Lethaia
AN INTERNATIONAL JOURNAL OF PALAEONTOLOGY AND STRATIGRAPHY

Inferring eco-climate parameters for the Pliocene Climate Optimum using frog body size as a new proxy

ALMUDENA MARTÍNEZ-MONZÓN, TOMÁŠ PŘIKRYL, CHRISTIAN SÁNCHEZ-BANDERA,
JOSEP F. BISBAL-CHINESTA, JORDI AGUSTÍ, GERARD CAMPENY VALL-LLOSERA,
BRUNO GÓMEZ DE SOLER AND HUGUES-ALEXANDRE BLAIN

LETHAIA

Climate conditions during the Pliocene Climate Optimum (3.2 – 2.5 Ma) are significant due to their proposed correspondence with future climate. There are various difficulties involved in obtaining terrestrial temperatures for this period, so new sources of information are therefore important. This work proposes a new approach based on frog body size, facilitating a palaeoclimate reconstruction of the palaeontological site of Camp dels Ninots (Caldes de Malavella, NE Spain), a Pliocene *Konservat-Lagerstätte,* dated at around 3.2 Ma. For this purpose, an extensive database of current populations of the genus *Pelophylax* from across Eurasia has been generated making it possible to establish a correlation between frog body size and eco-climate parameters such as temperature, precipitation rates and real evapotranspiration. Eco-climate values were obtained using OLS regression models and compared with previous palaeoclimate reconstructions from other archaeo-palaeontological sites of interest (Barranco León and Fuente Nueva 3, SE Spain). Our new proxy results in a palaeotemperature of 14.3 ± 2.6°C and a palaeoprecipitation rate of 846.8 ± 165.4 mm; according to primary productivity values, a 'Summer-green broad-leaved forest'-like biome is proposed for Camp dels Ninots, in line with previous palaeobotanical studies. The new values generated for the other sites follow the same trends as previous reconstructions, although with lower values in most cases, especially in terms of temperature. This method is a promising new approach to complement previous palaeoclimate reconstructions and could also generate new data.
☐ *Amphibians;* Pelophylax*; Primary productivity; Palaeoclimate; Camp dels Ninots; Spain*

Almudena Martínez-Monzón ✉ [amartinez@iphes.cat], Christian Sánchez-Bandera [csanchezbandera@gmail.com], Josep Francesc Bisbal-Chinesta [jbisbal@iphes.cat], Jordi Agustí [jagusti@iphes.cat], Gerard Campeny Vall-Llosera [gcampeny@iphes.cat], Bruno Gómez de Soler [bgomez@iphes.cat] and Hugues-Alexandre Blain [hablain@iphes.cat], IPHES-CERCA, Institut Català de Paleoecologia Humana i Evoluciò Social, Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain and Departament d'Història i Història de l'Art, Universitat Rovira i Virgili, Avinguda de Catalunya 35, 43002 Tarragona, Spain; Jordi Agustí [jagusti@iphes.cat], Institució Catalana de Recerca i Estudis Avançats (ICREA), Pg. Lluís Companys 23, 08010, Barcelona, Spain; Tomáš Přikryl [prikryl@gli.cas.cz], Institute of Geology, the Czech Academy of Sciences, Rozvojová 269, 165 00 Prague 6, Czech Republic; *manuscript received on 04/11/2022; manuscript accepted on 20/04/2023; manuscript published on 29/06/2023 in* Lethaia 56(2).

Today, one of the main focuses of climate research is on understanding how future increases in atmospheric carbon dioxide concentrations will influence temperature and general climate conditions (Haywood *et al*. 2019; Lunt *et al*. 2009). In this context, studies in the field of palaeoclimatology are looking closely at past warm periods, when CO_2 concentrations were analogous to current levels and those projected for the near future (Haywood *et al.* 2019). In this regard, the warm Pliocene climate is of great interest due to its similarity with the modelling predictions made for the future environment. Climate modelling simulations based on different scenarios of future greenhouse gas concentrations and other proxies indicates that the Mid-Piacenzian climate was the most recent period in the Earth's history with temperatures similar to those projected for the second half and the end of the 21st century (Burke *et al.* 2018; Lunt *et al.* 2009; Robinson *et al.* 2008; Dowsett *et al.* 2013). Additionally, this period known as the Pliocene climate optimum (3.2 to 2.5 Ma) is similar to today in many aspects, such as the position of the continents and oceans, the intensity of sunlight reaching the Earth's surface and the atmospheric CO_2 concentrations, for example (Robinson *et al.* 2008). Specifically, a less seasonal climate, 5°C warmer than present and 400–1000mm/year wetter, has been proposed for the middle Pliocene (ca. 3 Ma) in the European and Mediterranean region (Haywood *et al.* 2000).

Several methods of reconstructing past climates have been developed, for this and other geological periods, but none are exempt of difficulties (Blain *et al.* 2018a). There are a number of alternatives for reconstructing terrestrial temperatures and precipitation during the Pleistocene period as most species have extant representatives; however, the options decrease drastically when the line of the Pliocene is crossed. 'Nearest Living Relative' (NLR) palaeoclimate reconstruction methods, for both animal and plant taxa, entail the use of the current closest species to the fossil taxa (which does not itself have any living representatives). Using these proxies, the biological and ecological characters of the NRL are assumed to be the same as those of the fossil taxa, which at the outset generates a degree of uncertainty due to the possibility of evolutionary change in one or more traits.

In the field of palaeobotany, the physiognomic approach (i.e. the study of plant form) to palaeoclimate reconstruction does not require the identification of particular species, thus avoiding any possible biases related to NLR proxies (Spicer *et al.* 2021). Based on the plant form of woody dicots, a tool known as the Climate-Leaf Analysis Multivariate Program (CLAMP) has been developed, making it possible to derive climate parameters from macroscopic leaf traits commonly preserved in leaf fossils (see Spicer *et al.* 2021 for a review). In addition to the physiognomic approach, there are other plant-based palaeoclimate proxies, such as those involving fossil pollen records, as pollen is a well-established indicator of past vegetation changes (Chevalier *et al.* 2020). Even so, in some cases, these methods do rely on the use of NLRs.

In the animal kingdom, body size-metabolic rate approaches for reconstructing past conditions in poikilothermic animals, such as amphibians and reptiles, have yielded interesting results. For example, the study of the giant boid snake *Titanoboa cerrejonensis* from the Paleocene of South America (Head *et al.* 2009; 2013) has provided significant information about the equatorial climates during this period. This kind of approach complements other palaeoclimate reconstructions such as those utilising oxygen isotopes from planktonic foraminifera or palaeoflora (Head *et al.* 2009). The main weak point of this kind of analysis is still the fact that living relatives must be used instead of the exact species itself as a reference for the palaeoclimate reconstruction. There is ongoing debate about whether the ecology and biology of two related species can be considered equivalent or not (Blain *et al.* 2018a; Makarieva *et al.* 2009).

The palaeontological site of Camp dels Ninots (Caldes de Malavella, NE Spain) offers a golden opportunity to implement an actualistic approach for climatic reconstruction based on the body size of poikilothermic organisms while avoiding the shortcomings involved in the use of relative species as a current analogue. This Pliocene site, chronologically placed by various dating approaches into the mid-Piazencian during the Pliocene climate optimum, presents only two anuran taxa: representatives of the genus *Pelophylax* and a single specimen of the common toad (Bufo gr. *B. bufo*). In this case, there is no need to include related taxa in the method, as the first fossil record of the genus *Pelophylax* comes from the Early Oligocene of southern Germany (Sanchiz *et al.* 1993) and it has survived up to the present. *Pelophylax* is a widespread genus of green frogs currently ranging across Eurasia and north Africa. This genus, referred to as 'palaeartic water frogs', contains a high number of species as well as hybridogenic complexes. As suggested by its common name, *Pelophylax* is a very abundant group of frogs strongly linked to aquatic environments. For these reasons, the genus *Pelophylax* has the potential to fossilize in ponds, lakes and other aquatic environments, as happened in Camp dels Ninots and other *Konservat-Lagerstätte,* including the Miocene Libros site (Teruel, central Spain) (McNamara *et al.* 2012).

