovered in 2007, while constructing the Madrid-Levante high-speed railway. More than 10,000 macrofossils of different taxonomic groups of flora and fauna were unearthed. The stratigraphic position and associated fauna support a late Campanian–early Maastrichtian age [29, 67–68]. The "Lo Hueco" site outcrops in Garumn facies, which is the informal term that designates marl, clay, and gypsum, mainly of red color, deposited in shallow marine, coastal, and/or continental environments of southwestern Europe during the latest Cretaceous and the earliest Paleogene [69]. It corresponds to the upper part of the Villalba de la Sierra Formation (Fig. 2A), a lithological unit interpreted as a coastal marsh with distributary channels and sporadic establishment of sabkhas [29]. Six stratigraphic levels were defined at the "Lo Hueco" outcrop named V, G1, R1, G2, R2, and M from bottom to top [29] (Fig. 2B). This succession appears slightly modified laterally by a lower sulphate interval (S1) that cuts the V level in the eastern area of the outcrop, by a sandy channel structure (C) that interrupts V, G1, and R1 levels in the southern area, and an upper sulphate interval (S2) that cuts part of G2 in the northeastern area (Fig. 2B). Four bonebeds have yielded the majority of fossils: the C structure, the G1 and G2 levels and the lower part of the R2 level (Fig. 2B) [29, 68]. The G1 level is interpreted as a proximal muddy floodplain (close to the distributary channels) and vertebrate fossils usually appear complete and associated. More than 14 partially articulated sauropod skeletons were recovered from this level [28, 68]. Exceptionally well-preserved plant remains have been also described from this lithosome [30]. The G2 level corresponds to the distal part of a poorly drained muddy floodplain (distal from the distributary channels) and points to a relatively calm aquatic environment (i.e., marsh/swamp) exposed to partial or total desiccation, although there is a low degree of articulation of preserved skeletons [29, 68]. Recent fluid inclusion and geochemical analyses on the sulphates from S1 and S2 have pointed to a near coast playa-lake environment with mainly brackish and freshwater influence in the area, while not totally ruling out some extent of marine influence [70]. During the late Campanian–early Maastrichtian, the "Lo Hueco" locality was placed at a subtropical paleolatitude of $\sim 31^\circ$N.
Materials and Methods

The rich and diverse vertebrate assemblage of the “Lo Hueco” fossil site allowed us to collect multi-taxa samples including dinosaur (theropods: n = 11, sauropods: n = 4) and crocodyliform (n = 36) tooth enamel, turtle shell (n = 9) and gar ganoin (n = 19) from levels G1 and G2. Paleontological prospection and excavation undertaken at the “Lo Hueco” fossil site were authorized by the Dirección General de Patrimonio y Museos of the Junta de Comunidades de Castilla-La Mancha (Spain) (permit number: 04-0392-P11). “Lo Hueco” vertebrate remains are housed at Museo de las Ciencias de Castilla-La Mancha (Cuenca, Spain). Complete repository information including specimen number, stratigraphic situation and geographic location are given in S1 Dataset. Dinosaurs, crocodyliforms and turtles were analyzed for their $\delta^{18}$O$_{PO4}$, $\delta^{18}$O$_{CO3}$ and $\delta^{13}$C values, whereas gars were analyzed for their $\delta^{18}$O$_{PO4}$ values. Dinosaur dentine was also analyzed in order to check for diagenetic effects. Although three major groups of dinosaurs (theropods, sauropods and ornithopods) are represented in “Lo Hueco”, in this
study we had access to theropods belonging to Dromaeosaurinae and Velociraptorinae Eumaniraptora and to sauropods, which are presumably representing two titanosaurian species, one of them close to the genus *Ampelosaurus* [71–73]. Eusuchian crocodile remains are very abundant at this locality, although the record is monotonous and seems to be represented by two
genera close to *Allodaposuchus* [74]. Most of the turtle material probably belongs to two forms of PLEurodira, specifically to members of Bothremydidae [29, 75–76]. Finally, actinopterygians from "Lo Hueco" are mainly represented by lepisosteids, commonly known as gars [29]. We also performed δ¹³C analyses on bulk organic matter from the "Lo Hueco" G1 (n = 10) and G2 (n = 8) levels with the aim of characterizing the type of vegetation that was present in the area.

The carbon and oxygen isotope results are reported in the δ-notation. δXsample = [(Rsample−Rstandard)/Rstandard] × 1000, where X is the element, H is the mass of the rare, heavy isotope, and R = ¹³C/¹²C or ¹⁸O/¹⁶O. Vienna Pee Dee Belemnite (VPDB) is the standard for δ¹³C values, whereas δ¹⁸O values for both bioapatite carbonate and phosphate are reported relative to Vienna Standard Mean Ocean Water (VSMOW).

