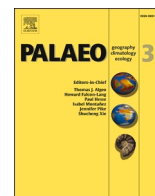




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Amphibians and reptiles as palaeoenvironmental proxies during the Late Pleistocene (MIS3): The case of Stratigraphic Unit V of El Salt, Alcoi, Spain



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ABSTRACT

The locality of El Salt (Alcoi, Spain) is a key site for understanding the extirpation of Neanderthals in the eastern part of Iberia. In this paper, we analyse an assemblage of amphibians and reptiles from Stratigraphic Unit V (45.2 ± 3.4 ka to 44.7 ± 3.4 ka), which corresponds to one of the last regional records of Neanderthals, to improve knowledge of the palaeoecology and palaeoclimate of this event. The assemblage comprises three anurans (*Pelodytes* sp., *Alytes obstetricans*, and *Epidalea calamita*), two lizards (Lacertidae indet. and *Chalcides bedriagai*), and five snakes (Colubridae indet., *Coronella* sp., *Coronella* sp./*Zamenis* sp., *Natrix maura*, and *Vipera latastei*). Palaeoclimatic reconstruction, based on the Mutual Ecogeographic Range method, indicates that climate was cooler and slightly wetter climate than the present day climate of the Alcoi area. Applying the Habitat Weighting Method, we infer that the area surrounding El Salt was dominated by open dry regions, alternating with rocky areas with scarce scrubs and forest patches that would have developed under mesomediterranean conditions. These results are not entirely consistent with those obtained with other proxies (charcoal and small mammal assemblages) from the same site, which suggest slightly warmer and drier conditions. We hypothesise that these divergences may be partly related to the current wide distribution of reptiles and amphibians across Iberia. A key finding is that the extirpation of the Neanderthals in Iberia coincided with aridification.

1. Introduction

Palaeoecological and palaeoclimatic reconstructions are two of the primary topics in Quaternary studies, which are primarily concerned with the history of our species and own relatives (e. g. Cohen et al., 2009; deMenocal, 2011; Birks et al., 2015). Numerous proxies have been used to perform palaeoclimatic and palaeoecological reconstructions

(Bradley, 1999; Rose et al., 1999; d'Errico and Sánchez Goñi, 2003; Evershed et al., 2007; Birks et al., 2010; Wolf et al., 2018, among others). The use of a natural system as a climate proxy must meet two requirements: it must contain a climatic signal and have a modern relative for comparison and calibration purposes (the uniformitarianism principle) (Bradley, 1999). According to Bradley (1999), the biological proxies are related to the presence of a particular taxon, the fossil

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assemblage, and its modern population distribution or its stable isotope composition.

Numerous marine cores allow for large-scale palaeoecological reconstructions in Quaternary sites, although it is not entirely clear that they can be applied to continental contexts (Jennerjahn et al., 2004; Beghin et al., 2016). Unfortunately, few continental cores can be used for this purpose (e.g. d'Errico and Sánchez Goñi, 2003; Sepulchre et al., 2007). Moreover, according to Holmes et al. (2010), only a specific-site reconstruction in which human remains have been found could provide a valuable environmental context for studying hominin evolution.

Although amphibians and reptiles have traditionally received less attention than mammals in palaeontological sites, they can be highly useful for clarifying some palaeoclimatic and landscape aspects of the study area. As ectothermic animals, they are quite sensitive to environmental and habitat changes; they also have low dispersal capabilities (Antúnez et al., 1988; Bailon and Rage, 1999; Araújo and Pearson, 2005; Rodríguez et al., 2005). Due to these characteristics, these specimens provide important local information on the climatic and ecological conditions that prevailed during the formation of the archaeological and palaeontological sites, as well as the possible effects of these conditions on Late Pleistocene human communities. For these reasons, in the last 10 years, amphibian and reptile assemblages have been widely used as palaeoclimatic and palaeoenvironmental proxies (Blain, 2009; Cruz et al., 2016; Blain et al., 2018, 2019; Villa et al., 2018a, 2018b). Therefore, numerous studies have examined on the palaeoclimatic and palaeoecological implications of both herpetofaunal and/or small mammal assemblages (e.g. López-García et al., 2011a, 2011b, 2012a, 2012b, 2012c, 2014; Blain et al., 2013; Rey-Rodríguez et al., 2016; Marquina et al., 2017) in order to elucidate the local context of the Neanderthals demise.

Neanderthals were a human species that inhabited Europe and the Middle East during the late-Middle and Late Pleistocene (e.g. Finlayson, 2004). The disappearance of Neanderthals occurred during Marine Isotope Stage (MIS) 3 (ca., 30–60 ka in accordance with Railsback et al. (2015)) (e.g. Mallol et al., 2012). This was an unstable climatic period in the Late Pleistocene that was characterised by alternating warm phases with expanding forests and cold phases when semi-arid areas developed (e.g. Fletcher and Sánchez-Goñi, 2008). A classical hypothesis proposed to explain the extinction of Neanderthals postulates competition and subsequent replacement by anatomically modern humans (AMH) (Mellars, 2004). However, direct contact between Neanderthals and AMH has not been directly confirmed in the Iberian Peninsula, apparently the last region inhabited by Neanderthals (e.g. Vaquero et al., 2006; Mallol et al., 2012). Human remains are scarce in the Late Pleistocene sites of the Iberian Peninsula (Strauss, 2018); therefore, their presence or absence is based on indirect evidence, such as lithic tools. It seems well established that Neanderthals manufactured Mousterian tools (Vaquero et al., 2006) whereas it is generally assumed that Aurignacian technology was produced by AMH (Vaquero et al., 2006). However, this attribution is highly controversial (Strauss, 2018). Moreover, there are several problems regarding the proposed dates for contact between both human populations: the studied period is close to the practical limit for radiocarbon dating; postdepositional disturbance processes on dated elements and archaeological evidences cannot be discarded; diagnostic elements in the lithic assemblage are lacking; and finally, some proposed radiocarbon dates are inaccurate due to the use of inadequate pretreatment protocols (Wood et al., 2013). These factors contribute to the uncertainty regarding the timing and possible causes of the Neanderthal extinction.

Some hypotheses for the Neanderthal disappearance focus on climate change and its environmental effects (e.g. Bradtmöller et al., 2012; Mallol et al., 2012), even though, during their existence, Neanderthals successfully coped with an unstable climate (Van Andel, 2003). These humans were severely affected by cold periods (Finlayson et al., 2001; Bradtmöller et al., 2012), and their distribution reached its northernmost limit during warm intervals (Stewart, 2005). Thus,

extirpation events and the abandonment of sites were common throughout Neanderthal history (Trinkaus, 1995). In this sense, the traditional view of this species as cold-adapted (Pearson, 2000) is doubtful (Finlayson, 2005). Recent studies of Neanderthal anatomy indicate certain traits that are actually characteristic of temperate-zone mammals (Aiello and Wheeler, 2004; Rae et al., 2011) and suggest that the robustness anatomical features of these humans are actually related to a powerful mode of locomotion (sprinting) (Stewart, 2005; Stewart et al., 2019). Moreover, the associated fauna in Neanderthal sites seem to be adapted to warm climatic conditions (Stewart, 2004; Finlayson and Carrión, 2007); for example, in Wallou Cave (Belgium), where occupation apparently alternated between Neanderthals and collared lemmings, an open cold-adapted species occurred (Stewart et al., 2019). Thus, the available palaeoecological evidence, along with Neanderthals' general anatomy, palaeogenomics, and likely ambush hunting behaviour (Schmitt et al., 2003) all seem to indicate that Neanderthals preferred warm forested habitats instead of cold open steppes (Stewart et al., 2019).

At the beginning of MIS 3, Neanderthals were nearly ubiquitous, although their distributional range was gradually shrinking towards the south (e.g. Stewart, 2009). Finally, they were limited to the Iberian Peninsula before their extinction (e.g. Finlayson and Giles-Pacheco, 2000). At the end of its existence, they apparently consisted of small and isolated populations living in a reduced ecological niche (Melchionna et al., 2018). The final demise of Neanderthals probably took place during Heinrich Event (HE) 4 (ca. 40.2–38.3 ka) (Bradtmöller et al., 2012) or just before its onset (ca. 40.2 ka) (Wood et al., 2013; Galván et al., 2014a; Wolf et al., 2018). In the Mediterranean coastal areas, this HE provoked severe aridity episodes (Sepulchre et al., 2007). However, according to Wolf et al. (2018), during MIS 3, the climate deterioration does not seem to have coincided with HE 4, at least in the interior area of the Iberian Peninsula.

The Middle Palaeolithic site of El Salt (Alcoi, Spain) is a key locality for studying the extirpation of Neanderthals in southeastern Spain. Its high value lies in the fact that the archaeological sequence of El Salt records different occupation phases, in which a transition from recurrent to sporadic human occupation –and finally, an abandonment of the site– have been identified (Galván et al., 2014a). Moreover, El Salt contains a rich lithic and vertebrate faunal assemblage, along with combustion structures and six Neanderthal teeth, possibly belonging to an individual from one of the last groups in the region (Garralda et al., 2014). The vertebrate faunal assemblage succession allows for studying and interpreting both the climatic evolution in the southeastern Iberian Peninsula during the Middle Palaeolithic and the possible impact of these changing climatic features on the local palaeoecology and, therefore, on the human populations inhabiting this zone. The aim of this study is to reconstruct the environmental conditions prevailing in Stratigraphic Unit (SU) V from the El Salt site, based on the amphibian and reptile assemblages. Our results are discussed within the debate about the Neanderthal extinction, focusing on the ecological context in which these events occurred.

2. Geological setting

The archaeological site of El Salt (Alcoi, Alicante) (716,673, 4,284,952, 30S) (Fig. 1) rests against a 38 m-high Paleocene limestone wall at 680 m above sea level (a.s.l.). The wall is the result of a thrust fault of Eocene limestone over Paleocene conglomerates. The presence of the limestone stopped the course of the Barxell River in the upper part of the wall, creating a palaeolake that outflowed over the fault. As a result, a large travertine building was created along more than 2.5 km in the foothills of the Serra de Mariola (Galván et al., 2014b).

According to Fumanal García (1994), the sedimentary sequence consists of thirteen lithostratigraphic units, which can be grouped into five segments based on their macroscopic textural appearance and archaeological content (Galván et al., 2014b) (Fig. 2a). From base to top,

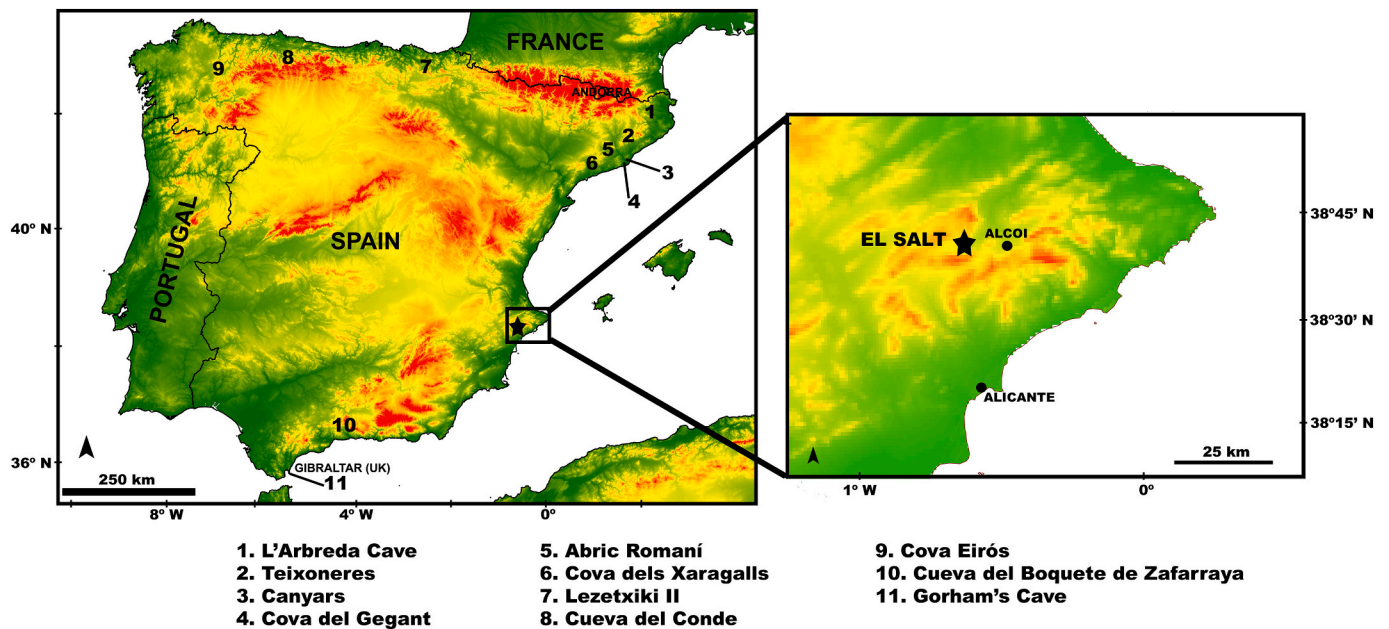


Fig. 1. Geographic location of the El Salt site (black star) in the Iberian Peninsula together with other MIS 3 localities mentioned in the text.

