UNIVERSITAT ROVIRA I VIRGILI

ECOLOGICAL TRAITS OF THE IBERIAN HERPETOFAUNA DURING THE PLIO-PLEISTOCENE: BODY SIZE AND SPECIES RICHNESS IN RELATION TO CLIMATE

Almudena Martínez Monzón

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ECOLOGICAL TRAITS OF THE IBERIAN HERPETOFAUNA DURING THE PLIO-PLEISTOCENE: BODY SIZE AND SPECIES RICHNESS IN RELATION TO CLIMATE

Almudena Martínez Monzón

Doctoral thesis

Supervised by

Dr. Hugues-Alexandre Blain

Tarragona

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UNIVERSITAT
ROVIRA i VIRGILI

Cover: illustrations by Sara Mª Gómez-Lobo P. Based on photographs of different specimens of *Pelophylax perezi* and *Epidalea calamita*; Pictures of skeletons included in the initial page of Chapters 2 and 4 come from different plates of Boulenger, G. A. (1897), *The tailless batrachians of Europe* (Nº. 74-75). Ray Society, London.

A mi hija, Vera

ALMUDENA MARTÍNEZ MONZÓN

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DOCTORAL THESIS

Supervised by
DR. HUGUES-ALEXANDRE BLAIN

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IPHES
Institut Català de Paleoecologia Humana i Evolució Social

I STATE that the present study, entitled "*Ecological traits of the Iberian herpetofauna during the Plio-Pleistocene: Body size and species richness in relation to climate*", presented by Almudena Martínez Monzón for the award of the degree of Doctor, has been carried out under my supervision at the Department of History and History of Art of the University Rovira i Virgili (Tarragona, Spain).

Tarragona, January 2023
Doctoral Thesis Supervisor/s

Dr. Hugues-Alexandre Blain
Director of the Doctoral dissertation

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FORMAT

This doctoral dissertation is presented as a compendium of publications. Three main works have been already published in international journals included in the Journal Citation Report (JCR), all of them in high impact journals included in the first Quartile. The last work is contained as an unpublished chapter but it has been sent to an indexed journal.

In addition to the articles which conform the Chapter 3. "*Results*", two previous Chapters ("Introduction" and "Material and Methods") have been included to settle the context and describe the material, technical instruments and main methodologies used. Also, a final chapter named "*General conclusions and future perspectives*" where a general analysis of the results obtained is presented, leading to the main conclusions derived from this PhD thesis.

To conclude, three appendixes are contained in this document, the first one is composed by five plates which constitute a representation of the material studied. The second appendix, compiles three works in the form of published articles in which I have a relevant participation, all of them related to the main research topic of this thesis. The last one is composed by six tables in which raw data of humeral measurements from the different sequences and the reference collections are presented.

The references of the main research works which compose the present thesis are:

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(8), 1307-1318.

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(5), 673-686.

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.

Martínez-Monzón, A., Přikryl, T., Sánchez-Bandera, C., Bisbal-Chinesta, J. F., Agustí, J., Campeny Vall-Llosera, G., Gómez de Soler, B., Blain, H.-A., 2022. Inferring eco-climatic parameters for the Pliocene climatic optimum using frog body size as a new proxy. Unpublished.

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Part 3

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

Figure 2. Ordinary Least Square (OLS) regression models performed between SVL (Snout to vent length) of populations of *Pelophylax* genus across Eurasia and A. Real evapotranspiration obtained by Turc's formula (RET; mm/year); B. Mean annual temperature (MAT; C°); C. Mean annual precipitation (MAP; mm).

Table 1. Relation database of the modern studied populations of the genus. The number of individuals (n) and the mean Snout-to-Vent Length (SVL) is presented as the Mean annual temperature (MAT), Mean annual precipitation (MAP) and Real evapotranspiration (RET) according to Turc's formula. References in the first column: [1]Papežík et al. (2021), [2]Zhelev et al. (2017), [3]Lukanov et al. (2014), [4]Wang et al. (2008), [5]Lou et al. (2012), [6]Karaica et al. (2016), [7]Conan et al. (2022), [8]Pille et al. (2021), [9]Tarkhnishvili and Gokhelashvili (1999), [10]Hoffmann et al. (2015), [11]Mayer et al. (2013), [12]Hatziioannou et al. (2022), [13]Tsiora and Kyriakopoulou-Sklavounou (2022), [14]Kyriakopoulou-Sklavounou et al. (2008), [15]Pafilis et al. (2019), [16]Bam-e-Zar et al. (2019), [17]Bam-e-Zar et al. (2020), [18]Fathinia et al. (2012), [19]Rajabi and Javanbakht (2019), [20]Comas et al. (2014), [21]Nakashima et al. (2021), [22]Togane et al. (2018), [23]Disi and Amr (2010), [24]Socha and Ogielska (2010), [25]Hermaniuk et al. (2020), [26]Spigonardi et al. (2012),[27]Balint et al. (2008), [28]Ivanova and Berzin (2019), [29]Svinin et al. (2021), [30]Sánchez-Montes and Martínez-Solano (2011), [31]Christiansen et al. (2010),[32]Erismis (2011), [33]Çiçek et al. (2011), [34]Gül et al. (2011), [35]Arısoy and Başkale (2019), [36]Özcan et al. (2021), [37]Başkale et al. (2017), [38]Alkaya and Şereflişan (2021), [39]Erismis and Chinsamy (2010), [40]Peskov (2019), [41]Stakh et al. (2016), [42]Kuzmin et al. (2020), [43]Reminnii (2007) in Fominykh and Lyapkov (2012),[44]Savchuk (2009) in Fominykh and Lyapkov (2012).

Table 2. Results of OLS regression models and Pearson correlation test between genus *Pelophylax* SVL (Snout-to-vent length) and eco-climatic 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. Regarding to the correlation test, in addition to the significance level and the degrees of freedom, the correlation coefficient and the T statistic are shown.

Table 3. Values of SVL (Snout-to-vent length) in mm from fossil populations of *Pelophylax* sp. and reconstructed eco-climatic parameters based on the OLS regression models presented in this work with its standard error. MAT (Mean annual temperature in °C); MAP (Mean annual precipitation in mm); RET (Real evapotranspiration in mm/year). Comparative with previous palaeoclimatic reconstruction from Orce archaeo-palaeontological sites (BL and FN3) obtained by means of the Mutual Ecogeographic Range method (MER) with its mean standard deviation (Sánchez-Bandera et al., submitted) and RET values derived from Turc's formula.

ABSTRACT

Climatic changes have affected diversity and evolution of amphibian and reptile species in all biomes and ecosystems of the planet. During the Plio-Pleistocene several events and variations in the climate dynamics at a global scale have occurred, making it an interesting period for the study of the herpetofauna reactions to such changes. The research of macroecological trends and rules in the fossil record constitutes a field of study with a huge spectrum of possibilities and several questions that remain unanswered. The palaecoecological analysis of the herpetofauna fossil assemblages provides a different approach to such macroecological questions, often studied at spatial scale, but not at temporal one. This work intends to define the macroecological patterns of herpetofauna reactions to climate changes and turn them over in order to develop a new methodology which can provide further palaeoclimatic insights. With this purpose, the main ecological traits studied here are the anuran body size and the diversity of the herpetofauna communities. The first one was selected as it influences endless aspects in biology and evolution of every organism, also of anurans. *Epidalea* (formerly *Bufo*) *calamita* and genus *Pelophylax* are the selected taxa due to their abundance in Plio-Pleistocene fossil assemblages in the Iberian Peninsula.

Main methodologies applied in this work are, in the first place, the anuran body size reconstruction based on humeral measurements. This method has been developed by means of the study of the dry osteological modern collections of the MNCN (Madrid, Spain). Then, in order to establish the relationship between anuran body size and eco-climatic parameters, several OLS regression models have been settled. To study herpetofauna diversity, the Simpson index as evenness (1-D) and also the species richness, have been taken as the reference parameters.

Several archaeo-palaeontological sites with special relevance in the field of human evolution have been studied due to their noteworthy fossil record, the geological period that encompass and also their location in the Iberian Peninsula. This land extension is constitutes one of the southernmost territories of Europe which has constituted a refugium during the coldest glacial eras and also, acts as a nexus between Europe and Africa.

At the Sierra de Atapuerca site complex, the body size of *E. calamita* has been analysed in relation to climatic variables. Also, in this extense in time and quite complete sequence (which includes the studied sites of the Sima del Elefante, Gran Dolina and Portalón) the herpetofauna diversity is analysed taking into account the main climatic events recorded in these sites. In the Guadix-Baza Basin sites (Barranco León and Fuente Nueva 3), the body size of *Pelophylax* cf. *perezi* and again the herpetofauna diversity are considered together and their variations are examined in relation to the climatic and environmental changes occurred in this period.

After the obtention of a general view about how anuran body size changes can be related to eco-climatic parameters, the generated knowledge intends to be the basis for the use of anuran body size as new climatic proxy. To do so, the palaeontological Pliocene site of Camp dels Ninots is presented as a case study. After building a model grounded on the body size of current populations of the whole genus *Pelophylax* across Eurasia, a novel palaeoclimatic reconstruction is presented for Camp dels Ninots based on the body size of the fossil remains of *Pelophylax* sp. of this site.

So, as main conclusions, in this PhD, it has been demonstrated that: (1) the reconstruction of anuran past body size based on humeral measurements can be done accurately for *Epidalea calamita* and *Pelophylax perezi*; (2) the temperature is the main factor influencing anuran body size (especially in females) and herpetofauna diversity; (3) due to their relationships with eco-climatic parameters, *Pelophylax* body size can be used to infer past climatic conditions; and finally (4) changes in the amphibian and reptile diversity reflect the main climatic events recorded in the studied sequences.

RESUMEN

Los cambios climáticos han afectado la diversidad y evolución de las especies de anfibios y reptiles en todos los biomas y ecosistemas del planeta a lo largo del tiempo. Durante el Plio-Pleistoceno se han producido varios eventos y variaciones en las dinámicas climáticas a escala global, lo que hace de este un período interesante para el estudio de las reacciones de la herpetofauna a tales cambios. La investigación de tendencias y reglas macroecológicas en el registro fósil constituye un campo de estudio con un enorme espectro de posibilidades y varias preguntas que permanecen sin respuesta. En esta tesis doctoral, el análisis paleoecológico de diversos conjuntos fósiles proporciona un enfoque diferente a este tipo de cuestiones macroecológicas, a menudo estudiadas en la escala espacial, pero no en la temporal. Este trabajo pretende definir los patrones macroecológicos de las reacciones de la herpetofauna a los cambios climáticos e invertirlos para desarrollar una nueva metodología que pueda proporcionar más conocimientos sobre el paleoclima. Con este propósito, los principales rasgos ecológicos estudiados en este trabajo son el tamaño corporal de los anuros y la diversidad de las comunidades de herpetofauna. Se seleccionó el primero ya que influye en un sinfín de aspectos en la biología y evolución de todos los organismos, también de los anuros. *Epidalea* (anteriormente *Bufo*) *calamita* y el género *Pelophylax* son los taxones seleccionados para su estudio en esta tesis doctoral debido a su abundancia en conjuntos fósiles del Plio-Pleistoceno en la Península Ibérica.

Las principales metodologías aplicadas en este trabajo son, en primer lugar, la reconstrucción del tamaño corporal de los anuros a partir de medidas del húmero. Este método ha sido desarrollado mediante el estudio de las colecciones osteológicas modernas del MNCN (Madrid, España). Luego, para determinar las relaciones entre el tamaño corporal de los anuros y los parámetros ecoclimáticos, se establecieron varios modelos de regresión OLS. Para el estudio de la diversidad de la herpetofauna se tomaron como parámetros de referencia el índice de diversidad de Simpson (1-D) y también la riqueza de especies.

Varios yacimientos arqueo-paleontológicos de especial relevancia en el campo de la evolución humana han sido estudiados debido a su destacable registro fósil, el periodo geológico que abarcan y también por su ubicación en la Península Ibérica. Esta área constituye uno de los territorios más meridionales de Europa que ha

actuado como refugio para diferentes especies durante los periodos glaciales más fríos y, además, debido a su localización actúa como nexo entre el continente africano y el europeo.

Dentro del complejo de yacimientos de la Sierra de Atapuerca se analizó el tamaño corporal de *E. calamita* en relación con las variables climáticas. Asimismo, en esta secuencia bastante completa y extensa en el tiempo (que incluye los sitios estudiados de la Sima del Elefante, Gran Dolina y Portalón) se analizó la diversidad de herpetofauna teniendo en cuenta los principales eventos climáticos registrados en estos sitios. En los yacimientos de la Cuenca de Guadix-Baza (Barranco León y Fuente Nueva 3) el tamaño corporal de *Pelophylax* cf. *perezi* y la diversidad de la herpetofauna se consideraron en conjunto y se examinaron sus variaciones en relación con los cambios climáticos y ambientales ocurridos en este período.

Después de haber obtenido una visión general sobre cómo los cambios en el tamaño corporal de los anuros pueden relacionarse con los parámetros ecoclimáticos, el conocimiento generado pretende ser la base para el uso del tamaño corporal de los anuros y la diversidad de herpetofauna como nuevos indicadores climáticos. Para ello, se presenta como caso de estudio el yacimiento paleontológico Plioceno del Camp dels Ninots. Tras construir un modelo basado en el tamaño corporal de las poblaciones actuales de todo el género *Pelophylax* en Eurasia, se presentó una nueva reconstrucción paleoclimática para Camp dels Ninots basada en el tamaño corporal de los restos fósiles de *Pelophylax* sp. de este sitio

Así, como principales conclusiones, en esta tesis doctoral se ha demostrado que: (1) la reconstrucción del tamaño corporal de los anuros fósiles basada en medidas del húmero se puede realizar con precisión para *Epidalea calamita* y *Pelophylax perezi*; (2) la temperatura es el principal factor que influye en el tamaño corporal de los anuros (especialmente en las hembras) y la diversidad de la herpetofauna; (3) debido a sus relaciones con los parámetros ecoclimáticos, el tamaño corporal de *Pelophylax* puede usarse para inferir condiciones climáticas pasadas; y finalmente (4) los cambios en la diversidad de anfibios y reptiles reflejan los principales eventos climáticos registrados en las secuencias estudiadas.

CHAPTER 1.
INTRODUCTION

SUMMARY

The first chapter of this PhD aims to settle the climatic, geological and ecological context necessary to understand and situate the rest of the work. In the first place, the time period encompassed in this study is defined according to the International Chronostratigraphic Chart (i. e the Pleistocene 258 to 11.7 ka and the Pliocene 5.3 to 2.58 Ma). Climatic dynamics during this period are characterized by the transition from relatively warm conditions of the Pliocene to a cooling climate and the changing glacial-interglacial dynamics characteristic from the Pleistocene. The main climatic events recorded within the studied sites/sequences are: The Pliocene Climatic Optimum; The Mid-Brunhes event and the Last Glacial Maximum (LGM). All the fossil assemblages studied in this work are placed in the Iberian Peninsula whose location and relief have been determinant for migrations, biodiversity and also play a key role in human evolution. Climatic changes occurred during the Plio-Pleistocene affected to all organisms, specifically amphibians and reptiles have been proved to be excellent bioindicators. The development of new methodologies for reconstructing past conditions during this period are of great interest for different research areas. The herpetofauna fossil record can contribute to this respect and also to the study of ecogeographical rules and macroecological patterns within the temporal dimension (instead of the classical spatial approach). Body size is one of the main traits studied in ecology due to its importance in all aspects of an organism life. Concretely anurans body size is influenced by several biotic and abiotic factors as temperature or precipitation. Despite the lack of consensus about their adhesion to Bergmann's rule, several works have found clear clines in the spatial dimension which are explained by diverse mechanisms: Temperature-size rule; heat-balance hypothesis; water availability hypothesis or starvation resistance hypothesis. Apart from that, molecular and genetic mechanisms and also sex-related traits are known to condition body size changes in anurans. To conclude, the main research questions and objectives of this PhD are presented at the end of this chapter.

This PhD thesis aims to study the body size and other ecological traits of the herpetofauna during the Plio-Pleistocene from the Iberian Peninsula. In this chapter a brief introduction to the climate of the Plio-Pleistocene period and the geological context of the Iberian Peninsula is settled. Then, a little background on the role of the fossil record of amphibians and reptiles as environmental proxies is presented together with some remarks about their diversity and community dynamics. Also, the literature referent to amphibian body size is reviewed as it is one of the main biological characters of every organism. Finally, the general research questions and objectives are contained within this chapter.

1.1 GENERAL CONTEXT OF THE PLIO-PLEISTOCENE CLIMATE AND THE IBERIAN PENINSULA

According to the data from the International Chronostratigraphic Chart (ICS; Cohen et al., 2013) Pleistocene Epoch which occurred during the Quaternary period (i.e. the last 2.6 million years), ranges from 258 to 11.7 ka and the Pliocene Epoch took place within 5.3 to 2.58 Ma at the end of the Neogene period. Both Neogene and Quaternary are subdivisions of the Cenozoic era and, all together the time-span studied comprises a period of more than five million years known as the Plio-Pleistocene. The fossil assemblages studied in this work have been dated within this period and altogether range from the Mid-Piazencian to the Middle-Late Pleistocene (Fig. 1). Pliocene climate is supposed to be generally warmer and wetter than current climate. Elevated atmospheric CO_2 concentrations was one of the main causes for the increased temperatures of this Epoch, in addition, the reduction of polar ice sheets generates an increase of sea levels which was higher than today and changes in the ice-albedo feedback contribute to the Pliocene warmth (Dowsett et al., 2010; Haywood and Valdes, 2004).

The Pliocene Epoch constitutes a transition period from relatively warm conditions to a cooling climate and the glacial-interglacial dynamics characteristic from the Quaternary (Salzmann et al., 2011). In southern Europe and specifically in the Iberian Peninsula, this transition culminates with the end of subtropical ecosystems around 1.2 Ma in favour to the current Mediterranean climate characteristic of the region (Robles et al., 2013), and fauna adapted to increasing aridity or at least periods of aridity during the year (summer in that case). In southern Europe, palaeoenvironments are known to have moved progressively from a seasonal forest present during Middle to Late Miocene, to warm-temperate laurel forest in the Pliocene and then to more open and arid Mediterranean conditions during the Early Pleistocene (Barrón et al., 2010).

Following the Pliocene, the Quaternary is a period characterized by its glacial-interglacial dynamics mainly determined by changes in the orbital configuration of the Earth. These changes in orbital parameters (obliquity, eccentricity and precession) generate cycles of periodicities of 20 – 100 ka known as Milankovitch cycles which drive changes in climate during this period.

These cycles, which can be observed in the changes of the proportion of oxygen isotopes derived from the study of fossil foraminifera in deep-sea sediment cores (Shackelton, 1995), also influence species ecological and evolutionary processes (Bennet, 1990). It is known that the ratio of oxygen-18 to oxygen-16 ($\delta^{18}O$) in the ocean increases with glaciation, and this ratio varies in cycles associated to changes in obliquity and precession (Hays et al., 1976). Other mechanisms also influence climatic dynamics of the Plio-Pleisocene as the changes in ice polar caps, the insolation or the changes in the carbon cycle. (Raymo and Huybers, 2008; Smith et al., 1999). During the mid-Pleistocene transition (MPT; i.e. between 1.2 and 0.6 Ma), the dominant cyclicity of glacial response changes from 41 to about 100 ka (Lisiecki and Raymo, 2007). Apart from the long-term cooling trend characteristic of the Pliocene, other mechanisms such as changes in sea ice formation, a switch from terrestrial to marine ice margins in Antarctica or a gradual increase in the insolation threshhold for ice-sheet ablation are also considered responsible for the change in the glacial dynamics at the mid-Pleistocene transition (see Lisiecki and Raymo, 2007 and the references therein).

Main climatic events recorded within the studied sequences are: 1. The Pliocene climatic optimum placed in Camp dels Ninots sequence (Caldes de Malavella, north-eastern Spain); 2. The Mid-Brunhes event together with the MIS 11 and MIS 19, present in Gran Dolina sequence (Atapuerca, Burgos, north-central Spain) and 3. The Last Glacial Maximum (LGM) located in the Portalón sequence (Atapuerca, Burgos, north-central Spain).

1.1.1 Pliocene Climatic Optimum

The Pliocene Climatic Optimum (3.2 to 2.5 Ma) occurred during the Mid-Piacenzian. During this period, global warmth reaches temperatures similar to those ones projected for the end of this century (Dowsett et al., 2013; Robinson et al., 2008) and it is similar to today in many aspects as the position of the continents and oceans, the intensity of sunlight reaching the earth surface or CO_2 atmospheric concentrations (Robinson et al., 2008). Specifically, for the mid-Pliocene (ca. 3 Ma) a less seasonal climate 5°C warmer than present and 400-1000mm/year wetter has been proposed for the European and Mediterranean region (Haywood et al., 2000). Even though these similarities, there are significant differences between these two analogues as during the mid-Pliocene the climate system response was dominated by the 41,000-year period of Earth's obliquity rather than by the latter 100,000-year period of glacial-interglacial cycles which leads the current climatic dynamic.

1.1.2 Mid-Brunhes event, MIS 11 and MIS 19

The Mid-Brunhes Event is a climatic transition between marine oxygen iso-tope stages (MIS) 13 and 11 after which the amplitude of glacial–interglacial climatic cycles increased substantially. Middle and late Pleistocene interglacials occurring after this event, (about 430,000 years ago) are characterized by greater warmth than the previous ones of the early-middle Pleistocene (780-450 ka). Reasons suggested to explain this warmer interglacials are mainly focused on the increased global mean temperatures during Northern Hemisphere winters. The increased insolation during this season, in conjunction

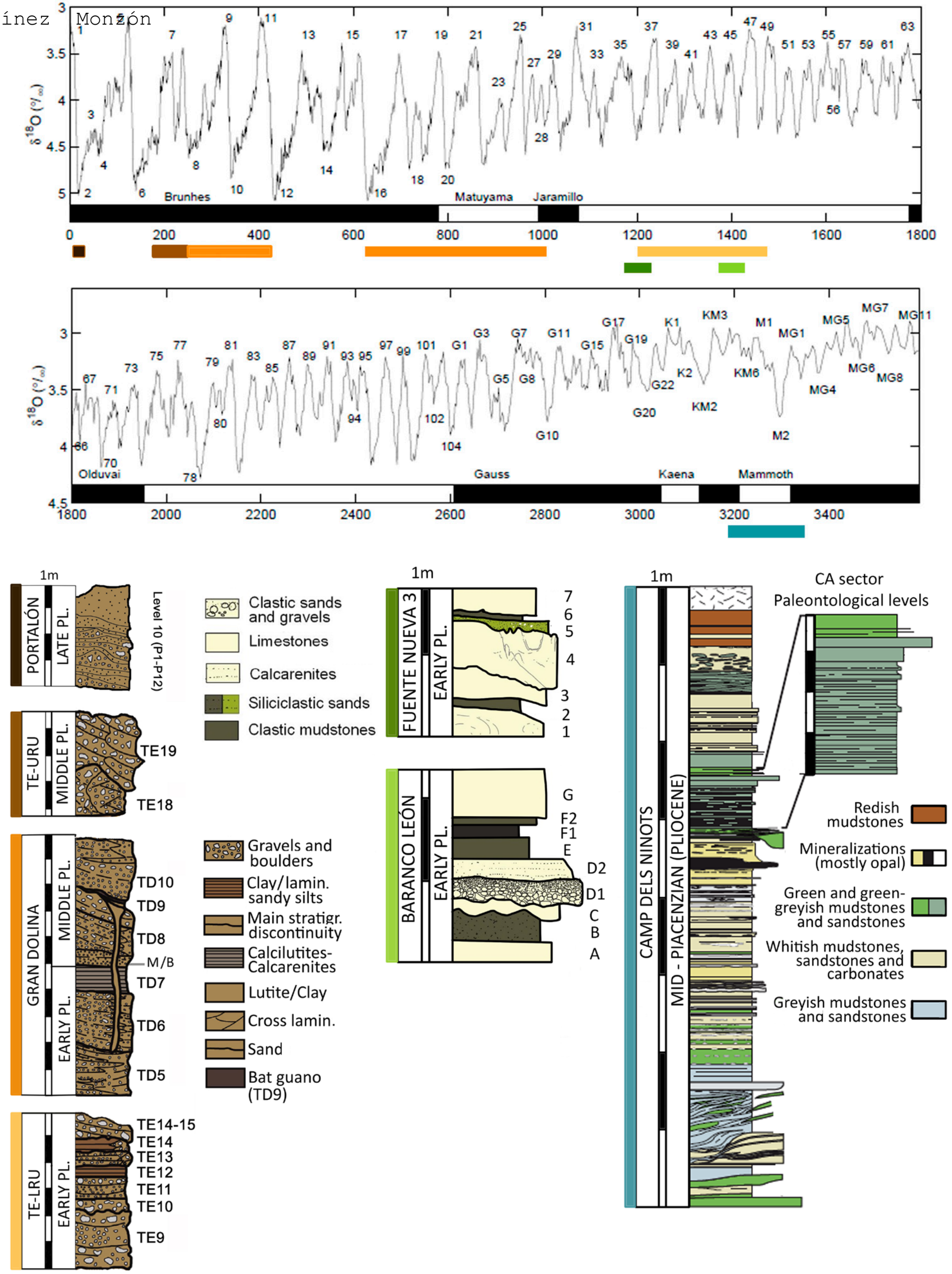

Figure. 1. Stratigraphic and chronological context of the present work, From left to right the stratigraphic sequences and levels from the Sierra de Atapuerca sites complex: TE-LRU (Trinchera Elefante Lower Red Unit), Gran Dolina, TE-URU (Trinchera Elefante Upper red Unit) and Portalón; Guadix-Baza Basin sites: Barranco León and Fuente Nueva 3 and Camp dels Ninots sequence, with a detail of the palaeontological levels from the Can Argilera sector. Within each sequence, the scale and the geological period are indicated at the left side. Also at this side, a colour code is presented in order to link the sequences with the LR04 benthic global $\delta^{18}O$ records (from Lisiecky and Raymo, 2005) at the top of the figure.

with the increased atmospheric greenhouse-gas concentrations arises as the main factors generating this warmth (Yin and Berger, 2010).

Even though this event is observable in diverse long-term climatic records such as the Mapping Spectral Variability in Global Climate Project (SPECMAP) and the European Project for Ice Coring in Antarctica (EPICA) (EPICA community members, 2004; Jouzel et al., 2007), and other ones (see for example Lisiecki and Raymo, 2005 or Winograd et al., 1997), its effect over fauna still poorly understood (Blain et al., 2012; Candy et al., 2010). Mid-Brunhes event is present in the sequence of Gran Dolina coinciding with MIS 11 at level TD10-4.

Marine Isotopic Stage 11 and 19 (MIS 11 and MIS 19 respectively), are considered to be two of the best analogues for the current interglacial due to its similarities with the current pattern of orbital configuration, insolation distribution and temperature (Berger et al., 2012; Yin and Berger 2010). Minimum values of eccentricity, CO_2 concentrations and human influence indicates that our current interglacial will be exceptionally long, the same as occurred during MIS 11 (Jouzel et al., 2007). MIS 19, also associated with a very low eccentricity, is the next best astronomical analogue for our Holocene interglacial (Berger et al., 2012). MIS 11 and MIS 19 both are present in our sequence, in levels TD10-4 and TD8a respectively, of the Gran Dolina site.

1.1.3 Last Glacial Maximum (LGM)

The Last Glacial Maximum (22–19 ka BP) constitutes one of the most relevant climatic events of the Pleistocene, which contrasts starkly with current interglacial. The LGM is a glacial period characterized by harsh climatic conditions with large changes in the greenhouse gases, aerosols, sea level, ice sheets and vegetation. During this event, the climatic situation was of maximum cold in the northern hemisphere and the greatest extension of ice at the polar caps occurred (Otto-Bliesner et al., 2006). The Iberian Peninsula is known to have exhibited gentler conditions than the rest of Europe during this period, thus acting as a refugium for certain Eurosiberian species (López-García et al., 2010; Bañuls-Cardona et al., 2014). The changes in species distributions induced by the ice ages have largely conditioned the present genetic structure of populations, species and communities (Hewitt, 2000), specially refugia (Stewart and Cooper, 2008).

Previous studies have located the LGM between levels P3 and P6 of the Portalón sequence due to the drastic decrease in the representation of both herpetofaunal and small-mammal taxa with respect to the underlying sublevels (López-García et al., 2010).

All these climatic events are of great importance for the study of current climate and also to understand the response of the fauna to such variations in climatic conditions. In the case of anurans, their reaction to these climatic periods or events considered as analogues of present and future climate turns out to be highly relevant for the future of this endangered group.

1.1.4 The Iberian Peninsula

From a geographical point of view, the fossil assemblages studied in this work are located in the Iberian Peninsula. This peninsula count with a land extension of 583,832 km2 and is welded to the European continent by means of a wide isthmus. The Iberian Peninsula or Iberia, occupies one of the southernmost points of Europe being located between this and the African continent. Its geological evolution can be divided in several periods of orogenesis and also erosive and sedimentary ones which have resulted in a very diverse territory in terms of rock type and relief modes (Lloidi, 2017). The Iberian Peninsula has a pentagonal shape with a huge central plateau or Meseta which constitutes the basic structural element of modern Iberia, around which the rest of the geological structures are attached. The Iberian Peninsula counts with an average elevation of ca. 600 m a.s.l. Main mountain ranges can be divided in two main groups, the Alpine Massifs (the Pyrenees, the Iberian Ranges, the Catalonian Coastal Ranges and the Baetic Ranges) and the Mesetan Massifs (Central Range and the Montes de Toledo). Along the borders of the Meseta there are other groups of massifs, such as the Cantabrian Range, the Sierra Morena and the Iberian System. (Lloidi, 2017). Within these ranges, there are four depressions or main valleys: Ebro, Duero, Tagus-Guadiana and Guadalquivir (Fig. 2). Regarding to current climate, the Iberian Peninsula present a wide variety in the range of climatic values as temperature and precipitation and two main climatic types can be identified, with several subtypes associated to them: Oceanic climate (Subtypes: Atlantic and Mountainous) and Mediterranean climate (Subtypes: Sub-Mediterranean; Continental; from Eastern Façade; Southern; Arid or from South-Eastern and Mountainous) (Castro et al., 2005).

Its independence and isolation from the rest of the European continent determines some of the characteristics of the diverse fauna and flora present in Iberia and also play a key role in migrations, acting as a refugium for several species during the glacial periods (see Gómez and Lunt, 2007 for a review). Regarding to human evolution, the fossil hominin remains and the lithic tools found in the Sierra de Atapuerca sites and in the Guadix-Baza Basin sites are widely considered to be among the oldest evidence of hominin occupation in western Europe (Oms et al., 2000; Carbonell and Rodríguez, 2006; Huguet et al., 2022).

1.2 ANURANS AS CLIMATIC AND ENVIRONMENTAL PROXIES AND HERPETOFAUNA DIVERSITY

Global climatic changes affect organisms in all biomes and ecosystems of the planet. Consecutive glaciation events characteristics of Pleistocene rose climate as a conditioning factor for presence and vital development of herpetofauna species, both at European and Iberian scale. In some cases, these climatic conditions have led to extinction or extirpation of some species or families (Blain et al., 2016). To avoid extinction without changing their distributions other species have developed adaptive response mechanisms which let them to cope with changes in climatic parameters and environmental conditions. There are some works which suggest that limits to such adaptation are greatest during periods of rapid climate change, such as those predicted for the future (Davis and Shaw 2001).

Apart from the implications of this fact in the development of current conservation strategies, the study of the herpetofauna has a great interest in characterizing reaction patterns of amphibians and reptiles in the face of climate change. In addition, amphibian and reptile fossil record is considered suitable both for the study of ecogeographical rules and patterns in the temporal dimension (instead to the classical spatial approach) and also to provide reconstructions of past conditions. It is so because of the high sample sizes available of fossil remains, the wide temporal range that archaeo-paleontological sites offer and the rapid adaptive response of these species to changes in the environment.

In addition, increasing our knowledge about Quaternary climate and specifically the Pleistocene can also provide new insights on the early human occupations of the Iberian Peninsula and the first human settlements of Europe.

With the aim of reconstructing past climates several methodologies for this and other geological periods have been developed, no one exempt of difficulties (Blain et al., 2018). There are quite a few alternatives for reconstructing terrestrial temperatures and precipitation during Pleistocene period as most species have extant representatives, but the options draw drastically when the line of Pliocene is crossed. Body size-metabolic rate approaches upon poikilothermic animals as amphibians and reptiles have yielded interesting results (Head et al., 2009; 2013). This kind of approach complements other palaeoclimatic reconstructions as those ones derived from planktonic foraminifer oxygen isotopes or palaeofloras (Head et al., 2009). As the main weak point of this kind of analysis, still the fact that the validity of the use of the living relatives instead of the same species as a reference point for the palaeoclimatic reconstruction remain unclear. There still a debate about whether the ecology and biology of two related species can be considered equivalent or not (Blain et al., 2018; Makarieva et al., 2009).

From a palaeontological point of view, amphibians are considered to be morphologically very stable and conservative organisms, showing little change in their assemblages over millions of years and also undergoing few extinction events, unlike other groups such as mammals or birds (Delfino, 2005). Actually, most species of herpetofauna present in Plio-Pleistocene localities in the Iberian Peninsula are considered identical to modern populations due to genetic distance data obtained by molecular clock techniques (Lobo et al., 2016; Barbadillo et al., 1997; Sanchiz, 1977). Therefore, the law of actualism, based on Hutton's Principle of Uniformity, can be applied to these species. Taking this fact into account, amphibians and reptiles of Plio-Pleistocene localities can constitute environmental proxies of past conditions thus avoiding the difficulties present in other methodologies and geological periods associated to the use of relative species.

With regard of amphibian and reptile community dynamics, it is known that temperature and precipitation have always played a key role driving diversity and distribution of herpetofauna by influencing their thermal biology, the amount of environmental resources, their growth patterns, etc. (Gibbons et al., 2000; Angilletta et al., 2004). Specifically, for ectotherms, thermal traits such as heat tolerance, evaporative water loss, variation in body temperature and a reduced dispersal rate are known to explain part of the sensitivity of amphibians and reptiles to habitat modification (Nowakowski et al., 2017).

The importance of the scale within the study of ecological traits of amphibian and reptile communities is mandatory. Different taxonomical levels must be studied separately as they are not influenced by the same determinants (LaBarbera, 1989). Assessments have been made of the importance of ecological scale in understanding the response of ecosystem communities when a perturbation occurs (Downing and Leibold, 2010). In addition to this, this PhD thesis aims to emphasise the importance of temporal scale in understanding not only short- but long-term responses of communities to climatic changes. The fossil

Figure 2. Map of the relief of the Iberian Peninsula. Red stars mark the location of the archaeo-palaeontological sites studied in this PhD: A. Sierra de Atapuerca sites complex; B. Camp dels Ninots and C. Guadix-Baza Basin sites. Map modified from (https://www.nationsonline.org).

record has already yielded promising results as a new source for compiling long-term data and contributing to a better understanding of long-term dynamics in ecological research (for example Araújo et al., 2008; Tietje and Rödel, 2018; Van der Sande et al., 2019). Different traits of amphibian and reptile communities can provide information about past conditions (see Blain et al., 2018 and references therein) but in this PhD thesis, amphibian body size and the diversity of the herpetofauna communities are the main studied traits.

1.3 BODY SIZE

Body size is one of the main traits studied in animal ecology due to its influence in endless aspects of biology and evolution. Due to its relevance for physiology and functional morphology, body size has become a main research topic in ecology and evolutionary biology of all groups across the animal kingdom. (LaBarbera, 1989). The organism's size is linked to metabolic rate, fertility, internal complexity, speed of movement or life span among other individual's characteristics (LaBarbera, 1989; Bonner, 2011). Upon the individual level, body size also influences population ecology traits as population density or home range.

As J. T. Bonner argues in the introduction of his book (*Why size matters*, 2011) the overarching character of body size in all matters biological, should situate to this trait of all living organisms as a supreme regulator and a prime mover in evolution. In this work he settled five rules that I bring up here as they sum up the importance of body size in all aspects of life:

1. *"Strength varies with size".*
2. *"Surfaces that permit diffusion of oxygen, of food, and of heat in and out of the body, vary with size".*
3. *"The division of labor (complexity) varies with size".*
4. *"The rate of various living processes varies with size, such as metabolism, generation time, longevity, and the speed of locomotion".*
5. *"The abundance of organisms in nature varies with their size".*

As can be derived from the five rules settled by Bonner (2011), a lot of physical parameters change with body size as for example the relative importance of gravity, inertia, viscosity or surface tension. Surface-to-volume ratios are also determined by body size, mainly when isometry occurs (constancy in shape with change in size). This relationship between area and volume is relevant in processes as diffusive transfer or heat loss which means that physiology in general is highly determined by body size (LaBarbera, 1989).

On this matter, the German physiologist Carl Bergmann proposed that larger species would occupy colder areas due to their higher heat conservation capacity, consequence of their low surface-to-volume ratio. He was the first to link body size with climate settling a global pattern, known as Bergmann's rule (Bergmann, 1848) and its associated mechanism (better heat conservation). In the nature, this rule has been widely supported by endothermic vertebrates as reviewed by Ashton et al. (2000) however, results are mixed in what concerns to the validity of this pattern for ectotherms. In some cases, no clear trend has been found (Hawkins and Lawton, 1995; Pincheira-Donoso et al., 2008), but support for Bergmann's rule has been found in others (Lindsey, 1966; Atkinson et al., 2003).

Even though, no single theory has been able to explain the generality of temperature–size relationships in ectotherms yet (Angilletta et al., 2004). Apart from heat conservation hypothesis, quite controversial since ectotherms do not generate their own heat, temperature-size-rule (Atkinson, 1994) rises as one of the main explanations to body size gradients in ectotherms. This general rule states that within this group, development at low temperatures leads to a delay in maturation and a larger final size. Given that in ectotherms there is a positive correlation between the size of the adult female and her fecundity, this delay in maturation is considered adaptive for ectotherms as they increase fertility and survival, thus adjusting reproduction and all the processes linked to it to the characteristics of the environment (Atkinson, 1994; Angilletta et al., 2004; Atkinson et al., 2003). This different explanation to Bergmann's clines in ectothermic organisms, can coexist with the "better heat-conservation" and other mechanisms proposed as they are not mutually exclusive.

Concretely in amphibians, even though previous studies into Bergmann's rule (and its intraspecific modification known as James's rule (James, 1970; Blackburn et al., 1999) have been carried out, no conclusive results have allowed to establish a clear trend for this group. Bergmann clines, the inverse pattern and even no clear trend in body size related to temperature have been found making this an unsolved issue within amphibian ecology (see the *"Results"* Chapter, Part 1.1 for more references). Also, in the cases where Bergmann clines in amphibians have been found, the mechanism proposed to justify this pattern is not always the classic explanation of better heat conservation but some other more complexes. For example, the heat-balance hypothesis establishes that, for ectothermic taxa below a certain body size threshold and with physiological and/or behavioural thermoregulatory abilities (such as burrowing or basking to enhance heat gain and/or heat conservation), larger body sizes would be favoured in cooler climates where their low-surface-to-volume ratio is better for conserving heat (Olalla-Tárraga and Rodríguez, 2007). In the case of anurans, they are below this size threshold and are considered to be thermoregulators.

Taking humidity as the focal point instead of temperature, the water availability hypothesis is also another common explanation to the physiological processes underlying Bergmann's clines in amphibians. Based on the same physical principle as Bergmann's heat conservation mechanism (i.e. surface-to-volume ratios), the water availability hypothesis predicts larger sizes for amphibians that inhabit more arid areas because they would have higher desiccation resistances (Olalla-Tárraga and Rodríguez, 2007). Some works support this idea (Olalla-Tárraga et al., 2009; Nabil and Sarra, 2011) and highlight the importance of humidity in amphibian biology

Other of the most accepted explanations to Bergmann's clines in ectotherms is the starvation resistance hypothesis (Boyce, 1979). This hypothesis states that larger animals are favoured in cooler, more seasonal environments due to their better capacity to store fat and use it to enhance survival during stress periods, mainly when overwintering.

Apart from that, other kind of molecular and genetic mechanisms are known to influence body size in amphibians. Even though many of the molecular mechanisms involved in regulation of growth rates and body size limits are not well known, the role of the cells, the subcellular structures and the genome has turned out to be key in development regulation and final body size of the organisms. Changes in genome size, cell size and body size of the adult individual are not always correlative in amphibians, although differences in genome size usually correlates with cell-size changes. Differences in genome and cell-size at the same adult size, generate diverse ways that significantly affect morphogenesis, growth and adult morphology (Levy and Heald, 2016). Regarding to amphibian development, size at the metamorphosis is characteristic of each species thus indicating a genetic component to metamorphic size determination, even though other environmental factors affect to how soon metamorphosis occurs.

Amphibians, as many other taxa, present a phenomenon referred to as indeterminate growth (Duellman and Trueb, 1986), which means that they can continue to grow after sexual maturity (Shine, 1979). Despite this, there is a great correlation between the size at maturity and the final size of the individual (Shine, 1990). In anurans, sexual dimorphism exists in terms of size (Sexual size dimorphism: SSD), with females being larger in most species (Duellman and Trueb, 1986). As said before, in amphibians, female body size is closely related to a higher fecundity due to the increase in the size and number of oocytes that can be produced. This correlation (female size - clutch size) occurs in a generalized way among ectotherms and usually implies a greater weight of the hatchlings and a greater probability of their survival (Blueweiss et al., 1978). Egg production is an extremely important event in the life of anurans and energetically very demanding for females (Slatkin, 1984), which take longer than males to reach sexual maturity, live longer and grow more slowly as a great amount of resources is devoted to the production of ovules and not to growth (Monnet and Cherry, 2002). Since sperm production is energetically less challenging (Reading, 1988), males can grow faster and reach sexual maturity earlier, thus extending their reproductive period. Despite this, their mortality rate is much higher due to the vulnerability and exposure during the breeding season (Shine, 1979; Monnet and Cherry, 2002), so they do not live long enough to reach larger sizes. Reproductive behaviour during the breeding season also entails a high energy expenditure for males, so during this period the resources allocated to growth are reduced to a minimum (Woolbright, 1989). Therefore, within a population the age structure tends to be different in reproductive males and females and that constitutes a relevant source of SSD variation (Monnet and Cherry, 2002). By the other side, intersexual differences in body-size variation in response to climate changes cannot be dismissed, as several works have detected that climate has a larger influence on the body size of amphibian females (Hemelaar, 1988; Schäuble, 2004; Leskovar et al., 2006).

Finally, density-dependent resource availability has been proved to be determinant for body size changes along with phenotypic plasticity (Green and Middleton, 2013). Due to the global character of the influence of body size in all aspects of organism's life, the number of factors conditioning this trait is immense. In this PhD thesis the influence of environmental factors upon body size rises as the main research topic and the detection of patterns in changes of amphibian body size takes prevalence over the explanation of the underlying mechanisms.

1.4 GENERAL RESEARCH QUESTIONS

Within this PhD thesis, several questions intend to be answered:

- Is it possible to accurately reconstruct past body sizes as SVL (Snout to vent length) of two different species of anurans (*Epidalea calamita and Pelophylax perezi*) based on humeral measurements? Is there a solid relationship?

- How reacts anuran body size to fluctuations and events in eco-climatic conditions? Is there any relationship between temperature, precipitation and primary productivity with changes in body size of anurans during the Plio-Pleistocene?

- Is the herpetofauna diversity affected by the changes in eco-climatic parameters and main climatic events during the Plio-Pleistocene?

- And conversely, can anuran body size be used as a new proxy to reconstruct past climatic features and ecosystem energy during this period?

1.5 GLOBAL OBJECTIVES

In order to answer these questions, we settled a series of steps to guide this project which have been translated in five global objectives:

- Establish the correlation between body size of *Epidalea calamita* and *Pelophylax perezi* and humeral measurements. Compile current data from osteological collections of the MNCN and generate statistical models in order to reconstruct amphibian past body sizes from fossil humeri.

- Reconstruct past body sizes from different archaeo-palaeontological sites which record key periods of the human evolution and/or interesting climatic events.

- Relate these data to eco-climatic parameters in order to understand the relationships between anuran body size and eco-climatic parameters. Also, integrate these data with the herpetofauna diversity.

- Use the generated knowledge to develop a new methodology intended to reconstruct past eco-climatic conditions thus complementing current methods.

- Within the current context of climatic change and anthropogenic impact over the environment, compare and contrast the present state of amphibian and reptile populations with its reaction to climatic fluctuations in the past.

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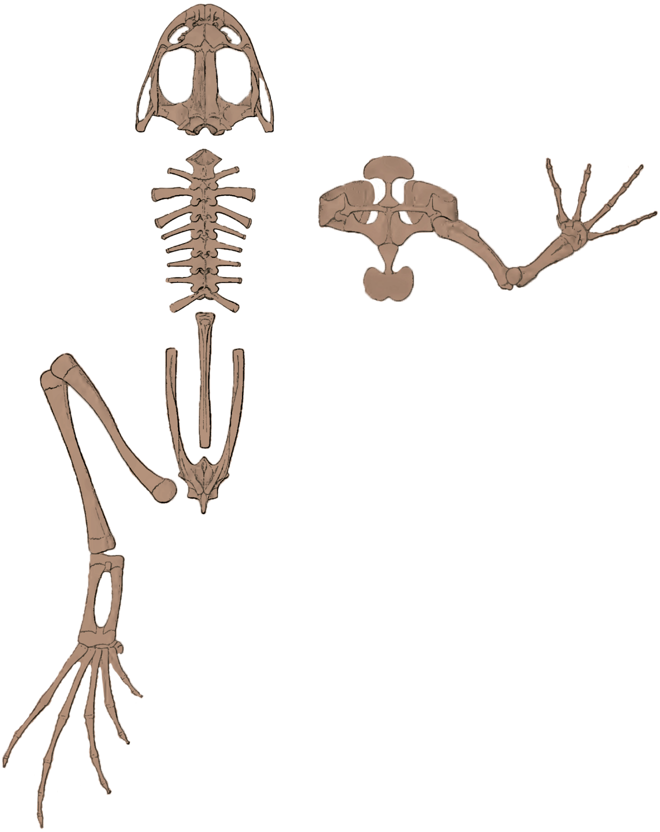
CHAPTER 2. MATERIAL AND METHODS



SUMMARY

This chapter contains some of the issues referent to the material analysed, the species studied, the field and laboratory work and also, the osteological reference collections consulted and the performed body size reconstruction. The two main species studied in this PhD are *Epidalea calamita* (Laurenti, 1768) and *Pelophylax perezi* (Seoane, 1885), also contemplated in some cases as the whole genus *Pelophylax*. The first one, also known as natterjack toad has been settled in Europe and specifically in the Iberian Peninsula for at least 16 or 17 Ma and is characterized for its ecological plasticity. *Pelophylax* is a genus of waterfrogs which appears in central Europe during the Oligocene and it is maintained until our days. *P. perezi* is also known as the Iberian waterfrog or common frog and it is the main representative of the genus in the Iberian Peninsula. These frogs are exclusively of aquatic habits and concretely *P. perezi* has few ecological requirements but altitude. Material studied in this PhD consists mostly in fossil disarticulated bone fragments from Atapuerca sites (Sima del Elefante, Gran Dolina and Portalón) located in Burgos (Central Spain), Guadix-Baza Basin sites (Barranco León and Fuente Nueva 3) situated in Orce (SE Spain) and Camp dels Ninots placed in Caldes de Malavella (NE Spain). A total of 3720 fossil humeri of *E. calamita* and genus *Pelophylax* have been measured for this PhD thesis. Also, material of the osteological reference collections from the MNCN (Museo Nacional de Ciencias Naturales, Madrid) has been studied and used to create both OLS regression models which allow for the reconstruction of past body sizes of *E. calamita* and *P. perezi* based on humeral measurements. The humerus has been selected as the reference osteological element for this PhD because, in addition to its high correlation with body size, it is relevant for the species attribution, permits to establish the sex of the individual and it is quite abundant in fossil samples unlike other elements which also may present correlation with body size. Main features by which the humerus of *E. calamita* and the waterfrogs of genus *Pelophylax* can be recognized are specified within this chapter and also are the humeral measurement selected for body size reconstruction and the technical material employed to this respect.

Even though most of the contents of this section are explained in the papers part of the Chapter 3 (*"Results"*), here some relevant issues referent to the material analysed will be explained more in detail, the studied species, the associated field and laboratory work and also, the reference collections consulted and the performed body size reconstruction.

2.1 *EPIDALEA CALAMITA* AND *PELOPHYLAX PEREZI*: ECOLOGICAL REMARKS AND THE ACTUALISTIC APPROACH

In this PhD thesis, the study of the body size of anurans has been focused on two species: *Epidalea calamita* (Laurenti, 1768), and *Pelophylax perezi*, (Seoane, 1885) studied also at genus level (*Pelophylax*). The selection of these two anurans for the study of its body size was due to its abundance in most of the archaeo-palaeontological sites from the Plio-Pleistocene of the Iberian Peninsula. In this section, a few insights of the biology of these species and its main ecological requirements, habitat or distribution are presented together with a brief description of their main traits, body size and sexual size dimorphism.

Epidalea calamita

Epidalea (formerly *Bufo*) *calamita* (Laurenti, 1768) commonly known as natterjack toad, is an anuran species belonging to the Bufonidae family, a group which presents a great physiological and morphological diversity and a wide distribution. *E. calamita* has been settled in Europe and specifically in the Iberian Peninsula for at least 16 or 17 Ma. Some fossil remains of this species are situated with certainty within the Pliocene and other ones could correspond to the Turolian Miocene (Sanchiz, 1998). The natterjack toad is a medium-sized toad, robust and plump in appearance whose coloration and design are highly variable but with the presence of a characteristic lighter midline on the back (Fig. 1C). Its distribution area includes a large part of the European continent (Beebee, 1983) (Fig.1.B) and, in the case of the Iberian Peninsula, *E. calamita* is found in most of the territory, although it is rarer in areas of the Norther coast and is absent in the Balearic and Canary archipelagos (Reques and Tejedo, 2002) (Fig. 1.A). Natterjack toads are well adapted to terrestrial environments, although, like other amphibians, they remain attached to water bodies where they return to reproduce and spawn (García-París et al., 2004). In general terms, this species is characterized by its high ecological plasticity, it can be found in several types of natural habitats and also in anthropic environments to which it easily adapts (García-París et al., 2004). In the same way, it is distributed along a wide pluviometric and altitudinal gradient (García-París et al., 2004; Reques and Tejedo, 2002).

According to García-París et al. (2004), *E. calamita* presents a light sexual size dimorphism, being the females somewhat larger than the males. The latter ones, on the other hand, have more robust forelimbs, possibly due to the greater musculature necessary for the amplexus, as occurs in most amphibian species.

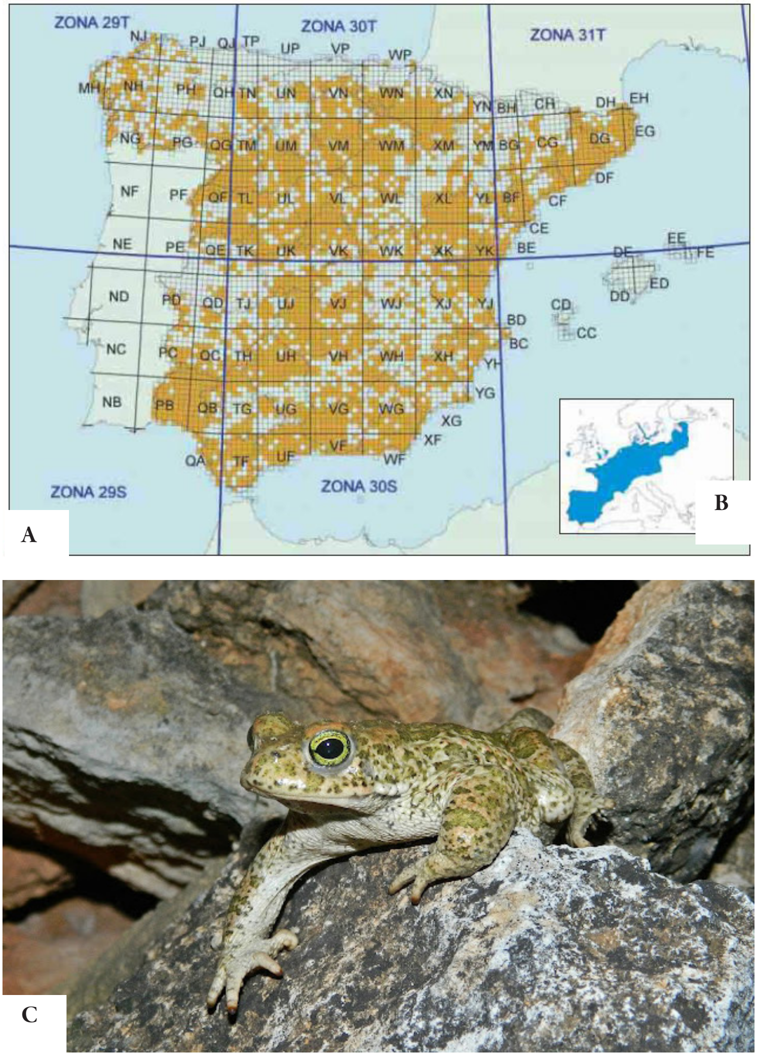


Figure. 1 *Epidalea calamita.* Distibution maps of Spain (**A**) and Europe (**B**) from Reques and Tejedo (2002). (**C**) Photograph of an adult individual (Photograph courtesy of J. F. Bisbal-Chinesta).

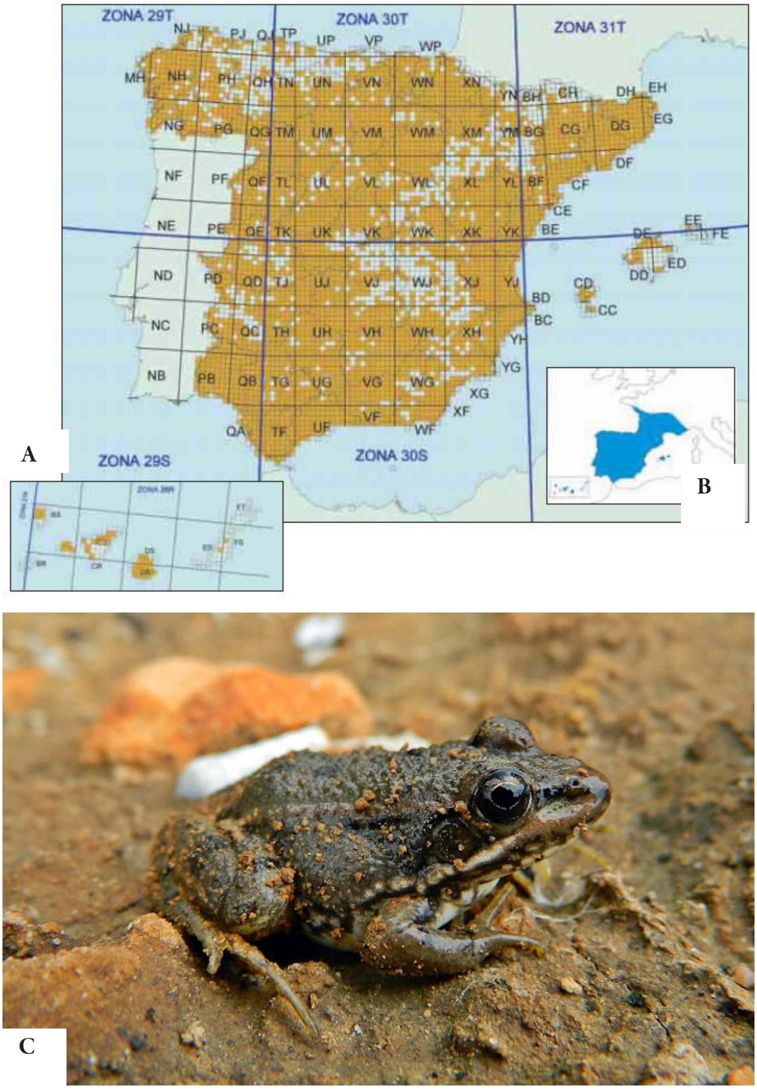


Figure. 2 *Pelophylax perezi*. Distribution maps of Spain (**A**) and Europe (**B**) from LLorente et al. (2002). (**C**) Photograph of an adult individual (Photograph courtesy of J. F. Bisbal-Chinesta).

Genus *Pelophylax* and *Pelophylax perezi*

The genus *Pelophylax* (Anura, Ranidae) appears in central Europe during the Oligocene (Sanchiz et al., 1993) and it is maintained until our days. *Pelophylax* is a widespread genus of green frogs with a current distribution around Eurasia and north Africa. This genus, known as "paleartic water frogs", counts with a high number of species and also with hybridogenic complexes. In Spain, the main representative of its genus is the Iberian waterfrog or common frog, *Pelophylax perezi* (Seoane, 1885). *P. perezi* is a medium-size frog with smooth dorsal and ventral skin and with a rounded snout (Fig. 1.C) (Egea-Serrano, 2014). Its worldwide distribution includes the entire Iberian Peninsula and southern France, though the northern limit is not clear (Fig. 1.B). Within the Iberian Peninsula, *P. perezi* is distributed throughout practically all the territory (Fig. 1.A), and is only absent in the regions of higher altitudes (more than 2400 meters above sea level in the Betic range). As occurs in the rest of Europe, hybridogenic populations of the common frog can be found in the Iberian Peninsula.

This species, which has few ecological requirements but altitude (Egea-Serrano, 2014; Llorente et al., 2002), occupies all kinds of biotopes, both in the Mediterranean and Eurosiberian bioclimatic regions. It can be found in places subjected to intense human action. *P. perezi*, as the rest of water frogs, is of exclusive aquatic habits and usually share its habitat with a great number of anuran species as adults and larval stages (Egea-Serrano, 2014). Also, the common frog is not very demanding with water quality and tolerates saline environments (Llorente et al., 2002). The Iberian waterfrog presents an elevated genetic variability and geographic variation in weight and body size. This diversity results in lower body sizes in the populations from southern Iberia (Egea-Serrano, 2014). Different from *E. calamita, P. perezi* presents an evident sexual size dimorphism being the females much bigger than males.

Like most amphibian species present in Pleistocene localities, *E. calamita* and *P. perezi* are considered identical to modern populations due to genetic distance data obtained by molecular clock techniques (Sanchiz, 1977; Barbadillo et al., 1997); therefore, the law of actualism, based on Hutton's Principle of Uniformity, can be applied to this species. This circumstance results favourable within the context of the methodologies developed to reconstruct past conditions based on the faunistic record. In this case, the use of current analogues of fossil species is avoided thus ensuring a strong correspondence between both fossil and current populations.

2.2 MATERIAL

Material studied in this PhD consist mostly in fossil disarticulated bone fragments collected by water screening from Atapuerca sites (Sima del Elefante, Gran Dolina and Portalón) and Guadix-Baza Basin sites (Barranco León and Fuente Nueva 3) and collected in situ within the main excavation in Camp dels Ninots (see Appendix 1, Plates 2, 3, 4 and 5). In this last palaeontological site, in addition to disarticulated elements, also articulated specimens appeared. In this work, these last specimens have been measured but not included in the final body size analysis due to the risk of bias generated by the flattening of specimens during fossilization that may have altered the original shape of the frogs (Sanchiz, 1977). Also, in most of the specimens, the orientation of the humerus prevents of taking the measurements required for the body size reconstruction. Fossil remains from Sima del Elefante were only included in the biodiversity analysis. Material coming from the rest of the sites of Sierra de Atapuerca (Gran Dolina and Portalón) and also the material from Guadix-Baza Basin sites was analysed from both perspectives, anuran body size and herpetofauna diversity.

A total of 3720 fossil humeri of *E. calamita* and genus *Pelophylax* have been measured for this PhD thesis. 3217 of them attributed to *E. calamita* are from Gran Dolina and 371 from Portalón. Of those ones assigned to the genus *Pelophylax*, 93 humeri (*Pelophylax* cf. *perezi*) come from Barranco León, 13 from Fuente Nueva 3 (*Pelophylax* cf. *perezi*) and 26 (*Pelophylax* sp.) from Camp dels Ninots. Apart from that, the analysis of the herpetofauna diversity was based on former faunal lists (Blain 2005; Blain et al., 2008, 2010, 2011, 2013; López-García et al., 2010) for Atapuerca sites and the one of Sánchez-Bandera et al., 2020 for Barranco León and Fuente Nueva 3, where stratigraphical information is taken into account.

2.3 FIELD WORK, LABORATORY WORK

Anuran fossil remains from Atapuerca sites and Barranco Léon and Fuente Nueva 3 have been recovered by the water-screening and sieving of the sediment coming from the main excavation sites. In both cases, sediment was collected in bags and transported to the washing area near to the river where was moved into buckets with water to soft and break the sediment up. Finally, it was water-screening (Fig. 3A, D) with two superimposed meshes of 10.5 and 0.5 mm. After that, once the resulted sediment was completely dry (Fig. 3B), the bone fragments were picked up by hand (Fig. 3C) and under a binocular microscope when it was necessary.

I personally participated in this process during the campaigns of 2014, 2015 and 2016 in Atapuerca sites and also in 2019 in the archaeopalaeontolgical complex of sites from the Orce Archaeological Area (among which are Barranco León and Fuente Nueva 3) (Fig. 3). The fossil remains were collected in minigrip bags with a label including the name of the site, the year, the date, the level, the square and the depth (z). Material coming from Barranco León and Fuente Nueva 3 is stored in the Museo Arqueológico y Etnológico de Granada (MAEGR; Granada, Spain) and the ones from Atapuerca sites are held in the University of Zaragoza (UNIZAR, Zaragoza, Spain).

Regarding to the laboratory work, it was carried out mostly at IPHES (Fig. 4A) (Tarragona, Spain) and an initial part at the Universidad de Alcalá (UAH, Madrid, Spain). Reference collections were loaned for its analysis as it was the fossil material included in this work. Measurements were taken by means of a binocular microscope equipped with a camera lucida (Askania, Technival 2) (Fig. 4F) in the case of the humerus of *E. calamita* from Atapuerca sites and, for the rest of the material, with a digital microscope (Dino-Lite USB 3.0 AM73000 Series) (Fig. 4D, E) which was also used to take photographs. For the study of osteological characters and drawings, a binocular microscope (Olympus SZX7) also equipped with a camera lucida (Olympus SZX-DA) (Fig. 4B, C).

Within this PhD, the analysis of the fossil material, the osteological reference collections and the measurements taking were the main technical work carried out. Apart from that,

Figure. 3 Field work at the Sierra de Atapuerca sites (**A-C**) and Guadix-Baza Basin sites (**D**). The pictures reflect the main phases of the sediment processing: Water-screening (**A, D**); Drying (**B**) and sorting (**C**).

Figure. 4 Main technical equipment used during the analysis of the material (**A**): Binocular microscope (Olympus SZX7) (**B**) equipped with a camera lucida (Olympus SZXDA) (**C**); Digital microscope Dino-Lite USB 3.0 AM73000 Series (**D, E**); and another binocular microscope (Askania,Technival 2) (**F**) equipped also with a camera lucida.

the laboratory work for this project involved the preparation of some specimens for my osteological collection (AMM) and also from the Blain Herpetological Collection (BHC) in Table 6 (Appendix 3, "*Data*") both stored at IPHES. After the data collection (place where the specimens were collected, date, name of the collector and other observations), the body size as SVL was recorded for all the specimens. For the preparation of the amphibians, the skin was removed (when possible) and then the specimens went through a period of maceration in water with successive changes of the liquid. Finally, the specimens were boiled in order to remove the remaining organic tissues and thus clean bones were obtained which afterwards were added to the named collections and to my body size database. All these procedures were also carried out in the Micropaleontology and Zooarchaeology laboratories of IPHES (Tarragona, Spain).

2.4 THE HUMERUS: MAIN FEATURES, MORPHOLOGICAL CHARA CTERS AND TAXONOMICAL ATTRIBUTION

For all the work regarding to anuran body size included in this PhD thesis, the humerus was the reference osteological element. This element has been selected because, in addition to its high correlation with body size, permits to relatively securely identify the species/genus and the sex of the individual. At these points, the humerus differs from other bones which also present correlation with body size. In addition to all the information provided by this osteological element, in fossil assemblages, the humerus is often well-represented and it is one of the best-preserved bones, concretely its distal epiphysis which is the place where the selected measurement for the body size reconstruction should be taken.

Even though the taxonomical attribution to the species studied was carried out in former works (Blain, 2005; Blain et al., 2008 and López-García et al., 2010 for *E. calamita*; Blain et al., 2011; Gómez de Soler et al., 2012; Sánchez-Bandera et al., 2020 for the genus *Pelophylax*), a study of the humerus and its characters has been carried out for this PhD thesis.

E. calamita remains were identified following the general criteria for anurans given in Böhme (1977), Sanchiz (1977), Bailon (1999) and Blain (2005, 2009) The main characters by which the humerus of *E. calamita* can be recognised (see Appendix 1, Plates 2 and 3) are the high curvature of its relatively short diaphysis, a condyle located laterally in relation to the main diaphysis axis, well developed radial and ulnar epicondyles, closed cubital fossa, absence of paraventral crest (but rudimentary in some cases; Sanchiz, 1977), and, only in males, the presence of a medial crest, key character to establish the sex of an individual.

For waterfrogs of genus *Pelophylax*, specifically *Pelophylax* cf. *perezi* for Barranco León and Fuente Nueva 3, and *Pelophylax* sp. for CN can be identified following the criteria from Blain (2005 and 2009) and Bailon (1999). In the case of CN, the specific attributions among the different species of *Pelophylax* has still to be resolved and this is why we preferred for the moment to let attribution to genus level. One of the main features by which the humerus of the genus *Pelophylax* can be recognized is its straight diaphysis in ventral view (more robust than in the group of brown frogs) which does not have a paraventral crest. It is also a distinctive trait of the ranids the presence of a well-rounded condyle situated in the extension of the diaphyseal axis. In male individuals belonging to genus *Pelophylax*, a

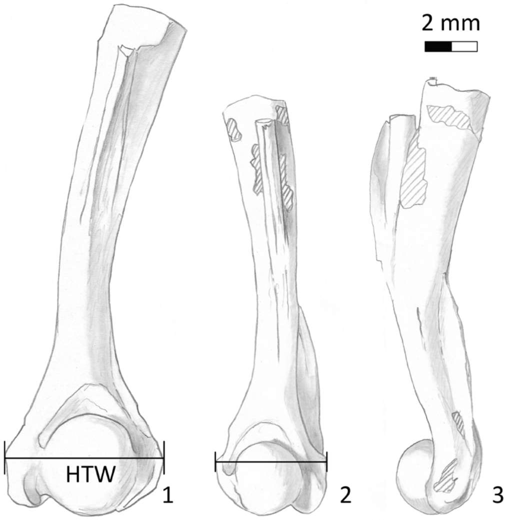


Figure. 5 Ventral and lateral views from female (1) and male (2, 3) Epidalea calamita humeri from the dry osteological reference collections of the Museo Nacional de Ciencias Naturales (Madrid, Spain) with identification numbers (MNCN-42577 and MNCN-22337 respectively). Ventral views (1, 2) shows the humeral total width (HTW), the measurement selected for the body size reconstruction.

short, transverse medial crest is present, which is characteristic of the green frogs group (see Appendix 1, Plates 1, 4 and 5). Even though the humerus of this group of waterfrogs can be identified at genus level (i. e. *Pelophylax*), in these ranids is the ilium the main distinctive osteological element which leads to the specific attribution.

2.5 REFERENCE COLLECTIONS, MEASUREMENTS AND BODY SIZE RECONSTRUCTION

The modern specimens consulted and measured in order to create a reference database for body size reconstruction are part of the osteological collections from the Museo Nacional de Ciencias Naturales (MNCN; Madrid, Spain). Founded in 1771, this institution is one of the most iconic centres pertaining to the Consejo Superior de Investigaciones Científicas (CSIC) (Fig. 4). From its osteological collections belonging to the Herpetology section, dry osteological material has been analysed and included in our database (Table 6 Appendix 3, "*Data*"). Together with other specimens belonging to my collection identified as AMM, and other ones from the collection of the Dr. Hugues-Alexandre Blain deposited at IPHES identified as BHC, a total of 66 individuals of *Epidalea calamita* (49 males and 17 females) and 104 of *Pelophylax perezi* (43 males and 61 females) have been included in the dataset (Table 6 in Appendix 3, "*Data*").

To reconstruct past body size of these anurans as SVL, the humeral total width (HTW) was the selected measurement as it presents the highest correlation with body size in the modern populations (to see details of the results of the OLS regression models

Fecha y lugar de colecta: 01/05-04-1985.- Plasencia, (Cáceres) Extremadura, España, Europa.
Colectó:
P LT: LCC

MNCN-15062 M.-Ad.-
EDP(A:07)+ETP (T:0664)
Taxon Pelophylax perezi // (Seoane, 1885)
Fecha y lugar de colecta: 01/05-04-1985.- Plasencia, (Cáceres) Extremadura, España, Europa.
Colectó:
P LT: LCC

MNCN-15061 M.-Ad.-

Fecha y lugar de colecta: 06-03-1983.- San Agustin de Guadalix, (Madrid) C. A. de Madrid, España, Europa.
Colectó: R. R. Talavera
P: 9 g LT: LCC 47 mm

MNCN Madrid

1885)
Fecha y lugar de colecta: 11-03-1983.- Cauce del rio Guadarrama, Villaviciosa de Odón, (Madrid) C. A. de Madrid, España, Europa.
Colectó: I. Doadrio & R. R. Talavera
P: 3'3 g LT: LCC 34 mm

MNCN-16452 Jv.-
EDP(A:07)
Taxon Pelophylax perezi // (Seoane, 1885)
Fecha y lugar de colecta: 11-03-1983.- Villaviciosa de Odón, (Madrid) C. A. de Madrid, España, Europa.
Colectó: I. Doadrio & R. R. Talavera
P: 1'5 g LT: LCC 23 mm

MNCN-16451 ?.-

Villamesias, (Cáceres) Extremadura, España, Europa.
Colectó: R. R. Talavera
P: 2 g LT: LCC 29 mm

MNCN-16460 H.-Ad.-
EDP(A:07)+ETP ()
Taxon Pelophylax perezi // (Seoane, 1885)
Fecha y lugar de colecta: 05-04-1983.- Villamesias, (Cáceres) Extremadura, España, Europa.
Colectó: R. R. Talavera
P: 22'57 g LT: LCC 66 mm

MNCN-16459 H.-Ad.-
EDP(A:07)+ETP ()
Taxon Pelophylax perezi //

Figure. 5 Museo Nacional de Ciencias Naturales de Madrid, Spain (MNCN). (**A**) Sample of its dry osteological collection of amphibians; (**B, C**) Different views of the main building and (**D**) logotype.

see the sections 1.1 and 1.3 from the Part 1 of the Results chapter). This measurement is defined as the maximum width of the humeral distal epiphysis with the humerus in ventral view (Fig. 4). Body size and other data from all the sequences studied are contained in the Appendix 3.

In this PhD all the main statistical analysis were conducted with R (R core team) and with PAST (Hammer et al., 2001). Different statistical approaches are explained in detail in the *"Material and methods"* section of each paper (see Chapter 3 *"Results"*).

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CHAPTER 3.
RESULTS

SUMMARY

This chapter compiles the three main publications that constitute this PhD and also an unpublished work. In general terms, each publication starts with and introduction where the main literature on the topic is revised and a material and methods section which explains the statistical analysis and the fossil assemblages studied. Then, the description of the results obtained is presented followed by a discussion of such results and the main conclusions of the work.

References of these publications are:

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(8), 1307-1318.

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Part 1.
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1.1

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Climate and amphibian body size: a new perspective gained from the fossil record

Almudena Martínez-Monzón, Hugues-Alexandre Blain, Gloria Cuenca-Bescós and Miguel Ángel Rodríguez

A. Martínez-Monzón (http://orcid.org/0000-0001-5120-9478) (almudena.martinezm@hotmail.com), H.-A. Blain, Inst. Català de Paleoecología Humana i Evolució Social (IPHES), Tarragona, Spain. AM-M also at: Àrea de Prehistòria, Univ. Rovira i Virgili (URV), Tarragona, Spain. H-AB also at: Univ. Rovira i Virgili (URV), Àrea de Prehistòria, Tarragona, Spain. – G. Cuenca-Bescós, Aragosaurus-IUCA, Dept of Earth Sciences, Univ. of Zaragoza, Zaragoza, Spain. – M. Á. Rodríguez and AM-M, Depto de Ciencias de la Vida, Edificio de Ciencias, Univ. de Alcalá, Madrid, Spain.