Sample chemical treatments followed those described in Bassett et al. [77] for phosphate in bioapatite, Koch et al. [78] for carbonate in bioapatite and Domingo et al. [79] for bulk organic matter. All samples were analyzed at the Stable Isotope Laboratory of the University of California Santa Cruz (USA). Bioapatite δ¹⁸OPO₄ values were measured using a Thermo Finnigan Delta plus XP isotope ratio mass spectrometer coupled via continuous flow to a high temperature conversion elemental analyzer (TCEA). Bioapatite δ¹³C and δ¹⁸OCO₃ analyses were conducted on a Thermo MAT253 dual-inlet isotope-ratio mass spectrometer coupled to a Kiel IV carbonate device. Bulk organic matter δ¹³C analyses were performed using a Carlo Erba 1108 elemental analyzer interfaced to a ThermoFinnigan Delta plus XP isotope ratio mass spectrometer. The standards used in the case of phosphates were Fisher Standard (δ¹³C = 8.4‰), UCSC Low standard (δ¹³C = 11.3‰), UCSC High standard (δ¹³C = 19.0‰) and Kodak standard (δ¹³C = 18.1‰) (all of them are silver phosphate). Standard deviations for repeated measurements of Fisher (n = 52), UCSC Low (n = 13), UCSC High (n = 16), and Kodak (n = 7) standards were 0.51‰, 0.55‰, 0.21‰, and 0.36‰ for δ¹⁸OPO₄. As suggested by Suarez et al. [20], we used NIST 120c as a quality control standard and not as a calibration standard since its value is highly dependent on both pretreatment and analysis methods. NIST 120c value (n = 8) was 21.5±0.4. Replicate δ¹⁸OPO₄ analyses were carried out in ~80% of the samples. The average absolute difference for δ¹⁸OPO₄ was 0.02‰ and the standard deviation of this average difference was 0.20‰. The standards used in the case of carbonates were Carrara Marble (CM, δ¹³C = 2.05‰ and δ¹⁸O = -1.91‰, both VPDB), NBS-18 (δ¹³C = -5.03‰ and δ¹⁸O = -23.01‰, VPDB) and NBS-19 (δ¹³C = 1.95‰ and δ¹⁸O = -2.20‰, VPDB). The standard deviations for repeated measurements of CM (n = 16), NBS-18 (n = 19), and NBS-19 (n = 10) were 0.03‰, 0.33‰, and 0.04‰ for δ¹³C, respectively, and 0.08‰, 0.07‰, and 0.09‰ for δ¹⁸O, respectively. Duplicate analyses were performed for ~50% of the samples. The average absolute difference for δ¹³C and δ¹⁸O was 0.03‰ and 0.14‰, respectively, and the standard deviations of these average differences were 0.02‰ and 0.05‰ for δ¹³C and δ¹⁸O, respectively. The standards used in the case of bulk organic matter analyses were Pugel (δ¹³C = -12.60‰) and Acetanilide (δ¹³C = -29.53‰). The standard deviations for repeated measurements of Pugel (n = 11) and Acetanilide (n = 3) were 0.15‰ and 0.02‰, respectively. Statistical tests were performed using the program SPSS PASW Statistics 18.0 software.

We used the following equations to calculate δ¹⁸Owater values from "Lo Hueco" vertebrates: Dinosaurs: δ¹⁸O_H₂O = 1.118δ¹⁸OPO₄−26.44 [16] (1) Crocodyliforms: δ¹⁸O_H₂O = 0.82δ¹⁸OPO₄−19.13 [80] (2) Turtles: δ¹⁸O_H₂O = 1.068δ¹⁸OPO₄−21.6 [81] (3) Equation (1) was calculated by Amiot et al. [16] constructing a database with modern mammalian δ¹⁸OPO₄ values and the δ¹⁸O value of meteoric water from IAEA stations. Since most of dinosaur samples from "Lo Hueco" belong to theropods, we considered them as endotherms following most authors [22–23, 45], and therefore we applied equation (1) as Amiot et al. [16] suggested in their study. Equation (2) was experimentally determined by Amiot et al. [80]
analyzing modern crocodilian $\delta^{18}$OPO$_4$ values and the $\delta^{18}$O value of the water in which they live. Equation (3) was determined by Coulson et al. [81] for freshwater and marine extant turtle datasets combining experimental and literature results. This equation was adjusted to correct for the difference in NIST 120c value obtained by Coulson et al. [81] (22.6‰) and in our study (21.5±0.4).

Once dinosaur, crocodyliform and turtle $\delta^{18}$OH$_2$O values were estimated, we used gar ganoine $\delta^{18}$OPO$_4$ values as an independent proxy to calculate temperature values and to eventually determine temperature offsets related to seasonal patterns (see Discussion). Following Domingo et al. [82], we selected lepisosteid middle flank scales since they record the greatest number of layers of ganoine per unit of time and grow all year round. In the case of dinosaurs, we have only used theropod $\delta^{18}$OPO$_4$ values on account of 1) the low number of sauropod samples, and 2) the uncertainty about whether sauropods obtained water mainly from drinking (i.e., obligate drinkers) or from vegetation (i.e., non-obligate drinkers).

