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Palaeoecological characterization of the Pliocene-Pleistocene transition on the Mediterranean littoral area: Almenara-Casablanca (Castellón, eastern Spain)

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ABSTRACT

The Pliocene-Pleistocene transition in the Almenara region (eastern Spain) is investigated through the analysis of herpetofaunal assemblages from ACB-4 (latest Pliocene, MN16) and ACB-1 (earliest Pleistocene, MN17), serving as proxies for palaeoclimate and palaeoenvironmental reconstructions. Our study revealed the presence of new taxa not identified in previous studies in ACB-4 site (*Tarentola mauritanica* and Testudines indet.), thus enlarging previous faunal lists. Palaeoecological reconstructions indicate a shift from forest and scrubland dominance in the Late Pliocene to open habitats in the Early Pleistocene, potentially influenced by the onset of the double seasonality (hot and dry summers, with rainfall concentrated during the other seasons and low temperatures during winter) that characterized the Mediterranean climate then. Palaeoclimatic analyses suggest cooler and wetter conditions during this transition than currently, with higher Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) during the earliest Pleistocene than in the latest Pliocene. Moreover, according to our results precipitations had a more seasonal character in ACB-1, which likely influenced the vegetation and habitat types in the region. The higher seasonality in ACB-1 may have played a significant role in the inferred ecological changes (shift from forest to open habitats), though other factors could also be involved.

These results have been contextualized in the regional palaeoclimatic evolution during the early Quaternary by comparing them with those provided by the palaeoherpetofaunal assemblage from ACB-3 site (Early Pleistocene), according to which open habitats became increasingly dominant and a slight increase in rainfall seasonality took place compared to ACB-1.

Overall, our findings contribute to a better understanding of the ecological and climatic dynamics that took place in the Pliocene-Pleistocene transition of the Almenara region, showing the importance of the integration of diverse proxies and methodological approaches for comprehensive reconstructions.

1. Introduction

The Pliocene-Pleistocene transition has been traditionally placed near the top of the Olduvai Subchron, dated astronomically at 1.806 Ma (Lourens et al., 2005). This boundary was defined by a Global Stratotype Section and Point (GSSP) at Vrica (Calabria, south-eastern Italy). The acceptance of the Plio-Pleistocene transition at 1.806 Ma was related to the first cooling event in the Mediterranean region on basis of the

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presence of marine cold-tolerant taxa there, i.e., first appearance of the mollusc *Arctica islandica* in the Italian sequences (Aguirre and Pasini, 1985). However, these taxa, named "northern guests", were present in the Mediterranean earlier than the above-mentioned chronology. For example, the ostracod *Cytheropteron testudo* has been recorded at 2.4 Ma within the Monte San Nicola section in Italy (Aiello et al., 1996). In fact, the planktic foraminifer *Neogloboquadrina atlantica* invaded the Mediterranean Sea at about 2.4 Ma, being the "true first cold guest" (Spaak, 1983; Zachariasse et al., 1990). Thus, Suc et al. (1997) proposed placing the Plio-Pleistocene transition at the Gauss-Matuyama reversal chron (c. 2.4–2.6 Ma), correlated with the cold Marine Isotope Stage (MIS) 104. Moreover, several climatic events seem to occur worldwide around 2.6 Ma, i.e., increased seasonality (difference between winter and summer surface sea temperatures) in the Northern Hemisphere, southward shift of the North Atlantic Current and Arctic Front, onset of aridity at Lake Baikal (southern Siberia), and modifications of the annual monsoon regimen in China, among others (Hennissen et al., 2015, and references herein). In this sense, the climate of the last 2.7–2.6 Ma appears to be mainly the result of feedback mechanisms involving a steep temperature gradient from the tropical zone to the poles, a temperature gradient from the western to the eastern equatorial Pacific, fluctuating CO_2 levels and permanent ice caps on both poles (Fedorov et al., 2013). Consequently, the base of the Quaternary was refined in June 2009. The new GSSP was established at Monte San Nicola (Sicily, Italy), currently dated at 2.58 Ma (Gibbard and Head, 2009, 2010). Thus, the Gelasian constitutes the oldest epoch of the Pleistocene. With this modification, the onset of the Quaternary exhibits greater coherence from the perspective of changes recorded both in physical systems (terrestrial climate and oceans) and in biota, coinciding with the Gauss-Matuyama magnetostratigraphic boundary and, approximately, with MIS 103 (Gibbard and Head, 2009; 2010).