In recent years several studies have been carried out to test the validity of Bergmann's rule for amphibians, and have generated varying results. Due to the lack of agreement on this topic, here we examine the relationship between climate and body size for one anuran species (*Bufo calamita*, commonly known as the natterjack toad) with a new methodological approach that uses the fossil record as the data source. We analysed bones from two archaeo-paleontological sites located close to each other in the Sierra de Atapuerca (Burgos, Spain) that together encompass more than one million years from Early to Late Pleistocene. We used ordinary least squares (OLS) simple regression models to integrate body size and palaeoclimatic data (temperature and precipitation) and describe the relationship between the amphibian's body size and climate along the entire temporal gradient. We found the body size of *B. calamita* to be negatively related to the mean annual temperature and the mean temperature of the coldest month, and positively related to December-to-February precipitation. The climatic influence was stronger in females, which were smaller than males in most cases, and therefore an inverse sexual size dimorphism pattern was found. Juvenile individuals or the limited sexual size dimorphism of this species may be causes of this unusual pattern. *Bufo calamita* populations showed a clear Bergmann cline during the Pleistocene period, and winter stands out as the most influential season. Although this new methodology can only be used to describe patterns, we discuss several mechanisms that could explain our results. We propose that starvation resistance and delayed maturation are the main causes for this increase in size in periods with cooler winters, and a fecundity-related hypothesis to explain why climate has a greater influence on female body size.

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1.1.1. INTRODUCTION

Due to the worldwide decline in amphibian populations it is crucial to take preservationist actions to avoid potential massive extinctions (Wake, 1991; Houlahan et al., 2000; Hussain and Pandit, 2012). The possible reasons behind this decline and the complex interactions between them have been studied in several works (Collins and Storfer, 2003; Beebee and Griffiths, 2005). In all cases the authors agree that climate change and its consequences are relevant factors in this process because they affect amphibian biology and distribution (Carey and Alexander, 2003; Reading, 2007; Li et al., 2013).

One of the main biological traits in amphibians that could be affected by these changes in climate is body size. Commonly studied in ecology, body size influences many physiological and biochemical processes and determines life history and ecological niche (Peters, 1983; LaBarbera, 1989; Bonner, 2011). Therefore, increasing our knowledge about how changes in climate affect amphibian's body size (identifying patterns and understanding the underlying mechanisms) is a priority for developing conservation strategies and also for understanding amphibian diversity, biology and biogeography better.

Karl Bergmann, a German physiologist, was the first to link body size with climate (Bergmann, 1848). He proposed that larger species would occupy cold areas due to their higher heat conservation capacity due to their low surface-to-volume-ratio. This global pattern, known as Bergmann's rule, and its associated mechanism (better heat conservation) have been supported by several studies for endothermic vertebrates (reviewed by Ashton et al., 2000; Ashton, 2002). Although to a lesser extent, body size gradients have also been studied in ectotherms. However, results are mixed as no clear trend has been found in some cases (Hawkins and Lawton, 1995; Pincheira-Donoso et al., 2008) but support for Bergmann's rule has been found in others (Lindsey, 1966; Atkinson et al., 2003), and the mechanism proposed to justify the pattern is not always better heat conserva¬tion. Although no single theory has been able to explain the generality of temperature–size relationships in ectotherms (Angilletta et al., 2004), these data suggest that the validity of Bergmann's rule may not only be limited to endotherms but may also be valid for ectotherms, which broadens the range of taxa to be studied.

Regarding amphibians, even though previous studies into Bergmann's rule (and its intraspecific modification known as James's rule (James, 1970; Blackburn et al., 1999)) have been carried out, no generally accepted trend has been established for this group (Tryjanowski et al., 2006). Discrepancies occur at the inter and intraspecific levels, studies have found Bergmann clines (Hemelaar, 1988; Schäuble, 2004; Olalla-Tárraga and Rodríguez, 2007), the inverse pattern (Leskovar et al., 2006; Olalla-Tárraga and Rodríguez, 2007; Cvetković et al., 2009) and even no clear trend in body size related to temperature (Laugen et al., 2005; Adams and Church, 2008; Olalla-Tárraga et al., 2009). As no conclusive results have been found at the geographic scale, we hope to contribute to this question by focusing on the problem from another perspective: by studying body size along a stratigraphic sequence, in other words, over time. Although climate dynamics are often studied in the long term (McCarroll, 2015), amphibian's responses to these variations are not; therefore, we propose a temporal scale study in which we will analyse the variations in body size of one anuran species and its relationship with climate over more than one million years based on the best source of information for long term studies: the fossil record.

After we had determined our novel approach, we selected two archaeological sites with abundant microvertebrate fossil records (Blain, 2005, 2009; Blain et al., 2008, 2009; Cuenca-Bescós et al., 2005, 2010, 2011, 2016; Cuenca-Bescós and García, 2007; López-García, 2008; López-García et al., 2010) that together cover more than one million years. These sites are Gran Dolina (Carbonell et al., 1995; Bermúdez de Castro et al., 1997) and Portalón (López-García et al., 2010), both located in the Sierra de Atapuerca, Burgos, Spain (Fig. 1). They are karstic sites separated by less than one kilometre; therefore, latitudinal and altitudinal variations and related variables that could potentially affect our results are avoided, unlike previous spatial-nature works in which climatic influence on body size can be masked by co-variant ecological features. The 11 layers of the cave of Gran Dolina (TD) site have provided an unusual supply of archaeological remains and fossils of large and small vertebrates that have been used to document human activity and its relationship to the environment in the last one million years (Carbonell et al., 1995, 2008; Bermúdez de Castro et al., 2008; Rodríguez et al., 2011; Rodríguez-Gómez et al., 2013). The stratigraphic layers of the site have been extensively excavated, studied and dated using numerous methods, such as biostratigraphy, luminescence, electron spin resonance and paleomagnetism (Cuenca-Bescós et al., 1999, 2015; Falguères et al., 1999; Parés and Pérez-González, 1999; Berger et al., 2008; Parés et al., 2013; Arnold et al., 2015). Gran Dolina contains one of the most complete Quaternary stratigraphic sequences in Spain from the Early to Middle Pleistocene, which comprises some 700 000 yr (1 Myr to 244 kyr BP: see the latest updates for the chronology of Gran Dolina in Alvarez-Posada et al., in press), while the Portalón Late Pleistocene stratigraphic sequence comprises at least 15 000 yr (30 to 16 kyr BP) (Table 1).

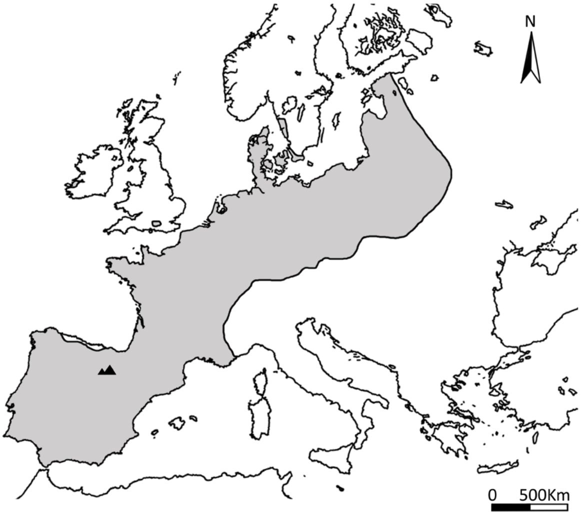

Figure 1. Geographic range (in grey) of *Bufo calamita* (modified from Beja et al., 2016) and location of the Gran Dolina and Portalón excavation sites at Sierra de Atapuerca (mountain range symbol).

Choosing Portalon to complement Gran Dolina allowed us to investigate a larger time span in the same location.

Due to its great abundance (more than 35 000 bones) and continued presence throughout the two sequences, the amphibian species selected to carry out this study is a bufo nid that is widespread in Europe and also very common in the Iberian Peninsula (Fig. 1): *Bufo calamita* (= *Epidalea calamita*) commonly known as the natterjack toad. Like most amphibian species present in Pleistocene localities, *B. calamita* is considered identical to modern populations due to genetic distance data obtained by molecular clock techniques (Sanchiz, 1977; Barbadillo et al., 1997); therefore, the law of actualism, based on Hutton's Principle of Uniformity, can be applied to this species.

Using the proposed temporal approach, we aim to examine variation in the body size of *B.calamita* populations over the entire Pleistocene period in the Sierra de Atapuerca (Burgos, Spain). In addition, we take climatic parameters into account to study the effect of climate on amphibian body size by testing five, not mutually exclusive hypotheses for ectotherm body size gradients: 1) the heat-balance hypothesis establishes that, for ectothermic taxa below a certain body size threshold and with physiological and/or behavioural thermoregulatory abilities (such as burrowing or basking to enhance heat gain and/or heat conservation), larger body sizes would be favoured in cooler climates where their low-surface-to-volume ratio is better for conserving heat (Olalla-Tárraga and Rodríguez, 2007). Anurans are below this size threshold and are considered to be thermoregulators. In particular, *B.calamita* is well known for showing behavioural adaptations like burrowing to avoid frost or desiccation (López Jurado, 1982; Gómez-Mestre and Tejedo, 2005; Oromí et al., 2010). Therefore, in agreement with this hypothesis, a Bergmann cline is predicted to take place among *B. calamita* populations, increasing their body size in cooler periods.

The same prediction would also be derived from two of the most accepted explanations for Bergmann's rule in ectotherms (reviewed by Ashton, 2002); namely, 2) the temperature–size rule (Atkinson, 1994) and 3) the starvation resistance hypothesis (Boyce, 1979). The former states that, for ectotherms, lower development temperature results in larger body size, which has been supported for different amphibian species by laboratory experiments (see Ashton, 2002 and references therein). Also, for *B. calamita*, temperature during the activity period between metamorphosis and first hibernation or aestivation has proved to be decisive for the final adult body size (Sinsch et al., 2010). Alternatively, the starvation resistance hypothesis states that larger animals are favoured in cooler, more seasonal environments due to their larger capacity to store fat and use it to enhance sur-vival during stress periods, mainly when overwintering. In this regard, although no relationship between energy storage and juvenile mortality was found in a German population of *B. calamita* (Sinsch and Schäfer, 2016), this does not rule out its potential importance for this species over vast time periods like the one studied here.

However, based on the same physical principle as Bergmann's heat conservation mechanism (i.e. surface-to-volume ratios), 4) the water availability hypothesis predicts larger sizes for amphibians that inhabit more arid areas because they would have higher desiccation resistances (Olalla-Tárraga and Rodríguez, 2007). Some works support this idea (Olalla-Tárraga et al., 2009; Nabil et al., 2011) and highlight the importance of humidity in amphibian biology.

Finally, intersexual differences in body-size variation in response to climate changes cannot be dismissed, as several works have detected that climate has a larger influence on the body size of amphibian females (Hemelaar, 1988; Schäuble, 2004; Leskovar et al., 2006). It is well known that an increase in female body size is closely related to a greater fecundity in ectotherms, including amphibians in general (Shine, 1979; Miaud et al., 1999; Monnet and Cherry, 2002; Han and Fu, 2013), and *B. calamita* in particular (Tejedo, 1992; García-París et al., 2004). This led us to propose 5) a fecundity-related hypothesis that states that increased female fecundity due to a larger body size is advantageous in harsh environments as it increases the probability of success in reproduction and juvenile survival (Atkinson, 1994; Angilletta et al., 2004).

Table 1. Stratigraphic levels, age estimates (extracted from Falguères et al., 1999; Berger et al., 2008; López-García et al., 2010), climate units and their averaged values for mean annual temperature (MAT), mean temperature of coldest month (MTC), mean temperature of warmest month (MTW), annual precipitation (AP), winter (DJF) precipitation (WP), and summer (JJA) precipitation (SP) at the Portalón (PI to PVI units) and Gran Dolina (DI to DVII) excavation sites in the Sierra de Atapuerca.

Level	Age (kyr BP)	Climate	Temperature (ºC)			Precipitation (mm)		
		unit	MAT	MTC	MTW	AP	WP	SP
P4/P3	<16.89 ± 0.08	PVI	8.4	1.7	16.5	1342.5	265	153
P11-P7	30.30 ± 0.19	PV	7.5	2.5	19.6	950	244	197
P12		PIV	8.8	2.1	17.6	1346	263	156
P13		PIII	7.3	2.5	19.6	950	244	197
P14		PII	9.4	3.3	20	860	244	197
P15		PI	7.3	2.5	19.6	950	244	197
TD10	244 ± 26	DVII	11.7	3.8	19.8	893.4	179.4	145.1
TD10	337 ± 29	DVI	12.6	3.8	20.3	981	148	153
TD8	586 ± 88	DV	12.6	3.8	20.3	981	148	153
TD7	734 ± 128	DIV	12.1	3.4	20.3	907	167	148
TD6	882 ± 91	DIII	12.3	3.6	20	975.8	155.4	150.8
TD5/TD6		DII	11.4	3.3	19.5	958	183.5	152.1
TD5	988 ± 225	DI	11.8	3.3	19.5	960.5	164.5	145.3

1.1.2 MATERIAL AND METHODS

The sites

The Gran Dolina and Portalón sites are part of the Sierra de Atapuerca, a small hill of late Cretaceous limestones located 14 km to the east of the city of Burgos in northern Spain (Fig. 1). This small limestone hill emerges among the characteristic flat landscape of the Castilian cereal-growing plains to around 1080 m a.s.l. The Atapuerca hill is in the middle of the Bureba Corridor that connects the Ebro and Duero basins, and thus constitutes the ecotone between the Eurosiberian and Mediterranean bioclimatic areas. These particular conditions are reflected in the high biodiversity of the area, which is characterized by a mixture of Mediterranean and Atlantic taxa (García-Antón and Sainz-Ollero, 1991; Bermúdez de Castro et al., 1995), a pattern that is also observed in the current herpetofauna assemblage (Diego-Rasilla and Ortiz-Santaliestra, 2009; Ortiz-Santaliestra et al., 2011). The Burgos area is considered one of the coldest regions in the Iberian Peninsula (Font Tullot, 2000), and has a Continental-Mediterranean climate with mean annual values for temperature and precipitation of 9.9°C and 572 mm respectively (meteorological station of Burgos Air Base, 891 m a.s.l. The Burgos region is characterized by its very contrasted seasonality: winters are cold including snowfalls and below freezing

Table 2. Mean, maximum and minimum values for humeral-total-width-based reconstructions of *Bufo calamita* body sizes (snout-to-vent-lengths in mm) in 13 climate units at the Portalón (top six rows) and Gran Dolina excavation sites in the Sierra de Atapuerca. Body size values were calculated for whole populations and for females and males separately. Ages of climate units increase downwards. The number of humeri measured for body size reconstructions is also provided (n).

Climatic	Population				Females				Males			
unit	mean	max	min	N	mean	max	min	N	mean	max	min	N
PVI	57.9	69.3	41.4	15	50.7	63.2	41.4	5	61.5	69.3	57.3	10
PV	52.2	81.1	6.8	272	47.8	81.1	6.8	152	57.9	67.7	44.6	120
PIV	54.0	58.6	47.2	6				1	54.2	58.6	47.2	5
PIII	58.0	64.3	45.5	7					58.0	64.3	45.5	7
PII	54.6	63.2	48.1	7		63.2	55.7	2	52.6	58.0	48.1	5
PI	55.4	70.4	19.8	55	52.4	68.4	19.8	26	58.1	70.4	51.4	29
DVII	47.2	67.9	9.0	435	40.1	66.7	9.0	196	53.0	67.9	34.3	239
DVI	47.4	68.5	6.7	393	41.2	68.5	6.7	178	52.5	65.7	35.4	215
DV	43.4	70.0	6.7	131	39.7	70.0	6.7	91	51.7	64.9	34.3	40
DIV	51.1	63.2	14.5	11	39.5	63.2	14.5	7	57.2	59.3	53.6	5
DIII	47.1	73.2	6.7	773	40.7	73.2	6.7	445	55.8	68.3	37.7	328
DII	50.8	74.7	6.7	934	46.2	74.7	6.7	516	56.6	70.9	40.7	418
DI	52.4	66.1	12.7	194	47.4	65.1	12.7	96	57.3	66.1	43.6	98

temperatures that reach –15°C, while summer mean temperatures are between 15 and 20°C (Font Tullot, 2000; Ninyerola et al., 2005).

The anuran amphibian fossil remains used for this study consist of disarticulated bone fragments collected by excavating the sediments with archaeological methods and then water-screening a restricted area within the sites, called the TDS (around 9 m² in Gran Dolina; Blain, 2005, 2009; Blain et al., 2008, 2009) and N10 squares (around 1 m² in Portalón; López-García et al., 2010). The remains were provisionally stored for study at the Inst. de Paleoecologia Humana i Evolució Social (Tarragona, Spain). From a total of 35 057 *B. calamita* remains, we analysed for this work 3217 fossil humeri from Gran Dolina and 371 from Portalón, and thus the sample size was 3588 humeri (the number of humeri per sex and climatic unit are shown in Table 2). The humerus was considered the most appropriate skeletal part for our purposes, as it is a well-ossified, robust, long bone, in particular the distal extremity, and also a highly diagnosable element at species level. Moreover, it is sexable, it constitutes an excellent indicator of body size and, as supported by our sample size, it is relatively abundant in most of the fossil samples.

Gran Dolina and Portalón are both cave systems where the origin of microvertebrate remains is mainly due to the action of small predators and/or in situ mortality (Bennàsar, 2010). Several facts, such as the high number of remains, the lack of digestion marks and the large number of bones per carcass, suggest that the causes for the *B. calamita* fossil accumulation were natural mortality that occurred during aestivation and, especially, hibernation (Blain, 2005, 2009; Blain et al., 2008; López-García et al., 2010). As both sites appear to show the same accumulation process and we found no evidence of bias, our sample seems to be representative of the Pleistocene *B. calamita* populations from the Sierra de Atapuerca.

Bufo calamita remains were identified following the general criteria for anurans given in Böhme (1977), Sanchiz (1977), Bailon (1999), Blain (2005, 2009) and by comparisons with modern osteological material belonging to the Museo Nacional de Ciencias Naturales de Madrid (MNCN). The main characters used to recognise *B. calamita* humeri (see Fig. 2 for anatomical features) are the high curvature of its relatively short diaphysis, a condyle that moves laterally and well developed radial and ulnar epicondyles, closed cubital fossa, absence of paraventral crest (but rudimentary in some cases; Sanchiz, 1977), and, only in males, the presence of a medial crest, key character to establish the sex.

Besides the fossil remains, we also sampled 66 modern individuals (49 males and 17 females) from the dry osteological collections of the MNCN to identify humerus features that could serve to reconstruct *B. calamita* body sizes, such as snout-to-vent-lengths (SVL). We measured the width of the distal epiphysis of the humerus (measurement named humeral total width, hereafter abbreviated as HTW) (Fig. 2), which was used to generate predictive regression models of SVL. The previously exposed methodology used to establish the sex, loses accuracy over individuals under 2.2 mm of HTW which are considered juveniles. For this reason, these individuals were excluded from analysis thus avoiding potential difficulties.

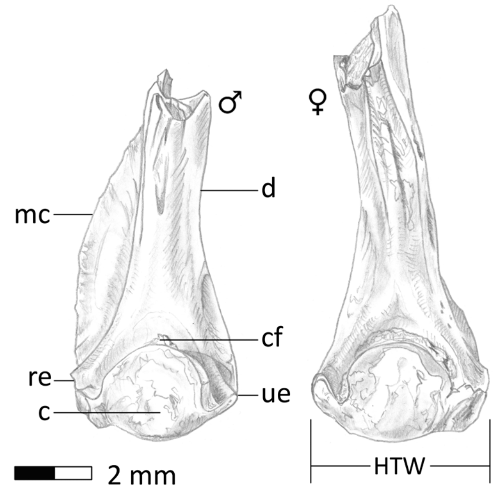

Figure 2. Fossil humerus of male (left) and female (right) *Bufo calamita* specimens from the late-Pleistocene Portalón excavation site in ventral view, showing humeral total width (HTW); i.e. the trait used for body size reconstruction, and significant osteological features. Abbreviations, c: condyle; cf: cubital fossa; d: diaphysis; mc: medial crest; re: radial epicondyle; ue: ulnar epicondyle.

Paleoclimate predictors

We obtained mean annual temperature, mean temperature of the coldest month, mean temperature of the warmest month, annual precipitation, winter (December-January-February; DJF) precipitation, and summer (June-July-August; JJA) precipitation data from the paleoclimate reconstructions conducted by López-García (2008), Blain et al. (2009, 2012, 2013), and López-García et al. (2010) using microvertebrate assemblages as climate proxies. We processed these data to generate six climate predictors of *B. calamita* body size, each comprising 13 climate units obtained based on mean values from the stratigraphic levels of the two excavation sites, seven corresponding to Gran Dolina (coded as DI to DVII) and six to Portalón (PI to PVI) (see Table 1, and Supplementary material Appendix 1 Table A1 for correspondence with archaeological sublevels and original climatic data).

Statistical analysis

We used simple ordinary least squares (OLS) regression to generate a predictive models of *B. calamita* snout-to-vent-length (in mm) for humeral total width extracted from modern specimens. For this, we tried both untransformed and log10-transformed HTW measurements, and albeit both data types performed similarly in terms of model fits, we preferred the latter as it showed lower heteroscedasticity (particularly for males), and resulted in enhanced normality in model residuals. We applied the resulting model to the measurements taken from the fossils in order to reconstruct past body sizes. Finally, we also employed simple OLS regression to relate the reconstructed body size data to the climate predictors. All analyses were conducted with R (R core team).

1.1.3 RESULTS

To reconstruct past snout-to-vent-lengths, the HTW derived model explained 82 and 78% of body size variance in modern male and female individuals respectively. Consequently, we employed the models including this feature to reconstruct animal sizes from fossil data. However, because male and female models showed slightly different intercept and slope (male SVL = 0.0557 1 0.00966 x Log_{10}HTW; Adj. $r^2 = 0.8239$; n = 47; $p << 0.001$; and female SVL = 0.27088 + 0.00642 x Log_{10}HTW; Adj. $r^2 = 0.779$; n = 15; $p << 0.001$), body size reconstructions were made separately for

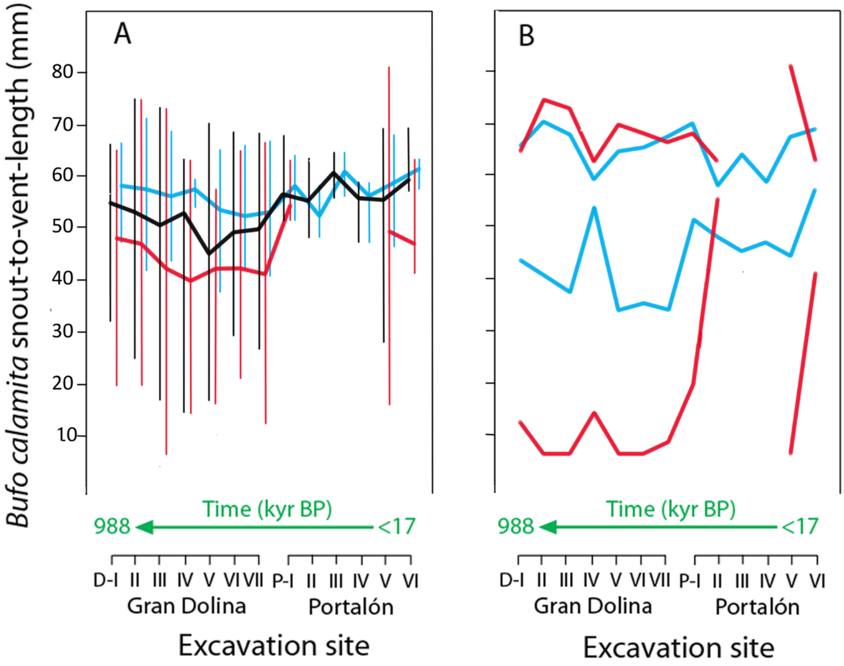

Figure 3. Evolution of *Bufo calamita* body size (as reconstructed SVL expressed in mm) over time. (**A**) Median values and size ranges (in vertical, at the lowest datum still within 1.5 IQR of the first quartile, and at the highest datum still within 1.5 IQR of the third quartile) for whole populations (black), females (red) and males (blue). (**B**) Maximum and minimum body sizes of the two sexes.

each sex. An extra advantage of using humeral total width as a predictive reference for body size reconstructions is that the distal epiphysis was generally better preserved in the fossilized humeri we processed than the other two diagnostic features tested.

Variation in *B. calamita* body size over time was strong throughout the last million years, albeit there was a tendency in both sexes to increase in size toward the end of the Pleistocene (Fig. 3 and Table 2). In addition, there was also an inverse pattern of sexual size dimorphism, with males being, on average, larger than females, an unusual trend that was apparent throughout most of the stratigraphic sequence (Fig. 3). However, females exhibited smaller minimum and larger maximum sizes than males in most instances, indicating that they had a larger body size variation (Fig. 3b and Table 2).

Underlying the temporal trend, our analyses also detected a strong climatic influence on the variation in body size, with animals being larger in periods with low annual and winter temperatures and high winter precipitation (Fig. 4). However, while this pattern was clear and strong for the entire population and female data, it was much weaker in the case of males, which showed a significant, but weak negative relationship with the mean temperature of the coldest month (Table 3).

1.1.4 DISCUSSION

In light of the results obtained, it is noteworthy that climate strongly constrains amphibian body size. Despite the generality of this statement, this fact deserves to be pointed out due to its implications in conservation biology and the inevitable effects of climate change on amphibian fauna. Overall, winter appeared to be the most influential period as temperature and precipitation variables have been shown to have a stronger influence on body size than summer ones. The climate has a larger influence on female body size, suggesting a sex-related response to climatic variations in amphibians.

Origin of the accumulation and sexual size dimorphism

The exceptional accumulation of *B. calamita* remains in Gran Dolina and Portalón has been largely attributed to natural mortality during hibernation (Blain, 2005, 2009; Blain et al., 2008; López-García et al., 2010). According to Sinsch and Schäfer (2016), this increased winter mortality would be higher for small individuals as they have less digging capabilities than larger animals and, consequently, they are more likely to be exposed to freezing and predation. However, we found a strong trend of body sizes to increase in periods with cold winters. Thus, if the expectation of Sinsch and Schäfer (2016) of increased winter mortality for small animals is true, then this would suggest that our findings are in fact an underestimation of a much larger effect, with cold periods harbouring much larger sized individuals than warm ones.

For *B. calamita,* although sexual size dimorphism is not extreme (García-París et al., 2004), and even absent in some cases (López Jurado, 1982; Sinsch, 1997; Leskovar et al., 2006), it seems to be always female-biased (Gómez-Mestre, 2009) as opposed to what we found in our sample. As amphibians exhibit continuous growth larger variance in female body size may be due to their increased longevity being older females able to reach the largest body sizes.

Despite this, although nowadays most anurans show female-biased sexual size dimorphism (Shine, 1979), the opposite pattern has also been observed in some amphibian species whose reproduction strategies involve territory defence, male–male combat, parental care or female sexual selection of larger males (Han and Fu, 2013; Hudson and Fu, 2013). In these cases, larger male sizes constitute a selective advantage (Shine, 1979; Han and Fu, 2013), thus leading to the development of male-biased sexual size dimorphism. Even if we are not able to infer sexually-related behavioural strategies from our sample, it is known that they can change between relative species (Kratochvil and Frynta, 2002; Schäuble, 2004) or even between populations of the same species (Shine and Fitzgerald, 1995); therefore, a change in reproduction strategies that could lead to an inverse sexual size dimorphism pattern cannot be ruled out.

Bergmann's rule and climatic influence

As some authors (Blackburn et al., 1999; Ashton, 2002) have previously pointed out about ecogeographic rules, like Bergmann's rule in this case, it is important to distinguish between the pattern itself (bigger sizes in cooler areas) and the mechanism proposed for justifying it (heat conservation); therefore, the invalidity of the mechanism does not invalidate the pattern (Mayr, 1956). Due to the correlational nature of our study, in most

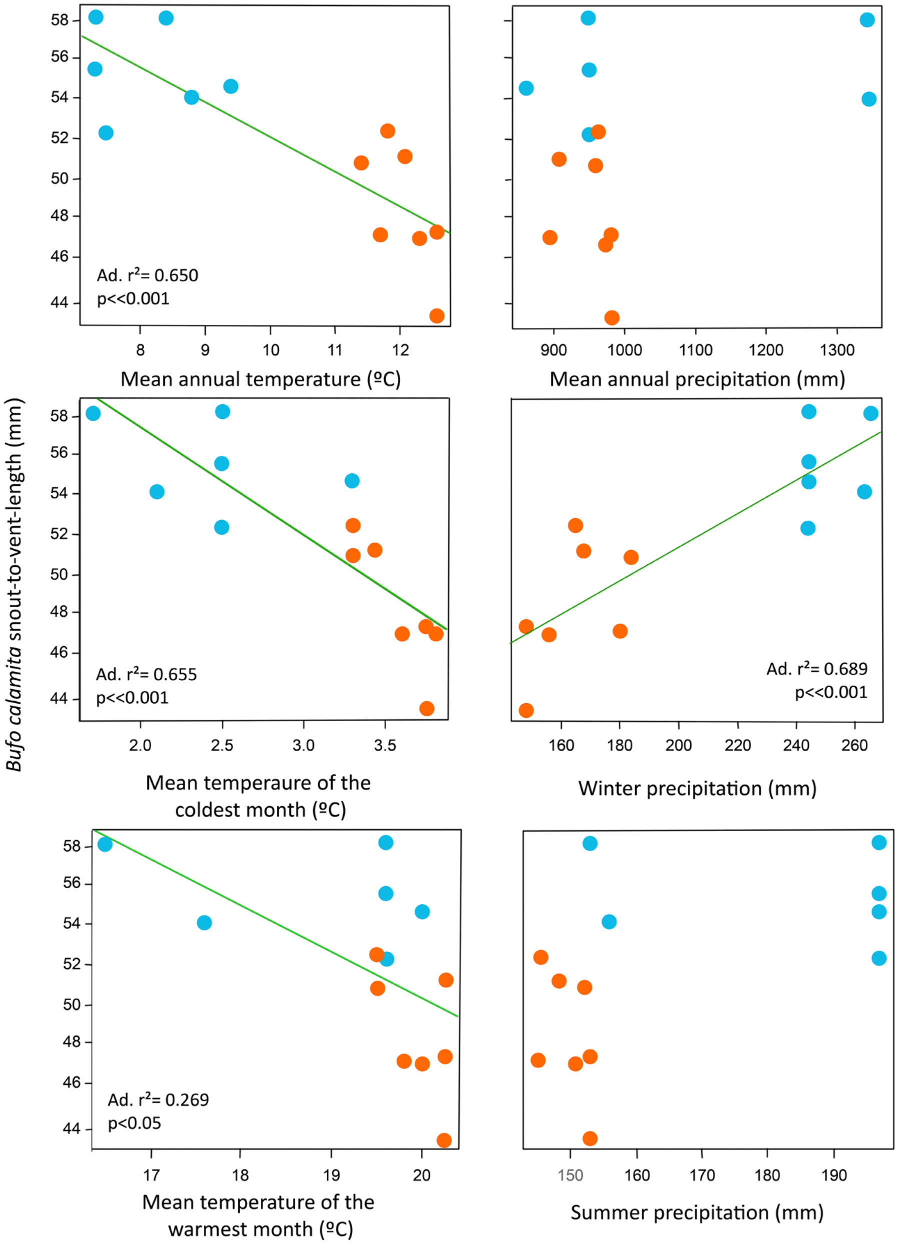

Figure 4. Relationships of *Bufo calamita* body size (reconstructed SVL in mm) with temperature and precipitation at Gran Dolina (orange) and Portalón (blue) excavation sites. Fitted lines correspond to significant OLS regression models for which adjusted coefficients of determination and p-values are also provided. Body size data include both females and males; regression results for each sex are included in Table 3.

Table 3. Proportions of variance described by linear regression models of female and male *Bufo calamita* body sizes (snout-to-vent-lengths) fitted with three temperature and three precipitation predictors. Similar models for whole population data (i.e. combining the data for females and males) are shown in Fig. 4.

Variable	Females		Males	
	Adjusted r^2	p-value	Adjusted r^2	p-value
Mean annual temperature	0.678	<<0.001	0.225	0.058
Mean temperature of coldest month	0.698	0.002	0.438	0.008
Mean temperature of warmest month	0.317	0.052	0.209	0.066
Mean annual precipitation	0.120	0.185	0.022	0.284
Winter precipitation	0.654	<<0.001	0.141	0.113
Summer precipitation	0.283	0.065	0.057	0.566

cases mechanisms cannot be identified only hypothesized, unlike patterns, which can be detected. Taking this into account, we can state that *B. calamita* populations follow a clear Bergmann cline during the Pleistocene in the Sierra de Atapuerca. Even at intraspecific level, these results have clear implications for the open debate about the validity of Bergmann's rule for amphibians (Ashton, 2002; Adams and Church, 2008).

Although we have just pointed out the importance of distinguishing between the pattern itself and the mechanism, here we explore some likely explanations for the observed trends. First of all, it is noteworthy that previous works on geographic body size variation in *B. calamita* (Leskovar et al., 2006; Sinsch et al., 2010) have found a negative relationship between temperature and body size, as opposed to our results. This implies a different body size variation pattern in geographic and temporal dimensions under the same climatic conditions. This divergence may have been generated by the secondary influence of other variables that change over space or time, or by methodological differences. In our case, by maintaining the location, several parameters, like altitude and geographic features, also remain constant, in contrast to what occurs in spatial-nature works. However, our results are concordant with predictions proposed by heat-balance (1), temperature-size rule (2), starvation resistance (3) and fecundity-related (5) hypotheses, which suggests that not one but various mechanisms could possibly explain our results.

In reference to the heat-balance hypothesis, an increase in body size in cooler periods is considered an adaptation to better heat conservation for ectotherms that are thermoregulators and are under a certain body size threshold. This hypothesis is partially supported by the thermoregulatory behaviour widely observed in *B. calamita* (López Jurado, 1982; Gómez-Mestre and Tejedo, 2005; Oromi et al., 2010), which evidences this species need to maintain body temperature under relative control. Although we still consider heat conservation to be a valid explication, there are other possible explanations that justify the observed pattern which also fit ectotherm biology.

For example, as proposed by the starvation resistance hypothesis, in cold environments, a high fat proportion (easily achieved by bigger individuals) would be an advantage for withstanding long hibernation periods and also emerging with a better body condition. Going further, this increase in fat storage would be used as an extra investment in the resources necessary for reproduction after overwintering (Tejedo, 1992; Chen et al., 2011), which becomes less frequent in cold environments due to a decrease in activity periods. Thus the probability of reproductive success would be maximized. This mechanism has already been proposed to justify bigger body sizes in cooler climates in some cases (Blackburn et al., 1999; Ashton, 2002; Schäuble, 2004; Yu et al., 2010), and also fits the fecundity-related hypothesis, based on the positive relationship between the fecundity of ectotherm females (translated into a higher number of better-quality eggs) and their body size (Tejedo, 1992; Atkinson, 1994; Atkinson et al., 2003; Angilletta et al., 2004).

Since this relationship only appears in females, and considering that female investment in reproduction is by far larger than male investment (Slatkin, 1984; Reading, 1991), the stronger response of female body size to climatic fluctuations, by increasing body size in cooler environments (Hemelaar, 1988; Schäuble, 2004), agrees with predictions derived from the fecundity-related hypothesis. Even though in Leskovar et al. (2006) *B. calamita* females showed an inverse Bergmann cline, they were more influenced by climate than males, which partially agrees with the fecundity-related hypothesis by pointing to a sexually dimorphic response to climatic fluctuations. The last temperature-mediated mechanism proposed to justify this pattern is derived from the temperature–size rule and consists in maturity being delayed to extend the growth period and achieve bigger final sizes (Von Bertanalaffy, 1960; Atkinson, 1994; Angilletta et al., 2004). Although this delay in maturity occurs in some amphibians, including *B. calamita* (Sinsch et al., 2010; Oromí et al., 2012), there is no agreement about its effect on final amphibian body size, as an overall increase in body size has been documented in some cases (Hemelaar, 1988; Miaud et al., 1999) and no relation in others (Sinsch et al., 2010).

With reference to humidity, our results do not agree with predictions derived from the water availability hypothesis given that we found a high positive correlation between DJF precipitation and body size. This trend could be related to the linked increase in resource availability. Higher precipitations linked with higher ecosystem productivity would favour growth and also energy storage required for successful overwintering and the following breeding. According to this hypothesis, Reading and Clarke (1995) found that *Bufo bufo* individuals entered hibernation with a poor body condition following a dry period, whereas natterjack toad clutches were more numerous during rainy periods (Tejedo and Reques, 1994). This increase in clutches, would require adult natterjack toads to have enough available energy to succeed in this breeding period after overwintering, and therefore bigger toads would be found under these conditions.

Overall, our climatic analysis concurs with the results from Schäuble (2004) in two species of the genus *Lymnodastes* in Australia and with Reading and Clarke (1995) in *Bufo bufo* from the United Kingdom. In these two works, body size increases towards lower temperature values and the climatic influence are both reflected most in female body size. Humidity also affects body size, and amphibians are bigger in areas where the dry period is shorter or where there is more rainfall.

The study of body size gradients based on fossil material and the effect of climatic changes on this biological trait is not only restricted to amphibians. Smith et al. (1995) proved that the woodrat *Neotoma cinerea* suffered a reduction of body size during periods of climatic warming of the interglacial-glacial cicles of the Pleistocene thus following predictions of Bergmann's rule, as occurs for *B. calamita*.

Both works as a whole supports the use of paleontological data to enlarge our knowledge about Bergmann's rule and their utility to disentangle effects of climate on vertebrate body size. In the particular case of amphibians, the reduction of body size during periods of global warming is aggravated by the effect of the aridity (which in Mediterranean areas is often linked to high temperatures). This fact makes difficult to maintain a good conservation status of amphibian populations in this area. Global warming due to human action will doubtless contribute to the decline of some amphibian species and the extinction of others, so imperative actions to reduce and slow down these natural climatic cycles are required.

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SUPPLEMENTARY MATERIAL

Table S1. Correspondence of the climatic levels named PI-VI and DI-VII (from Portalón and Gran Dolina respectively) with stratigraphic levels and archaeological divisions as "Tallas" (i.e. spits) in Gran Dolina (T0-74) and Sublevels in Portalón (P3-15) and original paleoclimatic data from Blain et al. (2009, 2012, 2013), López García (2008) and López-García et al. (2010).

Climatic unit	Strat-Level	Talla/ Sublevel	TEMPERATURE						PRECIPITATION					
			MTC		MTW		MAT		DJF		JJA		MAP	
			MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
PVI	N10	P3	1.5	2.3	16.4	1.2	8.4	2.2	270	86	153	51	1331	502
		P4	1.9	2.9	16.5	1.1	8.4	2.0	260	77	153	55	1354	420
PV		P7	2.5	0.5	19.6	1.0	7.1	1.6	244	0	197	0	950	87
		P8	2.5	0.5	19.6	1.0	7.3	1.5	244	0	197	0	950	87
		P9	2.5	0.5	19.6	1.0	7.3	1.5	244	0	197	0	950	87
		P10	2.5	0.5	19.6	1.0	7.3	1.5	244	0	197	0	950	87
		P11	2.5	0.5	19.6	1.0	7.3	1.5	244	0	197	0	950	87
PIV		P12	2.1	2.7	17.6	1.5	8.8	2.5	263	83	156	53	1346	357
PIII		P13	2.5	0.5	19.6	1.0	7.3	1.5	244	0	197	0	950	87
PII		P14	3.3	0.8	20.0	0.4	9.4	1.5	244	0	197	0	860	108
PI		P15	2.5	0.5	19.6	1.0	7.3	1.5	244	0	197	0	950	87
DVII	TD10	T0	3.49	1.95	19.59	1.67	11.45	1.94	187	44	140	28	975	206
		T1	3.70	2.00	19.90	1.44	11.60	1.83	178	44	145	26	876	153
		T2	3.74	2.13	19.56	1.53	11.29	2.06	189	52	154	33	990	202
		T4	3.70	2.00	19.90	1.44	11.60	1.83	178	44	145	26	876	153
		T5	3.70	2.00	19.90	1.44	11.60	1.83	178	44	145	26	876	153
		T6	4.25	0.73	19.61	1.21	11.75	0.78	211	14	132	22	811	121
		T8	3.49	1.95	19.59	1.67	11.45	1.94	187	44	140	28	975	206
		T9	4.16	1.98	21.02	1.20	12.68	1.33	146	41	149	23	864	126
		T10	3.70	2.00	19.90	1.44	11.75	0.35	178	44	145	26	876	153
		T12	2.93	1.91	18.98	1.63	11.28	1.92	183	52	151	33	923	122
		T15	3.70	2.00	19.90	1.44	11.60	1.83	178	44	145	26	876	153
		T16	3.75	0.35	19.75	0.35	11.75	0.35	167	53	134	5	750	212
		T17	5.67	1.41	20.00	1.37	12.89	0.68	161	53	154	27	867	101
		T18	2.98	1.89	19.32	1.51	11.18	1.92	189	53	152	33	955	116
DVI		T19	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T20	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T21	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
DV	TD8	T28	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
DIV	TD7	T30	3.43	1.46	20.27	0.80	12.07	1.08	167	50	148	25	907	169

Climatic unit	Strat-Level	Talla/ Sublevel	TEMPERATURE						PRECIPITATION					
			MTC		MTW		MAT		DJF		JJA		MAP	
			MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
DIII	TD6	T32	3.13	2.10	18.50	2.05	11.58	1.46	178	49	145	30	976	103
		T33	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T34	3.82	2.16	19.76	1.50	11.98	1.42	175	51	146	27	880	148
		T35	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T36	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T37	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T38	3.49	1.95	19.59	1.67	11.45	1.94	187	44	140	28	975	206
		T40	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T41	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T43	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T44	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T45	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T47	3.25	2.17	20.13	1.16	12.38	1.30	148	41	153	27	1025	46
DII		T48	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T49	2.98	1.89	19.32	1.51	11.18	1.92	189	53	152	33	955	116
		T50	3.75	1.87	20.25	1.16	12.56	1.18	148	41	153	27	981	46
		T51	3.72	1.65	19.56	1.28	11.47	1.59	192	58	156	36	983	162
		T52	2.76	2.31	18.98	1.79	10.74	2.31	198	57	159	36	943	137
		T53	2.91	2.16	19.30	1.64	11.05	2.14	185	51	152	33	961	102
		T54	2.91	2.16	19.30	1.64	11.05	2.14	185	51	152	33	961	102
		T55	3.19	2.01	18.88	1.58	10.74	2.14	203	51	156	38	1049	193
	TD5	T58	3.70	2.00	19.90	1.44	11.60	1.83	178	44	145	26	876	153
		T59	3.70	2.00	19.90	1.44	11.60	1.83	178	44	145	26	876	153
		T60	2.98	1.89	19.32	1.51	11.18	1.92	189	53	152	33	955	116
		T61	2.98	1.89	19.32	1.51	11.18	1.92	189	53	152	33	955	116
		T62	3.53	1.97	19.42	1.51	11.26	2.02	193	48	150	32	984	207
		T63	2.98	1.89	19.32	1.51	11.18	1.92	189	53	152	33	955	116
		T64	2.98	1.89	19.32	1.51	11.18	1.92	189	53	152	33	955	116
DI		T65	3.32	1.75	19.95	0.93	12.18	0.96	146	39	143	18	977	117
		T66	3.31	1.89	20.00	1.02	11.77	1.49	161	51	151	26	981	101
		T67	3.13	2.10	18.50	2.05	11.58	1.46	178	49	145	30	976	103
		T68	3.32	1.75	19.95	0.93	12.18	0.96	146	39	143	18	977	117
		T69	3.70	2.00	19.90	1.44	11.60	1.83	178	44	145	26	876	153
		T70	3.13	2.10	18.50	2.05	11.58	1.46	178	49	145	30	976	103
		T71	3.31	1.89	20.00	1.02	11.77	1.49	161	51	151	26	981	101
		T72	2.56	1.84	18.56	1.76	9.96	2.25	196	35	165	39	928	220
		T74	3.31	1.96	20.00	1.02	12.15	1.25	155	42	141	17	938	160

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ONE MILLION YEARS OF DIVERSITY SHIFTS IN AMPHIBIANS AND REPTILES IN A MEDITERRANEAN LANDSCAPE: RESILIENCE RULES THE QUATERNARY

by ALMUDENA MARTÍNEZ-MONZÓN[1,2], GLORIA CUENCA-BESCÓS[3], JOSEP-FRANCESC BISBAL-CHINESTA[1,2] *and* HUGUES-ALEXANDRE BLAIN[1,2]

[1]Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain; amartinez@iphes.cat, jbisbal@iphes.cat, hablain@iphes.cat
[2]Department of History & History of Art, Univ. Rovira i Virgili (URV), Tarragona, Spain; amartinez@iphes.cat, jbisbal@iphes.cat, hablain@iphes.cat
[3]Aragosaurus-IUCA, Department of Earth Sciences, University of Zaragoza, Zaragoza, Spain; cuencag@unizar.es

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Abstract: In contrast with the well documented strain on extant amphibian and reptile populations today, the Quaternary fossil record of these groups is very conservative showing few changes over long periods of time. In order to establish the non-human-induced effect of climate change on herpetofaunal diversity, we collected data from Pleistocene sites in the Sierra de Atapuerca complex (Burgos, Spain), which records the last few million years of changes. Diversity was measured in terms of richness and evenness indices and its relationship to the climatic parameters was analysed with OLS regression models. The highest diversity (richness and evenness; 1-D) occurred in periods considered to be analogues of the current interglacial, whereas minimum diversity values were reached during periods when conditions were harsher (cooler or glacial stage). In all cases, the diversity values were always restored subsequently, pointing to great resilience. Temperature proves to be the most influential climatic factor. Accordingly, amphibians and reptiles have been able to overcome previous climatic changes successfully. In contrast, the effects of anthropization have generated an uncommon loss of diversity, the like of which has not been seen in the last few million years. The data presented here demonstrate that the current amphibian loss seems to be driven by anthropogenic influence, with climate a factor of a secondary importance.

Key words: amphibian, diversity, Quaternary, reptile, resilience.

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1.2.1 INTRODUCTION

In the twentieth century, authors such as E. O. Wilson recognized the gravity of the problem of the loss of species. Wilson's work, The Diversity of Life had a major influence on the perception of modern society in the current loss of biodiversity on the planet (Wilson, 1999). McGill et al. (2015) confirmed the transformation of the biosphere by humans in the Anthropocene, raising the question of how to evaluate the biodiversity trend. However, the literature analysing present-day biodiversity is so overwhelming in scope that what should be a cause for global alarm (as much as or even more than climate change) ends up being engulfed by the avalanche of scientific literature. Moreover, the majority of data analysed are accounts of the last two centuries.

One impressive study is that of BioTIME (Dornelas et al., 2018), documenting the biodiversity at a global scale, including marine, freshwater and terrestrial taxa of plants and animals. The global decline in the amphibian and reptile population has been widely documented in the scientific literature in the last two decades (Gibbons et al., 2000; Kiesecker et al., 2001; Araújo et al., 2006). Quantitative evidence of this decline (Houlahan et al., 2000) and of the main factors driving it has also been identified (Collins and Storfer, 2003; Sodhi et al., 2008). The effects of human activity, habitat degradation, pollution and climate change are leading to an imminent and irreparable loss of biodiversity in our ecosystems. Several authors agree in pointing to climate change and its consequences as a relevant factor in this process, since these affect herpetofaunal diversity, distribution and community structure (Pounds, 2001; Duffy, 2003; Sheldon et al., 2011). Also, it has been pointed out that, in the case of amphibians, species with small geographic ranges (usually corresponding to those with larger body size), are more vulnerable to hábitat alterations (Sodhi et al., 2008). Climate change leads to loss or fragmentation of climatically suitable areas thus increasing the vulnerability of this kind of species which often displays poor dispersal ability (García et al., 2014). For this reason, we consider it crucial to go beyond a mere analysis of current biodiversity and look at the problem from a palaeontological–historical point of view in order to ascertain how the associations of fossil assemblages of species develop in deep time. With roughly a million species currently at risk of extinction, it is critical that these mechanisms are better understood.

From a palaeontological point of view, amphibians are considered to be morphologically very stable and conservative organisms, showing little change in their assemblages over millions of years and also undergoing few extinction events, unlike other groups such as mammals or birds (Delfino, 2005). Even though examples of species persistence through repeated periods of unfavourable climate are documented in the fossil record, the occurrence of extirpations and extinctions in the past (Holman, 1995; Blain et al., 2016) suggests that limits to adaptation are greatest during periods of rapid climate change, such as those predicted for the future (Davis and Shaw, 2001). It is known that temperature and precipitation have always played a key role driving diversity and distribution of amphibians and reptiles by influencing their thermal biology, the amount of environmental resources, their growth patterns, etc. (Gibbons et al., 2000; Angilletta et al., 2004). Specifically, for ectotherms, thermal traits such as heat tolerance, evaporative water loss, variation in body temperature and a reduced dispersal rate are known to explain part of the sensitivity of amphibians and reptiles to habitat modification

(Nowakowski et al., 2017), especially the rapid climate-induced habitat changes occurring nowadays (Gibbons et al., 2000; García et al., 2014).

A great deal of conservation activity is being carried out to put a stop to this freefall in biodiversity, yet the complexity and the large number of factors involved (Blaustein and Kiesecker, 2002) limit the effect of these actions and highlight the importance of prevention. Although there are few studies on the effect of climate upon the amphibian fossil record (Martínez-Monzón et al., 2018; Tietje et al., 2020), the general lack of knowledge about the long-term dynamics in terrestrial systems and the response of biodiversity to climatic perturbations makes it difficult to design and implement such conservation activities (Cottingham et al., 2001). Disentangling these questions will require years of research and studies at different scales. Assessments have been made of the importance of ecological scale in understanding the dynamics of resistance (defined as a measure of the initial response of ecosystems after a perturbation) and resilience (understood as the rate of recovery of ecosystems to pre-disturbance conditions) when a perturbation occurs (Downing and Leibold, 2010). In addition to this, we aim to show the importance of temporal scale in understanding not only short- but long-term responses of communities to climatic changes. To this end, the fossil record has already yielded promising results as a new source for compiling long-term data and contributing to a better understanding of long-term dynamics in ecological research (Araújo et al., 2008; Martínez-Monzón et al., 2018; Tietje and Rödel, 2018; Van der Sande et al., 2019).

The Quaternary (i.e. the last 2.6 million years) is a perfect scenario to shed light on this issue as it is a well-documented period with several recorded climatic changes. Glacial–interglacial cycles are characteristic of this period and other relevant climatic events such as the Last Glacial Maximum (LGM) have also been recorded. In addition, almost all the herpetofaunal species we can find during this period are considered to be identical to current species, so the data from our study can be transferred to present-day populations. The study of the fossil record of this period, also allows us to understand how amphibian and reptile populations react to climatic changes apart from the human presence. This is of vital importance since we must be able to distinguish the alterations produced by human impact from the natural development during a period of climate change in order to develop effective conservation strategies for these groups.

Here we apply a novel approach to analyse long-term responses to climatic changes in the diversity of amphibian and reptile communities over time. With data provided by the fossil record and with oceanic $\delta^{18}O$ isotope records (i.e. global climate records) taken from Lisiecky and Raymo (2005), we bring together palaeoclimatic and palaeoecological data from a Mediterranean riverine wetland with a high biodiversity during a period of marked climatic changes, in order to understand how the resistance and resilience of amphibian and reptile communities react to perturbations.

1.2.2 GEOLOGICAL SETTING AND SITE DESCRIPTION

The Atapuerca complex is situated in the Sierra de Atapuerca, a small hill located 14 km to the east of the city of Burgos (north Spain) (Fig. 1) at around 1080 m above mean sea level (a.s.l.) (Benito-Calvo et al., 2017). This área contains diverse landscapes, which provide the fauna with a great variety of niches and resources. Cereal-growing plains, mountains and riverine Mediterranean wetlands shape a varied landscape which connects the Ebro and Duero basins and thus constitutes an ecotone and a natural corridor for species between Mediterranean and Eurosiberian regions. This characteristic conjunction of geographical and ecological factors makes this an interesting study area with high biodiversity as a result of the mixture of Mediterranean and Eurosiberian taxa (García-Antón and Sainz-Ollero, 1991), a pattern that is well observed in the current herpetofaunal assemblage (Pleguezuelos et al., 2004; Ortiz-Santaliestra et al., 2011). The Sierra de Atapuerca constitutes an archaeopalaeontological complex known for its contributions to human evolution (Arsuaga et al., 1993; Bermúdez de Castro et al., 1997; Carbonell et al., 2008).

This study is based on data from stratigraphic levels of several localities in the Sierra de Atapuerca. The complex is a karstic cave system whose cave infills comprise various archaeo-palaeontological layers, which are well ordered stratigraphically. In the present study, we include a composite sequence of more than one million years (1200–16.8 kyr BP), using fossils from several sites separated from each other by less than one kilometre (Fig. 1).

From oldest to youngest, these sites are: Sima del Elefante (1200–1100 to 350–250 kyr BP) (de Lombera-Hermida et al., 2015); Gran Dolina (1000–925 to 430–250 kyr BP) (Cuenca-Bescós et al., 2010, 2011; Rodríguez et al., 2011); and Portalón (30.30 to 16.85 kyr BP) (López-García et al., 2010). Although this is one of the most complete sequences of this period in the Iberian Peninsula, there are two important chronological hiatuses: between MIS 16 and MIS 12 and between MIS 6 and MIS 3 (see Fig. 3, below). Sima del Elefante and Gran Dolina were dated using luminescence or electron spin resonance spectroscopy combined with U-series (ESR-U/Th) (see an overview in Rodríguez et al., 2011), while Portalón has been dated by means of ^{14}C accelerator mass spectrometry (AMS).

Sections from each site yield cave sediments that can be stratigraphically ordered. The stratigraphy is divided into sedimentary units and also into archaeological levels established during the process of excavation. Further, each site is designated by an abbreviation: Gran Dolina (TD); Sima del Elefante (TE); and Portalón (P). This abbreviation is also used in naming the levels of each site: for example, level 10 of the Gran Dolina site is named TD-10 (Benito-Calvo et al., 2017). The Burgos area has a continental–Mediterranean climate and is considered to be one of the coldest regions in the Iberian Peninsula (Font Tullot, 2000). Mean anual values for temperature and precipitation are 9.9°C and 572 mm respectively (meteorological station of Burgos Air Base, 891 m a.s.l.), and display a very marked seasonality: winters are cold and include snowfall and belowfreezing temperatures that reach −15°C, whereas summer mean temperatures are between 15 and 20°C (Font Tullot, 2000; Ninyerola et al., 2005).

1.2.3 MATERIAL AND METHOD

Species data and taphonomic remarks

The species data, in particular the number of individuals per level, were obtained from previous studies in which a taxonomic assessment was performed (Blain, 2005; Blain et al., 2008, 2010, 2011, 2013; López-García et al., 2010). These data are summarized in Martínez-Monzón et al. (2021, table S1). The

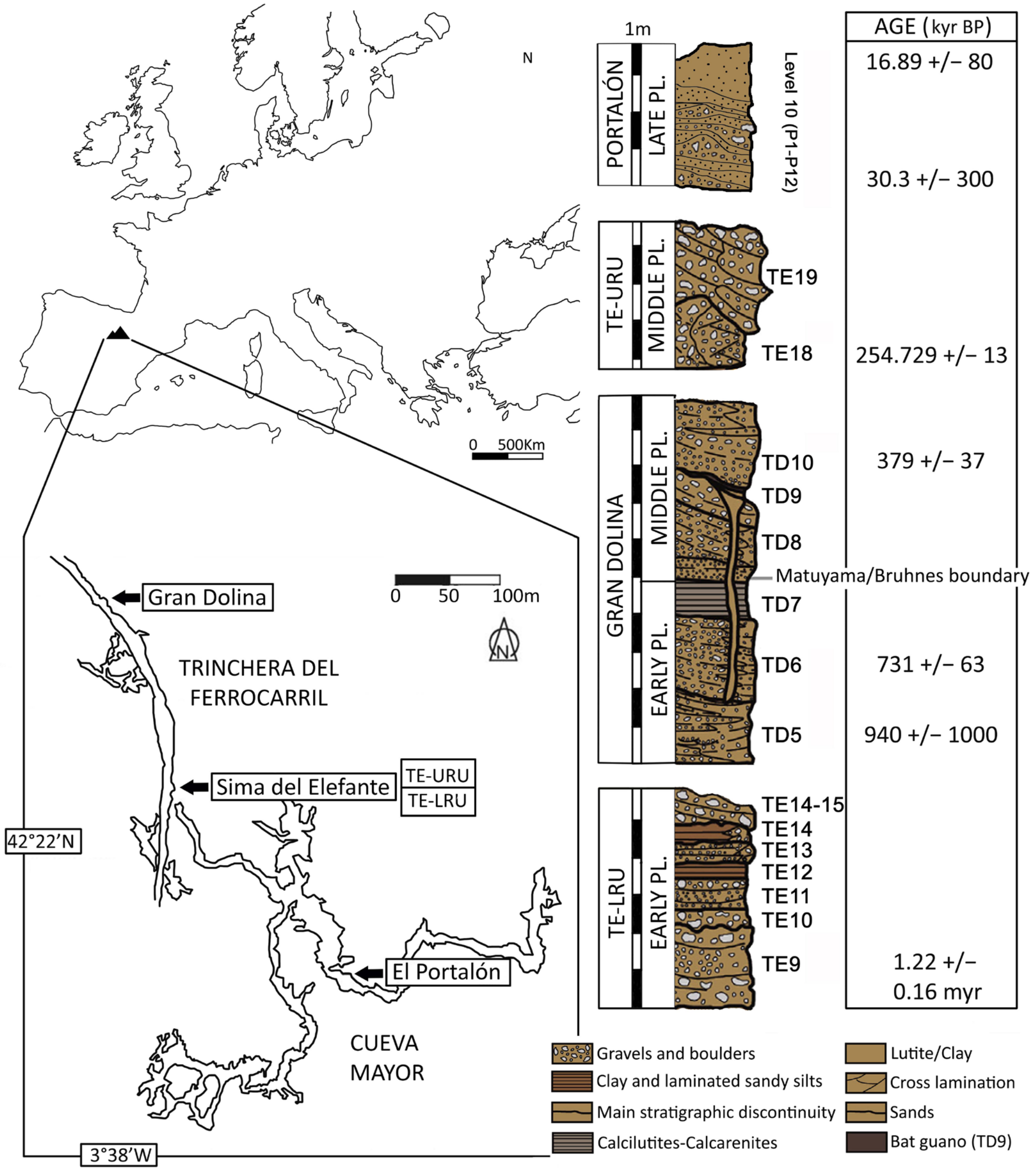

Figure. 1. Location of the Sierra de Atapuerca (Burgos, Spain). Detail: plan view of the two cave systems (Trinchera del Ferrocarril and Cueva Mayor). On the right, the studied sections of the composite stratigraphic sequence, indicating: site, geological period, stratigraphic sequence, level and age.

data for species present in the area nowadays correspond to those currently registered in the Universal Transverse Mercator (UTM) coordinate system squares of the area under study (data from Asociación Herpetológica Española, 2018).

Traditionally, bone-accumulating predators such as birds of prey are considered to be the main accumulating agent of small-vertebrate remains in caves (Andrews, 1990; Bennasar, 2010; Núñez-Lahuerta et al., 2019), together with other independent factors (autonomous entries, accidental falls, etc.) Nocturnal birds of prey show little variation and minimal biases in their individual preferences concerning the alimentary spectrum in pellets. They are highly efficient collectors and so the microvertebrate accumulations of Pleistocene sites, which are mainly derived from the pellets for these birds, are considered to be representative of the environment outside the cave (Andrews, 1990; Fernández-Jalvo and Andrews, 2016).

However, in this particular case, remains attributed to *Epidalea calamita* display a different accumulation pattern through most of the study sequence, being overrepresented in the lower and middle Pleistocene (TD and the lower part of TE). A high ratio of NISP (the number of identifiable bones) to MNI (the minimum number of individuals) is indicative of an elevated number of skeletal elements per carcass and *E. calamita* always shows values much higher than the other represented anuran species (Blain et al., 2008). This indicates that fossil individuals are represented by their whole skeleton in the cave, pointing to a greater in situ mortality during hibernation or aestivation as the major cause of such an accumulation (Blain et al., 2013). It is known that one of the main thermoregulatory strategies of the natterjack toad to cope with the constraints of environmental temperatura and water availability is to use of shelter microhabitats or borrowing in their own galleries (Gómez-Mestre, 2009). Due to this overrepresentation, *E. calamita* has been excluded from the evenness analysis, but not from that of richness, for which only presence/absence data are required.

By contrast, Lacertidae indet. constitutes a group of related species whose presence in the assemblage is quite relevant for the ecosystem's reconstruction. Unfortunately, the taxonomic identification of these species, which is based on osteological characters, can be faithfully performed only up to genus level. For this reason, this group has also been excluded from the evenness analysis but maintained in that of richness, classified as one species (which is the minimum number of species we can be sure is represented within this group). Despite these few taxonomical exceptions, the good representativeness of Atapuerca fossil record can be ascertain based on the fact that: (1) taphonomy does not suggest any alteration of the representation of the immediate environment; (2) our extensive fossil record (more than 50 000 amphibian and reptile specimens), documents 90.9% of the current herpetofauna of the area, a higher figure than usual for sites of the same period, indicating excellent preservation of the remains and thus a high representativeness of past biodiversity; (3) some fragile and small elements, such as toad parasphenoids and newt vertebrae, usually poorly represented in archaeological sites, are present among our fossils.

Climatic predictors

The climatic predictors used for this work are the palaeotemperature and palaeoprecipitation, given as the mean annual temperature (MAT) expressed in °C, and mean annual precipitation (MAP) in mm, obtained from previous studies

(Blain, 2005; López-García, 2008; Blain et al., 2009, 2011, 2012, 2013; López-García et al., 2010), as well as original new data presented in this work from TD4 and the upper part of TE (all of them contained in Martínez-Monzón et al., 2021, Table S1). The palaeoclimatic reconstructions are based on the characteristics of the herpetofaunal assemblage from each site and stratigraphic or archaeological level, using the method known as the mutual ecogeographic range (MER) (Blain et al., 2009).

To prevent any possible intrinsic circularity, we performed a correlation analysis between the geographic range (as number of 10 × 10 km UTM squares of the respective overlaps) and resulting climatic indicators. In both cases, the linear regression analysis displayed p-values over significance level (0.05) indicating that no relationship exists between MAT and MAP values and the geographical extension of the overlap. So, the overlap resulting from the species distributions is totally independent of the climatic variables used here, confirming their validity and suitability for the present study.

Diversity indices and statistical analysis

Diversity is measured in terms of richness and evenness indices. It was analysed on the basis of the indices that are a measure of α-diversity, which means the diversity of species in a given habitat, site or landscape unit (Whittaker, 1972). Roughly, richness corresponds to the total number of species in the community, whereas evenness constitutes a measure of the relative abundance of species within a community; it represents the opposite of dominance or Simpson's index (D) (Simpson, 1949):

$$D = \sum \left(\frac{n_i[n_i - 1]}{N[N - 1]} \right)$$

Where n_i is the number of individuals for a taxon i and N the total number of individuals (Magurran and McGill 2011). Evenness is expressed as the opposite of dominance (1-D). This value, which ranges from 0 to 1, rises as the dominance decreases and the assemblage becomes more even. As regards this index, it is considered that the greater the value, the greater the sample diversity. To avoid statistical problems related to different sample sizes, the raw values of MNI were standardized. These values were divided by their corresponding total simple abundance, thus obtaining percentages of MNI. Both calculations of evenness (1-D) and richness were analysed using PAST (Hammer et al., 2001). On the other side, the relation with the climatic parameters and the relation between evenness and richness was analysed, with ordinary least squares (OLS) regression models. These analyses together with Pearson correlation test and t-test were conducted with R version 3.2.5 (R Core Team, 2016), all of them taking on a significance level of $\alpha = 0.05$.

1.2.4 RESULTS

Diversity

Leaving aside present-day data, a relatively constant pattern in general evenness (1-D) can be observed in our data during the early and middle Pleistocene, reaching its maximum (0.87) in TE-19g, at the end of the middle Pleistocene. As we can see in Fig. 2, amphibians reach their maximum in TE-19f (0.79) whereas reptiles do so in TE19g, with a value of 0.82. By contrast with the previous period, evenness values significantly decrease during the part of the sequence that corresponds to the late Pleistocene as confirmed by the t-test performed between late Pleistocene and middle Pleistocene richness ($t = -6.51$; d.f. = 8.1; p

<<0.001). Mean richness for each period is 4.19 and 11.63 for the late and middle Pleistocene respectively. Minimum values for evenness are reached during this period in level P9 of the Portalón sequence (0.24 and 0.00 respectively for amphibians and reptiles), the absence of reptiles being a common feature of the Portalón sequence.

The maximum richness value (16 species) is reached in two levels close to one another in the Gran Dolina site: TD8a and TD10-4. For amphibians, the maximum richness is eight species, a value that can be seen in several levels of the early Pleistocene and the first part of the middle Pleistocene at the Gran Dolina site. Reptiles also reach their maximum richness values in Gran Dolina, particularly in two of the three sublevels of TD-10. The minimum value of general richness (three species) is found in the oldest part of the Portalón sequence (P16–P12). Both amphibians and reptiles reach their mínimum richness values (3 and 0 respectively) in the late Pleistocene in the Portalón site.

As a general trend, amphibian values for evenness are higher than reptile values through almost the whole sequence, with a few exceptions. Until the late Pleistocene part of the sequence, evenness for amphibians remains at quite stable values, unlike richness, which displays a more oscillating pattern. This pattern of richness becomes more constant during the levels corresponding to the late Pleistocene, when evenness is more variable (Figs. 2, 3). In the case of reptiles, neither evenness nor richness show particularly low or high values until the middle Pleistocene, when both start to show high peaks and great descents. After this period, the presence of reptile species is markedly reduced, even to zero in some levels.

In this study, richness proves to be the most representative measurement of diversity due to the particularities of the species assemblage commented above. The total richness of both amphibians and reptiles exhibits a similar pattern, which is more stable than the groups considered separately (Fig. 3). The highest peaks of richness are reached during the first half of the middle Pleistocene in levels TD10-4 and TD8a. This period, which started during the early Pleistocene, ends with a marked decrease in richness values in the late Pleistocene. Throughout the sample, total evenness and richness display a similar pattern, which is supported by the results of an OLS simple regression model (Adj. r^2 = 0.59; p<<0.001; slope = 17.48; d.f. = 39) and by a Pearson correlation test which shows the strength of the positive correlation between these two variables (correlation coefficient = 0.77; T = 7.59; p<<0.001; d.f. = 39) (Fig. 4). It is remarkable that the most substantial part of this OLS regression model is due to reptile values, since the amphibian correlation between richness and evenness is not significant.

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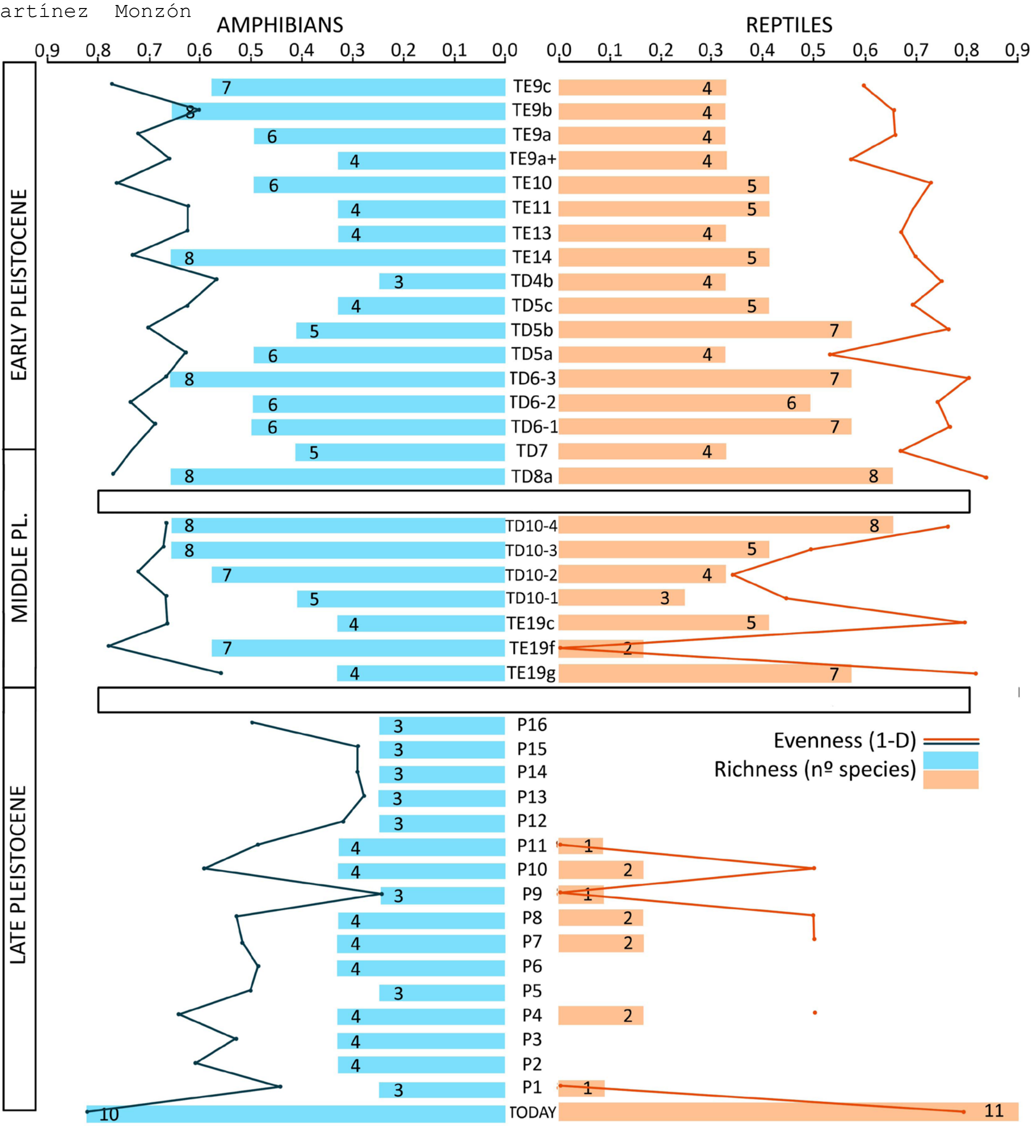

Figure. 2. Lines representing evenness (1-D) and bars representing richness (or number of species) plotted against time and divided by archaeological sites and levels. The whole Atapuerca sequence is represented, from late to early Pleistocene, together with the presentday data from the area. Blue bars and lines represent amphibians, and orange ones, reptiles. White spaces between bars represent the two chronological hiatuses present in the sequence.

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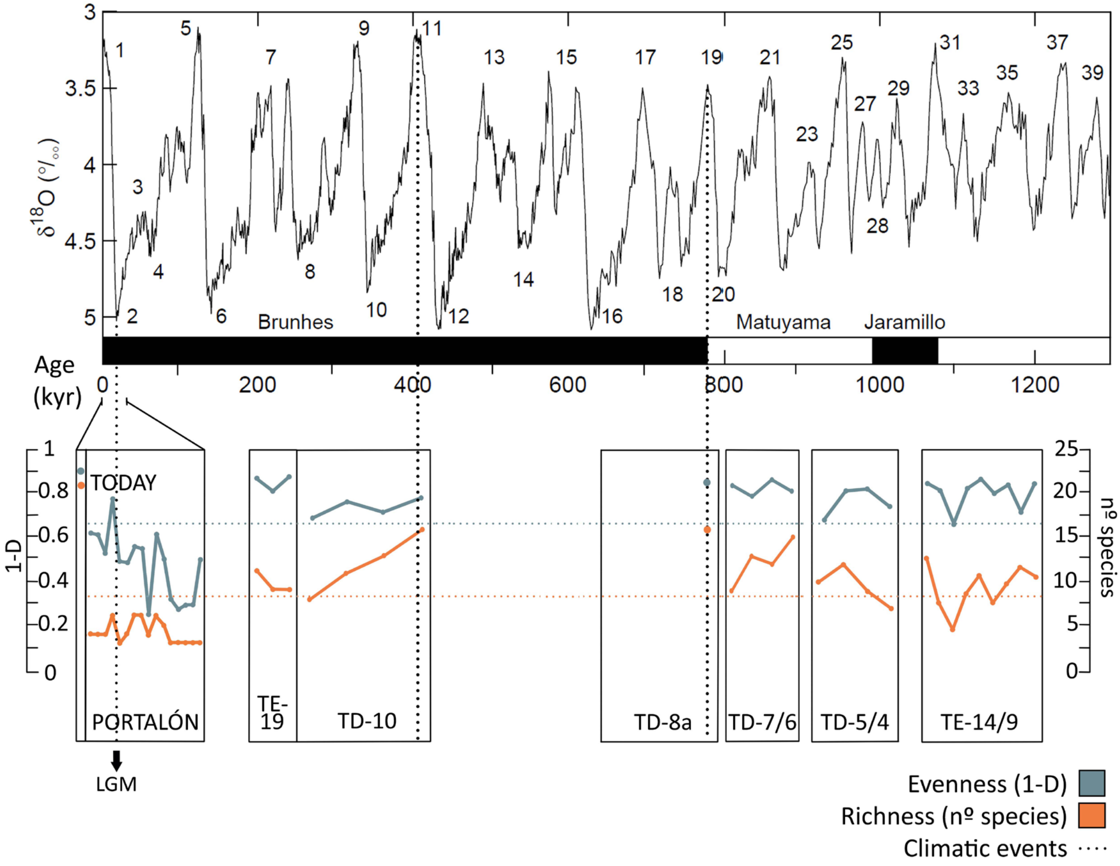

Figure. 3. The LR04 benthic global $\delta^{18}O$ records (from Lisiecky and Raymo, 2005) in relation to evenness (1-D) (blue line) and species richness (orange line). Dotted blue and orange lines indicate the average values for the two measures of diversity. Vertical dotted black lines represent the LGM, in the Portalón sequence, and MIS 11 and MIS 19 in their respective positions in the stratigraphic sequence. Each site is represented separately coinciding with the timespan it records. Dating was established based on the model by Blain et al. (2012) for the Dolina levels, data available from de Lombera-Hermida et al. (2015) for the Sima del Elefante site, and from López- García et al. (2010) for Portalón.