Different phosphate-water oxygen isotope fractionation equations have been proposed as paleothermometers based mainly on studies carried out on extinct and extant fish and invertebrate phosphates. The utilization of a given equation may yield significant differences in calculated temperature values when compared to other equations, which can be as large as 8–9°C [83–84]. Here, we applied three different equations in order to check whether they can be used to calculate temperature offsets related to seasonal patterns independently of the absolute temperature values yielded by each of them (see Discussion). We considered the following equations:

$$T(\degree C) = 119.3 \pm 12.9 - 4.38 \pm 0.54 \left(\delta^{18}O_{PO4} - \delta^{18}O_{H2O}\right) [51]$$ (4)

This equation was rescaled for a NBS 120b value of 21.4‰ (see [84])

$$T(\degree C) = 118.7 \pm 4.9 - 4.22 \pm 0.20 \left(\delta^{18}O_{PO4} - \delta^{18}O_{H2O}\right) [85]$$ (5)

$$T(\degree C) = 117.4 \pm 9.5 - 4.50 \pm 0.43 \left(\delta^{18}O_{PO4} - \delta^{18}O_{H2O}\right) [84]$$ (6)

**Results**

Table 1 shows dinosaur, crocodyliform, turtle and gar mean $\delta^{18}$OPO$_4$, $\delta^{13}$C, $\delta^{18}$OCO$_3$, and $\delta^{18}$OH$_2$O values. Individual values per sample and statistical tests are given in S1 and S2 Datasets, respectively.

**$\delta^{18}$OPO$_4$ results**

Fig. 3 shows mean $\delta^{18}$OPO$_4$ values for theropods, sauropods, crocodyliforms, turtles and gars. Mean $\delta^{18}$OPO$_4$ value for theropods is 20.8±0.9‰, with a non-significant increase of ~0.5‰ between G1 and G2 (t = -1.146, p = 0.276). Mean $\delta^{18}$OPO$_4$ value for sauropods is 20.9 ± 0.4‰ and there is also an increase of ~0.5‰ in $\delta^{18}$OPO$_4$ between G1 and G2, although in this case no statistical tests were done since only one sauropod per level could be sampled. Mean $\delta^{18}$OPO$_4$ value for crocodyliforms is 19.4 ± 0.9‰ with a significant increase of ~1.0‰ between G1 and G2 (t = -3.491, p = 0.002). Turtles show a mean $\delta^{18}$OPO$_4$ value of 18.3‰ ± 0.7‰, with a non-significant increase of ~0.8‰ between G1 and G2 (t = -2.208, p = 0.063). Crocodyliforms and turtles show statistically consistent lower $\delta^{18}$OPO$_4$ values than dinosaurs for the total dataset (Table 1 and S2 Dataset). Mean $\delta^{18}$OPO$_4$ value for gars is 19.8 ± 1.0‰, with a non-significant decrease of ~0.2‰ between G1 and G2 (t = -0.475, p = 0.641). ANOVA tests show significant differences for $\delta^{18}$OPO$_4$ values when comparing all taxa for the total dataset and for G1 and G2 independently (S2 Dataset).
δ\(^{18}\)O\(_{H2O}\) results

Mean calculated \(\delta^{18}O_{H2O}\) value for theropods is \(-3.5 \pm 1.0\)‰, with a non-significant increase of \(-0.6\)% between G1 and G2 \((t = -0.670, p = 0.566)\). Mean \(\delta^{18}O_{H2O}\) value for crocodyliforms is \(-3.2 \pm 0.7\)‰, with a significant increase of \(-0.9\)% between G1 and G2 \((t = 2.541, p = 0.019)\).
Turtle mean δ18OH2O value is -2.2 ± 0.7‰, with a non-significant increase of *0.9‰* between G1 and G2 (t = -2.215, p = 0.062). ANOVA test performed for the total dataset and for levels G1 and G2 showed significant differences in δ18OH2O value among theropods, crocodyliforms and turtles (S2 Dataset).

δ13C and δ18OCO3 results

Fig. 4 shows a biplot δ13C-δ18OCO3 graph for the “Lo Hueco” vertebrate assemblage. Theropod mean δ13C and δ18OCO3 values are -10.7 ± 0.8‰ and 30.0 ± 1.1‰, respectively, with a decrease in both values between G1 and G2, although only significant in the case of δ18OCO3 (t = 2.603, p = 0.022). Sauropod mean δ13C and δ18OCO3 values are -10.5 ± 0.8‰ and 29.0 ± 0.1‰, respectively, with a non-significant increase in δ13C between G1 and G2 (t = -0.334, p = 0.770) and with the same δ18OCO3 value in both levels. Crocodyliform mean δ13C and δ18OCO3 values are -10.4 ± 1.9‰ and 28.2 ± 1.0‰, respectively, with a non-significant decrease in δ13C between G1 and G2 (t = 0.214, p = 0.834) and a non-significant increase in δ18OCO3 between G1 and G2 (t = -0.204, p = 0.842). Finally, turtle mean δ13C and δ18OCO3 values are -11.8 ± 0.6‰ and 27.1 ± 0.3‰, respectively, with increases in both values between G1 and G2, although only significant in the case of δ13C (t = -14.300, p < 0.001). δ13C values do not show statistically significant differences among taxa for the total dataset, G1 and G2, whereas δ18OCO3 values do show significant differences in all cases (S2 Dataset).

Bulk organic matter mean δ13C value is -25.1 ± 1.4‰, with a non-significant increase of ~0.2‰ between G1 and G2 (t = -0.302, p = 0.767).