On the Iberian Peninsula, the use of amphibians and reptiles as environmental proxies is widely applied to the Quaternary, as these organisms are relatively sensitive to climate and environmental variations (see for example Blain *et al.* 2008; 2009; 2016; Martínez-Monzón *et al.* 2018a; 2018b; 2021; 2022). In addition, the current ecological niche of the species that comprise the herpetofaunal assemblages has been proved to constitute an excellent analogue to those of the past, thus generating accurate reconstructions of palaeoclimate conditions (Lobo *et al.* 2016). Nevertheless, most of the amphibian species found in European Pleistocene assemblages are still extant as this group behaved conservatively throughout the Neogene and Quaternary (Delfino 2005). This indicates the capacity of this group to cope with the successive climate and environmental variations that took place during this period by changing their bio-ecological features and adapting to new conditions (Martínez-Monzón *et al.* 2018b; 2021).

Body size is one of the main life-history traits used in ecology to evaluate how different biotic and abiotic factors, such as resources or climate, affect amphibian communities both in current populations as well as in the fossil record (Reading 2007; Lips *et al.* 2003; Martínez-Monzón *et al.* 2018a; 2022). This is because in poikilothermic animals like amphibians, body size is interlinked with a large number of key physiological, biochemical and ecological traits, including metabolic rate, fertility, thermoregulatory behaviour, water-conservatism, starvation resistance and many others (Bonner 2011; Angilletta *et al.* 2004; Olalla-Tárraga *et al.* 2009).

Previous studies of the fossil record have detected a strong relationship between temperature, primary productivity and anuran body size (Martínez-Monzón *et al.* 2018a; 2022). These works show that anuran body size increases when temperature decreases and resources are scarce. Despite the intricacies of the interrelationships between the different variables that influence body size changes, current data supports the patterns found in studies of the genus *Pelophylax*: a direct one for temperature (Amor *et al.* 2010; Gül *et al.* 2014; Erismis 2018); and an indirect one for primary productivity (Amor *et al.* 2010; Mohammadi *et al.* 2015). This relationship with eco-climate parameters opens up new ways to use anuran body size as a proxy for inferring past climate conditions. In addition to the work of Spicer et al. (2021) that uses leaf shape to reconstruct past climate conditions, physiognomy also has been applied to other groups such as non-biting midges (Diptera, Chironomidae) (Baranov *et al.* 2021). That work established a clear relationship between the latitudinal temperature gradient and the wing size of this group of insects, following a clear Bergmann cline (i.e. larger in colder environments).

The application of this finding to palaeoecological analysis is discussed because, as happens in most groups, methods based on reconstructing the climate tolerance of present-day Chironomidae that rely on NLR approaches turn out to be less effective the older the geological time periods studied. In these cases, using all available palaeoclimate proxies to reconstruct the past climate reduces the overall error of eco-climate estimations. With this in mind, this work looks at physiognomy as a valuable proxy when studying past climates and assesses the impact of climate on frog body size. The body size of *Pelophylax* sp. individuals from the Camp dels Ninots site are analysed and the data obtained is integrated with fossil and current data of *Pelophylax* body size, thus providing new insights into eco-climate reconstruction for this geological period, which is key in terms of research into future climates. Comparing the new data with previous reconstructions for other fossil assemblages, such as the Orce archaeo-palaeontological sites, is the key to validating this new method. The study of these sites makes the comparison possible, using *Pelophylax* body size as a new proxy together with other consolidated methods like the Mutual Ecogeographic Range (MER).

The study site: Camp dels Ninots

The Camp dels Ninots (from now on abbreviated as CN) palaeontological site is a Pliocene *Konservat-Lagerstätte* located in north-eastern Spain, in the town of Caldes de Malavella (Girona) (Fig. 1) at 84 m above sea level (Gómez de Soler *et al.* 2012). It is situated in an ancient volcanic area, known as the La Selva Depression, which forms part of the Catalan Volcanic Complex where today there is still important geothermal activity (Vehí *et al.* 2005). The site lies within a Pliocene palaeolake contained within a low-relief volcanic crater known as a maar. The lacustrine sedimentation led to the exceptional preservation of vertebrate faunal and floral remains (Gómez de Soler *et al.* 2012). The stratigraphical sequence of the Can Argilera excavation sector has been divided into four units, mainly comprising clays, carbonates and sandstones (Gómez

Fig. 1. Location of the studied populations of the genus *Pelophylax* across Eurasia. A red star marks the Camp dels Ninots fossil site (NE Spain). Link to the exact locations and their associated reference number (also in Table S1) in Google maps: (https://www.google.com/maps/d/u/1/edit?mid=12CnCKkAD_BrNM2PQqMe1_qNnZgR2oVA&usp=sharing).

de Soler *et al.* 2012). Within these divisions, it is in the 2.3 subunit (greenish laminated clays with diatoms, isolated sandstones and no carbonates) where most of the palaeontological remains have been found (Gómez de Soler *et al.* 2012).

The large mammal association suggests that CN is 'around the Mammals Neogene (MN) 15–16 transition or slightly later', about 3.2 Ma (Gómez de Soler *et al.* 2012). Additionally, stratigraphical and palaeomagnetic data points to an age within the interval 3.3 to 3.1 Ma (Jiménez-Moreno *et al.* 2013; Oms *et al.* 2015).

In general terms, palaeobotanical studies of CN point to a warm and wet environment, in line with the presence of tapirs (*Tapirus arvernensis*), as these may be indicative of a close humid environment, as this is the most likely habitat of this animal (Gómez de Soler *et al.* 2012). Botanical macroremains (leaves, wood, and seeds) found at CN indicate subtropical flora with lauroid-leaved evergreen trees (Gómez de Soler *et al.* 2012). The vegetation in the area is characteristic of a broadleaved riparian forest and laurel forest together with aquatic plants from the lake edge. This association is indicative of a pre-Mediterranean context characteristic of the mid-Piazencian, when subtropical ecosystems gave way to the establishment of the Mediterranean climate on the Iberian Peninsula (Robles *et al.* 2013). Estimated temperatures of this geochronological period are 2–3°C warmer than at present, a situation which has been projected for the end of the 21st century (Dowsett *et al.* 2013). Similar associations of plant taxa can be found today on the Canary Islands and in the humid subtropical forest of central Asia (Robles *et al.* 2013); these are both environments that display elevated ecosystem energy and a high biodiversity.

In terms of the faunal diversity recorded at CN, several vertebrate groups are represented, like freshwater fish, amphibians, reptiles, birds and mammals (Gómez de Soler *et al.* 2012; Přikryl *et al.* 2016). However, the species richness is rather low and to date only two taxa of anurans have been documented at CN. In Gómez de Soler *et al.* (2012), the fossil water frogs were attributed to *Pelophylax* cf. *perezi*, mainly based on biogeographical arguments, but a later biometric study suggested that the fossils may be within the variability of *Pelophylax* cf. *lessonae* (Blain *et al.* 2018b). As the taxonomical attribution has still to be investigated, in this work we refer to these fossils at the genus level only (*Pelophylax* sp.). As with anurans, CN has a low diversity of other animal groups as well as palaeoflora (Robles *et al.* 2013). Even though a deep taphonomical study has not yet been performed, the presence of a predominant semi-aquatic anuran may be due to 1) the taphonomic filter (aquatic taxa are preferentially preserved); 2) access difficulties and/or low light levels at the lake margins which would have limited the presence of other anuran species with a less marked aquatic character than genus *Pelophylax*.