Climatic predictors

Given the high correlation between the two diversity measurements (mainly due to reptile values), only richness was taken into account for this analysis, thus avoiding possible complications and biased results derived from the evenness data. The lack of correlation between richness and evenness in amphibians together with the overrepresentation and subsequent exclusion of one of the most common species along the sequence, leads us to consider data coming for richness analysis as a more reliable measure.

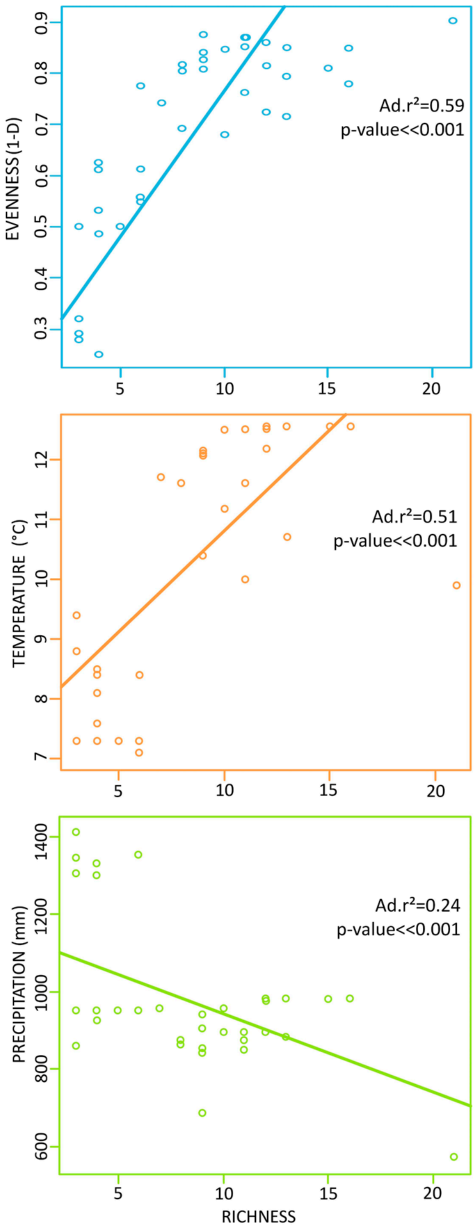

Figure. 4. From top to bottom, relationships of total richness (number of species) with evenness (1-D), mean annual temperatura (MAT; °C) and mean annual precipitation (MAP; mm). Fitted lines correspond to significant OLS regression models for which adjusted coefficients of determination and p-values are also provided. Richness and evenness data include both amphibians and reptiles; regression results for each group are included in Table 1.

Richness is in all cases significantly positively correlated with MAT (Fig. 4), especially for reptiles and the assemblage as a whole (Table 1). Likewise, MAP is negatively correlated with richness in all cases (Fig. 4), but to a lesser extent. In these correlations, the adjusted r^2 is under 0.3 for MAP (Table 1), thus showing a weaker tendency even though all correlations are at significant levels.

Table. 1. Results of OLS regression models between richness and climate.

	Adj.r²	p-value	D.F.	Slope
Amphibian richness				
MAT	0.355	<<0.001	39	0.568
MAP	0.128	0.012	39	−0.00425
Reptile richness				
MAT	0.5	<<0.001	39	0.97
MAP	0.262	<<0.001	39	−0.00844
Total richness				
MAT	0.508	<<0.001	39	1.539
MAP	0.237	<<0.001	39	−0.0127

Richness (or number of species) is differentiated by group: amphibians, reptiles and the whole community of herpetofauna (Total richness). Climate is represented by MAT (mean anual temperature) and MAP (mean annual precipitation). For each regression model, adjusted r^2, p-value, degrees of freedom (D.F.) and slope are shown.

1.2.5 DISCUSSION

Trends in diversity

As a general trend, richness displays high values which oscillate during the early and middle Pleistocene (Fig. 3). This probably follows climatic cycles of glacial–interglacial stages, as is suggested by the influence of temperatura (MAT) on the herpetofauna (Table 1; Fig. 4). The fact that richness rises in warm periods is a phenomenon widely documented in the literature for several groups (Hawkins et al., 2003; McCain and Grytnes, 2010). The character of the study area as an ecotone is also very likely to influence the number of species, thus increasing richness values (McCain and Grytnes, 2010).

When the climatic conditions turn cooler and wetter at the end of the late Pleistocene (Portalón site), both richness and evenness fall to minimum values, again revealing the influence of temperature on species number, and the lesser influence of precipitation. This is not surprising as temperature is a key parameter that shapes ecosystems by influencing energy-resource dynamics, population size and metabolic rates (Hawkins et al., 2003; Brown et al., 2004) particularly in the case of ectotherms, which depend on an external source of heat for their metabolic activity and embryonic development.

According to the literature, we initially expected that amphibians would be more conditioned by precipitation due to their greater dependence on water, whereas reptiles would be more influenced by temperature. Despite the substantial evidence pointing to a close relationship between amphibians and environmental moisture or precipitation, our present results contradict this hypothesis. The explanation we suggest for this resides in the nature of our precipitation measurement: MAP is a very broad parameter, which indicates the level of precipitation over the whole year, but not its distribution in time, the presence/absence of water courses, or the influence of other parameters such as plant cover or the capacity of the substrate for retaining water. For amphibians, the presence, number and type of nearby water courses and other ecological traits such as tree density cover prove to be very important factors conditioning their occurrence in ecosystems (Soares and Britto, 2007). In this case, it seems that the influence of MAP is of secondary importance, concurring with Sodhi et al. (2008), who showed that for 45% of known amphibians, the risk of decline decreases under higher ambient temperature and increases with greater precipitation seasonality and habitat loss. Finally, the study area is considered a Mediterranean riverine wetland, as it has three permanent water courses nearby that have been present throughout the Pleistocene to this day: the rivers Arlanzón, Pico and Vena (Ortega et al., 2013). These permanent water courses generate an area with all the necessary requirements to support a great number of amphibian species, overcoming small variations in MAP.

Climatic events

In terms of orbital configuration, insolation distribution pattern and temperature response, MIS 11 and MIS 19 are considered to be two of the best analogues for the current interglacial (Yin and Berger, 2012). Both are present in our sequence, in levels TD10-4 and TD8a respectively (Fig. 3). Our data reveal these levels to be the time of máximum diversity (richness) in our sequence, yielding the values closest to those in the area today. This is completely consistent with the established climatic correspondence between these two interglacials and the present time, again highlighting the influence of climate on diversity values. Also remarkable is the small discrepancy detected in the diversity maximums of amphibians and reptiles, which occur in two consecutive sublevels of TE (TE19g and TE19f respectively). The high resolution displayed by this part of the sequence may be revealing a complex pattern in which amphibians react first to climatic change in glacial–interglacial cycles. Although this is just an unconfirmed first postulate, it may be worth focusing research on this topic in the future.

On the other hand, one of the most relevant climatic events present in our study sequence is the Last Glacial Maximum (22–19 kyr BP), which contrasts starkly with current conditions. The LGM was a period of harsh climatic conditions characterized by maximum cold in the northern hemisphere, as well as the greatest extension of ice at the polar caps (Otto-Bliesner et al., 2006). The Iberian Peninsula is known to have exhibited gentler conditions than the rest of Europe during this period, thus acting as a refugium for certain Eurosiberian species (López-García et al., 2010; Bañuls-Cardona et al., 2014).

Previous studies have located the LGM between levels P3 and P6 of the Portalón sequence, a period characterized by a drastic decrease in the representation of both herpetofaunal and small-mammal taxa with respect to the underlying sublevels (López-García et al., 2010). Taking into account the δ18O records and their correlation with diversity data (Fig. 3), our analysis clearly reflects the impact of the LGM on the herpetofaunal assemblage, which translates into a marked decrease in evenness (1- D) and species richness, both in amphibians and reptiles (Figs. 2, 3). In addition, the presence of reptiles in these levels is almost non-existent (Fig. 2).

The LGM in the study area is characterized by cold and humid conditions (Fletcher and Sánchez-Goñi, 2008). The most humid periods of the study sequence occur in the Portalón site, coinciding with the coldest ones, including those of the LGM. This climatic association may be driving the relationships between diversity and MAP that we observe in our results, thus suggesting again that the influence of temperature outweighs that of rainfall.

Regarding the theoretical pattern of oscillations in herpetofaunal species richness driven by the glacial–interglacial cycles that was expected, our data can only give provisional insights. Well-characterized climatic events such as MIS 11, MIS 19, and the LGM, provide adequate study cases to try to approach this question. The LGM shows a great decrease in species richness associated with harsher conditions and an ensuing recovery of former richness values during the subsequent interglacial stage (Fig. 3 'Today' sample), pointing to a correlation between glacial cycles and diversity. By contrast, MIS 11 and MIS 19, which are considered warm interglacial analogues to the current one, display high richness values similar to those in the area today. Notwithstanding this evidence, further investigation of the topic is required to provide a definitive answer to this question.

Resilience

Several climatic changes have taken place during the timespan of our study sequence, generating fluctuations in the richness and evenness of the herpetofaunal assemblages. Even so, these parameters tend to re-establish themselves at values similar to those prior to the perturbation. Based on the literature and the features of the assemblage studied, we expect there to be a high level of resilience in both amphibian and reptile populations, facilitated by species richness. As can be observed in Fig. 3, perturbations occur throughout the sequence in the form of climatic changes, and subsequent increases/ decreases in species richness are recorded. In spite of this, a high level of resilience is shown for both studied groups, which in most cases recover high richness values, even though there is no uniformity in the recovery speed, probably on account of the multiple factors that may be influencing the resilience and recovery of the ecosystem. The time span between MIS 9 and MIS 8 constitutes an exception to this pattern; after the disturbance represented by MIS 10, richness values are lower in the next interglacial (MIS 9) and this decrease in richness continue in the next glacial (MIS 8). This may indicate that, in this case, the drop in richness was not entirely determined by changes in climate. The influence of other factors, such as intra and interspecific competition, diseases, predators or other ecological constraints, seems to overcome the influence of climate on richness during this period.

Despite the importance and impact of the LGM on the current distribution of species (Araújo et al., 2008), evenness and richness values were restored after this perturbation and, at present, the study area exhibits the highest levels of diversity in the whole sequence (Fig. 3). Of course, current diversity values were obtained using different sampling methods, which could constitute a bias. Whatever the case, the current values for diversity are the highest present in the study sequence, providing evidence of the restoration of herpetofaunal diversity after the great perturbation of the LGM.

There are many examples of populations of different plant and animal groups that adapted to climate change during Quaternary persisting in situ (e.g. Davis and Shaw, 2001), thus showing a resistance and/or resilience level high enough to cope with all perturbations that occurred during this period. This is particularly notable in herpetofaunal species that persisted throughout the Quaternary with few changes, and are considered to be the same species as those that can be found today in the Iberian Peninsula.

The effects of biodiversity on community resilience and resistance are far from clear (Ives et al., 2000; Cottingham et al., 2001). Several studies have found a variety of complex relationships between species-richness and stability, depending on traits such as community composition or interaction strength (Downing and Leibold, 2010). In our case, the high diversity displayed in the area, and its response to perturbations through time, clearly suggests a positive relationship between species richness and the resilience of the amphibian and reptile communities. Explanations of this pattern may include the insurance effect, the character of the study area as an ecotone, or a combination of these factors. As summarized by Downing and Leibold (2010), the theory of the insurance effect proposes that species-rich communities are able to buffer environmental variability because they are more likely to contain species with different responses (Yachi and Loreau, 1999) or because they are less likely to lose important functions thanks to their increased redundancy (Naeem, 1998).

The high level of resilience that we found in the Pleistocene herpetofauna of the Sierra de Atapuerca sites seems to be related to the character of the study area as an ecotone, together with the great variety of habitats (nearby mountains, floodplains, water-edge environments and riverine forests) present there. This habitat diversity allows the area to support a great number of species with different requirements, due to the abundance of different niches and resources. On the other hand, its geographical situation made the area a natural corridor, between the Mediterranean and the Atlantic, where both Eurosiberian and Mediterranean species can be found. Each group of taxa has different requirements, which contributes to the rapid recovery of diversity after perturbations, especially climatic changes. The high species flux in the area promotes the establishment of new species and the re-establish-ment of earlier ones, thus maintaining the local diversity.

Throughout the stratigraphic sequences of the several localities in the caves from the Sierra de Atapuerca, the composition of the herpetofaunal assemblage changes with climate and probably with other biotic and abiotic factors. By contrast, the species richness does not vary substantially, and when it does it recovers in most cases, thanks to the high level of resilience exhibited by these groups.

At present, amphibian and reptile communities are also facing a scenario of climate change, reinforced by anthropic effects such as pollution or habitat degradation, which were not present at the time of our study. As shown by our study of an inland Mediterranean landscape, herpetofaunal communities can face climate change by tending towards stability. Nonetheless, our results show that even though richness values may be maintained over time, the replacement of species often occurs. In a present-day context, this could mean the disappearance of endemic species and the proliferation of alien species, which has been established as another main cause of reduced herpetofaunal diversity. In addition, there are disagreements about the equivalence of the interglacials of the past and the current one (Giaccio et al., 2015). It has been suggested that anthropogenic greenhouse gas emissions are changing the natural course of glacial–interglacial cycles by disrupting the progressive cooling that should lead to the subsequent glacial period. This discrepancy with respect to past interglacials may interfere with the pattern of resilience shown by herpetofaunal communities until now.

What we currently see is a worldwide decline in amphibian and reptile populations, but with no evidence of the replacement of species or population recovery (Houlahan et al., 2000; Blaustein and Kiesecker, 2002). Authors such as Davis et al. (2018) have argued that the loss of species due to human activity leads to a loss of phylogenetic diversity and that millions of years will be required for it to recover. Even though the causes of amphibian and reptile decline are complex (Kiesecker et al., 2001), research is focused on disentangling the various factors driving the decline in amphibian and reptile populations and to what extent they are doing so, as well as ascertaining which preventive and corrective measurements should be implemented to stop this tendency. Species that are not capable of coping with this perturbation rate will unavoidably be led to reduction and extinction, as has already happened during the Pleistocene (Blain et al., 2016).

As regards the herpetofauna, habitat loss and degradation, pollution, invasive alien species, harvesting, persecution, human disturbance, disease and vehicle collision are identified as major present-day threats for this endangered group (Cox et al., 2006; Liu et al., 2014; Greenberg et al., 2018). It is remarkable that these threats are mostly derived from human activity or from its magnifying effect on climate change disturbances. As evidenced by the Quaternary records, climate change has occurred recurrently in the past, but not anthropization. Perturbations derived from human activity seem to constitute overriding factors that prevent species from adapting to new conditions, while climate change stays in the background.

1.2.6 CONCLUSIONS

1. Temperature changes are the most influencing factor conditioning richness values of amphibians and reptiles. An increase in temperature leads to a rise in richness probably by conditioning the energy-resource dynamics of these groups. Even though in our study case the influence of precipitation is not relevant, due to the complexity in the analysis of a palaeontological sample, the influence of precipitation cannot be dismissed as another ecological factor influencing diversity trends.

2. Levels corresponding to MIS 11 and MIS 19 display maximum diversity values, the closest to current ones. This is consistent with the established climatic correspondence between these two interglacials and the present time. Also, our analysis clearly reflects the impact of the LGM on the herpetofaunal assemblage, which translates into a marked decrease in evenness and species richness.

3. A high level of resilience is shown, except during the time span between MIS 9 and MIS 8. Our data suggests a positive relationship between species richness and resilience of the herpetofauna communities. The high level of resilience that we found in study area seems to be related to the ecotone character of the area, together with the great variety of habitats present in there.

4. Even though our data have shown an elevated capacity to couple with climatic changes, current conditions of pollution and habitat degradation sitúate herpetofaunal communities in a different scenario. Perturbations derived from human activity seem to constitute overriding factors that prevent species from adapting to new conditions, while climate change stays in the background.

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Data archiving statement

Data for this study are available in the Dryad Digital Repository:

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SUPPLEMENTARY MATERIAL

Table S1. Raw values of minimum number of individuals (MNI) per site or unit and per level: TE-LRU (Trinchera Elefante Lower Red Unit); Dolina (Gran Dolina); TE-URU (Trinchera Elefante Upper Red Unit) and Portalón. Species are fully named in the first page and abreviated in the next. Climatic data of MAT: Mean annual temperature and MAP: Mean annual precipitation are setted at the bottom of the table in ºC and mm respectively. Original data sources are specified in the main text within the section "Material and Methods".

AMPHIBIA

Site/Unit	**TE-LRU**								
Level	**TE9c**	**TE9b**	**TE9a**	**TE9a+**	**TE10**	**TE11**	**TE12**	**TE13**	**TE14**
Urodela									
Salamandra gr.*salamandra*		1							
Triturus marmoratus	1	1							1
Lissotriton helveticus									
Anura									
Alytes cf. obstetricans	6	9	3	3	2			1	5
Discoglossus sp.									
Pelobates cultripes	2	3	2		3	2	1		
Pelodytes punctatus	10	51	6	4	2	1		2	11
Bufo gr. *bufo-spinosus*	6	8	2		1	1			3
Epidalea calamita	226	375	135	48	30	10	10	10	37
Hyla gr.arborea-molleri									1
Rana gr.*temporaria-iberica*	10	13	9	4	4			1	2
Pelophylax sp.									2
TOTAL AMPHIBIA	**261**	**461**	**157**	**59**	**42**	**14**	**11**	**14**	**62**

	Site/Unit	**TE-LRU**								
	Level	**TE9c**	**TE9b**	**TE9a**	**TE9a+**	**TE10**	**TE11**	**TE12**	**TE13**	**TE14**
SQUAMATA	Amphisbaenia									
	Blanus gr. *cinereus-mariae*									
	Lacertilia									
	Chalcides striatus									
	Lacerta sl.	3	5	4	1	4	2	4	1	3
	Lacertidae indet.	42	94	26	8	80	27		7	48
	Anguis gr. *fragilis*									1
	Serpentes									
	Natrix maura					2				
	Natrix gr. *natrix-astreptophora*						1			
	Coronella cf. *austriaca*									
	Coronella cf. *girondica*	12	6	6	5	5	3	3	1	5
	Coronella sp.									
	Rhinechis scalaris									
	Vipera cf. *aspis*									
	Vipera cf. *latasti*									
	Vipera sp.	11	8	6	6	4	1	1	1	4
	TOTAL REPTILES	**68**	**113**	**42**	**20**	**95**	**34**	**8**	**10**	**61**
	TOTAL	**329**	**574**	**199**	**79**	**137**	**48**	**19**	**24**	**123**
CLIMATE	**MAT (°C)**	12.5	12.5	12.5	11.6	12.5	12.1	x	11.6	10.7
	MAP (mm)	897	897	897	864	897	687	x	864	883

	Site/Unit	**DOLINA**												
	Level	**TD4B**	**TD5C**	**TD5B**	**TD5A**	**TD6-3**	**TD6-2**	**TD6-1**	**TD7**	**TD8a**	**TD10-4**	**TD10-3**	**TD10-2**	**TD10-1**
AMPHIBIA	Urodela													
	S. gr.*salamandra*													
	T. marmoratus					2								
	L. helveticus													
	Anura													
	A. cf. *obstetricans*	1	1	115	47	162	7	95	2	18	19	31	32	29
	Discoglossus sp.													
	P. cultripes					9	2	5		9	3	3	1	
	P. punctatus		2	62	7	49	5	84	2	20	12	18	10	3
	Bufo gr.	6		33	8	24	1	6	1	3	80	108	31	14
	E. calamita		4	631	311	619	47	553	12	292	479	521	187	62
	Hyla gr.									3	2	2	1	
	Rana gr.	5		60	39	76	4	70	2	5	62	80	37	27
	Pelophylax sp.		1		1	3				3	1	1		
	TOTAL AMPHIBIA	**12**	**8**	**901**	**413**	**944**	**66**	**813**	**19**	**353**	**658**	**764**	**299**	**135**
	Amphisbaenia													
	Blanus gr.									1				
	Lacertilia													
	C. striatus													
	Lacerta sl.	1	1	9	1	27	3	11	1	3				
	Lacertidae indet.		2	74	2	113	11	28	5	27	46	24	29	13
	Anguis gr.			14		26	1	4			2			
	Serpentes													
	N. maura	1								2	16	2	1	1

	Site/Unit	**DOLINA**												
	Level	**TD4B**	**TD5C**	**TD5B**	**TD5A**	**TD6-3**	**TD6-2**	**TD6-1**	**TD7**	**TD8a**	**TD10-4**	**TD10-3**	**TD10-2**	**TD10-1**
	Natrix gr.		1	6	1	5		6		3				
	C. cf. *austriaca*	1	2	16		28	4	22	1	3	10	3	1	
	C. cf. *girondica*										1			
	Coronella sp.													
	R. scalaris	1	3	7	5	12	1	5	1	1	4			
	V. cf. *aspis*			34		24	2	20		3	12	13	8	2
	V. cf. *latasti*										2	1		
	Vipera sp.													
	TOTAL REPTILES	**4**	**9**	**160**	**9**	**235**	**22**	**96**	**8**	**43**	**93**	**43**	**39**	**16**
	TOTAL	**16**	**17**	**1061**	**422**	**1179**	**88**	**909**	**27**	**396**	**751**	**807**	**338**	**151**
CLIMATE	**MAT (°C)**	11.7	12.15	12.18	11.18	12.56	12.56	12.56	12.07	12.56	12.56	12.56	11.6	11.6
	MAP (mm)	956	938	977	955	981	981	981	907	981	981	981	876	876

	Site/Unit	**TE-URU**		
	Level	**TE19C**	**TE19F**	**TE19G**
AMPHIBIA	Urodela			
	S. gr.*salamandra*	1	1	
	T. marmoratus			
	L. helveticus		3	
	Anura			
	A. cf. *obstetricans*		1	
	Discoglossus sp.		1	
	P. cultripes			1
	P. punctatus		5	1
	Bufo gr.	1		5
	E. calamita	4		
	Hyla gr.	1	2	
	Rana gr.		1	1
	Pelophylax sp.			
	TOTAL AMPHIBIA	**7**	**14**	**8**
SQUAMATA	Amphisbaenia			
	Blanus gr.			
	Lacertilia			
	C. striatus	1		4
	Lacerta sl.		5	
	Lacertidae indet.	1	1	1
	Anguis gr.			
	Serpentes			4
	N. maura	1		1
	Natrix gr.			
	C. cf. *austriaca*			
	C. cf. *girondica*	1		2
	Coronella sp.			
	R. scalaris			
	V. cf. *aspis*	1		2
	V. cf. *latasti*			2
	Vipera sp.			
	TOTAL REPTILES	**5**	**6**	**16**
	TOTAL	**12**	**20**	**24**
CLIMATE	**MAT (°C)**	10.4	10.4	10
	MAP (mm)	854	843	850

	Site/Unit	**PORTALÓN**															
	Level	**P16**	**P15**	**P14**	**P13**	**P12**	**P11**	**P10**	**P9**	**P8**	**P7**	**P6**	**P5**	**P4**	**P3**	**P2**	**P1**
AMPHIBIA	Urodela																
	S. gr.*salamandra*																
	T. marmoratus																
	L. helveticus																
	Anura																
	A. cf. *obstetricans*	1	14	11	1	2	29	34	25	44	22	3	1	2	5	2	1
	Discoglossus sp.																
	P. cultripes																
	P. punctatus Bufo gr.						3	8		3	1	1		1	1	1	
	E. calamita	2	49	13	5	10	82	38	14	58	32	9	1	9	12	5	2
	Hyla gr.																
	Rana gr.	1	65	51	5	8	55	28	153	47	24	8	1	2	2	3	2
	Pelophylax sp.																
	TOTAL AMPHIBIA	**4**	**128**	75	**11**	**20**	**169**	**108**	**192**	**152**	79	**21**	**3**	14	**20**	**11**	5
SQUAMATA	Amphisbaenia																
	Blanus gr.																
	Lacertilia																
	C. striatus																
	Lacerta sl.																
	Lacertidae indet.						1	1	1	1	1			1			1
	Anguis gr.																
	Serpentes																
	N. maura																
	Natrix gr.																

	Site/Unit	**PORTALÓN**															
	Level	**P16**	**P15**	**P14**	**P13**	**P12**	**P11**	**P10**	**P9**	**P8**	**P7**	**P6**	**P5**	**P4**	**P3**	**P2**	**P1**
	C. cf. *austriaca*																
	C. cf. *girondica*																
	Coronella sp.																
	R. scalaris																
	V. cf. *aspis*																
	V. cf. *latasti*																
	Vipera sp.							1		1	1			1			
	TOTAL REPTILES	**0**	**0**	**0**	**0**	**0**	**1**	**2**	**1**	**2**	**2**	**0**	**0**	**2**	**0**	**0**	**1**
	TOTAL	**4**	**128**	**75**	**11**	**20**	**170**	**110**	**193**	**154**	**81**	**21**	**3**	**16**	**20**	**11**	**6**
CLIMATE	**MAT (°C)**	8.8	7.3	9.4	7.3	8.8	7.3	7.3	7.3	7.3	7.1	8.1	8.8	8.4	8.4	8.5	7.6
	MAP (mm)	1413	950	860	950	1346	950	950	950	950	950	1302	1305	1354	1331	925	950

	Site/Unit	**TODAY**
AMPHIBIA	Urodela	
	S. gr. *salamandra*	1
	T. marmoratus	25
	L. helveticus	16
	Anura	
	A. cf. *obstetricans*	9
	Discoglossus sp.	3
	P. cultripes	
	P. punctatus	4
	Bufo gr.	19
	E. calamita	16
	Hyla gr.	15
	Rana gr.	
	Pelophylax sp.	35
	TOTAL AMPHIBIA	**143**
SQUAMATA	Amphisbaenia	
	Blanus gr.	1
	Lacertilia	
	C. striatus	5
	Lacerta sl.	50
	Lacertidae indet.	29
	Anguis gr.	8
	Serpentes	
	N. maura	20
	Natrix gr.	8
	C. cf. *austriaca*	1
	C. cf. *girondica*	4
	Coronella sp.	
	R. scalaris	4
	V. cf. *aspis*	
	V. cf. *latasti*	9
	Vipera sp.	
	TOTAL REPTILES	**139**
	TOTAL	**282**
CLIMATE	**MAT (°C)**	9.9
	MAP (mm)	573

Part 2.
Guadix-Baza Basin sites: Barranco León and Fuente Nueva 3

2.

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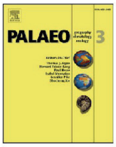

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Amphibian body size and species richness as a proxy for primary productivity and climate: The Orce wetlands (Early Pleistocene, Guadix-Baza Basin, SE Spain)

Almudena Martínez-Monzón [a,b,*], Christian Sánchez-Bandera [a,b], Ana Fagoaga [a,b,c,d], Oriol Oms [e], Jordi Agustí [a,b,f], Deborah Barsky [a,b], José Solano-García [g], Juan Manuel Jiménez-Arenas [h,i], Hugues-Alexandre Blain [a,b]

[a] *IPHES-CERCA, Institut Català de Paleoecologia Humana i Evolució Social, Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain*
[b] *Departament d'Història i Història de l'Art, Universitat Rovira i Virgili, Avinguda de Catalunya 35, 43002 Tarragona, Spain*
[c] *PVC-GIUV (Palaeontology of Cenozoic Vertebrates Research Group), Àrea de Palaeontologia, Universitat de València, Dr. Moliner 50, E-46100 Valencia, Spain*
[d] *Museu Valencià d'Història Natural, L'Hort de Feliu, P.O. Box 8460, E-46018, Alginet, Valencia, Spain*
[e] *Departament de Geología, Facultat de Ciències, Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain*
[f] *Institució Catalana de Recerca i Estudis Avançats (ICREA), Pg. Lluís Companys 23, 08010 Barcelona, Spain*
[g] *Departamento de Prehistoria y Arqueología, Facultad de Filosofía y Letras, Universidad de Sevilla, María de Padilla S/N, 41004 Sevilla, Spain*
[h] *Departamento de Prehistoria y Arqueología, Facultad de Filosofía y Letras, Universidad de Granada, Campus Universitario de Cartuja C.P, 18011 Granada, Spain*
[i] *Instituto Universitario de la Paz y los Conflictos, Universidad de Granada, c/Rector López Argüeta s/n, 18011 Granada, Spain*

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ABSTRACT

Amphibians are considered excellent indicators of ecological and climatic changes with a remarkable phenotypic plasticity. The study of such adaptative capacities is central to understanding the climate and environmental changes that occurred during the Early-Middle Pleistocene Transition, at around 1.2 Ma, when the persistence of subtropical ecosystems in Europe came to an end, and several reptile and tree taxa were extirpated. The SE Spain sites in the Guadix-Baza Basin offer an exceptional opportunity for studying this change, in addition to the significant findings made in this area in the field of human evolution.

We have analysed the body size of the most well-represented amphibian species in the sites, the Iberian waterfrog, *Pelophylax perezi*. In order to reconstruct past body sizes from fossil samples, a regression model from current osteological collections has been generated. Also, diversity of the herpetofauna community was studied at different levels as richness or species number. Finally, to study the relationships between body size, richness, climate and productivity, OLS regression models and Pearson correlations were applied. Also for this purpose, a productivity indicator was designed based on the addition of the two most productive ecosystems from previous habitat reconstruction.

Amphibian body size appears to be negatively associated with primary productivity, reaching minimum values during the interglacial stages, when species richness increased. In contrast, during glacial periods characterised by greater aridity and fewer resources, amphibian body size increased while species richness decreased. Main explanations proposed to justify this pattern are the “water-availability hypothesis” and a trade-off between somatic growth and reproductive opportunities for females. The study of herpetofaunal diversity shows a clear correlation to regional plant diversity and primary productivity. The results of this work indicate that species richness and amphibian body size are valuable proxies that can complement current environmental and climate reconstruction methods.

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2.1. INTRODUCTION

As one of the primary components of aquatic and terrestrial environments (Unrine et al., 2007), amphibians currently play a central role in many ecosystems. They influence ecosystem energy and trophic dynamics by controlling the insect population and by serving as a vital food source for many larger animals (Unrine et al., 2007; Sparling et al., 2010). Research into this group has revealed that, due to their semi-permeable skin and biphasic lifecycles, amphibians are highly sensitive to environmental changes, both in terrestrial and aquatic systems (Alford and Richards, 1999), making them excellent bioindicators of habitat alterations (Henry, 2000). Because amphibians live in multiple habitats, they are potentially exposed to a greater range of environmental and anthropogenic stresses at various spatial scales (Johnson et al., 2002) than would be expected for organisms that use only terrestrial or aquatic habitats. Several studies have documented the sensitivity of amphibians to landscape-scale anthropogenic threats, including habitat fragmentation (Kolozsvary and Swihart, 1999; Knutson et al., 2000; Willson and Dorcas, 2003), whereas other studies have highlighted the importance of local-scale factors such as hydroperiods (Pechmann et al., 1989) and introduced predators (Hecnar and M'Closkey, 1997; Adams, 1999). This suggests that amphibians can be used as biological indicators of overall ecological conditions and as a means of assessing the effects that environmental factors have on ecosystems.

All extant species of amphibians and reptiles in Europe have presumably existed since at least the Pliocene. Compared to other groups, they are regarded as relatively stable and conservative organisms during the Neogene and Quaternary, in contrast to their high level of sensitivity to environmental factors (Delfino, 2005). This suggests that these species have been able to adapt to successive variations in global climate conditions (cyclicity, seasonality, etc.) over the last 5 Myr by readjusting their ranges to microclimates (see Martínez-Monzón et al., 2018, 2021). In southern Europe, palaeoenvironments are known to have moved progressively from what was originally seasonal forest (Middle to Late Miocene) to warm-temperate laurel forest in the Pliocene and then to more open and arid Mediterranean conditions during the Early Pleistocene (Barrón et al., 2010). One of these thresholds has been identified as being around 1.2 Ma, marking the end of warm-temperate ecosystems in Europe and the extirpation of several reptile and tree taxa (see Bertini, 2010; Blain and Bailon, 2019).

At this threshold, prior to the first major cold peak (Marine Isotope Stage, MIS 22) of the Early-Middle Pleistocene Transition, climate variability (i.e., the difference between the interglacial and glacial stages) was much more pronounced than that subsequently experienced. As Altolaguirre et al. (2019, 2020) recently determined based on the pollen record from the Palominas core (from the Guadix-Baza Basin, SE Spain), the interglacials were warmer and more humid than those today, while the glacials were characterised by more moderate temperature values (similar to those today) and were notably drier than the interglacials. As the temperature in the Guadix-Baza Basin region does not seem to have been the sole determining factor at around 1.2 Ma, other related eco-climatic agents, such as increased aridity, habitat fragmentation, decreased primary productivity, or a combination of these, may have been critical in contributing to the extirpation of the various herpetofauna, including the subtropical genus of legless lizards *Ophisaurus*, agamid lizards, and green toads (Blain et al., 2010, 2014, 2016a; Blain and Bailon, 2019). A recent palaeoenvironmental study of material from two Early Pleistocene archaeological sites (Barranco León and Fuente Nueva 3) in the Guadix-Baza Basin found evidence of glacial-interglacial dynamics like those identified in the Palominas core (Sánchez-Bandera et al., 2020). These sites are known to have been located on the shore of a large fluctuating shallow Pleistocene lake, surrounded by marshland and riparian humid areas (Altolaguirre et al., 2021; Oms et al., 2011), thus offering a paradigmatic location for the study of climate and environmental variability.

At present, a range of approaches are being used to more precisely characterise the palaeoenvironmental and biotic changes driven by Early Pleistocene climate variability. The amphibian fossil record offers one of these perspectives, as amphibian adaptation and physiological reactions to environmental fluctuations are reflected in morphological changes, some of which are recognisable at an osteological level (Martínez-Monzón et al., 2018). To fully understand how amphibians reacted to eco-climatic changes in the context of the Guadix-Baza Basin sites, we propose two response variables that incorporate a combination of scales: herpetofaunal species richness, as a measure of community diversity; and the body size of the most well-represented amphibian species at the sites, the Iberian waterfrog, *Pelophylax perezi* (Anura, Ranidae). *P. perezi* is clearly one of the most successful taxa in the Iberian Peninsula in terms of its ability to cope with environmental and climate changes. Today, this frog is a medium-sized species with accentuated female-biased sexual size dimorphism (Egea-Serrano, 2014). It is found in all types of freshwater environments and is considered to be a species with elevated physiological plasticity, elevation being the only cited restriction to its distribution (Llorente et al., 2002). Like most extant amphibians, *P. perezi* individuals from Pleistocene localities have been determined to be identical to modern specimens based on genetic distance data obtained through molecular clock techniques (Sanchiz, 1977; Barbadillo et al., 1997).

An actualistic approach can therefore be applied to this species for further analysis. Because of its high degree of adaptability and apparent capacity to endure changes in climate, the phenotypic reflection of its physiological adaptations to such variations may facilitate a more accurate definition of the palaeoenvironmental changes that occurred in the freshwater or water-edge environments in the south-eastern Iberian Peninsula during the Early Pleistocene. Determining waterfrog morphological changes like body size variations may contribute to a better understanding of these environmental alterations, as this parameter (body size) has an enormous influence on most of the life-history traits and the physiological processes of this frog. The influence of eco-climatic parameters on body size in the genus *Pelophylax* has been the focus of several studies that have reported a negative relationship between body size and temperature (Amor et al., 2010; Gül et al., 2014; Erismis, 2018). Other studies have found no such trend (Lou et al., 2012). To our knowledge, no research has yet explicitly analysed the relationships between waterfrog body size and other climate factors, such as precipitation, resources, and primary productivity. However, indirect insights suggest the presence of a negative relationship between primary productivity and body size (Amor et al., 2010; Mohammadi et al., 2015).

This work aims to study the body size variations of *P. perezi* in terms of Early Pleistocene climate/environmental variability to use them as a new indicator for characterising palaeoenvironmental variables, such as eco-climatic parameters (primary productivity, temperature, and precipitation) in Mediterranean wetland areas.

2.2. GEOLOGICAL AND PALAEOECOLOGICAL SETTING

The Orce-Fuente Nueva-Venta Micena sector is located in southern Spain, in the north-eastern area of the Guadix-Baza Basin (Fig. 1). This region has one of the most important continental palaeobiological records in Europe for the Early Pleistocene and the transition towards the Late Pliocene (Agustí et al., 1999, 2010). The main archaeo-palaeontological sites are located 124 km north of the city of Granada (SE Spain), at approximately 950 m above sea level. The fossil hominin tooth recovered from the Barranco León site (BL) (Toro-Moyano et al., 2013) and the Oldowan (i.e., Mode 1) lithic artefacts discovered at the Fuente Nueva 3 (FN3) and Barranco León sites are widely considered to be among the oldest evidence of hominin occupation in western Europe (Oms et al., 2000b; Carbonell and Rodríguez, 2006). In addition to their exceptionally rich and well-documented stone tool assemblages (e.g., Barsky et al., 2015a, 2015b, 2018; Titton et al., 2018, 2020, 2021), these sites have yielded a remarkable large/small vertebrate record (e.g., Agustí et al., 2010, 2013, 2015a, 2015b; Saarinen et al., 2021).

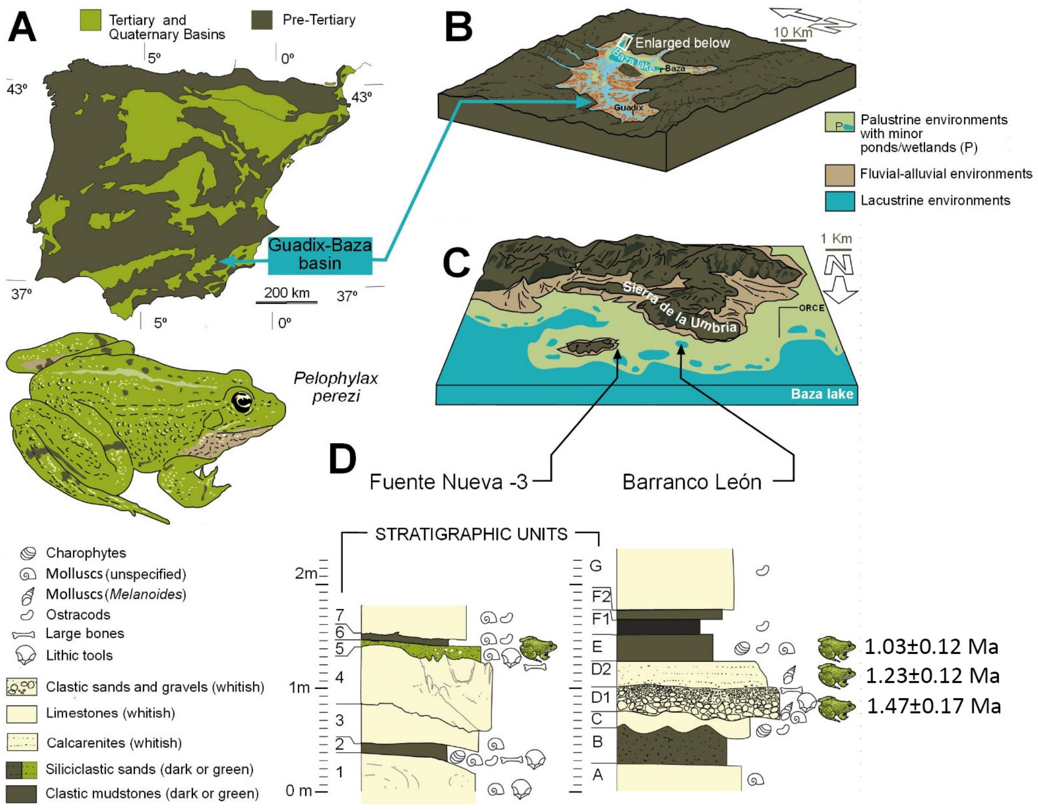

Figure. 1. A: Tertiary and Quaternary basins of the Iberian Peninsula showing the location of the Guadix-Baza Basin; **B**: General palaeogeographic diagram of Baza Lake in the framework of the basin; **C**: Detailed palaeogeographic map of the BL and FN3 sites (see location in B); **D**: Local archaeo-palaeontological sections of the FN3 and BL sites (redrawn from Sánchez-Bandera et al., 2020, and works therein).

Geologically, the Guadix-Baza Basin is an intramontane basin of about 3000 km^2 with an almost continuous sedimentary succession spanning the last 8 Myr (see Hüsing et al., 2010, and references therein). In the Orce area, the Baza formation (Vera, 1970) has three members (Vera et al., 1985; Oms et al., 2000a); the sites studied here belong to the upper silty calcareous member. The FN3 and BL sediments were deposited in a lacustrine-palustrine environment (Oms et al., 2011) characterised by shallow lakes/ponds and wetlands (see also Granados et al., n.d.). The sites are located on what was the marginal area of the larger saline Baza Lake (Anadón et al., 1987).

During periods of lake expansion, saline conditions extended throughout the basin, but when the main lake receded, the basin margins were fed by freshwater inputs of thermal origin and precipitation runoff (Anadón et al., 2015). Thus, water bodies close to the main saline lake could potentially preserve evidence of environmental changes during periods of lake regression. Presence of exclusively reverse magnetization throughout the stratigraphic sections, combined with the faunal assemblages, indicates a Pre-Jaramillo age for all levels of BL and FN3 (Oms et al., 2011).

Additionally, for a biochronological point of view, both micro and macromammal assemblages support that statement (Agustí et al., 2015a, 2015b; Toro-Moyano et al., 2013). In spite of BL-E1 dating younger (Duval et al., 2012) than FN3–5 (Duval et al., 2011), BL-E1 is considered here to be older than FN3–5 based on dental features of *Mimomys savini* (Lozano-Fernández et al., 2015).

In any case, it is worth to note that numerical datings are affected by the imprecision of the methods, which implies a high degree of overlap due to the wide confidence intervals. A combination of stratigraphical, geochronological and biostratigraphical approaches rises, therefore, as the best way to establish the chronological framework of the Guadix-Baza Basin sites.

Barranco León

The Barranco León site (BL) (37°43'28.4"N 2°27' 03.7"W) is located 3 km from the village of Orce (Fig. 1C, D), adjacent to the Sierra de la Umbría (one of the mountain ranges that delimits the north-eastern part of the Guadix-Baza Basin). This site is included in a stratigraphic sequence consisting of grey to yellow sands, mudstones, gravels, and limestones. The stratigraphy bounding the site is divided into nine levels, of which D1, D2, and E are considered the most important in archaeo-palaeontological terms (See Fig. 1D).

The origin of Level D1 is principally related to a sudden high-energy event, which transported gravels contain palaeontological and archaeological remains (Oms et al., 2011). This level is up to 65 cm thick and consists of sandy gravels. It is overlain by Level D2, comprising grey sands, which is around 20 cm thick. Despite this event, the observations of small vertebrate surfaces concluded that only a very little part of the microfauna may have been reworked (Titton et al., 2021), and it is in Level D2 where the more progressive sedimentation indicates an unquestionable in situ origin of the microfaunal remains (Oms et al., 2011). The stratigraphic sequence of BL has been dated using a variety of techniques, including large- and small-mammal assemblages, palaeomagnetic studies, and electron spin resonance (ESR). The latter has dated the sequence to between 1.2 ± 0.09 Ma at the top, and 1.88 ± 0.19 Ma at the base, which is in line with the stratigraphic and biochronological data (Toro-Moyano et al., 2013). The dates for Levels D1 and D2 reveal an Early Pleistocene age of 1.46 ± 0.17 Ma (Toro-Moyano et al., 2013).

The palaeomagnetic study shows reverse polarity throughout the BL stratigraphic section, placing it in the upper Matuyama chron (Oms et al., 2000b). From an environmental perspective, the invertebrate fauna from this site indicates a fresh water to oligosaline shallow lacustrine environment (Oms et al., 2011; Anadón et al., 2015). The main environmental features of Levels D1, D2, and E suggest that they were located in a marginal freshwater area of the main saline lake. According to the herpetofauna, in BL-D (i.e., D1 + D2) the hominin-bearing layer could represent a humid period corresponding to an interglacial stage (Sánchez-Bandera et al., 2020).

Fuente Nueva 3

The Fuente Nueva 3 site (FN3) (37◦42' 55.2"N 2◦23' 51.3"W) is located 2 km north of the Sierra Umbría, 7 km east of the village of Orce, and 4 km from the other main site, Barranco León (see Fig. 1C, D). The general section of FN3 contains up to 12 levels, including limestones, mudstones, and sandstones (Oms et al., 2011; see also Anadón et al., 2003). Levels 2 and 5 are particularly noteworthy due to the presence of abundant lithic industry and mammal remains.

Level 5 consists of greenish fine-grained sand and marly mudstones that infill the irregular top of Level 4 (Oms et al., 2011). ESR dating places the stratigraphic succession of FN3 within a chronological range from 1.67 to 1.34 Ma (Duval et al., 2012). The palaeomagnetic analyses reveal reverse polarity (Oms et al., 2000a), which, in conjunction with the ESR data, dates the site as prior to the Jaramillo subchron (1.07–0.99 Ma) (Oms et al., 2003; Álvarez et al., 2015).

The evolutionary differences between the *Mimomys savini* populations at BL and FN3 (both located in the same biozone) suggest that BL is older than FN3, with a proposed age of 1.2 Ma for FN3 (Lozano-Fernández et al., 2015). As in BL-D2 and E, at FN3 there is no evidence of high-energy events (Espigares, 2010; Oms et al., 2011; Titton et al., 2021). The FN3 succession is indicative of a palustrine environment, although the invertebrate fossils indicate minor changes in water salinity (Anadón et al., 2003, 2015).

Taphonomic studies suggest that this site was a waterhole where animals came to drink and were occasionally hunted by hypercarnivores (e.g., sabretooths and wild dogs) and subsequently scavenged by hyenas and hominins (Palmqvist et al., 2005; Toro et al., 2010). From a palaeoenvironmental perspective, Level 5 could represent a dry period corresponding to a glacial stage (Sánchez-Bandera et al., 2020).

2.3. MATERIALS AND METHODS

Species data, eco-climatic parameters and species richness

The material studied in this work comes from Levels D1, D2, and E of BL and primarily from Level 5 of FN3 (see Fig. 1 D). The amphibian and reptile fossil remains comprise disarticulated elements collected by means of water-screening the sediments obtained during the excavation campaigns at the studied sites. The taxonomic attributions can be found in Agustí et al. (2015a) and Sánchez-Bandera et al. (2020). The species data used here, in particular the minimum number of individuals (MNI) per level, were obtained from Sánchez-Bandera et al. (2020). Within the five major habitat categories defined in Blain et al. (2008) (i.e., open-dry, open-humid, woodland and woodland-edge, water-edge, and stony/rocky), woodland and open-humid exhibit the highest primary productivity given the greater quantity of biomass and environmental humidity (Smith and Smith, 2001). The first (i.e., woodland) has been defined as 'mature forest including woodland margins and forest patches, with moderate ground cover' while open-humid habitats consist of 'evergreen meadows with dense pastures and suitable topsoil' (Blain et al., 2008). Around the Baza palaeo-lake, more humid areas, such as Mediterranean wet woodlands and wet open meadows, correspond to the woodland and open-humid percentages of the palaeoenvironmental reconstructions by levels, as reported in Sánchez- Bandera et al. (2020). These primary data are consistent with ongoing sedimentological, palynological, and ecometric analyses applied to herbivores (see Saarinen et al., 2021).

Our primary productivity indicator involves the sum of the open-humid and woodland percentages. The high frequency of these two habitat types at the archaeo-palaeontological sites (Sánchez-Bandera et al., 2020) reflects periods in which the net primary production rose due to higher carbon inputs promoted by increased plant cover and evapotranspiration. The increase in woodland and open-humid habitats in the samples studied also reflects the combination of warm temperatures and adequate water availability for transpiration, together with several environmental factors, including the quantity of light and nutrients (Smith and Smith, 2001). The palaeoclimate values presented in this work come from (Sánchez-Bandera in Serrano-Ramos et al., 2021) and have been reconstructed using the mutual ecogeographic range method (MER; Blain et al., 2009, 2016b), a widely established approach that analyses the geographical overlap of the current distribution of all taxa (amphibians and reptiles, in this case) with extant representatives occurring in an archaeo-palaeontological locality or level.

Current spatial distributions were obtained from Loureiro et al. (2008) and Pleguezuelos et al. (2004). Once the common overlapping area of the species from the assemblage had been obtained, and in order to include the exotic taxon *Ophisaurus* sp., the basis of the UDA-ODA discrimination method (Fagoaga et al., 2019) was applied. The climate parameters selected for this work were mean annual temperature (MAT) expressed in ◦C, and mean annual precipitation (MAP) in mm (data from WorldClim 2, Fick and Hijmans, 2017). Diversity is measured in terms of richness, which in this case can be considered as a measure of α-diversity, representing the diversity of species in a given habitat, site, or landscape unit (Whittaker, 1972) and by definition includes two main variables: the species richness and the relative abundance of species (i.e., the number of individuals represented by any single species). Richness corresponds to the total number of species in the community. This has also been calculated for amphibians and reptiles separately, in order to establish the contribution of each group to the total richness value.

Reconstruction of body size

The waterfrog fossil remains studied here consist of disarticulated bone fragments collected together with other small vertebrate remains by excavating the sediments using archaeological methods and then wet-sieving using a 0.5 mm mesh. We analysed a total of 106 fossil humeri of *Pelophylax perezi* from Levels D1, D2, and E at BL, and Levels 5 and 6 at FN3 for this work (Table S1), representing a minimum number of 57 individuals (31 females and 26 males) (see a sample in Fig. 2). Due to the scarcity of fossil remains, the data from FN3 Level 6 were only included in the study of global body size variation and not in the other analyses performed by level. Humeri for which sex cannot be securely determined have been excluded from the analysis. The humerus (more specifically its distal epiphysis) was considered the most appropriate skeletal part for our purposes, as it is a well-ossified, robust long bone. It is also highly diagnosable at species level (Fig. 3) and sexable due to a medial crest that is only present in males (Fig. 3).

The humerus thus constitutes an excellent indicator of body size (see Martínez-Monzón et al., 2018) and it is relatively abundant in most of the fossil samples. In addition to the fossil remains, we also sampled 104 modern lections housed at the Museo Nacional de Ciencias Naturales de Madrid (MNCN) to identify humerus features that could serve to reconstruct *P. perezi* body size, such as snout-to-vent length (SVL). We measured the width of the distal epiphysis of the humerus (referred to as humeral total width, hereafter abbreviated as HTW) (Fig. 3; Table S1), which was used to generate predictive regression models of SVL. For the analysis of body size and eco-climatic parameters, only the data from the 61 fossil humeri corresponding to the females were used. Previous work with fossil samples has suggested a sex-related response to climatic variables in amphibians, with females reflecting greater sensitivity to climatic changes (Martínez-Monzón et al., 2018). The more pronounced response of female body size to climate fluctuations has also been reported in current populations (Hemelaar, 1988; Schäuble, 2004; Leskovar et al., 2006; Reading, 2007), pointing to a sexually dimorphic response. In addition, males of *P. perezi*, and indeed most anurans, have more robust forelimbs due to the strength required to perform amplexus (Egea-Serrano, 2014). This sexual-selection characteristic can affect bone structure and could have consequently biased our results, as we reconstructed body size based on the humerus.

Statistical analysis

To verify the main assumptions of the following tests (i.e., normality and homoscedasticity), the normality of the samples was determined by means of a quantile-quantile plot, commonly known as a Q-Q plot, as well as with a Shapiro-Wilk test if the Q-Q plot results were not definitive. Furthermore, the homogeneity of variance between the different samples was assessed using Bartlett's test, which is specifically indicated if there are differences in sample sizes, as in our case.

For the mean comparison of female body size values, the Welch's t-test was chosen as the best option for our data. This adaptation of the Student's t-test performs better if, as in our case, sample sizes are unequal between groups. As a complement to the Welch's t-test, Lubischew's test (Lubischew, 1962) was used to estimate the extent to which a single morphometric variable (body size, in this study) allows us to discriminate between pairs of samples.

Figure. 2. Selection of fossil disarticulated female (upper row) and male (lower row) humeri of *Pelophylax perezi* from the Orce archaeo-palaeontological sites. Fuente Nueva 3, Level 5 (**A** and **E**); Barranco-León, Level D1 (**B** and **F**); Level D2 (**D** and **G**); and Level E (**C** and **H**).

In brief, Lubischew's test works as follows: given that the percentage of misclassifications with a variable (X) is approximately the probability that a normal deviate exceeds $\sqrt[2]{K/2}$, the greater K is, the better X works as a discriminator. To reconstruct past body sizes, regression models of SVL from the dry osteological collections of the MNCN (SVL vs HTW) were constructed using simple ordinary least squares (OLS). The male and female models were developed independently, after which we applied the resulting models to the measurements taken from the fossils in order to reconstruct past body sizes.

For the correlation analysis using eco-climatic parameters, we employed a simple ordinary least squares (OLS) regression to generate a predictive model of female *P. perezi* body size (in mm) for the productivity indicator and climate parameters. The results of this model were complemented with a Pearson correlation analysis, a measurement of the linear dependence between two quantitative random variables. All the analyses were conducted using the R software environment (R Core Team) and a significance level of α = 0.05.

Finally, regarding species richness analyses, the samples have been standardized by the elaboration of rarefaction (interpolation) and prediction (extrapolation) curves with Hill numbers method (Colwell et al., 2012; Chao et al., 2014) in order to test whether expected species richness are significantly different. The curves were drawn on the basis of the integrated sample-size and sample-coverage analytic approaches (Chao and Jost, 2012)). Hill numbers include the three most widely used species diversity measures: species richness (q = 0), Shanon diversity (q = 1) and Simpson diversity (q = 2), and are increasingly dominated by the frequencies of the more common

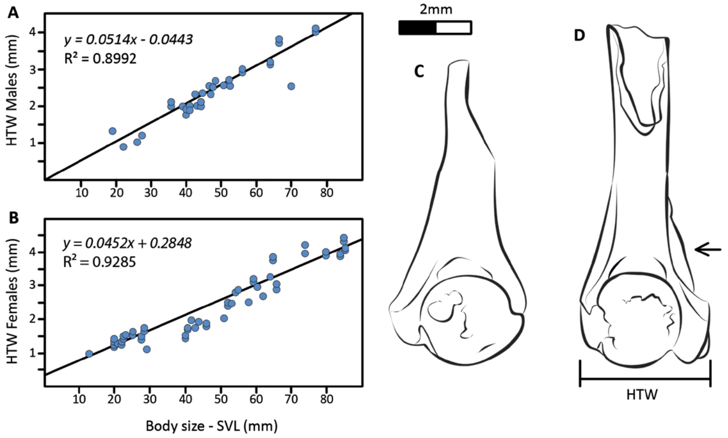

Figure. 3. Male (**A**) and female (**B**) OLS regression models of HTW (humeral total width) to SVL (snout-to-vent length), both in mm, of modern specimens of *Pelophylax perezi* from the osteological dry collections of the MNCN. The respective equations and adjusted coefficients of determination (R^2) are provided. On the right are diagrams of a left female (**C**) and right male (**D**) fossil humeri of *P. perezi* from the Early Pleistocene site of Barranco León (Level E and Level D2 respectively), in ventral view showing humeral total width (HTW); i. e., the trait used for body size reconstruction and, marked with an arrow, the medial crest present in males, the main osteological feature used for establishing sex.

species. Finally, the bootstrap method is used to construct 95% confidence intervals for the expected interpolated and extrapolated curves (Chao et al., 2014). Statistical analyses were processed using the iNEXT (iNterpolation/EXTrapolation) online freeware application R-based version (Chao et al., 2016).

2.4. RESULTS

Richness

Richness (i.e., the number of species documented in each level) reaches its maximum value in Level D1 of BL with 14 species (Table 1). At the same site, Levels D2 and E present intermediate values (10 and 9 species respectively), and the lowest value is in Level 5 of FN3, with 7 species. In terms of the contribution of the different species to these richness values, the number of reptile species is slightly higher in all cases than that of amphibians. However, differences in the number of species in the various samples follow the same trend for the two groups. The two extreme points are Level D1 of BL, which exhibits the greatest diversity, and Level 5 of FN3 with a richness only half that of D1. The decrease in richness is proportional in both amphibians and reptiles, with both values exactly halved in FN3–5, the point of minimum richness (Table 1).

Statistical analyses following the rarefaction and extrapolation with Hill number method corroborate the richness differences and trends inferred. The biodiversity comparison is based on 82 number of individuals (basic sample-size n = 82) as double the size of the sample for the level with the smallest number of individuals (FN3–5). Slight differences in term of species richness between the BL Levels (D1, D2 and E) are observed, when comparing diversity among the studied layers based on sample-size (Supplementary Fig. S1-A). However, these differences are not statistically significant (i.e., 95% confidence intervals overlap). When comparing BL with FN3–5, significant differences are detected (95% confidence intervals do not fully overlap when levels' sample-sizes are standardized). It is remarkable to note that partially overlapping intervals do not guarantee no significance (Schenker and Gentleman, 2001). According to Shannon and Simpson indices (q = 1 and q = 2, respectively; Supplementary Fig. S1-A), BL-D2 is less diverse in terms of evenness than the other levels, due to the fact that it is dominated by the waterfrog *Pelophylax* cf. *perezi*. In the other levels, the species are more equally distributed.

The results obtained were compared with coverage-based rarefaction and extrapolation curves (Supplementary Fig. S1-C), which confirms the order and significance of the biodiversity indices between the four levels detected in the sample-size based curves (Supplementary Fig. S1-A). Both curves were linked with the construction of a sample completeness curve (Supplementary Fig. S1-B), which allow us to examine how the sample completeness varies with sample size. The estimated sample coverage does not differ significantly between the four levels (BL-D1 = 0.8, BL-D2 = 0.9, BL-E = 0.8 and FN3–5 = 0.9), showing that all the levels have been equally sampled. There is therefore a correspondence between the conclusions regarding the values of biodiversity estimators drawn on the basis of both curve types.

Reconstructed body sizes and their variation

For the reconstruction of past snout-to-vent-lengths, the HTW-generated model explained

90% and 93% of body size variance in modern male and female individuals, respectively (Fig. 3). Consequently, we employed the models including this measurement (HTW) to reconstruct animal sizes from fossil data.

However, because the male and female models presented a slightly different intercept and slope (Fig. 3), the body size reconstructions were performed separately for each sex. The variation range of the samples was studied taking into account all individuals as well as the means of all the levels studied (Barranco León Levels D1 and D2; Fuente Nueva 3 Levels 5 and 6). The same analysis was replicated within different action ranges to avoid the influence of outliers and confirm the results obtained from the raw data. As expected, the maximum and minimum values of the reconstructed body sizes are higher when looking at the whole dataset than the mean values, which remain constant in both divisions (Table 2). In contrast, body size range is greater when looking at the level division (BL-D1, D2, E; FN3–5, 6) than the entire dataset, with males and females displaying 4.20 mm and 16.09 mm body size ranges, respectively (Table 2). In the dataset as a whole, females present the largest and smallest body sizes, higher mean values, and also a greater body size range than males at both scales (level division and the whole dataset).

In addition, females present a higher standard deviation and coefficient of variation than do males (SDMales = 8.57 / CVMales = 14.79; SDFemales = 11.34 / CVFemales = 18.25). To establish the normality of the female samples, several Q-Q plots were developed (Fig. 4). Subsequently, a Shapiro-Wilk test was performed for the BL-D1 sample due to its poor fit to the reference line in one of the tails of the dataset (Fig. 4). The results of the Shapiro-Wilk test confirm the normality of the data (W = 0.962; p-value = 0.519). Bartlett's test, performed to test the homogeneity of the variance, provided a non-significant p-value (over 0.05), thus confirming the homoscedasticity of our samples. Despite the normality of the data, the differences in sample size between levels led us to select the Welch's t-test to compare the body size means from the different levels, as this test best fits the characteristics of our data. Fig. 5 shows that females are larger in FN3–5, have an intermediate body size value in BL-E and exhibit the lowest body size values in BL-D1 and BL-D2. When performing the Welch's t-test between the most divergent levels, i.e., FN3–5 vs BL-D1/D2 (Table 3), p-values above 0.05 (the significance level) indicate that the differences present in the sample are not statistically significant. This may be due to the great difference in sample sizes between the different levels. The results of the Lubischew's test are summarised in Table 4. The data from all the pairs of samples provide a high degree of overlap. The lowest are those corresponding to females, specifically between the females of FN3–5 and those of the two BL Levels (D1 and D2).

Relationships between body size, productivity and climate

The productivity indicator presents the highest values in BL-D1 and D2, with the Level E values falling between these and those of FN3–5, which has the lowest value (Table 5). The data for the palaeoclimate reconstruction, from Sánchez-Bandera in Serrano-Ramos et al. (2021), indicate that temperature follows the same trend with a noticeable decrease in FN3–5, although its variation within the BL levels is less marked than the productivity indicator.

Table. 1. Distribution of amphibian and squamate remains throughout the stratigraphic sequence of Barranco León and Fuente Nueva 3 (Orce, Spain) in terms of mínimum number of individuals (MNI) (data from Sánchez-Bandera et al., 2020). On the right are the species occurring in the Orce area today (counted as number of field citations), corresponding to those currently registered in the 10 × 10 UTM of the study area (data from the A.H.E. [Spanish Herpetological Association], 2021). At the bottom of the table, richness in terms of herpetological species is expressed as a single number (RICHNESS), with a breakdown of the contribution of amphibians and reptiles, respectively, to that total.

Taxon	**Barranco León**			**Fuente Nueva 3**	**Orce**
	Level D1	**Level D2**	**Level E**	**Level 5**	
Amphibia, Anura					
Bufotes viridis s.l.	1				
Discoglossus sp.	13	22	16	11	
Discoglossus galganoi					1
Epidalea calamita	1	1	1		
Hyla sp.	1				
Pelobates cultripes	1	1	1	2	13
Pelodytes punctatus					6
Pelophylax cf. *perezi*	28	50	18	23	15
Squamata, Amphisbaenidae					
Blanus cinereus					3
Squamata, Lacertidae					
Lacertidae indet.	1	1	1	2	
Acanthodactylus erythrurus					3
Ophisaurus sp.	1	1	1		
Podarcis hispanica					10
Psammodromus algirus					11
Psammodromus edwardsianus					1
Psammodromus hispanicus					9
Tarentola mauritanica					2
Timon lepidus					11
Squamata, Scincidae					
Chalcides bedriagai					2
Squamata, Serpentes					
Colubrinae indet.	2			1	
cf. *Coronella* sp.	1	1	1		
Hemorrhois hippocrepis					3
Malpolon monspessulanus	1		1	1	6
Natrix maura	1	1	1	1	4
Natrix natrix s.l.	1	1			
Zamenis scalaris	1	1			6
RICHNESS	14	10	9	7	17
Amphibian richness	6	4	4	3	4
Squamate richness	8	6	5	4	13

Table. 2. Body sizes (expressed in mm) of male and female *Pelophylax perezi*, both for the entire dataset and considering the mean values of all the levels studied from the Fuente Nueva 3 (Levels 5 and 6) and Barranco León (Levels D1 and D2) sites. Maximum (Max), minimum (Min), mean and variation range (Range) values are expressed.

	Entire dataset				**Mean by levels**			
	Max	**Min**	**Mean**	**Range**	**Max**	**Min**	**Mean**	**Range**
♀	**89.1**	**40.8**	**62.2**	**48.3**	**69.6**	**53.5**	**62.0**	**16.1**
♂	**85.3**	**42.9**	**57.9**	**42.4**	**61.1**	**56.9**	**58.4**	**4.2**

Finally, precipitation data show a divergence from the previous eco-climatic pattern as the values within the BL levels peak in Level E, are intermediate in Level D2, and present the lowest value for this site in Level D1. On the other hand, for FN3–5, the precipitation values follow the pattern of the other eco-climatic parameters, with this level presenting the lowest values. To determine any possible relationships between female body size and productivity, an OLS simple regression model was constructed and yielded the following result: Adj.$r^2 = 0.891$; p-value = 0.037; slope = -0.22; D.f = 2. This reveals a marked negative relationship between the two variables, meaning that as productivity increases, female body size decreases. We confirmed this using a Pearson correlation test, which shows the strength of the negative correlation between these two variables (Correlation coefficient = -0.963; T = -5.056; p-value = 0.037; D. f = 2).

In terms of the relationship between female body size and climate, OLS regression models yielded no conclusive results (p-value >0.05). These outcomes are not unusual for samples in which only a few observations are available, although it is worth noting that in the warmest periods, related to BL-D1 and D2, female body sizes were smaller, while the largest body size recorded came from FN3–5, which corresponds to the coldest period (Fig. 5).

2.5. DISCUSSION

Richness data

The richness values calculated for the BL and FN3 levels are consistent with the palaeoclimate reconstructions (Table 1; Fig. 5). The fact that amphibians and reptiles follow the same trend, increasing or decreasing in richness in almost identical proportions in all levels (Table 1), indicates that external factors condition richness values to the same extent in both groups and at two different scales, as an entire community and at the group level. Sub-humid conditions during the late Early Pleistocene around the Baza palaeo-lake, warmer and more humid than today, probably supported a great diversity of species of both amphibians and reptiles.

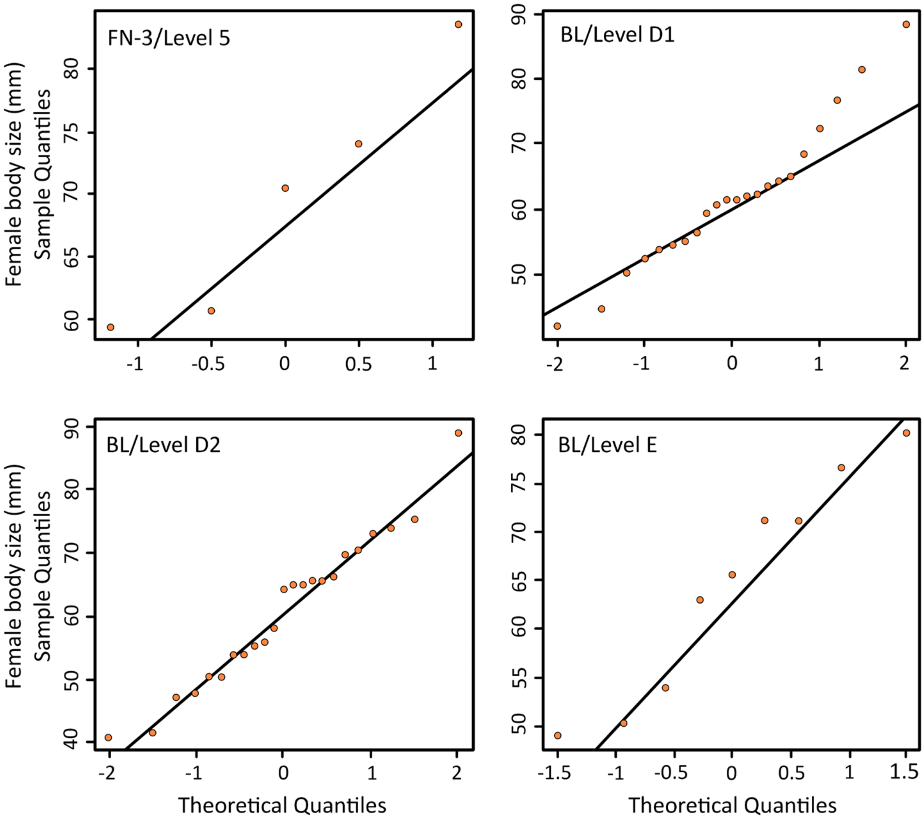

Figure. 4. Normality test quantile-quantile plots (Q-Q plots) for the female body size samples corresponding to the main levels studied (Fuente Nueva 3, Level 5, and Barranco León Levels D1, D2 and E).

Despite the higher aridity levels, the current overall richness of the area exceeds the maximum recorded in BL-D1, which is most likely due to the distinct sampling method. In addition, there are major differences in the assemblage structures between the two samples. Indeed, the current assemblage primarily comprises reptile species, with only a few amphibians (Table 1). The increased aridity at the present time (as well as the change in the hydrographic regime of the Guadix-Baza Basin compared to late Early Pleistocene conditions) represents a major barrier to the establishment and development of amphibian taxa, which generally require water sources for reproduction and are very susceptible to evaporative water loss through their mucosal skin. In general terms, periods with greater productivity, such as BL-D1 and BL-D2, support a higher number of species, which makes sense given that increased resource availability allows the ecosystem to maintain various habitats.

Additionally, the lower precipitation and temperature values correspond to the low richness found in FN3–5 and, in general

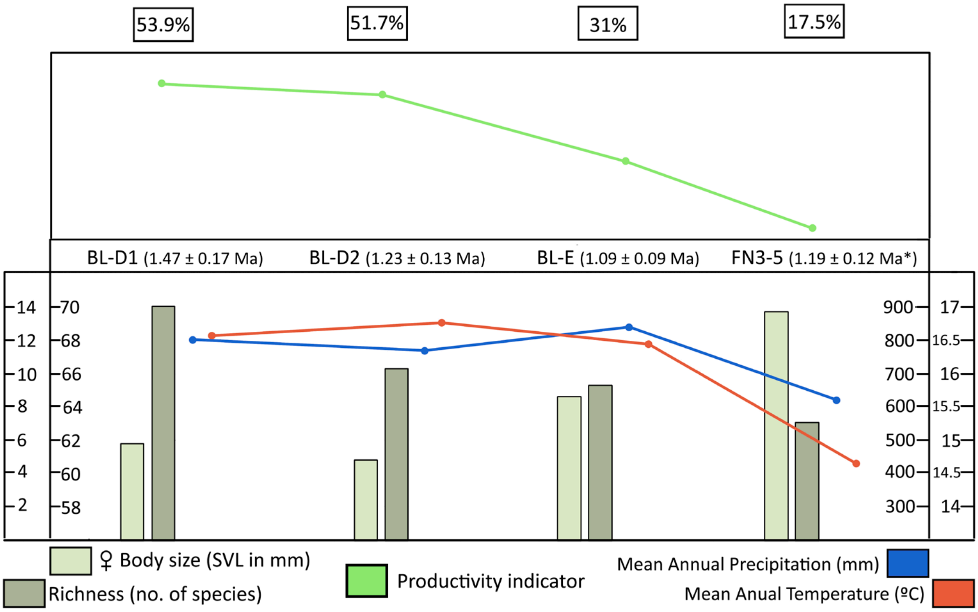

Figure. 5. Comparison of body size, species richness and productivity indicator for the composite Early Pleistocene succession of BL and FN3 (Guadix-Baza Basin, SE Spain). Age for each level is presented (*Nevertheless, it is assumed from a stratigraphical point of view that E1 is very close to D2). Temperature (mean annual temperature in ◦C) and precipitation (mean annual precipitation in mm) values are from Sánchez-Bandera in Serrano-Ramos et al. (2021). The productivity indicator percentage is also presented by level, together with female *Pelophylax perezi* body size in mm, as SVL (snout-to-vent length), and richness (number of species).

terms, the increased climate values are reflected in the higher diversity seen in the BL levels. This pattern of wetter, warmer, and more productive ecosystems having a higher degree of biodiversity, always conditioned by upper thresholds mainly in terms of temperature values, has been widely reported in the literature (see Gaston, 2000, for an overview).