Diagenesis

Several lines of evidence point to a low degree of diagenetic alteration for the “Lo Hueco” fossil vertebrates:

1) Tooth enamel was the selected tissue for dinosaurs, crocodyliforms, whereas ganoine was analyzed in the case of gars. Relative to dentine, bone and isopedine, tooth enamel and ganoine
have larger apatite crystals, a lower content of organic matter, and a low porosity, making them the least prone tissues to undergo diagenetic alteration [86].

2) Several studies of living organisms point to a difference between bioapatite $\delta^{18}OCO_3$ and $\delta^{18}OPo_4$ values ($\Delta^{18}OCO_3-PO_4$) of ~ 8.6–9.1‰ [87–88]. Obtaining a $\Delta^{18}OCO_3-PO_4$ value near this range in fossil bioapatite has been viewed as an indication that both phases retain pristine isotopic values [87, 89–91]. The mean $\Delta^{18}OCO_3-PO_4$ value for “Lo Hueco” dinosaurs is 9.1 ± 1.7‰ and thus, it is in the range of the expected equilibrium difference supporting a low degree of diagenetic alteration (Fig. 5). Although this relationship was established for endotherms, “Lo Hueco” turtle $\Delta^{18}OCO_3-PO_4$ value is also in that range (8.8 ± 0.5‰) (Fig. 5), probably reflecting sustained and constant body temperature during mineral growth (preferentially during summer months: [49–50]). The fact that we only sampled compact bone from the outermost part of turtle shells reduces the possibility of diagenetic alteration. $\Delta^{18}OCO_3-PO_4$ value could not be calculated for crocodyliforms since $\delta^{18}OCO_3$ and $\delta^{18}OPo_4$ values did not come from the same samples.

3) Dinosaur enamel and dentine $\delta^{18}OPo_4$ analyses were performed in order to evaluate the response of these tissues against postburial alteration. Several authors have observed higher isotopic values in dinosaur dentine compared to enamel (e.g., [24–26]). Fricke and Pearson [25] argued that this difference was due to a variable exposure of dentine to diagenetic fluids, as well as more isotopic exchange and/or secondary mineral formation in dentine compared to enamel. In the case of the “Lo Hueco” dinosaurs, we also observed higher isotopic values in dentine with theropods showing $\Delta^{18}OPo_4$ dentine-enamel = 1.04, and sauropods showing $\Delta^{18}OPo_4$ dentine-enamel = 1.34. Significant differences have been detected between both tissues when considering the total dataset ($t = -2.983$, $p = 0.007$).

4) An additional line of evidence to assess the preservation of original $\delta^{18}OPo_4$ values was outlined by Fricke and Rogers [22] when trying to determine the type of metabolism of dinosaurs. According to these authors, differences in body temperatures between ectotherms and endotherms give rise to differences in $\delta^{18}OPo_4$ values as a function of latitude in such a way that at high latitudes, ectotherms have higher $\delta^{18}OPo_4$ values than endotherms (due to lower body temperature for ectotherms). Conversely, at low latitudes, endotherms show higher $\delta^{18}OPo_4$ values than ectotherms. Amiot et al. [16] stated that diagenetic processes would bring
about the homogenization of isotopic values and therefore, the aforementioned differences would not be observable. The “Lo Hueco” fossil site was situated at a low paleolatitude (≈ 31°N) during the Late Cretaceous [92]. Theropod dinosaurs, which have been proposed to be endotherms [22–23, 93], show consistently higher δ\(^{18}\)O\(_{\text{PO4}}\) values in comparison to crocodyliforms and turtles (ectotherms) at the “Lo Hueco” fossil site when considering the total dataset as well as G1 and G2 levels separately (Table 1), in agreement with the results observed by Fricke and Rogers [22] and Amiot et al. [16]. In addition to the difference observed in δ\(^{18}\)O\(_{\text{PO4}}\) values between endotherms and ectotherms, lower δ\(^{18}\)O\(_{\text{H2O}}\) values for aquatic gars and semi-aquatic crocodyliforms and turtles, and higher δ\(^{18}\)O\(_{\text{PO4}}\) values for terrestrial theropods constitute another line of evidence pointing to the preservation of the original isotopic signal, as previously stated by other authors [19–20].