Many palaeoclimatic reconstructions rely on continuous oceanic records, while terrestrial sequences are scarcer, leaving local effects poorly understood (De Schepper et al., 2014). This means that the effects at the local level are poorly understood. In this sense, the correlation between the mentioned climatic dynamics and faunal turnovers could be hampered by the lack of long continental sections (Agustí et al., 2001). The rich palaeontological record of the continental Neogene in the Iberian Peninsula has allowed us to study the evolution of several biological groups of both flora and fauna during this chronological interval (Agustí et al., 1999, 2009; Aguirre, 2004; Prado et al., 2014; Postigo Mijarra et al., 2009). However, palaeoecological studies focusing on local changes are scarce. Among these, those carried out in the Teruel (Ezquerro et al., 2022) and Guadix-Baza (Agustí et al., 2001) basins stand out, covering in both cases the climatic evolution between the Miocene and Pleistocene. All of them are based on lacustrine sections. Although discontinuous because of the way in which they are formed, fissure infillings of karstic origin can provide valuable information in this regard (Agustí et al., 1999). Moreover, karst infillings can preserve components of the regional biota that are usually not preserved (Plotnick et al., 2015). For example, bats are rarely found in fluvial or lake deposits, in contrast they are reasonably well represented in karstic localities (Crespo et al., 2018; Galán et al., 2024). Reptiles and amphibians are favourably represented in karstic sites, too. Thus, work focused on areas of high concentration of sites and a good stratigraphic control, regardless of their nature, are crucial to understanding ecological and evolutionary responses of biological communities in climatic change scenarios. The Almenara-Casablanca (ACB) karst complex includes a Neogene-Early Quaternary succession of sites that span from the end of the Miocene to the beginning of the Pleistocene: ACB-M (MN13, Late Miocene), ACB-MB (MN14, Early Pliocene), ACB-4 (MN16, Late Pliocene), ACB-1 and ACB-6 (MN 17, earliest Pleistocene), and ACB-3 (late Early Pleistocene). Sampling in these sites has provided a well-documented small vertebrate succession that includes amphibians, reptiles, insectivores, bats, rodents, and lagomorphs (Agustí et al., 2011; Ruiz-Sánchez and Montoya, 2009; Mansino et al., 2016). Thus, these sites are key localities recording the evolution of the herpetofauna during the Pliocene-Pleistocene transition due to the rich, diversified and well-preserved remains they contain. This is especially interesting since herpetofaunal assemblages from this time interval are scarce in the Iberian Peninsula (i.e., Blain, 2005, 2009; Blain et al., 2007) or have been studied as part of broader works which include other faunas (i.e., Piñero et al., 2023). Evidence shows that palaeoclimatic variations during this period led to the extirpation of tropical/subtropical elements in Western Europe and the regionalisation of herpetofaunal communities, with thermophilic taxa retreating to southern regions (Bailon, 1991; Bailon and Blain, 2007; Blain et al., 2016a).

The aim of this study is to reconstruct the environmental conditions prevailing in the region of Almenara based on the amphibian and reptile assemblages recovered from ACB-4 and ACB-1. Our results are discussed within the debate about the palaeoclimatological variations of the Pliocene-Pleistocene transition, focusing on the ecological context in which these events occurred. In order to contextualize our results at a regional level, they will be briefly compared with those estimated for the younger ACB-3 site (see Supplementary Material 1).

2. Geological setting

The Almenara-Casablanca karstic complex is located in an abandoned quarry in Almenara (Castellón, Spain) (Fig. 1A). Its precise location is in the Muntanyeta Blanca, perhaps a more adequate name for this karst complex instead of the name of the municipality to which it belongs (Ruiz-Sánchez and Montoya, 2009); however, we maintain the name Almenara-Casablanca with which it has been known since its discovery, and the one used in all the literature referring to this site (i.e., Agustí et al., 2011). Muntanyeta Blanca belongs to the coastal ends of the Serra d'Espadà mountains (Iberian range). The latter is a mountainous alignment with a marked predominance of Lower and Middle Triassic materials. Sandstones, limestones and marls are the dominant rocks in the Serra d'Espadà, which condition both the relief and the hydrogeology of the region. There are abundant and extensive outcrops of the Buntsandstein and Muschelkalk limestones, as well as the Keuper clays and gypsum rocks (López et al., 2014).

The Almenara-Casablanca complex is a paleokarst developed in Muschelkalk limestones during the Neogene/early Quaternary. The dominating lithofacies are carniolas, micritic dolomite breccias and olivine dolomites, among others. The cavities, aligned according to NNW/SEE orientation, are mainly vertical and are completely filled with clays (*terra rossa*) and pebbles coming from the alteration processes within the cavity itself (Freixes, 2005). The area was exploited in the past for limestone extraction, but mining was not very profitable due to the presence of these karstic infills, and was consequently abandoned in the early 1980s (Santos-Cubedo et al., 2003). The quarry basin is divided into a southwestern area and a north-eastern one separated by a local road.

The Almenara-Casablanca karstic complex comprises at least ten different karstic infills, but only six of them have yielded fossil material, mainly vertebrates (Fig. 1B). In the southeastern area of the quarry the sites of ACB-M, ACB-MB and ACB-1 are found. The first two are the oldest infillings encompassing the Miocene/Pliocene transition. Unfortunately, after mining activities ceased this area was transformed into a recreational area compromising the preservation of the sites. The northeastern area contains the remaining sites (ACB-4, ACB-3, and ACB-6), which also underwent changes and was used for some time as a solid urban waste dump, currently closed. The sealing with debris of the quarry's basin used as a dump has had as a result the entombment of two of these fossiliferous deposits, ACB-3 and ACB-6. Comparing photographs taken by Dr. Francesc Gusí in 1984 with measurements taken from intact preserved milestones, Ruiz-Sánchez and Montoya (2009) have estimated that ACB-3 and ACB-6 are currently 8.33 and 7.00 m deep, covered by the debris and therefore inaccessible for study or resampling.