SU XIII is a subhorizontal travertine platform of unknown thickness. The top of this unit has been dated by U/Th as 81.5 ± 2.7 ka and 80.1 ± 4 ka (MIS 5a- ca. 82–71 ka) (Galván et al., 2014b). Whereas SU XIII is archaeologically sterile, the stratigraphic units SU XII to SU IX contain the highest concentration of archaeological remains and combustion features within the entire sequence. As a whole, these units consist of 1.5 m of horizontally bedded fine sand, with several large blocks at their base related to a first episode of roof collapse (Galván et al., 2014b). This part of the sequence has been dated, using thermoluminescence (TL), as 60.7 ± 8.9 ka (SU XII) and 52.3 ± 4.6 ka (SU X) (Galván et al., 2014a), placing the sequence at the beginning of MIS 3, before event HE 5 (Galván et al., 2014a). In contrast, from SU VIII to the middle part of SU V, human occupation evidences decrease and become spatially reduced. SU VI is covered by a significant accumulation of large blocks, produced by the collapse of the roof of the travertine structure. Six teeth attributed to a juvenile or young adult Neanderthal were recovered from the base of SU V (Garralda et al., 2014). These remains may represent one of the last occurrences of Neanderthals in the region (Garralda et al., 2014). The top of SU VI has been dated by TL as between 52.3 ± 4.6 and 47.2 ± 4.4 ka, whereas the base of SU V has been dated by optically stimulated luminescence (OSL) as 45.2 ± 3.4 ka (Galván et al., 2014a). The middle part of SU V has been dated by OSL as 44.7 ± 3.2 ka, before HE 4 (40.2–38.3 ka) (Galván et al., 2014a). The upper part of SU V consists of a 50 cm-thick layer, truncated by a Holocene erosive episode. It is constituted by massive sandy silt with heterogeneous gravel in the top 20 cm, from which two small flint blades, a few undifferentiated flakes, and a small combustion structure have been recovered (Garralda et al., 2014). Finally, SU IV to I consist of a 1.3 m-thick constituted by irregular beds of gravel and cobbles in a silty, clayey matrix. These SU are in a secondary position and separated by erosional contacts. In this deposit, Neolithic pottery mixed with lithic remains from the late Upper Palaeolithic, Epipalaeolithic, and Mesolithic have been recorded (Galván et al., 2014a).

3. Material, methods and abbreviations

The material we describe in this paper consists primarily of disarticulated elements collected during the 2013 and 2014 archaeological campaigns at El Salt. The excavation methodology implemented at the El Salt site is based on the identification of stratification planes through

sharp stratigraphic contacts, textural or lithological changes, and the presence of large objects, which identify the various palaeosurfaces. The remains studied here come from Upper Unit V: specifically, layers V-24, including excavation surfaces (S) 9, 8, and 7, from youngest to oldest, and V-25 (Fig. 2b). Both layers have been dated around 45 ka – that is, between HE 5 and HE 4 (Galván et al., 2014a). A total weight of 101.46 kg (V-25: 14.66 kg; V-24 S7: 23.42 kg; V-24 S8: 26.00 kg; V-24 S9: 37.38 kg) of sediment was sieved for this study.

Fossils were obtained from two distinct sources: i) sieving of the sediment using superimposed nested sieves of successively sized screens (5, 2, 1.25, 1, 0.75, and 0.5 mm), and ii) flotation with a 1-mm mesh during the process of separating macrobotanical remains from the sediment (see Vidal-Matutano, 2016). Unlike method (i) (sieving), with the flotation technique (ii) only the coarser fractions (> 1 mm) were recovered; therefore, fossils obtained through flotation were only recorded as presence/absence data. Fossils were picked, sorted, and classified under a Leica M55 binocular microscope. Measurements were taken with a Leica MZ75 binocular microscope connected to Sony Magnescale measuring equipment. Photographs were taken with a HITACHI 4800 scanning electron at the Servei Central de Suport a la Investigació Experimental (SCSIE) of the Universitat de València.

Herpetological fossils were assigned to different taxa following the criteria given by Bailon (1991, 1999), Sanchiz (1998), and Blain (2009) for Amphibia remains and following Szyndlar (1984), Barbadillo (1989), Bailon (1991), Barahona (1996), Barahona and Barbadillo (1997), Szyndlar and Rage (1999), and Blain (2009) for Squamata. Comparisons were carried out using the collections of dry skeletons of the Museo Nacional de Ciencias Naturales (CSIC) (Madrid, Spain), Muséum national d'Histoire naturelle (MNHN) (Paris, France), Gabinet de Fauna Quaternària of the Museu de Prehistòria de València (Valencia, Spain), and the Departament de Botànica i Geologia from the Universitat de València (Burjassot, Spain). The osteological nomenclature follows Roček (1984), Szyndlar (1984), and Bailon (1991, 1999). We follow the taxonomic nomenclature of Speybroeck et al. (2020) for reptiles and amphibians. All measurements were taken following Barahona (1996) and Barahona and Barbadillo (1997) for lacertids, and following Aufenberg (1967) and Blain (2009) for snakes.

The study of the palaeoclimatic and palaeoecological changes along the sequence are based on the study of the assemblage of amphibians and reptiles from SU Xb-11 S3 (Marquina et al., 2017). The

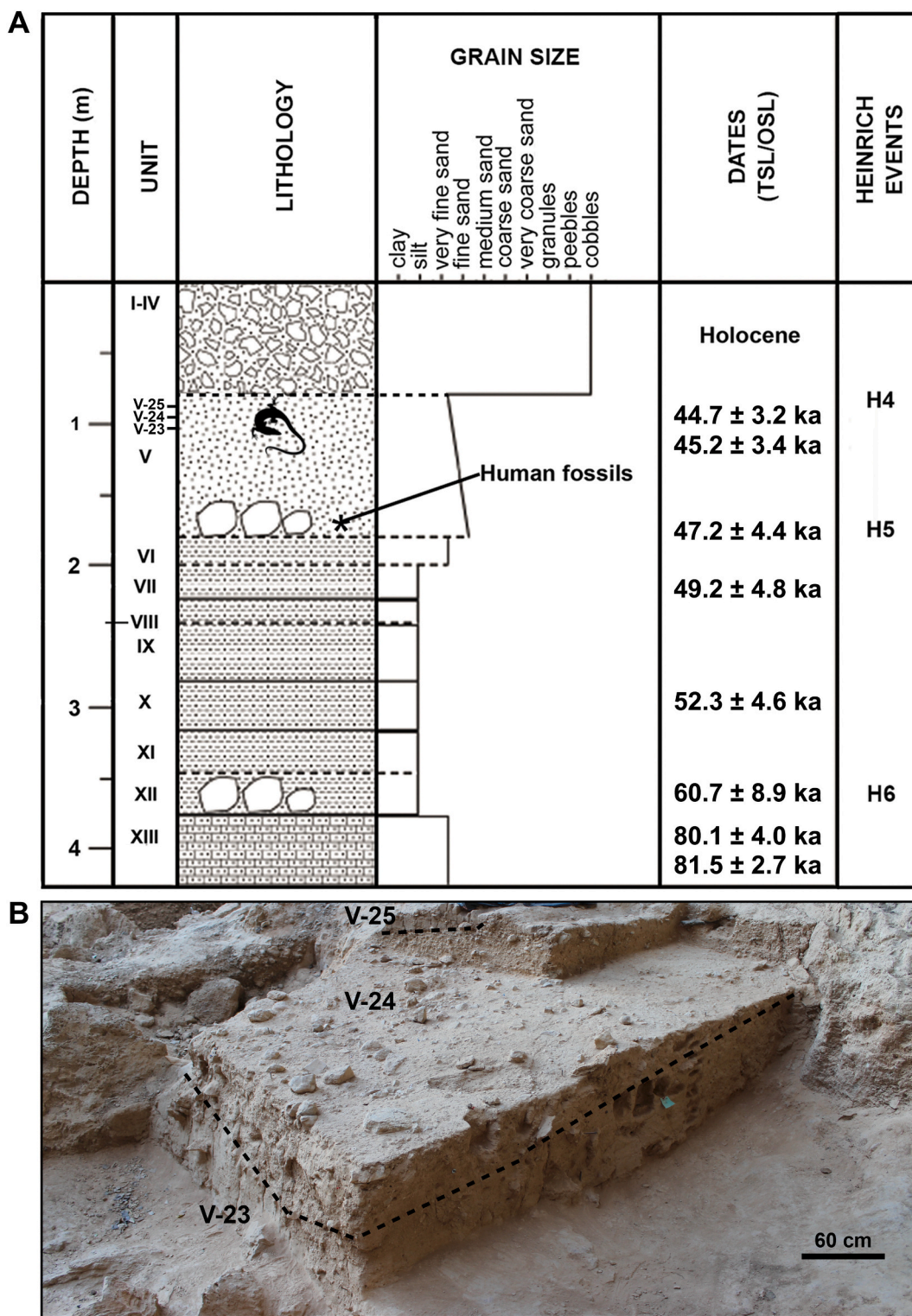


Fig. 2. A) Lithostratigraphic column of El Salt showing the different Stratigraphic Units described by Fumanal García (1994). Modified from Garralda et al. (2014a). The lizard’s silhouette indicates the stratigraphic position of the herpetofaunal remains studied in the present work. B) Picture of the sedimentary deposit of Unit V where the amphibian and reptile remains were recovered (Upper Unit V-24 and V-25). Modified from Fagoaga et al. (2019).

consideration of all these units (SU Xb and SU V) allows us to compare different moments of human occurrence.

To reconstruct the environment of SU V, we have applied the Habitat Weighting Method (HWM) (Evans et al., 1981; Andrews, 2006), which depends on the relative abundances of the different species determined in the assemblage. Therefore, only the material collected with the water-

sieving method (which considers all of the size fractions) was used here. HWM is based on distributing each amphibian and squamate taxon in the habitat(s) where they can be found currently in the Iberian Peninsula. With the exception of a few residual Early Pleistocene taxa (Bailon and Blain, 2007; Blain et al., 2016a; Blain and Bailon, 2019), Iberian Pleistocene amphibians and squamate reptiles are specifically identical

to modern populations (Bailon, 1991; Barbadillo et al., 1997; Blain, 2009). Based on these assumptions, the current species habitat distribution may be used for calculating the habitat-weighting index of taxa described in this work. In the original method, the habitats were sorted into five types (Cuenca-Bescós et al., 2005; Blain et al., 2008): (I) open-dry, (II) open-humid, (III) woodland, (IV) rocky areas, and (V) water edges (areas surrounding water bodies). Each species was given a proportional score depending on its occurrence in one or more habitats. The maximum possible score for each taxon is 1.00. Subsequently, all of these scores are related to the minimum number of individuals (MNI) to obtain the percentage weight of each species in the various assemblages. The distribution data are taken from multiple studies in the Iberian Peninsula (Pleguezuelos et al., 2002; Loureiro et al., 2008) and from palaeoenvironmental reconstructions based on HWM (Blain et al., 2011a, 2011b; López-García et al., 2011a, 2012a, 2012b, 2012c, 2013, 2014; Burjachs et al., 2012; Rey-Rodríguez et al., 2016; Garcia-Ibaibarriaga et al., 2018).