Material and methods

The studied material comes from the Can Argilera excavation sector, subunit 2.3 of CN and was recovered during the 2005 to 2022 campaigns. This material consists of disarticulated bone elements collected *in situ* in the excavation. The skeletal element used here is the humerus, as this correlates well with the body size of living individuals, and also makes it possible to establish the sex of the animal (Martínez-Monzón *et al.* 2018; 2022). Articulated frogs were not included in this work because in most cases the orientation or visibility of their humeri prevents any measurements being taken. Additionally, SVL (Snout to Vent Length) is not directly measurable on the articulated specimens, as indicated by Sanchiz (1977), the flattening of specimens during fossilization may have altered the original shape of the frogs.

The body size of frogs from CN was reconstructed according to the methodology proposed by Martínez-Monzón *et al.* (2022). This method involves measuring the total width of the humeral distal epiphysis and then obtaining the body size as SVL by means of an OLS regression model for which the linear equation is $y = 0.0514x + 0.0443$ for males ($R^2 = 0.9$) and $y = 0.0452x + 0.285$ for females ($R^2 = 0.9$) (see Martínez-Monzón *et al.* 2022).

To construct a relational database including the body size of current populations of the genus *Pelophylax* from across Eurasia and their associated climate parameters, an exhaustive bibliographical search was performed, mainly in the Scopus, Google Scholar, and Researchgate databases using the main research terms '*Pelophylax*; Water frogs; Pond frogs; Body size; Adult size; SVL; Morphometry; Morphology; Sexual Size Dimorphism; Body condition; Growth; Population; Demography; Ecology' combined with names of the countries in Europe and Asia and also with the complete names of the various species of the genus *Pelophylax* present in these areas (Fig. 1; Table S1). Only papers with the body size data expressed as SVL, written in English, published in indexed journals and with no evident bias that could affect body size were selected. Modern climate values (1970–2000) for mean annual temperature (MAT) and mean annual precipitation (MAP) were extracted from the climate layers of WorldClim v. 2.1 with 30-arc second resolution grids (Fick & Hijmans 2017). A buffer of 20 km was created around populational geographic data (points) to obtain more representative and accurate climate values. The same climate parameters were calculated for present-day Caldes de Malavella (1970–2000). The data sets were processed using the ArcGIS v. 10.3 app (ESRI, 2014). The mean and standard deviation were calculated using the statistical software IBM SPSS Statistics 22 (IBM Corporation, released 2013).

In relation to primary productivity, the real evapotranspiration (RET) was obtained using Turc's formula (Turc 1961, in Remenieras 1974), which enables the evapotranspiration data for both fossil assemblages and current locations to be obtained. RET values were converted into net primary productivity (NPP) via the Montreal model (Box 1988).

$$RET = \frac{P}{\sqrt{0.9 + P^2/L^2}}$$

Turc's real evapotranspiration formula in mm/year, where P indicates the average precipitation also expressed in mm/year and $L = 300 + 25t + 0.05t^3$, where t is the mean annual temperature in °C.

$$NPP = 1350\ (1 - e^{-0.0009695\ (RET-20)})$$

Montreal model (Box 1988) which relates NPP (in g C/m²) to RET (in mm/year).

Body size data from Eurasian *Pelophylax* populations and eco-climate parameters (i.e. MAT, MAP and RET) for current and fossil locations were integrated by means of an OLS regression model. In addition, a Pearson correlation was applied to complement the results of the regression models. All the analyses were conducted using R software (R Core Team), R version 3.2.5 (2016-04-14), and a significance level of $\alpha = 0.05$. The R-code and the related excel file are included as supplementary material.

Results

In this section the main results of the bibliographic search are translated into an extended dataset for current populations. On the basis of this database, models are developed that can be applied to fossil locations and used to reconstruct past eco-climate conditions.

Current populations and eco-climate parameters

A total of 72 populations of several species of the genus *Pelophylax* were analysed (Table S1). These populations are from 22 different countries in Europe and Asia, from the Azores (38°40′N 28°04′O38°40′N 28°04′O) to Japan (36°N 138°E) (Fig. 1). Using the data from these Eurasian populations, OLS regression models were developed involving the body size (SVL) of the whole population and three of the most relevant eco-climate predictors (MAT, MAP and RET). The results of these models are presented in Table 1 and are represented graphically in Figure 2. All of them were significant ($p < 0.05$) and in all cases a negative correlation with body size was found. The Pearson correlation test also supported these models. Despite other fits being tested, the linear model provided the best results for our data. The equations of these models are: $MAT = -0.137SVL + 21.453$; $MAP = -6.318SVL + 1178.388$; $RET = -3.581SVL + 747.656$. The MAT and RET models display higher adjusted R^2 and correlation coefficients, while the MAP model presents lower values (Table 1). Even though there is a non-minor standard error (MAT ± 2.6 °C; MAP ± 77.9 mm/year; RET ± 165.4mm), there is a clear relationship between these parameters and the SVL of the genus *Pelophylax* throughout its range.

Application to Camp dels Ninots

A total of 26 fossil humeri, representing 10 females and 16 males, were available for this study. Based on the method from Martínez-Monzón *et al.* (2022), the mean body size of the entire Camp dels Ninots frog population was established as 52.5 mm, with females being bigger than males (54.5 mm and 51.2 mm respectively).

Table 1. Results of OLS regression models and Pearson correlation test between *Pelophylax* SVL (snout to vent length) and eco-climate parameters (MAT: mean annual temperature; MAP: mean annual precipitation; RET: real evapotranspiration) across Eurasia. In the first case the adjusted R^2 is presented together with the significance level, the degrees of freedom and the slope. For the correlation test, in addition to the significance level and the degrees of freedom, the correlation coefficient and the T statistic are shown

OLS regression models				
Eco-climate parameter	**Adj. r^2**	**p-value**	**D.F.**	**Slope**
MAT	0.145	<0.001	70	−0.137
MAP	0.078	0.01	70	−6.318
RET	0.115	0.002	70	−3.581
Pearson correlation test				
Eco-climate parameter	**Correlation coefficient**	**p-value**	**D.F.**	**T**
MAT	−0.396	<0.001	70	−3.608
MAP	−0.302	0.01	70	−2.652
RET	−0.357	0.002	70	−3.193