### Discussion

#### Seasonal thermal variability in the Iberian Late Cretaceous

Controversy arises when discerning whether Middle and Late Cretaceous climate witnessed a lower mean annual range of temperatures (i.e., seasonal thermal equability) than today [34–39], although it seems that during the colder Late Cretaceous there was a higher seasonal thermal variability (i.e., lower equability) in comparison to the warmer Middle Cretaceous [38]. Multi-taxa studies as the one carried out here allow us to investigate this issue on account of differences in the timing of bioapatite growth, thus tracking different moments throughout the year. While in general, δ\(^{18}\)O\(_{\text{H2O}}\) values calculated for theropods, crocodyliforms and turtles from “Lo Hueco” correspond to typical precipitation waters in subtropical locations [94], theropods recorded consistently lower δ\(^{18}\)O\(_{\text{H2O}}\) and temperature values than crocodyliforms and turtles in G1 and G2 levels as well as in the total dataset (Table 1). Lower δ\(^{18}\)O\(_{\text{H2O}}\) values of terrestrial endothermic taxa such as theropods would correspond to ingested water probably consumed during the whole year and hence, recording all seasons. In contrast, δ\(^{18}\)O\(_{\text{H2O}}\) data of semiaquatic ectothermic taxa such as crocodyliforms and turtles would represent local meteoric waters over a shorter time scale when the conditions are favorable for apatite synthesis (i.e., growth during the warm season and higher δ\(^{18}\)O\(_{\text{H2O}}\) values) [21, 49, 80]. Temperature values calculated from theropod δ\(^{18}\)O\(_{\text{H2O}}\) values would track mean annual temperature (MAT), whereas temperature values estimated from crocodyliform and turtle δ\(^{18}\)O\(_{\text{H2O}}\) values would record temperature of the warmest months (TWMs), when apatite synthesis is more likely to occur. Albeit the seasonal thermal amplitude is usually calculated as the difference between temperature of the warmest months (TWMs) minus temperature of the coldest months (TCMs), in our approach it is not feasible to work out this latter value with the available proxies. We opted to infer the semi-seasonal thermal variability characterized as the difference between TWMs and MAT (ΔTWMs-MAT). Since the “Lo Hueco” site was located in a coastal subtropical setting, we created a database with modern meteorological information from coastal stations situated within the subtropics in both hemispheres (25°–35°) compiling MAT and TWMs (i.e., July, August, September) data and calculating ΔTWMs-MAT (S3 Dataset). We also considered seasonal data provided by Tethyan Cretaceous rudists [36, 38]. These authors argued that during the colder Early Cretaceous (late Barremian–middle Albian), seasonal thermal variability was more intense than during warmer Cretaceous episodes (late Albian–early Campanian). Fig. 6 shows ΔTWMs-MAT vs subtropical latitude range (25°–35°) for data calculated from vertebrate taxa from “Lo Hueco”, modern subtropical stations, and Santonian–Campanian eastern Tethyan rudists (Greece and Turkey: [36, 38]). ΔTWMs crocodyliforms,MAT\textsubscript{theropods} values from “Lo Hueco” are 2.2±0.1°C, 3.5±0.1°C, and 2.7±0.1°C for G1, G2, and the total dataset, respectively (S4 Dataset), whereas ΔTWMs turtles,MAT\textsubscript{theropods} yielded higher values of 6.1±0.2°C, 7.4
±0.20°C, and 6.7±0.2°C for G1, G2, and the total dataset, respectively (S4 Dataset). Similar ΔTWMs-crocodiles-MATtheropods and ΔTWMs-turtles-MATtheropods values were obtained when using equations (4), (5) and (6) (S4 Dataset). ΔTWMs-MAT values from modern data vary between minimum values of 2.8±0.4°C (Easter Island, Chile, 27.17°S) and maximum values of 8.1±0.3°C (Fuzhou, China, 26.08°N). Finally, the mean sea-surface ΔTWMs-MAT value from Late Cretaceous Tethyan rudists is 5.0±2.6°C (Greece and Turkey, ~30°N). No significant statistical differences have been found between the “Lo Hueco” ΔTWMs-MAT values and those shown by modern meteorological stations and Cretaceous rudists (S5 Dataset) indicating that the climatic conditions in the subtropical western area of the Tethys during the late Campanian-early Maastrichtian were not more significantly equable than those observed today.

Previous studies have suggested that during mid-Cretaceous greenhouse conditions the latitudinal thermal gradient was weaker than the one observed today, whereas during the cooler late-Cretaceous, the latitudinal thermal gradient has been proposed to be either weaker or similar to that observed today [6, 95–96]. Cool greenhouse periods, as Huber et al. [6] refer to mid-Campanian-Maastrichtian, showed warm temperatures in high latitudes and cool temperatures in the subtropics and tropics (e.g., [95]). Cooler conditions have been traditionally associated to a lower thermal equability and vice versa [37, 97] and in this vein, Steuber et al. [38], studying seasonal thermal variability on Tethyan rudists, observed a lower thermal seasonality during the warmer Cretaceous episodes, whereas cooler Cretaceous episodes show a higher thermal seasonality. “Lo Hueco” temperature data do not show a significant different seasonal thermal variability when compared to modern data pointing to a similar seasonal thermal
amplitude between central eastern Iberia during the late Campanian-early Maastrichtian and today (S3 and S5 Datasets). The determination of past seasonality remains a difficult issue to determine due to the limitation of the seasonal information yielded by paleoproxies and the shortage of these indicators in terrestrial settings. Isotopic studies of multi-taxon vertebrate assemblages as the one from the “Lo Hueco” locality help to characterize past seasonality. Future clumped isotope analyses on soil carbonate and invertebrate carbonate from the “Lo Hueco” locality may allow us to double-check TWMs values and compare them with those provided by crocodyliforms and turtles.