To conduct the palaeoclimatic reconstruction, we apply the Mutual Ecogeographic Range (MER) method (Blain, 2009; Blain et al., 2016b). This technique is based on the modern biogeographic co-occurrence of species described in a palaeontological or archaeological site. We have considered here the entire Iberian Peninsula, an area with natural geographical limits. The choice of this analytical unit is also supported by the fact that some species, that could potentially appear in the site are Iberian endemisms (e.g. *Chalcides bedriagai*). The biogeographic cartography of amphibians and reptiles for Spain is provided by the Servidor de Información de Anfibios y Reptiles de España (SIARE) (AHE, 2016); for Portugal, it is provided by Loureiro et al. (2008). Using ArcGIS 9.1®, the climatic parameters are estimated by overlapping the co-occurrence areas and the current climate layers with a 30-arcseconds resolution grid from WorldClim 1.4 (Hijmans et al., 2005). Both sets of data (co-occurrence areas and climate layers) are represented in the same spatial reference system (EPSG 25830, ETRS 1989 UTM datum coordinate projection system). The bioclimatic parameters extracted from the cartography supplied by Hijmans et al. (2005) are: BIO 1 (mean annual temperature), BIO 5 (maximum temperature of the warmest month), BIO 6 (minimum temperature of the coldest month), BIO 7 (temperature annual range), BIO 12 (annual precipitation), BIO 13 (precipitation of the wettest month), and BIO 14 (precipitation of the driest month).

To reconstruct the vegetal landscape and its bioclimatic determinants existing around the site at the time of its formation, we related (with the aid of GIS tools) the cartography of vegetation series in the Iberian Peninsula (Rivas-Martínez, 1987) to the mutual distribution range of the fossil species (currently extant) recorded in SU Xb and V at El Salt. We compared these results to those of the present vegetal landscape and the bioclimatic indices that characterise the surroundings of the site (Alcoi municipality), according to Rivas-Martínez (1987).

Finally, we conducted a preliminary taphonomic study of the reptiles and amphibians of SU V to discern the agent(s) responsible for the fossil accumulation and to verify the degree of reliability of the information provided by the fossil assemblages. Our taphonomical approach is based primarily on Pinto Llona and Andrews (1999), Stoetzel et al., 2011, Lebreton et al. (2020), and Bisbal-Chinesta et al. (2020a). These authors have studied skeletal representation, as well as bone fragmentation and modification. Thus, to identify the degree of preservation of skeletal elements per carcass, we calculated the ratio of the number of identifiable skeletal parts (NISP) to the minimum number of individuals (MNI) for every taxon described here.

The material described in this study is temporally housed in the Departament de Botànica i Geologia of the Universitat de València (Burjassot, Spain) until their definitive storage in the Museu Arqueològic Municipal Camil Visedo Moltó (Alcoi, Spain).

The abbreviations used in this text are as follows: AHE (Asociación Herpetológica Española); AMH (anatomically modern humans); H (months with probability of frost); HWM (Habitat Weighting Method);

HE (Heinrich Event); M (average of the maximum temperatures of the coldest month); It (thermicity index); m (average of the minimum temperatures of the coldest month); MAT (mean annual temperature); MAP (mean annual precipitation); MER (Mutual Ecogeographic Range method); MIS (marine isotope stage); MNI (minimum number of individuals); MinTC (minimum temperature of the coldest month); MaxTW (maximum temperature of the warmest month); NISP (number of identifiable skeletal parts); OD (Open Dry habitat); OH (Open Humid habitat); R (Rocky habitat); SCSIE (Servei Central de Suport a la Investigació Experimental, Universitat de València); S (excavation surface); SU (Stratigraphic Unit); TL (thermoluminescence dating method); W (Water habitat); WO (Woodland habitat).

4. Results

4.1. Herpetofaunal assemblage

A total of 551 remains of reptiles and amphibians were recovered from El Salt V-24 and V-25; they belong to 95 individuals distributed among 12 species. The association include three anurans (*Pelodytes* sp., *Alytes obstetricans* and *Epidalea calamita*), two lizards (Lacertidae indet. and *Chalcides bedriagai*) and five snakes (Colubridae indet., *Coronella* sp., *Coronella* sp. or *Zamenis* sp., *Natrix maura*, and *Vipera latastei*) (Table 1; Fig. 3). The description of the recovered material can be found in Supplementary Material 1. In general, all taxa are distributed throughout the entire sequence, except for some species that are only present in a particular surface, such as *Natrix maura* in V24-S8, along with *Pelodytes* sp. and *Coronella* sp. or *Zamenis* sp. in V24-S9.

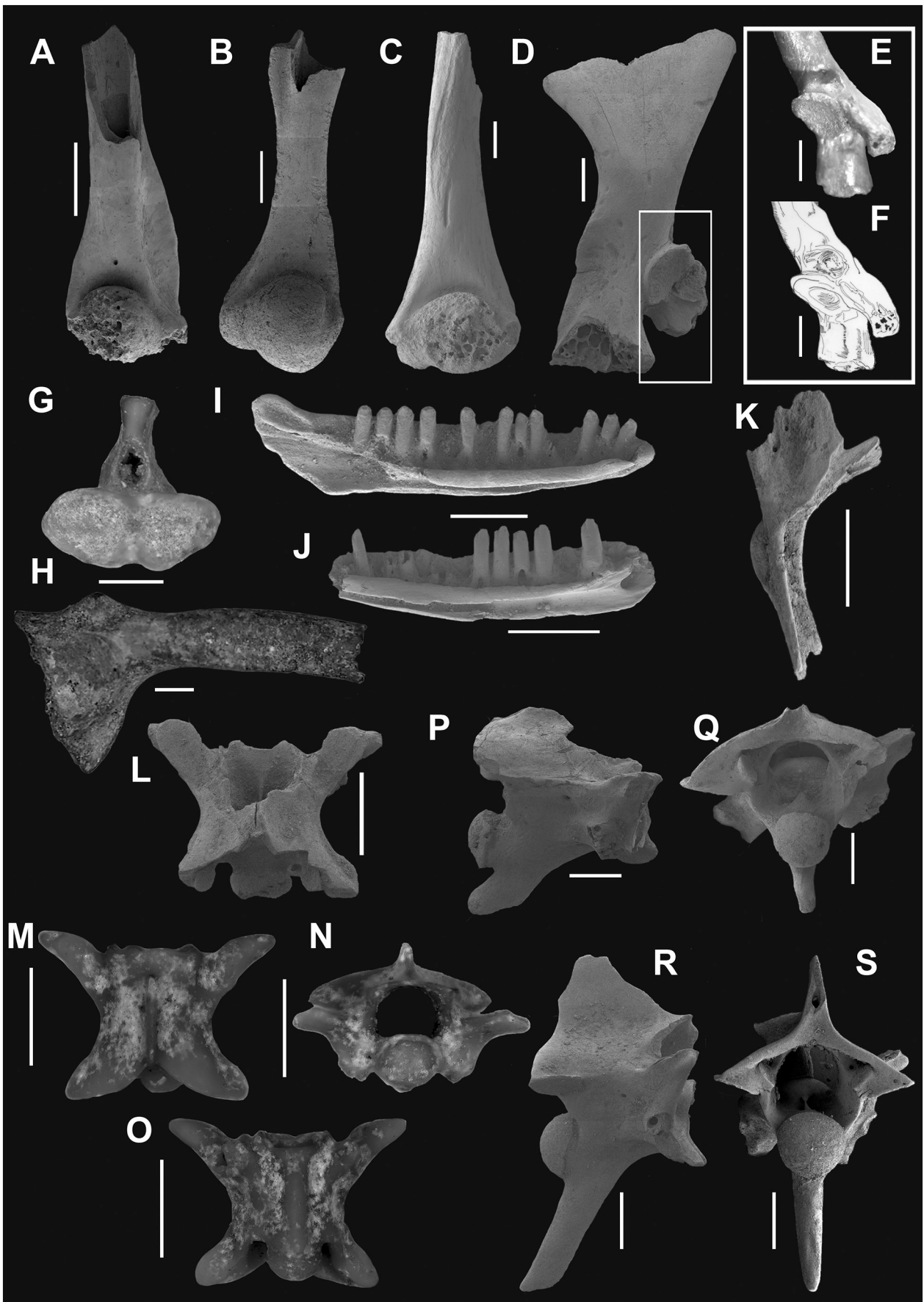
The herpetofaunal assemblage described here is composed of species widely distributed in the Iberian Peninsula (Pleguezuelos et al., 2002; Loureiro et al., 2008). With the exception of *Alytes obstetricans*, *Epidalea calamita*, and *Natrix maura*, which can be found outside the Iberian Peninsula, the rest of the species are Iberian endemisms (i.e. *Vipera latastei* and *Chalcides bedriagai*). Multiple authors (i.e. Vargas and Real, 1997; Sillero et al., 2009) have found the existence of two major chorotypes among the Iberian herpetofauna (Atlantic and Mediterranean), which are extremely coincident with the geoclimate and biogeography of the region. The species recovered from SU V are included within the Mediterranean chorotype of the Iberian herpetofauna, characterised by a wide distribution throughout the Mediterranean bioregion of the Iberian Peninsula and a broad presence in various habitat types (Sillero

Table 1

Comparative faunal list from Stratigraphic Units Xb (Marquina et al., 2017) and V (this work) at El Salt.

	Xb	V			
		24		25	
	S3	S9	S8	S7	-
Anura indet.	0	0	0	0	0
<i>Pelodytes</i> sp.	0	1	0	0	0
<i>Alytes obstetricans</i>	1	1	1	1	1
<i>Epidalea calamita</i>	1	1	1	1	1
<i>Bufo bufo</i> s.l.	1	0	0	0	0
<i>Blanus cinereus</i> s.l.	1	0	0	0	0
Lacertilia indet.	0	1	1	1	1
<i>Chalcides bedriagai</i>	1	1	1	1	1
Lacertidae indet.	0	1	1	1	1
cf. <i>Acanthodactylus erythrus</i>	1	0	0	0	0
Serpentes indet.	0	1	1	1	1
Colubridae indet.	0	1	1	1	0
<i>Coronella</i> sp.	0	1	0	1	0
<i>Coronella</i> sp./ <i>Zamenis</i> sp.	0	1	0	0	0
cf. <i>Zamenis scalaris</i>	1	0	0	0	0
<i>Natrix maura</i>	0	0	1	0	0
<i>Vipera latastei</i>	0	1	0	1	0

The faunal list of surfaces V-24 S9, V-24 S8, V-24 S7 and layer V-25 reflects only the material recovered with the sieving method. 1: presence; 0: absence.



(caption on next page)

Fig. 3. Amphibians and reptiles from SU V at El Salt. A) *Pelodytes* sp. Right humerus (ST-V24-1302) in ventral view. B) *Alytes obstetricans*, left humerus (ST-V24-1256) in ventral view. C–H) *Epidalea calamita*, left humerus (ST-V24-1298) in ventral view (C); left scapula (ST-V25-125) in ventral (D) and lateral (E and F) views; urostyle (ST-V25-101) in frontal view (G); right ilium (ST-V25-142) in lateral view (H). I) *Chalcides bedriagai*, left dentary (ST-V24-264) in lingual view. J) Lacertidae indet., right dentary (ST-V24-133) in lingual view. K) Lacertidae indet., right dentary (ST-V25-107) in ventral view. L) *Coronella* sp./*Zamenis* sp., trunk vertebra (ST-V24-1178) in dorsal view. M–O) *Coronella* sp., trunk vertebra (ST-V24-256) in dorsal (M), frontal (N) and ventral (O) views. P–Q) *Natrix maura*, trunk vertebra (ST-V24-1184) in lateral (P) and posterior (Q) views. R–S) *Vipera latastei*, trunk vertebra (ST-V24-1262) in lateral (R) and posterior (S) views. Scale bars equal 1 mm.

et al., 2009).