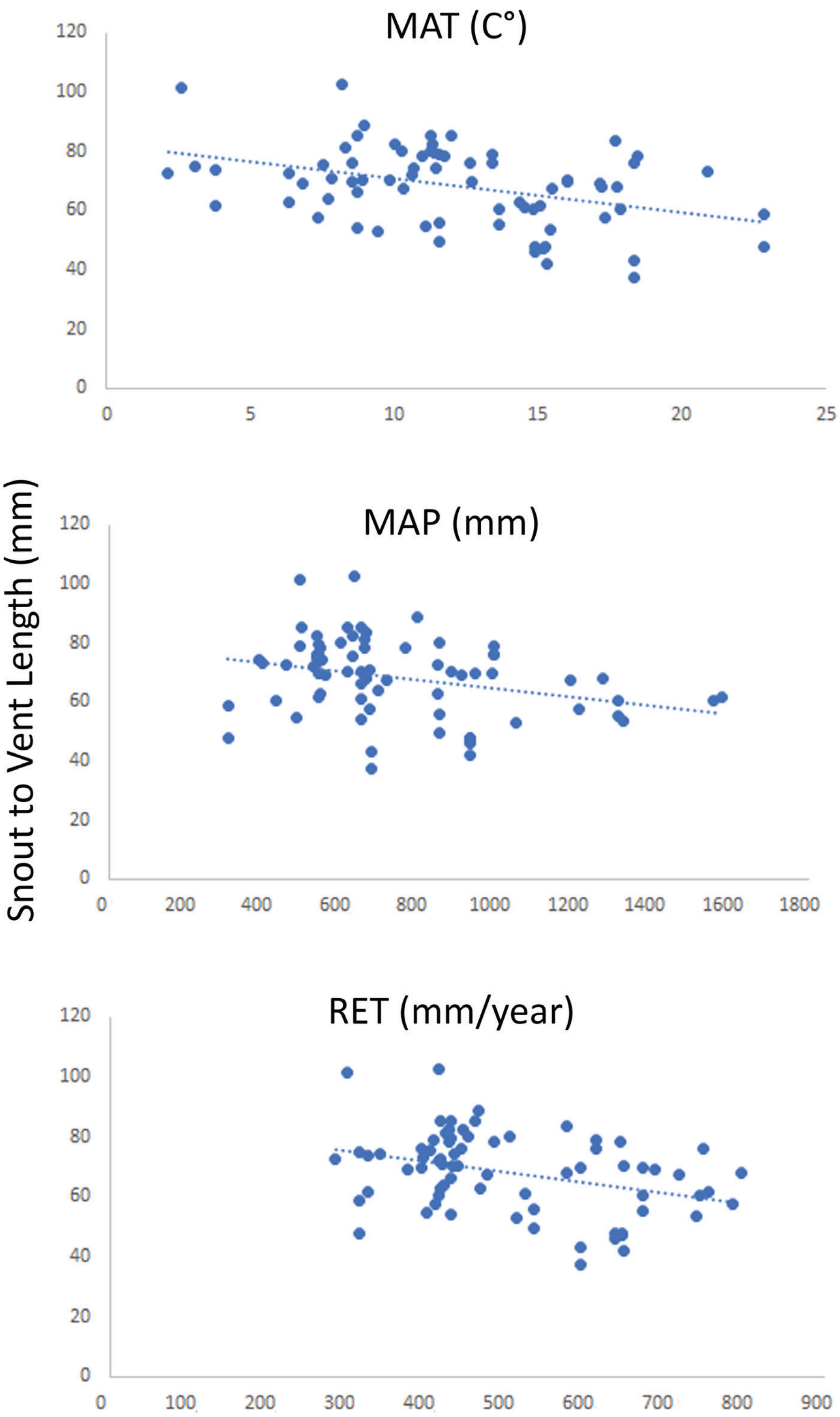

Fig. 2. Ordinary Least Square (OLS) regression models performed using the SVL (snout to vent length) of *Pelophylax* populations across Eurasia and Mean annual temperature (MAT; C°); Mean annual precipitation (MAP; mm) and Real evapotranspiration obtained using Turc's formula (RET; mm/year).

Table 2. SVL (snout to vent length) values in mm in fossil populations of *Pelophylax* sp. and reconstructed eco-climate parameters based on the OLS regression models presented in this work with the standard error. MAT (mean annual temperature in °C); MAP (mean annual precipitation in mm); RET (real evapotranspiration in mm/year). Comparison with previous palaeoclimate reconstructions from the Orce archaeo-palaeontological sites (BL and FN3) obtained using the Mutual Ecogeographic Range method (MER) with the mean standard deviation and RET values derived from Turc's formula

Sites		**SVL**	**MAT (±2.6)**	**MAT (± 1.1)**	**MAP (±165.4)**	**MAP (±143)**	**RET (±77.9)**	**RET**
CN		52.5	14.3		846.8		559.7	
Orce	BL-E	63.2	12.8	16.5	779.4	834.7	521.5	640.3
	BL-D2	58.9	13.4	16.6	806.1	792.8	536.7	624.7
	BL-D1	60.6	13.2	16.8	795.8	767.3	530.8	617.2
	FN3-5	62.9	12.9	14.7	780.9	617.7	522.4	510.7

After interpolating the Camp dels Ninots data into the literature-based models generated (Table S1; Table 1), MAT, MAP and RET were reconstructed for this site. Temperature and precipitation presented values of 14.3 ± 2.6°C and 846 ± 165.4 mm, respectively. The productivity of the ecosystem, expressed as RET, yielded a value of 559.7 ± 77.9 mm/year (Table 2). This latter value has been translated into NPP by means of the Montreal mode, giving a value of NPP = 550 g C/m^2 per year.

Application to other fossil assemblages: BL and FN3

In terms of applying these frog body size models to reconstruct past eco-climate parameters for fossil assemblages, they were also employed to obtain data of MAP, MAT and RET for the Orce archaeo-palaeontological sites: the three levels of Barranco León (E, D2 and D1) and level 5 from Fuente Nueva 3, from now on abbreviated as BL and FN3 respectively (Table 2).

Within the BL and FN3 sites, the mean body size of the water frog populations is between the maximum and minimum values of 58.9 mm in BL-D2 and 63.2 mm in BL-E (Table 2). Sex-separated data for the entire dataset can be found in Martínez-Monzón *et al.* (2022; Table 1). The minimum mean values of all the eco-climate parameters were recorded for BL-E, followed closely by FN3-5 in some cases, while the maximum values were found for BL-D2 (Table 2).

Discussion

Original data on the body size of the CN water frog population has been established with its consequent palaeoclimate implications. Applying the proposed models to fossil assemblages facilitated the first reconstructions of MAT, MAP and RET for CN, as well as some new data for the BL and FN3 sites.

Frog body size and climate: comparisons with fossil and current data

The water frog population from CN exhibits the sexual size dimorphism typical for the genus *Pelophylax,* with females being larger than males. Within the fossil assemblages studied, CN presents higher values of MAT and MAP, while BL and FN3 display lower values with a smaller variation rank between them (Table 2). The coldest temperatures in the studied levels were found in BL-E, with 12.8°C, which is also the driest, presenting a MAP of 779.4 mm. The same pattern is repeated with respect to RET, the higher primary productivity being at the CN site and the least in level BL-E (Table 2).

Body size values from CN are quite similar to those from BL level D2, with CN frogs being slightly smaller than those from BL-D2. From an environmental point of view, the BL and FN3 sites were part of a fresh water to oligosaline shallow lacustrine environment (Oms *et al.* 2011; Anadón *et al.* 2015). Herpetofauna and other proxies such as macrofauna indicate that the environments around the lake were characteristic of a Mediterranean woodland which probably represented a humid period corresponding to an interglacial stage (Sánchez-Bandera *et al.* 2020; Saarinen *et al.* 2021). Overall, the rich palynoflora (Ochando *et al.* 2022) together with the considerable number of large and small vertebrate taxa (Martínez-Navarro *et al.* 2010; Agustí *et al.* 2010) indicate that the BL and FN3 sites had a very diverse ecosystem. According to the negative body size – temperature relationship within the genus *Pelophylax* (Amor *et al.* 2010; Erismis 2018), as in other anurans (Hemelaar 1988; Schäuble 2004; Olalla-Tárraga & Rodríguez, 2007; Gül *et al.* 2014), this mean that the MAT at CN would have been higher than for BL-D2, which according to previous reconstructions was 16.6 ± 0.8°C. However, when looking at the values obtained using our new method, the temperature appears somewhat lower, specifically 13.4 ± 2.6°C (Table 2). The error in the two reconstructions generates an overlap between the figures, and in addition, the overall trend in the new MAT reconstruction for BL and FN3 follows the pattern previously established by Sánchez-Bandera *et al.* (2023) although with lower values, particularly in the case of BL-E (Table 2). In terms of precipitation, the mean values proposed for BL-D1 and D2 are generally in line with previously published data; this is not true of BL-E and FN3-5, where there is a slight divergence. Again, when the standard errors of the two reconstructions are taken into account, these differences disappear, thereby reinforcing this new method.