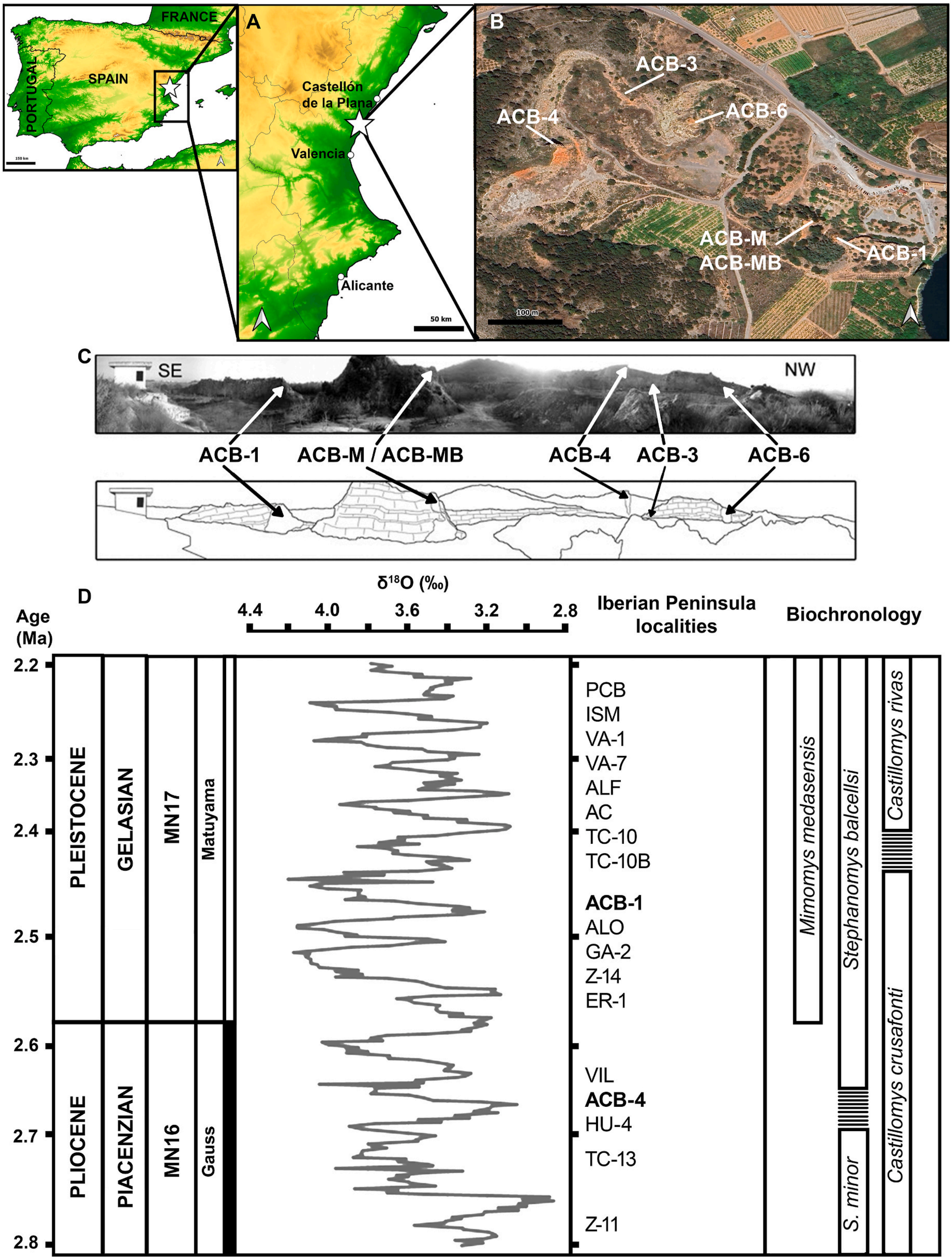

Fig. 1. A) Geographical location of Almenara-Casablanca karstic complex in the Iberian Peninsula. (B) Location of the different sites in the quarry. (C) Panoramic view with the location of the different karstic infilling in the Almenara-Casablanca karstic complex, modified from Agustí et al. (2011). (D) Biostratigraphic correlation between Almenara-Casablanca 1 and 4 sites and (A) the oxygen isotope record from Site 846 (taken from Shackleton et al., 1995) the geomagnetic polarity time-scale (GPTS), (B) various continental Iberian localities, and the biochronologies proposed by Agustí et al. (2015) and Piñero et al. (2018). White star denotes the location of ACB-1 and ACB-4. Abbreviations of the sites: AC, Alto de la Cerdaña; ACB-1, Almenara-Casablanca 1; ACB-4, Almenara-Casablanca 4; ALF, Alfarerías; ALO, Alozaina; ER-1, El Rincón 1; GA-2, Galera 2; HU-4, Huélago 4; ISM, Islas Medas; PCB, Pedrera del Corral d'en Bruach; TC-10, Tollo de Chiclana 10; TC-10B, Tollo de Chiclana 10B; TC-13, Tollo de Chiclana 13; VA-1, Valdeganga 1; VA-7, Valdeganga 7; VIL, Villaroya; Z-11, Zújar 11; Z-14, Zújar 14.

