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Long-term changes in composition and distribution patterns in the Iberian herpetofaunal communities since the latest Pleistocene

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ABSTRACT

The climate has undergone significant changes since the end of the Last Glacial Maximum and in the course of the Holocene, parallel to important cultural transformations and migrations in the human communities. The faunal record has also suffered the effects of climate change. Amphibians and reptiles in particular have been shown to be highly sensitive because they are very susceptible to temperature alterations due to their ectothermy. This research presents the first approach to the Iberian paleobiogeography of the different species of amphibians and reptiles from the Late Pleistocene (MIS3) to present times, based on a comparative synthesis of the latest research published in recent years and the fossil record of the 58 archaeo-paleontological sites with significant assemblages. The paleo-herpetofaunal associations make it possible to establish two major biotic regions during the Late Pleistocene. The first biotic region was located in the center and south of the Iberian Peninsula, with thermophilic species as the most representative taxa. The second biotic region was formed by the Atlantic-Cantabrian facade and the northeast Iberian area, dominated by hygrophilous and Euro-Siberian species, with an absence of Mediterranean species. After the Last Glacial Maximum there was an unprecedented concurrence in the northern Iberian Peninsula of autochthonous taxa from that area with thermophilic species. In the early Holocene, new species with no previous record in the Iberian Peninsula entered northern Iberia from eastern Mediterranean *refugia*. Finally, the introduction of North African species was the last significant biogeographical change during the Middle-Late Holocene.

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1. Introduction

The last 60,000 years of the Quaternary have been characterized in Western Europe by major climatic and environmental changes as a result of the occurrence of the last great glacial pulsation and the beginning of the current warm interglacial. This time interval begins in MIS 3 (ca. 60,000 to 26,900 B.P.), alternating between phases of warming and cooling climate that correspond to the decline or increase of forests and semi-desert environments until the onset of MIS 2 (26,900 to 14,900 B.P.). At this point there occurs a major cooling process and a remarkable expansion of open arid spaces, with vegetation typical of cold and dry environments and with

forest limited to areas of refuge (Fletcher and Sánchez-Goñi, 2008; Fletcher et al., 2010). MIS 1 (which starts at 14,900 B.P.) is characterized by a generalized warming of the climate, especially from the Holocene onwards (11,700 B.P.), and by a rapid increase in wooded areas. However, this phase also presents significant climatic fluctuations, though without outweighing the warm overall dynamic (Fletcher & Sánchez-Goñi, 2008; Fletcher et al., 2009; Walker et al., 2012; Naughton et al., 2015).

These large climatic and environmental changes have had a decisive impact on wildlife. The herpetofauna, reptiles and amphibians, is one of the animal groups that is most sensitive to temperature fluctuations due to the characteristic ectothermy of such organisms (Pough, 1980). This makes it a group of special interest for studying the effects that Quaternary climate changes have had on biodiversity (Araújo et al., 2008). All species of reptiles and amphibians in the Iberian fossil record of the Late Quaternary are currently represented in the Iberian Peninsula (Rage and Roček, 2002; Blain et al., 2011, 2014a, 2016). This facilitates actualist studies that allow us to observe the movements that have occurred

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in the geographical distribution of these groups leading to the current situation and to infer the possible paleoenvironmental and bioclimatic changes at a regional level (Blain, 2009).

To date, 51 species of reptiles and 28 species of amphibians have been described on the Iberian mainland, a herpetofaunal assemblage characterized by a great variability of thermal and ecological requirements (Masó and Pijoan, 2011). This includes typically Mediterranean taxa such as *Acanthodactylus erythrurus*, *Hemidactylus turcicus*, *Hemorrhois hippocrepis*, *Chamaeleo chamaeleon* and *Blanus cinereus*, and other species associated with Euro-Siberian climates such as *Lacerta agilis*, *Zootoca vivipara*, *Mesotriton (Ichthyosaura) alpestris* and *Rana temporaria*. The widespread mountainous terrain of the Iberian Peninsula has facilitated the emergence of species whose distribution is associated with high mountain climates, especially in northern Spain, examples being *Calotriton asper* and the genus *Iberolacerta* (Carretero et al., 2014). The high degree of knowledge currently available of the 79 herpetofaunal species with a current distribution in the Iberian Peninsula (Pleguezuelos et al., 2002; Masó and Pijoan, 2011; Salvador and Pleguezuelos, 2013; Carretero et al., 2014) results in a good bibliographical, biogeographical and statistical base for an analysis of the Iberian fossil herpetofauna. The biological requirements of each of these species generate particular restrictions that limit their biogeographical distribution and the viability of their populations, both at present and during the Quaternary, allowing us to infer the paleoclimate and the paleobiogeography by means of the fossil record (Blain et al., 2009a).

The phylogenies of different European species suggest the existence of a climatic refuge in the Iberian Peninsula through the successive glacial stages, from which these species would have subsequently repopulated the rest of the continent during the interglacial phases. This is a role similar to that played by the other peninsulas of southern Europe, the Balkans and Italy (Hewitt, 1996, 2000), made possible by the special climatic characteristics of their geographical location (Fletcher et al., 2010; Harrison and Sánchez-Goñi, 2010). In addition, the highly variable Iberian orography allowed the existence of a multitude of areas with different climatic and environmental characteristics, permitting the survival of species more adapted to temperate climates, in contrast to the situation in the rest of the continent (Nieto, 2011).