Study of body size

The data available for *P. perezi* indicate that the maximum body size recorded in Spain for this species is a SVL of 85 mm in males and 110 mm in females, while average body size values are 49.36 mm and 59.75 mm SVL in males and females, respectively (Egea-Serrano, 2014). The mean body size of *P. perezi* individuals in the Guadix-Baza Basin sites are slightly higher than the average body size values recorded for Spain, both for males and females (Table 1). Moreover, there is clear female-biased sexual dimorphism in terms of body size.

The body size variability ranges in the BL and FN3 populations differs for male and female specimens, with the values for the females in all cases higher than those for the males. The difference is less obvious when looking at the entire dataset (i.e., all individuals of each sex), but much more evident when considering the analysis by levels (4.2 mm in males and 16.09

mm in females). Furthermore, the standard deviation and coefficient of variation are consistent with these data, indicating that females exhibit a greater variation in body size, making them more suitable subjects for this study as their body size changes are more easily detectable than those in males. For the genus *Pelophylax*, several studies have reported greater variation in female body size in current populations (Lou et al., 2012; Gül et al., 2014; Erismis, 2018). This is in agreement with previous studies of fossil (Martínez-Monzón et al., 2018) and recent (Hemelaar, 1988; Schäuble, 2004; Leskovar et al., 2006; Reading, 2007; Lou et al., 2012) anurans, indicating that external factors have a greater influence on females and the existence of a sexually dimorphic response in terms of body size change. In all these studies, a fecundity-related hypothesis has been proposed to explain this pattern, linked to the greater energy investment in reproduction by female anurans. The largest females in the levels we analysed were found in FN3–5, intermediate sizes were in BL-E, and the smallest body sizes were recorded in BL-D1 and BL-D2.

Although the results of the Welch's t-test for the difference of means were not conclusive (possibly due to the high divergence in sample sizes), the differences in mean female body sizes between the levels merits discussion: the coefficients of variation (CV) of both sexes from FN3–5 (CVMales = 12.12; CVFemales = 14.30) are lower than those from BL-D1 (CVMales = 18.95; CVFemales = 17.96) and BL-D2 (CVMales = 12.40; CVFemales = 19.67). This is an intriguing result because the CV is highly dependent on sample size (Cope and Lacy, 1992; Foote, 1993); thus, the larger the sample, the lower the CV tends to be. In the case of FN3–5, even though this sample involves the lowest number of observations, it presents the lowest CV. These results permit us to strongly infer that colder and less humid climate conditions denote less body size variation in both sexes.

On the other hand, the Lubischew's test results indicate that all the mean comparisons present enormous overlap. However, two pairs of samples show the least overlap, with close to 70%: BL-D1♀/FN3–5♀ (71.88%); and

Table. 3. Results of the Welch's t-test of difference of means between Level 5 at Fuente Nueva 3 (FN3) and Levels D1 and D2 at Barranco León (BL). The value of the statistic (t) is presented, as are the degrees of freedom and the significance level (p-value).

Sites	Welch's t-test		
	T	Degrees of freedom	p-value
FN3-5 vs BL-D1	**1.571**	**6.474**	**0.164**
FN3-5 vs BL-D2	**1.733**	**6.78**	**0.128**

Table. 4. Results of the Lubischew's test. K expresses the coefficient of determination (Lubischew, 1962).

♂	$\sqrt[2]{K/2}$	% Overlap	♀	$\sqrt[2]{K/2}$	% Overlap
BL-D1/FN3-5	**0.06**	**95.21**	**BL-D1/FN3-5**	**0.36**	**71.88**
BL-D2/FN3-5	**0.03**	**97.61**	**BL-D2/FN3-5**	**0.38**	**70.04**
BL-D1/BL-D2	**0.09**	**92.82**	**BL-D1/BL-D2**	**0.04**	**96.81**

BL-D2♀/FN3–5♀ (70.04%). This could be interpreted to mean that the most marked differences in *P. perezi* body size are those found in the FN3–5 females compared to those of the two BL Levels (D1 and D2). Nevertheless, we must add two cautionary notes, as (1) even for the two abovementioned pairs the overlap is large (>70%), and (2) there is a considerable difference in the number of observations between the two levels due to the scarcity of FN3–5 material.

Climate and productivity

Palaeoclimate reconstruction (Sánchez-Bandera in Serrano-Ramos et al., 2021) and the productivity indicator suggest colder and less humid climate conditions and a less productive ecosystem in FN3–5 (Table 5; Fig. 5). The temperature and precipitation values are the lowest in this level, which agrees with previous data that identified FN3–5 as the most arid of the studied samples within the Early Pleistocene climate cyclicity of the Guadix-Baza Basin (Sánchez-Bandera et al., 2020). Nevertheless, the climate reconstruction for the late Early Pleistocene of the Guadix-Baza Basin suggests that the conditions were generally warmer and more humid than those recorded in the area today (Table 5). In contrast, within the BL levels, eco-climatic parameters indicate that BL-D1 and BL-D2 were quite similar in terms of temperature and productivity, although they differed slightly in terms of precipitation (Table 5).

These two levels appear to reflect the warmest periods, with a higher energy intake by the ecosystem, enabling the greater primary productivity seen in the studied samples. Finally, BL-E is presented as an intermediate step between BL-D1/D2 and FN3–5. Female *Pelophylax perezi* body size shows a clear trend towards increased body size in cooler and less productive periods (in terms of primary productivity of the ecosystem). This pattern is consistent with the predictions of Bergmann's rule, which establishes that larger species would occupy colder areas due to their higher heat conservation capacity promoted by their low surface-to-volume ratio (Bergmann, 1848). Although in ectothermic vertebrates such as amphibians no consensus has yet been reached about the adhesion to this pattern (Ashton, 2002), it is evident in this case, as the females are smaller in BL-D1 and D2, an intermediate size in BL-E, and larger in FN3–5, the level representing the coldest period of all the levels studied (Fig. 5). Possible mechanisms involved in such a pattern are discussed in the following section.

Global integration of results

In the dataset presented, female body size, richness and eco-climatic values have demonstrated a complex interrelationship, giving rise to several hypotheses which can contribute to explaining our results. However, due to the correlational nature of our study, these mechanisms often cannot be confirmed, only hypothesised, in contrast to the patterns which are clearly detectable. The data presented in this study suggest that the main eco-climatic parameter conditioning female body size is primary productivity, as this has a statistically significant correlation. This does not, however, mean that temperature and precipitation have no influence on female body size, as these variables are closely linked to primary productivity (Gaston, 2000; Smith and Smith, 2001) and this, in turn, is directly related to species richness. Despite the great extension of the heat-conservation hypothesis to justify Bergmann's clines, temperature does not seem the most likely explanation in our case. This is because during the Early Pleistocene in the study area, temperature variations were not as severe as the changes in aridity and resource availability caused by a decrease in plant diversity (Altolaguirre et al., 2021), one of the main limiting factors for species distribution.

In addition, no thermoregulatory behaviour has been described for *P. perezi* (Egea-Serrano, 2014); however, in the Canary Islands it has been reported that for a few months of the year adult individuals of this species

Table. 5. Palaeoclimate values for the Guadix-Baza sites: BL (Barranco León) and FN3 (Fuente Nueva 3). Palaeoprecipitation, shown as mean annual precipitation (MAP), and palaeotemperature, shown as mean annual temperature (MAT), are presented in mm and ◦C, respectively (Sánchez-Bandera in Serrano-Ramos et al., 2021). To the right, current climate data (1970–2000) for the Orce area (from WorldClim version2, Fick and Hijmans, 2017). In addition, the productivity indicator is also shown as the combination of the woodland and open-humid percentages from the environmental reconstruction (Sánchez-Bandera et al., 2020).

	Guadix-Baza sites				**Orce**
Eco-Climatic parameters	**BL-D1**	**BL-D2**	**BL-E**	**FN3-5**	
MAP (mm)	**767.31**	**792.77**	**834.74**	**617.65**	**437.29**
MAT (°C)	**16.77**	**16.75**	**16.45**	**14.65**	**12.89**
Productivity indicator	**53.9%**	**51.7%**	**31%**	**17.5%**	

seek refuge under rocks where there is still moisture (Báez and Luis, 1994; Egea-Serrano, 2014). In the Canary Islands, temperature does not vary greatly throughout the year, so the rainfall regime and aquatic habits of this species seem to trigger this water-conserving behaviour. Despite the lack of precedents relating to the species studied here, previous work on the genus has reported larger body sizes in more arid locations (Amor et al., 2010; Mohammadi et al., 2015), pointing to water conservation as having a greater influence than heat conservation on this species. Based on the same physical principle as Bergmann's heat conservation mechanism (i.e., surface-to-volume ratios), the water-availability hypothesis (Olalla-Tárraga and Rodríguez, 2007) establishes that larger amphibians would have an advantage in more arid environments because of their increased desiccation resistance.

Our observation of larger females being present in Level FN3–5, which also yielded the lowest precipitation values, is in line with this hypothesis. At the same time, precipitation and plant productivity in the ecosystem (which are closely related) have been shown to have a negative relationship to body size, with larger females being found in levels reflecting lower primary productivity. The most likely explanation for this pattern involves a fecundity-related argument: Despite the higher energy intake of the ecosystem, which translates into increased primary productivity and more resources, females do not need to store fat or increase in size before sexual maturity, thus increasing fecundity (Tejedo, 1992; Atkinson, 1994) as opportunities for successful reproduction are plentiful. Instead, females can balance their reproductive success by increasing their fecundity with an extended breeding season, thus producing more clutches per year.

In other words, no energy has to be invested into increasing survival and reproductive success by increasing body size, as the favourable climate conditions and abundant resources provide other feasible options. In contrast, larger female body sizes are observed in FN3–5, the level with the lowest values for temperature, humidity and plant productivity. In this case, the opposite reproductive strategy can be assumed: Harsher environmental conditions and fewer resources delay sexual maturity, making it possible for females to attain a larger size, thus increasing their fecundity (Atkinson, 1994; Morrison and Hero, 2003).

In addition, the shorter activity period and breeding season promotes the production of larger clutches and larger eggs by anuran females (Morrison and Hero, 2003). This investment in reproduction is possible due to the fat storage and larger female body sizes developed during periods with less favourable environmental conditions, decreased primary productivity, and fewer resources, such as those evidenced in FN3–5, in order to increase possibilities of successful reproduction.

Furthermore, during periods when the ecosystem is more productive, inter- and intraspecific competition can play a key role in energy allocation and the development of *P. perezi* individuals. In all the levels studied, richness and female body size exhibit an inverse pattern (Fig. 5), with BL-D1 and BL-D2 being the levels with the highest values of richness and the smallest female body sizes. These levels also represent times of greater primary productivity and warmer and more humid environmental conditions. It therefore seems possible that an elevated number of species gave rise to increased competition, generating a trade-off for *P. perezi* females between growth and reproduction. Even though *P. perezi* has proved to be an excellent competitor, both as an adult and at the larval stage (Egea-Serrano, 2014), earlier sexual maturity is an advantage in an extended breeding season where other anuran species will be occupying the water bodies, thus increasing competition between larvae. In other words, in the presence of sufficient resources, promoted by increased primary productivity and suitable environmental conditions, quantity and not quality is prioritised.

Additionally, intraspecific competition is not the only limitation in resource-rich ecosystems. Higher population densities, predation, and disease may also constrain somatic growth, thus favouring earlier sexual maturity. Finally, amphibians and reptiles, similarly to plants, are known to be very sensitive to changes in local climate and environmental conditions. In this study, this pattern seems to be apparent, as the loss of both arboreal cover and diversity during the Early Pleistocene glacial periods in the region (Altolaguirre et al., 2021) roughly correlates to decreased herpetofaunal richness. Thus, as a reflection of local environmental conditions small vertebrates may represent an interesting proxy as an indirect measure of overall resource availability for secondary consumers, such as Early Pleistocene hominin communities inhabiting the surroundings of the Baza palaeo-lake.

Variations in resource availability may have resulted in periods of higher competition among the members of the carnivore guild, including *Homo* sp. (see Rodríguez-Gómez et al., 2016). As suggested by Altolaguirre et al. (2021), increased aridity and decreased plant productivity may have forced hominin communities inhabiting the Orce region to seek resources in more steppe-like environments and mountainous regions, while during more humid phases, open Mediterranean woodlands, marshland, and lake systems provided access to a great variety of plant and animal resources. In contrast, waterfrogs have much more reduced dispersal abilities, and were therefore forced to adapt in situ to the new less favourable conditions, with females attaining larger body sizes, thus providing a new method for reconstructing the environments inhabited by these humans.

2. 6. CONCLUSIONS

1. Species richness at all scales (as an entire community and at the group level) reached maximum values during periods with greater plant productivity according to productivity indicator data, which coincided with warmer and more humid conditions (with the exception of Level BL-E). Both amphibians and reptiles followed the same trend in variation, thus indicating an equivalent influence of external factors.

2. Females of the species *Pelophylax perezi* exhibit a greater body size range than males, allowing variations within different climate periods to be easily detected. Differences in female body size by level are not statistically significant, probably due to the great difference in sample sizes. Even so, the coefficient of variation and overlap analysis, as well as the clear eco-climatic influence on this parameter, indicate that net differences in female body size should not be ignored.

3. Female body size negatively correlates with primary productivity. Although other climate variables show no statistically significant correlations, their influence cannot be dismissed as they are closely linked to primary productivity. On the other hand, female body size follows a Bergmann's cline; maximum sizes are attained during the coldest periods. A combination of the water-availability hypothesis, the fecundity-related hypothesis, and higher intra- and interspecific competition are proposed to explain female body size variation in relation to eco-climatic parameters. However, due to the correlational nature of our work, the mechanism behind these patterns can only be hypothesised, even though the patterns themselves are clear.

4. The study of fossil amphibian body size, herpetofaunal richness, and the relationship between these and climate parameters can be used as an indicator of ecosystem conditions, which, combined with other environmental and climatic proxies, can contribute to reconstructions of the Pleistocene ecological and climate context in which human dispersal events took place.

Supplementary data to this article can be found online at https://doi. org/10.1016/j. palaeo.2021.110752.

Declaration of Competing Interest

Authors who have participate in the development of this work declares no conflict of interest.

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SUPPLEMENTARY MATERIAL

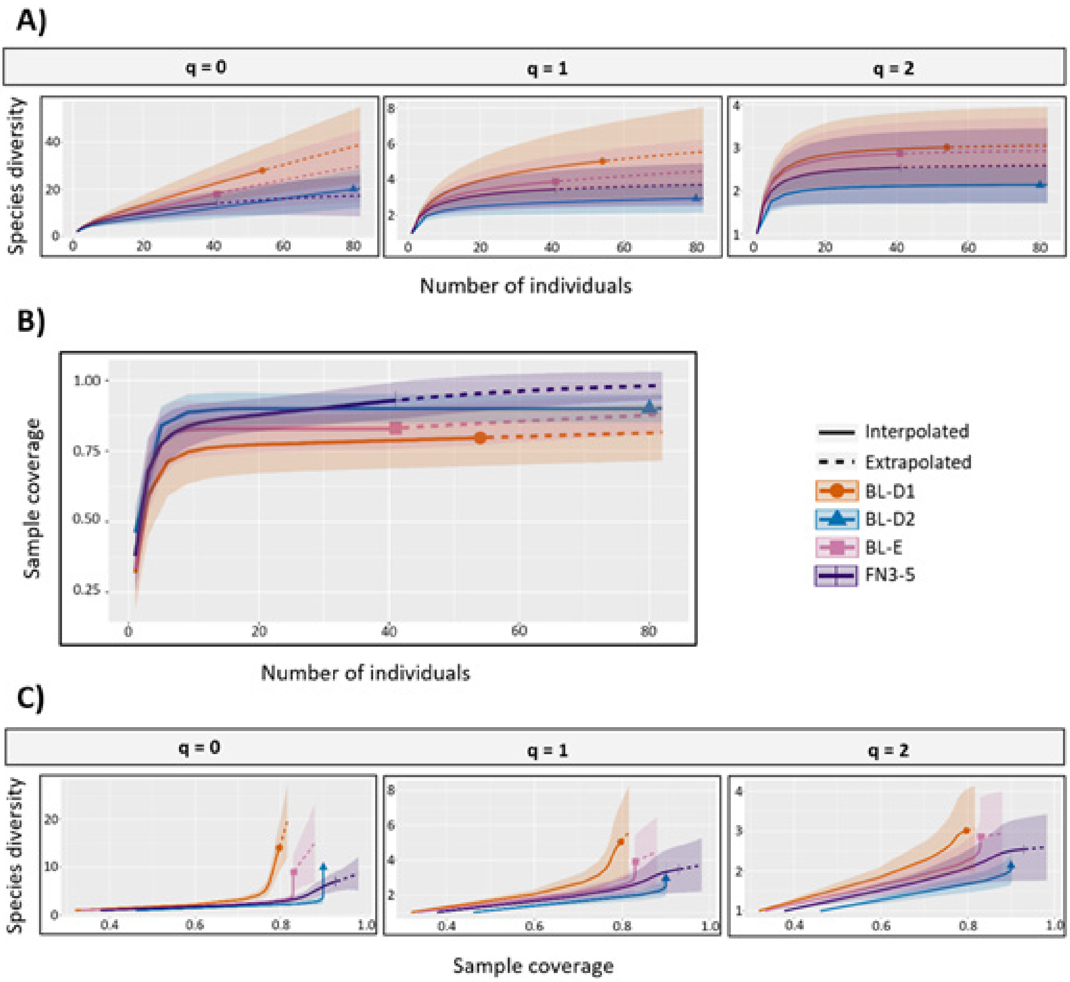

Figure S1: (**A**) Sample-size-based and (**C**) coverage-based rarefaction (solid segment) and extrapolation (dotted line segments) sampling curves with 95% confidence intervals (shaded areas) for the herpetofaunal data of Levels D1, D2 and E from BL and Level 5 from FN3, separately by diversity order: q=0 (species richness, left panel), q=1 (Shannon diversity, middle panel) and q=2 (Simpson diversity, right panel). The solid dots/triangles represent the reference samples. (**B**) Sample completeness curves linking curves in (**A**) and (**C**).

Table S1. Raw data from the Pelophylax perezi humeri of Guadix-Baza Basin sites. Humerus number, sex and laterality are indicated together with the site of which each humerus comes from and the year of excavation. Finally, in the last column, Humeral Total Width measurement (HTW) is provided in mm.

H(humerus) X(number) M-F(sex)/ L-R(laterality)	Site	Year of excavation	Level	HTW (mm)
H1M/R	FN3	2011	5	2.25
H2M/L	FN3	2011	5	3.13
H3M/L	FN3	2011	5	2.97
H4M/R	FN3	2011	5	3.28
H5F/L	FN3	2011	5	3.47
H6F/R	FN3	2011	5	3.03
H7F/R	FN3	2011	5	3.63
H8M/R	FN3	2014	5a	2.97
H9F/R	FN3	2014	5a	2.97
H10F/R	FN3	2014	5a	4.06
H11M/L	FN3	2017	5b	2.81
H12F/L	FN3	2017	6	2.88
H13F/R	FN3	2017	6	2.53
H14M/L	BL	2013	D1	2.78
H15M/L	BL	2013	D1	2.56
H16M/L	BL	2013	D1	3.34
H17M/L	BL	2013	D1	3.25
H18M/R	BL	2013	D1	2.25
H19M/R	BL	2013	D1	2.63
H20M/R	BL	2013	D1	2.69
H21M/R	BL	2013	D1	2.41
H22F/L	BL	2013	D1	2.78
H23F/L	BL	2013	D1	2.31
H24F/L	BL	2013	D1	3.06
H25F/L	BL	2013	D1	2.66
H26F/L	BL	2013	D1	2.19
H27F/L	BL	2013	D1	3.75
H28F/L	BL	2013	D1	3.38
H29F/L	BL	2013	D1	2.84
H30F/R	BL	2013	D1	3.06
H31F/R	BL	2013	D1	2.97
H32F/R	BL	2013	D1	2.75
H33F/R	BL	2013	D1	3.09
H34F/R	BL	2013	D1	3.56
H35M/R	BL	2010	D1	2.75
H36F/L	BL	2010	D1	3.16
H37F/R	BL	2011	D1	3.19
H38F/L	BL	2011	D1	2.72
H98M/L	BL	2011	D1	4.34
H99F/L	BL	2011	D1	3.97
H100M/R	BL	2011	D1	3.13
H101M/R	BL	2011	D1	3.38
H102F/L	BL	2011	D1	3.10
H103F/L	BL	2011	D1	4.28

H(humerus) X(number) M-F(sex)/ L-R(laterality)	Site	Year of excavation	Level	HTW (mm)
H104F/L	BL	2011	D1	2.56
H105F/R	BL	2011	D1	3.22
H106F/R	BL	2011	D1	3.03
H39M/L	BL	2011	D2	2.66
H40M/L	BL	2011	D2	3.84
H41M/L	BL	2011	D2	2.69
H42M/L	BL	2011	D2	3.09
H43M/L	BL	2011	D2	2.34
H44M/R	BL	2011	D2	3.00
H45M/R	BL	2011	D2	2.69
H46M/R	BL	2011	D2	2.72
H47M/R	BL	2011	D2	2.69
H48M/R	BL	2011	D2	3.03
H49M/R	BL	2011	D2	2.16
H50M/R	BL	2011	D2	2.94
H51F/L	BL	2011	D2	2.91
H52F/L	BL	2011	D2	3.22
H53F/L	BL	2011	D2	2.41
H54F/L	BL	2011	D2	2.72
H55F/L	BL	2011	D2	2.56
H56F/L	BL	2011	D2	3.19
H57F/L	BL	2011	D2	4.31
H58F/L	BL	2011	D2	2.16
H59F/L	BL	2011	D2	2.44
H60M/L	BL	2011	D2	3.22
H61F/R	BL	2011	D2	2.81
H62F/R	BL	2011	D2	2.72
H63F/R	BL	2011	D2	3.22
H64F/R	BL	2011	D2	3.63
H65F/R	BL	2011	D2	3.28
H66M/R	BL	2011	D2	3.41
H67M/R	BL	2011	D2	3
H68M/L	BL	2011	D2	3.06
H69M/L	BL	2011	D2	2.59
H70M/L	BL	2011	D2	2.63
H71F/L	BL	2011	D2	3.25
H72F/R	BL	2011	D2	2.13
H73F/R	BL	2011	D2	2.78
H74F/R	BL	2011	D2	3.69
H75F/L	BL	2010	D2	3.44
H76F/L	BL	2010	D2	3.47
H77F/L	BL	210	D2	3.59
H78M/R	BL	2013	D2	3.06
H79M/R	BL	2013	D2	2.84
H80M/R	BL	2013	D2	2.81
H81F/R	BL	2013	D2	3.25
H82F/L	BL	2013	D2	2.56
H83F/R	BL	2013	E	2.56
H84M/L	BL	2010	E	4.06
H85M/L	BL	2010	E	2.69
H86M/R	BL	2010	E	2.63
H87M/R	BL	2010	E	3.38

H(humerus) X(number) M-F(sex)/ L-R(laterality)	Site	Year of excavation	Level	HTW (mm)
H88M/R	BL	2010	E	2.84
H89M/R	BL	2010	E	2.97
H90F/L	BL	2010	E	3.50
H91F/R	BL	2010	E	2.72
H92F/R	BL	2010	E	2.50
H93F/R	BL	2010	E	3.75
H94F/R	BL	2010	E	3.13
H95F/R	BL	2010	E	3.91
H96F/R	BL	2010	E	3.25
H97F/R	BL	2013	E	3.50

Part 3.
Pliocene Konservat-Lagerstätte of Camp dels Ninots

3.

INFERRING ECO-CLIMATIC PARAMETERS FOR THE PLIOCENE CLIMATIC OPTIMUM USING FROG BODY SIZE AS A NEW PROXY

Inferring past conditions from anuran body size

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

The study of the climatic conditions of the Pliocene Climatic Optimum (3.2 – 2.5 Ma) is a relevant issue due to its proposed correspondence with future climate. The obtention of terrestrial temperatures for this period present several difficulties and new sources of information are significant. In this work a new approach based on frog's body size is proposed thus providing a palaeoclimatic reconstruction for the palaeontological site of Camp dels Ninots (Caldes de Malavella, NE Spain), a Pliocene Konservat-Lagerstätte, dated around 3.2 Ma. For this purpose, an extensive database of current populations of genus Pelophylax across Eurasia has been generated making possible to establish a correlation between waterfrogs' body size and eco-climatic parameters as temperature, precipitation and real evapotranspiration. Eco-climatic values have been obtained by means of OLS regression models and also confronted to previous palaeoclimatic reconstructions of other archaeo-palaeontological sites of interest (Barranco León and Fuente Nueva 3, SE Spain). Our new proxy comes up with a palaeotemperature of 14.3 ± 2.6°C and a palaeoprecipitation of 846.8 ± 165.4 mm and, according to primary productivity values, a "Summer-green broad-leaved forest" biome-like is proposed for Camp dels Ninots, in agreement with previous palaeobotanical studies. Regarding to the new values generated for the other sites, the same trend than previous reconstructions is followed, despite with lower values in most cases, especially for temperature. This new methodology rises as a promising approach to complement former palaeoclimatic reconstructions and also to generate new data.

Amphibians; Pelophylax; Primary productivity; Palaeoclimate; Camp dels Ninots; Spain

3.1. INTRODUCTION

Pliocene climate is of great interest due to its likely correspondence with future climate. Concretely, mid-Piacenzian climate is the most recent period in Earth's history which reveals quite similar temperatures to the ones projected for the end of the 21st century (Robinson et al., 2008; Dowsett et al., 2013). Also, this period known as the Pliocene climatic optimum (3.2 to 2.5 Ma) is similar to today in many aspects as the position of the continents and oceans, the intensity of sunlight reaching the earth surface or CO_2 atmospheric concentrations, for example (Robinson et al., 2008). Specifically, for the middle Pliocene (ca. 3 Ma) a less seasonal climate 5°C warmer than present and 400-1000mm/year wetter has been proposed for the European and Mediterranean region (Haywood et al., 2000).

With the aim of reconstructing past climates several methodologies for this and other geological periods have been developed, no one exempt of difficulties (Blain et al., 2018a). There are quite a few alternatives for reconstructing terrestrial temperatures and precipitation during Pleistocene period as most species have extant representatives, but the options draw drastically when the line of Pliocene is crossed. Body size-metabolic rate approaches upon poikilothermic animals 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 provide significant information about the equatorial climates during this period. This kind of approach complements other palaeoclimatic reconstructions as those ones derived from planktonic foraminifer oxygen isotopes or palaeofloras (Head et al., 2009). As the main weak point of this kind of analysis, still the fact that the validity of the use of the living relatives instead of the same species as a reference point for the palaeoclimatic reconstruction remain unclear. There still a 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 in poikilotermic body size but avoiding the use of relative species as a current analogue. This Pliocene site, chronologically placed by different methodologies into the mid-Piazencian during the Pliocene climatic optimum, presents a reduced biodiversity with only two anuran taxa: a representative of the genus *Pelophylax* and only one remain pertaining to the common toad (*Bufo* gr. *B. bufo*). In this case, there is no need to include related taxa in the methodology as the genus *Pelophylax* appears in southern Germany during the Early Oligocene (Sanchiz et al., 1993) and it is maintained until our days. *Pelophylax* is a widespread genus of green frogs with a current distribution around Eurasia and north Africa. This genus, known as "paleartic water frogs", counts with a high number of species and also with hybridogenic complexes. As pointed by its common name, *Pelophylax* is a group of frogs very abundant and strongly linked to water environments. For these reasons, this group of waterfrogs has a potential to fossilize in ponds, lakes and other aquatic environments as it happens in Camp dels Ninots and other konservat-lagerstätte as the Miocene Libros site (Teruel, central Spain) (McNamara et al., 2012).

In the Iberian Peninsula, the use of amphibians and reptiles as environmental proxies is widely extended during the Quaternary as these organisms are pretty sensitive to climatic and environmental variations (see for example Blain et al., 2008, 2009, 2016; Martínez-Monzón et al., 2018a, 2018b, 2021, 2022) besides, the current ecological niche of amphibian communities has been proved to constitute an excellent analogue to those ones in the past thus leading to accurate reconstructions of palaeoclimatic conditions (Lobo et al., 2016). By other side, most of the amphibian species found in European Pleistocene assemblages are present nowadays as this group has shown a conservative behaviour during Neogene and Quaternary (Delfino, 2005). That is an indication of the capacity of this group to cope with the successive climatic and environmental variations that took place during this period by changing bio-ecological features and adapting to new conditions (Martínez-Monzón et al., 2018b, 2021).

In particular, body size is one of the main life-history traits used in ecology to evaluate how different biotic and abiotic factors as resources or climate affect amphibian communities both in current populations as in fossil record (Reading, 2007; Lips et al., 2003; Martínez-Monzón et al., 2018a, 2022). This is because in poikilothermic animals as amphibians, body size is involved in a high number of physiological, biochemical and ecological characters of key importance as metabolic rate, fertility, thermoregulatory behaviour, water-conservatism, starvation resistance and much others (Bonner, 2011; Angilletta et al., 2004; Olalla-Tárraga et al., 2009). Regarding to the study of fossil record, previous works have detected a strong relationship between temperature, primary productivity and anuran body size (Martínez-Monzón et al., 2018a, 2022). In these works, body size of anurans increases when temperature decreases and the resources are scarce. Despite the intricacies of the interrelationships between the different variables that influence size changes, current data support the patterns found in those works within the genus *Pelophylax*, directly for temperature (Amor et al., 2010; Gül et al., 2014; Erismis, 2018), and indirectly for primary productivity (Amor et al., 2010; Mohammadi et al., 2015), thus opening a new path in the use of anuran body size as a proxy to infer past climatic conditions.

The use of all available palaeoclimatic proxies for reconstructing past climates reduces the overall error of eco-climatic estimations. With this aim this work assess the impact of climate upon frog body size and presents this biological trait as a valuable proxy in the study of past climates. Body size of *Pelophylax* sp. individuals of Camp dels Ninots will be analysed and the data obtained will be integrated with fossil and current data of *Pelophylax* body size thus providing new insights of eco-climatic reconstruction for this geological period so relevant in the research of future climate. Comparisons of the new data with previous reconstructions for other fossil assemblages as Orce archaeo-palaeontological sites is key to validate this new methodology. The study of these sites makes possible the comparison of both, the use of *Pelophylax* body size as a new proxy and also other consolidated methods as the Mutual Ecogeographic Range (MER).

3.2 .THE SITE: CAMP DELS NINOTS

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). The site is placed in an ancient volcanic area part of the Catalan Volcanic Complex, known as la

Selva Depression, where today still being an important geothermal activity (Vehí et al., 2005). The site consists in a Pliocene palaeolake contained inside a low-relief volcanic crater known as a maar. This lacustrine sedimentation generated an exceptional preservation of vertebrate fauna and flora remains (Gómez de Soler et al., 2012). The stratigraphical sequence of the Can Argilera excavation sector has been divided in four units mainly composed of clays, carbonates and sandstones (Gómez de Soler et al., 2012). Within those divisions, it is in the 2.3 subunit where most palaeontological remains have been found (Gómez de Soler et al., 2012). Greenish laminate clays with diatoms and isolated sandstones and no carbonates built up this section.

The large mammal association suggest that CN should be placed "around the mammals Neogene (MN) 15-16 transition or slightly latter", an age about 3.2 Ma (Gómez de Soler et al., 2012). Also, stratigraphic and palaeomagnetic data points to an age enclosed in the interval of 3.3 to 3.1 Ma (Jiménez-Moreno et al., 2013; Oms et al., 2015).

In general terms, the palaeobotanical studies of CN points to a warm and wet environment which is in accordance with the presence of tapirs (*Tapirus arvernensis*) that 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 in CN indicate a "subtropical type of flora with lauroid leaves of evergreen trees" (Gómez de Soler et al., 2012). The vegetation of the area is characteristic of a broadleaved riparian forest and laurel forest together with the aquatic plants from the lake edge. This association is indicative of a pre-Mediterranean context characteristic of the mid-Piazencian when the end of subtropical ecosystems arrives to give way to the establishment of Mediterranean climate in the Iberian Peninsula (Robles et al., 2013). Estimated temperatures of this geochronological period are 2-3°C warmer than present ones, situation which has been projected for the end of our century (Dowsett et al., 2013). Similar association of such vegetal taxa can be found nowadays at the Canary Islands and in the humid subtropical forest of central Asia (Robles et al., 2013), both environments that display an elevated ecosystem's energy and a high biodiversity.

Regarding to the faunal diversity present in CN, several vertebrate groups are represented as freshwater fishes, amphibians, reptiles, birds and mammals (Gómez de Soler et al., 2012; Přikryl et al., 2016). However, the diversity is rather low and for anurans only two taxa have been documented yet at CN. In Gómez de Soler et al. (2012), fossil waterfrogs were attributed to *Pelophylax* cf. *perezi*, mainly based on biogeographical arguments, but later a biometric study suggested that fossils may rather enter into the variability of *Pelophylax* cf. *lessonae* (Blain et al., 2018b). As the taxonomical attribution has still to be investigated, we refer here these fossils at level of the genus only (*Pelophylax* sp.). As it occurs for anurans, CN is not very diverse for other animal groups as well as for the palaeoflora (Robles et al., 2013). Even though a deep taphonomical study has not been performed yet, the presence of a predominant semi-aquatic anuran may be due to 1) to the taphonomical preservation (more aquatic taxa being preferentially preserved); 2) probably also to the difficulties on the access and/or also to a low light incidence in the lake margins which limits the presence of other anuran species with a less marked aquatic character than genus *Pelophylax*.

3.3 . MATERIAL AND METHODS

The studied material comes from the Can Argilera excavation sector, subunit 2.3 of CN and was recovered during the campaigns from 2005 to 2022. This material consists in disarticulated bone elements directly collected in situ in the excavation. In concrete, the skeletal element used for this work is only the humerus, as it presents a high correlation with the body size of living individuals and also it makes possible to establish the sex (Martínez-Monzón et al., 2018a, 2022). Articulated frogs have not been included in this work because in most cases the orientation or visibility of their humeri prevent any measurements to be done. Additionally, SVL is not directly measurable on those articulated specimens, as raised by Sanchiz (1977), the flattening of specimens during fossilization may have altered the original shape of the frogs.

Regarding methods, the reconstruction of frog body sizes from CN was done following the methodology proposed by Martínez-Monzón et al. (2022). This method consists in measuring the total width of the humeral distal epiphysis and then obtain the body size as SVL (Snout to Vent Length) by means of an OLS regression model whose 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).

In order to construct a relational database including the body size of current populations of the genus *Pelophylax* across Eurasia and their associated climatic parameters, an exhaustive bibliographic search has been performed mainly in Scopus, Google Scholar, and Researchgate databases (Fig. 1; Table 1). Only papers with the biometric data 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) have been extracted from the climatic layers of WorldClim v. 2.1 with 30-arc seconds resolution grid (Fick and Hijmans, 2017). A buffer of 20 km was created around populations' geographical data (points) in order to obtain more representative and accurate climatic values. The same climatic parameters were calculated for Caldes de Malavella nowadays (1970-2000). Data sets were processed using the ArcGIS v. 10.3 application (ESRI, 2014). The mean and standard deviation were calculated using the statistical software IBM SPSS Statistics 22 (IBM Corp. Released, 2013).

In relation to primary productivity, real evapotranspiration (RET) was obtained using the Turc's formula (Turc, 1961 in Remenieras, 1974) which permits the obtention of evapotranspiration data both in fossil assemblages and in current locations. The conversion of RET values into net primary productivity (NPP) was made by 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 average precipitation also expressed in mm/year and $L = 300 + 25t + 0.05t^3$, being t the mean annual temperature in °C.

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

Montreal model (Box, 1988) which relates NPP (in g C/m^2) with RET (in mm/year).

Integration of body size data of the populations of genus *Pelophylax* across Eurasia and eco-climatic parameters (i.e MAT, MAP and RET) from current and fossil locations was made by means of an OLS regression model. In addition, Pearson correlation test was applied in order to complement the results of the regression models. All the analyses were conducted using the R software (R Core Team) and a significance level of $\alpha = 0.05$.

3.4. RESULTS

In this section the main results of the bibliographic search are translated in the shape of an extended dataset for current populations. On the basis of this database, models are developed in order to apply them to fossil locations and reconstruct past eco-climatic conditions.

Current populations and eco-climatic parameters

A total of 72 populations belonging to several species of genus *Pelophylax* have been analysed (Table 1). These populations belong to 22 different countries of Europe and Asia, from the Azores islands (38°40'N 28°04'O38°40'N 28°04'O) to Japan (36°N 138°E) (Fig. 1).

Major biomes comprised within the studied area include (from north to south): the taiga or boreal forest in Russian populations; Temperate broadleaf and mixed forest in the most part of central and western Europe and eastern Asia (some populations from China nearer to the Pacific Ocean and the ones from Japan);

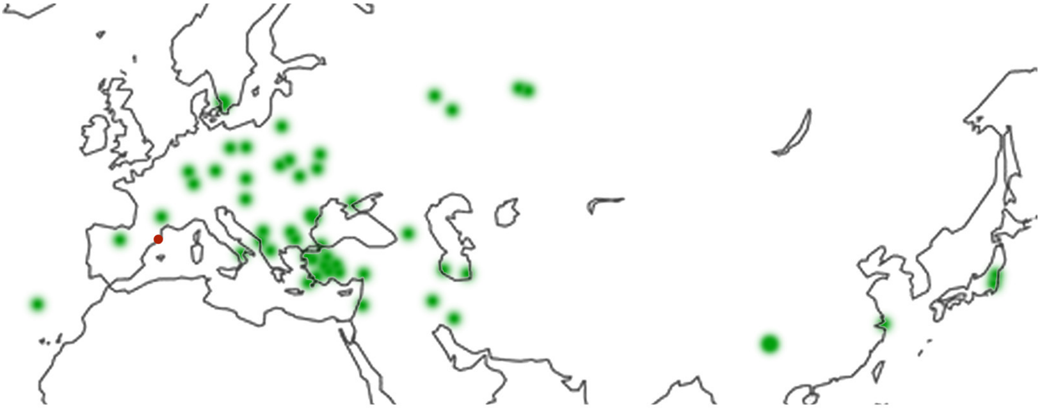

Figure 1. Location of the studied populations of the genus *Pelophylax* across Eurasia. Red circle marks the Camp dels Ninots fossil site (NE Spain). Link to the exact locations and their associated reference number (also in Table 1) in a map from Google maps: (https://www.google.com/maps/d/u/1/edit?mid=12CnCKkAD_BrNM2PQqMe1_qNn-ZgR2oVA&usp=sharing).

Temperate conifer forests in some regions of central Europe; Temperate grasslands, savannas and shrublands within easternmost Europe in populations surrounding Black Sea; Mediterranean forests, woodlands and scrub in the Mediterranean region; and finally desert and xeric shrublands in some populations of Iran (National Geographic Global Biomes map). Within those regions, the temperature range is comprised between 22.8°C in Iran (Sarfaryab) and 2.2°C in Russia (Physma), and precipitation between 1577.50 mm in Japan (Zushi) and 305.7 mm again in Iran (Sarfaryab) (Table 1).

Taking into account these populations of across Eurasia, OLS regression models have been performed between the body size (SVL) of the whole population and three of the most relevant eco-climatic representatives (MAT, MAP and RET). Results of these models are presented in Table 2 and its graphic representation in the Figure 2. All of them resulted significant (p-value under 0.05) and in all cases a negative relationship with the body size was found. Pearson correlation test also came back significative correlation results supporting these models. Despite other fits were tested, the linear model was the one which provides better results for our data. Equations of these models are: $MAT = -0.137SVL + 21.453$; $MAP = -6.318SVL + 1178.388$; $RET = -3.581SVL + 747.656$. MAT and RET models display the higher adjusted R^2 and correlation coefficients while MAP one remains in lower values (Table 2). Even though the non-despicable standard error (MAT ± 2.6 °C; MAP ± 77.9 mm/year; RET ± 165.4mm), a clear trend has been evidenced between these parameters and the SVL of the genus *Pelophylax* over its whole distribution area.

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 methodology from Martínez-Monzón et al. (2022), mean body size of the whole population of frogs from Camp dels Ninots has been established in 52.5 mm being females bigger than males (54.5 mm and 51.2 mm respectively).

After the application of the models generated from the database of current populations (Table 1; Table 2), MAT, MAP and RET have been reconstructed for CN. Regarding to climatic parameters, temperature and precipitation present values of 14.3 ± 2.6°C and 846 ± 165.4 mm respectively. The productivity of the ecosystem as RET, yielded a value of 559.7 ± 77.9 mm/year (Table 3). This latter value has been translated to NPP by means of the Montreal model providing a value of NPP = 550 g C/m^2 per year.

Application to other fossil assemblages: BL and FN3

Regarding to the application of these models to reconstruct past eco-climatic parameters in fossil assemblages based on frog body size, they have also been employed to obtain data for Orce archaeo-palaeontological sites: The three levels of Barranco León (E, D2 and D1) and the level 5 from Fuente Nueva 3, from now on abbreviated as BL and FN3 respectively (Table 3). In all cases, the body size of *Pelophylax* populations has derived in MAT, MAP and RET values.

Within BL and FN3 sites, mean body size of the waterfrogs populations are comprised between the maximum and minimum values of 58.9 mm of BL-D2 and 63.2 mm of BL-E

Table 1. Relation database of the modern studied populations of the genus. The number of individuals (n) and the mean Snout-to-Vent Length (SVL) is presented as the Mean annual temperature (MAT), Mean annual precipitation (MAP) and Real evapotranspiration (RET) according to Turc's formula. References in the first column: [1]Papežík et al. (2021), [2]Zhelev et al. (2017), [3]Lukanov et al. (2014), [4]Wang et al. (2008), [5]Lou et al. (2012), [6]Karaica et al. (2016), [7]Conan et al. (2022), [8]Pille et al. (2021), [9]Tarkhnishvili and Gokhelashvili (1999), [10]Hoffmann et al. (2015), [11]Mayer et al. (2013), [12]Hatziioannou et al. (2022), [13]Tsiora and Kyriakopoulou-Sklavounou (2022), [14]Kyriakopoulou-Sklavounou et al. (2008), [15]Pafilis et al. (2019), [16]Bam-e-Zar et al. (2019), [17]Bam-e-Zar et al. (2020), [18]Fathinia et al. (2012), [19]Rajabi and Javanbakht (2019), [20]Comas et al. (2014), [21]Nakashima et al. (2021), [22]Togane et al. (2018), [23]Disi and Amr (2010), [24]Socha and Ogielska (2010), [25]Hermaniuk et al. (2020), [26]Spigonardi et al. (2012),[27]Balint et al. (2008), [28]Ivanova and Berzin (2019), [29]Svinin et al. (2021), [30]Sánchez-Montes and Martínez-Solano (2011), [31]Christiansen et al. (2010),[32]Erismis (2011), [33]Çiçek et al. (2011), [34]Gül et al. (2011), [35]Arısoy and Başkale (2019), [36]Özcan et al. (2021), [37]Başkale et al. (2017), [38]Alkaya and Şereflişan (2021), [39]Erismis & Chinsamy (2010), [40]Peskov (2019), [41]Stakh et al. (2016), [42]Kuzmin et al. (2020), [43]Reminnii (2007) in Fominykh and Lyapkov (2012),[44]Savchuk (2009) in Fominykh and Lyapkov (2012).

Ref	**Country**	**Locality**	**Species**	**n**	**SVL (mm)**	**MAT (°C)**	**MAP (mm)**	**RET (mm/yr)**
1	Albania	Central plain region	*P. kurtmuelleri*	100	69.4	16	944.4	670.7
1	Albania	Nishaj	*P. shqipericus*	60	53.3	15.4	1321.6	737.8
2	Bulgaria	Vacha River. Krichim	*P. ridibundus*	50	74.5	11.4	546.8	434
3	Bulgaria	Chelopechene	*P. ridibundus*	25	78.9	11.5	489.1	407.6
4	China	Guoju and Qiuai (Ningbo)	*P. nigromaculata*	76	67.7	17.2	1271.7	794.6
5	China	Ningnan County	*P. pleuraden*	63	47.5	14.9	929.3	636.0
5	China	Ningnan County	*P. pleuraden*	42	46.1	14.9	929.6	636.2
5	China	Ningnan County	*P. pleuraden*	36	47.2	15.2	929.2	644.4
5	China	Ningnan County	*P. pleuraden*	52	42.2	15.3	928.7	647
5	China	Ningnan County	*P. pleuraden*	39	47.9	15.2	927.6	644.9
6	Croatia	Bjelovar-Bilogora	*P.* kl. *esculentus*	40	56	11.6	850.7	534.6
6	Croatia	Bjelovar-Bilogora	*P. lessonae*	16	49.6	11.6	850.7	534.6
7	France	Bas-Rhin (Vendenheim)	*Pelophylax* sp.	78	67.1	10.3	713.6	474.8
8	France	Larzac	*P. ridibundus*	736	80	10.3	849.7	504.5
9	Georgia	Borjomi Gorge	*P. ridibundus*	-	89	9	791.8	465.4
10	Germany	Döbern	*P.* kl. *esculentus*	70	70	8.9	649.3	432.4
11	Germany	Bavaria (Ratisbona)	*P.* kl. *esculentus*	61	66.1	8.8	646.7	429.1

11	Germany	Bavaria (Ratisbona)	*P. lessonae*	23	54	8.8	646.7	429.1
11	Germany	Bavaria (Ratisbona)	*P. ridibundus*	63	85.1	8.8	646.7	429.1
12	Greece	Pamvotida Lake. Amfithea	*P. epeiroticus*	85	69.9	12.7	985	591.9
13	Greece	Pamvotida Lake. Ioannina	*P. epeiroticus*	318	78.7	13.4	990.8	612.9
14	Greece	Vistonis Lake (Salpi)	*P. ridibundus*	108	76	13.4	990.8	612.9
1	Greece	Ioannina	*P. epeiroticus*	51	63	14.4	541.8	466.3
15	Greece	Argoni. Karpathos island (Olympos)	*P. cerigensis*	51	42.9	18.4	674.6	591.9
15	Greece	Nati. Karpathos island	*P. cerigensis*	25	37.6	18.4	674.6	591.9
16	Iran	Sarfaryab	*P. bedriagae*	181	47.5	22.8	305.7	315
17	Iran	Sarfaryab	*P. bedriagae*	85	58.8	22.8	305.7	315
18	Iran	Darre-Shahr	*P. ridibundus*	96	73.2	20.9	394.9	395.8
19	Iran	Rasht	*P. ridibundus*	20	67.5	15.5	1187.9	716
19	Iran	Sari	*P. ridibundus*	30	83.4	17.7	661	575
20	Italy	Calabria	*P.* kl. *hispanicus*	114	69.1	17.2	909.4	686.2
21	Japan	District T. Kaminokawa	*P. porosus porosus*	422	55	13.7	1309.1	671.9
21	Japan	District K. Kaminokawa	*P. porosus porosus*	222	60.5	13.7	1309.1	671.9
22	Japan	Hayamajina (Sagamihara)	*P. porosus porosus*	118	60.6	14.8	1556.3	742.8
22	Japan	Zushi	*P. porosus porosus*	184	61.7	15	1577.5	754.4
23	Jordan	Jordan Valley (Irbid)	*P. bedriagae*	156	60.4	17.9	429.3	414.4
24	Poland	Milicz	*P. ridibundus*	70	76.3	8.5	538.8	393.1
24	Poland	Milicz	*P. esculentus*	89	69.6	8.5	538.8	393.1
25	Poland	Biebrza	*P.* kl. *esculentus*	195	69.3	6.8	558.3	375.1
26	Portugal	São Jorge. Açores	*P. perezi*	45	57.7	17.3	1209.7	784.0
27	Romania	Dobromir	*P. ridibundus*	73	54.7	11.1	480.1	398.4
28	Russia	Reftinsky	*P. ridibundus*	>100	101.2	2.6	490.6	298.5
28	Russia	Pyshma	*P. ridibundus*	38	72.5	2.2	454.2	284.8
29	Russia	Mari-El / Tatarstan	*P. ridibundus*	57	75.1	3.1	534	314.2
29	Russia	Mari-El	*P. lessonae*	98	61.6	3.8	537.7	325.1
29	Russia	Mari-El	*P. esculentus*	67	73.9	3.8	537.7	325.1

Ref	**Country**	**Locality**	**Species**	**n**	**SVL (mm)**	**MAT (°C)**	**MAP (mm)**	**RET (mm/yr)**
1	Slovakia	Danube River (Bratislava)	*P. ridibundus*	89	82.2	10	628.2	445.0
30	Spain	Valdemanco	*P. perezi*	115	70.1	9.9	613.3	437.9
10	Sweden	Genarp	*P.* kl. *esculentus*	34	63.9	7.7	691.2	421.1
31	Sweden	Southern Sweden (Holmeja)	*P.* kl. *esculentus*	5051	70.8	7.9	670.6	419.1
10	Switzerland	Kloten	*P.* kl. *esculentus*	241	53.1	9.4	1048.3	511.4
32	Turkey	Akören Lake (Balmahmut)	*P. ridibundus*	250	72.3	10.6	525.7	414.6
33	Turkey	Sülüklü Göl (Ayvacik)	*P. bedriagae*	36	61.2	14.5	647	523.6
34	Turkey	Karagöl Lake (Manisa)	*P. ridibundus*	45	67.7	17.7	662	576.3
34	Turkey	Dörtyol	*P. ridibundus*	39	70.4	16	879.2	647.5
35	Turkey	Işıklı Lake (Çivril)	*P. caralitanus*	72	76.1	12.6	532.9	441.9
35	Turkey	Burdur Lake (Burdur)	*P. caralitanus*	70	85.1	12	495.2	416
36	Turkey	Kocagöl Lake (Serefler)	*P. bedriagae*	32	76.3	18.4	991.6	747.2
37	Turkey	Suğla Lake	*P. caralitanus*	21	78.6	11.8	657.1	483.6
37	Turkey	Akburun	*P. caralitanus*	25	79.9	11.3	594.9	452.2
37	Turkey	Gölcük Lake (Isparta)	*P. caralitanus*	23	79.4	11.4	538.7	430.2
37	Turkey	Yazıköy	*P. caralitanus*	24	78.5	18.4	762.9	643.7
37	Turkey	Ağlasun	*P. caralitanus*	23	78.5	11	543.3	427.2
38	Turkey	Gölbaşı Lake	*P. ridibundus*	48	74.4	10.7	385.6	341.1
39	Turkey	Beyşehir	*P. caralitana*	94	85	11.3	613.3	459.2
40	Ukraine	Territory of Crimea	*P. ridibundus*	133	82.4	11.3	535.8	427.7
41	Ukraine	Nyzhankovychi	*P. ridibundus*	67	81.3	8.3	657	423.6
41	Ukraine	Zhovtantsi	*P. ridibundus*	19	57.6	7.4	669.4	410.1
42	Ukraine	Northern Ukraine (Malin)	*P. esculentus*	57	62.9	6.4	845.1	417.0
42	Ukraine	Northern Ukraine (Malin)	*P. ridibundus*	86	72.6	6.4	845.1	417.0
43	Ukraine	Vinnitsia Oblast	*P. ridibundus*	-	75.4	7.5	625.8	403.2
44	Ukraine	Kitsman	*P.* kl. *esculentus*	-	102.8	8.2	629.4	414.8

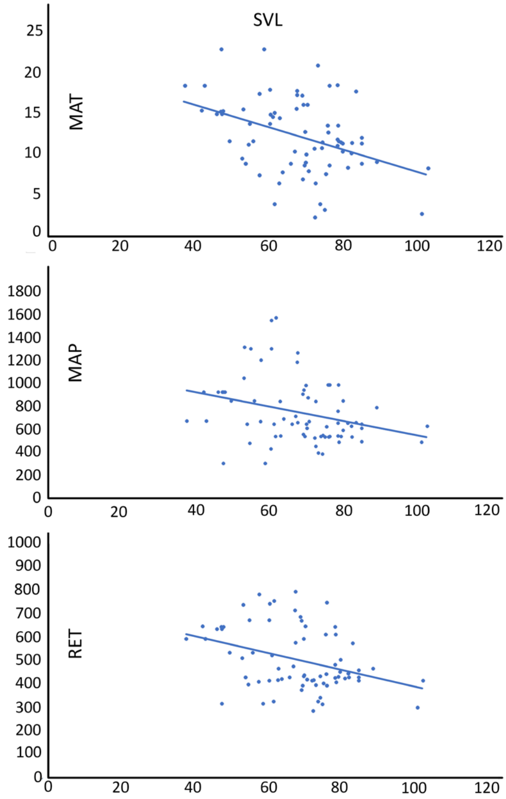

Figure 2. Ordinary Least Square (OLS) regression models performed between SVL (snout-to-vent length) of populations of *Pelophylax* genus across Eurasia and A. Real evapotranspiration obtained by Turc's formula (RET; mm/year); B. Mean annual temperature (MAT; C°); C. Mean annual precipitation (MAP; mm).

(Table 3). Data separated by sex for the entire dataset can be found in Martínez-Monzón et al. (2022; Table 2). Regarding to eco-climatic parameters, minimum mean values of all of them are reached in BL-E, followed by close of FN3-5 in some cases, while the maximum ones occurred in BL-D2 (Table 3).

3. 5. DISCUSSION

Subsequent to results section, original data about the body size of the CN waterfrog population has been settled with its implications upon palaeoclimatic inferences. The application of the models proposed to fossil assemblages came up with the first reconstructions of MAT, MAP and RET for CN and some new ones for BL and FN3 sites.

Frog's body size and climate of Camp dels Ninots. Comparisons with fossil and current data

The waterfrog population from CN maintains the typical sexual size dimorphism of the genus being females bigger than males. Within the fossil assemblages studied, higher values of MAT and MAP are present in CN while BL and FN3 display lower values with a smaller variation rank between them (Table 3). In relation to temperature, the coldest level studied is BL-E with 12.8°C, which is also the driest one presenting a MAP of 779.4 mm. The same pattern is repeated with respect to RET, being the higher primary productivity in CN site and the lesser ones in BL-E (Table 3).

Values of body size from CN are quite similar to those ones from the site of BL level D2, being CN frogs slightly smaller than those ones of BL-D2. From an environmental point of view, BL and FN3 sites were in a fresh water to oligosaline shallow lacustrine environment (Oms et al., 2011; Anadón et al., 2015). Herpetofauna and other proxies as macrofauna indicate that the environments around the lake were characteristic of a Mediterranean woodland which probably represent a humid period corresponding to an interglacial stage (Sánchez-Bandera et al., 2020; Saarinen et al., 2021). Overall, the rich palynoflora (Ochando

Table. 2. Results of OLS regression models and Pearson correlation test between genus *Pelophylax* SVL (snout-to-vent Length) and eco-climatic 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. Regarding to 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-climatic 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-climatic parameter	Correlation coeficient	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

et al., 2022) together with the considerable number of taxa of large and small vertebrates (Martínez-Navarro et al., 2010; Agustí et al., 2010) makes of BL and FN3 sites a very diverse fossil ecosystem. According to the negative relationship found between body size and temperature within the genus *Pelophylax* (Amor et al., 2010; Erismis 2018) as in other anurans (Hemelaar, 1988; Schäuble, 2004; Olalla-Tárraga and Rodríguez, 2007; Gül et al., 2014), this mean that MAT in CN would be warmer than BL-D2 which according to previous reconstructions is 16.6 ± 0.8°C.

Instead, when looking to the values obtained by our new methodology temperature is quite lower, concretely 13.4 ± 2.6°C (Table 3). Error of both reconstructions generates an overlap between these two numbers, besides, the overall trend in the new reconstruction of MAT from BL and FN3 sites follows the pattern previously settled by Sánchez-Bandera et al. (submitted for publication) although with lower values specially in the case of BL-E (Table 3). In relation to precipitations, mean values proposed for BL-D1 and D2 are pretty much in accordance with former data, not so BL-E and FN3-5 where a light divergence exists. Again, when standard errors of both reconstructions are taking into account these differences disappear thus reinforcing this new methodology.

From a different approach, laurel forests in the Canary Islands have been proposed as a current analogue to the ecosystem of CN (Robles et al., 2013). In these communities, Walter and Lieth

(1967) in Morales et al. (2002) have registered a mean annual temperature of 14°C, with a mean daily maximum of the warmest month of 22.6°C and a mean daily minimum of the coldest month of 6.9°C. When looking at precipitation data, mean values of the Canary Islands (MAP = 733 mm. Data from Walter and Lieth (1967) in Morales et al. (2002)) are barely lower than MAP from CN (Table 3), difference that disappears if standard error is taking into account. In the case of the Canary Islands precipitation pattern, a dry period takes place during summer months. Laurel forest ecosystems of this region are classified according to Köppen's climate classification (Köppen, 1918) and Kottek maps (Kottek et al., 2006) as a Csb type of climate, which means temperate with a warm and dry summer. This climate also presents a high air humidity (annual mean relative humidity was 82%) (Morales et al., 2002) and mean monthly precipitations during humid period above 100 mm.

The comparison with both current and fossil data leads to a Csb type of climate for CN (following Köppen's classification). MAT would be around 14°C, and MAP comprised between 700 - 850 mm a climatic proposal in line with the pre-Mediterranean context in which CN is situated.

New insights about the primary productivity of 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-climatic parameters being female waterfrogs smaller as the primary productivity increases (Martínez-Monzón et al., 2022). Based on this statement, the inverse relationship yielded by our OLS regression model between body size and RET at a global scale fits the pattern. This model comes up with a proposed RET of 559.7 ± 77.9 mm/year for CN according to the waterfrogs' body size. In this case, as it happened for temperature, RET values are lower than those ones previously settled (Table 3). Unlike with the other climatic parameters, RET reconstructions for BL and FN3 sites with the different methodologies does not overlap even if standard error is considered.

On the basis of the climatic record provided by Walter and Lieth (1967) in Morales et al. (2002) and by means of Turc's formula, the RET value obtained for the Canary Islands is of 551.42 mm/year. This data, pretty close to the reconstructed RET for CN (Table 3), buttressed the analogy settled between CN fossil environment and this archipelago. The high amount of biomass of subtropical environments, as the one suggested for CN, and the high environmental humidity characteristic of forest and lake-riparian ecosystems is also in accordance 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 within the NPP data of major biomes estimated by global scale models as Montreal model (Alexandrov et al., 2002, see Table 1), CN palaeontological site would be represented by a "Summer-green broad-leaved forest" which concurs with the past vegetal communities derived from the analysis of the palaeoflora (Robles et al., 2013).

New data for Camp dels Ninots and Pliocene climate

Regarding the current knowledge about Pliocene climate, our data results controversial with previous works that indicate that Pliocene temperatures are 5°C warmer than today and also 400-1000 mm/year wetter in the European and Mediterranean region (Haywood et al., 2000). Following these predictions, about 19.4°C and a range of 1170-1770 mm are expected for the Pliocene climatic optimum in the location of CN (Caldes de Malavella, current MAT and MAP 14.4°C and 743 mm respectively). Even though the comparisons with other fossil assemblages provide higher palaeotemperatures than our new methodology (Table 3), in any of those cases the temperature predicted for the Pliocene climatic optimum is reached even if the standard error is considered. Palaeotemperature for CN would be as maximum 3°C warmer than present ones when looking at the comparisons with BL-D2 and 2.5°C warmer with our new proxy.

Instead for palaeoprecipitations, our new data for CN almost fits the predictions with a maximum value of 1012.2 mm. The higher correspondence with other palaeoclimatic reconstructions (Sánchez-Bandera et al., submitted) and also with the predicted values for the Pliocene climatic optimum for precipitations rather than for temperatures may be related to the strong aquatic character for the genus *Pelophylax*.

Despite the discordance generated with the new CN temperature data regarding to the Pliocene climatic optimum, our eco-climatic parameters are in accordance with the palaeobiome suggested by the palaeoflora and micro/macrofaunal assemblage. This fact gives more value to our reconstruction than the general trend settled for the Mediterranean region because of the restricted studied area. CN probably constitutes a more temperate moment within the transition to the Mediterranean climate and that the increase of temperatures up to 5°C warmer to present would take place earlier or later.

Warmer temperatures predicted for the end of the 21st century will generate a change in the ecosystem that undoubtedly affect amphibian communities. The fossil record has shown that climatic change affect anurans, but in previous studies in the Iberian Peninsula those

Table. 3. Values of SVL (snout-to-vent length) in mm from fossil populations of Pelophylax sp. and reconstructed eco-climatic parameters based on the OLS regression models presented in this work with its standard error. MAT (Mean annual temperature in °C); MAP (Mean annual precipitation in mm); RET (Real evapotranspiration in mm/year). Comparative with previous palaeoclimatic reconstruction from Orce archaeo-palaeontological sites (BL and FN3) obtained by means of the Mutual Ecogeographic Range method (MER) with its mean standard deviation (Sánchez-Bandera et al. submitted) and RET values derived from Turc's formula.

Sites		**SVL**	***MAT* *(±2.6)***	**MAT (±2.6)**	***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**

changes allow for its physiological adaptation and resilience (Martínez-Monzón et al., 2021, 2022). If the Pliocene climatic optimum of CN results in an analogue of future climate, changes of MAT and MAP may not be the main threat for anuran populations as there is no evidence of such a decline. So, other threats related to climate change may be the distribution of the precipitation throughout the year that could cause intense summer draught periods in the Mediterranean region. Even though, the human impact which leads to habitat degradation, pollution, introduction of alien species and vehicle collision has proved to be determinant for the survival of this endangered group (Cox et al., 2006; Greenberg et al., 2018).

3.6. CONCLUSIONS

1. There are clear negative linear relationships between eco-climatic parameters (MAT, MAP and RET) and SVL of genus *Pelophylax* across Eurasia.

2. Body size of *Pelophylax* sp. population from CN is of 52.5 mm and follows the current pattern of sexual size dimorphism being females bigger than males. Comparing with current data, waterfrogs' body size of *Pelophylax* sp. from CN suggest a temperate climate with a warm and dry summers. Our new method has yielded a palaeotemperature of 14.28 ± 2.63°C and a palaeoprecipitation of 846.76 ± 165.43 mm. Instead, our new data compared with former ones of BL and FN3 fossil assemblages allude to higher values of mean annual temperature for CN, above 16.55°C.

3. Regarding to primary productivity of the ecosystem, NPP values points to a "Summer-green broad-leaved forest" biome-like. Probably, the environment of CN palaeontological site constitutes a past analogue of the current laurel forest of the Canary Islands as previous palaeobotanical studies suggest.

4. Reconstructed MAT for CN does not match with the proposals for the Pliocene climatic optimum, being lower than expected. Precipitations instead, show values much closer to the settled ones for this period. Despite this divergence in temperature data, all reconstructed eco-climatic parameters match the approach of a "Summer-green broad-leaved forest" biome-like previously made for CN site.

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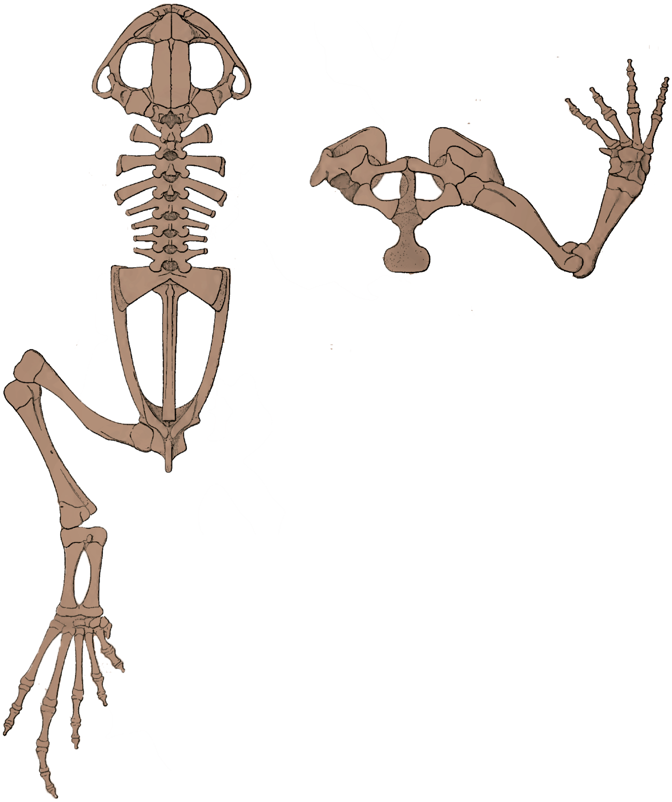
CHAPTER 4. GENERAL CONCLUSIONS AND FUTURE PERSPECTIVES



SUMMARY

Subsequent to the *"Results"* chapter where most of the discussion of the results obtained is presented, in this chapter five general conclusions derived for the work carried out in this dissertation are presented. They are as follows:

1. Reconstruction of anuran past body size based on humeral measurements can be done accurately for *Epidalea calamita* and *Pelophylax perezi*.

2. Temperature is the main factor influencing anuran body size and herpetofauna diversity, probably due to its close relationship with the energy-resources dynamics and primary productivity of the ecosystems.

3. Female body size constitutes a better indicator than male's one, but due to the limitations associated to fossil samples and current references is not always easy its study apart from males.

4. Due to its relationships with eco-climatic parameters, *Pelophylax* body size can be used to reconstruct past conditions even though results must be taking with caution and should be integrated with other proxies, if any.

5. Amphibian and reptile diversity changes have reflected the main climatic events recorded in the sequences studied.

To conclude this PhD, a brief report of future perspectives is contemplated within this chapter.

After the Chapter 3. (*"Results"*) where most of the discussion of the work carried out in this dissertation have been exposed, this section aims to put in relation all the former studies in the shape of five global conclusions. These conclusions are related to the initial methodological work, the palaeoecological analysis and the application of the obtained results to develop a new methodology for reconstruct past conditions. Finally, a brief section of limitations and future perspectives closes the manuscript.

4.1. GENERAL CONCLUSIONS

In the first place, the methodology proposed in this PhD in order to reconstruct past body sizes based on humeral measurements has provided excellent results. Even though other fits were considered, linear models applied to the data of modern osteological reference collections always provide the best statistical outcomes. The well-adjusted OLS regression models generated constitute a useful tool which can be used for the study of anuran body size based on fossil samples. For these reasons, it can be stated that:

1. Reconstruction of anuran past body size based on humeral measurements can be done accurately for *Epidalea calamita* and *Pelophylax perezi*.

Regarding to climate, the work carried out in this PhD proves that environmental factors strongly constrain anuran body size. Bergmann's clines have been found in the Sierra de Atapuerca sites, in Camp dels Ninots and in the Guadix-Baza Basin sites for *E. calamita* and *P. perezi* (or *Pelophylax* sp.). This assignment has been made by means of a correlation analysis in the two first cases and by the study of maximum values in the last one. Temperature together with primary productivity seems to be the main factors driving body size changes in anurans during the Plio-Pleistocene of the Iberian Peninsula. The close association between these two variables, which often covary, make difficult to establish a single mechanism to explain the pattern detected (i. e. bigger body sizes in colder climates with less primary productivity). By other side, influence of precipitations over body size cannot be dismissed as it is correlated with changes in body size of current populations of genus *Pelophylax*. For the whole genus, bigger body sizes can be found in the more arid environments.

Regarding to species richness, temperature and primary productivity also have proved to be the main determinants for species number, occurring the more diverse assemblages in warmer, high-productivity periods.

The correlational nature of the studies performed in this PhD has made possible to detect clear relationships between anuran body size / herpetofauna diversity and eco-climatic parameters. Despite, this kind of analysis prevents obtaining a full understanding of the underlying mechanisms to the detected patterns.

As a global conclusion referent to the influence of eco-climatic parameters upon body size, it can be established that:

2. Temperature is the main factor influencing anuran body size and herpetofauna diversity, probably due to its close relationship with the energy-resources dynamics and primary productivity of the ecosystems.

Among the different fossil assemblages and studied anuran species, the climate has shown a larger influence on female body size, suggesting a sex-related response to climatic variations in amphibians. It is probably due to the differences between males and females in energy and resource allocations related to their reproductive biology and behaviour. The widely accredited association between female body size and fecundity probably determines a larger influence of external factors over this trait in this sex.

Even though female body size has proved to be a better climatic proxy than male one, in fossil assemblages some features as the sample size makes difficult to only take into account female individuals. Also, data of current references required for applying an actualistic approach are not always available by sex, thus forcing a sex-independent approach. As a conclusion referent to sex-related differences in the response of body size against eco-climatic changes it can be stated that:

3. Female body size constitutes a better indicator than male's one but, due to the limitations associated to fossil samples and modern data, it is not always easy to study them separately.

Anuran body size and herpetofauna diversity have been revealed as valuable climatic and environmental proxies, reinforcing the role of amphibians and reptiles as indicators of past conditions. Regarding to herpetofauna diversity, main climatic events recorded within the sequences studied have exerted an influence over amphibians and reptiles during the Plio-Pleistocene. In general, after the climatic perturbations, herpetofauna communities shows a high level of resilience, which seems to be positively related to species richness.

The models generated based on current populations of the genus *Pelophylax* across Eurasia, constitute a new and valuable tool for increasing our knowledge about past climates and environments. This new methodology can be applied to Plio-Pleistocene localities where some of the current species of the genus *Pelophylax* are present. This would mean a complement to former reconstructions in locations that already counts with palaeoclimatic reconstructions based in other proxies, but as in Camp dels Ninots, it could mean the first reconstruction which comes with numerical values. So, it can be said that:

4. Due to its relationships with eco-climatic parameters, *Pelophylax* body size can be used to reconstruct past conditions even though results must be taking with caution and should be integrated with other proxies, if any.

5. Amphibian and reptile diversity changes have reflected the main climatic events recorded in the studied sequences.

Subsequent to the discussion of the results obtained and the proposal of the five main conclusions derived from this work, it is appropriate to say that the general research questions have been answered for the most part and the objectives settled in the introduction have been fully accomplished.

4.2. FUTURE PERSPECTIVES

All the work carry through these years has not been extent of difficulties and each of them constitute a new opportunity to open a new research line, parallel to the main topic of this dissertation. Unfortunately, everything comes to an end and the time and resources destined to this PhD are not an exception. There are several issues I would have liked to spend more time on.

In the first place, there is the influence exerted for taphonomy on sexual size dimorphism in cave environments. As the cave systems are used for the hibernation of some amphibians which have the habit of burrowing for protection against the harsh conditions of winter (as is the case of *E. calamita*), a lot of remains of such species can be found. In the case of the Gran Dolina, the smallest individuals, often the most fragile and with less fat deposits, are the ones which usually die the most. In this PhD some hypothesis at this respect have been settled within the Chapter 3 (Part 1, Section 1.1). Personally, I have observed the same pattern in other archaeo-palaeontological sites with similar characteristics as in Camino (Pinilla del Valle, Madrid). This other site is also a cave environment in which remains of *E. calamita* exhibits a very similar pattern to the ones of the Gran Dolina. This subject would deserve to be studied more in depth in order to better understand which is the main cause of the inverse pattern of sexual size dimorphism present in these accumulations.

By other side, several attempts to achieve good osteological preparations with the aim to perform a skeletochronological study on anuran fossil samples have been made, without good results. I would like to keep trying to achieve this goal by applying different methodologies. I personally consider that knowing the age distribution and growth pattern of the fossil amphibian populations belonging to the Plio-Pleistocene of the Iberian Peninsula will constitute a remarkable advance for the study of the palaeoecology of these communities and also an advantage for the taphonomical studies of this group.

Apart from these two different research paths that I would like to take up, the perspective of pursuing the study of body size and implementing the new developed methodology to other fossil assemblages seems very interesting to me. Also, I would like to perfect and improve this new method in order to make it more certain and accurate for its application to fossil locations, as a complement for other methodologies, and why not as a new reliable proxy itself.

Finally, I personally would like to explore the applications of all the knowledge obtained from fossil record to the development of effective conservation strategies for amphibians and reptiles. Nowadays these endangered groups are facing a challenging scenario where the influence of human impact is overwhelming. The knowledge about how they have coped with climatic perturbations in the past, could be useful to contribute to its protection facing the future.

APPENDIX 1.
PLATES

This appendix compiles six plates which constitute a sample of the material studied for this PhD. A selection of fossil humeri of *Epidalea calamita* and *Pelophylax perezi* (or *Pelophylax* sp.) from most of the sites studied (Gran Dolina, Portalón, Barranco León, Fuente Nueva 3 and Camp dels Ninots) have been photographed in some cases (Plates 2, 4 and 5) and drawn with a camera lucida in others (Plate 3). In addition, drawings of some humerus of *Pelophylax perezi* from the osteological reference collection of the MNCN (Museo Nacional de Ciencias Naturales) are presented in the Plate 1.