4.2. Taphonomical approach

Although taphonomical studies of micromammals are common, those addressing herpetofauna are scarce (Lyman, 1994; Bailon, 2011). In fact, papers exclusively focused on amphibian and/or reptilian taphonomy are extremely rare (Pinto Llona and Andrews, 1999; Stoetzel et al., 2011; Bisbal-Chinesta et al., 2020a); they have usually been incidental to other studies (i. e., Castillo et al., 2001). However, some observations can be made. At El Salt, the herpetological remains show very few marks of digestion, whereas weathering or chemical alteration marks are common (Fig. 4a). There is a high degree fragmentation; intact bones are extremely rare. The fracture plane is primarily angular due to the fragmentation in situ after its deposition. No fossils show

abraded or polished surfaces or edges, which suggests short or null transport prior to their burial. The colour of the remains is homogeneous, without remarkable differences. Root marks and black traces (Fig. 4b) are rare on the surface of the studied material. The lack of intense digestion marks (Fig. 4c) on some remains suggests that they could have been accumulated by owls, whose gastric juice action on bones is smoother than that in carnivorous mammals (Pinto Llona and Andrews, 1999). The preliminary taphonomic study of the small mammals from SU V at El Salt suggests the European eagle owl (*Bubo bubo*) as the most plausible agent for the concentration of this assemblage (Fagoaga et al., 2019). *Bubo bubo* is characterised by a wide range of prey (Lebreton et al., 2020); however, amphibians and reptiles generally constitute only sporadic prey for the European eagle owl, at least in Mediterranean ecosystems (Jasić and Martí, 1984). Nevertheless, some individual owls have been reported to show some degree of

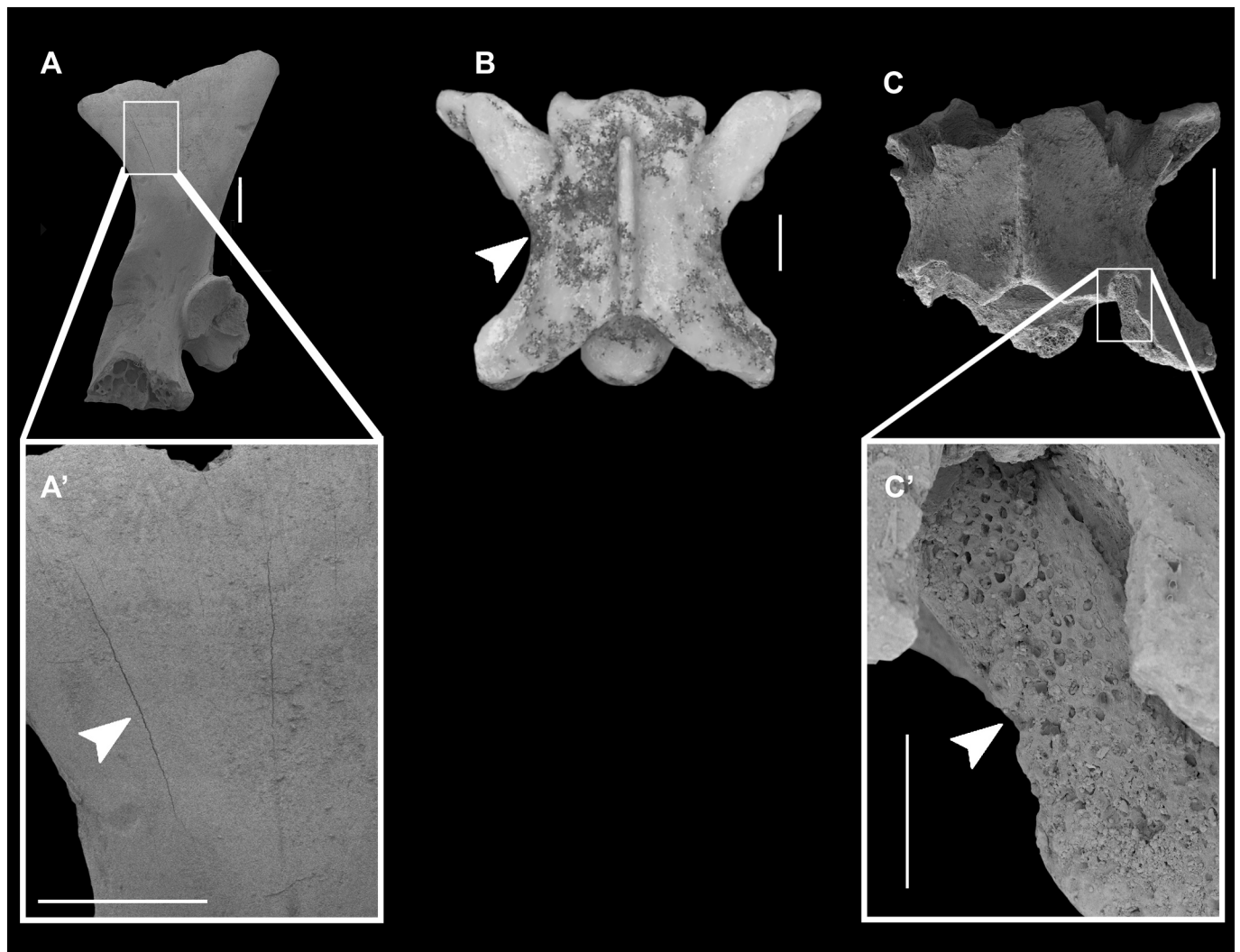


Fig. 4. Alteration marks (shown by white arrows) identified in some herpetofaunal remains from SU V of El Salt. A) *Epidalea calamita*, left scapula (ST-V25-125) in ventral view, with weathering alteration on the bone's surface (longitudinal cracking). A') amplified box showing the weathering alteration mark. B) *Coronella* sp., trunk vertebra (ST-V24-251) in dorsal view, with black traces on its surface related with chemical precipitation (probably of manganese oxides). C) Colubridae indet., trunk vertebra (ST-V24-1202) in dorsal view, with digestion marks. C') amplified box showing the digestion alteration mark.

specialisation on amphibians (Andrews, 1990). Bisbal-Chinesta et al. (2020a) describe a fossil assemblage clearly dominated by *Hyla* gr. *arborea* (representing 84% of the association). The taphonomic analysis suggests that the assemblage was generated by the predation of a medium-large nocturnal raptor (possibly *B. bubo* or *Strix aluco*). This is an interesting case of opportunistic exploitation of an abundant seasonal resource during the reproductive agglomerations of that anurans (Bisbal-Chinesta et al., 2020a). However, predation is not the only process responsible for herpetological taphocoenosis (Cochard, 2004). Reptiles and amphibians use caves and rock fissures for brumation and/or aestivation as a response to changes in weather conditions (Vitt and Caldwell, 2013). The lack of digestion marks also may be attributed to natural death as the primary origin for at least part of the assemblage. Unfortunately, the absence of studies focusing on the taphonomy of reptiles and amphibians precludes further conclusions about the possible biological agents that produced this accumulation.

Table 2 shows the values of NISP and MNI from the material recovered with the sieving method. Supplementary Material 2 includes the results yielded by both the sieving method and the flotation method.

4.3. Palaeoenvironmental reconstruction

The application of the HWM method to the different assemblages recorded in SU V (V-24 S7, S8, and S9, as well as V-25) of the El Salt site indicates a landscape dominated by an Open Dry habitat (OD) throughout the sample studied (Table 3; Fig. 5a). The reconstruction shows a peak of clearly dominant Open Dry habitats, at V-25, which could be related to a scenario of higher aridity. Moreover, Fig. 5 shows an increasing trend of Open Dry habitat values from the oldest samples to the youngest. *Pelodytes* sp., *Epidalea calamita*, and *Chalcides bedriagai* suggest the presence of dry meadows under seasonal climate change. Conversely, the Open Humid habitat (OH) – represented by the presence of *Alytes obstetricans*, *Coronella* sp., and *Vipera latastei* – undergoes, generally the opposite evolution, with a decreasing tendency from older to younger surfaces (V-24 S9: 6%; V-24 S8: 7%; V-24 S7: 7%; V-25: 4%) (Fig. 5).

The rocky areas habitat (R) shows high values throughout the studied SUs, with its highest value (28%) in V-24 S7 and the lowest value in V-24 S8 (23%) (Table 3). Taxa linked to rocky habitats are *Coronella* sp., *Epidalea calamita*, and *Vipera latastei* (Table 2). Additionally, rocky areas provide abundant fissures, that can be used by trogophilic species such as *Pelodytes* sp. (Thomas and Triolet, 1994).

The Woodland habitat type (WO) shows an erratic evolution. The highest values are obtained in V-24 S7 (27%) and V-24 S9 (26%); the lowest values are obtained in V-25 (23%) and V-4 S8 (22%) (Table 3).

In general, the presence of the water-related habitat (W) is anecdotal,

Table 2

Minimum number of individuals, percentage and habitat classification of the species from Unit V at El Salt.

	V-24 S9			V-24 S8			V-24 S7			V-25			Habitat Weighting Method				
	NISP	MNI	%	NISP	MNI	%	NISP	MNI	%	NISP	MNI	%	OD	OH	WO	R	W
<i>Pelodytes</i> sp.	1	1	4										0.5		0.2	0.1	0.2
<i>Alytes obstetricans</i>	2	1	4	2	1	8	4	1	5	6	1	6		0.6	0.2		0.2
<i>Epidalea calamita</i>	8	1	4	9	1	8	4	1	5	26	3	18	0.75			0.25	
<i>Chalcides bedriagai</i>	31	11	48	26	6	46	35	11	58	31	10	59	0.4		0.3	0.3	
Lacertidae indet.	29	4	17	12	2	15	18	3	16	14	3	18					
Colubridae indet.	4	2	8	4	2	16	1	1	5								
<i>Coronella</i> sp.	3	1	4				6	1	5				0.125	0.375	0.25	0.25	
<i>Coronella</i> sp./ <i>Zamenis</i> sp.	2	1	4														
<i>Natrix maura</i>				1	1	8											1
<i>Vipera latastei</i>	2	1	4				1	1	5				0.375		0.25	0.375	
TOTAL	149	23	100	111	13	100	103	19	100	123	17	100					

Data correspond to the material recovered with the sieving method. NISP: number of identifiable skeletal parts; MNI: minimal number of individuals. Wo, Woodland; OD: Open Dry; OH: Open Humid; Wa: Water; R: Rocky. The habitat percentage values for every taxa have been based on Pleguezuelos et al. (2002), Loureiro et al. (2008), Blain et al. (2011a, 2011b), López-García et al. (2011a, 2012a, 2012b, 2012c, 2013, 2014), Burjachs et al. (2012), Rey-Rodríguez et al. (2016), Marquina et al. (2017) and García-Ibaibarriaga et al. (2018).

Table 3

Results of the palaeoclimatic reconstruction after the application of the Habitat Weighting Method to the fossil assemblage of amphibians and reptiles.

	OD	OH	WO	R	W
Xb-11 S3	27	24	30	6	13
V-24 S9	38	6	26	27	3
V-24 S8	35	7	22	23	13
V-24 S7	38	7	27	28	1
V-25	45	4	23	27	1

Data for layer Xb-11 S3 are from Marquina et al. (2017).

except in the case of V-24 S8. This anomalous value is due to the presence of *Natrix maura* in the recovered fossil association. The only limiting factor in the distribution of this species is the presence of water bodies in the environment (Santos et al., 2002; Santos, 2008); for this reason, its entire ecosystem weight is recorded in the water habitat type. Only a single individual of *Natrix maura* (MNI = 1) has been found in V-24 S8, although it represents 7% of all the individuals (14) recovered from this sample (14). Thus, the ‘percentage weight’ in the results of this taxon is elevated. In fact, if we remove *N. maura*, the Open Dry is the most important habitat in the sample (39%) followed by Rocky (26%) and Woodland (25%) habitats. The occurrence of *Alytes obstetricans* and *Natrix maura* indicates permanent water bodies in the surrounding area of El Salt, while *Pelodytes* sp. and *Epidalea calamita* are indicators of ephemeral water bodies. The palaeoenvironmental reconstruction given here should be taken with caution, considering the low MNI (13–23 individuals) yielded by the different studied surfaces of SU V.

4.4. Palaeoclimatic reconstruction

The results of the application of the MER method are represented in Fig. 6. The absence of grids in the south of the Iberian Peninsula derived from the mutual distribution area linked to SU V is explained by the distribution of *Alytes obstetricans* (Fig. 5). On the other hand, the lack of records in the northernmost regions of the peninsula results from the absence in these regions of species such as *Chalcides bedriagai* and *Vipera latastei* (Pleguezuelos et al., 2002; Loureiro et al., 2008) (Fig. 6). Finally, the discontinuous distribution of *V. latastei*, present primarily in mountainous regions (Saint Girons, 1980), results in the discrimination of a large number of grid units, especially in those regions outside of mountainous systems (Fig. 5). The mutual distribution area is located primarily in the eastern and western Iberian Peninsula. The absence of records in the central region is probably related to areas containing low herpetological data, such as the Southern Plateau (Pleguezuelos et al., 2002; Sillero et al., 2009).