Using a different approach, the Canary Island laurel forests have been proposed as a current analogue to the CN ecosystem (Robles *et al.* 2013). 31 leaf macroremains have been recovered from CN and attributed to eight angiosperm taxa belonging to the families Lauraceae, Juglandaceae, Fagaceae, Betulaceae, Salicaceae, Fabaceae, and the superorder Poanae. Within this leaf assemblage, the Lauraceae family is the most abundant and is represented by *Laurophyllum* sp. and *Daphnogene polymorpha*. The palaeoflora present at Camp dels Ninots comprises a combination of Arcto-Tertiary and palaeotropical elements in a pre-Mediterranean context in which three main plant associations can be distinguished: firstly, there was some aquatic vegetation characteristic of the shallow waters at the margin of the *maar*; secondly, there was a riparian mesophilic forest and, finally, a dense and shady laurel forest, considered to be one of the last representatives of this type of vegetation on the Iberian Peninsula (Robles *et al.* 2013). Despite the differences in the orography and other physical determinants, the most similar current flora to that evidenced from the Camp dels Ninots site is found in the subtropical humid forests of central and southern Asia and the laurel forest of the Canary Islands. These forests are composed of broad-leaved evergreen trees, arboreal and scarcer shrubby deciduous elements and sometimes coniferous ones.

Specifically to the Canary Island laurel forest communities, Walter & Lieth (1967, reported in Morales *et al.* 2002) recorded a mean annual temperature of 14°C, with a mean daily maximum in the warmest month of 22.6°C and a mean daily minimum in the coldest month of 6.9°C. When looking at precipitation data, the mean values from the Canary Islands (MAP = 733 mm. Data from Walter & Lieth (1967 *in* Morales *et al.* 2002) are only very slightly lower than the MAP modelled for CN (Table 2), and that difference disappears if the standard error is taken into account. In the case of the Canary Island precipitation pattern, there is a dry period over the summer months. Laurel forest ecosystems in this region are classified according to Köppen's climate classification (Köppen 1918) and Kottek's maps (Kottek *et al.* 2006) as a Csb type of climate, meaning that they are temperate with a warm dry summer. This climate also presents high air humidity levels (an annual mean relative humidity of 82%) (Morales *et al.* 2002) and a mean monthly precipitation during the humid period of more than 100 mm.

The comparison with both current and fossil data suggests a Csb-type climate for CN (following Köppen's classification). The MAT would be around 14°C, and the MAP from 700 - 850 mm, a climate proposal in line with the pre-Mediterranean context of the CN site.

New insights into primary productivity at Camp dels Ninots

Previous work has shown that female body size in *Pelophylax perezi* correlates with primary productivity in fossil assemblages more than with other eco-climate parameters, with female water frogs becoming smaller as primary productivity increases (Martínez-Monzón *et al.* 2022). The inverse relationship yielded by our OLS regression model between body size and RET at a global scale fits this pattern. This model proposes a RET of 559.7 ± 77.9 mm/year for CN according to water frog body size. In this case, as with temperature, the RET values are lower than those previously established (Table 2). Unlike the other climate parameters, the RET reconstructions for the BL and FN3 sites using the different methods do not overlap even if the standard error is taken into account.

On the basis of the climate record provided by Walter & Lieth (1967 *in* Morales *et al.* 2002) and using Turc's formula, the RET value obtained for the Canary Islands is 551.42 mm/year. This figure is fairly similar to that reconstructed for CN (Table 2), supporting the analogy established between the CN fossil environment and the Canary archipelago. The high quantity of biomass in subtropical environments, as suggested for CN, and the high environmental humidity characteristic of forest and lake-riparian ecosystems is also in line with this data. Translating this RET data to NPP by means of the Montreal model (Box 1988), a value of NPP = 550 g C/m^2 per year for CN is obtained. Integrating this number into the NPP data for major biomes estimated by global scale models such as the Montreal model (Alexandrov *et al.* 2002, see Table S1), the CN palaeontological site would have been a 'Summer-green broad-leaved forest', in line with the past plant communities as evidenced by the analysis of the palaeoflora (Robles *et al.* 2013).

New data for Camp dels Ninots and the Pliocene climate

According to current knowledge of the Pliocene climate, our results are somewhat controversial in terms of previous studies indicating that the Pliocene was 5°C warmer than today, and also 400–1000 mm/year wetter in the European and Mediterranean region (Haywood *et al.* 2000). In line with these predictions, a temperature of about 19.4°C and a precipitation range of 1170–1770 mm would be expected for the Pliocene climate optimum in the CN location (Caldes de Malavella, current MAT and MAP 14.4°C and 743 mm, respectively). Even though the comparison with BL-D2 suggests higher palaeotemperature for CN than our new method (Table 2), in any of those cases the temperature predicted for the Pliocene climatic optimum is reached even if the standard error of the reconstructions is considered. The palaeotemperature for CN would have been at most 3°C warmer than the present day when looking at the comparisons with BL-D2, and 2.5°C warmer with our new proxy. However, in terms of palaeoprecipitation, our new data for CN is generally in line with the predictions, with a maximum value of 1012.2 mm. The greater correspondence with other palaeoclimate reconstructions (Sánchez-Bandera *et al.* 2023) as well as the predicted values for the Pliocene climate optimum for precipitation rather than for temperatures may be related to the strong aquatic character of the genus *Pelophylax*.

Despite the discordance generated by the new CN temperature data in terms of the Pliocene climate optimum, our eco-climate parameters are in line with the palaeobiome suggested by the palaeoflora and micro/macrofaunal assemblage. This fact gives more weight to our reconstruction than the general trend established for the Mediterranean region, due to the restricted studied area. The CN deposits probably represent a more temperate moment within the transition to the Mediterranean climate, and the increase of temperatures up to 5°C warmer to present predicted for the Pliocene climate optimum in the Mediterranean region would take place earlier or later.

The warmer temperatures predicted for the end of the 21st century will generate ecosystem changes that will undoubtedly affect amphibian communities. The fossil record has shown that climate change affects anurans, but previous studies on the Iberian Peninsula show that those changes were accompanied by physiological adaptation and resilience (Martínez-Monzón *et al.* 2021; 2022). If the Pliocene climate optimum at CN is an analogue of future climate, changes in the MAT and MAP may not be the main threat for anuran populations, as there is no evidence of a population decline. Nevertheless, other climate change related threats may involve the distribution of precipitation over the year, which could cause periods of intense summer droughts in the Mediterranean region. Even so, the human impact, which leads to habitat degradation, pollution, the introduction of alien species and vehicle collisions, has proved to be a determining factor in the survival of this endangered group (Cox *et al.* 2006; Greenberg *et al.* 2018).

Conclusions

The following conclusions may be drawn from this study:

1. There are clear negative linear relationships between eco-climate parameters (MAT, MAP and RET) and the SVL of frogs from the *Pelophylax* genus across Eurasia.
2. The average body size of the *Pelophylax* sp. population at CN is 52.5 mm and follows the current pattern of sexual size dimorphism where females are bigger than males. Comparing this with current data, the body size of *Pelophylax* sp. from CN suggests a temperate climate with a warm and dry summers. Our new method yielded a palaeotemperature of 14.28 ± 2.63°C and a palaeoprecipitation rate of 846.76 ± 165.43 mm. Our new data compared with that formerly elicited for the BL and FN3 fossil assemblages alludes to higher mean annual temperature values at CN, above 16.55°C.
3. In terms of the ecosystem's primary productivity, the NPP values point to a 'Summer-green broad-leaved forest'-like biome. It is likely that the environment at the CN palaeontological site is a past analogue of the current laurel forest on the Canary Islands, as suggested by previous palaeobotanical studies.
4. The reconstructed MAT for the CN site is not in line with the proposals for the Pliocene climate optimum, being lower than expected. In contrast, the precipitation rates do show values much closer to those established for this period. Despite this divergence in temperature data, all reconstructed eco-climate parameters match the 'Summer-green broad-leaved forest'-like biome suggested previously for the CN site.