In the present study, by means of a comparative statistical analysis of the herpetofaunal associations from a total of 118 levels of 38 Iberian archaeo-paleontological sites in the Iberian Peninsula from the last 60,000 years (Fig. 1), we intend to identify the main changes in the distribution, composition and diversity of the reptiles and amphibians during the time interval analyzed. Our aim is to determine the main biogeographical movements of the different herpetofaunal species throughout the Iberian Peninsula and the role of the peninsula as a climate refuge during the Last Glacial Maximum and as a starting point for the subsequent recolonization of northern areas.

2. Material and methods

2.1. Data matrix

First, a bibliographical search has been carried out in the major journals of archaeology, paleontology and zooarchaeology, as well as a search through the major Internet search engines (mainly Google, Yahoo and Bing). For our statistical studies, the taxa identified in 118 levels of 38 paleo-archaeological sites chronologically dated to between early MIS 3 (ca. 60,000 B.P.) and the Bronze Age (ca. 3500 B.P.) have been compiled. These were then separated into three data matrices on the basis of biogeographical factors (Appendix A, B & C). For each level all the species present in the

herpetological record have been included. In the case of genera with a single Iberian species (e.g., genus *Pelobates*), either currently or in the Quaternary fossil record (genus *Testudo*) (Morales and Sanchis, 2009), these have been assigned to the only species in question. The same goes for taxonomic identifications assigned to families that only have a single species present in the Iberian Peninsula (Geoemydidae or Emydidae). However, we have not included the genus-level citations of genera that have two or more species present in the Iberian Peninsula (e.g., genera *Bufo* sensu lato and *Natrix*).

In addition, we have applied some corrections to the data matrix to reduce dispersion and facilitate interpretation. The genus-level citations of the genera *Hyla*, *Lacerta* and *Vipera* from levels in the northern area have been included because of their biogeographical significance. For the same reason, the genus-level citations of *Pelodytes* and *Alytes* have also been included, despite the lack of species-level identification in some cases (e.g., Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013; Blain et al., 2013). Due to the problems in the paleontological literature of differentiating between *R. temporaria* and *Rana iberica* by osteological criteria (e.g., Zubeldia et al., 2007; Murelaga et al., 2011; Garcia-Ibaibarriga et al., 2015), these two species have been grouped together as *R. temporaria-iberica* in the data matrix of the northern region. The citations of *Elaphe* sp., a snake genus that previously grouped together the current species *Zamenis scalaris* and *Zamenis longissimus*, have been assigned to *Z. scalaris* in the cases from Las Orcillas 1 and Lloma de Betxí, in accordance with the Iberian thermophilic tendencies of the herpetofaunal associations from their respective levels (Fernández et al., 2010; Tormo and De Pedro, 2013).

There are 20 levels with herpetofaunal record that have not been included in the matrix data. The chelonian citations from the paleo-archaeological sites of Gruta da Oliveira, Foz do Enxarrique, Abrigo de la Quebrada, Abric del Pastor, Cueva de San Luís, Cova Canet, Gruta do Escoural, Cova de l'Or, Ereta del Pedregal, Pic dels Corbs, Roca dels Bous, Cova del Gegant, Cova del Teixó, Can Sadurní, La Draga, Pont de Sadernes, El Pastoral, Cal Tintorer and Bòbila Madurell, as well as levels NV13, NM14 and NM4-2 of Cueva de Nerja (Jiménez Fuentes, 1986; Fernández Peris and Martínez Valle, 1989; Pérez Ripoll, 1990; Jiménez-Fuentes et al., 1998; Gómez and Jiménez Fuentes, 1998; Brugal and Raposo, 1999; Crespo, 2002; Mora et al., 2003; Budó et al., 2005; Félix et al., 2006; Morales and Sanchis, 2009; Aura et al., 2010; Jordá et al., 2011; Daura and Sanz, 2012; Sanchis et al., 2013, 2015; Pérez Ripoll, com. pers.), the citation of *Tarentola mauritanica* from level A.sup of Cova Colomera (López-García et al., 2010a), the citation of *R. iberica* from Cueva Millán (Esteban and Sanchiz, 1990) and the citation of *C. chamaeleon* from Cueva de Rincón de la Victoria (Talavera and Sanchiz, 1983) have been excluded from the northeastern and central-southern data matrices, to avoid statistical deviations owing to the large number of mono-specific citations without any other herpetofaunal taxa, although they are included in the subsequent discussion. Also, the citations of the genus *Testudo* that date from the Holocene of the northeastern area (Budó et al., 2005) have not been included because of the taxonomic revision they have undergone (Félix et al., 2006; Morales and Sanchis, 2009).

In order to compare the fossil record with the current situation, we have collected data on the present-day herpetofaunal assemblages from the same 10 × 10 km UTM's as the archaeo-paleontological sites included in the regional data matrices, through the "Especies por UTM" (species per UTM) function of the SIARE application website (Sistema de Información de Anfíbios y Reptiles de España) (AHE, 2016).

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