The samples we study here suggest a palaeoclimatic scenario similar

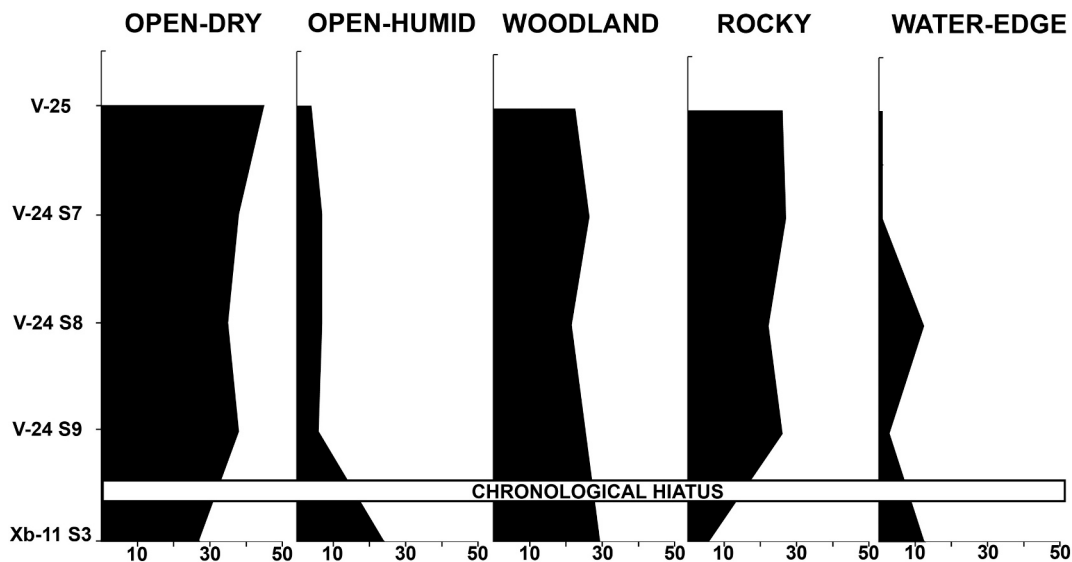


Fig. 5. Palaeoenvironmental reconstruction of El Salt based on fossil herpetofauna from the different surfaces of SU V (S9, S8 and S7 in V-24, and V25) and SU Xb (S3) (Marquina et al., 2017). The reconstruction is based on the herpetofaunal association.

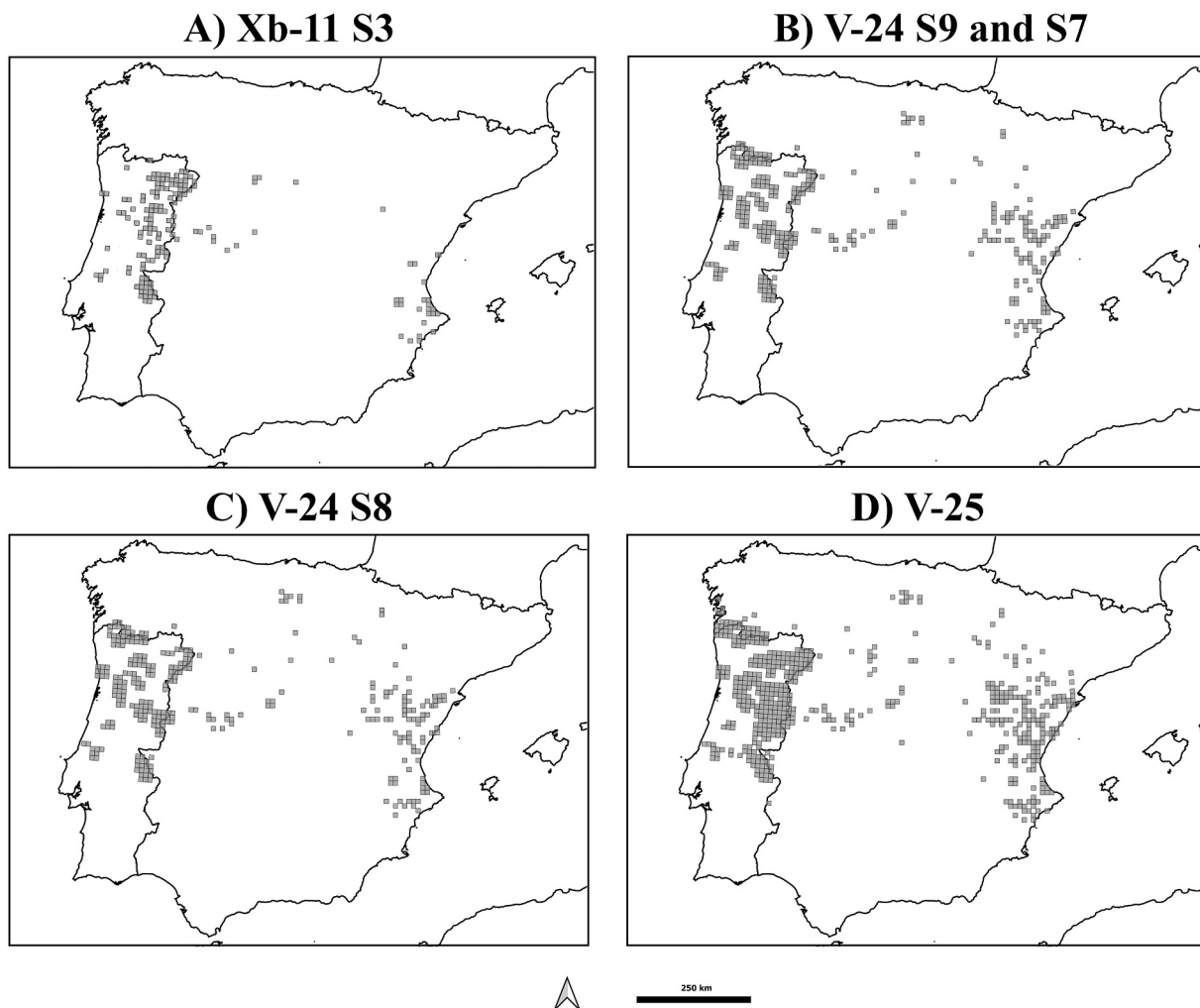


Fig. 6. Mutual distribution area for the whole amphibians and reptiles association determined in Xb-11 S3 (A), V-24 S9 (B), V-24 S8 (C), V-24 S7 (B), and V-25 (D) after applying the MER method. V-24 S9 and S7 have the same assemblage; therefore, both samples share the same mutual distribution area. The distribution area is represented by 10×10 km UTM grids. Data extracted from Loureiro et al. (2008) and AHE (2016). The distribution map of Xb-11 S3 is modified from Marquina et al. (2017).

to the current one at El Salt, with little variation in the bioclimatic parameters. Based on our results, the climate was slightly cooler (from -0.87 to -1.3 °C) and more humid (from $+305.31$ to $+137.5$ mm) than the present climate (Table 4). Thus, the highest differences in MAT have been obtained in samples V-24 S7 and V-24 S9 (-1.3 °C). The other temperature parameters (MinTC and MaxTW) show the same pattern as MAT. Both MaxTW and MinTC are slightly lower than today. Mean MaxTW values range from 27.19 °C in V-24 S8 to 27.64 °C in V-25, whereas mean MinTC values oscillate between 0.98 °C in V-24 S7 or V-24 S9 and 1.74 °C in V-24 S8 (Table 4).

Rainfall parameters show strong differences from their current average values in Alcoi. MAP values are higher than today in all samples (differences range from $+137.5$ mm in V-24 S7 and V-24 S9 to $+305.31$ mm in V-24 S8) (Table 4). A similar trend is apparent for PWM, with the highest differences recorded in V-24 S8 (PWM: $+44.13$ mm) and the lowest differences recorded in V-24 S7 and V-24 S9 ($+18.98$ mm). As for PDM, samples V-24 S7 and V-24 S9 have yielded the highest difference ($+3.25$ mm), whereas the lowest difference ($+1.37$ mm) is obtained at V-24 S8.

4.5. Thermoclimatic belts/vegetation stages

When we overlap the areas of the Iberian Peninsula where the distribution of the species identified in SU Xb and V of El Salt are currently occurs with the map of the vegetation series of Spain (Rivas-Martínez, 1987), we observe that the dominant thermoclimatic belts represented in the surrounding area of El Salt in both SUs were, mesomediterranean (results vary from 62.78 to 49.03%) and supramediterranean (45.72 to 31.34%) (Table 5). The mesomediterranean belt is characterised by the

Table 4

Values of the climatic parameters estimated using the MER methodology.

		MEAN	σ	MAX	MIN	Δ
F25	MAT	12.77	2.47	18.4	4	-0.87
	MaxTW	27.64	2.51	34	19.4	-0.85
	MinTC	1.44	2.84	8.1	-7	-0.25
	MAP	692.53	303.89	1798	276	148.95
	PWM	95.69	46.34	273	41	21.42
	PDM	17.62	8.7	50	3	2.31
	F24-S7	MAT	12.34	2.62	18.3	4
MaxTW		27.23	2.49	34	19.4	-1.26
MinTC		0.98	2.91	7.8	-7	-0.71
MAP		681.08	292.31	1798	312	137.5
PWM		93.25	43.28	272	41	18.98
PDM		18.56	9.06	48	4	3.25
F24-S8		MAT	12.61	2.38	18.2	4.1
	MaxTW	27.19	2.53	33.6	19.4	-1.3
	MinTC	1.74	2.7	7.8	-6.7	0.05
	MAP	848.89	331.03	1798	357	305.31
	PWM	118.4	50.46	272	42	44.13
	PDM	16.68	8.8	47	5	1.37
	F24-S9	MAT	12.34	2.62	18.3	4
MaxTW		27.23	2.49	34	19.4	-1.26
MinTC		0.98	2.91	7.8	-7	-0.71
MAP		681.08	292.31	1798	312	137.5
PWM		93.25	43.28	272	41	18.98
PDM		18.56	9.06	48	4	3.25
ALCOY		MAT	13.64			
	MaxTW	28.49				
	MinTC	1.69				
	MAP	543.58				
	PWM	74.27				
	PDM	15.31				

MAT (mean annual temperature, °C); MaxTW (maximum temperature of the warmest month, °C); MinTC (minimum temperature of the coldest month, °C); MAP (mean annual precipitation, mm); PWM (mean rainfall of the wettest month, mm); PDM (mean rainfall of the driest month, mm); ALCOY (current situation). σ (standard deviation of obtained values); Δ (difference between the values obtained from the fossil assemblages of El Salt and current values in Alcoi).

Table 5

Percentage values of thermoclimatic belts (%) inferred from the assemblages of fossil amphibians and reptiles analysed in Stratigraphic Units Xb and Upper V at El Salt.

	Xb-11 S3	V-24 S9	V-24 S8	V-24 S7	V-25
Alpine	0.00	0.00	0.00	0.00	0.00
Subalpine	0.00	0.00	0.00	0.00	0.00
Montane	0.00	2.10	0.87	2.10	1.34
Coline	0.00	2.25	1.03	2.25	3.61
Cryoromediterranean	0.00	0.00	0.00	0.00	0.00
Oromediterranean	0.14	0.30	0.25	0.30	0.26
Supramediterranean	31.34	45.08	38.71	45.08	40.68
Mesomediterranean	62.78	49.03	58.29	49.03	52.70
Thermomediterranean	5.73	1.23	0.85	1.23	1.42

following thermicity indexes: mean annual temperature (MAT): 13 – 17 °C; average of the minimum temperatures of the coldest month (m): 1 – 4 °C; average of the maximum temperatures of the coldest month (M): 9 – 14 °C. The supramediterranean belt is characterised by MAT: 8 – 13 °C; m: 1 – 4 °C; M: 2 – 9 °C (Rivas-Martínez, 1987). The results show a clear evolution between Xb-11 S3 and V-25 with a progressive increase in the presence of the supramediterranean thermoclimatic belt, although it never surpasses mesomediterranean belt values. Sample V-24 S8 records a peak of the representativeness of the mesomediterranean belt and a fall in the supramediterranean percentage (Table 5).