From a biochronological point of view, the presence of the arvicoline *Kislangia cappettai* places ACB-4 at the end of the Pliocene (between ca. 2.7–2.6 Ma) in MN16 (Agustí et al., 2011) (Fig. 1D). The record of this taxon, found together with the murids *Castillomys crusafonti* and *Stephanomys minor* is also found in other Iberian localities correlated with the latest Pliocene. For instance, in Huélago 4 (Sesé, 1989), *K. cappettai* and *C. crusafonti* are found, together with a more evolved species of murid *Stephanomys balcellsi*, indicating a somewhat younger age than ACB-4. Earlier than ACB-4, with a chronology between 3.0 and 2.7 Ma, are the associations from Tollo de Chiclana 13 and 3 (Minwer-Barakat et al., 2004) characterized by the presence of *C. crusafonti* and *S. minor*, but with more archaic arvicoline forms such as *Mimomys minor* or *Kislangia ischus*. For its part, ACB-1 can be placed according to its rodent assemblage, at the beginning of the Early Pleistocene, between 2.6 and 2.4 Ma, in the MN17. The most significant biochronological elements which appear in ACB-1 are the arvicolines *M. medasensis* and *K. gusii* that appear together with the murines *S. balcellsi* and *C. crusafonti* (Agustí et al., 2011). Similar rodent assemblages with *M. medasensis* and *C. crusafonti* are found in other Iberian sites such as El Rincón 1 (Alberdi et al., 1997) or Alozaina (Aguilar et al., 1993). Of slightly younger age (between 2.4 and 2.2 Ma) are sites such as Tollo Chiclana 10 and 10B (Minwer-Barakat et al., 2004) or Pedrera del Corral d'en Bruach (López-García et al., 2024), where *M. medasensis* and *S. balcellsi* are still present, but *C. crusafonti* has already be replaced by an evolved form, *C. rivas*.

3. Material and methods

3.1. Systematic review

In this work we present an update of the herpetofaunal assemblages of ACB-4, ACB-1, and ACB-3 previously described by Blain (2005, 2009) and Blain et al. (2007) for amphibians and squamates, and the turtles from ACB-1 originally studied by Jiménez Fuentes (1985). To this review, we have added new chelonian and gekkotan remains from ACB-4 and ACB-3 which remained unstudied until now. The taxonomical attribution of the undescribed chelonian material is based mainly in Cheylan (1981) and Hervet (2000) and Villa et al. (2018) for the gekkotan material. Photos of the fossil amphibians and reptiles were taken with the digital microscope Leica MZ75, housed at the Departament de Botànica i Geologia of the Universitat de València (Valencia, Spain). 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).

3.2. Palaeoclimatic reconstruction

To conduct the palaeoclimatic reconstruction, we have applied the Mutual Ecogeographic Range (MER) method (Blain et al., 2009; Blain et al., 2016b) and the Uncertain and Occupied Discrimination Area (UDA-ODA) discrimination technique (Fagoaga et al., 2019) using the amphibian and reptile assemblage from the palaeontological sites of Almenara-Casablanca (ACB) 4, 1, and 3. This method is based on the application of an ecological criterion to distinguish those areas that are ecologically habitable for each species (ODA) from those that, a priori, lack the necessary requirements to be occupied by the taxon (UDA). Once these two types of areas are identified, the method searches the modern biogeographic co-occurrence of the ODAs of species represented in a given palaeontological or archaeological site. To define the favourable areas we have used altitude ranges for each species due to its importance as a biogeographical variable in the distribution of Iberian amphibian and reptile species, based on data from diverse herpetological atlases of Spain and Portugal that provide information at different territorial levels (national, autonomic/regional, provincial, particular protected area and, even at mountainous system), which is easily integrated in Geographical Information System softwares (Marquina-Blasco et al., 2022).