Acknowledgements.– This study is part of the projects 'The Late Pliocene lower vertebrates (fishes and frogs) from the *Konservat-Lagerstätte* Camp dels Ninots (north-eastern Spain)' of the Czech Science Foundation (GAČR 21-33751S), 'El Plio-pleistocè del Camp dels Ninots i la depressió prelitoral: evolució paleoclimàtica, dispersions faunístiques i humanes III' of the Servei d'Arqueologia i Paleontologia (Direcció General del Patrimoni cultural, Generalitat de Catalunya, CLT009/22/00043), and 'Estudio paleontologico y preparación de los microvertebrados del Plioceno de Camp dels Ninots, Girona' of the Spanish Ministry of Science and Innovation (CGL2011-13293-E/BTE). We thank the excavation team of Camp dels Ninots and two anonymous reviewers for their comments. AM-M, CS-B, J-FB-C, JA, GCV, BGS and H-AB are funded by the CERCA Programme/Generalitat de Catalunya; AM-M, CSB and H-AB by Project PID2021-122533NB-I00; and JA, GCV and BGS by Project PID2021-123092NB-C21 from the Spanish Ministry of Science and Innovation (MICINN/AEI/10.13039/501100011033/FEDER 'Una manera de hacer Europa'). AM-M is supported by the Agència de Gestió d'Ajuts Universitaris i de Recerca (AGAUR) and the Departament d'Empresa i Coneixement de la Generalitat de Catalunya grant 2021 FI_B2 00207. TP was supported by the Institute of Geology of the Czech Academy of Sciences (RVO67985831). CS-B is supported by a FPI Predoctoral Scholarship (PRE2020-094482) associated to project CEX2019-000945-M-20-1 with the financial sponsorship of the Spanish Ministry of Science and Innovation. AM-M, CS-B, J-FB-C, JA, GCV, BGS and H-AB belongs to the Consolidated Research Group 'Paleoecology of Pliocene and Pleistocene and Human Dispersals (PalHum)', AGAUR-Generalitat de Catalunya, 2021SGR-1238. The Institut Català de Paleoecologia Humana I Evolució Social (IPHES-CERCA) received financial support from the Spanish Ministry of Science and Innovation through the 'María de Maeztu' programme for Units of Excellence (CEX2019-000945- M).

References

Agustí, J., Blain, H.-A., Furió, M., De Marfá, R. & Santos-Cubedo, A. 2010: The Early Pleistocene small vertebrate succession from the Orce region (Guadix-Baza Basin, SE Spain) and its bearing on the first human occupation of Europe. *Quaternary International 223–224*, 162–169. https://doi.org/10.1016/j.quaint.2009.12.011

Alexandrov, GA., Oikawa, T. & Yamagata, Y. 2002: The scheme for globalization of a process-based model explaining gradations in terrestrial NPP and its application. *Ecological Modelling 148*, 293–306. https://doi.org/10.1016/S0304-3800(01)00456-2

Amor, N., Farjallah, S., Merella, P. & Said, K. 2010: Karyological and morphometric variation of the North African green frog *Pelophylax saharicus* (Anura) in north-eastern Africa. *Current Zoology 56*, 678–686. https://doi.org/10.1093/czoolo/56.6.678

Anadón, P., Oms, O., Riera, V. & Julià, R. 2015: The geochemistry of biogenic carbonates as a paleoenvironmental tool for the Lower Pleistocene Barranco León sequence (BL-5D, Baza Basin, Spain). *Quaternary International 389*, 70–83. https://doi.org/10.1016/j.quaint.2014.09.062

Angilletta Jr, M.J., Steury, T.D. & Sears, M.W. 2004: Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology 44*, 498–509. https://doi.org/10.1093/icb/44.6.498

Baranov, V., Jourdan, J., Hunter-Moffatt, B., Noori, S., Schölderle, S., & Haug, J.T. 2021: Global size pattern in a group of important ecological indicators (Diptera, Chironomidae) is driven by latitudinal temperature gradients. *Insects 13*, 34. https://doi.org/10.3390/insects13010034

Blain, H.A., Bailon, S. & Cuenca-Bescós, G. 2008: The Early–Middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxies at the Gran Dolina site, Atapuerca, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology 261*, 177–192. https://doi.org/10.1016/j.palaeo.2008.01.015

Blain, H.-A., Bailon, S., Cuenca-Bescós, G., Arsuaga, J.L., Bermúdez de Castro, J.M. & Carbonell, E. 2009: Long-term climate record inferred from early-middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca, Spain. *Journal of Human Evolution 56*, 55–65. https://doi.org/10.1016/j.jhevol.2008.08.020

Blain, H.-A., Lozano-Fernández, I., Agustí, J., Bailon, S., Menéndez, L., Espígares Ortiz, M.P., Ros-Montoya, S., Jiménez Arenas, J.M., Toro, I., Martínez-Navarro, B. & Sala, R. 2016: Refining upon the climatic background of the early Pleistocene hominid settlement in Western Europe: Barranco León and Fuente Nueva-3 (Guadix- Baza basin, SE Spain). *Quaternary Science Reviews 144*, 132–144. https://doi.org/10.1016/j.quascirev.2016.05.020

Blain, H.A., Cruz-Silva, J.A., Jiménez-Arenas, J.M., Margari, V. & Roucoux, K. 2018a: Towards a Middle Pleistocene terrestrial climate reconstruction based on herpetofaunal assemblages from the Iberian Peninsula: State of the art and perspectives. *Quaternary Science Reviews 191*, 167–188. https://doi.org/10.1016/j.quascirev.2018.04.019

Blain, H.-A., Lozano-Fernández, I., Martínez-Monzon, A., Přikryl, T., Oms, O., Anadón, P., Rodríguez-Salgado, P., Agustí, J., Campeny, G. & Gómez de Soler, B. 2018b: Water Frogs (Anura, Ranidae) from the Pliocene Camp dels Ninots Konservat-Lagerstätte (Caldes de Malavella, NE Spain), 162–163. *IAVCEI – 7th International Maar Conference*, Olot.

Bonner, J. T. 2011: *Why Size Matters: from Bacteria to Blue Whales*. Princeton University Press, Princeton.

Box, E.O. 1988: Estimating the seasonal carbon source–sink geography of a natural, steady-state terrestrial biosphere. *Journal of Applied Meteorology and Climatology 27*, 1109–1124. https://doi.org/10.1175/1520-0450(1988)027<1109:ETSCSS>2.0.CO;2

Burke, K.D., Williams, J.W., Chandler, M.A., Haywood, A.M., Lunt, D.J. & Otto-Bliesner, B.L. 2018: Pliocene and Eocene provide best analogs for near-future climates. *Proceedings of the National Academy of Sciences 115,* 13288–13293. https://doi.org/10.1073/pnas.1809600115

Chevalier, M., Davis, B.A., Heiri, O., Seppä, H., Chase, B.M., Gajewski, K., Lacourse, T., Telford, R.J., Finsinger, W., Guiot, J., Kühl, N., Maezumi, S.Y., Tipton, J.R., Carter, V.A., Brussel, T., Phelps, L.N., Dawson, A., Zanon, M., Vallé, F., Nolan, C., Mauri, A., de Vernal, A., Izumi, K., Holmström, L., Marsicek, J., Goring, S., Sommer, P.S., Chaput, M. & Kupriyanov, D. 2020: Pollen-based climate reconstruction techniques for late Quaternary studies. *Earth-Science Reviews 210,* 103384. https://doi.org/10.1016/j.earscirev.2020.103384

Cox, N., Chanson, J. & Stuart, S. 2006: *The Status and Distribution of Reptiles and Amphibians of the Mediterranean Basin* (No. 2). IUCN.