Plate 1. Reference collections, *Pelophylax perezi* (Seoane, 1885), selection of humeri from the osteological reference collection of the Museo Nacional de Ciencias Naturales (Madrid, Spain) and Blain Herpetological Collection (BHC) stored at the IPHES (Tarragona, Spain). All humeri in ventral view: **1 – 2** Male humeri, (1) MNCN-16442, left and (2) MNCN-16475 right; **3 – 4** Female right humeri, (3) BHC-PePe6 and (4)

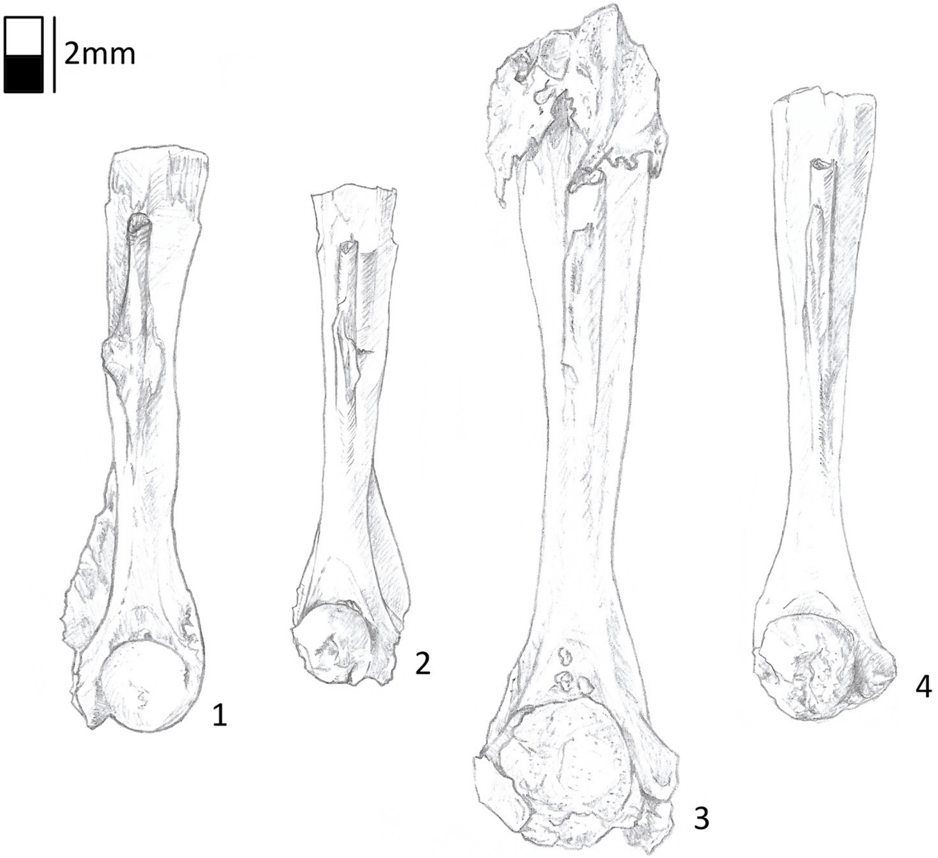

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Plate 2. Gran Dolina, TDS. Atapuerca archaeo-palaeontological complex, Central Spain). *Epidalea calamita* (Laurenti, 1768), selection of fossil disarticulated humeri. **1 - 3** Female left humerus: (1) Ventral, (2) lateral and (3) dorsal views; The rest of humeri in ventral view: **4 – 10** Females: (4 – 6) Left and (7 - 10) right; **11 – 15** Males: (11 - 12) Left and (13 – 15) right; **16 – 20** Juvenile individuals: (16 – 17) Left and (18 – 20) right.

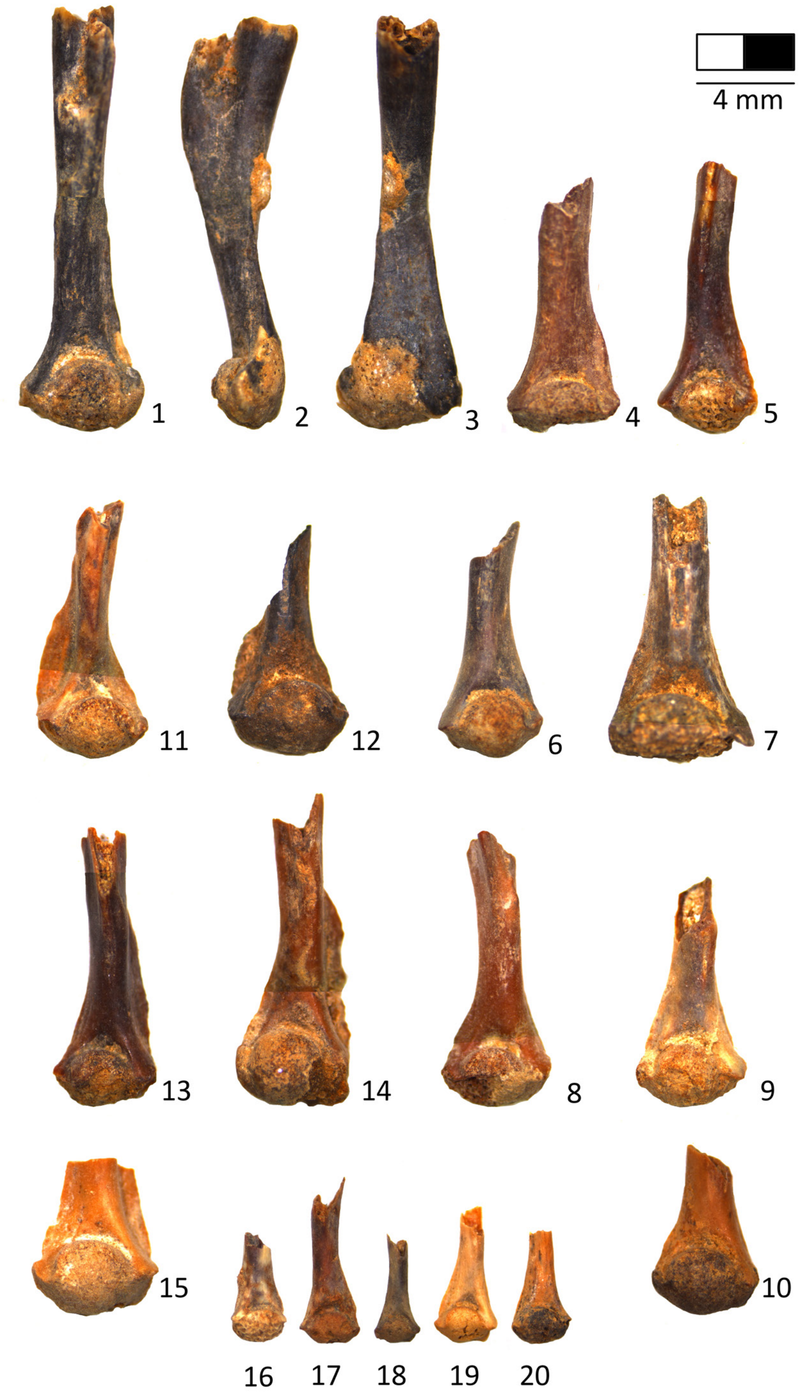
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Plate 3. Portalón, P. Atapuerca archaeo-palaeontological complex, Central Spain). *Epidalea calamita* (Laurenti, 1768), selection of fossil disarticulated humeri drawn with a clear camera. **1 - 5** Male humeri in ventral view (1, 5) right and (2) left; (3) lateral and (4) dorsal views; **6 – 10** Female humeri in ventral view (6, 9) right and (7) left; (8) dorsal and (10) lateral views.

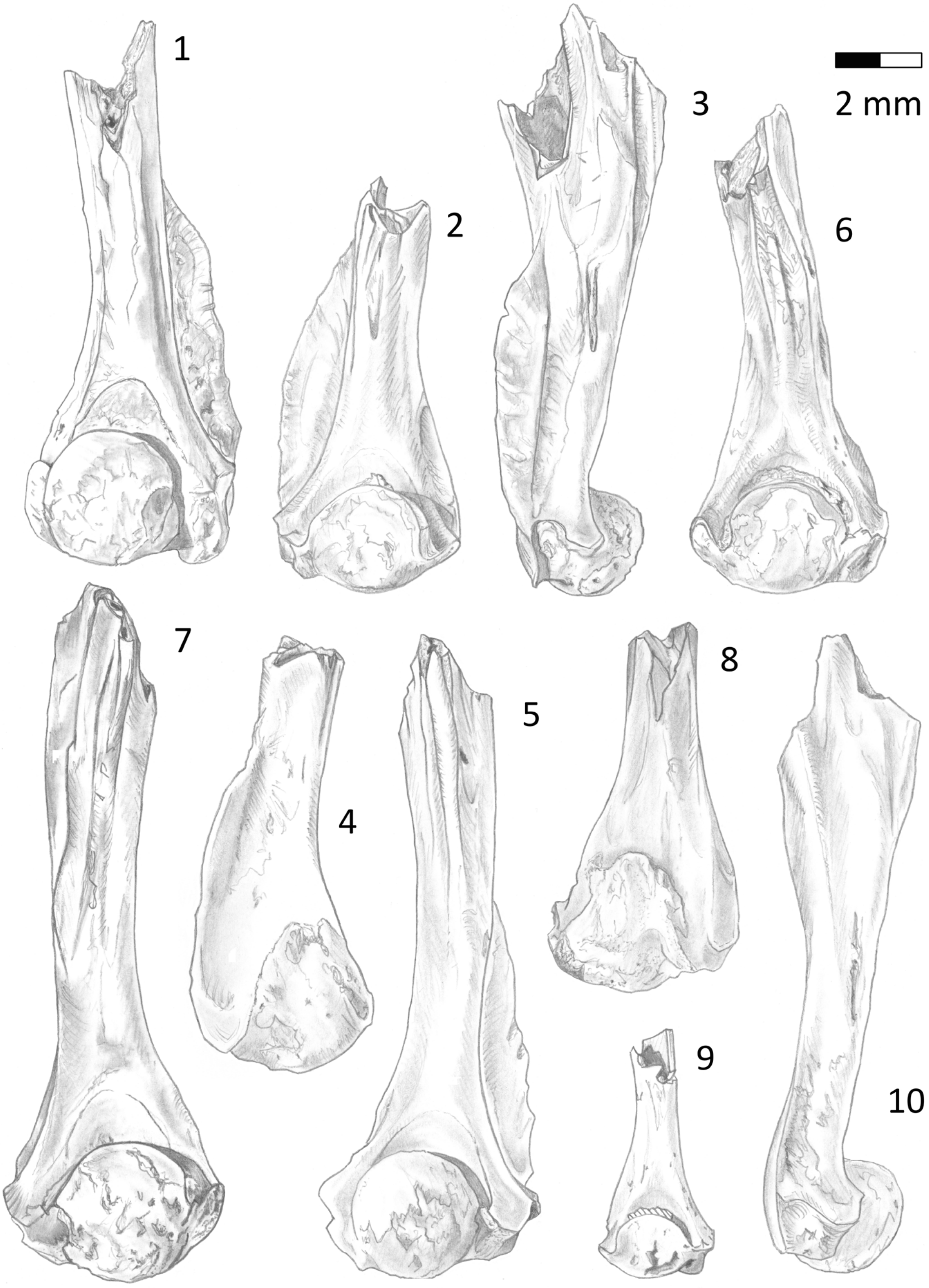
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Plate 4. Barranco León and Fuente Nueva 3, Barranco León, levels D1; D2; E. Fuente Nueva 3 level 5. Orce archaeo-palaeontological site complex, SE Spain). *Pelophylax* cf. *perezi* (Seoane, 1885), selection of fossil disarticulated humeri in ventral view. Humeri from Barranco León site: **1 – 4** Females (1 – 2) Left and (3 – 4) right; **5 – 8** Males: (5 – 6) Left and (7 – 8) right. Humeri from Fuente Nueva 3: **9 -10** Females, right; **11 - 12** Males right and left respectively.

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Plate 5. Camp dels Ninots I, Can Argilera Sector, NE Spain *Pelophylax* sp., selection of fossil disarticulated humeri in ventral and lateral views. **1 – 4** Male left humerus: (1) Ventral, (2) right lateral, (3) dorsal, (4) left lateral views. Remaining humeri in ventral view. **5 – 9** Females: (5 -6) Left and (7 – 9) right; **10 – 15** Males: (10 – 12) Left and (13 – 15) right.

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APPENDIX 2.
OTHER WORKS

This appendix contains three research papers which are related to some the main research topics of this PhD. All of them have been published in national and international indexed journals with impact factor. The first work entitled *"El Cuaternario ibérico como escenario para el estudio de patrones globales biogeográficos y macroecológicos en anfibios y reptiles"* was published in a monographic volume of the Ecosistemas Journal, part of the Spanish Association of Terrestrial Ecology (AEET). In this work I participated as the main author and in the two other works which constitute this appendix, I have made significant contributions specified later in each chapter. The titles of these other works are *"Early-Middle Pleistocene freshwater ecosystems in the Sierra de Atapuerca (northern Iberia) based on the Gran Dolina fish record"* published in the journal *"Palaeogeography, Palaeoclimatology, Palaeoecology"* and *"The middle to Late Pleistocene herpetofaunal assemblages from the Jarama and Manzanares valleys (Madrid, central Spain): An ecological synthesis"* contained in the journal *"Quaternary International"*.

A2.1 Iberian Quaternary as a scenario for the study of global biogeographic and macroecological patterns in amphibians and reptiles (El Cuaternario ibérico como escenario para el estudio de patrones globales biogeográficos y macroecológicos en anfibios y reptiles)

The present work belongs to a monographic volume entitled *"Paleoecología, analizando la cuarta dimension de la biodiversidad"* of the Ecosistemas journal (AEET) edited by Dra. Sara Varela. A publication of the Spanish Association of Terrestrial Ecology (AEET). In this work, my role was of the main and corresponding author. Dr. Hugues-Alexandre Blain and Dr. Josep Francesc Bisbal-Chinesta, collaborated to this publication by writing the sections ("Palaeobiogeography") and ("Extinction or extirpation") of the aforementioned work. I wrote the section of ("Macroecology") and put together all these parts by writing the introduction, discussion and conclusions of this publication.

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El Cuaternario ibérico como escenario para el estudio de patrones globales biogeográficos y macroecológicos en anfibios y reptiles

A. Martínez-Monzón[1,2,*], J.F. Bisbal-Chinesta[1,2], H.-A. Blain[1,2]

(1) IPHES, Institut Català de Paleoecología Humana i Evolució Social, Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, España.
(2) Àrea de Prehistòria, Universitat Rovira i Virgili, (URV), Avinguda Catalunya 35, 43002 Tarragona, España.

* Autor de correspondencia: A. Martínez-Monzón [almudena.martinezm@hotmail.com]

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Los cambios climáticos globales afectan a los organismos en todos los biomas y ecosistemas del planeta. Durante el Pleistoceno, las sucesivas glaciaciones han hecho del clima un factor condicionante para la presencia y desarrollo vital de las especies de herpetofauna tanto a nivel europeo como ibérico. Durante este periodo glacial, la península ibérica actúa como refugio meridional para especies termófilas que posteriormente expanden su distribución hacia el tercio norte pasado esta etapa fría hacia el inicio del Holoceno. En algunos casos, dichas condiciones climáticas conducen a la extinción o extirpación de ciertas especies o familias con un claro patrón geográfico de retirada progresiva norte-sur. Para evitar la extinción sin cambiar su distribución, algunas especies desarrollan mecanismos adaptativos como sucede en ciertas poblaciones de anuros en las que se registra un aumento de tamaño durante los periodos más fríos siguiendo el patrón propuesto por la regla de Bergmann y la TSR o temperature-size rule. En esta publicación daremos a conocer la aportación de los yacimientos arqueo-paleontológicos del Cuaternario de la península ibérica al conocimiento de los patrones globales evolutivos y biogeográficos en anfibios y reptiles.

Palabras clave: extinción; Holoceno; macroecología; paleobiogeografía; paleoherpetología; Pleistoceno

Martínez-Monzón, A., Bisbal-Chinesta, J.F., Blain, H.-A. 2018. Iberian Quaternary as a scenario for the study of global biogeographic and macroecological patterns in amphibians and reptiles. *Ecosistemas* 27(1): 87-95. Doi.: 10.7818/ECOS.1435

Global climatic changes affect organisms in all biomes and ecosystems of the planet. During Pleistocene, consecutive glaciation events rise climate as a conditioning factor for presence and vital development of herpetofauna species, both at European and Iberian scale. During this glacial period, Iberian Peninsula constitutes a meridional refuge for thermophilous species which lately expand their distribution towards the northern area at the end of this cold phase when Holocene begins. In some cases, these climatic conditions have led to extinction or extirpation of some species or families in a clear north-south retreat geographic pattern. To avoid extinction without changing their distribution some species have developed adaptive mechanisms as occurs in certain amphibian populations which experiment an increase of body size following the pattern derived from Bergmann's rule and TSR or temperature-size rule. In this paper, we will present the contribution of Quaternary archaeo-paleontological sites of the Iberian Peninsula to our knowledge on global evolutionary and biogeographical patterns in amphibians and reptiles.

Keywords: extinction; Holocene; macroecology; paleobiogeography; paleoherpetology; Pleistocene

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1.1 INTRODUCCIÓN

A pesar de que el Cuaternario (2.6 Ma - actualidad) es un periodo científicamente reconocido por su relevancia en el campo de la evolución humana, también lo es para entender la sistemática, diversidad y distribución del resto de especies de vertebrados que encontramos en la actualidad entre los que se encuentran los anfibios y reptiles (Jansson, 2003; Araújo et al., 2008). Durante este periodo, reconocido climáticamente por la alternancia de fases glaciales e interglaciales, el estudio de la herpetofauna reviste un gran interés a la hora de caracterizar las normas de reacción de anfibios y reptiles ante los cambios climáticos. El material fósil de anfibios y reptiles es además considerado apto para el estudio de reglas y patrones ecogeográficos en la dimensión temporal dados los elevados tamaños muestrales de los que se dispone, el amplio rango temporal que los yacimientos arqueo-paleontológicos ofrecen y la rápida respuesta adaptativa de estas especies ante cambios ambientales. Desde el punto de vista osteológico, las especies de herpetofauna presentes en yacimientos del Cuaternario (concretamente del Pleistoceno) en la península ibérica se consideran idénticas a las que constituyen las poblaciones modernas, lo cual ha sido confirmado por datos genéticos basados en la aplicación de relojes moleculares (Lobo et al., 2016; Barbadillo et al., 1997; Sanchiz, 1977). Este hecho reviste una importancia crucial pues permite aplicar el principio de actualismo a las muestras procedentes de yacimientos de este periodo.

El estudio de la herpetofauna fósil presenta una enorme cantidad de posibilidades a la hora de plantear experimentos, aportar datos y solventar dilemas en diversas ramas de la biología y especialmente en paleoecología. En este trabajo nos centraremos en ilustrar mediante una serie de ejemplos, cómo el estudio del registro fósil ibérico contribuye al entendimiento de los patrones biogeográficos regionales a través del tiempo, y de las respuestas de las especies a los cambios climáticos globales.

1.2 PALEOBIOGEOGRAFÍA

A pesar de la gran cantidad de estrategias que diversos clados de anfibios y reptiles han desarrollado para hacer frente a condiciones adversas, la herpetofauna en general se considera altamente susceptible a las oscilaciones térmicas debido al carácter ectotérmico de dichos organismos (Pough, 1980), lo cual la convierte en un grupo de especial interés para estudiar los efectos que los cambios climáticos del Cuaternario han tenido sobre la biodiversidad y su distribución espacial (Araújo et al., 2008). Sus restricciones fisiológicas, junto a la generalizada tendencia conservadora a nivel osteológico del grupo, permiten documentar a través del registro fósil cambios en la distribución geográfica de diferentes grupos hasta la actualidad, así como inferir posibles fluctuaciones bioclimáticas a escala regional (Blain, 2009). Los estudios filogenéticos y filogeográficos de diferentes especies presentes en la Europa transpirenaica apuntan a la existencia de un refugio climático en la península ibérica a lo largo de las sucesivas fases glaciales, desde el cual las especies habrían expandido su distribución por el continente durante los periodos interglaciales, papel semejante al desempeñado por el resto de penínsulas del sur europeo, los Balcanes e Italia (Hewitt, 1996, 2000), gracias a las características climáticas favorables asociadas a su situación geográfica (Fletcher et al., 2010; Harrison y Sánchez-Goñi, 2010).

El Cuaternario final se ha caracterizado en Europa Occidental por los grandes cambios climáticos y ambientales a consecuencia del desarrollo de la última gran pulsación glacial y el inicio del actual interglacial. Estos grandes cambios climáticos y ambientales han tenido un impacto determinante sobre la fauna, siendo los reptiles y anfibios especialmente susceptibles a contraer o expandir sus áreas de distribución espacial según los cambios de gradiente térmico de cada momento.

Las asociaciones de herpetofauna fósil documentadas permiten establecer dos grandes regiones bióticas durante el Pleistoceno superior final (ca. 60 000 – 14 900 a.B.P.) (Bisbal-Chinesta y Blain, 2018) (Fig. 1A). La primera está formada por el centro y sur de la península ibérica, con las especies *Epidalea calamita, Timon lepidus, Bufo spinosus, Zamenis scalaris* y, en menor medida, *Pelobates cultripes, Testudo hermanni, Malpolon monspessulanus, Pleurodeles waltl* y *Vipera latastei* como los taxones más representativos de su registro, formando una asociación general de tendencia termófila y plenamente mediterránea. La segunda gran región biótica es la conformada por las regiones cantábrica y nororiental ibéricas, que comparten el binomio de tendencias eurosiberianas e higrófilas de *Rana temporaria* y *Anguis fragilis* como las especies dominantes de las secuencias.

En el área cantábrica este binomio es acompañado por *B. spinosus, E. calamita, Alytes obstetricans* y *Vipera* sp. como taxones más representativos, acentuando todavía más el carácter higrófilo de la asociación; mientras que el registro del noreste de la península ibérica *R. temporaria* y *A. fragilis* aparecen mayoritariamente junto con *A. obstetricans, E. calamita, B. spinosus, Coronella girondica* y *Pelodytes punctatus,* detectándose gracias a estas dos últimas especies la existencia de cierta influencia mediterránea.

Los principales cambios biogeográficos se producen a partir del inicio de la fase postglacial del Pleistoceno superior terminal y Holoceno, que conllevará la expansión de las especies más termófilas hacia el norte de la península ibérica (Fig. 1B), posiblemente aprovechando la existencia de corredores naturales, como el Valle del Ebro o el litoral atlántico (Bisbal-Chinesta y Blain, 2018). Esto es especialmente visible en el registro herpetológico del MIS 1 (14 900 a.B.P. - actualidad) de la franja cantábrica. La herpetofauna documentada durante los MIS 3 y 2 (60 000 – 26 900 a.B.P. y 26 900 – 14 900 a.B.P., respectivamente) se compone de taxones generalistas, pero con tendencias higrófilas, que pueden tolerar un amplio espectro climático y ambiental (*B. spinosus, E. calamita, A. fragilis y Vipera* sp.), aunque significativamente la secuencia regional está monopolizada por *R. temporaria*, especie de significada preferencia por ambientes húmedos y condiciones climáticas eurosiberianas.

La primera aparición de una especie plenamente termófila en el registro fósil es el ofidio mediterráneo *M. monspessulanus,* en la Unidad Inferior de Valdavara-1 (15 120 ±70 – 13 770 ±70 a.B.P) (López-García et al., 2011), cuya aparición en el área gallega se puede relacionar con un proceso de colonización a partir de un refugio meridional ibérico gracias a la subida de las temperaturas después del final del MIS 2.

A lo largo del MIS 1, aparecen nuevos taxones hasta entonces ausentes en el registro regional del Pleistoceno superior, como *Lacerta sensu lato, Natrix maura, Natrix natrix* sensu lato y *Coronella austriaca* en la misma Unidad Inferior de Valdavara-1 (López-García et al., 2011); *Ichthyosaura* (=*Mesotriton*) *alpestris, Lissotriton helveticus, Triturus marmoratus, Hyla* sp., *Chalcides striatus, Lacerta* sp., *C.*

girondica, Zamenis longissimus e *Hierophis viridiflavus* en los niveles III a I de Cueva de Santa Catalina (12 425 ±90 a.B.P. a 9180 ±110 a.B.P.) (Bailon y Garcia-Ibaibarriaga, 2014); *T. lepidus, M. monspessulanus, Natrix* sp. y *Zamenis-Rhinechis* (=*Elaphe* sp. sensu lato) en los niveles C.II-I de Las Orcillas-1 (8610 ±50 a.B.P) (Fernández et al., 2010); y finalmente *Chioglossa lusitanica, Discoglossus galganoi, C. striatus, T. lepidus, N. maura, C. austriaca* y *M. monspessulanus* en la Unidad Inferior de Valdavara-1 (4490 ±40 a.B.P.) (Blain et al., 2009b; López-García et al., 2011).

Las secuencias de Las Orcillas-1 y Valdavara-1 posiblemente indican dos vías de penetración hacia el norte de la península ibérica para las especies de influencia mediterránea y para las especies hoy en día propias del noroeste pero más sensibles a las pulsaciones climáticas glaciales:

1. La vía occidental, representada por Valdavara-1, estaría enmarcada en la fachada litoral atlántica hacia las costas gallegas y habría sido utilizada tanto por especies de origen mediterráneo (por ejemplo: *D. galganoi, T. lepidus* y *M. monspessulanus*) como por especies típicamente occidentales (*C. lusitanica* y posiblemente *Lacerta schreiberi*), generalistas y/o tolerantes a condiciones eurosiberianas (por ejemplo: *N. maura* o *C. striatus*) para colonizar el noroeste ibérico y la franja cantábrica.

2. La vía oriental, marcada por Las Orcillas-1, estaría configurada por el Valle del Ebro y, aparentemente según el registro fósil, habría sido utilizada por especies mediterráneas (*T. lepidus, M. monspessulanus* y posiblemente *Z. scalaris*). Ya en la región nororiental, en pleno valle del Ebro, la concurrencia holocénica termófila de *P. cultripes, T. lepidus* y *M. monspessulanus* proveniente de Balsa la Tamariz (ca. 3600 - 3400 a.B.P.) (Laplana y Cuenca-Bescós, 1995), junto con la presencia del gecko *Tarentola mauritanica* en el nivel superior de Cova Colomera (3490 ±50 a.B.P.) (López- García et al., 2010a), situada sobre uno de los afluentes del Ebro, pueden correlacionarse con la existencia del corredor natural del Valle del Ebro, a partir del cual las especies termófilas propias del ámbito mediterráneo penetrarían hacia el interior.

3. Paralelamente, se produciría la entrada a través de los extremos de los Pirineos de nuevas especies provenientes de Italia a través de los extremos pirenaicos, que posiblemente vieron su expansión frenada en el norte de la península por la colonización contemporánea de las especies mediterráneas propias del ámbito ibérico. Es el caso de *Z. longissimus,* cuyo primer registro corresponde con los niveles II y I de Santa Catalina (Bailon y Garcia-Ibaibarriaga, 2014), seguido por la secuencia Aziliense-Edad del Bronce de Aizkoltzo (Murelaga et al., 2008) y el nivel calcolítico de El Mirón (Sanchiz et al., 2012) y cuyas dataciones concuerdan con el escenario de expansión holocénica propuesto a partir de los estudios filogenéticos (Musilová et al., 2010). Otras especies de origen oriental con biogeografías parecidas y susceptibles de haber efectuado una expansión paralela reciente son *H. viridiflavus* y *Lacerta bilineata* (Böhme et al., 2007; Joger et al., 2007).

Los cambios climáticos y ambientales ligados a las últimas fases glacial e interglacial del Cuaternario no han tenido aparentemente grandes efectos sobre la composición del registro fósil herpetológico del centro y sur de la península ibérica. Así pues, se ha constatado la presencia continuada de especies termófilas durante el Pleistoceno superior y su pervivencia también en el Último Máximo Glacial, como se muestra gracias a la asociación típicamente

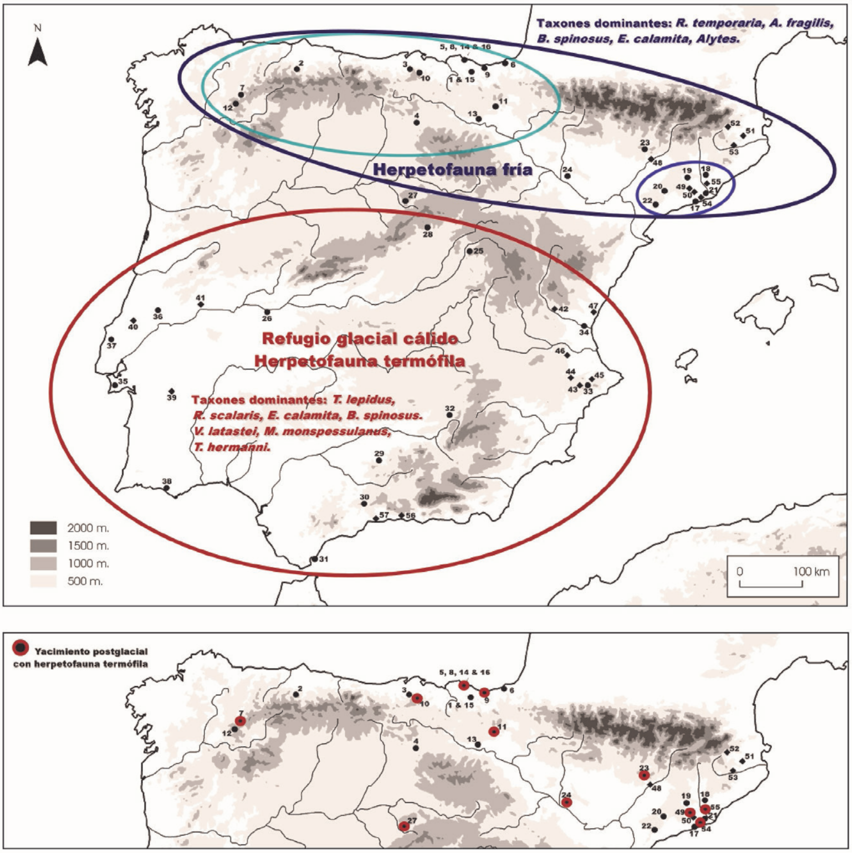

Figura 1. A. Yacimientos paleo-arqueológicos de la península ibérica del Cuaternario final (60 000 – 3000 a.B.P.) con presencia de herpetofauna: 1) Askondo, 2) Cueva del Conde, 3) Cueva de Cobrante, 4) El Portalón, 5) Santimamiñe, 6) Erralla, 7) Valdavara-1, 8) Laminak II, 9) Aizkoltzo, 10) El Mirón, 11) Las Orcillas-1, 12) Cova Eirós, 13) Peña Larga, 14) Antoliñako Koba, 15) Dolmen of Errekatxuetako Atxa, 16) Santa Catalina, 17) Cova del Gegant, 18) Cova Teixoneres, 19) Abric Romaní, 20) Cova dels Xaragalls, 21) Riera de Canyars, 22) Cova dels Galls Carboners, 23) Cova Colomera, 24) Balsa la Tamariz, 25) Cueva de los Torrejones, 26) Sala de las Chimeneas of Maltravieso, 27) Peña de Estebanvela, 28) Ventana, 29) Sima de Abraham, 30) Boquete de Zafarraya, 31) Gorham's Cave, 32) Castillejo del Bonete, 33) Abric del Salt, 34) Lloma de Betxí, 35) Gruta da Figueira Brava, 36) Gruta do Caldeirâo, 37) Gruta Nova da Columbeira, 38) Guia of Albufeira, 39) Gruta do Escoural, 40) Gruta da Oliveira, 41) Foz do Enxarrique, 42) Abrigo de la Quebrada, 43) Abric del Pastor, 44) Cova Canet, 45) Cova de l'Or, 46) Ereta de Pedregal, 47) Pic dels Corbs, 48) Roca dels Bous, 49) Cova del Toixò, 50) Can Sadurní, 51) La Draga, 52) Pont de Sadernes, 53) El Pasteral, 54) Cal Tintorer, 55) Bòbila Madurell, 56) Cueva de Nerja, 57) Cueva de Rincón de la Victoria. A. Biogeografía de los taxones de herpetofauna durante el Pleistoceno superior glacial (60 000-14 900 a.B.P.). B. Yacimientos del norte de la península ibérica con presencia de herpetofauna termófila a partir del final del Último Máximo Glacial (14 900 a.B.P.) hasta finales de la Edad del Bronce (3000 a.B.P.)

Figure 1. A. Late Quaternary (60 000-3000 yrs. B.P.) archaeo-paleontological sites of the Iberian Peninsula with herpetofaunal presence: 1) Askondo, 2) Cueva del Conde, 3) Cueva de Cobrante, 4) El Portalón, 5) Santimamiñe, 6) Erralla, 7) Valdavara-1, 8) Laminak II, 9) Aizkoltzo, 10) El Mirón, 11) Las Orcillas- 1, 12) Cova Eirós, 13) Peña Larga, 14) Antoliñako Koba, 15) Dolmen of Errekatxuetako Atxa, 16) Santa Catalina, 17) Cova del Gegant, 18) Cova Teixoneres, 19) Abric Romaní, 20) Cova dels Xaragalls, 21) Riera de Canyars, 22) Cova dels Galls Carboners, 23) Cova Colomera, 24) Balsa la Tamariz, 25) Cueva de los Torrejones, 26) Sala de las Chimeneas of Maltravieso, 27) Peña de Estebanvela, 28) Ventana, 29) Sima de Abraham, 30) Boquete de Zafarraya, 31) Gorham's Cave, 32) Castillejo del Bonete, 33) Abric del Salt, 34) Lloma de Betxí, 35) Gruta da Figueira Brava, 36) Gruta do Caldeirâo, 37) Gruta Nova da Columbeira, 38) Guia of Albufeira, 39) Gruta do Escoural, 40) Gruta da Oliveira, 41) Foz do Enxarrique, 42) Abrigo de la Quebrada, 43) Abric del Pastor, 44) Cova Canet, 45) Cova de l'Or, 46) Ereta de Pedregal, 47) Pic dels Corbs, 48) Roca dels Bous, 49) Cova del Toixò, 50) Can Sadurní, 51) La Draga, 52) Pont de Sadernes, 53) El Pasteral, 54) Cal Tintorer, 55) Bòbila Madurell, 56) Cueva de Nerja, 57) Cueva de Rincón de la Victoria. A. Herpetofaunal biogeography during the glacial Late Pleistocene (60 000-14 900 yrs.B.P.). B. North Iberian sites with presence of thermophilous herpetofauna from Last Glacial Maximum (14 000 yrs.B.P.) to latest Bronze Age (3000 yrs.B.P.)

mediterránea de *B. spinosus, E. calamita, Pelophylax perezi, T. lepidus,* (cf.) *N. maura, C. girondica* y *V. latastei* del nivel A de la Sala de las Chimeneas de la cueva de Maltravieso (19 500-18 700 cal. a.B.P. y 19 700-18 750 cal. a.B.P) (Bañuls-Cardona et al., 2012).

Los escasos movimientos detectados son la contracción hacia el norte del límite meridional de la distribución del género *Alytes* y *Lissotriton boscai* en la región de Cádiz (Blain et al., 2013), la extinción de *Testudo hermanni* (Morales y Sanchis, 2009) y la posible extirpación regional y posterior recolonización de *Mauremys leprosa* desde el Magreb (Velo-Antón y Pinya, 2015). Asimismo, la aparición de nuevas especies, como *Hyla meridionalis* y *Chamaeleo chamaeleon,* también desde el norte de África y datadas en tiempos relativamente recientes por los estudios genéticos, de las cuales también se sospecha la intervención humana (Paulo et al., 2002; Recuero et al., 2007), protagonizarán los últimos procesos de distribución expansiva entre la herpetofauna en territorio ibérico.

1.3 EXTINCIÓN O EXTIRPACIÓN

Cuando los organismos no consiguen adaptarse a los nuevos entornos generados por las variaciones climáticas mediante cambios en su distribución hacia ambientes térmicos más favorables, primeramente, tiene lugar una reducción de su rango de distribución geográfica, seguida por un colapso demográfico que puede llevar a una extinción global o local (extirpación). Por su situación geográfica y sus condiciones climáticas más templadas que en el resto de Europa, la península ibérica presenta todas las características para ser una zona de refugio donde las especies termófilas sobreviven durante los periodos más fríos, especialmente en su

parte meridional. En el registro pleistoceno ibérico se documentan la última aparición de ciertas familias de reptiles escamosos y de un grupo de anuros que no cuentan con representantes actuales en la península ibérica, e incluso en algunos casos ni siquiera están representados en todo el subcontinente europeo por lo que hablaremos de extirpación, a falta de poder profundizar más en la determinación a nivel de especie de ciertos de estos fósiles.

En el continente europeo, el registro fósil documenta un retroceso progresivo hacia la zona Mediterránea para muchas familias y géneros de anfibios y reptiles durante el Plioceno conduciendo a sus consiguientes extirpaciones durante el Plioceno y el Pleistoceno inferior en la península ibérica (y otras penínsulas como la itálica o la balcánica), probablemente asociadas con la intensificación de las pulsaciones frías en el hemisferio norte (Bailon y Blain, 2007; Rage, 2013; Blain et al., 2016). A finales del Plioceno inferior (hace aproximadamente 3.2 Ma), las familias con afinidades tropicales como los varanos (Varanidae), las serpientes falsa coral (Aniliidae s.l.) y las cobras (Elapidae) desaparecen de Europa occidental, con sus últimos representantes descritos en España o el Sur de Francia.

En torno a hace 2.6 Ma (el límite actual entre el Plioceno y Pleistoceno), las boas de la arena (Erycinae, Boidae) desaparecen de la península, mientras que durante este periodo otros grupos de reptiles termófilos como los agámidos (Agamidae), las culebrillas ciegas (Blanidae), algunos ánguidos (Anguidae), algunas culebras (Colubridae) y el grupo de las víboras orientales de gran tamaño, sufren un retroceso en su distribución hacia la vertiente mediterránea de la zona sur. Los últimos escamosos "exóticos" (según criterios modernos) que se refugian (o sobreviven) en el sur de la península ibérica donde acaban por extinguirse a finales del Pleistoceno inferior (en torno a 1.3 Ma) son los agámidos y los ánguidos del genero Dopasia (o *Hyalosaurus*).

En cuanto a los anfibios, de momento se ha descrito un único grupo "exótico" en el Pleistoceno ibérico: el grupo de los sapos verdes (*Bufo viridis* s.l.) recientemente separados en varias especies. Aunque posiblemente ligados al registro fósil Mio-Plioceno franco-ibérico, no es descartable una dispersión de los sapos verdes desde Europa central o el Norte de África a finales del Pleistoceno inferior (1.4 Ma), al mismo tiempo que la llegada de los primeros homininos a Europa occidental. La última cita de este grupo se da en el yacimiento murciano de Cueva Victoria en niveles datados recientemente en torno a 900 000 años (Blain et al., 2010; Blain, 2015), la cual resulta más o menos contemporánea del primer pico frío importante (el MIS 22).

Para ilustrar estos eventos de retroceso hacia el sur de familias muy termófilas y las consiguientes extinciones, el registro fósil de un grupo como el de los lagartos agámidos resulta de gran interés, tanto a nivel europeo como ibérico (Fig. 2). Los agámidos son una familia de lagartos de tamaño mediano que viven actualmente en África, Asia, Australia, y en algunas zonas restringidas del sur-este de Europa (Pough et al., 2001; Zug et al., 2001). Los únicos géneros presentes actualmente en Europa son *Stellagama* (Baig et al., 2012) o *Laudakia* (Gasc et al., 1997; Sillero et al., 2014), *Trapelus*, y *Phrynocephalus,* los cuales solo se encuentran en la periferia sureste de este continente, en una pequeña zona de la Grecia continental (región de Thessaloniki) y en unas pocas islas (Corfu, archipiélago de las Cícladas y algunas islas griegas enfrente de las costas turcas) (Gasc et al., 1997; Sillero et al., 2014) (ver Fig. 2).

Del otro lado del Mediterráneo, los géneros *Agama* y *Trapelus* (Bons y Geniez, 1996; Trape et al., 2012) habitan el noroeste de África. Tanto los representantes europeos como africanos frecuentan las sabanas, estepas y desiertos, y poseen un modo de vida ligado a ambientes cálidos y áridos en zonas rocosas o arenosas.

Sus representantes mediterráneos se encuentran principalmente en los pisos bioclimáticos termo- y meso-Mediterráneos, con unas temperaturas medias anuales entre 15 y 18ºC, una temperatura del mes más calido superior a los 24 o 26ºC y del mes más frío entre 5 y 11ºC, y unas precipitaciones anuales bajas (menos de 300 mm) (Önol y Semazzi, 2009).

Las reconstrucciones paleoclimáticas cuantitativas para los yacimientos ibéricos de principios del Pleistoceno con presencia de agámidos han revelado unas condiciones climáticas similares (Agustí et al., 2009).

Ahora bien, al tomar en cuenta el registro fósil europeo de la familia entera (Fig. 2), los primeros fósiles atribuidos a agámidos se han descrito en el Eoceno inferior del Oeste y Norte del continente europeo y después en el Oligoceno de Francia (Augé y Smith, 1997; Augé, 2005). Durante el Mioceno, los agámidos tenían una distribución europea bastante amplia; desde Francia hasta Ucrania (Delfino et al., 2008; Rage, 2013). Más tarde, en el Plioceno, la distribución de esta familia queda restringida a yacimientos localizados en la zona mediterránea, principalmente el sur de Francia, Italia y España (Bailon, 1987; Bailon y Blain, 2007; Delfino et al., 2008). En la península ibérica, los fósiles de agámidos han sido escasamente documentados y, con la excepción del yacimiento plioceno de Sarrión 1 en la provincia de Teruel (Delfino et al., 2008), muchas de sus citas corresponden ahora al Pleistoceno inferior.

Han sido descritos agámidos en el Pleistoceno inferior inicial de las Islas Medas (Girona: Bailon, 1991), de Almenara-Casablanca-4 en la provincia de Castellón, y de Estepa-1 (Sevilla: Blain, 2009; Blain et al., 2016), y posteriormente en el Pleistoceno inferior de Vallirana (Barcelona) y Almenara-Casablanca-1 (Castellón) (Blain y Bailon, 2006; Blain, 2009; Rage, 2013; Blain et al., 2016). Más recientemente, se han descrito unos 50 dentarios de especies pertenecientes a este mismo grupo en el yacimiento de Canal Negre 1 en la provincia de Barcelona, con un contexto cronológico poco preciso y comprendido entre el Mioceno superior final y el Pleistoceno medio (Guillén Castejón, 2010). Finalmente, su última aparición en el registro fósil ibérico tiene lugar en el Pleistoceno inferior final (en torno a 1.3 Ma) en el yacimiento de Quibas, localizado en la provincia de Murcia, hoy en día una de las áreas más áridas del sureste peninsular (Blain et al., 2014). Las nuevas campañas de excavación emprendidas desde 2015 bajo la dirección conjunta del IPHES (Tarragona) y del Museo Nacional de Ciencias Naturales de Madrid en este yacimiento permitirán seguramente en un futuro cercano afinar la cronología y las causas probables de esta extirpación en la península ibérica.

1.4 MACROECOLOGÍA

La dificultad para establecer con certeza una relación causaefecto supone uno de los principales problemas para los estudios en macroecología enfocados a entender los efectos del cambio climático sobre la fauna (Olalla-Tárraga, 2014). Esta clase de trabajos normalmente se centran en el estudio de patrones dentro de una escala espacial, pues tal y como señalan Kerr et al. (2007), la mayoría de procesos de cambio climático suceden a lo largo de una amplia área geográfica. A su vez, los cambios climáticos también suceden en un amplio espacio de tiempo y, a pesar de que normalmente las dinámicas climáticas se estudian a largo plazo, las respuestas de los organismos ante dichos cambios no. Las relaciones causales entre fluctuaciones en las variables climáticas y variaciones en caracteres biológicos, como puede ser el tamaño o la

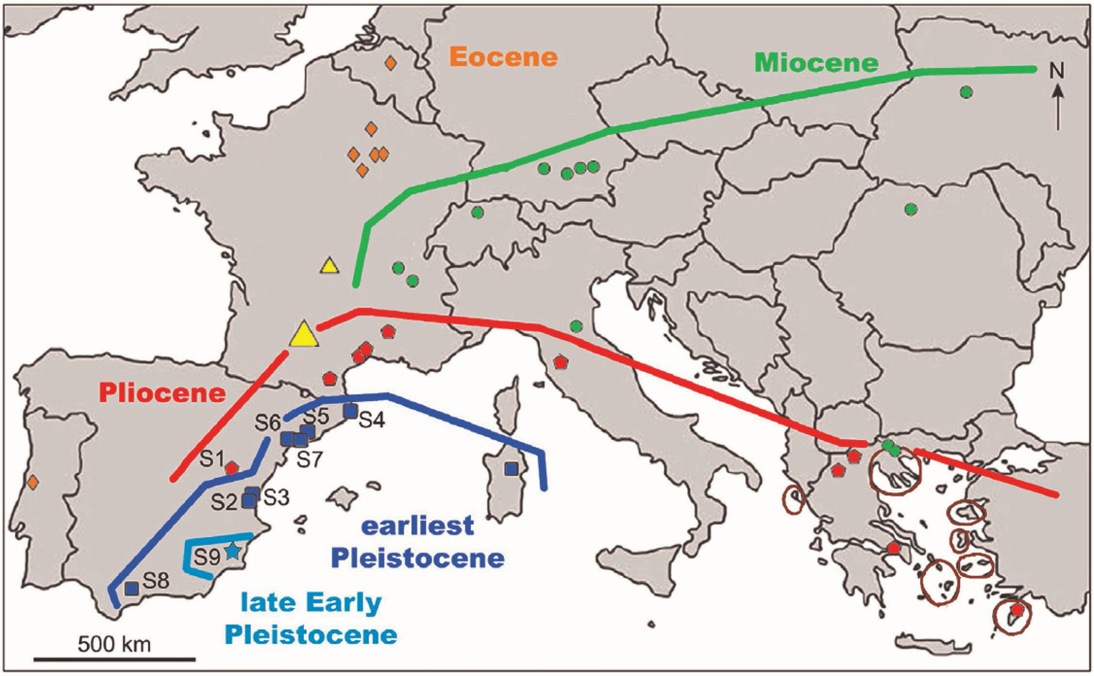

Figura 2. Regresión climática seguida por una extirpación en la península ibérica en base al registro fósil europeo de los lagartos agamidos (familia Agamidae), modificado de Blain et al. (2016). Símbolos: rombo naranja, Eoceno; triangulo amarillo, Oligoceno; circulo verde, Mioceno; pentágono rojo, Plioceno; cuadrado azul oscuro, Pleistoceno inferior inicial; estrella azul claro, Pleistoceno inferior-final. La distribución geográfica actual europea de *Laudakia stellio* está representada por elipses vacíos de color marrón. España: S1, Sarrion 1 (*Agama* sp.; Plioceno); S2, Almenara-Casablanca-4 (Agamidae indet.; Pleistoceno inferior); S3, Almenara-Casablanca-1 (Agamidae indet.; Pleistoceno inferior); S4, Islas Medas (*Agama* sp.; Pleistoceno inferior); S5, Cova Bonica (Agamidae indet.; Pleistoceno inferior); S6, Vallirana (Agamidae indet.; Pleistoceno inferior); S7, Canal Negre 1 (*Agama* sp.; Pleistoceno inferior?, Guillén Castejón, 2010); S8, Estepa-1 (Agamidae indet., Pleistoceno inferior, Blain et al., 2016); S9, Quibas (Agamidae indet., Pleistoceno inferior final, Blain et al., 2014).

Figure 2. Climate-related regression followed by an Iberian extirpation based on the European fossil record of agamid lizards (family Agamidae), modified from Blain et al. (2016). Symbols: orange diamond, Eocene; yellow triangle, Oligocene; green circle, Miocene; red pentagon, Pliocene; dark blue square, Earliest Pleistocene (formerly Late Pliocene, MN17); light blue star, late Early Pleistocene. The approximate European modern range of *Laudakia stellio* is represented by the brown empty ellipses. Spain: S1, Sarrion 1 (Cerro de los Espejos) (*Agama* sp.; Pliocene); S2, Casablanca-Almenara 4 (Agamidae indet.; from Earliest Pleistocene); S3, Casablanca-Almenara 1 (Agamidae indet.; from Earliest Pleistocene); S4, Medas Islands (*Agama* sp.; Early Pleistocene); S5, Cova Bonica (Agamidae indet.; Earliest Pleistocene); S6, Vallirana (Agamidae indet.; Earliest Pleistocene); S7, Canal Negre 1 (*Agama* sp.; Earliest Pleistocene?, Guillén Castejón, 2010); S8, Estepa-1 (Agamidae indet., Earliest Pleistocene, Blain et al., 2016); S9, Quibas (Agamidae indet., late Early Pleistocene, Blain et al., 2014).

diversidad de especies, deberían acontecer del mismo modo independientemente de la dimensión (espacial o temporal) en la que sean estudiados.

Por lo tanto, el análisis de patrones y reglas ecogeográficas a largo plazo en la escala temporal durante el periodo Cuaternario, cobra importancia como una nueva fuente de datos que, al ser integrados con los resultados de estudios procedentes de otras ramas de la ecología y biología en general, ayudarán a establecer con mayor seguridad y precisión las relaciones causa-efecto, los mecanismos y los procesos que generan la distribución actual y futura de las especies y la influencia del clima sobre las mismas. En concreto, uno de los factores más determinantes en la biología de las especies y más estudiados en macroecología es su tamaño.

Este puede verse influido directa o indirectamente por factores abióticos como la temperatura o la humedad (p. ej. Atkinson, 1994; Gillooly et al., 2002; Indermaur et al., 2010) y repercute directamente en aspectos de su fisiología y ecología (LaBarbera, 1989). En concreto, la relación entre la temperatura y el tamaño de los organismos constituye el eje central de dos reglas ampliamente estudiadas en ecología: regla de Bergmann (Bergmann, 1847) y la TSR (“Temperature- Size-Rule”) (Atkinson, 1994). Ambas proponen la presencia de individuos de mayor tamaño en climas más fríos, es decir el mismo patrón, mientras que el mecanismo subyacente varía en cada caso siendo, a grandes rasgos, una mejor conservación del calor en el caso de la regla de Bergmann y el retraso de la maduración junto con un aumento de la fecundidad de las hembras y una mayor supervivencia de juveniles en el caso de la TSR (Atkinson, 1994; Atkinson et al., 2003; Angilletta et al., 2004).

Ante la falta de consenso en cuanto a la relación del tamaño de los anfibios (y de animales ectotermos en general) con las variables climáticas (ver revisión en Ashton, 2002) y la importancia de resolver esta cuestión tanto desde el punto de vista teórico como por sus posibles aplicaciones, el registro fósil puede aportar nuevos datos desde una perspectiva diferente.

Un ejemplo lo constituye el caso del sapo corredor (*Epidalea calamita*) cuyo tamaño fue estudiado a partir de muestras fósiles procedentes de dos de los yacimientos pleistocénicos de la Sierra de Atapuerca (Burgos, España) donde la acumulación de restos de *E. calamita* se debe en su mayor parte a mortalidad natural durante la hibernación junto con la acumulación ocasional por la acción de predadores oportunistas (Blain et al., 2008, 2009a); estos son la Gran Dolina y el Portalón de Cueva Mayor.

El conjunto de ambas secuencias comprende más de un millón de años en la misma localización geográfica (Fig. 3) evitando así posibles sesgos espaciales en el estudio de la influencia de la temperatura y la humedad sobre el tamaño (longitud hocico-cloaca o SVL: Snout to Vent Length) de dicho anuro, constituyendo así la localización ideal para llevar a cabo este trabajo.

Los datos de tamaño se obtuvieron a partir de medidas tomadas sobre el húmero, considerado un elemento identificable a nivel de especie (Sanchiz, 1977; Bailon, 1999) además de un excelente indicador de tamaño y sexo del individuo vivo (Martínez-Monzón, 2017). La integración de estos datos de tamaño junto con los valores de temperatura y humedad procedentes de las reconstrucciones paleoclimáticas de ambos yacimientos basadas

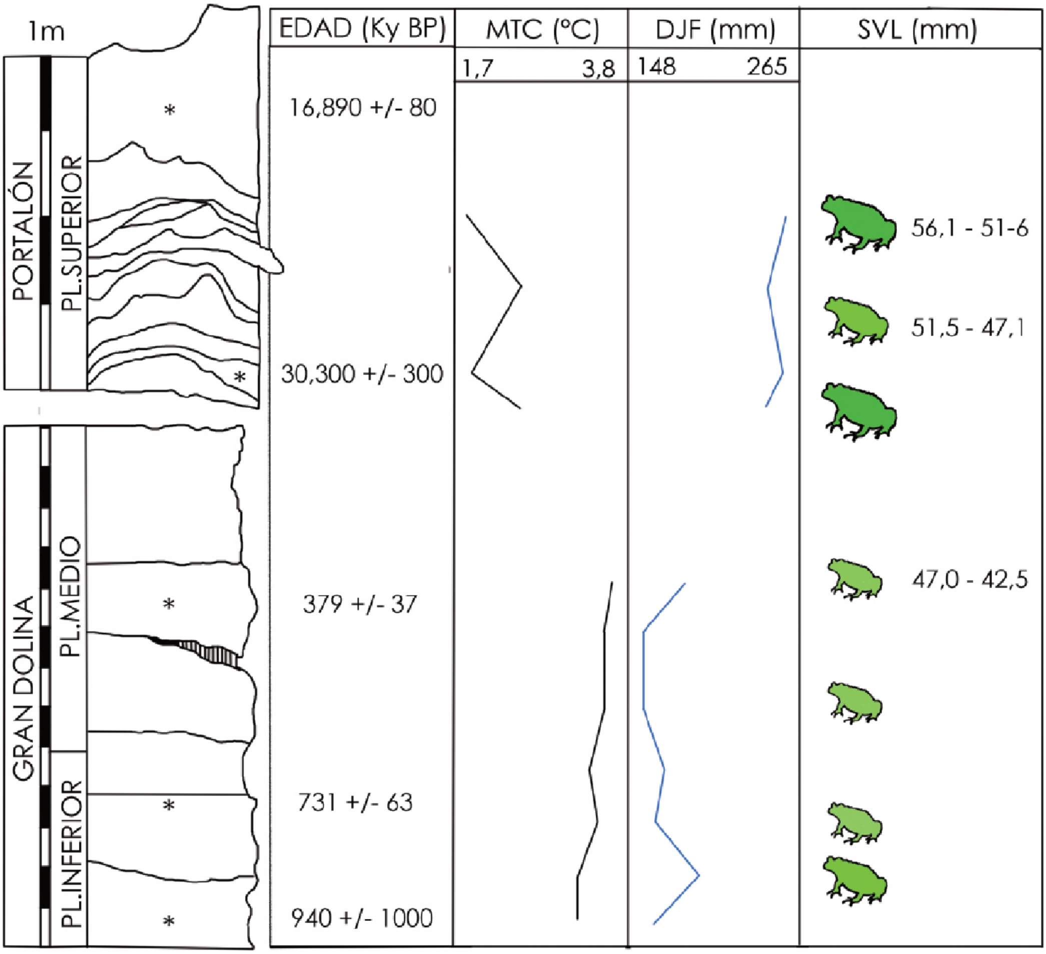

Figura 3. De izquierda a derecha: Yacimiento, periodo geológico, secuencia estratigráfica de ambos yacimientos modificadas de López-García et al. (2010b) y de Parès y Pérez-González (1999) y cronología absoluta basada en dataciones de diferentes puntos de la secuencia (ver síntesis en Blain et al., 2012). Se presentan los valores de la temperatura media del mes más frío; MTC (Mean Temperature of the Coldest Month) y de la precipitación de invierno; DJF (December-January-February precipitation) a lo largo de ambas secuencias junto con la SVL (Snout to Vent Length) dividida en tres rangos de tamaño.

Figure 3. From left to right: Site, geologic period, stratigraphic sequence of both sites modified from López-García et al. (2010b) and Parès y Pérez-González (1999) and absolute chronology based on datings from different points of the sequence (cf. synthesis in Blain et al., 2012). Values for Mean Temperature of the Coldest Month (MTC) and winter precipitation (December-January-February precipitation; DJF) are shown along both sequences together with SVL (Snout to Vent Length) divided in three body size ranges.

en la microfauna (López-García, 2008; López-García et al., 2010b; Blain et al., 2009a, 2012), reveló una elevada influencia de dichas variables climáticas sobre el tamaño de *E. calamita* alcanzándose mayores tamaños en periodos más fríos y húmedos en invierno (Fig. 3). Al igual que sucede actualmente en diferentes especies de anfibios, la respuesta observada en las poblaciones de *E. calamita* ante las variaciones climáticas sucedidas a lo largo de ambas secuencias no fue equivalente en ambos sexos habiéndose registrado una mayor influencia del clima sobre las hembras lo cual, respalda los datos obtenidos en poblaciones actuales de diversos anuros (Hemeelar, 1988; Schäuble, 2004; Leskovar et al., 2006).

En este caso, la relación entre el tamaño de *E. calamita* y la temperatura se ajusta al patrón derivado tanto de la regla de Bergmann como de la TSR. Este hecho constituye un nuevo dato a favor del cumplimiento de dichas reglas en ectotermos y concretamente en anfibios, además de reforzar la validez de esta nueva metodología basada en el registro fósil para el estudio de reglas y patrones en macroecología. Por otro lado, dado que ninguna de dichas reglas contempla la humedad como factor determinante a la hora de explicar las variaciones de tamaño, en este caso concreto, el mecanismo propuesto consiste en la combinación de una maduración retrasada en climas fríos unido a una mayor disponibilidad de recursos en climas húmedos, lo cual se traduce en un aumento de tamaño en climas fríos y húmedos (principalmente en invierno) permitiendo así un mayor acumulo de grasa y un aumento de la fertilidad de las hembras con las ventajas adaptativas que esto supone (Martínez-Monzón, 2017).

Dado que los datos de tamaño resultan relativamente fáciles de inferir a partir de muestras fósiles gracias a la alta correlación entre ciertas medidas de algunos huesos (como el húmero) y el tamaño del individuo vivo, esta metodología resulta aplicable a una gran variedad de muestras de diferentes especies de anfibios y reptiles donde la mayoría de elementos del esqueleto postcraneal se consideran identificables a nivel de especie. Extender dicha metodología a reptiles contribuiría a su vez al establecimiento de generalidades dentro de los vertebrados ectotérmicos.

En el caso concreto de anfibios, contar con datos de otras especies y aplicar dicha metodología a muestras procedentes de otros yacimientos permitirá la comparación de la respuesta a los cambios ambientales entre diferentes especies y localizaciones geográficas dentro del mismo periodo temporal, haciendo posible corroborar el seguimiento de unas normas de reacción generales en anfibios o, por el contrario, desmintiendo la existencia de dichas generalidades promoviendo así el estudio de cada caso de manera individual.

1.5 DISCUSIÓN

Los casos de estudio anteriormente presentados ponen de manifiesto que los trabajos científicos basados en material fósil de herpetofauna, darán lugar a una nueva fuente de conocimiento con una gran cantidad de implicaciones, especialmente en el campo de la paleoecología. El estudio de las poblaciones de anfibios y reptiles del Cuaternario nos ayudará a conocer de qué manera se ha generado la distribución y diversidad de las especies actuales, así como a identificar, caracterizar y entender procesos tales como la aparición o la extinción de especies, la evolución de las mismas y los procesos de adaptación a variaciones ambientales mediante cambios en el fenotipo.

Los resultados de esta línea de investigación ayudarán a comprender la evolución y la situación actual de las especies y a utilizar ese conocimiento para poder prever en la medida de lo posible las reacciones, tendencias y/o patrones de las poblaciones de las especies de anfibios y reptiles ante los actuales y futuros cambios en las condiciones ambientales, así como a la viabilidad y plasticidad fenotípica de sus poblaciones.

La paleoherpetología también resulta de gran utilidad a la hora de esclarecer o reafirmar las relaciones filogenéticas vigentes en anfibios y reptiles pues el registro fósil constituye la fuente principal de puntos de calibración a la hora de estimar tiempos de divergencia mediante la aplicación de relojes moleculares.

Para cerrar la discusión del artículo, cabe resaltar que el material fósil de herpetofauna, ha pasado prácticamente desapercibido en el contexto de la biología de la conservación y aún en la actualidad, su potencial está lejos de ser explotado completamente. La integración de los datos aportados por la paleoherpetología junto con los datos actuales procedentes de otras ramas de la biología podría dar lugar a estudios multidisciplinares de gran envergadura cuyos resultados serán sin duda originales y enriquecedores para el conjunto de la biología y ecología animal.

1.6 CONCLUSIONES

1. La península ibérica constituye actualmente una región de importanciacapital para la diversidad de la herpetofauna europea y ha constituido en el pasado un refugio climático para la mayoría de especies de anfibios y reptiles. El registro paleontológico ibérico del Pleistoceno superior final permite observar una contracción de la distribución de las especies más termófilas y típicas de los ambientes mediterráneos en las regiones meridionales y centrales ibéricas, mientras que el tercio norte presentaba una herpetofauna menos rica, pero con una mayor adaptabilidad a climas y ambientes fríos, en congruencia con el fenómeno de glaciación que tuvo su mayor auge en el Último Máximo Glacial. Este escenario cambiará con el final del período glacial y especialmente con el inicio del Holoceno, con la colonización del tercio norte a partir de los refugios meridionales, si bien también se produce la llegada de nuevas especies mediterráneas a través de los Pirineos y desde el Magreb. Esto nos muestra la rápida capacidad que presentan las especies de herpetofauna para colonizar nuevos espacios y ampliar su distribución con escenarios climáticos favorables, así como la existencia de fenómenos de contracción espacial en su distribución en el caso contrario.

2. Los anfibios y reptiles en Europa occidental han sufrido una progresiva disminución de la diversidad de especies con la desaparición progresiva de varias familias durante el Plioceno y el principio del Pleistoceno. En la península ibérica, yacimientos del Pleistoceno inferior (2.6 a 0.8 Ma) siguen documentando la presencia de taxones "exóticos", los cuales habrían desaparecidos en el resto de Europa, como las víboras orientales, los agámidos, los ánguidos (una especie fósil del genero *Pseudopus* y *Dopasia*), y un representante del grupo de los sapos verdes (*Bufo viridis* sensu lato). Como se ha demostrado en el caso bien ilustrado de los agámidos, el patrón geográfico (retirada progresiva norte-sur) y temporal (correspondiéndose con los primeros picos de clima frío) de estas extinciones (o extirpaciones) en el territorio ibérico sugiere una influencia importante de los factores climáticos, afectando a cada taxón de manera diferente según sus requerimientos climáticos.

3. El registro fósil se presenta como una nueva herramientapara el estudio de la influencia del clima sobre el tamaño de las poblaciones de anfibios y por tanto de las reglas o patrones ecogeográficos que relacionen dichas variables.

Los resultados del caso de estudio expuesto centrado en el sapo corredor (*Bufo calamita*), apoyan la validez de la regla de Bergmann y la TSR en anuros habiéndose registrado la presencia de individuos de mayor tamaño durante los periodos con inviernos más fríos. Por otro lado, se registró dimorfismo sexual en la respuesta a un descenso de las temperaturas siendo las hembras el sexo más susceptible y el que presentó mayor variación de tamaño.

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A2.2 Early-Middle Pleistocene freshwater ecosystems in the Sierra de Atapuerca (northern Iberia) based on the Gran Dolina fish record

This work published in the journal Palaeogeography, Palaeoclimatology, Palaeoecology has been written by Ángel Blanco-Lapaz (University of Tübingen) in the framework of his PhD. He developed all the work corresponding to the main signatory author. My contribution to this publication was the analysis and discussion of the results corresponding to the section 3. “Body size evolution of *S. trutta* through the sequence and its relationship with temperature”.

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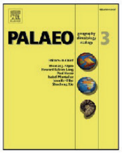

Early-Middle Pleistocene freshwater ecosystems in the Sierra de Atapuerca (northern Iberia) based on the Gran Dolina fish record

Angel Blanco-Lapaz [a,b,*], Almudena Martínez-Monzón [c,d], Hugues-Alexandre Blain [c,d], Gloria Cuenca-Bescós [e]

[a] Senckenberg Centre for Human Evolution and Paleoenvironment (SHEP), Hölderlinstrasse 12, 72070 Tübingen, Germany
[b] Institute for Archaeological Sciences, University of Tübingen, Rümelinstrasse, 23, 72070 Tübingen, Germany
[c] Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain
[d] Universitat Rovira i Virgili, Departament d'Història i Història de l'Art, Avinguda de Catalunya 35, 43002 Tarragona, Spain
[e] Aragosaurus-IUCA, Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, c. Pedro Cerbuna 12, 50009 Zaragoza, Spain

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ABSTRACT

Fish bones are common in Pleistocene cave deposits in Europe. In this paper, we report on fish remains from the Gran Dolina cave (Trinchera del Ferrocarril) in the Sierra de Atapuerca in Spain, to increase what is known of the freshwater ecosystems close to the cave. The 19-m-thick section, divided into 11 stratigraphic levels, represents an Early to Middle Pleistocene time span as dated by biostratigraphy, ESR, U-series, and magnetostratigraphy. We focus on the Sondeo South site, excavated from 1993 to 1999, which has yielded 1087 fish bones comprising the following taxa: brown trout (*Salmo trutta*), the common European eel (*Anguilla anguilla*) and chub (*Squalius* sp.). Taphonomic studies suggest that the European eagle owl (*Bubo bubo*) was the most likely predator responsible for the accumulation. Changes observed in the body size of brown trout through the sequence cannot be attributed to climate change (contravening Bergmann's rule). Our study documents the presence of a pre-mountain river system characterized by permanent, oxygen-rich, relatively cold flowing waters around the Sierra de Atapuerca during Early-Middle Pleistocene times.

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* Corresponding author at: Senckenberg Centre for Human Evolution and Paleoenvironment (SHEP), Hölderlinstrasse, 12, 72070 Tübingen, Germany.
E-mail address: angel.blanco-lapaz@uni-tuebingen.de (A. Blanco-Lapaz).

2.1 INTRODUCTION

Microvertebrate remains are commonly recovered from Pleistocene contexts in Europe. Over the course of the last few decades, abundant small-vertebrate remains from the Gran Dolina cave (Trinchera del Ferrocarril) in the Sierra de Atapuerca in Spain have been published: remains belonging to rodents and insectivores (Cuenca-Bescós et al., 2005, 2011, 2017; Cuenca-Bescós and García, 2007; Rofes and Cuenca- Bescós, 2009, 2011), bats (Galán et al., 2019), birds (Sánchez-Marco, 1999; Bennássar, 2010; Núñez-Lahuerta et al., 2019), and amphibians and reptiles (Blain, 2005, 2009; Blain et al., 2008, 2009, 2013). All these studies significantly expand our knowledge of the biochronology, depositional processes and paleoenvironmental conditions (see Rodríguez et al., 2011; Cuenca-Bescós et al., 2010, 2011, 2016).

Fish remains from the very first field campaigns (1987–1994) were mentioned by Doadrio (in Sanchíz, 1987) and published by Aguirre (1995), describing the presence of Salmo trutta and unidentified cyprinids. However, this was just a faunal list, and the references did not go any deeper into an interpretation of the remains. Other assemblages of fish remains belonging to neighboring sites have been cited as well. Cuenca-Bescós et al. (1997) mention the presence of *Salmo* sp. and *Leuciscus* sp. in the Middle Pleistocene site of Sima de los Huesos. Cuenca-Bescós et al. (2015) and Huguet et al. (2015) document the presence of the same taxa in the Early Pleistocene site of Sima del Elefante (TE), and the authors link the accumulation of fish and aquatic bird remains with the presence of the white-tailed sea eagle (*Haliaeetus albicilla*), recovered in level TE9c.

Finally, Blanco-Lapaz and Vergès (2016) document the presence of *S. trutta* in the Neolithic site of El Mirador cave. Previous archaeozoological studies and analyses, all of them based on Middle-Late Pleistocene sites, provide evidence of the exploitation of aquatic vertebrates by hominins in southwest and central Europe. Most of these pertain to marine coastal archaeological sites (e.g. Cleyet-Merle, 1990; Morales-Muñiz and Roselló-Izquierdo, 1988; Roselló-Izquierdo et al., 1995; Roselló-Izquierdo and Morales-Muñiz, 2005; Brown et al., 2011; Zilhão et al., 2020), and fewer studies are related to inland sites close to rivers and lakes (e.g. Morales, 1980; Russ and Jones, 2011; Conard et al., 2013; Rey-Rodríguez et al., 2018; Blanco-Lapaz, 2019; Guillaud et al., 2021). As regards the Iberian Peninsula, the previous studies based on Middle-Late Pleistocene sites indicate the presence of salmonids (*Salmo* sp., *S. trutta*) (Cueva Amalda, Cueva Millán, Cova dels Ermitons), the common eel (*Anguilla anguilla*) (Cueva Millán) and cyprinids (the *Pseudochondrostoma polylepis* group) (Cueva Millán) (Roselló- Izquierdo and Morales-Muñiz, 2005).

However, not all the fish assemblages recovered in Pleistocene archaeological sites were accumulated by humans. Other predators, such as small carnivores and birds of prey, have also been implicated (Nicholson, 1991, 2000; Le Gall, 1999; Russ, 2010b; Russ and Jones, 2011; Guillaud et al., 2017, Guillaud et al., 2018; Böhme, 2019). From a paleoecological point of view, body size is one of the most significant biological traits in fishes, as it determines the life history and several physiological and biochemical processes (Bonner, 2011). Bergmann (1847) proposed the tendency of organisms to be smaller at high temperatures and low latitudes and larger at low temperatures and high latitudes. This global pattern, known as Bergmann's rule, has been relatively little studied in marine fishes (Alonso-Fernández et al., 2014; Fernández-Torres et al., 2018;

Saunders and Tarling, 2018), freshwater fishes (Mousseau, 1997; Belk and Houston, 2002; Watt et al., 2010; Rypel, 2014; Adhikari, 2015), and particularly in Iberian freshwater fishes (Parra et al., 2009; Arranz-Urgell, 2017).

In general, it has been proved that Bergmann's rule applies to freshwater fish, but the strength varies with size and trophic levels. Arranz-Urgell (2017), for example, proved that temperature affects the size metrics for perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), ruffe (Gymnocephalus cernuus), white bream (*Abramis brama*), and zander (*Sander luciperca*) in the Iberian Peninsula, showing that these species are relatively smaller as adults at higher water temperatures.

On the other hand, Rypel (2014) evaluated the body size of various North American freshwater fish species in correlation with the mean annual temperature and the elevation. Bergmann's rule was observed for 11 (all of them cool- or cold-water species) out of 29 species, whereas the converse Bergmann rule was observed in 10 (all of them warm-water species) out of 29. Two non-native species, *S. trutta* (cold-water) and *Cyprinus carpio* (Cyprinidae) (warm-water), were also studied but in these cases, no correlation with Bergmann's rule was observed, proving that some freshwater fish species do not express this macroecological pattern, but the study suggests that a major and relatively unexplored link exists between the thermal requirements of species and the evolution of body size variation (Rypel, 2014). Previous studies in Gran Dolina using natterjack toad (*Epidalea calamita*) remains analyzed the correlation between body size and climate, proving the validity of Bergmann's rule for this amphibian on the basis of the fossil record (Martínez-Monzón et al., 2018). The authors found the body size for this species to be negatively related to the mean annual temperature and the mean temperature of the coldest month (showing an increase in size in periods with cooler winters), and positively related to winter precipitation.

In accordance with Bergmann's rule, we expected that the brown trout individuals in Gran Dolina might be bigger in colder periods and smaller in warmer periods. Although some fish assemblages have previously been studied in the Sierra de Atapuerca (Aguirre, 1995; Cuenca-Bescós et al., 1997, 2015; Huguet et al., 2015), the present paper describes for the first time the fish remains from the Gran Dolina Sondeo South (TDS) excavations, exploring the origin and characteristics of this Early-Middle Pleistocene fish assemblage from a taxonomic, taphonomic and ecological point of view. This adds to our knowledge of the freshwater ecosystems of the Sierra de Atapuerca during the late Early and Middle Pleistocene.

2.2 GEOLOGICAL SETTING

The site of Gran Dolina (42º21'09"N 3º31'06"W; 900 m.a.s.l.) (in the railway Trench, labeled, TD) is a cave infilled by at least 25 m of Pleistocene sediments, located in the Sierra de Atapuerca (Burgos, Spain) (Fig. 1). The Gran Dolina sedimentary deposits reveal a rather common succession in karstic tiered caves that developed in relation to the progressive incision of the Arlanzón river. The stratigraphy of the cave comprises 11 layers, TD1 to TD11 from bottom to top. It reflects a broad evolution and includes cave interior deposits at the bottom (including silts, clays, and flowstones) below unit TD4, and an assemblage of diamictons and gravels, often showing channel cut-and-fill structures with abundant sand and silts, from TD4 to the top of the sequence (Campaña et al., 2017). Gran Dolina provides an unusual supply of archaeological remains and fossils of large and small vertebrates that have been used to document human activity and its relationship to the environment over the last one million years (Carbonell et al., 1995, 2008; Bermúdez de Castro et al., 1997, 2008; Rodríguez et al., 2011; Rodríguez-Gómez et al., 2013; Cuenca-Bescós et al., 2010, 2016; Saladié et al., 2021).