The faunal list is based on Jiménez Fuentes (1985) and Blain (2009) for ACB-1; Blain (2009) for ACB-4; and Blain (2009) and Blain et al. (2007, 2010) for ACB-3. The herpetofaunal assemblages include taxa still present in the Iberian Peninsula, but they also include some "exotic taxa" (*sensu* Blain et al., 2016a), such as the anguid *Ophisaurus* s.l. sp., Agamidae indet., and *Bufotes viridis* s.l. (Blain, 2009; Blain et al., 2007, 2010). The methods of palaeoenvironmental reconstruction are based on the use of the ecological requirements of the recent representatives of the taxa identified in each site. This principle is basically of easy use with palaeoherpetofauna since most of the taxa found in the sites considered in this paper are still extant, have undergone no apparent evolutionary change and there is no basis to consider differences in ecological requirements. However, there are some exceptions, specifically among those referred to as "exotic taxa" by Blain et al. (2016a). For instance, when dealing with palaeontological material *Ophisaurus* s.l. sp., is a taxon that includes in fact three extant genera, which although morphologically similar, they belong actually to distinct lineages that radiated at least as early as the early Oligocene. One clade includes *Ophisaurus* s. s., geographically restricted to North America, and *Dopasia*, from southeastern Asia, and the other clade groups Western Eurasian-North African taxa (Lavin and Girman, 2019). The latter clade only includes the genus *Hyalosaurus*. This is a monospecific taxon, which only includes *Hyalosaurus koellikeri* that inhabits exclusively North Africa. The importance of this taxon, stands in the fact that it has been used by Sánchez-Bandera et al. (2023) as the modern palaeoecological proxy for the *Ophisaurus* s.l. sp. material found in the sites of Barranco León and Fuente Nueva 3 (Guadix-Baza Basin, SE Spain; Early Pleistocene). These authors used mainly the current ecological preferences and altitudinal and distribution area of *H. koellikeri*, but also some remarks about altitudinal distribution of the Asian clade *Dopasia* (i.e., *Dopasia harti*), as proxy for its palaeoecological reconstruction of the above-mentioned sites. Under similar criteria, we have looked for a modern proxy for the agamid taxon described in ACB-4 and ACB-1 (Blain, 2009). Agamids are a highly diverse taxon of squamates distributed in Eurasia, Africa, Asia, and Australia (Vitt and Caldwell, 2009; Speybroeck et al., 2016). In Europe, agamids are currently represented by six species with a restricted distribution in the continent (Speybroeck et al., 2016, 2020). However, during the Neogene the group was more widely distributed in Europe (Delfino et al., 2008), reaching the Iberian Peninsula probably during the Miocene-Pliocene transition (i.e., Bailon and Verbeke, 2019; Piñero et al., 2023). There is evidence they persisted in Western Europe until the Early Pleistocene of southeastern Iberia, according to the fossils recovered in Quibas (Blain et al., 2013). Although currently absent on the northern coast of the western Mediterranean, agamids are common on its southern coast. Three genera inhabit the northwestern Africa: *Agama*, *Trapelus*, and *Uromastyx* (Trape et al., 2012). *Agama* is represented in the area by at least seven species (Gonçalves et al., 2012), although only one, *Agama bibronii*, has colonized the Mediterranean bioclimatic zone (Gonçalves et al., 2012). Interestingly, *A. bibronii* is the only agamid species sympatric with *Hyalosaurus koellikeri* (Escoriza and Comas, 2015). *A. bibronii* is particularly common in Morocco, found in a wide variety of environments (Bons and Geniez, 1996; Znari et al., 1998) including humid, sub-humid, semi-arid, and arid zones, although it is rare in the desertic region of the Sahara (Bons and Geniez, 1996).

We consider here the entire Iberian Peninsula as an area with natural geographical limits. The choice of this analytical unit is also supported by the fact that some species described in the sites are Iberian endemisms (e.g., *Chalcides* cf. *bedriagai*, *Blanus cinereus* s.l., and *Vipera latastei*). The biogeographic cartography of amphibians and reptiles for Spain is provided by the Servidor de Información de Anfibios y Reptiles de España (SIARE) (AHE, 2021); for Portugal, it is provided by Loureiro et al. (2008). Both sources show the distribution of each species in 10 × 10 km UTM grids. The altitude ranges for each species are applied to differentiate between ODA and UDA. Using QGIS 3.28 Firenze, the climatic parameters are estimated by overlapping the co-occurrence areas and the current climate layers with a 30-arcsecond resolution grid from Wordclim 2 (Fick and Hijmans, 2017). Both sets of data (co-occurrence areas and climate layers) are represented in the same spatial reference system (EPSG 4326, WGS 84 UTM datum coordinate projection system). The bioclimatic parameters extracted from the cartography supplied by Fick and Hijmans (2017) are BIO 1 (Mean Annual Temperature, MAT), and BIO 12 (Mean Annual Precipitation, MAP). Additionally, we have implemented the monthly weather data for 1970–2000 at a spatial resolution of 2.5 min. The monthly bioclimatic parameters that have been considered are the mean monthly precipitation (MMP) and mean monthly temperature (MMT). For comparison purposes, the same climatic parameters were calculated for the Almenara municipality nowadays (1970–2000, with a 27.62 km^2 area).

The software GNU PSPP 1.6.2-g78a33a was used to perform the statistical analysis.

3.3. Palaeoecological reconstruction

In order to reconstruct the existing environment at the time each site was formed, we have used the method of habitat weighting (Blain et al., 2008). This method is based on the pattern of distribution exhibited by each amphibian and squamate taxon regarding the habitat(s) where each taxon can potentially be found today in the Iberian Peninsula. In the method originally described by Blain for the herpetofauna (Blain et al., 2008), the habitats are arranged in five types: (I) open-dry, (II) open-humid, (III) woodland, (IV) rocky areas, and (V) water edges (areas surrounding to water areas). Depending on its occurrence, each species is given a proportional score for each habitat type, the sum of these scores must be 1.00. To obtain the habitat reconstruction of a particular site, the habitat scores of each taxon present in the assemblage are recalculated considering the percentage in which they are represented in it, based on the MNI (minimum number of individuals). The habitat-weight data for each taxon used in this paper have been taken mainly from Blain et al. (2014, 2019).

3.4. Species diversity

As the studied and compared assemblages (i.e., ACB-4, ACB-1 and ACB-3) present different sample sizes, 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). This method also allowed us to compare the species diversity, which incorporates species richness and the relative abundance of each species, between the studied samples. 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 ($q = 0$), Shannon diversity ($q = 1$) and Simpson diversity ($q = 2$), and are increasingly dominated by the frequencies of the more common 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 iNEXT (iNterpolation/EXTrapolation) online freeware application R-based version (Chao et al., 2016).