“Lo Hueco” vertebrate isotopic paleoecology

Carbon isotope data have not been widely investigated in Cretaceous multi-taxon assemblages and studies have mainly focused on herbivore terrestrial taxa (e.g., [24–26]). We have analyzed δ13C values of sauropods, theropods, crocodyliforms and turtles as well as δ13C values of the bulk organic matter from the “Lo Hueco” sediments. Sauropod mean δ13C value is -10.5±0.8‰ and bulk organic matter mean δ13C value is -25.1±1.4‰ (Fig. 7). While we are aware that the low number of “Lo Hueco” sauropod tooth enamel samples may prevent us from attaining conclusive results, we still believe that it is worth discussing them in the context of other isotopic studies focused on herbivore dinosaurs. The “Lo Hueco” bulk organic matter mean δ13C value is almost identical to the estimated Late Cretaceous C3 vegetation mean δ13C value (-25.5‰), assuming a Δ13CatmCO2 value of ~ -6‰ for the late Campanian-early Maastrichtian [57] and the modern fractionation value of ~-19.5‰ between Δ13CatmCO2 and C3 vegetation δ13C values [60]. This suggests a pure C3 environment for the “Lo Hueco” locality for that time period. Assuming that the “Lo Hueco” bulk organic matter mean δ13C value is representative of the δ13C value of the vegetation present in the area, then the fractionation between the “Lo Hueco” sauropod enamel and diet (Δ13C enamel–diet) would be ~15‰. This offset lies between the one estimated for mammals and ostriches (12 to 14‰: [61–63, 66]) and the one estimated for sauropod dinosaurs and ostriches (~16‰: [32, 65], respectively), and it is narrower when compared to the one estimated for ornithischian dinosaurs (i.e., 18‰: [25–26]).

Stanton-Thomas and Carlson [24], Fricke and Pearson [25] and Fricke et al. [26] obtained higher δ13C values for hadrosaur and ceratopsian tooth enamel (-4‰ to -5.9‰) from different Late Cretaceous North American localities located in the vicinity of the Western Interior Seaway when compared to “Lo Hueco” sauropod δ13C values. Since bioapatite δ13C values of terrestrial vertebrates are ultimately controlled by δ13C values of diet giving rise to consistent Δ13C enamel–diet values [63, 86], the difference between the fractionation values obtained in our study and those from Stanton-Thomas and Carlson [24], Fricke and Pearson [25] and Fricke et al. [26] might be likely associated to metabolic differences among taxonomic groups (sauropods vs. ceratopsians and hadrosaurs) (Fig. 8) [22–23, 46–48]. Bulk organic matter mean δ13C values showed by Fricke and Pearson [25] are ~ -24.0‰, just 1‰ higher than our bulk organic matter mean δ13C values, supporting differences in dinosaur metabolism in a scenario with similar isotopic values of vegetation (Fig. 7). Fricke and Pearson [25] pointed out that differences in the methane production in herbivore dinosaur stomachs during digestion along with different utilization of plant organic compounds (e.g., carbohydrates, proteins, lipids) and/or plant parts (e.g., leaves, seeds, wood) may also explain the differences observed in Δ13C enamel–diet. The larger ceratopsian and hadrosaur Δ13C enamel–diet may be due to their ability to incorporate low quality, fibrous vegetation [25], whereas the smaller sauropod Δ13C enamel–diet value may be indicative of consumption of more digestible food items (e.g., soft leaves), fact also supported by the dental morphology of “Lo Hueco” titanosaur sauropods (i.e., chisel-like teeth) more adapted to leave behind the least digestible tissues [98–99]. The 3‰ difference observed in Δ13C enamel–diet values
for ornithischians from Fricke and Pearson [25] and Fricke *et al* [26] and sauropods from our study is statistically significant ($t = -4.481$, $p = 0.003$), and therefore, even considering the variability yielded by dinosaur and bulk organic matter $\delta^{13}C$ values, these two sets of data do not significantly overlap. Stanton-Thomas and Carlson [24] stated that higher $\delta^{13}C$ values observed in hadrosaurs might be related to ingestion of vegetation subject to high salinity levels and/or consumption of gymnosperms (which show an enrichment of ~1.1 to 2‰ compared to mean C3 $\delta^{13}C$ values). "Lo Hueco" sauropods may have relied heavily on angiosperms as revealed by the palynological content of the "Lo Hueco" sediments showing pollen assemblages dominated by angiosperms (93%: [100]). Specifically, the palynological assemblage from "Lo Hueco" is dominated by freshwater palynomorphs, spores and pollen grains related to swamp or local wetland vegetation [100]. The preferential incorporation of angiosperms by "Lo Hueco" sauropods may also lie behind the difference observed between our $\Delta^{13}C_{\text{enamel-diet}}$ value and the one estimated by Tütken [32]. Interestingly, in the compilation of sauropod $\delta^{13}C$
values carried out by this author, *Ampelosaurus* showed the lowest δ¹³C values, and according to Knoll et al. [73], one of the “Lo Hueco” sauropod taxa remains close to this genus. These uncertainties regarding herbivore dinosaur isotopic paleoecology open up new lines of investigation dealing with the question of the type of dietary behavior and physiology of different genera giving rise to different Δ¹³C enamel-diet offsets.