5. Discussion

5.1. Herpetofaunal assemblage

In accordance with the SIARE program (AHE, 2016), the current community of herpetofauna present in the UTM square 10×10 30SYH18 (where the archaeological site of El Salt is located) is composed of the following species: one newt (*Pleurodeles waltl*), five anurans (*Pelodytes hespericus*, *Alytes obstetricans*, *Epidalea calamita*, *Bufo spinosus*, and *Pelophylax perezi*), six lizards (*Tarentola mauritanica*, *Blanus rufus*, *Chalcides bedriagai*, *Psammotromus algerus*, *Podarcis hispanicus*, and *Timon nevadensis*) and six snakes (*Coronella girondica*, *Hemorrhoids hippocrepis*, *Zamenis scalaris*, *Natrix maura*, *Malpolon monspessulanus*, and *Vipera latastei*). The only turtle species recorded is *Trachemys scripta*, a North American species recently introduced in the Iberian Peninsula, at the end of the 20th century (Pérez-Santigosa et al., 2008). All of the species described in this work are present today in the study area. This stability in the association of amphibians and reptiles is common in numerous archaeo-palaeontological sites from MIS 3 to MIS 1 in the centre and south of the Iberian Peninsula (Bisbal-Chinesta and Blain, 2018). The major changes in the communities of amphibians and reptiles in the southeast of the Iberian Peninsula in the latest 40,000 years were the extirpation of *Testudo (Chersine) hermanni* (Morales Pérez and Sanchis Serra, 2009) and the anthropic introduction during historical times of species such as *Chamaeleo chamaeleon* (Paulo et al., 2002), *Testudo graeca* (Álvarez et al., 2000), and *Chalcides ocellatus* (Bisbal-Chinesta et al., 2020b). Conversely, the record of small mammals from the SU V yielded species currently absent in the area, such as *Arvicola sapidus*, *Microtus arvalis*, *Microtus (Iberomys) cabreranae*, and *Talpa occidentalis* (Fagoaga et al., 2019), thus reflecting that amphibians, reptiles and at least some small mammals show different responses to environmental change scenarios.

Previous research with fossil amphibians and reptiles in the El Salt site have reported the presence in SU Xb of three taxa of anurans (*Alytes obstetricans*, *Bufo bufo* s.l., and *Epidalea calamita*), one tortoise (*Testudo [Chersine] hermanni*), one blaniid (*Blanus cinereus* s.l.), two lizards (*Chalcides bedriagai* and cf. *Acanthodactylus erythrurus*), and one snake (cf. *Zamenis scalaris*) (Morales Pérez and Sanchis Serra, 2009; Marquina et al., 2017). When compared with the faunal list of SU V, the largest difference is the absence in SU V of the most marked thermophilous taxa

(*Testudo [Chersine] hermanni* and *Blanus cinereus* s.l.) and the disappearance of *Bufo bufo* s.l., a species that inhabits a wide range of habitats in Europe, North Africa, and western Asia. The only environmental requirement of *Bufo bufo* seems to be the presence of quiet or low-energy and preferably permanent water bodies with vegetation during its breeding season (Lizana, 2002). Thus, the faunal composition of the recovered assemblages in Units Xb and V shows a strong conservative character, only perturbed by a probable climatic fluctuation, reflected primarily in the relative abundance of the different taxa of the palaeo-community in the time span represented between Units Xb (52.3 ± 4.6 ka) and V (44.7 ± 3.2 ka). However, it is not clear whether the extinction of *T. (C.) hermanni* was the result of climate change (Morales Pérez and Sanchis Serra, 2009), human over-exploitation (Nabais and Zilhão, 2019) or a synergy of both. This stability in the herpetofaunal community is also generally present in other contemporaneous sites. Thus, the determined taxa of amphibians and reptiles are all currently present in Cova dels Xaragalls (López-García et al., 2012b), Cova del Gegant (López-García et al., 2012c), Cova Eirós (Rey-Rodríguez et al., 2016) and Lezetxiki II Cave (García-Ibaibarriaga et al., 2018). In other sites (such as Abric Romaní, Canarys, or Teixoneres in northeastern Spain), some identified taxa are not present in the region. Thus, the absence of the species *Rana temporaria*, *Coronella austriaca*, and *Vipera aspis* is related to the southward shift of the distribution area of that taxa during the Late Pleistocene and a posterior regression (Burjachs et al., 2012; López-García et al., 2013, 2014). A similar case is the presence in Cueva del Boquete de Zafarraya of *C. austriaca* (Barroso Ruiz and Bailon, 2003), a Eurosiberian species with relict populations in the south of the Iberian Peninsula related to the alternation of climatic phases during the Quaternary (Santos et al., 2008). Barroso Ruiz and Bailon (2003) also note the presence of remains belonging to *Testudo* sp., whose absence in the region is discussed above. Finally, in Gorham's Cave, the current absence of *Lissotriton* sp., *Alytes* sp., and *T. (C.) hermanni* may be related to the disturbance caused by the human occupation of the territory (Blain et al., 2013). Although Blain et al. (2013) point out that *Triturus* cf. *pygmaeus*, *Discoglossus* sp., *Acanthodactylus erythrurus*, and *Natrix maura* are absent in Gibraltar, all of these taxa are present today in that region (AHE, 2016).

5.2. Habitat reconstruction

The increasing importance of Open Dry and Rocky habitats observed in SU V probably indicates a more arid environment. The herpetofauna-based palaeoenvironmental reconstruction of SU Xb F11-S3, dated as 52.3 ± 4.6 ka, shows a landscape composed of bushland and forest patches, in which some open areas were present (Marquina et al., 2017). These results suggest a turnover in the dominant habitat-type from Woodland to Open Dry at the end of the Middle Palaeolithic in the surroundings of Alcoi (Fig. 6). The reconstruction based on the fossil small mammal assemblages points to a similar scenario, with a substantial increase in Open Dry habitats (from Units Xb to Upper V), although open forests were still prevalent (Fagoaga et al., 2019). The study of anthracological remains from El Salt, conducted by Vidal-Matutano (2016), describes a forest clearly dominated by *Pinus nigra-sylvestris* during the Middle Palaeolithic (reaching 79.89% of all woody taxa remains in SU V-24). These pine trees are cryophilous species currently present in medium-high Mediterranean mountains. At SU V, a slight increase in *Juniperus* sp. has been interpreted as indicating a trend to colder and drier palaeoclimatic conditions (Vidal-Matutano, 2016). In summary, herpetofauna, small mammals, and charcoal all suggest a tendency towards more open and drier conditions towards the upper part of the sequence.

The dominance of forested landscapes has been reported in numerous Iberian MIS 3 archaeological sites, such as Cueva del Boquete de Zafarraya (Barroso Ruiz and Bailon, 2003; Barroso Ruiz et al., 2003), Cueva del Conde (López-García et al., 2011a), Gorham's Cave (López-García et al., 2011b), Cova dels Xaragalls (López-García et al., 2012a,

2012b, 2012c), Teixoneres (López-García et al., 2014), Canarys (López-García et al., 2014), Cova del Gegant (López-García et al., 2014), L'Arbreda Cave (López-García et al., 2015), Cova Eirós (Rey-Rodríguez et al., 2016), Lezetxiki II Cave (García-Ibaibarriaga et al., 2018), and Abric Romaní (Fernández-García et al., 2018, 2020). Nevertheless, the aridification trend has also been reported in other contemporaneous Iberian sites, including the Gorham's Cave (Blain et al., 2013), L'Arbreda Cave (López-García et al., 2015), and Abric Romaní (Fernández-García et al., 2018).

The application of the HWM to small vertebrates' assemblages from various northeastern Spain localities shows that, during MIS 3, the regional landscape was dominated by open-forest formations regardless of climatic fluctuations (López-García et al., 2014). In contrast to northeastern Spain sites (Cova de L'Arbreda, Teixoneres, Abric Romaní, Cova del Gegant, Canarys and Cova del Xaragalls) the results at El Salt (southeastern Iberia) indicate a greater presence of open habitats (Marquina et al., 2017; Fagoaga et al., 2018, 2019; this work) (Fig. 7). This discrepancy may be related to the groups included in the palaeoenvironmental reconstructions. As shown in Fig. 7, reconstructions based exclusively on mammals (Fernández-García et al., 2018, 2020; Fagoaga et al., 2019) yield higher forest values than those based on herpetofauna (Marquina et al., 2017; this work). In sites where HWM was applied to both faunas (amphibians and reptiles and small mammals), more balanced results are obtained between both types of habitats, albeit always with predominant forests (López-García et al., 2011b, 2012a, 2012b, 2012c, 2014, 2015). The Canarys site constitutes a special case: the assemblage of small vertebrates suggests a landscape with an important component of open habitats (López-García et al., 2014). However, this may stem from the influence of colder and more arid conditions during HE 4 (Daura et al., 2013) or from a predominance of amphibians and reptiles (MNI: 14 individuals) over mammals (MNI: 11) and the resulting bias in the HWM calculations (see López-García et al., 2014). In general, the Iberian amphibians and reptiles of the Mediterranean bioregion have a wide distribution area (Sillero et al., 2009). The different taxa show high ecological plasticity, allowing them to occupy a diverse range of habitats (Sillero et al., 2009). At a small scale, they only select those areas that accomplish specific conditions; for example, humid and cool microhabitats are essential for the survival of many amphibian species due to their high water dependence (Boone et al., 2003). However, the defined habitat groups are too generalised to consider these microhabitat preferences, which results in biased results. This discrepancy may also result from the particular geographic location of El Salt, as compared to the other sites. This is related to the marked climatic gradient in the Iberian Peninsula, with a clear rainfall decrease from north to south and from west to east (Ninyerola et al., 2005). In fact, high-resolution pollen analyses from lacustrine sequences in the east of Spain, covering from MIS 5 to MIS 1, demonstrated that the arboreal cover was always higher in the north than in the south (Burjachs et al., 1996).

5.3. Thermoclimatic belts/vegetation stages

A thermoclimatic belt is composed of areas that share rainfall and temperature conditions and similar plant communities (Rivas-Martínez, 1987). Vegetation responds to climate change modifying its distribution area (Turner and Hannon, 1988). Therefore, the study of the fossil assemblages of reptiles and amphibians, along with the comparison to the current herpetofauna, may shed light on these distributional changes. Relating the overlapping distribution area to the vegetation maps series of Spain (Rivas-Martínez, 1987) allows for the determination of the regional dominant thermoclimatic belt in the past.

Currently, the Spanish inland territory is divided into two bioregions: the Eurosiberian region, which is limited to the north of the Iberian Peninsula, and the Mediterranean region, which accounts for the rest of the territory (Rivas-Martínez, 1987). According to Rivas-Martínez (1987), the Mediterranean region occupies 84.70% of the territory,

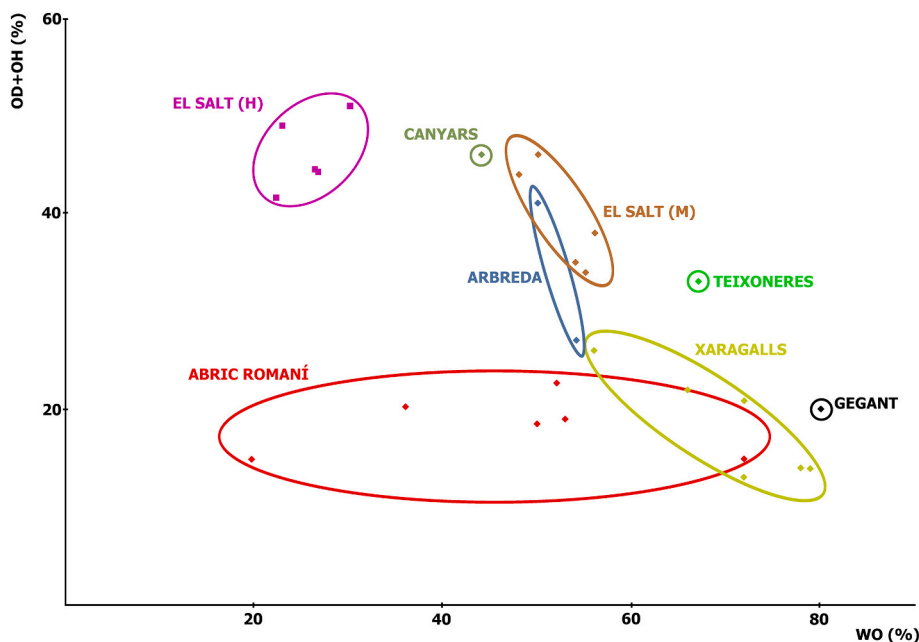


Fig. 7. Representation of Woodland (WO) and open habitats types (OD + OH, the sum of Open Dry and Open Humid habitats) based on the palaeoenvironmental reconstruction in different sites of eastern Spain. The different points represent the levels and units of each site. From North to South: Cova de L'Arbreda (López-García et al., 2015); Teixonereres (López-García et al., 2014); Abric Romaní (Fernández-García et al., 2018, 2020); Cova del Gegant (López-García et al., 2014); Canyars (López-García et al., 2014); Cova dels Xaragalls (López-García et al., 2012a, 2012b, 2012c) and El Salt (Fagoaga, 2019) for small mammals (M) and herpetofauna (H) (this work).

whereas the Eurosiberian region represents only 15.30% of inland Spain. Following the different stages within the Mediterranean region, the mesomediterranean belt is represented in 42.49% of the current inland Spanish territory, whereas the supramediterranean belt occupies 29.19% (Table 6). At present, the mesomediterranean stage is predominant in the Alcoi region, whereas the supramediterranean is restricted to higher areas, such as the Font Roja Natural Park (Fagoaga et al., 2018), located 1000 m in altitude. The studied fossil assemblages show the dominance of mesomediterranean conditions, albeit with a strong representation of the supramediterranean stage in V-24. These results may be explained by the current distribution of each species described in the work, mostly recorded in the mesomediterranean stage and to a lesser extent in the supramediterranean (Table 7); alternatively, both stages are the current dominant thermoclimatic belts in Spanish territory. Regarding the first point, in the Eurosiberian region, the most represented belts in the distribution of the studied species are the montane and coline belts, which show bioclimatic parameters equivalent to the supra- and mesomediterranean belts of the Mediterranean region (Table 6).