3.5. Abbreviations

The abbreviations used in this text are as follows: ACB (Almenara-Casablanca); AHE (Asociación Herpetológica Española); CV (Coefficient of Variation of the Precipitation); GSSP (Global Stratotype Section and Point); IUGS (International Union of Geological Sciences); MAT (mean annual temperature); MAP (mean annual precipitation); MMP (mean monthly precipitation); MMT (mean monthly temperature); MNI (minimum number of individuals); MPD (Mean precipitation of the driest month); MPW (Mean precipitation of the wettest month); MTC (mean temperature of the coldest month); MTW (mean temperature of the warmest month); NISP (number of identifiable remains); ODA (Occupied Distribution Area); PCI (Precipitation Concentration Index); SIARE (Servidor de Información de Anfibios y Reptiles de España); UDA (Uncertain Distribution Area), σ (Standard Deviation).

4. Results

4.1. Update of the herpetological assemblages

The review of the material from the studied sites has allowed the addition of new taxa to the previously published faunal lists (Table 1; Fig. 2). Although no new amphibian taxa have been identified, the reptile list has been increased with several taxa not included in the previous one.

Until the present work, chelonians were only reported in ACB-1 by Jiménez Fuentes (1985). He described the presence of *Testudo* sp. and Emydidae indet. A review of Figs. 1 and 2 in this paper, the tortoise remains have been reassigned to the genus *Chersine* on the basis of the presence of an epiplastron with not-well developed lips and shallow epiplastral pockets, and of the humeropectoral sulcus in the hioplastron, which is directed anteriorly forming a pronounced curvature that connects with the axillary notch (Cheylan, 1981; Hervet, 2000; Lapparent de Broin et al., 2006). This reassignment is reinforced by palaeobiogeographical evidence, since *Chersine* is the only genus of small-medium sized tortoise present during the Pleistocene in the Iberian Peninsula (Morales Pérez and Sanchis Serra, 2009). Although still under discussion (Díaz-Paniagua and Andreu, 2015), it seems that the current presence of *Testudo graeca* in the southern areas of the Iberian Peninsula is probably due to an ancient human introduction. Unfortunately, the remains from ACB-4 and ACB-3 are too fragmentary for a precise taxonomic attribution. Besides the generic reassignment of the chelonian remains, a new taxon, previously undetected in the ACB-4 material has been identified. It is *Tarentola mauritanica,* which was left out of the faunal lists of previous studies by Blain (2005, 2009) as it was considered a possible contamination with recent skeletal remains in the site. *Tarentola mauritanica* has a marked preference for rocky outcrops and stony areas, and can be locally quite abundant (Salvador, 2016). After a visual inspection, the remains show similar colour and degree of fracture found in the remaining fossils of the assemblage, thus there is no reason to consider a different origin for the *T. mauritanica* material and have considered them autochthonous. The taxonomic attribution is based in the presence of (i) fused frontal with a smooth dorsal surface without any lateral grooves and a few developed medial process, and (ii) gracile dentary with a closed Meckelian groove, which is open in the proximal end of the bone by a U-shaped notch (Villa et al., 2018). Following these criteria, we propose that the gekkotan material from ACB-1 belongs to *T. mauritanica*, having been referred to previously by Blain (2005, 2009), as *Tarentola* sp.

4.2. Palaeoclimatic reconstruction

The results of the application of the MER method and UDA/ODA discrimination technique are represented in Fig. 3A and B. The size of the current overlapping distribution area is 3743.59 km^2 (ACB-4) and 789.76 km^2 (ACB-1). These areas are distributed mainly in the southern half of the Iberian Peninsula. Thus, no grids in northern Iberia have been detected due to current distribution of some taxa (i.e., *Chalcides bedriagai*, *Malpolon monspessulanus*, *Vipera latastei*) from that region (Loureiro et al., 2008; AHE, 2021). As to the inferred climatic conditions defined by the overlapping distributions, they are defined on the basis of *Hyalosaurus koellikeri* and *Agama bribonii*, conditions that are currently found in central Iberia (Extremadura, Castilla-La Mancha, Madrid, and

Table 1

Herpetofaunal faunal lists from the latest Pliocene and earliest Pleistocene Almenara-Casablanca (ACB) 4 and 1, palaeontological sites (Castellón, Spain), revised from Jiménez Fuentes (1985), Blain (2009) and Blain et al. (2007, 2010), and the index assigned according to habitat preference in the Iberian Peninsula. NISP: number of identifiable skeletal parts; NMI: minimum number of individuals; WO, Woodland; OD: Open Dry; OH: Open Humid; W: Water; R: Rocky. The habitat percentage values for each taxon are based on Blain et al. (2014, 2019).