The stratigraphic layers of the site have been extensively excavated, studied and dated using numerous methods, such as biostratigraphy, luminescence, electron spin resonance and paleomagnetism (Cuenca-Bescós et al., 1999, 2001, 2016; Falguéres et al., 1999; Parés and Pérez-González, 1999; Berger et al., 2008; Parés et al., 2013; Arnold et al., 2013). Gran Dolina contains one of the most complete Quaternary stratigraphic sequences in Spain, running from the Early to Middle Pleistocene and comprising some 700,000 years (1 Ma to 244 ka: see the latest updates on the chronology of Gran Dolina in Álvarez-Posada et al., 2018).

Regarding the current environment and climatic parameters of the study area, the province of Burgos is considered one of the coldest regions in the Iberian Peninsula (Font-Tullot, 2000); it has a continental Mediterranean climate with mean annual temperature values of 9.9 ◦C (meteorological station of Burgos Air Base, 891 m.a.s.l.). The Burgos region is characterized by its highly contrasting seasonality: winters are cold, including snowfalls and below-freezing temperatures that reach -15 ◦C, whereas summer mean temperatures are between 15 and 20 ◦C (Font-Tullot, 2000; Ninyerola et al., 2005). On the other hand, the region connects the Eurosiberian and Mediterranean bioclimatic regions of the Iberian Peninsula, which is reflected in the high biodiversity of the area.

2.3 MATERIALS AND METHODS

The fish remains from Gran Dolina layers TD4-TD8 (Early Pleistocene) and TD10 (Middle Pleistocene) were recovered during the 1991, 1993–1994 and 1996–1997 field campaigns, during the latter of which a test pit (TDS, around 9 m2) was made. We here study the fossil assemblage, comprising 1087 fish remains (Table 1).

The fish remains were collected by applying standard water-screening techniques (lowest mesh 0.5 mm) to the sediments excavated during the archaeological campaigns excavations. The anatomy and taxonomy of each of the studied specimens were identified using material from the comparative collection housed in the Senckenberg Center for Human Evolution (University of Tübingen). Traces of human activities such as butchery or burning, animal modifications such as gnawing, pits and digestion marks, as well as environmental alterations, were also checked during this study.

All the elements were classified, and the bone surface was observed using a binocular microscope (OPTIKA SZM-2); pictures were taken using a Zeiss Stemi 305 EDU microscope. Bone surface damage was allocated to three categories of digestion mark: null-light (0), moderate (1) and moderate-heavy (1_2) (modified from Andrews, 1990; Fernández-Jalvo et al., 2016; Guillaud et al., 2015, 2018) (Table 3, Figs. 2 and 4B). For each level, the number of identified specimens (NISP) was determined. Several fish studies have determined the season of death (seasonality) using sclerochronological methods (Van Neer et al., 1999; Le Gall, 2003; Guillaud et al., 2017) based on scales and vertebrae.

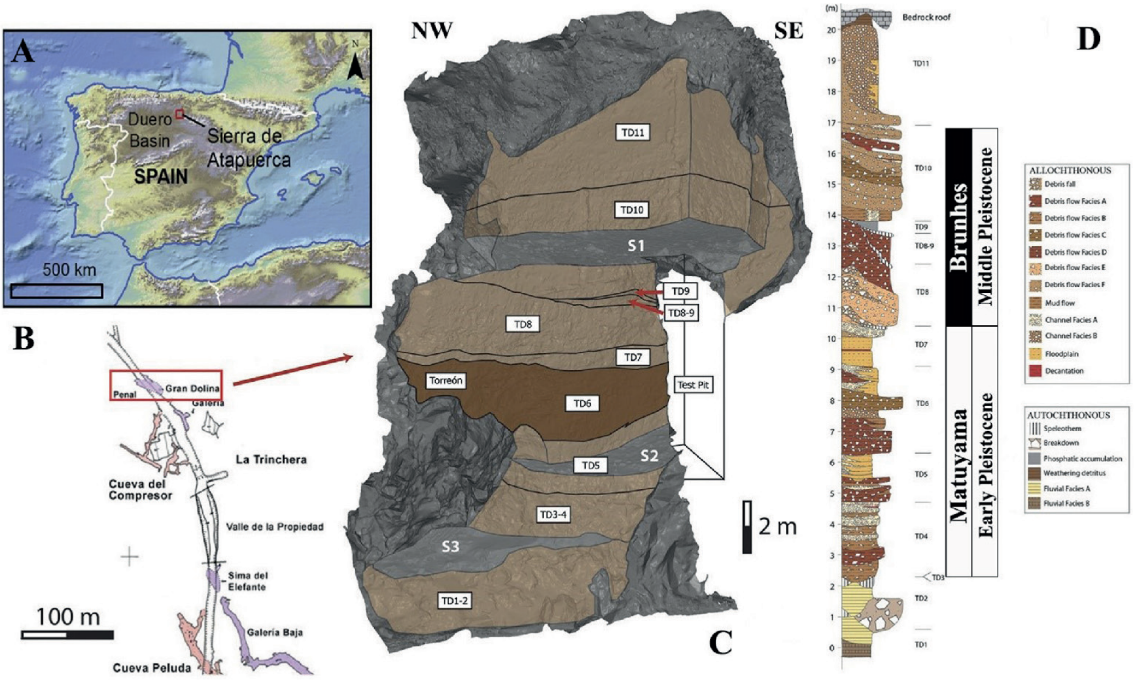

Figure. 1. (**A**) Location of the Sierra de Atapuerca. (**B**) Location of the Gran Dolina site situated in a railway trench ("Trinchera"). (**C**) General 3D model of the Gran Dolina site in 2012. Brown areas indicate stratigraphic units. Grey areas are the wall and roof of the cave. (D) Stratigraphic units (TD1 to TD11) and sedimentary facies of the Gran Dolina site. 1A map created by ArcGis 10.1 using the elevation data of the free access dataset SRTM90 (http://www.cgiar-csi.org/data/srtm-90m-di gital-elevation-database-v4-1). 3D model of 1C created by 3DReshaper 8.1 software (http://www.3dreshaper.com/en/) (modified from Campaña et al., 2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Here, however, the high degree of mineralization observed on the vertebrae together with the absence of fossil scales prevent any study using such a methodology. In accordance with Martínez-Monzón et al. (2018), the climatic values of the mean annual temperature (MAT), the mean temperature of the coldest month (MTC) and the mean temperature of the warmest month (MTW) were obtained from the paleoclimate reconstructions conducted by Blain et al. (2009, 2012, 2013) using herpetofaunal assemblages as climate proxies (Table 4). Due to the abundance of *Salmo trutta*, this species was selected to infer the average total body length from well-preserved vertebrae based on published regressive statistics using the total length of the vertebrae (BL) (Prenda et al., 2002; Blanco-Lapaz and Vergès, 2016) (Table 2, Figs. 3A, B and 4C). In order to understand the relationships between body size and temperature, we performed simple least square (OLS) regression models conducted with R (R core team) taking on a significance level of $\alpha = 0.05$.

Table. 1. Fish taxa identified in the Early and Middle Pleistocene layers of Gran Dolina (Sierra de Atapuerca, Spain). NISP: number of identified specimens; % Percentage of the assemblage.

Levels	Salmonidae				Anguillidae		Cyprinidae				Unidentified		NISP
	S. trutta		Unidentified		*A. anguilla*		*Squalius* sp.		Unidentified				
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	
TD10-1	6	85.7							1	14.3			7
TD10-2	8	61.5							5	38.5			13
TD10-3	33	76.7			5	11.6			5	11.6			43
TD10-4	63	63.0	1	1.0	6	6.0	4	4.0	26	26.0			100
TD8a	13	54.2							11	45.8			24
TD8b													0
TD7					2	100.0							2
TD6-1	216	89.6	1	0.4	1	0.4			23	9.5			241
TD6-2													0
TD6-3	349	95.9	2	0.5					11	3.0	2	0.5	364
TD5a	131	99.2			1	0.8							132
TD5b	109	89.3			1	0.8	1	0.8	11	9.0			122
TD5c									1	100.0			1
TD5d	1	100.0											1
TD4	37	100.0											37
NISP	966		4		16		5		94		2		1087
%	88.9		0.4		1.5		0.5		8.6		0.2		

2.4 RESULTS

A total of 1087 fish remains were identified in the Early to Middle Pleistocene layers of the Gran Dolina TDS sequence. All the levels yielded some evidence of fish, with the exception of levels TD6-2 and TD8b. The levels with the highest number of remains were TD6-3 and TD6-1, followed by TD5a, TD5b and TD10-4.

Taxonomic composition

The whole fish assemblage comprises three different families: Salmonidae, Cyprinidae and Anguillidae (Table 1, Fig. 4A). The predominant fish family is Salmonidae (90.3%), and most of the remains belong to the brown trout (S. trutta) (Fig. 3A–B) (88.9%). This species is represented almost exclusively by vertebrae and teeth. Less frequent are remains of Cyprinidae (carp family) (9.1%), The genus *Squalius* was identified in levels TD10-4 and TD5b based on two pharyngeal arches characteristic of this taxon (Fig. 3C–E).

The rest of the cyprinid remains correspond to vertebrae that are not possible to identify to genus or species level due to the similar vertebral morphology in this family (Prenda and Granado-Lorencio, 1992; Russ, 2010a). The assemblage also shows the presence in levels TD5a, TD5b, TD6-1, TD7, TD10-3 and TD10-4 of the common European eel (*Anguilla anguilla*) (1.5%), only represented by vertebrae (Fig. 3F) and constituting the first record of this species in the Early-Middle Pleistocene sites of Atapuerca.

Salmonidae

As mentioned above, Salmonidae and particularly the species *S. trutta* is the most represented taxon in the whole assemblage. Of the 37 fish remains recovered in TD4, only the brown trout (*S. trutta*) was identified. The sub-levels of TD5 are dominated by the same species (94.1%) although no item was recovered in level TD5c, only one vertebra in TD5d (100% of the sample), and the rest of the brown trout remains are distributed between TD5b (NISP = 109; 89.3%) and TD5a (NISP = 131; 99.2%).

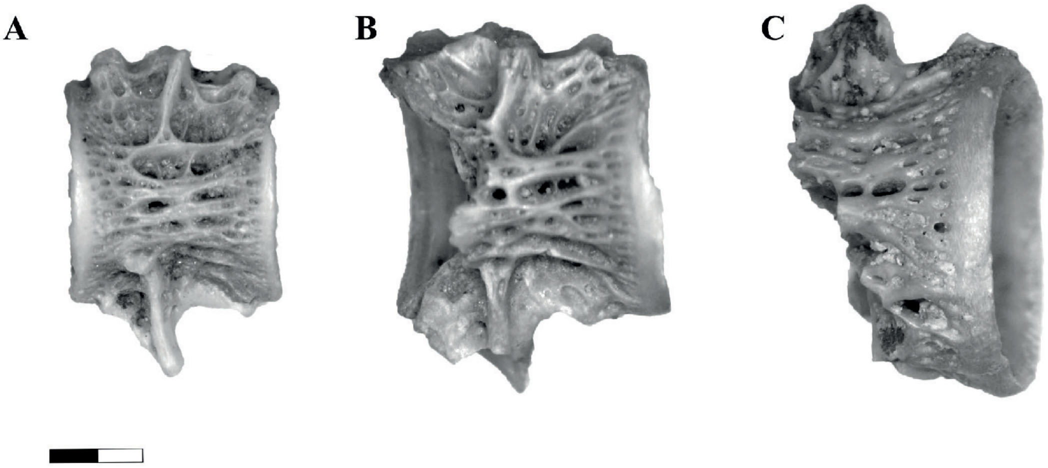

Figure. 2. Categories of digestion marks on *S. trutta* caudal vertebrae in lateral view (TD6-3). (**A**) null-light digestion (category 0). (**B**) almost complete vertebra showing moderate digestion (category 1). (**C**) vertebra showing damage in more than 50% of the bone, moderate-heavy (category 1_2). Scale 5 mm.

Table. 1. Body size estimations for *Salmo trutta* individuals from the Early-Middle Pleistocene of Gran Dolina (Sierra de Atapuerca, Spain).

Levels	<10 cm		10–20 cm		20–30 cm		30–40 cm		40–50 cm		50–60 cm		+ 60 cm		Total NISP
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	
TD10-1			3	100.0											3
TD10-2			1	25.0			1	25.0			2	50.0			4
TD10-3			8	36.4	6	27.3	3	13.6	3	13.6	1	4.5	1	4.5	22
TD10-4			8	17.8	11	24.4	13	28.9	8	17.8	3	6.7	2	4.4	45
TD8a			4	33.3	5	41.7	1	8.3	2	16.7					12
TD7															0
TD6-1	8	4.1	187	95.9		0.0		0.0							195
TD6-3			4	1.4	149	51.4	76	26.2	43	14.8	16	5.5	2	0.7	290
TD5a			7	5.9	13	10.9	47	39.5	46	38.7	6	5.0			119
TD5b	2	2.2	27	29.0	30	32.3	16	17.2	14	15.1	4	4.3			93
TD5c															0
TD5d															0
TD4			3	8.8	29	85.3	2	5.9							34
Total NISP	10		252		243		159		116		32		5		817
%	1.2		30.8		29.7		19.5		14.20		3.92		0.61		

In TD6, salmonids are also the most represented taxon in both sub-levels, TD6-3 (96.4%) and TD6-1 (90.0%). *S. trutta* is again the predominant species (TD6-3, NISP = 216; TD6-1, NISP = 349), although unidentified salmonid remains were recovered in both sub-levels (TD6-3, NISP = 1; TD6-1, NISP = 2). TD7 does not include any salmonid remains. The TD8a assemblage is also dominated by the brown trout (NISP = 13, 54.2%).

In all the TD10 sub-levels, Salmonidae is the most represented family, and its highest peak is reached in TD10-1, where only S. trutta is present (NISP = 6, 85.7%), although a decrease in the number of remains is observed from TD10-4 (NISP = 63) to TD10- 1 (NISP = 6) (Fig. 4A).

Cyprinidae

Cyprinids do not occur in the assemblage until sub-level TD5c, where they are the only represented taxon (NISP = 1). Cyprinid remains correspond to 9.8% of the sample in TD5b (NISP = 12), where only two remains are identified at genus level as *Squalius* sp. Thereafter cyprinids appear again and represent 3% of the sample in TD6-3 (NISP = 11). The percentage and number of cyprinid remains increase in TD6-1, where 9.5% of the sample corresponds to this family (NISP = 23).

Then the percentage further increases from TD8a to TD10-1 with some variations. TD8a has the highest representation for the family in the whole TDS assemblage, reaching 45.8% (NISP = 11), and in TD10 the percentages fluctuate from one sub-level to another, with TD10-4 (30%), TD10-3 (11.6%), TD10-2 (38.5%) and TD10-1 (14.3%). The percentage of cyprinid remains increases in the TD10 sub-levels in comparison with other levels, where cyprinids are less represented in the sample (less than 10%) (Fig. 4A).

Anguillidae

The family Anguillidae, only represented here by one species, *A. anguilla*, is present in TD5b and TD5a, representing 0.8% of the sample in both cases (NISP = 1). *A. anguilla* is the only species in TD7, with two remains. This species appears again in TD10-4, representing 6% of the sample (NISP = 6) and in TD10-3, with 11.6% (NISP = 5). The species is missing in TD10-2 and TD10-1.

Fish bone representation and taphonomy

The TDS samples are characterized by mainly postcranial elements in all levels. Vertebrae are the only postcranial remains recovered (total NISP = 1067; 98.2%), whereas cranial bones (NISP = 20; 1.8%) are clearly underrepresented and are absent in levels TD10-1/2, TD8a, TD7, TD5c-d and TD4 (Fig. 4D). The cranial bones recovered correspond to teeth in the case of *S. trutta* and to pharyngeal arches in the case of cyprinids. No scales, spines or ribs were recovered in this assemblage. Bone modification analysis indicates no damage in the form of deformation, rounding or polishing.

The absence of bite marks or crushed bones means that chewing action by carnivores or humans can be ruled out (Nicholson, 1993). No evidence of human activities such as butchery or burning was documented in any item either. Only digestion marks are observed in our assemblage. As outlined above, three categories of digestion marks were distinguished depending on the intensity of digestion (modified from Andrews, 1990 and Guillaud et al., 2015, 2018): null-light (category 0) (Fig. 2A), where the elements show no less is damaged, the shape of the bone remaining unchanged; moderate (category 1) (Fig. 2B), showing a loss of part of the bone although affecting less than 50% of the bone's surface area; moderate-heavy (category 1_2) (Fig. 2C), characterized by a major loss of bone (more than 50%) or compressed bones. The taphonomic alteration of bones is quite similar from one level to another, and no relevant differences are observable between the Middle and Early Pleistocene layers in Gran Dolina. In the

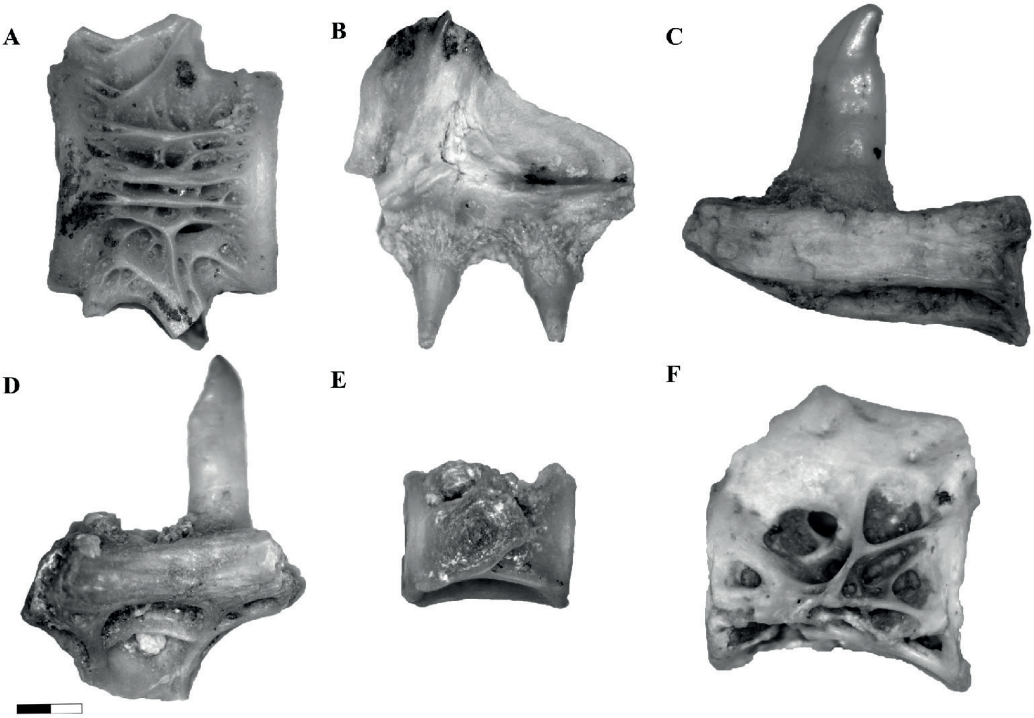

Figure. 3. Fish taxa from the Early and Middle Pleistocene of Gran Dolina (Spain). (A) Caudal vertebra of S. trutta in lateral view (TD6-1). (B) Premaxillary fragment of S. trutta in medial view, showing two teeth on the top (TD5b). (C) Branchial arch fragment of Squalius sp. in ventral-external view (TD10-4). (D) Pharyngeal arch fragment of Squalius sp. in dorsal-internal view (TD10-4). (E) Thoracic vertebra of unidentified cyprinid in lateral view (TD6-1) and (F) Thoracic vertebra of A. anguilla in lateral view (TD10-3). Scale 5 mm.

Early Pleistocene levels (TD4-TD8), the most represented category is 0, which ranges between 70.6% and 100% of the samples, whereas category 1 ranges between 0% and 17.9%. The third category, 1_2, is underrepresented, and the maximum percentage is 11.5%, which is present in TD6-3. The proportion in the Middle Pleistocene levels (TD10-1/TD10-4) is similar: although the percentage of category 1 increases and ranges between 15.4% and 57.1%, the most common category is 0, which ranges between 42.9% and 69.2%. Category 1_2 is also relatively more represented, its values ranging between 10% and 20.9%, although in TD10-1 it is missing (Table 3, Fig. 4B). As a whole, the Gran Dolina sequence shows the most represented category to be 0 (NISP = 808, 74.3%), followed by category 1 (NISP = 187, 17.2%) and category 1_2 (NISP = 92, 8.5%).

Salmonidae

Category 0 is the one most represented among the Salmonidae remains, amounting to 71.4% (NISP = 623) of the total; 18.5% (NISP = 161) correspond to category 1, and 10.1% to category 1_2 (NISP = 88) (Table 3).

Cyprinidae

All the remains belonging to Squalius sp. from TD5b (NISP = 1) and TD10-4 (NISP = 4) show category 1. For the unidentified cyprinid remains, category 0 represents 85.1% (NISP = 80) of the sample; category 1 represents 12.7% (NISP = 12); and category 1_2 is present only in 2.2% (NISP = 2) of the total (Table 3).

Anguillidae

The common European eel remains are slightly different in that more samples are characterized as category 1 (56.3%, NISP = 9) than category 0 (43.7%, NISP = 7). No eel vertebra shows category 1_2 (Table 3).

Body size evolution of S. trutta through the sequence and its relationship with temperatura

In general terms, significant body size variability is observed for S. trutta throughout the TDS sequence. This differs from the brown trout assemblage described in the Neolithic site of El Mirador cave, also in Atapuerca, where the probable accumulating agent was humans (Blanco-Lapaz and Vergès, 2016). This conclusion was based on the fact that only S. trutta was recovered in the assemblage, on the absence of any digestion marks, and on a body size range between 10 and 40 cm, indicating a more bounded body size (Blanco-Lapaz and Vergès, 2016). El Mirador corresponds to a typical anthropic fish accumulation as described by Russ (2010b) and Russ and Jones (2011).

The least represented body size corresponds to individuals smaller than 10 cm and is only present here in TD5b and TD6-1. Individuals with an estimated length between 10 and 20 cm are present in all levels, but their percentage varies between 1.4% in TD6-3 and 95.9% in TD6-1. In TD8a, it decreases again to 33.3%, remaining more or less stable during the first Middle Pleistocene layers (TD10-1, 17.8%; TD10-2, 36.4%; TD10-3, 25%) and reaching 100% in TD10-4 although in this case it is probably not significant since only three vertebrae were analyzed. Over the course of the sequence, two periods show greater variability in body size: the first period corresponds to the Early Pleistocene layers TD5b- TD6-3, whereas the second period corresponds to the Middle Pleistocene layers (TD10-4-TD10-2).

For both periods, the variability in body size is substantial, and all sizes between 10 and 60 cm are represented, indeed even sizes greater than 60 cm in TD6-3, TD10-4, and TD10-3 (Fig. 4C). The results of the regression models between the different measurements of temperature (MAT, MTC and MTW) and body size show no significant relationship (p-value >0.05).

2.5 DISCUSSION

Freshwater ecosystems around the Sierra de Atapuerca

The fish assemblages described here permit a better description of the freshwater ecosystems around the Sierra de Atapuerca. The common brown trout, *S. trutta*, requires oxygen-rich water and a specific temperature for hatching and growing.

Nowadays, *S. trutta* is the only native salmonid species in the Iberian Peninsula (Elvira, 1995; Elvira and Almodóvar, 2001) and is usually found in cold running water with temperatures ranging from 0 to 20 ◦C (Jonsson and Jonsson, 2009; Elliott and Elliott, 2010).

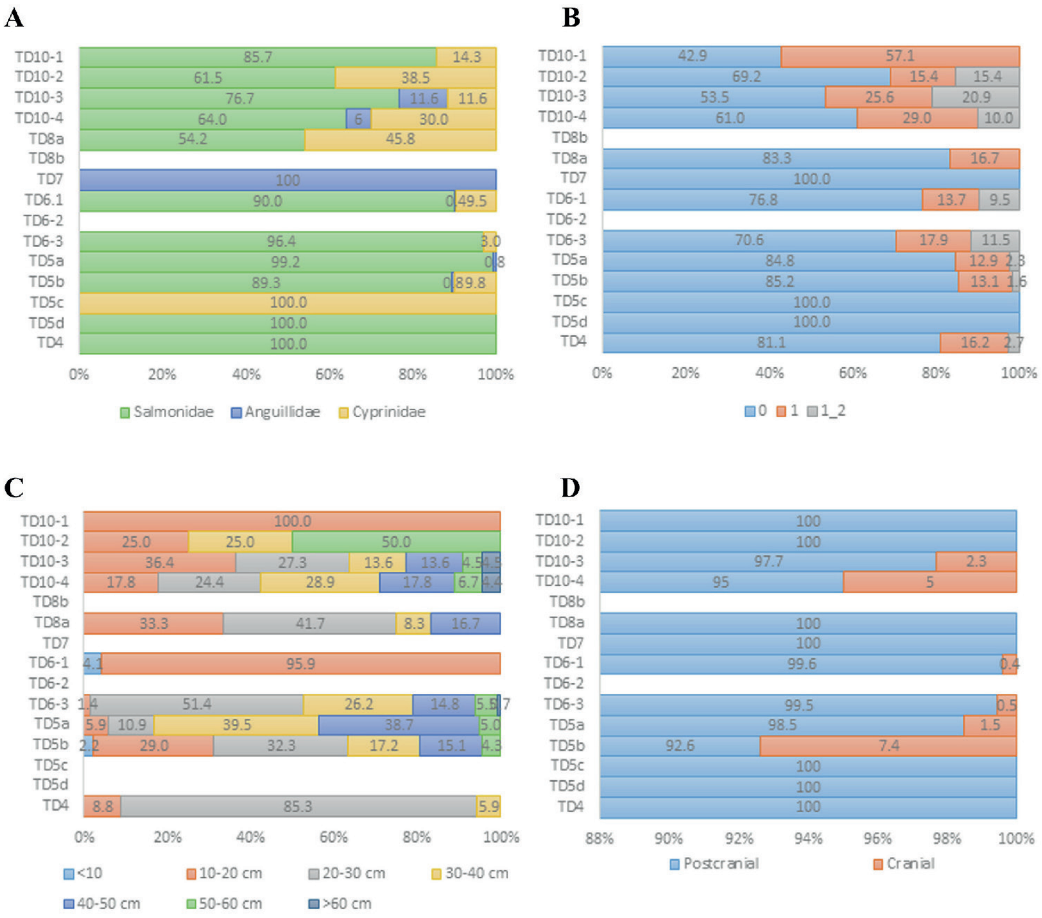

Figure. 4. Evolution through the Early and Middle Pleistocene sequence of Gran Dolina (Atapuerca, Spain) in %. (**A**) % for each taxon (based on Table 1). (**B**) categories of digestion marks (based on Table 3. (**C**) *S. trutta* size categories (based on Table 2 and (**D**) fish bone representation (postcranial and cranial).

Cyprinids are more typical of temperate waters and live in water temperatures between 10 and 25 ◦C (Doadrio, 2002; Tissot and Souchon, 2010). Accordingly, cyprinids such as the genus *Squalius* can be found in salmonid zones, as they also thrive in running water. However, cyprinids in general are present in multiple environments, showing enormous diversity in their diet, which includes arthropods and other fishes (Doadrio, 2002). The third taxon represented in our assemblage is the common European eel (*A. anguilla*), a catadromous fish present in all watersheds but strongly limited by dams today (Mota et al., 2016). The development of the eel occurs in rivers up to the beginning of sexual maturity; then they leave the continent for the Bermuda area, where they reproduce. After reproduction, they return to the Iberian Peninsula to lay their eggs. In the archaeological record, therefore, we could find remains belonging to both periods of their life. In the Iberian Peninsula, the eel has disappeared today from most of the Ebro, Tajo, Duero and Guadiana catchment areas (Doadrio, 2002).

In present-day terms, all three main groups of fishes, *Salmo trutta*, Cyprinidae and *Anguilla* are present in pre-mountain river sections in western Europe and the Iberian Peninsula (Fig. 3D). Understanding the role of these fish as part of the faunal assemblage is important in adding to our knowledge of the freshwater ecosystem in Gran Dolina (TD), corroborating the image of a typical river forest with the presence of limestones (Allué et al., 2015). The Sierra de Atapuerca sites are known to have been very close to river systems such as the Duero and Ebro basins, with the Arlanzón river as a main feature. Geomorphology too suggests that the Arlanzón was closer to the cave than today (Ortega et al., 2014).

Other small-vertebrate groups studied in the TDS also indicate a faunal association characteristic of Mediterranean wetland and associated freshwater ecosystems. Amphibian and reptile assemblages suggest that aquatic environments were quite well developed throughout the TDS sequence, with the presence of the viperine snake (*Natrix maura*) in all the levels of TD10, TD8a and TD4 and the rarer occurrence of the water frog (genus *Pelophylax*) in levels TD10-4, TD10-3, TD8a, TD6-3 and TD5a. Additionally, water-edge taxa (*Triturus* sp., *Pelodytes punctatus* and *Natrix natrix/astreptophora*) are well represented throughout the whole sequence (Blain et al., 2008, 2009, 2012).

The viperine snake (*N. maura*) is a snake of aquatic habits, which appears in all types of continental water bodies. It has been observed in natural environments such as rivers, lagoons, ponds, and marshes. In the former, it occupies all stretches from the lower to the upper part, although it avoids the points of greatest current (Santos et al., 2002). Pelophylax perezi is today the most widespread water frog in the Iberian Peninsula. It is a strictly aquatic species with low ecological requirements (Llorente et al., 2002). It rarely moves more than 5 m from the water-edge (Lizana et al., 1989). It occupies all types of aquatic environments (Malkmus, 1982, 1997; Meijide et al., 1994; Lizana et al., 1995), both temporary and permanent, although it cannot be considered a species characteristic of temporary environments. It avoids water bodies with cold water, mountain streams with excessive slopes, and water courses with closed vegetation (Malkmus, 1979, 1982, 1997). Its presence has been recorded in both lotic environments (rivers, streams, irrigation ditches), where it selects areas with little current, and lentic environments (ponds, agricultural ponds, marshes, ditches, reservoirs) (Gracia and Pleguezuelos, 1990; Pollo et al., 1998).

The larval stages of *P. perezi* are typical bottom dwellers of water bodies (Díaz-Paniagua, 1985). Given the late reproductive period of the species, they occupy water bodies with summer characteristics: smaller dimensions, less vegetation cover, higher temperature, and lower oxygen concentrations (Díaz-Paniagua, 1983, 1988). They almost always occupy relatively deep and permanent waters (García- París, 1989). In the latter bodies of water, the larvae of this species show a clear preference for occupying areas densely covered by submerged aquatic vegetation (thus showing a certain depth), avoiding deeper areas where aquatic vegetation is non-existent (Díaz-Paniagua, 1987). Sánchez-Marco (1999) analyzed the bird remains from TD6. The only aquatic bird classified to species level was Anas

Table. 3. Identified digestion mark categories: 0 (null-light), 1 (moderate) and 1_2 (moderate-heavy) in the Early and Middle Pleistocene layers of Gran Dolina (Sierra de Atapuerca, Spain).

Levels	Categories	Salmonidae				Anguillidae		Cyprinidae				Pisces indet.		Total NISP
		Salmo trutta		Unidentified		*A. anguilla*		*Squalius* sp.		Unidentified				
		NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	
TD10-1	0	2	66.7							1	33.3			3
	1	4	100.0											4
	1_2													0
TD10-2	0	5	55.6							4	44.4			9
	1	1	50.0							1	50.0			2
	1_2	2	100.0											2
TD10-3	0	16	69.6			3	13.0			4	17.4			23
	1	8	72.7			2	18.2			1	9.1			11
	1_2	9	100.0											9
TD10-4	0	38	62.3			2	3.3			21	34.4			61
	1	18	62.1			4	13.8	4	13.7	3	10.3			29
	1_2	7	70.0	1	10.0					2	20.0			10
TD8a	0	10	50.0							10	50.0			20
	1	3	75.0							1	25.0			4
	1_2													0
TD7	0					2	100							2
	1													0
	1_2													0
TD6-1	0	166	89.7							19	10.3			185
	1	28	84.8			1	3.0			4	12.1			33
	1_2	22	95.7	1	4.3									23
TD6-3	0	243	94.6	2	0.8					10	3.9	2	0.8	257
	1	64	98.5							1	1.5			65
	1_2	42	100.0											42
TD5a	0	112	100.0											112
	1	16	94.1			1	5.9							17
	1_2	3	100.0											3
TD5b	0	94	90.4							10	9.6			104
	1	13	81.3			1	6.3	1	6.3	1	6.3			16
	1_2	2	100.0											2
TD5c	0									1	100.0			1
	1													0
	1_2													0
TD5d	0	1	100.0											1
	1													0
	1_2													0
TD4	0	30	100.0											30
	1	6	100.0											6
	1_2	1	100.0											1
Total NISP		966		4		16		5		94		2		1087
%		88.9		0.4		1.5		0.5		8.6		0.2		100.0

crecca, although Núñez-Lahuerta et al. (2019) confirmed the presence of many anseriforms using eggshells remains, also in TD6.

The Eurasian green-winged teal (*Anas crecca*) is a common and widespread duck that breeds in temperate Eurosiberia and migrates south in winter. It is a highly gregarious duck outside the breeding season and can form large flocks. It is commonly found in sheltered wetlands and feeds on seeds and aquatic invertebrates. It nests on the ground, near water and under cover. In the breeding season, it is a common inhabitant of sheltered freshwater wetlands with some tall vegetation, such as taiga bogs or small lakes and ponds with extensive reedbeds. In winter, it is often seen in brackish waters and even in sheltered inlets and lagoons along the seashore (Carboneras, 1992). Piscivorous birds of prey such as the European eagle owl, *Bubo* (Russ, 2010b; Guillaud et al., 2018), or the white–tailed sea eagle, *Haliaeetus albicilla*, have also been found in the Sierra de Atapuerca. Most of the fish diet of the European eagle owl corresponds to salmonids and cyprinids (Russ, 2010a, 2010b), although other authors have described the presence of clupeids and anguillids in their diet (Guillaud et al., 2018).

The fish diet of *H. albicilla* is mainly constituted by cyprinids, pike (Esox lucius) and perch (Perca fluviatilis) (Mlíkovský, 2009; Van Rijn et al., 2010). Finally, some small-mammal associations recovered in Gran Dolina are also related to aquatic ecosystems. These include *Arvicola* aff. *sapidus* (in TD10), *Mimomys savini* (in TD4 to TD7), *Castor fiber* (in T4 to TD10), and the eulipotyphlans *Neomys* sp. and *Dolinasorex glyphodon* (in TD4 to TD6), indicating the presence of a water edge, above all during the transition TD5-TD6 and in particular during the aquatic habitat maximum in TD10, accompanied by a slight decrease in the open dry habitatsand a minor increase in open humid and woodland ones (Rofes and Cuenca-Bescós, 2009, 2011; Moya-Costa et al., 2019). Water-foraging bats such as *Myotis capaccinii* and *Myotis nattereri* are recovered from these levels (TD5-TD6), also indicating water resources (Galán et al., 2019). In conclusion, though concordant with other paleoenvironmental proxies, the fish remains from TDS studied here make it possible for the first time to offer a more detailed description of some of the freshwater ecosystems around Gran Dolina during the Early-Middle Pleistocene, in particular the presence of a pre-mountain river system characterized by permanent, oxygen-rich, relatively cold running waters.

The accumulator of the fish remains

To understand whether the fossil assemblage is a reflection of the natural communities around the sites, it is important, in Pleistocene caves and rock shelter sites, to identify the accumulator of the small vertebrates (Russ, 2010b) and in this case the fishes. Previous studies indicate that the amphibians and reptiles in Gran Dolina are of mixed provenance. Some of them may certainly have been accumulated inside the cave by a predator, as in the case of small mammals, but for others, such as the natterjack toad *Epidalea calamita*, a more probable origin is in situ mortality within the cave during wintering (Blain et al., 2008; Martínez-Monzón et al., 2018). For small-mammal assemblages, taphonomic observations corroborate the hypothesis that large accumulations of rodents and insectivores stem mostly from fossil pellets that enter the cave with sediment and are allochthonous in origin (Fernández-Jalvo and Andrews, 1992). Given the type of digestion and the breaks in the fossils, these are mostly due to nocturna*l birds of prey such as the barn owl (*Tyto alba) and the eagle owl (*B. bubo*), opportunists that hunt a broad range of prey (Bennássar, 2010).

The role of birds of prey and above all the eagle owl has been studied in various European regions, such as France (Bayle, 1994; Cochard, 2008), as well as in the Iberian Peninsula (Cramp, 1985; Lloveras et al., 2009). According to our results on the different taphonomic categories, all percentages (Fig. 4B) are similar to those obtained by Guillaud et al. (2018) in their study of *Bubo* pellets, indicating that this bird of prey was probably the main accumulator of fish remains, capturing the fish from spring to autumn.

The European eagle owl is a nocturnal, opportunistic predator that shows a generalist and very varied diet (including medium-sized mammals such as hedgehogs and lagomorphs but also small rodents, birds, and amphibians); the resultant deposits of partially digested skeletal remains are present in the vicinity of the nest area (Andrews, 1990). The diversity of species represented in the assemblage would thus also be a typical characteristic for this accumulator of fish remains (Russ and Jones, 2009; Russ, 2010b; Guillaud et al., 2018). Fish consumption by *B. bubo* has also been studied in the Grotte du Bourrouilla (France) by Le Gall (1999), indicating that the fish eaten by this species measure from a few centimeters up to 40 cm, although the majority in our *S. trutta* samples are between 10 and 30–40 cm in size (Table 3, Fig. 4C). The fact that we describe the presence of different body size classes among our *S. trutta* indicates non-selectivity of prey among the brown trout community. Many other studies have indicated the Eurasian eagle owl (*B. bubo*) as a possible accumulating agent at European archaeological sites. These include Andrews (1990), Sanchís-Serra (2000), Laroulandie (2002), De Cupere et al. (2009) and Russ (2010b). Other predators documented in Gran Dolina can be ruled out, such as hominins and carnivores (canids, felids, mustelids, bears and hyenas), as well as other birds of prey such as other Strigiformes and diurnal raptors (Accipitriformes). Several fish-feeding experiments and studies involving carnivores (*Canis familiaris*) (Jones, 1984, 1986) and humans (*Homo sapiens*) (Jones, 1984, 1986; Nicholson, 1993) identified various characteristics for recognizing digested material.

However, these signals have proved not to be species-specific and can only establish whether the remains were digested or not. As there are no chewed or crushed fish bones in the TDS fossil assemblage, we can rule out humans and carnivores as possible accumulator candidates, as these are known to produce such types of modification. Hyenas, for example, produce substantial and characteristic damage on the bone surface and the total destruction of bones. Experimental research by Russ and Jones (2011) on four female brown bears (Ursus arctos) showed that bears focus on large salmonids (longer than 30 cm in total length). The bears selected head elements, but whole fish were also consumed, and digested fish remains were only present in feces deposited in the wider environment but never within the caves (Russ and Jones, 2009, 2011). Other mammalian carnivores such as the otter (*Lutra lutra*) (not described in Gran Dolina but comparable with other small-medium-sized carnivores) and wolf (*Canis lupus*) (Russ and Jones, 2009) produce greater damage on fish bones (Guillaud et al., 2015). Previous studies of the feces of small-medium-sized felids show that the digestion processes of these animals generally produce extremely broken bones with high levels of rounding and polishing (Andrews and Evans, 1983; Andrews, 1990; Matthews, 2002).

The other birds of prey (mainly Strigiformes) represented as fossils in Gran Dolina, such as Tyto alba, are too small compared with *Bubo* to have been able to catch the larger specimens of *S. trutta* documented in some of the layers (Broughton et al., 2006; Russ, 2010a, 2010b). Although most of the diet of *H. albicilla* is constituted by aquatic birds, fish are also part of their food acquisition (Mlíkovský, 2009; Van Rijn et al., 2010). Taphonomic studies of accipitriform pellets confirm severe and extreme digestion on the bone surface (Lloveras et al., 2008; Fernández-Jalvo et al., 2016). Such modification is not reported on any of the fish remains from TDS. In conclusion, the great diversity of fish species, the fish bone representation and the less destructive digestion suggest the European eagle owl (*Bubo bubo*) as the potential fish bone accumulator in Gran Dolina, also proving the presence of a river system close to the cave, since the vital domain of these nocturnal birds of prey is an area of around 2.3 km2 during incubation (around 500 m away) and parental care (around 250 m away) (Penteriani and Delgado, 2008, Penteriani et al., 2015).

Fish body size and climate

Two differentiated peaks can be observed among our fish assemblages, indicating maximum average body size values of S. trutta in the timespan between the sub-levels TD5b and TD6-3 and from sub-levels TD10-4 to TD10-3 respectively (Table 4, Fig. 5A). Both peaks also represent the group of sub-levels with the highest body size variability in the assemblage, encompassing lengths from less than 10 cm to more than 60 cm. In accordance with Bergmann's rule, the brown trout individuals in Gran Dolina would be expected to be bigger under colder temperatures and smaller under warmer temperatures.

At first sight, this seems not to be the case here, because the two observed peaks of higher sizes (TD5b/TD6-3 and TD10-4/TD10-3) correspond to different estimated MATs (11.4 ◦C and 12.6 ◦C respectively (Table 4, Fig. 5D)). In addition, no statistical relationship between the body size of *S. trutta* and temperature is found. This indicates that, in this concrete case, the species in question does not follow Bergmann's rule (either standard or converse). Moreover, no relevant relationship is evidenced between body size and MTW and MTC (Fig. 5 C–D). Even though there is no statistical relationship between temperature and body size, it is noteworthy that the maximum mean body size of *S. trutta* is reached in the coldest period of the entire sequence (TD5b/ TD6-3), which falls within the Early Pleistocene. In addition, during the levels corresponding to this period (TD5a to TD6-1), the variation in body size of *S. trutta* follows Bergmann's rule, whereas in the upper levels of the sequence corresponding to the Middle Pleistocene (TD8a to TD10-1), it does not show any recognizable pattern. Furthermore, the Middle Pleistocene levels are those with the lowest numbers of remains, and although the sample size for these layers is considered enough to provide adequate and representative statistical results, this difference in the number of remains analyzed per level may generate some bias in our results. On the other hand, the level with the lowest sample size (TD8a) is almost in accordance with the trend exhibited during the Early Pleistocene, which may constitute an indication of the suitability of the present sample sizes for this kind of analysis.

The most likely explanation for this divergence affecting the Middle Pleistocene is that other ecological factors such as competition, resources or predation are influencing the changes in body size of *S. trutta* to a greater extent than climate during this period. In any case, both Bergmann's rule and the converse Bergmann rule have been found in freshwater fishes (Rypel, 2014). Likewise, it has also been widely reported that these organisms may not show any pattern relating climate and body size (Rypel, 2014; Belk and Houston, 2002). Specifically for *S. trutta*, some studies have obtained no clear results on its adhesion to Bergmann's rule (Rypel, 2014), whereas the converse Bergmann rule has been found in others (Parra et al., 2009). It seems that studies of macroecological patterns such as Bergmann's rule in poikilothermic organisms and particularly in freshwater fish such as *S. trutta* have not yet reached a clear consensus, so further investigation is required. Even though this study has not yielded conclusive results about body size patterns, investigators should keep on considering the fossil record as a valuable source of new data for paleoecological studies.

The unique characteristics of the fossil record (for example, the absence of overexploitation of larger individuals, or the huge timespans it provides for study) make it an excellent source of data that will contribute to the resolution of current macroecological questions. On the other hand, one of the problems in paleoarchaeological investigation is that fish remains will often be identified and interpreted separately from other faunal remains. In order to identify the potential predator, the ecosystem and the paleoenvironment, however, we must consider the faunal register as a whole, especially when fish are mixed with other small vertebrates. Hopefully, the results of this paper will encourage further fish studies in European Pleistocene sites to increase our knowledge of freshwater ecosystems, using fish remains as part of paleoenvironmental and paleoecological reconstructions to interpret their role during this period and in human evolution.

2.6 CONCLUSIONS

The fish taxa identified in this paper permit us to enlarge the faunal list of the Gran Dolina site (northern Iberia), adding to other small-vertebrate taxa such as amphibians, reptiles, small mammals, and birds and providing a valuable overview of the freshwater ecosystems around the Sierra de Atapuerca during the Early-Middle Pleistocene. In addition to *Salmo trutta* (brown trout), which is the most represented taxon, this study provides the first record in Sierra de Atapuerca for *Squalius* sp. (chub) and *Anguilla anguilla* (common European eel). The origin of the fish assemblage is also clarified, in that the presence of digestion marks on the bone surface categorized from null to medium-high in intensity point to *Bubo bubo* (European eagle owl) as a potential predator. This accumulating agent has been identified in other sites in the Sierra de Atapuerca such as Sima del Elefante, as well as at other Pleistocene sites in Spain, France, Belgium, and Germany and for other taxa such as micromammals and herpetofauna.

This thus suggests that human activity in Gran Dolina was not the potential accumulator of the fish remains. Other criteria, such as bone representation, the body size of the fishes, and species representation, also need to be taken into account to investigate the potential fish bone accumulator in archaeological cave sites. For the first time in an Iberian Pleistocene site, this research also reveals that the body size of *Salmo trutta* does not follow Bergman's rule, unlike other taxa such as amphibians or lacustrine fish species.

Table. 4. *Salmo trutta* body size estimations in Gran Dolina (Sierra de Atapuerca, Spain), organized according to the climate units established by Martínez Monzón et al. (2018) and averaged values for mean annual temperature (MAT), mean temperature of coldest month (MTC) and mean temperature of warmest month (MTW) (from Blain et al., 2009, 2012, 2013).

Level	Body size *Salmo trutta* (mm)							Average	Total NISP	Temperature (°C)		
	<100	100–200	200–300	300–400	400–500	500–600	>600			MTW	MTC	MAT
TD5b	2	25	24	14	12	3		273.3	80	19.5	3.3	11.8
TD5b/TD6-3		10	118	127	91	23	2	352.3	371	19.5	3.3	11.4
TD6-3/TD6-1	8	191	51					165.1	250	20	3.6	12.3
TD8a		4	5	1	2			172.9	12	20.2	3.7	12.6
TD10-4/TD10-3		8	12	14	10	3	2	348.7	49	20.2	3.7	12.6
TD10-3/TD10-1		9	6	3	1	3	1	295.6	23	19.8	3.8	11.7

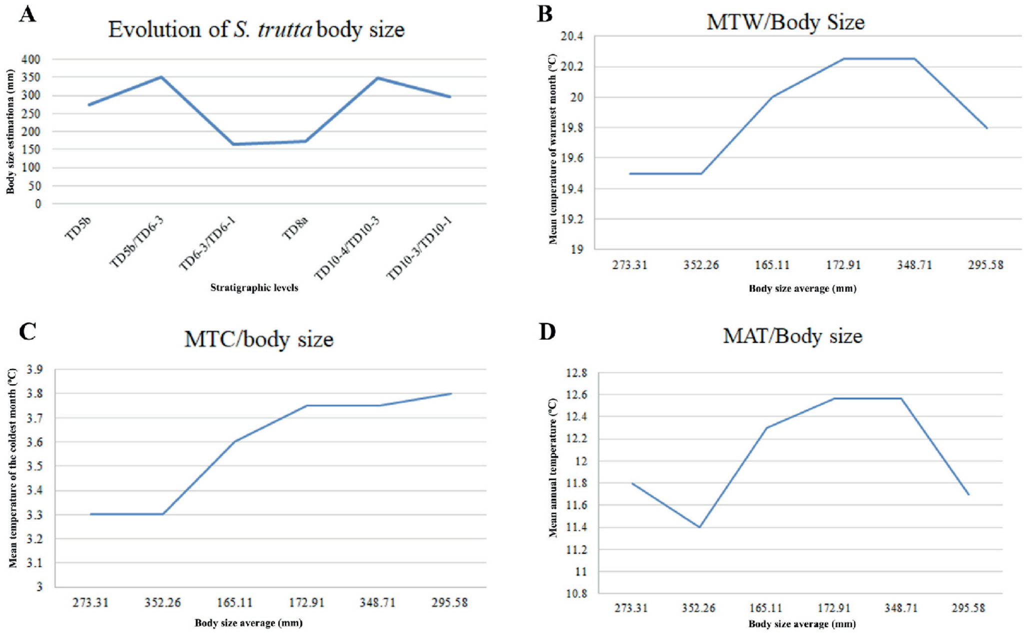

Figure. 5. Body size/climate correlation for *S. trutta* in the Early and Middle Pleistocene of Gran Dolina (Sierra de Atapuerca, Spain). (**A**) Evolution of the average body size through stratigraphic levels, (**B**) Correlation of the average body size and the averaged values for mean temperature of warmest month (MTW), (**C**) Correlation of the average body size and the averaged values for mean temperature of coldest month (MTC), (**D**) Correlation of the average body size and the averaged values for mean annual temperature (MAT).

Declaration of Competing Interest

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

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A2.3 The Middle to Late Pleistocene herpetofaunal assemblages from the Jarama and Manzanares valleys (Madrid, central Spain): An ecological synthesis

This last work, leaded by the senior researcher Dr. Hugues-Alexandre Blain, was published in the journal Quaternary International within the special issue "A fundamental archive for the European Pleistocene: The Manzanares and Jarama Valleys", edited by Joaquín Panera, Susana Rubio-Jara and Alfredo Pérez-González. My contribution to this synthesis was the analysis of the diversity and species richness of the herpetofauna communities from the middle-late Pleistocene of the Jarama and Manzanares valleys (Madrid, central Spain). My contribution is contemplated within the subsections "Diversity and species richness" and "Biodiversity" from "Material and methods" and "Results" sections respectively.

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The Middle to Late Pleistocene herpetofaunal assemblages from the Jarama and Manzanares valleys (Madrid, central Spain): An ecological synthesis

Hugues-Alexandre Blain [a, b, *], Josep Francesc Bisbal-Chinesta [a, b], Almudena Martínez-Monzón [a, b], Joaquín Panera [c], Susana Rubio-Jara [c], David Uribelarrea [d], José Yravedra Saínz de los Terreros [e], Alfredo Pérez-González [c]

[a] *IPHES, Institut Català de Paleoecologia Humana i Evolució Social, Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain*
[b] *Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain*
[c] *CENIEH, Centro Nacional de Investigación sobre la Evolución Humana, Paseo de la Sierra de Atapuerca 3, 09002 Burgos, Spain*
[d] *Departamento de Geodinámica, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, C/ Jose Antonio Novais 2, E-28040 Madrid, Spain*
[e] *Departamento de Prehistoria, Universidad Complutense de Madrid, C/ Prof. Aranguren s/n, 28040 Madrid, Spain*

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ABSTRACT

The successive fossil amphibian and reptile assemblages from the Middle to Late Pleistocene sites from the Manzanares and Jarama River Valleys (Madrid, central Spain) permitted the reconstruction of part of the climate instability with high-amplitude and rapid shifts of the last 450 ka and their associated landscapes: Áridos-1 (MIS11b), Valdocarros II (MIS8a/7e), Estanque de Tormentas de Butarque ETB-H02 (MIS7d or MIS6), PRERESA (MIS7/6 or MIS5a) and HAT (MIS5a). This work aims to present a regional synthesis of the palaeoclimatic and palaeoenvironmental data obtained from the herpetofaunal assemblages for these two valleys and their influence on the biodiversity during the Pleistocene. As a whole, these archaeo-paleontological localities document a total of 20 taxa (8 anurans and 12 reptiles) thus representing 76.9% of the modern authochtonous herpetofauna of the southeast of the Region of Madrid. Taking as a reference the modern situation in the area, the successive herpetofaunal assemblages permits a hypothetical landscape reconstruction where three different periods are represented with a glacial landscape (ETB-H02), a landscape of transition from cool to temperate climatic conditions (Valdocarros II), and an interglacial landscape (Áridos-1, HAT, PRERESA, and today). Environment is particularly open during dry periods, independently of if it is cold or warm. The main difference between an interglacial and a glacial period is the opposite representation of woodlands vs. moist environments: the last ones being more represented during cold periods than during warm periods. Finally, as documented by the succession from Valdocarros II, periods of transition between cold and warm climate are more forested but at the expense of humid meadows progressively. According to the relation between richness, biodiversity and climatic and environmental factors, a clear correlation appears between reptile richness and woodlands. In a similar way, mean annual precipitation (MAP) is revealed to be the most influent factor on reptile local diversity certainly because of its implications on vegetal cover extension and ecosystem productivity and resources. For amphibians the MAP does not influence dominancy but species richness: anuran richness being higher for lower MAP. Such an unusual pattern is certainly due to the fact that there are no strict forest-dweller anurans within the archaeological assemblages and that most of the anurans present in the sites are well adapted to arid conditions.

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3.1 INTRODUCTION

The pattern of the varying terrestrial climatic conditions (deduced from the vegetation development) in southern Europe over the last 450 ka is well known fromthe long pollen records that have been produced for sedimentary sequences from Greece (Tzedakis, 1993, 1994; Tzedakis et al., 1997, 2003, 2006; Fletcher et al., 2013; Sadori et al., 2016), France (Reille and de Beaulieu, 1995; Reille et al., 1998, 2000; Beaulieu de et al., 2001), Spain (Desprat et al., 2009; Valdeolmillos-Rodríguez et al., 2011), and off Portugal (Roucoux et al., 2006). These sequences have revealed a pattern of forested intervals alternating with periods characterized by more open vegetation, varying on time scales of 10.000-100.000 years that represent a response to the Milankovitch-driven global climatic changes recorded in marine isotope records of global ice volume. Deep-ocean sediment cores have also provided more quantitative and better-dated evidence for temperatures and total ice volumes.

Due to their incompleteness and dating uncertainties, the correlation and comparison of paleoecological proxies from archaeological sites with such long and detailed pollen or marine records is far from easy. In this context, the study of long (even if mainly fragmentary) archaeological successions in a same environment is a key to understand the differences between global and regional climate evolution and its forcing on flora and fauna.

The successive fossil amphibian and reptile assemblages from the Middle to Late Pleistocene sites from the Manzanares and Jarama River Valleys (Madrid, central Spain) permitted the reconstruction of part of the climate instability with high amplitude and rapid shifts of the last 450 ka and their associated landscapes: Áridos-1 (MIS 11b), Valdocarros II (MIS 8a/ MIS 7e), Estanque de Tormentas de Butarque H-02 (MIS 7d or MIS 6), PRERESA (MIS 7/6 or MIS 5a) and HAT (MIS 5a). This work aims to present a regional synthesis of the palaeoclimatic and palaeoenvironmental data obtained from the herpetofaunal assemblages for these two valleys and their influence on the biodiversity during the Pleistocene.

3.2 GEOGRAPHICAL AND CHRONOLOGICAL SETTINGS

The valleys of the Jarama and Manzanares rivers are located in the Tagus basin, within the South Sub-Meseta of the Iberian Peninsula (Fig. 1). These valleys are characterized by the development of a great number of fluvial terraces related to Quaternary climatic oscillations, and both rivers are responsible for the terraces configuration, tectonics (Alia, 1960; Pérez-González, 1980; Silva et al., 1988a,b; Pérez-González, 1994), isostatic rising and blocks adjustment, as well as lithological structural controls (Pérez-González, 1971).

In the Jarama valley, 19 stepped terraces between +3 and 5 m and +190 m high have been recorded in the high-middle trench of the river. However, in the lower part of the valley, Miocene evaporite-gypsum have facilitated synsedimentary subsidence processes in the underlying karst, affecting terraces lower than +40 m, which overlap the oldest ones and give rise to the Complex Terrace of Arganda (CTB) (Pérez-González, 1971, 1994; Panera et al., 2011, Fig. 1). This Complex Terrace is made up of successively stacked fluvial sequences, named Arganda I, II, III, which match up with terraces +30e32 m, +23e24 m, and +18e20 m respectively (Pérez-González and Uribelarrea del Val, 2002; Panera et al., 2011). The sitesÁridos-1, Valdocarros II and HAT are located in units Arganda I, Arganda II and Arganda IV respectively.

From a chronological point of view, the Brunhes-Matuyama boundary (780 ka) has been recorded in the Jarama river valley between the T+60-65 m, with reverse polarity, and the T+55-60 m, with normal polarity (Pérez-González et al., 2013). The chronological framework of the Complex Terrace of Arganda has been built through biostratigraphy data (López Martínez, 1980; Sesé et al., 2011), amino-acid racemization analysis (AAR; Panera et al., 2011), and ESR dating (Moreno et al., in press). In Arganda I and Arganda II, the micromammals associations from Áridos-1 and Valdocarros suggest a late Middle Pleistocene age for these deposits. According to the AAR results (332 ± 38 ka and 379 ± 45 ka at Maresa site), ESR data (314 ± 50 ka and 275 ± 62 ka), and the climatic requirements of the microfauna assemblage, Arganda I unit belongs to the last part of MIS 11 or early MIS 9, which is consistent with the micromammals evolutionary stage (López-Martínez, 1980). In Arganda II unit, at Valdocarros site, there are two AAR dating (254 ± 47 and 262 ± 07 ka), two ESR ages on quartz (ESR-Al: 255 ± 31 ka; ESR-Ti-Li: 286 ± 54 ka), and two ESR ages on teeth (360 ± 46 ka and 301 ± 73 ka). These data, together with the herpetofaunal assemblage (Blain et al., 2012a, b) at Valdocarros II, suggest that this unit was deposited between the last part of MIS 8 and the beginning of MIS 7, which is consistent with Valdocarros II rodent evolutionary stage (Sesé et al., 2011). ESR dating suggests that the Arganda III unit was deposited during the MIS 6 (Moreno et al., in press). Finally, at Arganda IV, several numerical ages were obtained by Thermoluminescence TL (112 + 36/-22 ka and 85 + 18-13 ka at Torreblanca; 74 + 16-12 ka at HAT) and Optically Stimulated Luminescence OSL (80 ± 7 ka at Valdocarros and 74 ± 5 ka at Maresa), suggesting that is was deposited during MIS 5 (Panera et al., 2011).

In the Manzanares valley 13 terrace levels, between +4 and 5 m and +95 m, have been recorded upstream from Madrid (Pérez-González, 1994). This system of stepped terraces gives way to a system of complex terraces, named Complex Terrace of Butarque (Goy et al., 1989), which includes the terraces +25-30 m, +18-20 m and +12-15 m, formed over evaporitic rocks (Pérez-González and Uribelarrea del Val, 2002). These terraces are overlapped and affected by the synsedimentary subsidence, as it has been described in those from the Jarama valley. The terraces higher than T+60 m have been assigned to the Early Pleistocene (Pérez-González and Uribelarrea del Val, 2002; Rubio-Jara et al., 2016). The Complex Terrace of Butarque has been ascribed to the Middle Pleistocene due to the presence of Acheulean industry, which was found to the bottom of the terrace (Rubio-Jara et al., 2016), as well as to the remains of large mammals such as Elephas (Palaeoloxodon) antiquus, Dicerorhinus hemitoechus or Bos primigenius (Sesé and Soto, 2000). The available numerical dates indicate that the visible deposits of the Complex Terrace of Butarque, which to T+18-20 m, date from the Middle-Late Pleistocene (Pérez-González et al., 2008; Silva et al., 2008, 2012; Domínguez- Alonso et al., 2007; Laplana et al., 2015). The dates range between 133 ka and 134 ka after two dates obtained through TL in Arriaga sand quarry (Silva et al., 2011, 2013), which are consistent with those obtained from the bottom of the Complex Terrace of Butarque at Los Estragales by OSL (107 + 39/-22 ka) and TL (122 ± 11 ka) respectively, and the date obtained from the top of the sequence of Los Estragales by OSL (91 ± 9 ka; Perez-Gonzalez et al., 2008).

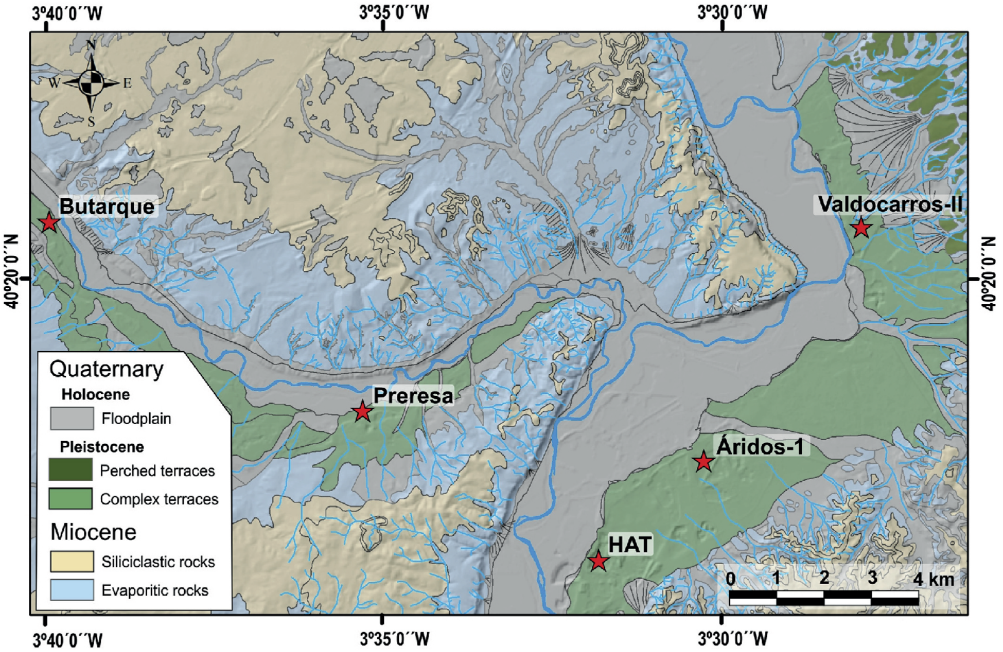

Figure. 1. Geographical and geological location of the Middle to Late Pleistocene archaeological sites of Áridos-1, Valdocarros II, Estanque de Tormentas de Butarque H-02, PRERESA and HAT (Madrid, central Spain).

In the Estanque de Tormentas de Butarque H-02, the TL dates provide values such as 84.6 + 12.6/-11. 2 ka and 74.9 + 10.2/-9.2 ka (Domínguez-Alonso et al., 2007), which have been interpreted as minimum dates owing to the identification of *Microtus brecciensis* among the micromammals preserved in this site (Laplana et al., 2015). In previous publications, the chronology of the site is attributed to the MIS 6 or MIS 8 (Laplana et al., 2015) and to the MIS 6 (Blain et al., 2017). Here we follow the new proposal by Moreno et al. (this issue) where the ESR age obtained from PRERESA constrain the age of ETB-H02 to be MIS 6 or MIS 7d. PRERESA has an OSL date of 84 ± 5.6 ka (Rubio-Jara, 2011; Yravedra et al., 2012). However, recently obtained ESR dates (Moreno et al., in press) suggest a chronological range between 169 ka and 270 ka. Taking into account the presence of Microtus cabrerae and the site, and the fact that it has also been recorded in MIS 6 sites (Foury et al., 2016; Laplana et al., 2015), the most probable date of the range given by ESR in PRERESA would be early MIS 6 (Moreno et al., in press). Chronological attribution of the archaeological localities under study are synthetized in Table 1.

3.3 MATERIAL AND METHODS

The synthesis proposed here lies basically on a critical review of diverse publications describing the herpetofaunal assemblage(s) of the Middle to Late Pleistocene sites of the south-eastern area of Madrid: Áridos-1 (Blain et al., 2014, 2015), Valdocarros II (Blain et al., 2012b), Estanque de Tormentas de Butarque H-02 (Blain et al., 2017) and HAT and PRERESA (Blain et al., 2013). All these publications used the same standardized systematical nomenclature and methodologies thus making easier the comparison between the different sites.

Paleoclimatic inferences

Paleoclimatic interpretations were based on the presence of herpetofaunal species from each site and/or stratigraphical or archaeological level, using the mutual ecogeographic range (MER; Blain et al., 2009, 2016). The MER method involves simply the identification of a geographic region (divided into 10 x 10km UTM squares) in which all of the species present in a given archaeological level currently live. Analysis of the MER of each archaeological level is based on distribution atlases available for Iberian herpetofauna (e.g. Godinho et al., 1999; Pleguezuelos et al., 2004) and various climatic maps of the Iberian Peninsula (Ninyerola et al., 2005).

A total of 26 climatic parameters have been calculated for each of these sites, as mean monthly temperature and precipitation, mean annual temperature (MAT) and precipitation (MAP). The record from weather station 3182E of Arganda 'Comunidad' (Ninyerola et al., 2005), located close to the archaeological locality, has been used for comparison with current data.

To measure aridity we used the Gaussen, Lautensach-Meyer, Dantin-Revenga and De Martonne indexes. The Gaussen index (P < 2 x T) dictates that a month is dry if the pluviometric level for that month (P), measured in mm, is less than twice the value of the average temperature in °C for that month (T). The Lautensach- Mayer index is a classification of climates based on the number of dry months according to the Gaussen index. The Dantin-Revenga index is calculated as (100 x MAT/ MAP), and the De Martonne aridity index as MAP/(MAT + 10), where MAT = mean anual temperatura and MAP = mean annual precipitation.

Paleoenvironmental inferences

Paleoenvironmental reconstruction has been done using the habitat weighting method applied to amphibians and reptiles (see Blain et al., 2008), distributing each taxon in the habitat(s) where it is possible to find them at present in the Iberian Peninsula. Because Spanish Pleistocene amphibians and reptiles are considered specifically identical to modern populations, the current species habitat distribution may be used for the habitat weighting. The habitats were divided into five types: open land in which dry and wet meadows are distinguished, woodland with woodland-margin and scrubland areas, areas surrounding water, and rocky areas.

Each species was given a maximum possible score of 1.00, which was broken down according to the habitat preference of that species, so that if an animal occurred in more than one habitat type, its score was proportional to its habitat preference. Scores for higherlevel taxonomic categories (providing no representatives have opposite ecological requirements) were calculated by counting the individual species

Table. 1. Chronological framework of the studied archaeological localities within the Manzanares and Jarama valleys, according to the numeric dating, biochronological information (mainly based on rodents) and MIS correlation.

Sites	Numeric Dating (method)		Biochronology	MIS correlation
Arganda I at Maresa quarry ~Áridos-1 (Jarama Valley)	379 ± 45 BP ka (AAR) 332 ± 38 BP ka (AAR)	Panera et al., 2011	middle Middle Pleistocene (López Martínez, 1980; Sesé et al., 2011)	late MIS 11/early MIS 9 (Panera et al., 2011)
	211 ± 54 ka (ESR Al center)	Moreno et al., in press		MIS 11b (Blain et al., 2014, 2015; this work)
	403 ± 115 ka (ESR Ti center)			MIS 9 and 10 (Moreno et al., in press)
Arganda I at Valdocarros quarry ~Áridos-1	314 ± 50 ka (ESR Al center) 275 ± 62 ka (ESR Ti center)			
Valdocarros II (Jarama Valley)	254 ± 47 ka BP (AAR) 262 ± 0.7 ka BP (AAR)	Panera et al., 2011	last third of the Middle Pleistocene (Sesé et al., 2011)	late MIS 9/early MIS 7 (Panera et al., 2011)
	255 ± 31 ka BP (ESR Al center) 286 ± 54 ka BP (ESR Ti center) 301 ± 73 ka BP (US-ESR) 360 ± 46 ka BP (US-ESR)	Moreno et al., in press		MIS 7d/8a (Blain et al., 2012a, 2012b; this work) MIS 8 and MIS7 (Moreno et al., in press)
PRERESA (Manzanares Valley)	84 ± 5.6 ka BP (OSL)	Rubio-Jara, 2011; Panera et al., 2014	early Late Pleistocene (Sesé et al., 2011)	
	157 ± 46 ka (ESR Al center) 223 ± 47 (ESR Al center)	Moreno et al., in press		MIS 5a (Blain et al., 2013) MIS 7/early MIS 6 (Moreno et al., in press)
	200 ± 31 (ESR Ti center) 206 ± 42 ka BP (US-ESR) 235 ± 32 ka BP (US-ESR)			MIS 7/6 or 5a (this work)
ETB-H02 (Manzanares Valley)	>84.6 + 12.6/−11.2	Domínguez-Alonso et al., 2007	late Middle Pleistocene (Laplana et al., 2015)	MIS6 or MIS 8 (Laplana et al., 2015)
	>74.9 + 10.2/−9.2,			Late MIS 6 (Blain et al., 2017) MIS 6 or 7d (this work)
HAT (Jarama Valley)	74 + 16/-12.1 ka BP (TL)	Panera et al., 2005	early Late Pleistocene (Sesé et al., 2011)	MIS 5a (Blain et al., 2013)

scores of all the species contained. Family-level groups or groups containing species currently with opposite ecologies (such as lacertids) were disregarded. To avoid large deviations in graphics, strictly aquatic species have been excluded from these analyzes.

The distribution data are from Pleguezuelos and Martínez-Rica (1997), Salvador (1997), Carrascal and Salvador (2002-2016), García-París et al. (2004) and Pleguezuelos et al. (2004). Please note here that some of the habitat percentages have been adapted from the original publications corresponding to more precise information about the local ecology of the species represented as fossil in the different localities.

Diversity and species richness

Diversity was analyzed taking into account two parameters: richness and evenness. Richness corresponds to the number of species in the community represented as S. Evenness constitutes a measure of the relative abundance of species within a community; it represents the opposite of dominance. Simpson's index (D) (Simpson, 1949) was used to measure evenness. In its initial form, Simpson index gave the probability of any two individuals drawn random from an infinitely large community belonging to the same species. The approach of this index for a finite community is:

$$D = \sum \left(\frac{n_i[n_i - 1]}{N[N - 1]} \right)$$

where ni is the number of individuals for a taxon i and N the total number of individuals (Magurran and McGill, 2011). Despite of this, Simpson index is usually expressed as the complement of dominance (1-D) so its value, which ranges from 0 to 1, will rise as the assemblage becomes more even or, what is the same, the homogeneity of the community decreases.

To avoid statistical problems related to different sample sizes, initial values of minimal number of individuals (MNI) were standardized by dividing by their corresponding total sample abundance thus obtaining percentages of MNI. Both, Simpson index (1-D) and Richness (S) were obtained using the Paleontological Statistics Program (PAST) (Hammer et al., 2001). Finally, relation with climatic parameters was analyzed with OLS regression models

taking on a significance level of $\alpha = 0.05$.

3.4 RESULTS

Amphibian and reptile assemblages

Amphibian and reptile fossils recovered from the sites under study here mainly correspond (with a few exceptions in Áridos-1) to disarticulated elements recovered by water-screening the sediments at the different localities (Table 2). Smallest mesh used in all sites was 0.2mmin size, thus avoiding any bias during the recovery of these tiny elements. From a taphonomical point of view, these sites have been deposited in still water environment (small ponds or lateral meander of the main river). No important difference between depositional environments has been evidenced, beside maybe the distance from the site to the main river, thus influencing the proportion of aquatic taxa in the assemblages. Accumulation of the small vertebrate remains has been demonstrated to be the consequence of both in situ mortality (burrowing toads and aquatic taxa) as well as by the action of opportunistic predators (birds of prey or small carnivores) (Blain et al., 2012b, 2013, 2014, 2017).

As a whole, the archaeo-paleontological localities of Áridos-1, Valdocarros II, Estanque de Tormentas de Butarque H-02, HAT and PRERESA document a total of 20 taxa (8 anurans and 12 reptiles) thus representing 76.9% of the modern autochthonous herpetofauna of the southeast of the Region of Madrid: 88.9% of the amphibians, 50% of the turtles, and 80% of the squamates. Taxa that are living today in the area but not represented in the fossil localities are *Pleurodeles waltl,* various exotic turtles (*Graptemys pseudogeographica, Pseudemys nelsonii* and *Trachemys scripta*), *Tarentola mauritanica, Acanthodactylus erythrurus, Podarcis virescens, Macroprotodon brevis and Malpolon monspessulanus.* Besides allochtonous turtles that have recently been introduced in the southeast of the Region of Madrid (Barquero, 2001; Pleguezuelos, 2004; Mingot et al., 2003), many of these absences can be considered significant as these taxa are well represented today in the area (with the exception of the snake *M. brevis*; Table 2). The depositional environment can also be evoked for some squamates as the gecko *T. mauritanica*, and maybe also *Podarcis* and *Acanthodactylus,* that are rather unlikely found as fossil in fluvio-lacustrine localities.