The small mammal associations of the same SU yield different results: in SU Xb, the dominant stage is clearly the supramediterranean, whereas in SU V, it is the mesomediterranean (Fagoaga et al., 2018, 2019). Differences between herpetofauna and small mammals are related to the wide distribution of the common area of amphibian and reptile species (mainly east and west of the Iberian Peninsula), as opposed to the much more restricted distribution of mammals (north and northwest). The study of charcoal from SU Xb (Vidal-Matutano

et al., 2018) and SU V (Vidal-Matutano, 2016) reveals that the supra-mediterranean was the dominant stage during the Middle Palaeolithic in El Salt's surrounding area, as in other Iberian localities (Vidal-Matutano, 2018). The differences recorded between this proxy and the results obtained from the study of small vertebrate associations may stem from a different area of the home range of humans and the accumulation agent of small vertebrates (in this case, *Bubo bubo*).

5.4. Palaeoclimatic reconstruction

Regarding temperatures, the palaeoclimatic reconstruction suggests a context with lower temperatures in the younger unit (SU V) than in the older one (SU Xb). Differences of values obtained between the oldest sample (SU Xb) and more modern samples (SU V) range between $-1.66\text{ }^{\circ}\text{C}$ (V24-S9 and V24-S7) and $-1.23\text{ }^{\circ}\text{C}$ (V25) (Fig. 8). During the time span considered, rainfall experienced the opposite trend than the latter case. Thus, MAP, PWM, and PDM show lower values from SU Xb than in SU V. This scenario in modern units of more rainfall is not congruent with the results obtained in the palaeoecological reconstruction (major representation of open habitats in SU V). The results obtained show a high standard deviation (Table 4), due to the wide geographical range reached by the mutual distribution area (Fig. 6). As a result, the set of data used for the calculation of the palaeoclimatic parameters show a strong data dispersion (i.e., $\text{MAP}_{\text{max}} = 1798\text{ mm}$ and $\text{MAP}_{\text{min}} = 276\text{ mm}$ in V-25) because the Iberian Peninsula is a highly mountainous region and that obtained mutual distribution area is formed by two differentiated areas: one in western Iberia and another in

Table 6

Area and Bioclimatic parameters of the dominant bioclimatic stages in inland Spain: Coline and Montane (Eurosiberian region) and Mesomediterranean and Supramediterranean belts (Mediterranean region).

Region	BIOCLIMATIC BELT	T	M	M	It	H	Total (ha)	% Spain	% Region
Eurosiberian (7,308,834.39 ha)	Montane	12 to 6 °C	2 to -4 °C	10 to 3 °C	240 to 50	IX-VI	3,785,771.87	7.57	51.8%
	Coline	>12 °C	>2 °C	>10 °C	>240	XI-IV	3,020,004.83	6.04	41.3%
Mediterranean (42,563,953.02 ha)	Supramediterranean	13 to 8 °C	-1 to -4 °C	9 to 2 °C	210 to 60	IX-VI	14,595,158.33	29.19	34.2%
	Mesomediterranean	17 to 13 °C	4 to -1 °C	14 to 9 °C	350 to 210	X-IV	21,245,402.84	42.49	49.9%
Total area of Spain (50×10^6 ha)									

Data from Rivas-Martínez (1987). MAT (mean annual temperature, °C); m (average of the minimum temperature of the coldest month, °C); M (average of the highest temperature of the coldest month, °C); It (thermicity index); H (months with probability of frost); % Spain (percentage of the surface of the mainland Spain occupied by the bioclimatic belt); % Region (percentage of its respective bioregion occupied by the bioclimatic belt).

Table 7
Representation (%) of the different thermoclimatic belts in the current distribution of the species recorded in the fossil association.

	<i>Alytes obstetricans</i>	<i>Bufo bufo</i> s.l.	<i>Epidalea calamita</i>	<i>Blanus cinereus</i> s.l.	<i>Chalcides bedriagai</i>	<i>Natrix maura</i>	<i>Vipera latastei</i>
Alpine	0.02	0.00	0.00	0.00	0.00	0.01	0.00
Subalpine	0.38	0.00	0.04	0.00	0.00	0.13	0.04
Montane	4.84	0.00	1.37	0.00	0.21	2.09	1.26
Coline	4.98	0.00	1.30	0.00	0.69	1.76	0.57
Cryoromediterranean	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oromediterranean	0.14	0.09	0.09	0.09	0.24	0.10	0.26
Supramediterranean	39.12	11.60	26.07	11.60	23.53	25.74	40.86
Mesomediterranean	49.87	79.23	68.12	79.23	69.01	66.62	54.65
Thermomediterranean	0.65	9.08	3.00	9.08	6.32	3.56	2.37

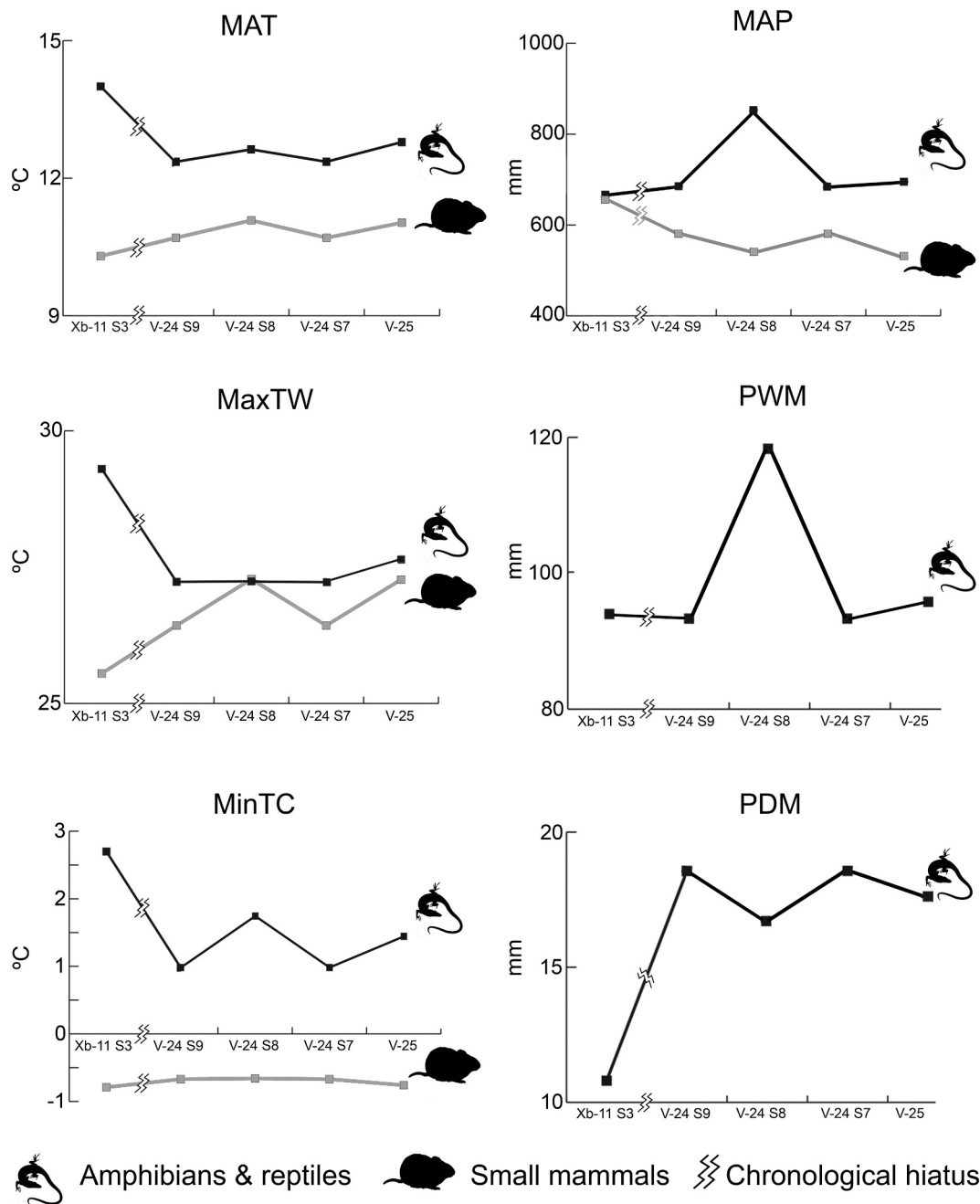


Fig. 8. Evolution of the bioclimatic parameters after the application of the MER method to the fossil assemblages of herpetofauna and small mammals from Stratigraphic Units Xb and V of El Salt. MAT (mean annual temperature, °C); MaxTW (maximum temperature of the warmest month, °C); MinTC (minimum temperature of the coldest month, °C); MAP (mean annual precipitation, mm); PWM (mean rainfall of the wettest month, mm); PDM (mean rainfall of the driest month, mm).

the east of Spain.

The palaeoclimatic analysis based on small mammals, developed by Fagoaga et al. (2019) in the same levels of El Salt, points to conditions wetter and cooler than those prevailing today. In contrast to our results based on herpetofauna, the temperature parameters provided by Fagoaga et al. (2019), based on small mammals, show higher MAT, MaxTW, and MinTC for the youngest bed (SU V) than for the older Xb-11 S3. For all calculated parameters, the resulting absolute values based on small mammals are lower than those based on the assemblages of amphibians and reptiles (Fig. 8). These differences are related to the current mutual distribution area obtained in each case. The presence of mammal species such as *Microtus arvalis* (present in all of the SUs and surfaces studied) and the punctual record of *Talpa occidentalis* (only recorded in sample V24-S9) restrict the distribution to the northwestern quadrant of the Iberian Peninsula (Fagoaga et al., 2018, 2019), whereas the common distribution of amphibians and reptiles is located in medial latitudes in the East and West of the Iberian Peninsula, both in SU Xb and SU V (Marquina et al., 2017; present work). Fagoaga et al. (2019) propose that the climatic parameters obtained for SU V should be placed between values considered for cold and temperate stages, although nearer to temperate ones.

The separate application of the MER method to the association of small mammals (López-García et al., 2011b) and the herpetofauna (Blain et al., 2013) in Gorham's Cave yields a difference in results similar to our case. Thus, at level IV of this locality, the analysis based on the small mammal assemblage resulted in a lower MAT ($-4.2\text{ }^{\circ}\text{C}$) and a higher MAP (+61.4 mm) than the analysis based on amphibians and reptiles (López-García et al., 2011b; Blain et al., 2013). This difference is explained by the presence of two shrews, *Sorex minutus* and *Sorex gr. coronatus-araneus*, which currently live in northern Spain (Blain et al., 2013). Thus, based on all of these results, herpetofauna seem to provide higher temperatures than small mammals. As for rainfall, the difference in the results may be related to the extension of the species distribution. Therefore, in theory, the presence of a taxon with a restricted distribution would result in a geographically more limited common area and in less-dispersed climatic results. Another possibility is the existence in the assemblage of a high number of taxa, which is true of the palaeoclimatic reconstruction of level IV at Gorham's Cave, based on the herpetofaunal assemblage (Blain et al., 2013).

Overall, our results in this study and those obtained for other contemporaneous eastern Iberian sites (L'Arbreda Cave, Teixoneres, Abric Romaní, Canyars, and Cova dels Xaragalls) reveal that the

palaeoclimatic conditions were cooler and wetter than current conditions (Table 8). In the time interval considered, all of the Iberian sites show a clear trend towards a gradual fall of the MAT and MAP (López-García et al., 2012a, 2012b, 2012c, 2014, 2015; Fernández-García et al., 2020).