	ACB-4		ACB-1						
	NISP	MNI	NISP	MNI	OD	OH	WO	R	W
cf. *Discoglossus* sp.			1	1					1
			6	3	0.50		0.20	0.10	0.20
Pelodytes cf. *punctatus*									
	2	1			0.50		0.20	0.10	0.20
Pelodytes sp.									
	8	1	4	1	0.10	0.30	0.40		
Bufo bufo s.l.									
Pelophylax sp.	1	1	1	2					1
			16	3	0.25		0.50	0.25	
Chersine sp.									
Emydidae indet.			3	1					1
	9		27						
Testudines indet.									
Agamidae indet.	36	3	34	4	0.33		0.33	0.33	
Tarentola mauritanica	20	3	56	13					
Chalcides cf. *bedriagai*			19	4	0.40		0.30	0.30	
Timon cf. *lepidus*	2	1	13	2	0.50			0.50	
Lacertidae indet.	35		365						
Blanus cinereus s.l.	71	1	768	9	0.45	0.10	0.45		
Ophisaurus sp.	3	1	16	1			1		
Natrix maura			7	1					1
	3	1	18	1	0.25	0.25	0.25	0.25	
Coronella girondica									
Zamenis scalaris			9	1	0.35	0.15	0.30	0.20	
Malpolon monspessulanus	3	1	18	1	0.35	0.15	0.25	0.25	
Vipera latastei	2	1	6	1	0.40		0.20	0.40	
TOTAL	186	15	1387	49					

the central area of Comunidad Valenciana) and in southern Iberia (Betic range, the Spanish-Portuguese border between Western Andalucía and Baixo Alentejo, and Algarve).

Our results suggest a cooler and more humid scenario than nowadays at the Almenara area (Table 2). The highest differences in MAT were obtained for ACB-4 (−2.29 °C). Other temperature parameters (mean temperature of the coldest month, MTC, and mean temperature of the warmest month, MTW) present a similar scenario. Thus, January is in all cases the month with the lowest temperatures, which were lower than today's. The difference in this parameter is higher in ACB-4 (−3.74 °C), than in ACB-1 (−1.79 °C). On the other hand, although the inferred MTW values are also lower than today's (−0.44 in ACB-4 and -0.82 °C in ACB-1), the hottest month was July instead of August, as it is currently the case.

The estimated rainfall gives stronger differences with current average precipitation in Almenara than those obtained for temperatures. Thus, the obtained MAP values were higher for all the studied samples, the differences ranging from +78.77 mm in ACB-1 to +17.25 mm in ACB-4 (Table 2). Interestingly, the MPD (Mean precipitation of the driest month) values are lower in the studied sites than today's. In both sites, the lowest mean monthly precipitation is recorded in July. Concerning MPW (Mean precipitation of the wettest month), this parameter shows a clear rise between the Late Pliocene and the earliest Early Pleistocene. Thus, the value from ACB-4 is distinctly lower than from the value obtained for ACB-1 (56.57 and 79.06 mm, respectively). More importantly, whereas during the Late Pliocene MPW was below present values in Almenara (−13.57 mm), during the earliest Early Pleistocene this value was higher (+8.92 mm). During the Pliocene and the Pleistocene, the MPW had occurred in December, nowadays it is registered in October (Table 2).

The standard deviation (σ) is higher in the results obtained for ACB-4 and ACB-1, than those recorded today at Almenara. The variation of the values of MAT shows some degree of overlap for ACB-1, but not in ACB-4. The present values in Almenara varies between 17.29 and 16.78 °C (Fig. 4A). The maximum value for ACB-1, 16.97 °C, slightly overlaps with the lower value proposed for Almenara. Regarding MAP, the σ shows an overlap between ACB-4 and the current precipitation in the region. Thus, the lower range of MAP in ACB-4 totally overlaps with the values for Almenara in the period 1970–2000 (Fig. 4B).

Thus, according to the palaeoclimatic reconstruction, mean temperatures were only slightly lower when the older assemblage (ACB-4) was formed, with a difference of −0.97 °C between ACB-4 and ACB-1 (Table 2). At the same time, rainfall underwent a more complex change involving changes both in the average precipitation values (the difference of MAP between ACB-4 and ACB-1 is +65.34 mm), and in the distribution pattern of rainfall along the year (Table 2).

The estimated monthly precipitation values (MMP) and temperature (MMT) indicate that hot summers and mild winters occurred. Rainfall was abundant with an irregular distribution, occurring mainly during winter and spring. The aridity indexes suggest a semi-arid (or arid according to the Dantin-Revenga index), continental Mediterranean climate with four dry months in the summer (Table 3; Fig. 3C).

4.3. Palaeoenvironmental reconstruction

The application of the HWM to ACB-4 and ACB-1, indicates a landscape dominated by the presence of Open Dry (OD) and Woodland (WO) environments in both sites (Fig. 3D). Comparing the older with the younger assemblage, an apparent increase in the importance of OD environments is seen, with its corresponding reduction in tree cover. Whereas in ACB-4, woodland was somewhat better represented (31.25%) than open dry habitats (28.98%), this situation is reversed in ACB-1, with OD (32.63%) slightly higher than WO (30.96%) (Fig. 3D).