Finally the only remains that may represent a species absent today from this area is Hyla sp. from Áridos-1 and PRERESA. The fossil remains of Hyla represented in these sites do not match the Iberian species *H. molleri,* but coincide better with the morphology of the African immigrant *H. meridionalis* (Blain et al., 2013, 2014).

Table. 2. Amphibians and squamates from the Manzanares and Jarama valleys (compilation from Blain et al., 2012b, 2013, 2014, 2017) according to their taxonomic attribution (tax.), minimum number of individuals (MNI), and number of sighting records (REC) currently registered in the five UTM squares of the localities under study (data from A.H.E., 2016; see Supplementary Information Table A1).

Species	Áridos-1		Vald. II level 2		Vald. II level 3		Vald. II level 4		ETB-H02		PRERESA		HAT		Today
	tax	MNI	tax	MNI	tax	MNI	tax	MNI	tax	MNI	tax	MNI	tax	MNI	REC
Pleurodeles waltl		–		–		–		–		–		–		–	15
Alytes sp.	aff.	1		–		1		–		–		–		–	–
Alytes obstetricans		–		–		–		–		–		–		–	16
Discoglossus galganoi	cf.	2		–		–		–		–		–		–	16
Discoglossus sp.		–		–		–		–		2		–		–	–
Pelobates cultripes		19		1		4		5		20		17		8	15
Pelodytes punctatus		–		–		–		–		–		–		–	24
Pelodytes sp.		–		–		2		–		1		2		11	–
Bufo spinosus		4		–		–		1		13		5		1	63
Epidalea calamita		–		1		3		7		1		16		–	81
Hyla gr. *H. arborea*		–		3		–		–		–		–		–	3
Hyla sp.		2		–		–		–		–		2		–	–
Pelophylax perezi		10		8		2		3		21		17		4	86
Emys/Mauremys		–		–		–		–		1		–		1	–
Emys orbicularis		3		–		–		–		–		–		–	10
Graptemys pseudogeographica		–		–		–		–		–		–		–	1
Mauremys leprosa		–		–		–		–		–		–		–	32
Pseudemys nelsonii		–		–		–		–		–		–		–	1
Trachemys scripta		–		–		–		–		–		–		–	21
Blanus cinereus		–		–		–		–		–		–		–	28
Blanus sp.		–		–		–		–		–		–		1	–
Chalcides striatus		–		–		–		1		–		–		–	8
Chalcides sp.		–		–		1		1		–		–		–	–
Tarentola mauritanica		–		–		–		–		–		–		–	33
Acanthodactylus erythrurus		–		–		–		–		–		–		–	16
Podarcis virescens		–		–		–		–		–		–		–	94
Psammodromus algirus		–		4		46		51		–	cf.	18		–	50
Psammodromus hispanicus	cf.	18		–		–		–		–		–		–	36
Timon lepidus		9		5		6		3		–		5		3	64
Coronella girondica		2		2		3		4		2		–		–	7
Coronella sp.		–		–		–		–		–		1		1	–
Macroprotodon brevis		–		–		–		–		–		–		–	8
Malpolon monspessulanus		–		–		–		–		–		–		–	40
Natrix maura		–		1		5		4		–		1		–	15
Natrix natrix		3		–		–		–		6		–		–	–
Rhinechis scalaris		5	cf.	1		–		–		–		–		–	68
Vipera latastei		–		–		–		–		–		7		1	–
Vipera sp.		–		1		2		–		–		–		–	–
Total		78		27		75		80		67		91		31	836

This species has been suggested, from mitochondrial DNA analyses, to be a very recent colonizer of southwestern Europe and the Canary Islands from Morocco (Recuero et al., 2007). In the Iberian Peninsula, this species is currently well represented in the southwestern part, quite reaching the Region of Madrid in the North and reaching in the East the littoral of the Province of Almeria and the north of the Province of Murcia. Populations from Catalonia and southern France have been supposedly introduced recently (Recuero et al., 2007). The fossils from Áridos-1 (and maybe also from PRERESA) might represent a previous dispersal event of this species onto the Iberian Peninsula, as it has been suggested for the Early Pleistocene locality of Barranco León(Guadix-Baza Basin, southeastern Spain; Blain and Bailon, 2010, Blain et al., 2011, 2016).

Paleoclimatic data

In the site of Áridos-1, the application of MER methodology to the herpetofaunal assemblage gives an overlap of 34 UTM squares, occurring in central and southwestern Spain. The estimated MAT is 15.6 ± 2.7 °C, and the MAP is 682 ± 140mm (Fig. 2, Table 3). The

climate at the time of Áridos-1 has been defined as warm with warm summer and temperate winter. Rainfall is low and its distribution irregular, occurring principally during winter and late autumn. The calculated aridity indexes suggest a semi-arid (or semi-humid according to the De Martonne index), continental Mediterranean climate with four dry months in summer. In comparison with the current climatic data from the Arganda 'Comunidad' 3182E weather station, the estimated MAT for Áridos-1 is warmer (ΔMAT = +1.7 °C). The increase in temperature is higher for winter (ΔMTC = +3.6 °C) than for summer (ΔMTW = +0.9 °C).

The total amount of rainfall is higher (ΔMAP = +223.9 mm) than the current level in Madrid. This is clearly supported by the De Martonne aridity index, indicating that today conditions are more arid than during MIS 11b. Nevertheless, differences can be seen in the distribution of precipitation over the year, with more abundant precipitation during the winter months, at the beginning of spring and at the end of fall (from October to March) and less precipitation than today during the summer months and at the end of spring (from May to August). This suggest stronger rainfall seasonality between winter and summer than is currently the case, with slightly warmer and dryer summers by contrast with muchwarmer and rainier winters.

The overlaps obtained for Valdocarros II (levels 2, 3 and 4) correspond to various areas within the Iberian Peninsula, thus suggesting different climatic conditions between the different levels of this site.

For level 2, the overlap gives 67 UTM squares, mainly occurring in central and southwestern Spain, yet they occur more abundantly in the north. This is mainly due to the occurrence of *Hyla* gr. *arborea*, which is currently absent from large areas in the south of the Iberian Peninsula (Pleguezuelos et al., 2004). The MAT is 12.1 ± 2.3 °C, and the MAP is 745 ± 152mm (Fig. 2, Table 3). The climate is relatively cold with a high atmospheric temperature range. The summer is rather warm and the winter is cold, with three months with mean temperatures below 6 °C. Rainfall is low and its distribution is fairly regular, occurring throughout the year (with highest levels during winter) and with two months during summer (July and August) with low rainfall. The aridity indexes suggest a semi-humid to humid, cold, continental Oceanic climate with two dry months in summer.

For the uplying levels 3 and 4, the overlap yields 90 and 145 UTM squares respectively. These overlaps are more extended than for level 2, reaching the Mediterranean seashore in the east for level 3 and in the northeast for level 4. For level 3, the MAT is 13.8 ± 3.1 °C and the MAP is 711 ± 169mm (Fig. 2, Table 3). The climate is temperate with warm summer and temperate winter. Rainfall is low and its distribution is fairly regular, occurring throughout the year with a similar pattern to that in level 2 but with a lower amount. The aridity indexes suggest a semi-humid to humid, continental Oceanic climate with two dry months in summer.

For level 4, the MAT is 15.3 ± 2.6 °C, and the MAP is 759 ± 163mm (Fig. 2, Table 3). The climate is warm with a high atmospheric temperature range. Rainfall is low and its distribution is fairly regular, occurring principally during winter and to a lesser extent during spring and late autumn. The aridity indexes suggest a semi-humid to humid, continental Mediterranean climate with three dry months in summer.

In comparison with current climatic data from the Arganda 'Comunidad' 3182E weather station, all the MER-estimated MATs are somewhat higher, excepted for level 2. The level 2 shows the coolest temperature of the sequence; with MAT 1.8 °C lower than today. Overall, the winter is generally warmer and the summer similar in warmth to current ones. In level 2, the cooler climatic conditions are mainly linked with a greater decrease in the summer temperature (-1.5 °C) than in the winter temperature (-1.0 °C).

The total amount of rainfall is higher than the current level in Madrid. This is well suggested by the values of the De Martonne index, suggesting more humid conditions during the transition from MIS 8 to MIS 7 than today.

For the Estanque de Tormentas de Butarque (H-02) site, the overlap obtained from the herpetofaunal assemblage gives 16 UTM squares occurring in north-central and eastern Spain. The mean value of the MER-estimated MAT is 10.9 ± 2.3 °C, and for the MAP 581.3 ± 40.3mm (Fig. 2, Table 3). The climate at the time of ETBH02 can be defined as cold with a very high atmospheric temperature range. The summer is reasonably warm, and the winter is cold. Rainfall is low, even if higher than today, but its distribution is fairly regular with higher amounts during winter and spring. The aridity indexes suggest a semi-humid (or humid according to the Dantin-Revenga index), continental Mediterranean (transitional to Oceanic) climate with only two dry months in summer (Fig. 2).

In comparison with the current climatic data from Arganda 'Comunidad' weather station 3182E, the MER-estimated MAT for ETB-H02 is much colder (ΔMAT=-3.0 °C). The decrease in temperature is in evidence for all the seasons of the year. Although the total amount of rainfall is only slightly higher (ΔMAP = +122.8 mm) than the current level in Madrid, the rainfall is more regularly distributed throughout the year, reducing the duration of summer aridity. This is clearly supported by the values of the aridity indexes, which all indicate a semi-humid or humid climate for ETB-H02, whereas current values are characteristic of a semi-arid climate, implying moister conditions in the area during MIS 6 or MIS 7d than today.

At PRERESA the overlap corresponds to 92 UTM squares, distributed on the whole Iberian Peninsula, on an axis oriented south-westenorth-east from Atlantic to the Mediterranean seashores, and encompassing the central Meseta. Estimated MAT is 14.2 ± 3.2 °C and MAP 693 ± 131mm (Fig. 2, Table 3). The aridity indexes suggest a continental semi-arid Mediterranean climate with three months of dryness during the summer and the beginning of fall (Fig. 2). The comparison with the current climatic data from Arganda 'Comunidad' weather station 3182E shows that the estimated MAT for PRERESA are slightly higher to present values (ΔMAT = +0.3 °C). The difference between the temperature of the warmest and coldest months is lower than today, due to the fact that winter temperatures are higher (ΔMTC=+1.2 °C) and summer only slightly higher (ΔMTW = +0.1 °C), thus suggesting a less pronounced continentality. MAPs remain low for PRERESA even if their

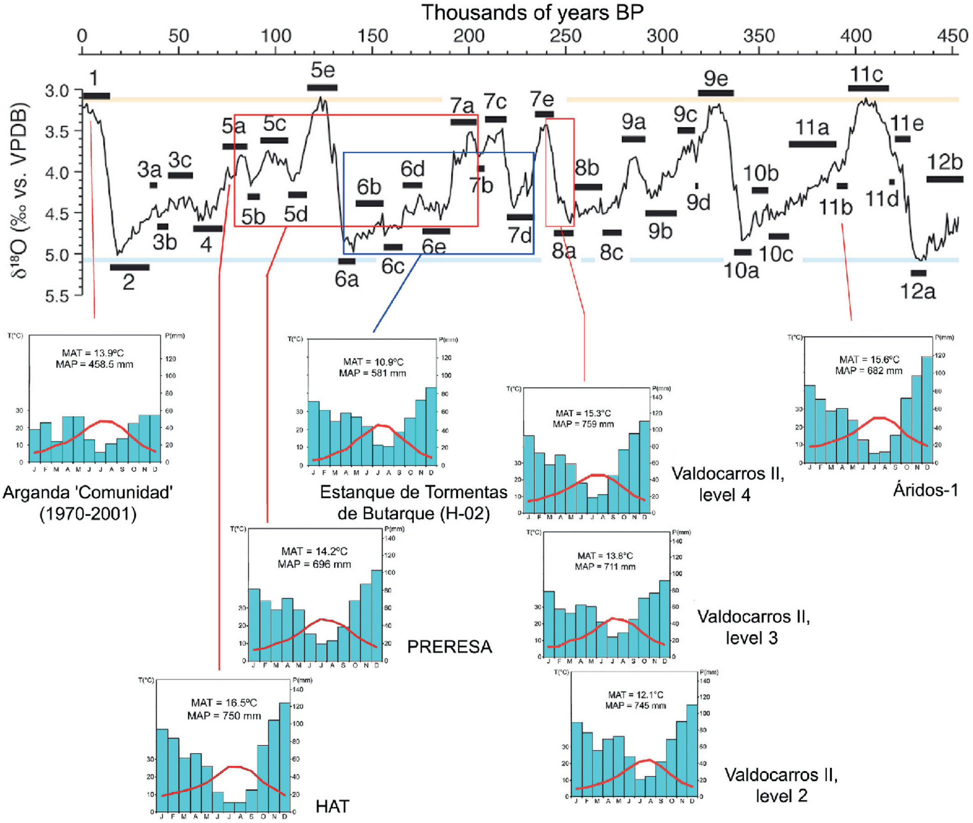

Figure. 2. Paleoclimatic reconstruction according to the mutual ecogeographic range method of the archaeo-paleontological sites from the Manzanares and Jarama valleys. Abbreviations: MAT, mean annual temperature; MAP, mean annual precipitation. Isotopic oxygen record and optimized scheme of lettered marine isotope substages from Railsback et al. (2015).

total amount are slightly higher than present values ($\Delta MAP = +235$ mm). The period of aridity during summer lasts three months (from June to August) thus well corresponding to a semi-arid Mediterranean climate.

For HAT, the overlap corresponds to some 45 UTM squares, all located in the south-westernmost Iberian Peninsula. Such a situation is partly linked to the presence of the amphisbaenian Blanus sp., restricted today to the Mediterranean bioclimatic area. In HAT, MAT is 16.5 ± 2.0 °C and MAP 750 ± 137mm (Fig. 2, Table 3).

Summer is warm and winter is temperate. Rainfall is rather low with an irregular distribution over the year, mainly occurring during the winter and in a lesser amount during spring. The aridity indexes suggest a continental semi-arid Mediterranean climate with four months of dryness during the summer and

Table. 3. Climatic parameters (in °C for temperature and mm for precipitation) calculated by the mutual ecogeographic range method and aridity indexes for the localities from the Manzanares and Jarama valleys (compilation from Blain et al., 2012b, 2013, 2014, 2017). Mean annual temperature (MAT), mean annual precipitation (MAP), N = number of 10 x 10 km UTM squares of the overlap, SD = standard deviation, D = comparison with the climatic values (1970-2001) from the weather station 3182E of Arganda 'Comunidad' (Ninyerola et al., 2005).

		Áridos-1	Vald. II level 2	Vald. II level 3	Vald. II level 4	ETB-H02	PRERESA	HAT	Today
	N	34	67	90	145	16	92	45	
MAT	MEAN	15.6	12.1	13.8	15.3	10.9	14.2	16.5	
	SD	2.7	2.3	3.1	2.6	2.3	3.2	2.0	
	Δ	1.7	−1.8	−0.1	1.4	−3.0	0.3	2.6	
MTC	MEAN	8.8	4.2	6.4	7.2	3.1	6.4	8.7	
	SD	3.5	2.7	3.5	3.9	2.7	3.5	2.7	
	Δ	3.6	−1.0	1.2	2.0	−2.1	1.2	3.5	
MTW	MEAN	24.9	22.2	23.7	23.3	22.4	24.1	25.5	
	SD	2.3	2.6	2.0	1.9	2.1	2.1	1.5	
	Δ	0.9	−1.5	−0.3	−0.7	−1.6	−0.1	1.5	
MAP	MEAN	682	745	711	759	581	693	750	
	SD	140	152	169	163	40	131	137	
	Δ	223.5	286.5	252.5	300.5	122.5	234.5	291.5	
Gaussen Index		Mediterranean	Oceanic	Oceanic	Mediterranean	Oceanic	Mediterranean	Mediterranean	Mediterranean
Lautensach-Mayer Index		semi-arid	semi-humid	semi-humid	semi-humid	semi-humid	semi-arid	semi-arid	semi-arid
Dantin-Revenga Index		semi-arid	humid	humid	humid	humid	semi-humid	semi-arid	semi-arid
De Martonne Index		semi-humid	humid	subhumid	subhumid	subhumid	semi-arid	semi-humid	semi-arid

the beginning of fall (Fig. 2). The comparison with the current climatic data shows that the estimated MAT for HAT are higher to present values (ΔMAT = +2.6 °C). The difference between the temperature of the warmest and coldest months is lower than today, due to the fact that winter temperatures are higher (ΔMTC = +3.5 °C) and summer (ΔMTW = +1.5 °C), thus suggesting a less pronounced continentality.

MAPs remain low for HAT even if their total amount are slightly higher than present values (ΔMAP = +292 mm). The period of aridity during summer lasts four months (from June to September) thus well corresponding to a semi-arid Mediterranean climate.

Overall paleoclimatic comparison between the studied sites, suggest two different climatic patterns: an interglacial "warm-temperate" pattern and glacial "cold" one. During relatively "warm" periods (MIS 11b, MIS 5a and today) the climate is clearly Mediterranean, with mild winters and a long period of dryness (4 months) in summer and early autumn and by contrast during "cold" periods (MIS 8 and MIS 6) the climate is more Oceanic (or continental Mediterranean), although preserving some dryness (two months) during the summer. However transitional stages may exist with sites like Valdocarros II, where summer dryness last 3 months and that seems to be rainier than the other reconstructions, with the exception of HAT that is very warm and humid.

Paleoenvironmental data

The distribution by habitat for each amphibian and reptile species used in this work is done in Table 4. Environmental reconstruction from the Áridos-1 herpetofaunal assemblage during MIS 11b suggests the existence of a landscape predominantly open dry (48.5%) with an uneven distribution of vegetation cover of scrub and forest (19.4%), rocky and stony habitats (11.3%) and wet meadows (9.8%) (Fig. 3, Table 5). This deviation to a mostly dry and open environment is marked quantitatively by a significant presence of *Timon lepidus, Psammodromus hispanicus* and, especially, *Pelobates cultripes.* The lacertid *T. lepidus* is very adaptable but usually occurs in dry habitats, and restricts its presence on account of the existence of shelters and not by vegetation cover (Llorente et al., 1995; Díaz et al., 2006). The small lacertid *P. hispanicus* prefers open habitats with sparse vegetation and to a lesser extent areas of low scrub, avoiding high vegetation and forest environments (Carrascal et al., 1989; Gosá and Bergerandi, 1994).

The adult toad *P. cultripes* prefers sandy or loose soils that allow it to bury itself as daytime refuge and during its periods of aestivation, but like all Iberian amphibians, also depends on the existence of wáter points for breeding and larval development (Recuero, 2014). The same happens to the other amphibians documented in Áridos-1 assemblage, which vary according to their adaptability to diverse terrestrial habitats as *Alytes* and *Bufo spinosus*, to humid meadows as *Discoglossus galganoi* and genus *Hyla* (*Hyla molleri*) or strictly aquatic as *Pelophylax perezi.* This last species of frog, plus the turtle *Emys orbicularis,* mark the presence of a fully aquatic environment (11%) due to the proximity of the river itself. The snake *Natrix natrix* (sensu lato, tentatively Iberian *Natrix astreptophora*), which also presents aquatic trends, is mostly terrestrial, preferring wet meadows as well as, to a lesser extent, forest areas (Santos et al., 2004). The combination *N. natrix, B. spinosus, D. galganoi* and *Hyla* is consistent with the presence of wetlands, both open or with vegetation cover. Concurrently, the presence of the snakes *Rhinechis scalaris* and *Coronella girondica* corroborates the diversity of different environments but in a dry and thermophilic general scenario (Pleguezuelos and Honrubia, 1997; Santos and Pleguezuelos, 2009).

Table. 4. Distribution by habitats of the taxa recovered as fossil in the archaeopaleontological localities and of the other species represented today in the Manzanares and Jarama valleys (see Supplementary Information Table A1). Abbreviations: OD, open-dry; OH, open-humid; WB, woodland/bush; R/S, rocky/stony environments; Wa, water-edge.

Species	Habitat distribution				
	OD	OH	WB	R/S	WE
Pleurodeles waltl	–	–	–	–	1
Alytes sp.	0.2	0.4	0.2	–	0.2
Alytes obstetricans	0.2	0.4	0.2	–	0.2
Discoglossus galganoi	–	0.4	–	–	0.6
Discoglossus sp.	–	0.4	–	–	0.6
Pelobates cultripes	0.8	–	–	–	0.2
Pelodytes punctatus	0.5	–	0.2	0.1	0.2
Pelodytes sp.	0.5	–	0.2	0.1	0.2
Epidalea calamita	0.45	–	0.2	0.25	0.1
Bufo spinosus	0.1	0.3	0.4	–	0.2
Hyla molleri	–	0.5	0.2	–	0.3
Hyla sp. *(meridionalis)*	–	0.6	0.2	–	0.2
Pelophylax perezi	–	–	–	–	1
Emys/Mauremys	–	–	–	–	1
Emys orbicularis	–	–	–	–	1
Graptemys pseudogeographica	–	–	–	–	1
Mauremys leprosa	–	–	–	–	1
Pseudemys nelsonii	–	–	–	–	1
Trachemys scripta	–	–	–	–	1
Blanus cinereus	0.45	0.1	0.45	–	–
Blanus sp.	0.45	0.1	0.45	–	–
Chalcides striatus	0.3	0.3	0.2	0.2	–
Chalcides sp.	x	x	x	x	x
Tarentola mauritanica	–	–	0.25	0.75	–
Acanthodactylus erythrurus	0.7	–	0.3	–	–
Podarcis virescens	0.4	0.1	–	0.5	–
Psammodromus algirus	0.2	0.1	0.5	0.2	–
Psammodromus hispanicus	0.5	–	0.3	0.2	–
Timon lepidus	0.5	–	0.25	0.25	–
Coronella girondica	0.25	0.25	0.25	0.25	–
Coronella sp.	0.25	0.25	0.25	0.25	–
Macroprotodon brevis	0.3	0.1	0.3	0.3	–
Malpolon monspessulanus	0.35	0.15	0.25	0.25	–
Natrix maura	–	0.2	–	–	0.8
Natrix natrix	–	0.5	0.25	–	0.25
Rhinechis scalaris	0.35	0.15	0.3	0.2	–
Vipera latastei	0.4	–	0.2	0.4	–
Vipera sp.	0.4	–	0.2	0.4	–

In contrast, the Valdocarros II sequence (MIS 8/7) is characterized by a progressive increase in vegetation cover at the expense of open habitats and aquatic strictly within a warm climatic context, in correspondence with the thermophilic herpetofaunal associations. So, in level 2 the open dry habitats have still the highest values of the set (30.5%), followed by scrubby or forested environments (25.5%), the rocky and stony areas (16.8%), wet meadows (14.5%) and aquatic environments (12.6%) (Fig. 3, Table 5). Level 3 and level 4 show very similar percentages: the habitats of scrub and forest are those with higher values in the last level (38.5%), compared to the open dry environments (26.6%), the rocky/stony areas (18.3%), the wet meadows (9.9%) and aquatic habitats (6.7%) (Fig. 3, Table 5).

The great increase in vegetation cover matches the appearance on the regional fossil record of *Psammodromus algirus*, which prefers dry environments with some vegetation cover, especially thickets, avoiding open areas in contrast to *P. hispanicus* (Carrascal et al., 1989; Díaz and Carrascal, 1991). This species becomes more abundant in the record with the advance of stratigraphy. This increase coincides with the decline of *P. cultripes*, reaching mínimum values in MNI of all the regional sequence. Also appear for the first time on regional fossil record the genera *Vipera* and *Pelodytes* and the species *Epidalea calamita*, *Hyla gr. H. arborea, Chalcides striatus* and *Natrix maura.* The skink *C. striatus* usually prefers open hábitats such as meadows, grasslands, pastures or low scrub (Pollo, 2012), although it may appears in stony zones next to the other mentioned areas. The snake *N. maura* is much more linked to the aquatic environment than *N. natrix*, absent in the Valdocarros II sequence, but also can be found in open environments near water points. The toad *E. calamita,* in its adult phase, presents a clear deviation towards open and well sunny environments, with sparse vegetation or lesser developed plant cover (Romero and Real, 1996).

The continued association of *T. lepidus, P. algirus, C. girondica, E. calamita* and *P. cultripes* at all three levels of Valdocarros II shows a deviation towards dry conditions with open areas and a vegetative cover of thicket and scrubland with low development. This environmental situation is also consistent with the intermittent appearance of other taxa such as genera *Alytes, Pelodytes* and *Vipera* and species *C. striatus* and *R. scalaris.* Also, although decreasing, the fluvial influence is still noticeable with the presence of *P. perezi* and *N. maura.* The environment documented by the herpetofauna from Estanque de Tormentas de Butarque ETB-H02, attributed to MIS 7d or MIS 6 (i.e. the Penultimate Glacial Period), shows significant changes from the previous stages, with significant increases of the aquatic environments and open moist and open dry habitats (Fig. 3, Table 5). So, the open dry environments have again the highest values (41.7%), followed by aquatic habitats (21.3%) and open wet environments (18.2%), being in the latter two cases the higher values for these types of habitats throughout the whole analyzed sequence. Instead, areas of vegetation cover decay (16.9%) while areas of rocky and stony habitats become insignificant (1.9%).

The association of ETB-H02 consists almost exclusively by taxa related with aquatic environment, with *Coronella girondica* as the only terrestrial exception. It also highlights the apparent absence of more thermophilic taxa, which are typical in the previous fossil record, as *T. lepidus, R. scalaris, P. algirus* and *Vipera* genus, a fact that explains the very low percentage attributable to the rocky and stony habitats, as well the low values of vegetation cover environments.

The taphonomical study of the remains indicates the existence of a very short transport of them and the possibility of a high percentage of in situ mortality. Therefore possibly it is a fully perifluvial association, from the closest environments to the river. Hence, there is likely a bias in the fossil assemblage from ETB-H02 that has only allowed the representation of the closest species to the river area. Or otherwise, it is also possible that the absence of thermophilic species which have been mentioned above is due to a much cooler climate, according to the glacial chronology of the level.

The herpetofaunal assemblages of HAT (MIS 5a) and PRERESA (MIS 5a or MIS 7/6), both with interglacial climatic conditions, show a general scenario of dominance of open dry habitats, although with significant differences (Fig. 3, Table 5). In HAT the prevalence of open dry environments is accentuated (56.2%), to the detriment of open wet areas (2.5%), vegetation cover of woods and/ or scrublands (16.4%) and rocky zones (9.6%). In PRERESA the open dry habitats are also predominant (42.5%), while the remaining habitats are better represented compared to HAT (open-humid: 6.7%; woodland: 24.2%; and rocky: 16.4%).

Thermophilic Mediterranean species reappear in the fossil record, as *T. lepidus, P. algirus* and *V. latastei.* In addition, the genus Blanus has its first regional record in the herpetofaunal assemblage of HAT. *Blanus* is a legless reptile associated with warm Mediterranean environments and is adapted to underground life in loose soils with presence of stones on the surface, avoiding the most compact and clayey soils (Martín et al., 1991; López et al., 1998). The significant conjugation in the quantitative aspect of *E. calamita* and *P. algirus* in the PRERESA assemblage, in contrast to their absences in HAT, coupled with the increased representation of *V. latastei,* are consistent with the existence of greater vegetation cover of shrubby type and of refuge areas as scree. The small differences observed between PRERESA and HAT, including those related to the development of aquaticenvironment and wet meadows, could be explained according to the distance of these sites regarding the river.

In conclusion, the application of the method of hábitat weighting on the herpetofauna currently documented in the UTM 10 x 10km squares where are located the sites under study (AHE, 2016; Supplementary Information Table A1) shows a varying scenario, with a predominance accentuated moderately of open dry environments (34.4%), followed by habitats with vegetation cover (23.9%) and rocky and stony areas (22.9%), and a smaller proportion of wet meadows (10.9%) and aquatic environments (7.9%). The observed environmental differences with respect to the fossil record should be related to the significant impact that human activity, such as agriculture and urbanization, have had and have yet over the territory. Especially, the large representation in rocky and stony environments today that is certainly due to the large aggregate extraction activity and the proliferation of quarries on riverterraces.

Biodiversity

The region's extraordinary environmental heterogeneity in terms of climatology, types of geological substrates, vegetation and orography contributes to there being a relatively high number of herpetofaunistic species in relation to surface area today in the Region of Madrid, with a total of 42 autochthonous species (18 amphibians and 24 reptiles) (Martínez-Solano et al., 2004). However, the southeastern part of the region, where the archaeological localities under study are located, is at a considerable distance from any major mountains and is poorer in terms of the number of herpetofaunistic species, with only 9 amphibian and 17 reptile autochthonous species (Table 2).

Throughout the different archaeological localities, the amphibians and reptiles showed different patterns for evenness and richness (Table 6). For amphibians, Simpson index (1-D) reached its highest value in the level 3 of Valdocarros II and its lowest value in the level 2 of the same locality which also held the maximum evenness value for reptiles. Minimum value for Simpson index for reptiles occurs in the level 4 of Valdocarros II.

Total values for richness, comprised between 10 and 12 species throughout the whole sequence, can be considered rather constant. However amphibians and reptiles component for richness changes between sites. For amphi-

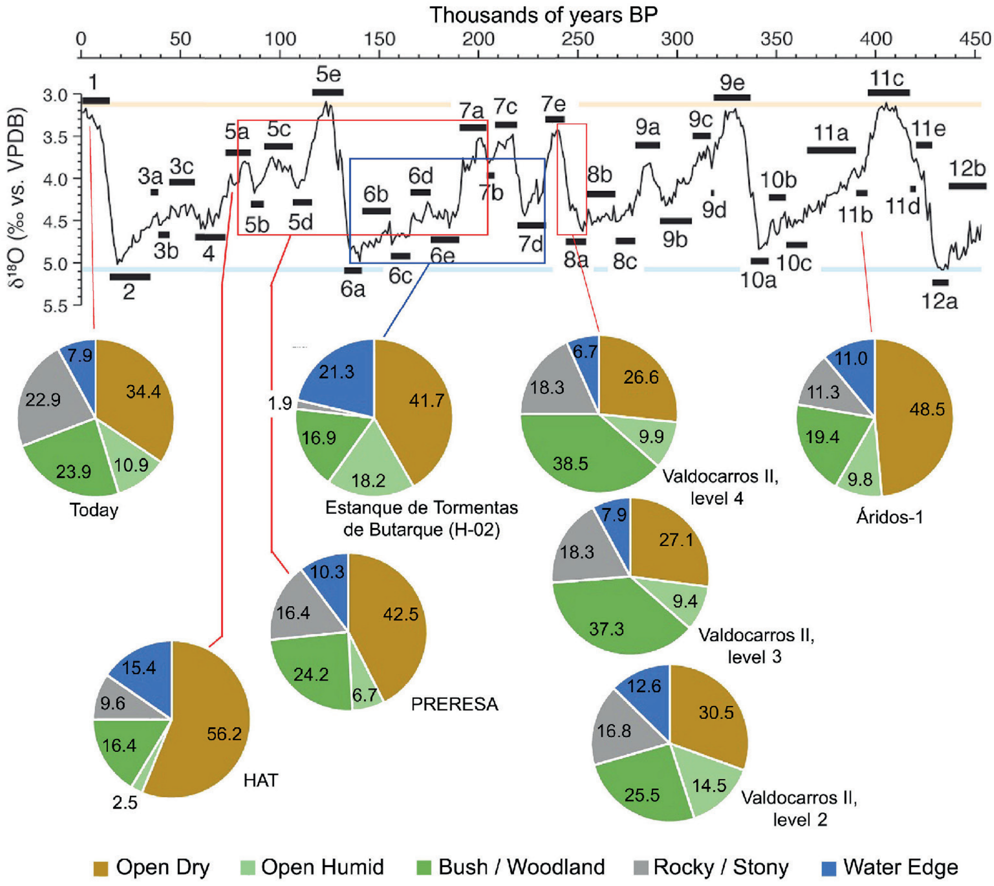

Figure. 3. Paleoenvironmental reconstruction according to the habitat weighting method of the archaeo-paleontological sites from the Manzanares and Jarama valleys. Isotopic oxygen record and optimized scheme of lettered marine isotope substages from Railsback et al. (2015).

bians, in the level 2 of Valdocarros II where minimum value of evenness occurred, the dominant species is *Pelophylax perezi*. For reptiles, *Psammodromus* cf. *algirus* is the dominant species in the levels 3 and 4 of Valdocarros II where the environment is more homogeneous (Fig. 3).

When comparing this data with the modern values for Simpson index in the area, both amphibians and reptiles are under current values for evenness which are rather high (Table 6). However such result can also be the case of a certain taphonomical bias in the representation of some rare species in the archaeological sites. Climate does not seem to be a determining factor for evenness, instead for total richness which seems to be influenced by MAP (Table 7). For reptiles, there is a high positive correlation with MAP, and vegetal cover (bush/woodland; Table 8) while for amphibians richness correlation with MAP is negative.

Remaining climatic correlations have adjusted r2 under 0.3 or are not significant (have p-value over 0.05). According to the correlates, only reptiles seem to be influenced by the terrestrial environment. The percentages for forested and water-edge habitats within the whole environment are negatively correlated with reptiles' evenness and richness respectively becoming a more even and rich (in terms of number of species) assemblage when the woodland and water-edge habitats decrease.

3.5 DISCUSSION AND CONCLUSION

The configuration and temporal evolution of the reconstructed habitats by the herpetofaunal assemblages suggest the existence, in the lower valleys of the Jarama and Manzanares Rivers, of a landscape with gallery forests along watercourses. Parallel to these forested areas would be the presence of wet meadows in the flood plain. Then, according to the distance from the river, they would give way, on the surrounding plateau, to shrubby and finally dry grasslands and steppe zones, with areas of scattered rocky (Fig. 4).

The changes observed over the sequence could be related to the retractions of the wettest environments and the increase of dry habitats in accordance with the fluctuations of the river water regime and rainfalls. Such a situation is in accordance with the overall climate comparison between the studied sites that suggest two different climatic patterns (+a transitional one): an interglacial "warm" pattern and a glacial "cold" one. During relatively "warm" periods (MIS 11b, MIS 7, MIS 5a and today) the climate is clearly Mediterranean, with mild winters and a long period of dryness in summer and early autumn and by contrast during "cold" periods (MIS 8 and MIS 6) the climate is more Oceanic (or continental Mediterranean), although preserving some dryness during the summer.

As far as herpetofaunal assemblages are concerned, a striking difference with modern data is the very low representation of reptiles in the archaeological localities (4-7 compared with the authochtonous 17 species currently represented in the southeastern part of the Region of Madrid): but as said before this can be due, in some way, to a taphonomical bias. At the contrary richness for anurans seems to have been quite the same (4e6 against 8 today in the area). Such pattern in biodiversity suggest 1) a quite similar diversity of anurans between cold and warm periods; 2) an impoverishment of the squamate Mediterranean fauna during cold periods (as put in evidence in ETB-H02; Blain et al., 2017); 3) an absence of any

Table. 5. Landscape reconstruction according to the habitat weighting method applied to the herpetofaunal assemblages from the archaeo-paleontological localities of the southeastern part of the Region of Madrid.

	Open Dry	Open Humid	Woodland/Bush	Rocky/Stony	Water Edge
Áridos-1	48.5%	9.8%	19.4%	11.3%	11.0%
Valdocarros II, level 2	30.5%	14.5%	25.5%	16.8%	12.6%
Valdocarros II, level 3	27.1%	9.4%	37.3%	18.3%	7.9%
Valdocarros II, level4	26.6%	9.9%	38.5%	18.3%	6.7%
ETB-H02	41.7%	18.2%	16.9%	1.9%	21.3%
PRERESA	42.5%	6.7%	24.2%	16.4%	10.3%
HAT	56.2%	2.5%	16.4%	9.6%	15.4%
Present	34.4%	10.9%	23.9%	22.9%	7.9%

Table. 6. Values obtained for Simpson index (evenness) and richness (number of species).

		Áridos-1	Valdocarros II			ETB-H02	PRERESA	HAT	Today
			level 2	level 3	level 4				
Simpson Index (1-D)	amphibians	0.663	0.556	0.764	0.672	0.698	0.751	0.649	0.809
	reptiles	0.718	0.755	0.448	0.374	0.64	0.609	0.736	0.904
	total	0.846	0.831	0.604	0.584	0.820	0.847	0.815	0.936
Richness (S)	amphibians	6	4	5	4	6	6	4	9
	reptiles	6	6	6	7	4	5	6	17
	total	12	10	11	11	10	11	10	26

Table. 7. Values of correlations between climatic parameters and Simpson index (1-D) and Richness. Adjusted R^2 (Adj-R^2), sign of the slope (Slope) and p-value of the regression model. As significance value was established in $\alpha = 0.05$, all correlations with higher p-value are consider not significant and not taken into account. Significant correlations are highlighted in bold.

		MAT			MTC			MTW			MAP		
		Adj-R^2	slope	p-value	Adj-R^2	slope	p-value	Adj-R^2	slope	p-value	Adj-R^2	slope	p-value
Simpson	amphibians	−0.193	+	0.871	−0.186	+	0.818	−0.135	+	0.614	−0.052	−	0.440
	reptiles	−0.191	−	0.850	−0.199	−	0.947	−0.162	+	0.702	−0.171	−	0.741
	total	−0.168	−	0.725	−0.186	−	0.816	−0.176	+	0.762	−0.044	−	0.426
Richness	amphibians	−0.114	−	0.561	−0.186	+	0.818	−0.196	−	0.907	**0.586**	**-**	**0.027**
	reptiles	0.311	+	0.112	0.242	+	0.149	−0.115	+	0.563	**0.740**	+	**0.008**
	total	0.061	+	0.291	0.200	+	0.175	−0.0004	+	0.364	−0.198	+	0.927

Table. 8. Values of correlations between environmental parameters and Simpson index (1-D) and Richness. Adjusted R^2 (Adj-R^2), sign of the slope (Slope) and p-value of the regression model. As significance valuewas established in $\alpha = 0.05$, all correlations with higher p-value are consider not significant and not taken into account. Significant correlations are highlighted in bold.

		Open-dry			Open-humid			Woodland			Rocky			Water		
		Adj-R^2	slope	p-value	Adj-R^2	slope	p-value	Adj-R^2	slope	p-value	Adj-R^2	slope	p-value	Adj-R^2	slope	p-value
Simpson	amphibians	−0.197	−	0.916	−0.144	−	0.735	−0.115	+	0.564	−0.198	+	0.928	−0.152	−	0.666
	reptiles	0.361	+	0.090	−0.200	+	0.980	**0.699**	**-**	**0.012**	0.062	−	0.291	0.221	+	0.161
	total	0.407	+	0.073	−0.160	+	0.855	−0.196	−	0.903	0.122	−	0.234	0.249	+	0.145
Richness	amphibians	−0.103	+	0.536	−0.121	+	0.580	−0.043	−	0.425	0.008	−	0.353	−0.115	+	0.564
	reptiles	−0.071	−	0.472	0.038	−	0.317	0.233	+	0.154	0.407	+	0.073	**0.518**	**-**	**0.041**
	total	−0.198	−	0.938	−0.141	−	0.633	−0.108	+	0.548	−0.057	+	0.449	0.264	−	0.136

typically cold Euro-Siberian or higher altitude taxa during cold periods (i.e. brown frogs); and 4) the absence of any strong thermophilous reptile (as are today *Macroprotodon brevis, Malpolon monspessulanus, Acanthodactylus erythrurus* or *Tarentola mauritanica*) during the warm periods, even when reconstructed climate is supposed to be higher than current one.

According to the relation between richness, biodiversity and climatic and environmental factors (Tables 7 and 8), a clear correlation appears between reptile richness and woodlands. In particular in the site of Valdocarros II, it is possible to observe the dominancy of reptiles against the reconstructed percentages of woodlands. For a higher percentage of forest, reptile evenness is lower and thus dominancy is higher. In a similar way, mean annual precipitation (MAP) is revealed to be the most influent factor, certainly because of its implications on vegetal cover extension and ecosystem productivity and resources. For amphibians (here only anurans) the MAP does not influence dominancy but species richness: anuran richness being higher for lower MAP. Such an unusual pattern is certainly due to the fact that there are no strict forestdweller anurans within the archaeological assemblages and that most of the anurans present in the site are well adapted to arid conditions. However even if the correlation rank is high, variation among richness values is rather low (comprised between 4 and 6; Table 6) and thus it can be considered that there is not a lot of differences.

For reptiles, MAP is the most influent parameter on species richness (Table 7). In this case the relation is positive, with a higher number of species for higher MAP. Even if the variation rank of the values is low (comprised between 7 and 4), the adjustment degree is higher than for amphibians. This fit quite well with the relation between the Simpson's Index and the percentage of woodland (Table 8), thus suggesting that for a higher MAP, woodland are more represented in the area together with higher resources and ecological niches. In that way, the ecosystem can support a higher number of species with a species succession reaching a more evolved state (climax) favoring the possible dominancy of one of the species and thus leading to a decrease of the Simpson's Index. A clear example of dominancy is visible in the levels 3 and 4 of Valdocarros II (Table 2), where the dominant species is the lizard Psammodromus cf. algirus (reaching in both cases more than 60% of the whole association).

Today, the abundance of that species is positively correlated with bush cover (over 20 cm high) and with food availability; parameters also correlated with vegetal cover and the presence of leaves litter on the ground (Díaz and Carrascal, 1991). In the Region of Madrid meadow environments, its abundance is higher for a higher representation of scrub covering (Martín and López, 2002), reaching up to 13-18 individuals per hectare in holm oak forest ("encinares") (Cano, 1984), or between 30 and 22.5 adults per hectare in oak forest ("robledales") (Díaz, 1993). In the surrounding mountain environments *Psammodromus* cf. *algirus* has been reported to reach much higher densities up to 130 specimens per hectare in the Sierra de Guadarrama (Salvador and Veiga, 2001) and up to 178 individuals per hectare in the Sierra de Gredos (Gil Costa, 1992). In a same way a higher vegetal cover (low scrubs) has been showed to be highly correlate with the survival rates of newborns (Civantos et al., 1999).

Taking as a reference the modern situation in the area, the successive herpetofaunal assemblages from Áridos-1 (MIS 11b),

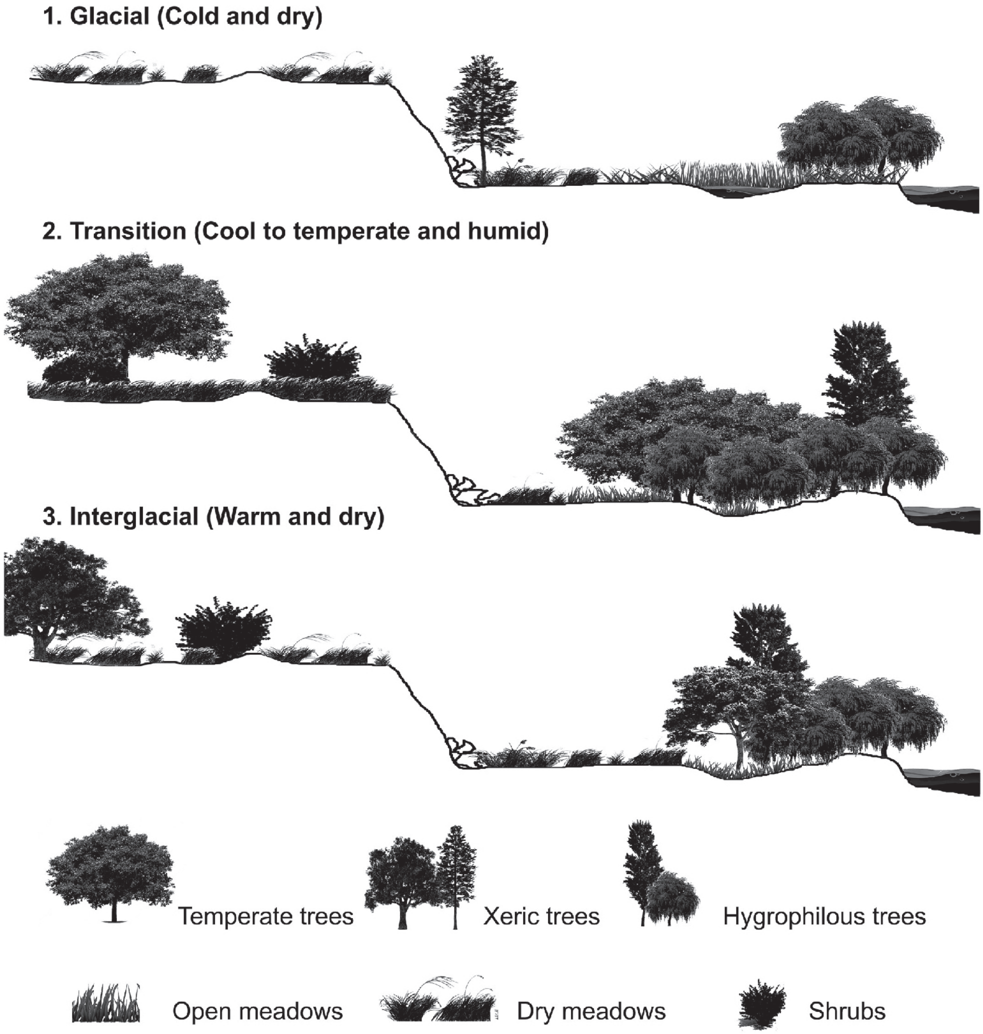

Figure. 4. . Schematic representation of the environmental succession in the vicinity of major rivers in central Iberian Peninsula as reconstructed from the herpetofaunal assemblages of the archaeo-paleontological sites of Aridos-1 (MIS 11b), Valdocarros II (MIS 8a/MIS 7e), Estanque de Tormentas de Butarque H-02 (MIS 6 or MIS 7d), PRERESA (MIS 5a or MIS 7/6) and HAT (MIS5a).

Valdocarros II (MIS 8a/MIS 7e), Estanque de Tormentas de Butarque H-02 (MIS 6 or MIS 7d), PRERESA (MIS 5a or MIS 7/6) and HAT (MIS 5a) permits a hypothetical landscape reconstruction as represented in Fig. 4. Three different periods are then represented with a glacial landscape (ETB-H02; Fig. 4.1), a landscape of transition from cool to temperate climatic conditions (Valdocarros II; Fig. 4.2), and an interglacial landscape (Áridos-1, HAT, PRERESA and today; Fig. 4.3).

Environment is particularly open during dry periods (independently of if it is cold or warm) with a percentage of open-dry environment about 40%. Themain difference between an interglacial and a glacial period is the opposite representation of woodlands vs. moist environments (water-edge + open-humid): the last ones being more represented during cold periods than during warm periods. Finally, as documented by the succession from Valdocarros II (from level 2 to level 4), periods of transition between a cold and warm climate are more forested (40% of the total landscape) but at the expense of humid meadows progressively.

As a conclusion, even if highly hypothetical and waiting for a confirmation by pollen studies, such landscape reconstructions may serves as a general background to put into context the large mammalian fauna represented in each sites as well as the hominin activities along water courses in central Iberian Peninsula.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/jquaint.2018.03.004.

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APPENDIX 3.
DATA

Abstract

In this section, raw data of the total width (in mm) from the humeri of the studied sequences (i. e. Gran Dolina; Portalón; Barranco León; Fuente Nueva 3 and Camp dels Ninots) are presented in five different tables. Also, in each table the year of excavation, level, square and other identifiers are contemplated together with the species and the sex of the individuals. Finally a sixth table with the measurements from the studied reference collections is contained in this appendix.

Table 1. Gran Dolina. Raw data of humeral Total width (HTW) in mm from the fossil humeri of *Epidalea calamita* from the Gran Dolina archaeo-palaeontological site (Sierra de Atapuerca, Spain). Year of excavation, level, talla, talla and sex of each individual is presented.

Table 2. Portalón. Raw data of humeral Total width (HTW) in mm from the fossil humeri of *Epidalea calamita* from Portalón archaeo-palaeontological site (Sierra de Atapuerca, Spain). Year of excavation, level and sex of each individual is presented.

Table 3. Barranco León. Raw data of humeral Total width (HTW) in mm from the fossil humeri of *Pelophylax* cf. *perezi* from Barranco León archaeo-palaeontological site (Guadix-Baza Basin, Spain). Year of excavation, level and sex of each individual is presented.

Table 4. Fuente Nueva 3. Raw data of humeral Total width (HTW) in mm from the fossil humeri of *Pelophylax* cf. *perezi* from Fuente Nueva 3 archaeo-palaeontological site (Guadix-Baza Basin, Spain). Year of excavation, level and sex of each individual is presented.

Table 5. Camp dels Ninots. Raw data of humeral Total width (HTW) in mm from the fossil humeri of *Pelophylax* sp. from Camp dels Ninots palaeontological site (Caldes de Malavella, Spain). Year of excavation, level, and sex of each individual is presented.

Table 6. Data of humerus of *Epidalea calamita* and *Pelophylax perezi* from modern osteological collections of the MNCN and also from the Dr. Hugues-Alexandre Blain collection (Blain Herpetological Collection; BHC) and Almudena Martínez's collection (AM). The sex (M, F) and the identification number of each specimen are specified in the table as they are the body size (Snout-to-ventlength) and humeral measurements (Humeral total width) both expressed in mm.

Table 1. Gran Dolina

Epidalea calamita; TD10; ATA 93

Talla (T)	Sex	HTW (mm)
T0	M	4.19
T0	M	3.63
T0	M	3.25
T0	M	4,00
T0	F	3,00
T0	F	4.13
T0	F	3.75
T0	M	3.06
T0	M	4,00
T0	M	3.13
T0	M	4.25
T0	F	3.75
T0	F	3,00
T0	F	2.88
T0	F	2.31
T0	F	3.25
T0	F	2.81
T1	F	3.44
T2	M	3.94
T2	M	3.75
T2	M	4,00
T2	M	3.38
T2	F	4.06
T2	F	3.38
T2	F	3.38
T4	M	4.06
T4	M	3.75
T4	M	3.25
T4	M	4,00
T4	M	3.25
T4	M	3.63
T4	M	4.25
T4	M	3.94
T4	M	5.13
T4	M	4.25
T4	F	3.13
T4	F	2.69
T4	F	3.06
T4	F	3.63
T4	F	3.31
T4	F	3.56
T4	F	3.44
T4	M	3.75
T4	M	4.63
T4	M	4.31
T4	F	3.25
T4	F	3.75
T5	M	2.69
T5	M	3.94
T5	M	4,00
T5	M	3.38
T5	F	3.06
T5	F	2.75
T5	F	3,00
T5	F	3.63
T5	F	3.38
T5	M	4.31
T5	M	3.19
T5	F	3.13
T5	F	3.75
T5	M	3.5
T5	F	2.44
T6	M	4.38
T6	M	3,00
T6	M	3.69
T6	M	3.44
T6	M	3.81
T6	M	3.94
T6	F	3.25
T6	F	3.38
T8	M	4,00
T8	M	4.63
T8	F	4.31
T8	F	3.13
T8	F	4,00
T8	F	3.13
T8	M	3.5
T9	M	3.44
T9	M	4.13
T9	M	3.5
T9	M	3.81
T9	M	4.13
T9	M	4,00
T9	M	3.63
T9	M	4,00
T9	F	2.63
T9	F	2.13
T9	F	3.69
T9	F	3.56
T9	F	3.13
T10	M	3.38
T10	M	3.44
T10	M	3.69
T10	F	2.88
T10	F	2.75
T10	F	3.38
T11	F	3,00
T12	M	4,00
T12	M	3.88
T12	F	3.81
T12	F	4.63
T12	M	3.75
T12	M	4.31
T12	M	3.88

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T12	M	3.88
T12	M	3.75
T12	M	3.44
T12	M	3.69
T12	M	3.75
T12	M	3.63
T12	M	3.5
T12	M	3.94
T12	M	3.44
T12	M	3.88
T12	M	5,00
T12	M	3.69
T12	M	3.06
T12	M	3.5
T12	F	2.31
T12	F	3.63
T12	F	3.38
T12	F	4.13
T12	F	3.69
T12	F	3.88
T12	F	3.31
T12	F	2.25
T12	F	4,00
T12	F	3.5
T12	F	3.44
T12	F	3.31
T12	F	1.88
T12	F	3.5
T12	F	3.75
T12	F	2.5
T12	F	2.88
T12	F	3.75
T12	F	4.75
T15	M	4.06
T15	M	3.38
T15	M	3.63
T15	M	3.75
T15	M	3.63
T15	M	4,00
T15	M	3.5
T15	M	2.44
T15	M	4.06
T15	F	3.63
T15	F	3,00
T15	F	3.94
T15	F	3.94
T15	F	4.38
T15	F	3.94
T15	F	3.75
T15	M	3.63
T15	M	4,00
T15	M	3.56
T15	M	3.75
T15	M	3.88
T15	M	3.06
T15	M	3.75
T15	M	3.63
T15	M	4.25
T15	M	3.5
T15	M	4.5
T15	F	3.56
T15	F	4,00
T15	F	3.75
T15	F	2.63
T15	F	4.13
T15	F	3.25
T15	F	3.69
T15	F	2.56
T15	F	2.38
T15	F	3.38
T16	M	4.31
T16	M	3.94
T16	M	3.19
T16	M	3.63
T16	M	3.94
T16	M	4,00
T16	M	3.56
T16	M	4.13
T16	M	3.44
T16	M	3.88
T16	M	4,00
T16	M	3.94
T16	M	4.63
T16	M	3.94
T16	M	3.25
T16	M	3,00
T16	M	3.25
T16	M	3.38
T16	M	3.31
T16	F	4,00
T16	M	3.5
T16	F	3.5
T16	F	3.63
T16	F	4.5
T16	F	3.25
T16	F	3,00
T16	F	4.63
T16	F	4.19
T16	F	2.63
T16	F	2.63
T16	F	3.38
T16	F	3.13
T16	F	3.75
T16	F	3.5

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T16	F	3.25
T16	F	3.38
T16	F	4.13
T16	F	3.88
T16	F	2.88
T16	F	3,00
T16	F	5,00
T16	F	4,00
T16	F	3.63
T16	M	3.75
T16	M	3.5
T16	M	3.63
T16	M	3.88
T16	M	3.5
T16	M	3.5
T16	M	3.75
T16	M	3.88
T16	M	3.5
T16	M	3.25
T16	M	3.5
T16	M	3.38
T16	M	4.06
T16	M	3.63
T16	M	3.56
T16	M	3.75
T16	M	3.44
T16	M	3.63
T16	M	3.38
T16	M	3.25
T16	M	3.38
T16	M	2.94
T16	M	2.88
T16	F	2.88
T16	F	3.38
T16	F	3.63
T16	F	3.5
T16	F	3.25
T16	F	3.5
T16	F	3,00
T16	F	3.25
T16	F	3.5
T16	F	3.13
T17	M	2.88
T17	M	3.13
T17	M	4.25
T17	M	3.94
T17	M	3.63
T17	M	3.5
T17	M	3.5
T17	M	3.63
T17	M	3.5
T17	M	3.63
T17	F	3.06
T17	F	2.81
T17	F	2,00
T17	F	3,00
T17	F	3.75
T17	F	2.75
T17	F	3.56
T17	F	3.88
T17	F	3.25
T17	F	4,00
T17	M	3.38
T17	M	4.06
T17	M	3.19
T17	M	4.25
T17	M	3.13
T17	M	3.75
T17	M	3.94
T17	F	3,00
T17	F	3.5
T17	F	3.88
T17	F	3.5
T17	F	2.63
T17	M	2.81
T17	M	3.13
T17	M	3.25
T17	M	3.63
T17	M	3.69
T17	M	4,00
T17	M	3.69
T17	M	3.94
T17	M	3.81
T17	M	3.94
T17	M	3.56
T17	M	3.94
T17	M	4.5
T17	M	4.13
T17	M	3.5
T17	M	3.31
T17	M	3.38
T17	F	3,00
T17	F	3.56
T17	F	3.13
T17	F	3.88
T17	F	3.88
T17	F	3.69
T17	F	3.44
T17	F	3.06
T17	M	5.15
T17	M	4.13
T17	M	4,00
T17	M	4,00
T17	M	3.63

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T17	M	3.88
T17	M	3.63
T17	M	4,00
T17	M	3.88
T17	M	3.81
T17	M	3.75
T17	F	5,00
T17	F	4.5
T17	F	3.94
T17	F	4,00
T18	M	3.56
T18	M	3.75
T18	M	4.38
T18	M	4.44
T18	M	4.25
T18	M	4.38
T18	M	3.88
T18	M	3.5
T18	M	3.44
T18	M	3.94
T18	M	3.25
T18	M	3.13
T18	M	4.81
T18	M	4,00
T18	M	4.19
T18	M	3.88
T18	M	3.38
T18	M	4,00
T18	F	4.38
T18	F	3.94
T18	F	3.88
T18	F	3.5
T18	F	4.38
T18	F	3.56
T18	F	3.63
T18	F	3.38
T18	F	3.31
T18	F	4,00
T18	F	3.06
T18	F	3.75
T18	F	4.13
T18	F	2.94
T18	F	3.56
T18	F	3.5
T18	F	2.25
T18	F	3.75
T18	F	3.44
T18	F	2.88
T18	M	4,00
T18	M	4.06
T18	M	3.81
T18	M	4.06
T18	M	3.63
T18	M	3.25
T18	F	3.13
T18	F	2.63
T18	F	2.69
T18	F	4.13
T18	M	3.94
T18	M	4.06
T18	M	3.38
T18	M	4.19
T18	M	3.75
T18	M	3.69
T18	M	3.25
T18	M	3.06
T18	M	3.44
T18	M	3.31
T18	M	3.81
T18	F	3.69
T18	F	3.75
T18	F	3.13
T18	F	2.88
T18	F	2.38
T18	F	3.63
T18	F	3.88
T18	F	4.13
T18	F	2.38
T18	F	3.69
T18	F	3.56
T18	F	2.81
T18	F	3.81
T18	F	3.19
T18	M	3.88
T18	M	3.63
T18	M	3.5
T18	M	3.63
T18	M	4.13
T18	M	3.81
T18	M	3.31
T18	M	3.75
T18	M	3.25
T18	M	3.25
T18	M	3.81
T18	M	3.75
T18	M	3.38
T18	M	4.13
T18	M	4.19
T18	M	3.63
T18	M	3.5
T18	M	3.5
T18	M	3.5
T18	M	3.75
T18	M	3.5

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T18	M	3.69
T18	M	3.56
T18	M	3.38
T18	F	3.31
T18	F	3.25
T18	F	2.5
T18	F	3.38
T18	F	3.06
T18	F	2.69
T18	F	4.19
T18	F	3,00
T18	F	2.5
T18	F	1.88
T18	F	4.31
T18	F	3.63
T18	M	3.31
T18	F	3.5
T18	F	3.38
T18	F	3.5
T18	F	3.63
T18	F	3.38
T18	F	2.63
T18	F	2.38
T18	F	3.88
T19	M	3.69
T19	M	3.75
T19	M	4,00
T19	M	3.44
T19	M	3.81
T19	M	3.5
T19	M	3.81
T19	M	3.5
T19	M	3.19
T19	M	3.38
T19	M	3,00
T19	M	3.63
T19	M	3.38
T19	M	3.5
T19	M	3.31
T19	M	3.88
T19	M	3,00
T19	F	3.13
T19	F	2.69
T19	F	4,00
T19	F	2.56
T19	F	3.38
T19	F	2.56
T19	F	3.38
T19	F	3.38
T19	F	3.38
T19	F	3.56
T19	F	2.31
T19	F	3.75
T19	F	3.63
T19	F	3.5
T19	F	3.88
T19	F	3.75
T19	F	3.69
T19	M	4,00
T19	M	3.75
T19	M	3.38
T19	M	3.81
T19	M	3.56
T19	M	3.5
T19	M	3.19
T19	M	3.5
T19	M	3.38
T19	M	3.63
T19	M	4.25
T19	M	4.5
T19	M	4.25
T19	M	3.38
T19	M	3.75
T19	M	3.25
T19	F	4.56
T19	F	4.88
T19	F	3.56
T19	F	3.13
T19	F	3.38
T19	F	3.69
T19	F	4.13
T19	F	4,00
T19	F	3.56
T19	F	2.88
T19	M	4.9
T19	M	3.19
T19	M	3.81
T19	M	3.63
T19	M	4.75
T19	M	3.88
T19	M	3.63
T19	M	2.94
T19	M	3.63
T19	M	4,00
T19	M	3.63
T19	M	3.75
T19	M	3.94
T19	M	3.94
T19	F	3.56
T19	F	3.5
T19	F	3.38
T19	F	2.06
T19	F	3,00
T19	F	3.63

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T19	F	3.19
T19	F	4.38
T19	F	5.13
T19	F	3.25
T19	F	3.75
T19	F	3.88
T19	F	3.56
T19	F	3.38
T19	F	3.44
T19	F	3.38
T19	M	3.13
T19	M	3.69
T19	M	4,00
T19	M	3.63
T19	M	4.06
T19	M	3.25
T19	M	4.06
T19	M	3.56
T19	M	3.81
T19	F	3.56
T19	F	3.38
T19	F	3.88
T19	F	3.44
T19	F	3.56
T19	F	3.88
T19	F	4.88
T19	F	3.63
T19	F	2.81
T19	F	2.94
T19	F	2.38
T19	F	3.5
T19	F	3.63
T19	F	3.75
T19	F	3.38
T19	F	2.88
T19	F	3.13
T19	F	2.56
T19	F	2.94
T19	F	3.31
T19	M	4.38
T19	M	3.75
T19	M	3.5
T19	M	3.69
T19	M	3.25
T19	M	3.63
T19	F	4.56
T19	F	3.81
T19	F	3.63
T19	F	3.75
T19	F	3.75
T19	F	3.88
T20	M	3.75
T20	M	3.94
T20	M	3.75
T20	M	3.63
T20	M	3.13
T20	M	3.13
T20	F	3.38
T20	M	4.06
T20	M	4,00
T20	M	3.75
T20	M	4,00
T20	M	4,00
T20	M	4.63
T20	M	3.5
T20	M	3.75
T20	M	3.25
T20	M	3.38
T20	M	4.69
T20	M	4.13
T20	M	4.44
T20	M	4.69
T20	M	3.94
T20	M	3.25
T20	M	3,00
T20	M	3.5
T20	F	4,00
T20	F	3.75
T20	F	3.44
T20	F	4.88
T20	F	3.56
T20	F	4,00
T20	F	3.5
T20	F	3.38
T20	F	4.75
T20	F	3.75
T20	F	3.13
T20	F	3.75
T20	F	3.88
T20	F	3.56
T20	M	4.56
T20	M	3.75
T20	F	2.94
T20	F	4.25
T20	M	3.13
T20	M	3.88
T20	M	3.94
T20	M	3.5
T20	M	3.38
T20	M	4,00
T20	M	3.13
T20	M	3.38
T20	M	3.5
T20	M	3.25

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T20	M	3.56
T20	F	3.56
T20	M	3.5
T20	M	3.13
T20	M	3.63
T20	M	3.44
T20	M	3.63
T20	M	4.25
T20	M	3.38
T20	M	4.19
T20	M	3.13
T20	F	3.75
T20	F	3.88
T20	F	3.38
T20	F	3.38
T20	F	3.88
T20	F	3.63
T20	F	4,00
T20	F	3.75
T20	F	3.25
T20	F	3.06
T20	M	3.13
T20	M	2.88
T20	F	3.5
T20	F	3,00
T20	M	3,00
T20	M	3.88
T20	M	3.88
T20	M	4,00
T20	M	4.25
T20	F	3.19
T21	M	3.88
T21	M	4.19
T21	M	3.63
T21	M	3.63
T21	M	3.44
T21	M	3.25
T21	M	3.13
T21	M	3.25
T21	F	3.13
T21	F	3.75
T21	F	4.13
T21	F	3.13
T21	F	3.15
T21	M	3.56
T21	M	4,00
T21	M	4.5
T21	M	3.75
T21	M	4.69
T21	M	4.06
T21	M	4,00
T21	M	3.81
T21	M	4.13
T21	M	3.25
T21	M	3.75
T21	M	3.63
T21	M	3.25
T21	M	4.13
T21	M	3.75
T21	M	3.25
T21	M	3.56
T21	M	2.63
T21	M	3.63
T21	F	3.75
T21	F	3.75
T21	F	2.88
T21	F	3.75
T21	F	3.88
T21	F	3.88
T21	F	3.63
T21	F	3.5
T21	F	3,00
T21	F	3.5
T21	F	3.63
T21	F	3.06
T21	F	3.25
H18	F	1.94
T21	M	3.25
T21	M	3.5
T21	M	3.63
T21	M	3.44
T21	M	4.25
T21	M	3.88
T21	M	3.63
T21	M	4.13
T21	M	3.75
T21	M	3.81
T21	M	3.5
T21	M	4,00
T21	M	2.94
T21	M	2.5
T21	F	3.69
T21	F	3.44
T21	M	4.13
T21	F	2.56
T21	F	4.5
T21	F	3.63
T21	F	2.94
T21	F	4,00
T21	F	3,00
T21	F	3.63
T21	M	3.86
T21	F	2.25
T21	M	3.88

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T21	F	3.75
T21	F	2.75
T21	F	3.44
T21	F	1.88
T21	M	4.88
T21	M	4.06
T21	M	4.75
T21	M	3.88
T21	M	3.38
T21	M	3.88
T21	M	3.75
T21	M	3.63
T21	M	3.88
T21	M	3.69
T21	M	3.75
T21	M	3.69
T21	M	3.5
T21	M	3.38
T21	M	3.63
T21	M	3.69
T21	M	3.25
T21	M	3.25
T21	M	3.19
T21	M	3,00
T21	M	3.69
T21	M	3.44
T21	M	3,00
T21	M	3.5
T21	M	3.13
T21	M	3.88
T21	M	4.38
T21	M	4.19
T21	M	3.75
T21	M	3.63
T21	M	3.63
T21	M	3.75
T21	M	3.25
T21	M	3.38
T21	M	3.88
T21	M	4.06
T21	M	4,00
T21	M	3.31
T21	M	3.38
T21	M	4,00
T21	M	3.81
T21	M	3.75
T21	M	3.75
T21	M	3.5
T21	M	3.63
T21	M	3.19
T21	M	3.5
T21	M	3.19
T21	M	3.63
T21	M	3.75
T21	M	4.19
T21	F	3.63
T21	F	3.69
T21	F	3.56
T21	F	4.38
T21	F	3.69
T21	F	4.19
T21	F	3.56
T21	F	3.88
T21	F	3.31
T21	F	3.13
T21	F	3.63
T21	F	3.5
T21	F	3.81
T21	F	3.38
T21	F	3.25
T21	F	3,00
T21	F	3.31
T21	F	3.63
T21	F	2.88
T21	F	3,00
T21	F	2.19
T21	F	2.31
T21	F	2.94
T21	F	3.5
T21	F	3.38
T21	F	3,00
T21	F	3.88
T21	F	3.44
T21	F	4,00
T21	F	2.63
T21	F	3.06
T21	F	3.38
T21	F	3.38
T21	F	3.38
T21	F	3.31
T21	F	3.56
T21	F	2.63
T21	F	2.75
T21	F	2.69
T21	F	2.75
T21	F	2.75
T21	F	3.13
T21	F	2.38
T21	F	3.75
T21	M	3.94
T21	M	3.88
T21	M	4.13
T21	M	4.06
T21	M	3,00

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T21	F	5.13
T21	F	3.44
T21	F	4.13
T22	M	3.75
T22	M	3.88
T22	M	3.75
T22	M	4.81
T22	M	4,00
T22	M	3.13
T22	M	3.75
T22	M	3.38
T22	M	4.25
T22	M	3.31
T22	M	3.38
T22	M	3.63
T22	M	3.13
T22	M	4.06
T22	M	4,00
T22	M	4.25
T22	M	4.06
T22	M	3.25
T22	M	3.88
T22	M	3.31
T22	M	3.75
T22	M	2.88
T22	M	4,00
T22	F	3.19
T22	F	3.56
T22	F	3.88
T22	F	3.75
T22	F	3.25
T22	F	3.44
T22	F	3.56
T22	F	2.81
T22	F	2.69
T22	F	3.06
T22	F	3.75
T22	F	3.19
T22	F	2.88
T22	F	2.81
T22	F	3.25
T22	F	3.75
T22	F	3.63
T22	F	4.13
T22	F	4.63
T22	F	3.56
T22	F	3,00
T22	F	3.63
T22	M	3.5
T22	M	3.56
T22	M	3,00
T22	M	3.44
T22	F	3.13
T22	F	2.5
T22	F	3.5
T22	M	4.13
T22	M	3.63
T22	M	3.81
T22	M	3.75
T22	F	3.31
T22	M	3.5
T22	M	4,00
T22	M	3.81
T22	M	3.94
T22	M	4.38
T22	M	4,00
T22	M	4,00
T22	M	3.94
T22	M	3.56
T22	M	3.94
T22	M	4.25
T22	M	3.31
T22	M	3.81
T22	M	4.13
T22	M	3.88
T22	M	4,00
T22	M	2.69
T22	M	3,00
T22	M	4,00
T22	M	4.38
T22	M	3.88
T22	M	4.81
T22	M	3.88
T22	M	4,00
T22	M	4.13
T22	M	5.31
T22	M	3.88
T22	M	3.44
T22	M	3.69
T22	M	3.13
T22	M	3.63
T22	M	3.06
T22	F	3.13
T22	F	3.81
T22	F	3.56
T22	F	4.13
T22	F	4.63
T22	F	3.31
T22	F	3.5
T22	F	2.75
T22	F	2.81
T22	F	2.88
T22	F	3.25
T22	F	2.5

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T22	F	2.13
T22	F	3.88
T22	F	3.5
T22	F	3.25
T22	F	3.63
T22	F	3.88
T22	F	3.63
T22	F	3.19
T22	F	3.25
T22	F	3,00
T22	F	2.75
T22	F	3.56
T22	F	3,00
T22	F	4.5
T22	F	3.38
T22	F	3.63
T22	M	3.63
T22	M	3.38
T22	M	3.88
T22	M	2.88
T22	M	3.38
T22	F	3.06
T22	F	3.56
T22	F	3.38
T22	F	2.13
T22	F	3.25
T22	M	3.38
T22	M	4.75
T22	M	3.38
T22	M	4.13
T22	M	3.88
T22	M	3.75
T22	M	3.38
T22	M	3.63
T22	M	3.06
T22	M	4.63
T22	M	3.63
T22	M	3.5
T22	M	3.5
T22	M	3.06
T22	M	3,00
T22	M	3.19
T22	M	3,00
T22	M	3.25
T22	M	3.75
T22	M	4.5
T22	M	3.88
T22	M	3.38
T22	M	3.38
T22	M	4,00
T22	M	3.94
T22	M	3.88
T22	M	4,00
T22	M	3.13
T22	M	3.5
T22	M	3.63
T22	M	3.88
T22	M	3.5
T22	M	3.5
T22	M	3.13
T22	F	3.5
T22	F	3.63
T22	F	3.63
T22	F	3.63
T22	F	3.5
T22	F	3.75
T22	F	2.88
T22	F	2.38
T22	F	3.88
T22	F	2.5
T22	F	2.63
T22	F	3.13
T22	F	3.13
T22	F	3.75
T22	F	5.25
T22	F	3.25
T22	F	4.69
T22	F	3.25
T22	F	3.19
T22	F	3.31
T22	F	2.56
T22	F	2.94
T22	F	3,00
T22	F	3.25
T22	F	2.63
T22	F	3.06
T22	F	3.25
T22	F	3.25
T22	F	2.69
T22	F	2.19
T22	F	3,00
T22	F	2.94
T22	F	2.5
T22	F	3,00
T22	M	3.5
T22	M	4,00
T22	M	4.63
T22	M	3.63
T22	M	4.25
T22	M	3.75
T22	M	3.75
T22	M	3.5
T22	M	4.5
T22	M	3.38