“Lo Hueco” theropod mean δ¹³C value is -10.7±0.8‰, statistically indistinguishable from the sauropod mean δ¹³C value (-10.5±0.8‰) (Fig. 4, S2 Dataset). To the best of our knowledge, there are no isotopic studies dealing with herbivore and carnivore dinosaur feeding.
paleoecology from the same locality. Isotopic studies on ancient vertebrate predator-prey systems have mainly focused on Quaternary mammals [64, 101–103] and to a lesser extent on Miocene mammals [104]. Clementz et al. [64] observed a $\delta^{13}$C offset between predators (wolves) and their prey (moose and elks) ($\Delta^{13}$C$_{\text{carnivore-herbivore}}$) of $\sim$ -1.3‰. These authors argued that lower tooth enamel $\delta^{13}$C values for carnivores might be due to differences in their digestive physiology in comparison to herbivores. The lack of significant differences between “Lo Hueco” carnivore and herbivore dinosaur tooth enamel $\delta^{13}$C values ($\Delta^{13}$C$_{\text{carnivore-herbivore}}$ = $\sim$ 0.2‰, S2 Dataset) may be due to differences in metabolic and/or physiological mechanisms between dinosaurs and mammals, however a more plausible explanation is that titanosaur sauropods were not likely prey for theropods belonging to Dromaeosaurinae and Velociraptorinae subfamilies on account of body mass differences. Interestingly, the lack of significant differences in $\delta^{13}$C values between both theropod subfamilies (t = 0.516, p = 0.618), along with the similarity in their body masses and likely hunting strategies point to some degree of resource overlap. Also, the lack of significant differences in variance of $\delta^{13}$C values between these subfamilies of theropods (Levene test; F = 1.582, p = 0.240) suggests that none was more versatile than the other in resource utilization.

In the case of aquatic ectotherms (crocodyliforms and turtles), $\delta^{13}$C values are a reflection of food oxidation (respiration) and ambient water (e.g., dissolved inorganic carbon or DIC can constitute an additional source of carbon) [105–106]. “Lo Hueco” crocodyliforms belong to the genus Allodaposuchus [74]. Since it is not possible to determine physiological tolerance to salinity from the morphological standpoint in the basal Eusuchia from “Lo Hueco”, (J.L. Sanz and F. Ortega, personal communication), the information supplied by stable isotopes may shed light about salt tolerance, dietary behavior and habitat occupancy. We have compared the isotopic values of “Lo Hueco” crocodyliforms to those provided by Wheatley et al. [107] for Louisiana and Florida modern crocodylians. We are aware that extrapolation between extinct and extant organisms is not straightforward due to unknown physiological mechanisms in ancient taxa as well as different environmental conditions. However, we still believe that a comparison can be made since 1) the marine-freshwater isotopic threshold values are well established not only in modern studies, but also in the past, 2) the marine $\delta^{18}$O value has remained fairly constant throughout the geological time and 3) the Wheatley et al. [107]’s study considered modern crocodylians from Louisiana and Florida with a similar latitude to the one suggested for “Lo Hueco” (25°–30°N for Louisiana and Florida vs 31°N for “Lo Hueco”). “Lo Hueco” crocodyliforms show a mean $\delta^{13}$C value, which is statistically indistinguishable from the value observed by Wheatley et al. [107] for Louisiana and Florida modern coastal Alligator mississippiensis (p = 0.999) and Florida modern coastal Crocodylus acutus (p = 0.868), while it is significantly different from Florida modern inland A. mississippiensis (p < 0.001), whereas “Lo Hueco” crocodyliforms show a significantly lower mean $\delta^{18}$O$_{\text{CO}_3}$ value, when compared to coastal and inland A. mississippiensis (p = 0.019 and p = 0.001, respectively) and coastal C. acutus (p < 0.001) (Fig. 9A). These results pose interesting issues concerning the salinity discrimination and osmoregulation capacity of the “Lo Hueco” eusuchian crocodyliforms. Jackson et al. [108] in a study of salinity tolerance and osmoregulation mechanisms by modern crocodilians argued that reptiles inhabiting marine and estuarine waters keep a constant plasma osmolality by behavioral modifications (avoiding drinking seawater) and/or morphological adaptation (salt-secreting glands and reduced integumental permeability). Crocodyliforms from “Lo Hueco” are under study and with the current information we cannot determine their physiological tolerance to salinity from a morphological standpoint (e.g., presence or absence of salt-secreting glands) (IL Sanz and F Ortega, personal communication, 2014). While waiting for these morphological studies, isotopic results suggest that the “Lo Hueco” crocodyliforms may have incorporated food items from brackish waters as
shown by their $\delta^{13}$C values, whereas they avoided ingesting this water and consumed preferentially freshwater, as suggested by their $\delta^{18}$O values. Clementz and Koch [109] and Wheatley et al. [107] argued that animals incorporating marine food items and drinking seawater show a lower variability in their $\delta^{18}$O values. Even though “Lo Hueco” crocodyliforms likely drank freshwater, its $\delta^{18}$O variability (1.0‰) is not as high as that shown by either inland (2.2‰).
and coastal (1.8‰) *A. mississippiensis*, and it is more similar to the one shown by saltwater tolerant *C. acutus* (0.8‰) (Fig. 9B). This might indicate that δ¹⁸O values of the water ingested by the “Lo Hueco” crocodyliforms may have remained homogeneous during the time window in which bioapatite mineralized (i.e., warmest months of the year).