Delfino, M. 2005: The past and future of extant amphibians. *Science 308*, 49–51. https://doi.org/ 10.1126/science.308.5718.49c

Dowsett, H.J., Foley, K.M., Stoll, D.K., Chandler, M.A., Sohl, L.E., Bentsen, M.B.L., Bragg, F. J., Chan, W.-L., Contoux, C., Dolan, A.M., Haywood, A.M., Jonas, J.A., Jost, A., Kamae, Y., Lohmann, G., Lunt D.J., Nisancioglu, K.H., Abe-Ouchi, A., Ramstein, G., Riesselman, C.R., Robinson, M.M., Rosenbloom, N.A., Salzmann, U., Stepanek, C., Strother, S.L., Ueda, H., Yan, Q. & Zhang, Z. 2013: Sea surface temperature of the mid-Piacenzian ocean: a data-model comparison. *Science Reports 3*, 1–8. https://doi.org/10.1038/srep02013

Erismis, U.C. 2018: Age, size, and growth of the Turkish endemic frog *Pelophylax caralitanus* (Anura: Ranidae). *The Anatomical Record 301*, 1224–1234. https://doi.org/10.1002/ar.23758

Environmental Systems Research Institute (ESRI) 2014. ArcGIS. Release: 10.3. Redlands.

Fick, S.E. & Hijmans, R.J. 2017: WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology 37*, 4302–4315. https://doi.org/10.1002/joc.5086

Gómez de Soler, B., Campeny Vall-Llosera, G., van der Made, J., Oms, O., Agustí, J., Sala, R., Blain, H.-A., Burjachs, F., Claude, J., García Catalán, S., Riba, D. & Rosillo, R. 2012: A new key locality for the Pliocene vertebrate record of Europe: the Camp dels Ninots maar (NE Spain). *Geologica Acta 10*, 1–17. https://doi.org/10.1344/105.000001702

Greenberg, D.A., Palen, W.J., Chan, K.C., Jetz, W. & Mooers, A.Ø. 2018: Evolutionarily distinct amphibians are disproportionately lost from human-modified ecosystems. *Ecology Letters 21*, 1530–1540. https://doi.org/10.1111/ele.13133

Gül, S., Özdemir, N., Kumlutas, Y. & Ilgaz, Ç. 2014: Age structure and body size in three populations of *Darevskia rudis* (Bedriaga, 1886) from different altitudes. *Herpetozoa 26*, 151–158.

Haywood, A.M., Valdes, P.J., Aze, T., Barlow, N., Burke, A., Dolan, A.M., von der Heydt, A. S., Hill, D.J., Jamieson, S.S.R., Otto-Bliesner, B.L., Salzmann, U., Saupe, E. & Voss, J. 2019: What can palaeoclimate modelling do for you?. *Earth Systems and Environment 3*, 1–18. https://doi.org/10.1007/s41748-019-00093-1

Haywood, A.M., Sellwood, B.W. & Valdes, P.J. 2000: Regional warming: Pliocene (3 Ma) paleoclimate of Europe and the Mediterranean. *Geology 28*, 1063–1066. https://doi.org/10.1130/0091-7613(2000)28<1063:RWPMPO>2.0.CO;2

Head, J.J., Bloch, J.L., Hastings, A.K., Bourque, J.R., Cadena, E.A., Herrera, F.A., Polly, P.D. & Jaramillo, C.A. 2009: Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature 457*, 715–717. https://doi.org/10.1038/nature07671

Head, J.J., Grinell, G.F., Holroyd, P.A., Hutchison, J.H. & Ciochon, R.L. 2013: Giant lizards occupied herbivorous mammalian ecospace during the Paleogene greenhouse in Southeast Asia. *Proceedings of the Royal Society B: Biological Sciences 280*, 20130665. https://doi.org/10.1098/rspb.2013.0665

Hemelaar, A. 1988: Age, growth and other population characteristics of *Bufo bufo* from different latitudes and altitudes. *Journal of Herpetology 22*, 369–388. https://doi.org/10.2307/1564332

IBM Corp. Released 2013. IBM SPSS *Statistics for Windows, Version 22.0*. Armonk, New York.

Jiménez-Moreno, G., Burjachs, F., Expósito, I., Oms, O., Carrancho, Á., Villalaín, J.J., Agustí, J., Campeny, G., Gómez de Soler, B. & van der Made, J. 2013: Late Pliocene vegetation and orbital-scale climate changes from the western Mediterranean area. *Global and Planetary Change 108*, 15–28. https://doi.org/10.1016/j.gloplacha.2013.05.012

Köppen, W. 1918: Klassifikation der Klimate nach Temperatur, Niederschlag und Jahreslauf. *Petermanns Geographische Mitteilungen 64*, 243–248.

Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F. 2006: World Map of Köppen-Geiger Climate Classification updated. *MeteorologischeZeitschrift 15*, 259–263. https://doi.org/10.1127/0941-2948/2006/0130

Lips, K.R., Reeve, J.D. & Witters, L.R. 2003: Ecological traits predicting amphibian population declines in Central America. *Conservation Biology 17*, 1078–1088. https://doi.org/10.1046/j.1523-1739.2003.01623.x

Lobo, J.M., Martínez-Solano, I. & Sanchiz, B. 2016: A review of the palaeoclimatic inference potential of Iberian Quaternary fossil batrachians. *Palaeobiodiversity and Palaeoenvironments 96*, 125–148. https://doi.org/10.1007/s12549-015-0224-x

Lunt, D.J., Haywood, A.M., Schmidt, G.A., Salzmann, U., Valdes, P.J. & Dowsett, H.J. 2010: Earth system sensitivity inferred from Pliocene modelling and data. *Nature Geoscience, 3*, 60–64. https://doi.org/10.1038/ngeo706

Makarieva, A.M., Gorshkov, V.G. & Li, B.L. 2009: Re-calibrating the snake palaeothermometer. *Nature 460*, E2–E3. https://doi.org/10.1038/nature08223

Martínez-Monzón, A., Blain, H.A., Cuenca-Bescós, G. & Rodríguez, M.Á. 2018: Climate and amphibian body size: a new perspective gained from the fossil record. *Ecography 41*, 1307–1318. https://doi.org/10.1111/ecog.03440

Martínez-Monzón A.M., Bisbal-Chinesta, J.F. & Blain, H.-A. 2018b: El Cuaternario ibérico como escenario para el estudio de patrones globales biogeográficos y macroecológicos en anfibios y reptiles. *Ecosistemas 27*, 87–95. https://doi.org/10.7818/ECOS.1435

Martínez-Monzón, A., Cuenca-Bescós, G., Bisbal-Chinesta, J.F. & Blain, H.A. 2021: One million years of diversity shifts in amphibians and reptiles in a Mediterranean landscape: Resilience rules the Quaternary. *Palaeontology 64*, 673–686. https://doi.org/10.1111/pala.12547

Martínez-Monzón, A., Sánchez-Bandera, C., Fagoaga, A., Oms, O., Agustí, J., Barsky, D., Solano-García, J., Jiménez-Arenas, J.M. & Blain, H.A. 2022: Amphibian body size and species richness as a proxy for primary productivity and climate: the Orce wetlands (Early Pleistocene, Guadix-Baza Basin, SE Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology 586*, 110752. https://doi.org/10.1016/j.palaeo.2021.110752