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T22	M	3.31
T22	M	3.63
T22	M	4,00
T22	F	3.75
T22	F	4.44
T22	M	3.5
T22	F	3.25
T22	F	4.06
T22	F	2.75
T22	M	4.06
T22	F	2.94
T22	F	3.38
T22	F	3.5
Epidalea calamita; TD8; ATA94.		
T27	M	3.44
T27	M	3.88
T27	M	3.5
T27	M	3.38
T27	M	3.69
T27	M	4,00
T27	M	4.25
T27	M	4.38
T27	M	3.75
T27	M	3.63
T27	M	4.13
T27	M	3.69
T27	M	3.75
T27	M	3.69
T27	M	3.94
T27	M	3.56
T27	M	4.06
T27	M	3.56
T27	F	4.5
T27	F	3.13
T27	F	4.44
T27	F	3.63
T27	F	3.56
T27	F	4.06
T27	F	3.56
T27	M	3.19
T27	F	3.94
T27	F	3.38
T27	F	3.94
T27	F	3.88
T27	F	3.63
T27	F	3.63
T27	F	3.81
T27	F	3,00
T27	F	3.44
T27	F	2.63
T27	F	2.88
T27	F	2.75
T27	F	2.88
T27	F	2.94
T27	F	3.06
T27	F	2.63
T27	F	2.56
T27	F	3.06
T27	F	4.19
T27	F	4,00
T27	F	4.63
T27	F	3.75
T27	F	2.75
T27	F	4.44
T27	F	3.44
T27	F	3.5
T27	F	3.38
T27	F	3.63
T27	F	2.81
T27	F	3,00
T27	F	3.75
T27	F	3.63
T27	F	3.19
T27	F	4.13
T27	F	3.63
T27	F	3.63
T27	F	2.06
T27	F	2.06
T27	M	4,00
T27	M	3.81
T27	M	3.13
T27	M	3.81
T27	M	3.38
T27	M	3.13
T27	M	2.81
T27	F	3.25
T27	F	3.63
T27	F	2.75
T27	F	3.75
T27	F	2.94
T27	F	3.38
T27	F	2.5
T27	F	3,00
T27	F	3.13
T27	F	2.44
T27	F	2.69
T27	F	4.5
T27	F	3.94
T27	F	3.44
T27	F	3,00
T27	F	3.13
T27	F	3.5

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)									
T27	F	4,00	T28	M	4.81	T28	F	3.56	T28	F	3.38
T27	F	2.88	T28	M	4.5	T28	F	3.63	T28	F	2.88
T27	F	2.63	T28	M	3.88	T28	F	3.81	T28	F	3.63
T27	F	2.63	T28	M	3.75	T28	F	3.75	T28	F	3.5
T27	F	3,00	T28	M	3.88	T28	F	3.63	T28	F	3.75
T27	F	2.25	T28	M	3.31	T28	F	4.25	T28	F	3.63
T28	M	4.25	T28	M	3.81	T28	F	4.13	T28	F	3.5
T28	M	4.19	T28	M	3.75	T28	F	3.75	T28	F	3.5
T28	M	3.94	T28	M	3.13	T28	F	2.75	T28	F	2.63
T28	M	3.94	T28	M	3.25	T28	F	3.44	T28	F	3.5
T28	M	3.63	T28	M	3.25	T28	F	3.19	T28	F	3.31
T28	M	3.69	T28	M	2.44	T28	F	3.44	T28	F	2.63
T28	M	3.69	T28	M	2.63	T28	F	3.19	T28	F	4.38
T28	M	4.25	T28	M	3.13	T28	F	2.75	T28	F	2.75
T28	M	4.44	T28	M	3.81	T28	F	4,00	T28	F	3,00
T28	M	3.63	T28	M	3.44	T28	F	3.5	T28	F	2.75
T28	M	3.94	T28	M	2.75	T28	F	2.38	T28	F	3.38
T28	M	3.13	T28	M	3.69	T28	F	2.5	T28	F	2.75
T28	M	3.75	T28	M	2.81	T28	F	2.75	T28	F	4,00
T28	M	3.19	T28	M	3.75	T28	F	3.44	T28	F	2.5
T28	M	3.25	T28	F	3.38	T28	F	3.56	T28	F	4.13
T28	M	3.75	T28	F	4.13	T28	F	3.81	T28	F	5.25
T28	M	3.81	T28	F	3.31	T28	F	4.25	T28	F	3.19
T28	M	3.63	T28	F	3.19	T28	F	3.69	T28	F	4,00
T28	M	3.06	T28	F	3.99	T28	F	4.13	T28	F	3.63
T28	M	4.25	T28	F	3,00	T28	F	3.25	T28	F	3.5

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T28	F	3.13
T28	F	4.25
T28	F	3.94
T28	F	3.25
T28	F	3.38
T28	F	3.31
T28	F	3.5
T28	F	2.81
T28	F	3.75
T28	F	3.75
T28	F	3.5
T28	F	3.75
T28	F	3.56
T28	F	3.5
T28	F	3.63
T28	F	3.81
T28	F	3.75
T28	F	3.38
T28	F	4.06
T28	F	3.5
T28	F	3.06
T28	F	3.13
T28	F	3.19
T28	F	2.75
T28	F	3.63
T28	F	3.25
T28	F	2.88
T28	F	2.63
T28	F	3.13
T28	F	2.75
T28	F	2.5
T28	F	2.13
T28	F	2.06
T30	M	4.25
T30	M	4,00
T30	M	3.75
T30	M	4.25
T30	F	3.06
T30	F	3.75
T30	F	4.75
Epidalea calamita; TD7; ATA94		
T30	M	4.06
T30	F	2.31
T30	F	3.38
T30	F	4,00
T30	F	2.75
Epidalea calamita; TD6; ATA94-97		
T32	M	3.56
T32	F	4.63
T32	F	4.63
T32	F	4.13
T32	F	2.88
T32	F	3.88
T32	F	4.63
T32	F	4.81
T32	F	4.13
T32	M	3.88
T32	M	3.75
T32	F	3.25
T32	F	3.88
T32	F	2.88
T32	F	3.13
T32	F	3.63
T32	M	4.13
T32	M	4.13
T32	M	3.88
T32	M	3.69
T32	M	4.38
T32	M	4.38
T32	M	5.13
T32	M	4.69
T32	F	4.06
T32	F	3.75
T32	F	3.13
T32	F	4.25
T32	F	3.63
T32	F	4.13
T32	F	4.19
T32	F	3.5
T32	F	4.13
T32	M	3.88
T32	M	3.75
T32	F	3.25
T32	F	3.88
T32	F	2.88
T32	F	3.13
T32	F	3.63
T32	M	4.13
T32	M	4.13
T32	M	3.88
T32	M	3.69
T32	M	4.38
T32	M	4.38
T32	M	5.13
T32	M	3.38
T32	F	4.06
T32	F	3.75
T32	F	3.13
T32	F	4.19
T32	F	4.25
T32	F	3.63
T32	F	4.13

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T32	F	3.5
T33	M	4,00
T33	M	3.13
T33	M	3.88
T33	M	5.19
T33	M	4.13
T33	M	4.25
T33	F	4.19
T33	F	3.63
T33	F	4.75
T33	F	4.25
T33	F	3.88
T33	F	3.44
T33	M	3.69
T33	F	4.5
T33	M	3.69
T33	M	3.5
T33	M	4.63
T33	M	4.06
T33	F	3.44
T33	F	4,00
T33	F	3.94
T33	M	5.06
T33	M	3.75
T33	M	3.81
T33	M	4.31
T33	M	3.75
T33	M	4,00
T33	M	4.31
T33	M	4.5
T33	F	3.88
T33	F	3.5
T33	F	3.38
T33	F	3.75
T33	M	4,00
T33	M	3.88
T33	M	4.06
T33	M	4.06
T33	F	3.5
T33	F	3.13
T33	F	4,00
T33	F	2.5
T33	M	3.81
T33	M	4,00
T33	M	3.81
T33	F	3.88
T33	F	3.63
T33	F	3,00
T33	F	2.5
T33	F	3.56
T33	F	2.69
T34	M	3.5
T34	M	4.75
T34	M	4.31
T34	M	4,00
T34	M	4.38
T34	M	4.13
T34	M	4.69
T34	M	4,00
T34	M	4.63
T34	F	3.75
T34	F	4.13
T34	F	3,00
T34	F	4,00
T34	F	4.56
T34	F	3.31
T34	M	4.13
T34	M	4,00
T34	M	4.19
T34	M	4.63
T34	F	4.5
T35	M	3.88
T35	M	3.06
T35	M	4.56
T35	M	3.5
T35	M	3.81
T35	M	3.94
T35	M	4.63
T35	M	4.88
T35	M	4.88
T35	M	4.25
T35	M	4.69
T35	M	3.88
T35	M	4.38
T35	M	4.38
T35	M	4,00
T35	M	3.88
T35	M	4,00
T35	M	4.38
T35	M	4.25
T35	M	4.19
T35	M	3.94
T35	M	3.25
T35	F	4.38
T35	F	4,00
T35	F	3.88
T35	F	4.56
T35	F	3.88
T35	F	4,00
T35	F	2.69
T35	F	2.5
T35	F	3.88
T35	F	4.19
T35	F	2.75

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T35	F	4.06
T35	F	2.75
T35	F	3.63
T35	F	4,00
T35	F	4,00
T35	F	4.38
T35	F	4.25
T35	F	4,00
T35	F	2.63
T35	F	3.31
T35	F	3.31
T35	F	2.94
T35	F	3.88
T35	M	3.88
T35	M	3.81
T35	M	4.5
T35	M	4.75
T35	M	3.69
T35	M	3.94
T35	M	4.13
T35	M	4.63
T35	M	4.18
T35	M	3.88
T35	M	4,00
T35	M	3.81
T35	M	3.88
T35	M	3.94
T35	M	3.13
T35	F	2.88
T35	F	3.88
T35	F	3.81
T35	F	4.13
T35	F	3.63
T35	F	2.5
T35	F	2.63
T35	F	4.63
T35	F	4.38
T35	F	3.75
T35	F	4.06
T35	F	4.13
T35	F	2.75
T35	M	4.5
T35	M	4.13
T35	M	4.38
T35	F	3.5
T35	F	3.25
T35	F	3.13
T35	F	2,00
T35	M	4.31
T35	M	4.63
T35	M	3.25
T35	M	3.38
T35	M	3.75
T35	M	4.63
T35	M	4.13
T35	M	4.31
T35	M	4.63
T35	M	3.25
T35	M	3.38
T35	M	4.63
T35	M	3.75
T35	M	4.13
T35	M	4.25
T35	F	3.06
T35	F	3.38
T35	F	3.63
T35	F	3.25
T35	M	4.06
T35	M	3.38
T35	M	3.25
T35	M	3.38
T35	M	4,00
T35	M	4.56
T35	F	3.5
T35	F	3.25
T35	F	2.25
T35	F	2.81
T35	F	3.63
T35	F	3.69
T35	F	5.31
T35	F	4.63
T35	F	4.56
T35	F	4.75
T35	F	3.5
T35	F	3.63
T35	F	2.38
T35	F	3.38
T35	F	3.44
T35	F	3.94
T35	F	2.88
T35	F	3.25
T35	F	2.81
T35	M	3.88
T35	M	4.38
T35	M	4,00
T35	M	3.25
T35	M	4.31
T35	F	2.81
T35	F	3.69
T35	F	2.31
T35	F	3.19
T35	F	2.56
T35	F	2.38
T35	F	4.13

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T35	F	3.88
T35	F	3.13
T35	F	3.38
T35	M	3.94
T35	M	4.13
T35	M	4.5
T35	F	4.38
T35	F	3.94
T35	F	3.5
T35	F	3.25
T35	F	4.13
T35	F	3.94
T35	F	4.81
T35	M	3.75
T35	M	3.88
T35	M	3.88
T35	M	4.38
T35	M	4.38
T35	M	3.69
T35	M	4.31
T35	F	4.44
T35	F	2.5
T35	F	3.25
T35	F	2.44
T36	M	4,00
T36	M	3.63
T36	M	4,00
T36	M	4.88
T36	M	3.94
T36	M	4.25
T36	M	4.38
T36	M	3.5
T36	M	4.25
T36	M	4.38
T36	F	3.75
T36	F	2.81
T36	F	4.13
T36	F	2.56
T36	F	3.75
T36	F	3.94
T36	F	3,00
T36	F	4.06
T36	F	4.06
T36	F	3.63
T36	F	3.88
T36	F	4.25
T36	F	3.88
T36	F	4.31
T36	M	4.5
T36	M	3.31
T36	M	4.19
T36	M	4.38
T36	M	3.75
T36	F	2.81
T36	F	4.25
T36	F	3.5
T36	F	4.38
T36	F	3.69
T36	F	3.88
T36	F	4.06
T36	F	2.63
T36	F	2.13
T36	F	2.88
T36	F	1.75
T36	F	3.75
T36	F	3,00
T36	F	3.13
T36	F	3.56
T36	M	4.38
T36	M	4.13
T36	M	3.75
T36	M	4.38
T36	M	4.06
T36	F	2.63
T36	F	3,00
T36	F	3.38
T36	F	2.88
T36	F	3.56
T36	F	3.44
T36	F	3.38
T36	F	2.88
T36	F	2.13
T36	F	3.38
T36	M	4.13
T36	M	4,00
T36	M	4.06
T36	M	3.56
T36	F	2.88
T36	F	3.75
T36	F	4.38
T36	F	4.25
T36	F	3.13
T36	F	3.94
T36	F	3.75
T36	F	3.56
T36	F	3.75
T36	F	2.88
T36	F	3.06
T36	F	2.5
T36	F	3.5
T36	F	3.5
T36	F	4.06
T36	F	3.88
T36	M	4.63

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T36	M	3.88
T36	M	4.25
T36	M	3.94
T36	M	3.88
T36	M	4.63
T36	M	3.25
T36	M	3.94
T36	M	3.63
T36	M	4.25
T36	M	3,00
T36	M	3.94
T36	F	4.25
T36	F	3.38
T36	F	3.75
T36	F	3.31
T36	F	4.5
T36	M	3.88
T36	M	3.88
T36	M	4.63
T36	M	4.19
T36	M	4.25
T36	M	4.06
T36	M	3.5
T36	M	3.75
T36	M	4,00
T36	M	3.75
T36	M	4.13
T36	M	4.25
T36	M	3.75
T36	M	3.88
T36	M	3.94
T36	M	4.31
T36	M	3.75
T36	M	2.75
T36	M	3.38
T36	F	3.75
T36	F	3.75
T36	F	3.19
T36	F	4,00
T36	F	3.5
T36	F	3.25
T36	F	4.25
T36	F	4.25
T36	F	2.31
T36	F	3.94
T36	F	2.56
T36	F	3.13
T36	F	2.5
T36	F	4.13
T36	F	4,00
T36	F	2.75
T36	F	3.44
T36	F	4.5
T36	F	3.94
T36	F	3.38
T36	F	4.5
T36	F	3.94
T36	F	5,00
T36	F	3.81
T36	F	2.63
T36	F	2.88
T36	F	4,00
T36	F	2,00
T36	F	3.06
T36	F	3.94
T36	F	2.63
T36	F	2,00
T36	F	2.38
T36	F	3.63
T36	F	3.5
T36	F	2.44
T36	F	2.75
T36	F	4,00
T36	F	4.75
T36	F	2.56
T36	M	4.56
T36	M	3.75
T36	M	3.69
T36	F	3.13
T36	F	3.44
T36	F	3.69
T36	F	2.38
T37	M	3.69
T37	M	4.13
T37	M	4.63
T37	M	4.5
T37	M	3.63
T37	M	4.13
T37	M	3.94
T37	F	4.13
T37	F	4.38
T37	F	3.19
T37	F	3.63
T37	F	4.38
T37	F	2.25
T37	F	3.38
T37	F	3.75
T37	F	3.81
T37	F	3.38
T37	M	4.38
T37	M	4.44
T37	M	4.63
T37	M	4.06
T37	M	3.69

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T37	M	4.13
T37	F	4.06
T37	F	3.75
T37	F	3.75
T37	F	4.13
T37	F	4.06
T37	F	4.5
T37	F	3.88
T37	F	4.5
T37	F	2.75
T37	M	3.56
T37	M	3.44
T37	M	4.5
T37	M	3.69
T37	M	4.44
T37	M	3.63
T37	M	4.5
T37	M	3.81
T37	M	3.31
T37	M	3.31
T37	F	2.94
T37	F	2.88
T37	F	3.5
T37	F	3.75
T37	F	2.19
T37	F	2.13
T37	F	2.06
T37	F	3.31
T37	F	3.63
T37	F	3.5
T37	F	2.81
T37	M	3.88
T37	M	3.44
T37	M	5.06
T37	M	3.56
T37	M	5,00
T37	M	4.06
T37	M	3.88
T37	M	3.75
T37	M	3.75
T37	M	4.06
T37	M	3.13
T37	F	3.31
T37	F	4.44
T37	F	4,00
T37	F	2.75
T37	F	3.88
T37	F	4.13
T37	F	3.94
T37	F	3.88
T37	F	3.38
T37	F	2.94
T37	F	3.25
T37	F	3.19
T37	M	3.56
T37	M	4.13
T37	M	4.25
T37	F	4,00
T37	F	2.88
T37	F	2.13
T37	F	4.5
T37	F	3.13
T37	F	2.56
T37	M	3.88
T37	M	4.5
T37	M	3.5
T37	M	4.13
T37	M	3.88
T37	M	4.19
T37	M	4,00
T37	M	4.38
T37	M	3.88
T37	M	4.5
T37	M	4.5
T37	F	3.5
T37	F	3.19
T37	F	3,00
T37	F	3.38
T37	F	3.25
T37	F	2.56
T37	F	3.63
T37	F	2.75
T37	F	3.5
T37	F	3.56
T37	F	2.88
T37	F	3.88
T37	F	2.31
T37	F	2.88
T37	F	2.63
T38	M	3.88
T38	M	3.5
T38	M	3.31
T38	M	3.5
T38	F	3.69
T38	F	2.25
T38	F	2.06
T38	F	3.56
T38	M	3.88
T38	M	4.06
T38	M	3.56
T38	M	3.25
T38	F	5.5
T38	F	4,00
T40	F	4.31

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T40	F	3.94
T40	M	3.38
T40	M	4.06
T40	F	1.94
T40	F	4.06
T40	F	3.94
T40	F	3.81
T40/45	M	3.94
T40/45	M	4.63
T40-41	M	3.63
T40-41	F	3.19
T40-41	F	3.94
T40-41	M	4.5
T40-41	F	3.13
T40-41	F	3.75
T40-41	F	3.75
T40-41	F	2.69
T40-41	F	3.56
T42	F	4.13
T42	F	4.31
T42	F	2.88
T42	F	3.75
T43	M	4.13
T43	M	4.38
T43	M	4.13
T43	M	4.06
T43	M	4.25
T43	M	3.44
T43	M	3.44
T43	M	4.63
T43	M	3.5
T43	M	3.88
T43	M	3.75
T43	F	3.88
T43	F	4.25
T43	F	3.25
T43	F	3.13
T43	F	4.19
T43	F	2.25
T43	F	2.88
T43	F	2.88
T43	F	3.13
T43	F	3.75
T43	F	3.69
T43	F	2.25
T43	F	2.13
T43	F	3.63
T43	F	3.25
T43	F	3.06
T43	F	3.06
T43	F	4.13
T43	F	3.44
T43	F	2.81
T43	F	2.94
T43	F	2.63
T43	F	2,00
T43	M	3.81
T43	M	3.88
T43	M	3.5
T43	M	4.13
T43	F	3.38
T43	F	3.81
T43	F	4.19
T43	F	3.56
T43	F	2.38
T43	F	3.88
T43	M	4.25
T43	M	3.94
T43	M	3.5
T43	F	3.88
T43	F	3.56
T43	F	4.63
T43	F	3.13
T43	F	2.19
T43	F	2.25
T43	F	3,00
T43	F	3.63
T43	F	3.31
T43	F	3.5
T43	M	4.25
T43	M	3.88
T43	F	4.13
T43	F	2.75
T43	F	3.13
T43	F	2.5
T43	F	2.06
T43	F	3.31
T43	F	3.75
T43	F	3.38
T43	F	3.63
T43	F	2,00
T43	F	3.06
T44	M	3.94
T44	M	3.75
T44	M	4.13
T44	M	3.5
T44	M	3.5
T44	M	4.06
T44	F	3.44
T44	F	4,00
T44	F	2.88
T44	F	2.19
T44	F	2.13
T44	F	4,00

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T44	F	4.06
T44	F	4.5
T44	F	4,00
T44	F	3.94
T44	F	2.75
T44	F	4,00
T44	F	3.75
T44	F	2.38
T44	F	3,00
T44	F	3.5
T44	F	3.06
T44	F	2.25
T44	M	3.75
T44	M	4.19
T44	F	3.56
T44	F	3.44
T44	F	3.5
T44	F	3.5
T44	F	3,00
T44	F	3.38
T44	F	3,00
T44	M	3.38
T44	M	4.75
T44	F	2.94
T44	F	3.44
T44	F	2.75
T44	F	3.13
T44	M	3.75
T44	M	3.75
T44	M	3.94
T44	F	2.75
T44	F	3.31
T44	M	3.69
T44	M	3.13
T44	F	3.75
T44	F	2.94
T44	F	3.63
T44	F	2.94
T45	M	3.94
T45	M	3.69
T45	M	3.94
T45	F	3.56
T45	F	3.75
T45	F	3.38
T45	F	3.75
T45	M	3.88
T45	M	3.5
T45	F	2,00
T45	F	2.75
T45	F	2.94
T45	F	3.31
T45	F	2.75
T45	F	1.94
T45	M	4.25
T45	M	4,00
T45	M	3.56
T45	F	3.75
T45	M	3.94
T45	F	3.31
T45	F	3.06
T45	F	3.88
T45	F	4.06
T47	M	3.94
T47	M	3.56
T47	M	3.69
T47	M	2.63
T47	M	4.31
T47	M	4.13
T47	F	3.69
T47	F	3.06
T47	F	4.06
T47	F	2.88
T47	F	3,00
T47	F	2.63
T47	F	2.81
T47	F	2.44
T47	F	3.56
T47	M	3.63
T47	F	2.75
T47	F	2.13
T47	F	3.38
T47	F	3.88
T47	F	1.88
T47	M	3.88
T47	M	3.94
T47	M	4.25
T47	M	3.5
T47	M	3.56
T47	F	3.5
T47	F	2.75
T47	F	2.88
T47	M	3.31
T47	F	3.31
T47	F	2.69
T47	F	3,00
T47	F	2.69
T47	F	3.19
T47	F	2.56
T47	F	3.94
T47	F	3.75
T47	F	3.88
T47	F	3.88
T47	F	3.56
T47	M	4.06

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T47	M	3.69
T47	F	2.69
T47	F	2.44
T47	F	3.19
T47	F	3.81
T48	M	4.38
T48	M	3.56
T48	M	3.5
T48	M	3.38
T48	M	4.13
T48	M	3.31
T48	F	3.63
T48	F	4.13
T48	F	3.88
T48	F	3.25
T48	F	3.88
T48	F	2.94
T48	F	3.94
T48	F	3.25
T48	M	3.44
T48	M	3.5
T48	M	4.06
T48	M	3.56
T48	M	3.75
T48	M	4.38
T48	F	2.75
T48	F	3.38
T48	F	2.81
T48	F	3.56
T48	F	3.44
T48	F	3.56
T48	F	3.5
T48	M	4.38
T48	M	3.75
T48	F	3.56
T48	F	3.38
T48	F	3.31
T48	F	3.69
T48	F	3.38
T48	F	3.81
T48	F	2.81
T48	F	3.88
T48	M	4.25
T48	M	3.25
T48	M	3,00
T48	F	3.19
T48	F	2.38
T48	F	3.56
T49	M	3.88
T49	M	3.81
T49	M	3.5
T49	F	3.56
T49	F	3.88
T49	F	4,00
T49	F	3.63
T49	M	4.13
T49	M	3.38
T49	F	4.25
T49	F	1.94
T49	F	3.5
T49	F	3.06
T49	F	2.25
T49	F	2.63
T49	M	4.5
T49	M	3.63
T49	M	3.38
T49	M	3.25
T49	M	3.56
T49	F	4.06
T49	F	4.13
T49	F	3.56
T49	F	3.56
T49	F	3.63
T49	F	3.94
T49	F	3.5
T49	M	3.75
T49	M	4.19
T49	M	4.5
T49	M	3.19
T49	M	2.81
T49	F	3.63
T49	F	3.69
T49	F	2.56
T49	F	3.5
T49	F	2.5
T49	F	3.19
T49	F	4.25
T49	M	3.63
T49	M	3.13
T49	M	4.13
T49	F	3.75
T49	F	3.38
T49	M	4,00
T49	M	3.5
T49	F	3.25
T50	M	3.88
T50	M	4.06
T50	M	3.19
T50	M	4,00
T50	M	4.25
T50	M	4.38
T50	F	3.94
T50	F	2.81
T50	F	3.5

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T50	F	3.44
T50	F	2.19
T50	F	3.63
T50	F	2.94
T50	F	3,00
T50	F	2.56
T50	M	3.88
T50	M	3.63
T50	M	3.75
T50	M	3.44
T50	M	3.25
T50	M	2.88
T50	F	4.25
T50	M	4.25
T50	M	3.88
T50	M	3.88
T50	M	3.75
T50	M	4.13
T50	M	4,00
T50	M	3.88
T50	F	3.5
T50	F	3.75
T50	F	2.31
T50	F	3.63
T50	F	3.69
T50	F	3.69
T50	F	2.75
T50	F	3.38
T50	M	3.13
T50	M	3.69
T50	F	3.44
T50	F	3.88
T50	M	3.63
T51	M	4,00
T51	F	3.94
T51	F	3.38
T51	F	4.38
T51	F	3.5
T51	F	3.63
T51	F	2.75
T51	M	3.81
T51	M	3.56
T51	M	4.06
T51	M	3.75
T51	M	3.56
T51	M	3.75
T51	M	3.5
T51	F	3.13
T51	F	2.44
T51	F	4.19
T51	M	3.94
T51	M	3.56
T51	M	3.13
T51	F	3.56
T51	F	3.13
T51	F	2.94
T51	F	3.63
T51	F	3.38
T51	F	4.25
T52	M	3.88
T52	M	3.44
T52	M	3,00
T52	M	4.06
T52	M	4,00
T52	M	4.06
T52	M	3,00
T52	F	3.69
T52	F	2.56
T52	F	2,00
T52	F	2.38
T52	F	3.19
T52	F	2.44
T52	F	3,00
T53	M	3.5
T53	F	3.25
T53	F	3.88
T53	F	2.63
T53	F	3.81
T53	F	3.63
T53	F	3.38
T53	F	4,00
T53	M	4.13
T53	M	4,00
T53	M	3.56
T53	F	4,00
T53	F	3.75
T53	F	3.81
T53	F	3.63
T53	F	3.31
T53	M	3.38
T53	F	2.06
T53	F	4.5
T53	F	2.13
T53	M	3.56
T53	M	4.75
T53	M	3.75
T53	M	4.56
T53	M	4,00
T53	M	4.75
T53	M	4.31
T53	M	4.5
T53	F	3.81
T53	F	4.5
T53	F	3.88

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T53	F	4.13
T54	M	4.63
T54	M	2.81
T54	F	2.13
T54	F	3.06
T54	F	2.13
T54	M	4.13
T54	M	4.25
T54	M	3.31
T54	M	3.88
T54	M	3.88
T54	M	4.81
T54	M	4.38
T54	F	4.5
T54	F	3.75
T54	F	3.63
T54	F	4.13
T54	F	3.31
T54	F	3.56
T54	F	3.44
T54	F	4.13
T54	F	3.94
T54	F	3.5
T54	F	3.13
T54	M	4.38
T54	F	3.25
T54	F	3.88
T54	F	3.13
T54	F	4.38
T54	F	3.56
T54	F	4.06
T54	F	3.75
T54	F	4.06
T54	M	3.75
T54	M	1.75
T54	M	3.25
T54	M	3.81
T54	F	3.94
T54	F	3.69
T54	F	3.75
T54	F	3.38
T54	F	3,00
T54	M	4.25
T54	M	3.63
T54	M	3.88
T54	M	4.31
T54	M	4.25
T54	F	3.88
T54	F	3.69
T54	F	4.31
T54	F	2.88
T54	F	4.06
T54	F	4.63
T54	F	3,00
T54	F	4,00
T54	F	3.19
T54	M	4.06
T54	F	3.69
T54	F	4.69
T54	M	4.5
T54	M	4.06
T54	M	4.38
T54	M	3.75
T54	F	4.44
T54	F	4.25
T54	F	4.31
T54	F	4.06
T54	F	4.5
T54	F	3.63
T54	F	4.38
T54	F	3,00
T54	F	4.38
T55	M	4.38
T55	M	4.75
T55	M	3.69
T55	M	4.25
T55	M	4.19
T55	M	3.81
T55	M	4.38
T55	M	3.75
T55	M	3.75
T55	M	3.88
T55	M	3.63
T55	M	4.94
T55	M	4.81
T55	M	3.44
T55	F	4,00
T55	F	4.38
T55	F	4.5
T55	F	4.5
T55	F	4.13
T55	F	4,00
T55	F	4.06
T55	F	3.81
T55	F	4.38
T55	F	3.13
T55	F	2.75
T55	F	3.63
T55	M	1.94
T55	M	3.88
T55	M	4,00
T55	M	3.69
T55	M	4.44
T55	M	3.38

Table 1. Gran Dolina

Talla (T)	**Sex**	**HTW (mm)**									
T55	M	4.06	T55	M	4,00	T56	M	4.31	T58	M	4.44
T55	M	3.88	T55	M	4.25	T56	M	4.5	T58	M	5.13
T55	F	4.56	T55	F	4.19	T56	M	4.06	T58	M	4.56
T55	F	3.75	T55	F	4.63	T56	M	4.13	T58	M	3.56
T55	F	2.5	T55	F	3.63	T56	F	4.25	T58	M	4.19
T55	F	4.06	*Epidalea calamita*; TD5/TDE5; ATA97-99			T56	F	4.81	T58	M	4.81
T55	F	4.13				T56	F	4.4	T58	M	3.8
T55	F	3.63	T56	M	4.88	T56	F	3.81	T58	M	4.19
T55	F	4.69	T56	M	4.81	T56	F	4.38	T58	M	2.93
T55	F	3.44	T56	M	4,00	T56	F	4.25	T58	M	3.88
T55	F	3.88	T56	M	4.13	T57	F	4.75	T58	M	4.56
T55	F	4.25	T56	M	4.63	T57	M	3.94	T58	M	4.13
T55	F	4,00	T56	F	4.63	T57	M	4.06	T58	M	4.13
T55	F	3.63	T56	F	3.94	T57	M	5,00	T58	M	4.19
T55	M	4.5	T56	F	4.63	T57	M	5.5	T58	M	4.38
T55	M	5.13	T56	M	4.38	T57	M	4.18	T58	M	5,00
T55	M	4.56	T56	M	4.38	T57	M	4.31	T58	M	5.19
T55	M	3.75	T56	M	3.88	T57	M	4.44	T58	M	4.38
T55	M	3.69	T56	M	3.63	T57	F	3.88	T58	M	4.06
T55	F	4.5	T56	F	4.38	T57	F	4.13	T58	M	5.31
T55	F	3.81	T56	F	4.06	T57	F	3.81	T58	M	4.13
T55	F	3.31	T56	F	4.19	T57	F	4.38	T58	M	4.06
T55	F	3.75	T56	M	4.5	T58	M	4.19	T58	M	4.63
T55	M	4.38	T56	M	4.5	T58	M	4.69	T58	M	4.06
T55	M	3.38	T56	F	2.94	T58	M	4.63	T58	M	4.81
T55	M	4.25	T56	M	4.13	T58	M	3.25	T58	M	3.36

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T58	M	5,00
T58	M	4.06
T58	M	4.69
T58	M	3.63
T58	M	3.25
T58	M	4.44
T58	M	3.63
T58	M	4.75
T58	M	2.81
T58	M	4,00
T58	M	4.5
T58	M	4,00
T58	M	4,00
T58	M	4.94
T58	M	4.13
T58	M	4,00
T58	M	3.34
T58	F	3.13
T58	F	3.13
T58	F	2.81
T58	F	3.36
T58	F	4.13
T58	F	3.36
T58	F	4.19
T58	F	4.63
T58	F	5.25
T58	F	4.94
T58	F	4.5
T58	F	4.13
T58	F	4.63
T58	F	5,00
T58	F	3.94
T58	F	4.5
T58	F	4.63
T58	F	4.75
T58	F	3.94
T58	F	4.19
T58	F	4,00
T58	F	3.18
T58	F	5.63
T58	F	4.31
T58	F	4,00
T58	F	4.94
T58	F	4.63
T58	F	4.13
T58	F	3.31
T58	F	3.56
T58	F	4.94
T58	F	4.88
T58	F	4.75
T58	F	4.88
T58	F	4.06
T58	F	4.13
T58	F	4,00
T58	F	4.69
T58	F	4.38
T58	F	3.81
T58	M	5,00
T58	M	4.5
T58	M	4.06
T58	M	4.25
T58	M	4.56
T58	M	4.69
T58	F	4.13
T58	M	5.38
T58	M	4,00
T58	M	4.13
T58	M	2.94
T58	M	3.88
T58	M	3.69
T58	M	3.94
T58	M	4.81
T58	M	4.44
T58	M	2.81
T58	F	3.63
T58	F	5.56
T58	F	4.13
T58	F	4,00
T58	F	3.13
T58	F	3.89
T58	F	3.94
T58	M	4.25
T58	M	4,00
T58	M	4.63
T58	M	4.38
T58	M	4.31
T58	M	4.25
T58	M	4.38
T58	M	3.81
T58	M	4.94
T58	M	4.75
T58	F	4.19
T58	F	4.06
T58	F	3.94
T58	F	4.44
T58	F	4.06
T58	F	2.5
T58	F	3.69
T58	M	4,00
T58	M	3.69
T58	M	4.31
T58	M	4.69
T58	M	5,00
T58	M	3.94

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T58	M	5.13
T58	M	5.25
T58	M	4.56
T58	M	4.25
T58	M	4.06
T58	M	3.75
T58	M	4.13
T58	M	4.38
T58	M	4.13
T58	M	5.25
T58	F	4.06
T58	F	4.06
T58	F	3.69
T58	F	4.13
T58	F	4.13
T58	F	4.5
T58	F	4.63
T58	F	4.38
T58	F	4.56
T58	F	4.69
T58	F	4.81
T58	F	3.75
T58	F	4,00
T58	F	3.75
T58	F	3.56
T58	F	3.81
T58	M	3.38
T58	M	3.88
T58	M	3.94
T58	M	3.75
T58	M	4.06
T58	F	3.38
T58	F	4.38
T58	F	4,00
T58	F	3.69
T59	M	5.5
T59	M	4.31
T59	M	4.5
T59	M	4.88
T59	M	4.06
T59	M	4.13
T59	M	4,00
T59	M	5,00
T59	M	5.13
T59	M	3.75
T59	F	5.13
T59	F	3.63
T59	F	3.25
T59	F	4.5
T59	F	4.81
T59	F	4.19
T59	F	4.19
T59	F	2.88
T59	M	4.31
T59	F	4.88
T59	F	2.69
T59	F	3.2
T59	M	5.19
T59	F	5.57
T59	F	4.75
T59	F	4.63
T59	M	3.69
T59	M	3.75
T59	F	4.25
T59	F	3.63
T59	F	4.56
T59	M	5,00
T59	M	5,00
T59	M	4.25
T59	M	4.25
T59	M	4.06
T59	M	3.69
T59	M	5.25
T59	M	4.63
T59	M	4.25
T59	M	3.94
T59	M	4.38
T59	M	3.44
T59	F	4.38
T59	F	3.44
T59	F	4.19
T59	F	5,00
T59	F	4.5
T59	F	3.5
T59	F	4,00
T59	F	4.25
T59	F	4.75
T59	F	4.25
T59	F	4.44
T59	F	4.25
T59	F	4.13
T59	F	4.25
T60	M	4.19
T60	F	3.75
T60	F	4.44
T60	M	4.19
T60	M	4.56
T60	F	4.38
T60	M	3.88
T60	M	4.19
T60	M	4.25
T60	F	5.06
T60	F	4.25
T60	F	5,00

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T60	F	2.88
T60	F	4.44
T60	M	3.31
T60	M	3.88
T60	M	3.13
T60	M	4.13
T60	F	3.88
T60	F	1.94
T60	F	3.25
T60	F	4,00
T60	F	3.06
T60	F	2.75
T60	F	3.5
T60	F	3.94
T60	F	3.5
T60	F	3.31
T60	F	3.38
T60	F	4.25
T60	F	3.25
T60	F	2.88
T60	M	4.69
T60	M	3.38
T60	M	3.81
T60	F	4.31
T60	F	3.31
T60	M	4.06
T60	M	3.63
T60	M	3.75
T60	F	4.56
T60	F	4.5
T60	F	4.19
T60	F	3.75
T60	F	3.69
T60	F	4.63
T60	F	3.75
T61	F	4.31
T61	M	4.13
T61	M	3.63
T61	M	5.31
T61	M	4.38
T61	M	4.06
T61	M	5.13
T61	M	3.88
T61	M	3.81
T61	M	4.5
T61	M	4.25
T61	M	3.75
T61	M	2.94
T61	M	4.06
T61	M	3.75
T61	M	3.63
T61	F	4,00
T61	F	3.06
T61	F	3.81
T61	F	4.63
T61	F	3.63
T61	F	3,00
T61	F	4.13
T61	F	3.38
T61	F	4.63
T61	F	2.63
T61	F	3.19
T61	F	3.25
T61	F	2.75
T61	F	3.5
T61	F	4.19
T61	M	4.13
T61	F	3.13
T61	F	2.56
T61	M	3.75
T61	F	3.94
T61	F	3.13
T61	F	4.13
T61	F	3.38
T61	M	3.88
T61	M	3.5
T61	F	4.38
T61	F	3.75
T61	F	3.94
T61	F	3.5
T61	F	3,00
T61	F	2.56
T62	F	3.31
T62	M	4.56
T62	F	3.75
T62	M	3.17
T62	M	4.13
T62	M	4.25
T62	M	4.25
T62	M	4.06
T62	F	4.44
T62	F	3.38
T63	F	2.88
T63	F	4.06
T63	M	4.31
T63	M	3.5
T63	F	4,00
T63	F	4,00
T63	F	4.06
T63	F	4.06
T63	F	4.25
T63	F	4.06
T63	M	3.69
T63	M	4.06

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T63	M	4.38
T63	M	3.25
T63	M	4.88
T63	M	3.69
T63	F	3.38
T63	F	3.56
T63	F	4.44
T63	F	3.54
T63	F	3.56
T63	F	2.38
T63	F	4.94
T63	F	3.94
T63	F	3.75
T63	M	4.75
T63	M	3.69
T63	F	3.19
T63	M	3.94
T63	M	3.19
T63	F	4.38
T63	M	3.75
T63	F	4,00
T63	F	3.13
T63	F	4.25
T63	F	3.56
T63	F	3.94
T64	M	4.5
T64	M	3.5
T64	M	3.88
T64	F	3.75
T64	M	3.56
T64	F	3.44
T64	F	3.75
T64	F	3.31
T64	F	3.75
T64	F	4.5
T64	F	3.5
T64	F	1.88
T64	M	3.69
T64	F	2.5
T64	F	3.5
T64	F	4,00
T64	F	4.19
T64	M	3.38
T64	F	2.69
T64	F	3.5
T64	M	3.56
T64	M	4.25
T64	M	3.94
T64	M	4.25
T64	M	3.38
T64	F	4.19
T65	F	3.5
T65	M	4.19
T65	M	3.31
T65	M	4.38
T65	M	4.13
T65	M	3.5
T65	M	4.13
T65	M	4.25
T65	M	3.88
T65	M	3.63
T65	M	4.44
T65	F	3.94
T65	F	3.69
T65	F	4,00
T65	F	3.13
T65	F	4.25
T65	F	4.06
T65	M	4.19
T65	M	5.19
T65	M	4.13
T65	M	4.75
T65	F	5.25
T65	F	4.06
T65	F	3.25
T65	F	3.63
T65	F	3.19
T65	F	2.69
T65	F	3.06
T65	F	3.63
T65	F	3.75
T65	F	3.31
T65	F	3.63
T65	F	4.13
T65	F	4.38
T65	F	2.88
T65	F	4.63
T65	M	4.13
T65	M	3.63
T65	M	4.25
T65	M	4,00
T65	M	4.19
T65	M	3.81
T65	M	3.94
T65	M	3.13
T65	F	4.06
T65	F	3.69
T65	F	4.38
T65	F	3.25
T65	F	4.44
T65	F	3.44
T65	F	3.63
T65	F	2.44
T65	F	2.19

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T65	F	4.06
T65	F	3.69
T65	F	3.31
T65	F	3.25
T65	F	3.44
T65	M	2.81
T65	F	2.63
T66	M	3.38
T66	M	3.88
T66	M	3.06
T66	M	3.56
T66	M	4.38
T66	M	4.31
T66	M	3.75
T66	M	3.3
T66	M	3.75
T66	M	3.38
T66	F	3.38
T66	F	3.44
T66	F	1.94
T66	F	2.69
T66	F	3.13
T66	M	2.88
T66	M	4.38
T66	M	4,00
T66	M	3.56
T66	M	4.36
T66	F	3.63
T66	F	4.5
T66	F	4.31
T66	F	3.19
T66	F	2.75
T66	F	4.63
T66	F	4,00
T66	F	3.44
T66	F	3.19
T66	F	3,00
T66	F	3.5
T66	F	3.81
T66	F	3.5
T66	F	4.19
T66	F	4.25
T66	F	2.5
T66	F	3,00
T66	M	4.38
T66	M	4.94
T66	M	3.94
T66	M	3.15
T66	M	4.38
T66	M	3.44
T66	M	4.75
T66	M	4.38
T66	M	4.63
T66	M	4.13
T66	M	4.25
T66	F	3.31
T66	F	3.5
T66	F	3.94
T66	F	3.13
T66	F	3.63
T66	F	3.13
T66	F	3.38
T66	F	2.88
T66	F	2.25
T66	F	3.31
T66	F	3.94
T66	F	4,00
T66	F	3.69
T66	F	3.44
T66	M	4.06
T66	F	3.5
T66	F	3.25
T66	F	3.69
T66	F	4.25
T66	F	3.75
T66	F	2.06
T66	M	3.63
T66	M	4.63
T66	M	3.5
T66	M	3.25
T66	M	4.31
T66	M	3.69
T66	M	3.81
T66	M	2.94
T66	M	3.88
T66	M	4.19
T66	M	4.38
T66	M	2.88
T66	M	4.25
T66	F	3.44
T66	F	3.75
T66	F	2.94
T66	F	4.25
T66	F	3.88
T66	F	3.75
T66	F	4,00
T66	F	3.75
T66	F	2.44
T66	F	3.81
T66	F	3.38
T66	F	3.38
T66	F	3.63
T66	F	3.63
T66	F	2.81

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T66	M	3.88
T66	M	4,00
T66	M	4.06
T66	F	3.5
T66	F	4.38
T66	F	5.06
T66	F	3.88
T66	F	3.69
T66	F	3.75
T66	F	3.88
T66	F	4.81
T67	M	4.06
T67	M	4.13
T67	M	3.63
T67	M	4.56
T67	M	4.25
T67	F	4.38
T67	F	3.75
T67	F	3.56
T67	F	3.81
T67	F	3,00
T67	F	2.75
T67	F	3.19
T67	F	3.56
T67	M	3.38
T67	M	3.81
T67	M	3.44
T67	F	3.63
T67	F	4,00
T67	F	4.5
T67	M	3.88
T67	M	3.88
T67	M	3.81
T67	M	3,00
T67	F	3.88
T67	F	3.5
T67	F	3.63
T67	F	4.25
T67	M	3.81
T67	F	4.06
T67	F	3.88
T67	F	4.25
T67	M	4.88
T67	F	4.44
T67	F	3.25
T67	F	4,00
T68	M	4.5
T68	M	4.63
T68	M	4.38
T68	M	3.75
T68	M	4.25
T68	F	3.19
T68	F	3.44
T68	F	2.44
T68	F	3.88
T68	F	3.81
T68	F	4.63
T68	F	3.88
T68	F	3.13
T68	F	3.06
T68	F	4.13
T68	M	3.94
T68	M	3.81
T68	M	3.69
T68	M	3.69
T68	M	4.44
T68	M	3.75
T68	M	3.75
T68	M	3.94
T68	M	4,00
T68	M	3.25
T68	M	4.19
T68	M	3.88
T68	M	4.56
T68	M	4.25
T68	M	3.88
T68	F	4.19
T68	F	3.69
T68	F	4.56
T68	F	4.25
T68	F	4.19
T68	F	3.75
T68	F	4.31
T68	F	3.81
T68	F	4.19
T68	F	3.44
T68	F	3.06
T68	F	4.06
T68	F	3.06
T68	M	3.63
T68	M	3.63
T68	M	3.63
T68	M	4.38
T68	F	4.13
T68	F	4.56
T68	F	5.13
T68	F	4.06
T68	M	4.5
T68	M	3.81
T68	M	4.06
T68	M	4.63
T68	M	4.06
T68	M	4.31
T68	M	4.38

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T68	M	3.44
T68	M	4.38
T68	M	3.94
T68	M	3.75
T68	M	4.5
T68	M	4.13
T68	M	4.44
T68	M	4.63
T68	M	4.25
T68	M	4.94
T68	M	4.31
T68	M	3.88
T68	M	4.5
T68	F	4.38
T68	F	3.69
T68	F	3.5
T68	F	4.5
T68	F	4.06
T68	F	4.06
T68	F	4.69
T68	F	4.38
T68	F	4.44
T68	F	3.56
T68	F	3.13
T68	F	3.19
T68	F	4,00
T68	F	4.25
T68	F	3.63
T68	F	3.81
T68	F	3.25
T68	F	3.56
T68	F	2.25
T68	M	4.88
T68	M	4.13
T69	M	4.5
T69	F	4.19
T69	M	3.94
T69	M	3.31
T69	M	4.31
T69	M	3.69
T69	M	4.94
T69	M	3.81
T69	M	3.38
T69	M	4.31
T69	M	4.63
T69	M	4.5
T69	F	4.38
T69	F	3.38
T69	F	3.31
T69	F	3.31
T69	F	3.56
T69	F	4.13
T69	F	4,00
T69	M	3.5
T69	M	4,00
T69	M	3,00
T69	M	4,00
T69	M	4.13
T69	F	4.88
T69	F	3.69
T69	F	3.31
T69	F	3.44
T69	F	2.63
T69	F	1.88
T69	F	4.06
T69	F	4.5
T69	F	4.56
T69	F	2.5
T69	M	4.19
T69	M	3.75
T69	M	4.5
T69	M	4.38
T69	F	4.69
T69	F	3.38
T69	F	4.25
T69	F	3.31
T69	M	4.13
T69	M	4.25
T69	M	4.13
T69	F	4.25
T69	F	3.56
T69	M	4.06
T69	M	4.5
T69	M	4.25
T69	M	4.13
T69	M	4.31
T70	M	4.13
T70	M	4,00
T70	M	4.31
T70	M	4,00
T70	M	3.81
T70	M	4.56
T70	F	3.56
T70	F	3.38
T70	F	4.69
T70	F	4.56
T70	F	3.44
T70	F	4.25
T70	M	3.81
T70	M	4,00
T70	M	4.81
T70	M	4.25
T71	F	4,00
T71	M	4.06

Table 1. Gran Dolina

Talla (T)	Sex	HTW (mm)
T71	**F**	**2.88**
T72	**F**	**3.81**
T74	**F**	**2.63**
T74	**F**	**4.38**
	TOTAL	**3219**

Table 2. Portalón

Talla (T)	Sex	HTW (mm)
Epidalea calamita; ATA05		
P2	M	4.13
P2	M	4.38
Epidalea calamita; ATA05		
P3	M	4.19
P3	M	4.25
P3	M	4.25
P3	M	4.56
P3	M	4.06
P3	F	4.75
P3	F	3.75
P3	F	3.44
P3	F	3.63
Epidalea calamita; ATA05		
P4	M	4.63
P4	M	5.31
P4	M	4.63
P4	M	4.38
P4	M	4.50
P4	F	4.31
Epidalea calamita; ATA05		
P5	M	3.38
Epidalea calamita; ATA05		
P6	M	4.25
P6	M	4.13
P6	M	4.00
P6	F	4.50
P7	M	4.13
P7	M	3.19
P7	M	4.25
P7	M	4.88
P7	M	3.88
P7	M	4.25
P7	M	4.19
P7	M	4.44
P7	M	4.00
P7	M	4.63
P7	M	4.06
P7	M	3.31
P7	M	3.56
P7	M	3.25
P7	F	4.38
P7	F	4.13
P7	F	4.50
P7	F	3.75
P7	F	3.44
P7	F	3.25
P7	F	4.19
P7	F	3.63
P7	F	3.19
P7	F	2.63
P7	F	2.44
P7	F	3.25
P7	F	3.56
P7	F	3.06
P7	F	4.25
P7	F	2.06
P7	F	4.31
P7	F	3.81
P7	F	3.38
P7	F	4.44
Epidalea calamita; ATA05		
P8	M	4.06
P8	M	4.88
P8	M	3.75
P8	M	4.69
P8	M	3.63
P8	M	4.63
P8	M	4.69
P8	M	3.88
P8	M	4.19
P8	M	3.81
P8	M	4.50
P8	M	4.50
P8	M	4.31
P8	M	4.38
P8	M	4.13
P8	M	4.81
P8	F	4.31
P8	F	4.50
P8	F	3.81
P8	F	3.75
P8	F	4.00
P8	F	2.94
P8	F	3.38
P8	F	4.19
P8	F	4.50
P8	F	3.50
P8	F	4.13
P8	F	4.25
P8	F	3.13
P8	F	3.63
P8	F	3.69
P8	F	3.94
P8	F	4.06
P8	F	4.63
P8	F	4.69
P8	F	4.13
P8	F	4.63
P8	F	3.69
P8	F	4.50
P8	F	3.38
P8	F	4.38
P8	F	3.56
P8	F	3.81

Table 2. Portalón

Level	**Sex**	**HTW (mm)**
P8	F	3.81
P8	F	4.19
P8	F	2.69
P8	F	3.25
P8	F	3.25
P8	F	3.38
P8	F	3.63
Epidalea calamita; ATA05		
P9	M	5.13
P9	M	4.44
P9	M	3.88
P9	M	4.31
P9	F	4.38
P9	F	4.25
P9	F	3.56
P9	F	4.06
P9	F	6.19
P9	F	3.31
Epidalea calamita; ATA05		
P10	M	4.38
P10	M	4.56
P10	M	4.44
P10	M	3.88
P10	M	4.63
P10	M	4.38
P10	M	3.81
P10	M	4.38
P10	M	4.06
P10	M	4.44
P10	M	3.38
P10	M	3.56
P10	M	4.06
P10	M	3.63
P10	M	4.00
P10	M	4.44
P10	M	3.38
P10	M	5.13
P10	M	3.50
P10	M	3.94
P10	M	4.19
P10	M	4.25
P10	M	3.70
P10	M	3.06
P10	M	3.75
P10	M	3.38
P10	F	4.56
P10	F	3.38
P10	F	4.13
P10	F	2.50
P10	F	3.50
P10	F	4.25
P10	F	4.56
P10	F	2.88
P10	F	2.94
P10	F	3.31
P10	F	2.88
P10	F	4.44
P10	F	4.56
P10	F	3.81
P10	F	4.50
P10	F	4.44
P10	F	4.06
P10	F	4.44
P10	F	3.38
P10	F	3.13
P10	F	2.75
P10	F	3.31
P10	F	4.13
Epidalea calamita; ATA05		
P11	F	3.31
P11	F	5.06
P11	F	2.38
P11	F	4.75
P11	F	4.50
P11	F	4.50
P11	F	4.25
P11	F	4.06
P11	F	3.94
P11	F	4.25
P11	F	4.63
P11	F	3.88
P11	F	4.06
P11	F	4.25
P11	F	3.69
P11	F	3.63
P11	F	4.13
P11	F	3.75
P11	F	4.25
P11	F	3.38
P11	F	2.75
P11	F	3.63
P11	F	3.88
P11	F	3.25
P11	F	2.88
P11	F	3.13
P11	F	3.06
P11	F	3.19
P11	F	4.31
P11	F	3.25
P11	F	3.25
P11	F	3.13
P11	F	4.38
P11	F	3.50

Table 2. Portalón

Level	Sex	HTW (mm)
P11	F	3.38
P11	F	4.44
P11	F	4.63
P11	F	5.19
P11	F	4.13
P11	F	4.25
P11	F	3.94
P11	F	4.25
P11	F	4.63
P11	F	3.70
P11	F	4.44
P11	F	4.50
P11	F	4.06
P11	F	4.50
P11	F	4.00
P11	F	3.44
P11	F	4.63
P11	F	3.63
P11	F	2.75
P11	F	4.56
P11	F	4.25
P11	F	4.31
P11	F	2.81
P11	F	4.56
P11	F	3.44
P11	F	4.19
P11	F	3.50
P11	F	3.44
P11	F	3.50
P11	F	4.31
P11	F	5.00
P11	F	3.25
P11	F	3.69
P11	F	2.94
P11	F	4.06
P11	M	4.75
P11	M	4.50
P11	M	4.38
P11	M	4.25
P11	M	4.38
P11	M	3.88
P11	M	4.25
P11	M	3.94
P11	M	4.13
P11	M	4.50
P11	M	4.25
P11	M	3.88
P11	M	4.31
P11	M	4.38
P11	M	4.38
P11	M	4.44
P11	M	4.88
P11	M	3.75
P11	M	3.88
P11	M	3.88
P11	M	4.25
P11	M	3.38
P11	M	3.88
P11	M	3.63
P11	M	3.63
P11	M	4.50
P11	M	3.44
P11	M	4.19
P11	M	3.44
P11	M	4.69
P11	M	5.13
P11	M	4.63
P11	M	4.94
P11	M	4.00
P11	M	4.50
P11	M	4.94
P11	M	4.38
P11	M	4.13
P11	M	4.69
P11	M	3.94
P11	M	3.75
P11	M	4.13
P11	M	4.31
P11	M	4.75
P11	M	4.31
P11	M	4.69
P11	M	3.94
P11	M	3.44
P11	M	4.56
P11	M	4.00
P11	M	4.25
P11	M	4.19
P11	M	3.50
P11	M	4.25
P11	M	3.35
P11	M	4.19
P11	M	4.13
P11	M	3.44
P11	M	3.94
P11	M	4.63
Epidalea calamita; ATA05		
P12	M	3.56
P12	M	4.19
P12	M	3.94
P12	M	4.13
P12	F	4.06
P12	M	3.25

Table 2. Portalón

Level	Sex	HTW (mm)
Epidalea calamita; ATA06		
P13	M	4.38
P13	M	3.94
P13	M	4.75
P13	M	3.13
P13	M	4.50
P13	M	3.94
P13	M	4.50
Epidalea calamita; ATA06		
P14	M	3.63
P14	M	4.13
P14	M	3.44
P14	M	3.31
P14	M	3.88
P14	F	4.25
P14	F	4.75
Epidalea calamita; ATA06		
P15	M	4.19
P15	M	4.00
P15	M	4.13
P15	M	4.56
P15	M	3.94
P15	M	3.70
P15	M	4.25
P15	M	3.56
P15	M	4.44
P15	M	3.94
P15	M	4.00
P15	M	4.38
P15	M	4.06
P15	M	4.69
P15	M	3.63
P15	M	4.69
P15	M	5.44
P15	M	4.13
P15	M	3.75
P15	M	4.13
P15	M	4.44
P15	M	4.00
P15	M	3.70
P15	M	4.13
P15	M	4.25
P15	M	4.56
P15	M	4.13
P15	M	3.56
P15	M	4.31
P15	F	4.13
P15	F	4.13
P15	F	4.19
P15	F	5.07
P15	F	4.44
P15	F	4.75
P15	F	4.13
P15	F	4.50
P15	F	2.50
P15	F	4.25
P15	F	4.50
P15	F	4.13
P15	F	3.00
P15	F	3.25
P15	F	4.38
P15	F	4.25
P15	F	4.19
P15	F	4.31
P15	F	5.13
P15	F	4.13
P15	F	4.13
P15	F	4.00
P15	F	4.38
P15	F	4.25
P15	F	2.88
P15	F	3.63
Epidalea calamita; ATA06		
P16	F	3.75
P16	M	3.94
TOTAL		371

Table 3. Barranco León

Level	Sex	HTW (mm)
***Pelophylax* cf. *perezi;* BL10,11,13**		
D1	M	2.78
D1	M	2.56
D1	M	3.34
D1	M	3.25
D1	M	2.25
D1	M	2.63
D1	M	2.69
D1	M	2.41
D1	F	2.78
D1	F	2.31
D1	F	3.06
D1	F	2.66
D1	F	2.19
D1	F	3.75
D1	F	3.38
D1	F	2.84
D1	F	3.06
D1	F	2.97
D1	F	2.75
D1	F	3.09
D1	F	3.56
D1	M	2.75
D1	F	3.16
D1	F	3.19
D1	F	2.72
D1	M	4.34
D1	F	3.97
D1	M	3.13
D1	M	3.38
D1	F	3.10
D1	F	4.28
D1	F	2.56
D1	F	3.22
D1	F	3.03
Pelophylax* cf. *perezi; BL10, 11, 13		
D2	M	2.66
D2	M	3.84
D2	M	2.69
D2	M	3.09
D2	M	2.34
D2	M	3.00
D2	M	2.69
D2	M	2.72
D2	M	2.69
D2	M	3.03
D2	M	2.16
D2	M	2.94
D2	F	2.91
D2	F	3.22
D2	F	2.41
D2	F	2.72
D2	F	2.56
D2	F	3.19
D2	F	4.31
D2	F	2.16
D2	F	2.44
D2	M	3.22
D2	F	2.81
D2	F	2.72
D2	F	3.22
D2	F	3.63
D2	F	3.28
D2	M	3.41
D2	M	3
D2	M	3.06
D2	M	2.59
D2	M	2.63
D2	F	3.25
D2	F	2.13
D2	F	2.78
D2	F	3.69
D2	F	3.44
D2	F	3.47
D2	F	3.59
D2	M	3.06
D2	M	2.84
D2	M	2.81
D2	F	3.25
D2	F	2.56
Pelophylax* cf. *perezi; BL10, 13		
E	F	2.56
E	M	4.06
E	M	2.69
E	M	2.63
E	M	3.38
E	M	2.84
E	M	2.97
E	F	3.50
E	F	2.72
E	F	2.50
E	F	3.75
E	F	3.13
E	F	3.91
E	F	3.25
E	F	3.50
TOTAL		**93**

Table 4. Fuente Nueva 3

Level	Sex	HTW (mm)
Pelophylax* cf. *perezi; FN3 11, 14, 17		
5	M	2.25
5	M	3.13
5	M	2.97
5	M	3.28
5	F	3.47
5	F	3.03
5	F	3.63
5a	M	2.97
5a	F	2.97
5a	F	4.06
5b	M	2.81
6	F	2.88
6	F	2.53
TOTAL		**13**

Table 5. Camp dels Ninots

Level	Sex	HTW (mm)
Pelophylax* sp.; *CN05		
10	**H**	**3.46**
Pelophylax* sp.; *CN10-22		
11	**M**	**2.68**
11	**M**	**2.38**
11	**M**	**2.33**
11	**M**	**2.5**
11	**M**	**2.5**
11	**H**	**3.48**
11	**H**	**2.7**
11	**M**	**2.66**
11	**M**	**2.68**
11	**H**	**3.8**
11	**M**	**2.29**
11	**H**	**2.46**
11	**H**	**1.99**
11	**H**	**1.95**
11	**H**	**2.03**
11	**M**	**2.92**
11	**H**	**2.84**
11	**M**	**2.92**
11	**M**	**2.65**
11	**M**	**2.76**
11	**M**	**2.58**
11	**M**	**2.61**
11	**M**	**2.56**
11	**H**	**2.78**
11	**M**	**2.4**
TOTAL		**26**

Table 6. Reference collections

Id. Nº	SPECIES	SEX	SVL (mm)	HTW (mm)
MNCN-15464	*Epidalea calamita*	M	44	*1.92*
MNCN-40953	*Epidalea calamita*	M	46	*3.00*
MNCN-40952	*Epidalea calamita*	M	60	*3.71*
MNCN-40952	*Epidalea calamita*	M	60	*3.71*
MNCN-15472	*Epidalea calamita*	M	62	*5.11*
MNCN-22336	*Epidalea calamita*	M	77	*6.00*
MNCN-22336	*Epidalea calamita*	M	77	*5.78*
MNCN-15461	*Epidalea calamita*	M	60	*5.25*
MNCN-15462	*Epidalea calamita*	M	75	*6.25*
MNCN-15467	*Epidalea calamita*	M	73	*5.00*
MNCN-15456	*Epidalea calamita*	M	71	*5.25*
MNCN-22341	*Epidalea calamita*	M	72	*5.50*
MNCN-22341	*Epidalea calamita*	M	72	*5.50*
MNCN-15471	*Epidalea calamita*	M	64	*5.00*
MNCN-15469	*Epidalea calamita*	M	22	*1.70*
MNCN-15470	*Epidalea calamita*	M	29	*2.13*
MNCN-15463	*Epidalea calamita*	M	62	*5.25*
MNCN-22340	*Epidalea calamita*	M	67	*5.25*
MNCN-22340	*Epidalea calamita*	M	67	*5.63*
MNCN-40954	*Epidalea calamita*	M	63	*4.50*
MNCN-40954	*Epidalea calamita*	M	63	*4.63*
MNCN-22238	*Epidalea calamita*	M	70	*5.25*
MNCN-22335	*Epidalea calamita*	M	86	*7.50*
MNCN-22335	*Epidalea calamita*	M	86	*7.50*
MNCN-40955	*Epidalea calamita*	M	63	*4.50*
MNCN-40955	*Epidalea calamita*	M	63	*4.60*

Table 6. Reference collections

Id. Nº	SPECIES	SEX	SVL (mm)	HTW (mm)
MNCN-22344	*Epidalea calamita*	M	65	*4.80*
MNCN-22344	*Epidalea calamita*	M	65	*5.00*
MNCN-15458	*Epidalea calamita*	M	64	*5.20*
MNCN-15466	*Epidalea calamita*	M	68	*6.00*
MNCN-15474	*Epidalea calamita*	M	65	*5.75*
MNCN-22339	*Epidalea calamita*	M	91	*7.50*
MNCN-22339	*Epidalea calamita*	M	91	*7.63*
MNCN-22239	*Epidalea calamita*	M	59	*4.36*
MNCN-40951	*Epidalea calamita*	M	61	*4.55*
MNCN-40951	*Epidalea calamita*	M	61	*4.36*
MNCN-40953	*Epidalea calamita*	M	46	*3.06*
MNCN-40953	*Epidalea calamita*	M	46	*3.25*
MNCN-15460	*Epidalea calamita*	M	63	*5.63*
MNCN-15457	*Epidalea calamita*	M	68	*5.50*
MNCN-15468	*Epidalea calamita*	M	62	*4.73*
MNCN-22342	*Epidalea calamita*	M	66	*5.00*
MNCN-22342	*Epidalea calamita*	M	66	*5.00*
MNCN-22343	*Epidalea calamita*	M	62	*5.20*
MNCN-22343	*Epidalea calamita*	M	62	*5.40*
MNCN-42577	*Epidalea calamita*	M	64	*4.18*
MNCN-42577	*Epidalea calamita*	M	64	*4.62*
AM-EpCa1	*Epidalea calamita*	M	60	*4.00*
AM-EpCa1	*Epidalea calamita*	M	60	*4.06*

Total males = 49

Table 6. Reference collections

Id. Nº	SPECIES	SEX	SVL (mm)	HTW (mm)
MNCN-15473	*Epidalea calamita*	F	63	*4.67*
MNCN-15449	*Epidalea calamita*	F	69	*4.36*
MNCN-15464	*Epidalea calamita*	F	75	*5.45*
MNCN-15448	*Epidalea calamita*	F	77	*4.73*
MNCN-22337	*Epidalea calamita*	F	78	*6.22*
MNCN-22337	*Epidalea calamita*	F	78	*6.22*
MNCN-15451	*Epidalea calamita*	F	55	*4.75*
MNCN-15450	*Epidalea calamita*	F	61	*4.75*
MNCN-22338	*Epidalea calamita*	F	79	*5.75*
MNCN-22338	*Epidalea calamita*	F	79	*6.00*
MNCN-15452	*Epidalea calamita*	F	66	*5.50*
MNCN-15459	*Epidalea calamita*	F	73	*5.50*
MNCN-15453	*Epidalea calamita*	F	75	*6.00*
MNCN-15454	*Epidalea calamita*	F	28	*2.35*
MNCN-15455	*Epidalea calamita*	F	71	*5.33*
AM-EpCa2	*Epidalea calamita*	F	50	*4.38*
AM-EpCa2	*Epidalea calamita*	F	50	*4.38*

Total females = 17

TOTAL = 66

Id. Nº	SPECIES	SEX	SVL (mm)	HTW (mm)
AM-PePe13	*Pelophylax perezi*	M	35.7	*2.1*
AM-PePe13	*Pelophylax perezi*	M	35.7	*2.06*
AM-PePe14	*Pelophylax perezi*	M	19	*1.33*
AM-PePe14	*Pelophylax perezi*	M	19	*1.3*
BHC-PePe3	*Pelophylax perezi*	M	70	*2.56*
BHC-PePe4	*Pelophylax perezi*	M	39	*2*
BHC-PePe4	*Pelophylax perezi*	M	39	*1.97*
MNCN-13388	*Pelophylax perezi*	M	41	*1.88*
MNCN-13396	*Pelophylax perezi*	M	48.5	*2.69*
MNCN-13399	*Pelophylax perezi*	M	52	*2.72*
MNCN-14939	*Pelophylax perezi*	M	47.5	*2.53*
MNCN-14940	*Pelophylax perezi*	M	52	*2.59*
MNCN-14943	*Pelophylax perezi*	M	44.5	*2.34*
MNCN-16440	*Pelophylax perezi*	M	64	*3.19*
MNCN-16440	*Pelophylax perezi*	M	64	*3.16*
MNCN-16442	*Pelophylax perezi*	M	77	*4.13*
MNCN-16442	*Pelophylax perezi*	M	77	*4.03*
MNCN-16443	*Pelophylax perezi*	M	47	*2.53*
MNCN-16444	*Pelophylax perezi*	M	40	*1.94*
MNCN-16445	*Pelophylax perezi*	M	43	*2.03*
MNCN-16446	*Pelophylax perezi*	M	41	*2*
MNCN-16446	*Pelophylax perezi*	M	41	*2.03*
MNCN-16447	*Pelophylax perezi*	M	51	*2.56*
MNCN-16462	*Pelophylax perezi*	M	26	*1*
MNCN-16463	*Pelophylax perezi*	M	27.5	*1.19*

Table 6. Reference collections

Id. Nº	SPECIES	SEX	SVL (mm)	HTW (mm)
MNCN-16470	*Pelophylax perezi*	M	40	*1.78*
MNCN-16470	*Pelophylax perezi*	M	40	*1.88*
MNCN-16474	*Pelophylax perezi*	M	22	*0.91*
MNCN-16474	*Pelophylax perezi*	M	22	*0.88*
MNCN-16475	*Pelophylax perezi*	M	44	*2.13*
MNCN-16475	*Pelophylax perezi*	M	44	*2*
MNCN-20579	*Pelophylax perezi*	M	56.1	*3*
MNCN-20579	*Pelophylax perezi*	M	56.1	*2.94*
MNCN-20580	*Pelophylax perezi*	M	66.6	*3.81*
MNCN-20580	*Pelophylax perezi*	M	66.6	*3.75*
MNCN-20582	*Pelophylax perezi*	M	52.2	*2.53*
MNCN-20582	*Pelophylax perezi*	M	52.2	*2.56*
MNCN-20586	*Pelophylax perezi*	M	47	*2.31*
MNCN-20586	*Pelophylax perezi*	M	47	*2.31*
MNCN-20587	*Pelophylax perezi*	M	43	*2.31*
MNCN-20587	*Pelophylax perezi*	M	43	*2*
MNCN-20588	*Pelophylax perezi*	M	41	*2.03*
Total males = 43				
MNCN-20588	*Pelophylax perezi*	M	41	*2.03*
AM-PePe1	*Pelophylax perezi*	F	28.5	*1.77*
AM-PePe1	*Pelophylax perezi*	F	28.5	*1.73*
AM-PePe2	*Pelophylax perezi*	F	22	*1.4*
AM-PePe2	*Pelophylax perezi*	F	22	*1.41*
AM-PePe3	*Pelophylax perezi*	F	27.5	*1.52*

Table 6. Reference collections

Id. Nº	SPECIES	SEX	SVL (mm)	HTW (mm)
AM-PePe3	*Pelophylax perezi*	F	27.5	*1.47*
AM-PePe4	*Pelophylax perezi*	F	20	*1.33*
AM-PePe4	*Pelophylax perezi*	F	20	*1.33*
AM-PePe5	*Pelophylax perezi*	F	23	*1.55*
AM-PePe5	*Pelophylax perezi*	F	23	*1.49*
AM-PePe6	*Pelophylax perezi*	F	20	*1.44*
AM-PePe6	*Pelophylax perezi*	F	20	*1.4*
AM-PePe7	*Pelophylax perezi*	F	12.5	*1*
AM-PePe7	*Pelophylax perezi*	F	12.5	*1*
AM-PePe8	*Pelophylax perezi*	F	25	*1.6*
AM-PePe8	*Pelophylax perezi*	F	25	*1.64*
AM-PePe9	*Pelophylax perezi*	F	22	*1.3*
AM-PePe9	*Pelophylax perezi*	F	22	*1.33*
AM-PePe10	*Pelophylax perezi*	F	21	*1.28*
AM-PePe10	*Pelophylax perezi*	F	21	*1.28*
AM-PePe11	*Pelophylax perezi*	F	20	*1.25*
AM-PePe11	*Pelophylax perezi*	F	20	*1.23*
AM-PePe12	*Pelophylax perezi*	F	22.5	*1.52*
AM-PePe12	*Pelophylax perezi*	F	22.5	*1.47*
BHC-PePe1	*Pelophylax perezi*	F	40	*1.5*
BHC-PePe1	*Pelophylax perezi*	F	40	*1.54*
BHC-PePe5	*Pelophylax perezi*	F	84	*3.99*
BHC-PePe5	*Pelophylax perezi*	F	84	*3.94*
BHC-PePe6	*Pelophylax perezi*	F	85	*4.34*
BHC-PePe6	*Pelophylax perezi*	F	85	*4.45*

Table 6. Reference collections

Id. Nº	SPECIES	SEX	SVL (mm)	HTW (mm)
BHC-PePe7	*Pelophylax perezi*	F	65	*3.82*
BHC-PePe7	*Pelophylax perezi*	F	65	*3.87*
MNCN-14942	*Pelophylax perezi*	F	60.5	*2.97*
MNCN-14944	*Pelophylax perezi*	F	54.5	*2.81*
MNCN-14945	*Pelophylax perezi*	F	41.5	*1.97*
MNCN-14947	*Pelophylax perezi*	F	66	*3.09*
MNCN-16448	*Pelophylax perezi*	F	55	*2.84*
MNCN-16456	*Pelophylax perezi*	F	51	*2.06*
MNCN-16457	*Pelophylax perezi*	F	62	*2.69*
MNCN-16458	*Pelophylax perezi*	F	58	*2.53*
MNCN-16459	*Pelophylax perezi*	F	46	*1.88*
MNCN-16459	*Pelophylax perezi*	F	46	*1.91*
MNCN-16460	*Pelophylax perezi*	F	66	*2.91*
MNCN-16461	*Pelophylax perezi*	F	29	*1.13*
MNCN-16467	*Pelophylax perezi*	F	53	*2.5*
MNCN-16468	*Pelophylax perezi*	F	44	*1.94*
MNCN-16469	*Pelophylax perezi*	F	43	*1.78*
MNCN-20578	*Pelophylax perezi*	F	79.9	*4.03*
MNCN-20578	*Pelophylax perezi*	F	79.9	*3.97*
MNCN-20581	*Pelophylax perezi*	F	85.4	*4.16*
MNCN-20581	*Pelophylax perezi*	F	85.4	*4.13*
MNCN-20583	*Pelophylax perezi*	F	52.2	*2.47*
MNCN-20583	*Pelophylax perezi*	F	52.2	*2.53*
MNCN-20584	*Pelophylax perezi*	F	74	*3.97*
MNCN-20584	*Pelophylax perezi*	F	74	*4.22*

Id. Nº	SPECIES	SEX	SVL (mm)	HTW (mm)
MNCN-20589	*Pelophylax perezi*	F	59.3	*3.22*
MNCN-20589	*Pelophylax perezi*	F	59.3	*3.16*
MNCN-20592	*Pelophylax perezi*	F	40.8	*1.78*
MNCN-20592	*Pelophylax perezi*	F	40.8	*1.75*
MNCN-40876	*Pelophylax perezi*	F	64	*3.28*
MNCN-40876	*Pelophylax perezi*	F	64	*3.25*

Total females = 61

TOTAL = 104

UNIVERSITAT ROVIRA I VIRGILI

ECOLOGICAL TRAITS OF THE IBERIAN HERPETOFAUNA DURING THE PLIO-PLEISTOCENE: BODY SIZE AND SPECIES RICHNESS IN RELATION TO CLIMATE

Almudena Martínez Monzón

IPHES
Institut Català de Paleoecologia
Humana i Evolució Social

UNIVERSITAT
ROVIRA i VIRGILI