“Lo Hueco” turtle mean δ¹³C and δ¹⁸O_Co₃ values are the lowest when compared to dinosaurs and crocodyliforms (Fig. 4) (although significant differences are only observed between turtles and dinosaur δ¹⁸O_Co₃ values, S2 Dataset). “Lo Hueco” turtles belong to two forms of Pleurodira, specifically to members of Bothremydidae [29, 75–76]. They are omnivore freshwater turtles, so low δ¹³C values may be indicative of a diet based on a mixture of aquatic and terrestrial C₃ vegetation and/or invertebrates, whereas low δ¹⁸O values may indicate ingestion of water with an inland source. Unlike crocodyliforms, there are not isotopic studies dealing with bone carbonate of freshwater turtles from the subtropics and they focused on marine turtles [105–106]. As observed in the case of “Lo Hueco” crocodyliforms, “Lo Hueco” turtles show a low variability in their mean δ¹⁸O_Co₃ value, in spite of inhabiting freshwater environments, when compared to modern marine loggerhead turtles reported by Wheatley et al. [107] (0.3‰ vs. 0.6‰, for “Lo Hueco” and marine loggerhead turtles, respectively) pointing to a low variability of δ¹⁸O_Co₃ values and presumably of the δ¹⁸O values of the ingested water for the time of bioapatite mineralization (i.e., warmest months of the year).

**Conclusions**

Isotopic analyses on the multi-taxa terrestrial vertebrate assemblage of the “Lo Hueco” locality (central eastern Spain) provides valuable information about climatic and environmental conditions existing in southeastern Iberia during the late Campanian-early Maastrichtian (Late Cretaceous). Seasonal thermal variability has been inferred as the difference between temperature of the warmest months (TWMs), supplied by crocodyliforms and turtles (whose bioapatite mineralizes during the warm season) and mean annual temperature (MAT), provided by theropods (that record ingested water throughout the year). “Lo Hueco” ΔTWMs-MAT results do not point to a significant different seasonal thermal variability to that observed today. From the paleoecological standpoint, δ¹³C values of the “Lo Hueco” taxa point to consumption of pure C₃ vegetation, fact that agrees well with bulk organic matter δ¹³C values from the “Lo Hueco” sediments. The estimated fractionation between sauropod enamel and diet (Δ¹³C enamelediet) is ~ 15‰, lower than other fractionation values calculated for sauropods (~ 16‰) and ornithischians (~ 18‰), and likely indicating differences in metabolic and/or physiological processes or different utilization of plant organic compounds and/or plant parts. Since “Lo Hueco” titanosaur sauropods may have not been likely prey for theropods belonging to Dromaeosaurinae and Velociraptorinae subfamilies on account of differences in their body mass, no conclusive information concerning dinosaurian predator-prey δ¹³C offset could be attained. Although “Lo Hueco” crocodyliform material remains under study and no paleoecological conclusions have been drawn from a morphological standpoint, isotopic results indicate that they may have incorporated food items from brackish waters as shown by their δ¹³C values, whereas they avoided ingesting saline water and consumed preferentially freshwater, as suggested by their δ¹⁸O_Co₃ values, when compared with isotopic values of modern crocodilians inhabiting sub-tropical regions. “Lo Hueco” turtles show the lowest δ¹³C and δ¹⁸O_Co₃ values of the vertebrate assemblage likely indicating a diet based on a mixture of aquatic and terrestrial C₃ vegetation and/or invertebrates and ingestion of water with an inland source, a fact that agrees well with their taxonomic designation.
Supporting Information

S1 Dataset. Signature, level, sample, δ18OPO4 (‰ VSMOW), δ13C (‰ VPDB), δ18OCO3 (‰ VSMOW), and δ18OH2O (‰ VSMOW) values.

(XLS)

S2 Dataset. ANOVA and post-hoc tests for δ18OPO4, δ18OH2O, δ13C and δ18OCO3 values for the total dataset (TOTAL), and G1 and G2 levels.

(XLS)

S3 Dataset. Continent, country, station, latitude, longitude, altitude, year of record, mean annual temperature (MAT), temperature of the warmest months (July, August, September) (TWMs) and difference between TWMs and MAT (ΔTWMs-MAT).

(XLS)

S4 Dataset. A) ΔTWMs crocodyliforms-MATtheropods and ΔTWMs turtles-MATtheropods calculated using equations (4), (5) and (6) for the total dataset (TOTAL) and independently for levels G1.

(XLS)

S5 Dataset. Post-hoc Tukey p-values comparing pairs of ΔTWMs-MAT values for “Lo Hueco” locality, Late Cretaceous eastern Tethyan rudists [36, 38] and modern meteorological stations from different continents (http://www-naweb.iaea.org/napc/ih/IHS_resources_isohis.html).

(XLS)

Acknowledgments

We thank JL Sanz (Universidad Autónoma de Madrid), F Ortega (Universidad Nacional de Educación a Distancia), A Pérez-García (Universidad Complutense de Madrid) and A Torices (University of Alberta) for the access to the analyzed material and suggestions that helped to improve the manuscript. We are indebted to PL Koch (University of California Santa Cruz) for valuable comments and access to his laboratory, and to D Andreasen (University of California Santa Cruz) for his help with stable isotope analyses. O Sanisidro is acknowledged for illustrations. We thank editor P Dodson and reviewers C Suarez and R Amiot for their valuable comments.

Author Contributions

Conceived and designed the experiments: LD FBB OCM. Performed the experiments: LD. Analyzed the data: LD FBB OCM. Contributed reagents/materials/analysis tools: LD FBB OCM. Wrote the paper: LD FBB OCM.

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