Martínez Navarro, B., Palmqvist, P., Madurell Malapeira, J., Ros Montoya, S., Espigares, M.P., Torregrosa, V. & Pérez Claros, J.A. 2010: '*La fauna de grandes mamíferos de Fuente Nueva-3 y Barranco León-5: estado de la cuestión*', 197–236. In: Toro, I., Martínez-Navarro, B., Agustí, J. (eds), *Ocupaciones humanas en el Pleistoceno Inferior y Medio de la cuenca de Guadix-Baza*. Consejería de Cultura,

McNamara, M.E., Orr, P.J., Alcalá, L., Anadón, P. & Peñalver, E. 2012: What controls the taphonomy of exceptionally preserved taxa—environment or biology? A case study using frogs from the Miocene Libros konservat-lagerstätte (Teruel, Spain). *Palaios 27*, 63–77. https://doi.org/10.2110/palo.2010.p10-126r

Mohammadi, Z., Khajeh, A., Ghorbani, F. & Kami, H.G. 2015: A biosystematic study of new records of the marsh frog *Pelophylax ridibundus* (Pallas, 1771) (Amphibia: Ranidae) from the southeast of Iran. *Journal of Asia-Pacific Biodiversity 8*, 178–182. https://doi.org/10.1016/j.japb.2015.04.001

Morales, D., Jiménez, S.M., González-Rodríguez, A.M. & Cermák, J. 2002: Laurel forests in Tenerife, Canary Islands. *Trees 16*, 529–537. https://doi.org/10.1007/s004680050055

Ochando, J., Carrión, J., Altolaguirre, Y., Munuera, M., Amorós, G., Jiménez-Moreno, G., Solano-García, J., Barsky, D., Luzón, C., Sánchez-Bandera, C., Serrano-Ramos, A., Toro-Moyano, I., Saarinen, J., Blain, H.-A., Bocherens, H., Oms, O., Fortelius, M. & Jiménez-Arenas, J.M. 2022: Palynological investigations in the Orce Archaeological Zone, Early Pleistocene of Southern Spain. *Review of Palaeobotany and Palynology 304*, 104725. https://doi.org/10.1016/j.revpalbo.2022.104725

Olalla-Tárraga, M.Á. & Rodríguez, M.Á. 2007: Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann's rule, urodeles its converse. *Global Ecology and Biogeography 16*, 606–617. https://doi.org/10.1111/j.1466-8238.2007.00309.x

Olalla-Tárraga, M.Á., Diniz-Filho, J.A.F., Bastos, R.P. & Rodríguez, M.Á. 2009: Geographic body size gradients in tropical regions: water deficit and anuran body size in the Brazilian Cerrado. *Ecography 32*, 581–590. https://doi.org/10.1111/j.1600-0587.2008.05632.x

Oms, O., Anadón, P., Agustí, J. & Julià, R. 2011: Geology and chronology of the continental Pleistocene archaeological and paleontological sites of the Orce area (Baza basin, Spain). *Quaternary International 243*, 33–43. https://doi.org/10.1016/j.quaint.2011.03.048

Oms, O., Bolós, X., Barde-Cabusson, S., Martí, J., Casas, A., Lovera, R., Himi, M., Gómez de Soler, B., Campeny Vall-Llosera, G., Pedrazzi, D. & Agustí, J. 2015: Structure of the Pliocene Camp dels Ninots maar-diatreme (Catalan Volcanic Zone, NE Spain). *Bulletin of Volcanology 77*, 98. https://doi.org/10.1007/s00445-015-0982-3

Přikryl, T., Gómez de Soler, B., Campeny, G., Oms, O., Roubach, S., Blain, H.-A. & Agustí, J. 2016: Fish fauna of the Camp dels Ninots locality (Pliocene; Caldes de Malavella, province of

Girona, Spain) – first results with notes on palaeoecology and taphonomy. *Historical Biology 28*, 347–357. https://doi.org/10.1080/08912963.2014.934820

R Core Team 2020: R: *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. URL https://www.R-project.org/

Reading, C.J. 2007: Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia 151*, 125–131. https://doi.org/10.1007/s00442-006-0558-1

Remenieras, G. 1974: *Tratado de Hidrología Aplicada*, 2nd ed., Barcelona

Robinson, M.M., Dowsett, H.J. & Chandler, M.A. 2008: Pliocene role in assessing future climate impacts. *Eos, Transactions American Geophysical Union 89*, 501–502. https://doi.org/10.1029/2008EO490001

Robles, S., Barrón, E. & Cebolla, C. 2013: Preliminary Palaeobotanical study of the Pliocene paleontological site Camp dels Ninots (Caldes de Malavella, Girona, Spain). Macroflora of Can Argilera sector. *Boletín de la Real Sociedad Española de Historia Natural, Sección Geológica 107*, 75–89.

Saarinen, J., Oksanen, O., Žliobaitė, I., Fortelius, M., DeMiguel, D., Azanza, B., Bocherens F., H., Luzón, C., Solano-García, J., Yravedra, J., Lloyd A.C., Blain, H.-A., Sánchez-Bandera, C., Serrano-Ramos, A., Rodriguez-Alba, J.J., Viranta, S., Barsky, D., Tallavaara, M., Oms, O., Agustí, J., Ochando, J., Carrión, J. & Jiménez-Arenas, J.M. 2021: Pliocene to Middle Pleistocene climate history in the Guadix-Baza Basin, and the environmental conditions of early Homo dispersal in Europe. *Quaternary Science Reviews 268*, 107132. https://doi.org/10.1016/j.quascirev.2021.107132

Sánchez-Bandera, C., Oms, O., Blain, H.-A., Lozano-Fernández, I., Bisbal-Chinesta, J. F., Agustí, J., Saarinen, J., Fortelius, M., Titton, S., Serrano-Ramos, A., Luzón, C., Solano-García, J., Barsky, D. & Jiménez-Arenas, J. M. 2020: New stratigraphically constrained palaeoenvironmental reconstructions for the first human settlement in Western Europe: the Early Pleistocene herpetofaunal assemblages from Barranco León and Fuente Nueva 3 (Granada, SE Spain). *Quaternary Science Reviews 243*, 106466. https://doi.org/10.1016/j.quascirev.2020.106466

Sánchez-Bandera, C., Fagoaga Moreno, A., Serrano-Ramos, A., Solano-García, J., Barsky, D., DeMiguel, D., Ochando, J., Saarinen, J., Piñero, P., Lozano-Fernández, I., Courtenay, Ll. A., Titton, S., Luzón, C., Bocherens, H., Yravedra, J., Fortelius, M., Agustí, J., Carrión, J.S., Oms, O., Blain, H.-A. & Jiménez-Arenas, J.M. 2023. Glacial/interglacial climate variability in southern Spain during the late Early Pleistocene and the climate backdrop for early Homo in Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 111688. https://doi.org/10.1016/j.palaeo.2023.111688

Sanchiz, B. 1977: *Nuevos anfibios del Neógeno y Cuaternario de Europa. Origen, desarrollo y relaciones de la batracofauna española*. Universidad Complutense de Madrid, Spain.

Sanchiz, B., Schleich, H. H. & Esteban, M. 1993: Water frogs (Ranidae) from the Oligocene of Germany. *Journal of Herpetology 27*, 486–489. https://doi.org/10.2307/1564847

Schäuble, C. S. 2004: Variation in body size and sexual dimorphism across geographical and environmental space in the frogs *Limnodynastes tasmaniensis* and *L. peronii*. *Biological Journal of the Linnean Society 82*, 39–56. https://doi.org/10.1111/j.1095-8312.2004.00315.x

Vehí, M., Bach, J., Roqué, C. & Linares, R. 2005: Relationship between thermal ground-water and environmental genesis of wetlands: The case of the Prats de Sant Sebastià, northwestern Mediterranean margin. *Journal of Soil and Water Conservation 60(6)*, 331–338.