The differences between past and present MAT and MAP at a particular locality are difficult to interpret, since these parameters are influenced by the altitude (current and past) of the site and the effect of coastal tempering during the time period under consideration. For example, sea level does not appear to have risen above about -60 m during MIS 3 on the Mediterranean French coast (Lambeck and Bard, 2000). Despite this possible bias, some similarities with present conditions can still be seen, such as the northernmost localities showing lower values of MAT and higher MAP than the southernmost localities.

The differences in MAT most similar to those at El Salt are shown in the Cova dels Xaragalls levels C5 ($-3.04\text{ }^{\circ}\text{C}$) and C8 ($-2.92\text{ }^{\circ}\text{C}$) and in the Abric Romaní level N ($-3.10\text{ }^{\circ}\text{C}$) (López-García et al., 2012a, 2012b, 2012c; Fernández-García et al., 2020). As for the MAP results, the Cova dels Xaragalls level C8 (+100 mm) and the Cova de L'Arbreda level H (+142 mm) are the closest to the SU V of El Salt (López-García et al., 2012a, 2012b, 2012c, 2015). The Abric Romaní level N has been chronologically assigned to Interstadial (IS) 16 (Burjachs et al., 2012); level C8 of Cova dels Xaragalls has been assigned to IS 15 or IS 16 (López-García et al., 2012a, 2012b, 2012c); and level H of Cova de L'Arbreda has been assigned to IS 10 (López-García et al., 2015). Based on these similarities, our palaeoclimatic reconstruction seems to indicate a cool and humid phase during MIS 3, which is congruent with the consideration of the interstadials as generally warm and wet moments, as opposed to the stadial periods, which are generally cold and dry (Sánchez Goñi et al., 2009). According to the proposed chronology (Galván et al., 2014a), Unit V may be correlated to Interstadial 12 or 13.

The Iberian Peninsula presents a remarkable climatic diversity due to its mountainous topography and its location in middle latitudes. Iberian climate gradients are characterised by two clear trends: temperature rises from north to south and rainfall decreases from north to south and from west to east (Ninyerola et al., 2005). Similar trends are expected to have occurred during the Quaternary. In this sense, the overall palaeoclimatic reconstructions based on small vertebrates in eastern Spain seem to show a progressive positive trend in the MAT and a negative trend in the MAP from north to south (Fig. 9). The northernmost considered site, Cova de L'Arbreda, shows lower MAT and higher MAP than the rest of the localities, whereas El Salt represents the opposite situation.

5.5. Implications for the last Neanderthals from El Salt

The drier scenario inferred from the palaeoenvironmental reconstructions of the older (SU Xb) and younger units (on SU V) at El Salt may have had a negative impact on the human populations that inhabited the region. In this sense, the major concentration of human activity (archaeological remains, combustion residues, and abundant faunal remains associated with lithic tools) has been found in the interval represented by SU XII to IX (Galván et al., 2014a), in which the assemblages of small vertebrates indicate humid conditions with dominant forest formations (SU Xb) (Marquina et al., 2017; Fagoaga et al., 2018, 2019) in a supramediterranean sub-humid context (Vidal-Matutano et al., 2018). The record of SU V reveals a change in depositional dynamics from gravitational to wind sedimentation and an increase in the episodes of roof collapse (Gómez de la Rúa et al., 2010). Both events, which occurred after the final abandonment of the site (Mallol et al., 2012), may be related to colder climatic conditions. Thus, aeolian sedimentation has been related to an increase in wind intensity in the Mediterranean area, due to changes in atmospheric circulation over the North Atlantic region during the D/O stadials and HE (Moreno et al., 2002). Moreover, the disaggregation of the travertine, limestone bedrock, along with n-alkane chain analyses, is consistent with a dry or

Table 8

MAT and MAP values obtained using the MER methodology from Eastern Iberian sites contemporaneous to El Salt.

Site	Level	Age (ka)	MAT ($^{\circ}\text{C}$)	MAP (mm)	ΔMAT ($^{\circ}\text{C}$)	ΔMAP (mm)
Cova de L'Arbreda	H	41.64–38.29	8.4	950	-6.70	+142
L'Arbreda	I	45.84–41.41	6	1500	-9.10	+692
Abric Romaní	D	45.6–44.4	11.6	981	-3.70	322
	E	49	9.7	950	-5.60	291
	J	50.4–49.3	9.9	719	-5.40	60
	N	54.5	12.2	925	-3.10	266
Canyars	O	54.2	11.1	840	-4.20	181
	–	39.4	10.11	757.6	-5.19	98.6
Teixoneres	II	44.21–33.06	7.6	1008	-7.70	349
Cova dels Xaragalls	C3	–	7.92	1092	-5.48	463
	C4	45.12–48.24	8	925	-5.40	296
	C5	–	10.36	664	-3.04	35
	C6	>43.5	8	950	-5.40	321
	C7	–	8.67	900	-4.73	271
C8	–	10.48	729	-2.92	100	

From North to South: Cova de L'Arbreda (López-García et al., 2015); Teixoneres (López-García et al., 2014); Abric Romaní (López-García et al., 2014; Fernández-García et al., 2020); Canyars (López-García et al., 2014) and Cova dels Xaragalls (López-García et al., 2012a). ΔMAT and ΔMAP : differences between past and present MAT and MAP values.

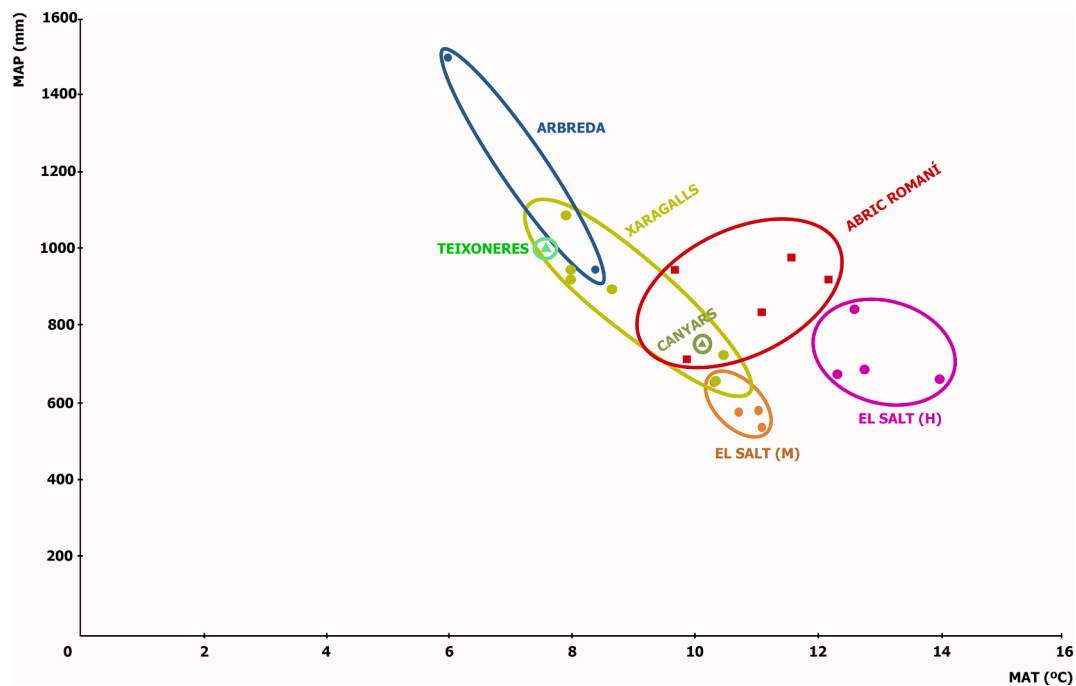


Fig. 9. MAT (°C) and MAP (mm) north-to-south gradient during the Quaternary, based on small vertebrates' palaeoclimatic reconstructions in different sites of eastern Spain. The different points represent the levels and units of each site. From north to south: Cova de L'Arbreda (López-García et al., 2015); Teixonerres (López-García et al., 2014); Abric Romaní (Fernández-García et al., 2018, 2020); Canyars (López-García et al., 2014), Cova dels Xaragalls (López-García et al., 2012b) and El Salt (Fagoaga et al., 2018, 2019) based on small mammals (M) and herpetofauna (H) (this work).

semi-dry climatic context with a prevalence of herbaceous species (Galván et al., 2014a). TL dating of the roof collapse at the base of SU V, in addition to OSL dating obtained for its middle part, places this segment between HE 5 and HE 4 (Galván et al., 2014a). In contrast to the lower units, upper SUs (VIII to VI) present very few, smaller, and thinner combustion structures and significantly smaller faunal and lithic assemblages (Galván et al., 2014a). In other words, the archaeological record of El Salt points to a sudden extirpation of the Neanderthals in a context of an environmental aridification. Latter on, after an occupational hiatus, the territory was once again occupied by an indeterminate group of humans (Galván et al., 2014a). A similar pattern has been observed in other Iberian sites (Mallol et al., 2012).

6. Conclusions

The conclusions obtained from the study of the assemblage of fossil amphibians and reptiles from SU V at El Salt are as follows:

- The herpetofaunal assemblage of SU V (44.7 ± 3.2 ka) is composed of three anurans (*Pelodytes* sp., *Alytes obstetricans*, and *Epidalea calamita*), two lizards (Lacertidae indet. and *Chalcides bedriagai*) and five snakes (Colubridae indet., *Coronella* sp., *Coronella* sp. or *Zamenis* sp., *Natrix maura*, and *Vipera latastei*). These taxa have been recovered from all the studied samples, except *Natrix maura*, which is found exclusively in V-24 S8, and *Pelodytes* sp. and *Coronella* sp. or *Zamenis* sp., which are found only in V24-S9. As for Xb11-S3 (SU Xb; 52.3 ± 4.6 ka), the only difference is the absence of *Testudo* (*Chersine*) *hermanni*, *Blanus cinereus* s. l., and *Bufo bufo* s. l.
- All of the species recorded in SU V at El Salt are currently present in the Mediterranean bioregion, although some taxa are not exclusive to it. Currently, all of the identified species of amphibians and reptiles are extant in the surrounding area.
- According to the proposed palaeoecological reconstruction, the landscape in the surrounding area of El Salt around 44.7 ± 3.2 – 45.2 ± 3.4 ka (SU V) would have been dominated by open dry habitats

throughout the studied sequence (V24-S9, V-24 S8, V-24-S7, and V25). The representation of this habitat is higher in the modern samples (SU V), whereas in SU Xb (52.3 ± 4.6 ka), forest habitat was the dominant habitat type.

- Our results indicate the dominance in the region of the meso-mediterranean thermoclimatic belt in both SU Xb and SU V. These results are not coincident at all with other proxies of the site, which suggest a dominance of the supramediterranean stage (Vidal-Matutano, 2016; Vidal-Matutano et al., 2018) or a turnover of the supramediterranean from SU Xb (Fagoaga et al., 2018) to a dominance of mesomediterranean in SU V (Fagoaga et al., 2019).
- The palaeoclimatic reconstruction draws a more or less stable context. The climate was cooler (-0.87 °C to -1.3 °C) and more humid ($+305.31$ mm to $+137.5$ mm) than the current climate in the area.
- Although our results are generally coincident with those inferred from mammals, the absolute values of the different bioclimatic parameters based on herpetofauna are higher than those based on small mammal assemblages.
- Whereas the studied bioclimatic parameters related with the temperature show a lower value for SU V than for SU Xb, the bioclimatic parameters related to rainfall (MAP, PDM, and PWM) are higher for the modern SU (SU V) than for the older SU Xb. Other proxies of the same site suggest the opposite situation (lower values for MAP, PDM, and PWM in SU V than those obtained in Xb).
- Differences between the palaeoclimatic and palaeoecological reconstructions based on herpetofauna and small mammals may stem from the generally wide distribution range of the Iberian amphibians and reptiles in the Mediterranean bioregion and/or from some physiological particularities not detected in this study.
- Whether or not climate played a decisive role in the disappearance of Neanderthals remains uncertain. The extinction process of Neanderthals was complex and was probably the result of a synergy of multiple factors, rather than the product of a single cause. Moreover, the factors that provoked the disappearance of these humans could

not have been the same in the different regions of their distribution area. In this sense, a multidisciplinary study is necessary to elucidate the causes that drove Neanderthals to their demise in the different regions of Iberia. In the case of El Salt, the climatic worsening scenario coincides with the progressive decrease in human activity, although this does not necessarily imply a causal connection.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2021.110372>.

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