Considering the ecological preferences of certain taxa represented in the assemblages, a habitat of dry meadows under seasonal climate change has been linked to the presence of cf. *Discoglossus* sp., *Pelodytes* cf. *punctatus*, *Pelodytes* sp., and *Chalcides* cf. *bedriagai*. On the other hand, *Bufo bufo* s.l., *Ophisaurus* sp. s. l., and other taxa favour scrublands and

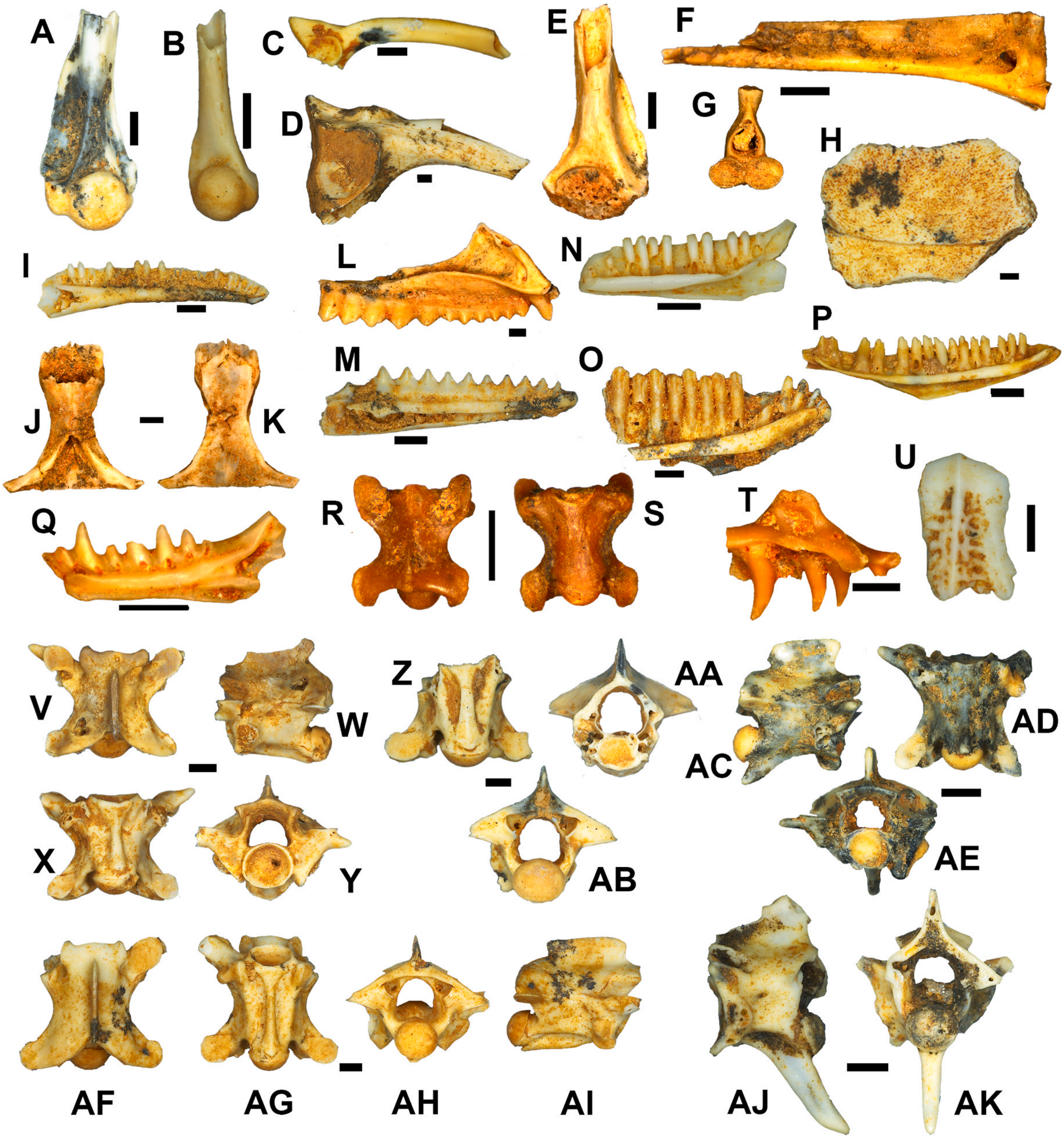

Fig. 2. Amphibians and reptiles from the latest EarltPliocene and earliest Pleistocene Almenara-Casablanca (ACB) 4 and 1 palaeontological sites (Almenara, Castellón, Spain). A, cf. *Discoglossus*, left humerus (ACB-1) in ventral view; B-C, *Pelodytes* cf. *punctatus*, right humerus (B, ACB-1) in ventral view and right ilium (C, ACB-1) in lateral view. D-E) *Bufo bufo* s.l., right ilium (D, ACB-1) in lateral view and right humerus (E, ACB-4) in ventral view. F-G, *Pelophylax* sp., urostyle (ACB-1) in lateral (F) and anterior (G) views. H, Testudines indet., fragment of an undetermined plate (ACB-4) in dorsal view. I-K) *Tarentola mauritanica*, left dentary (ACB-1) in lingual (I) view and frontal (ACB-4) in ventral (J) and dorsal (K) views. L-M, Agamidae indet., left maxilla (ACB-4) and left dentary (ACB-1) in lingual (L and M, respectively) view. N, *Chalcides* cf. *bedriagai*, right dentary (ACB-1) in lingual (N) view. O, *Timon* cf. *lepidus* s.l., left dentary (ACB-1) in labial (O) view. P, Lacertidae indet., left dentary (ACB-1) in lingual view. Q-S, *Blanus cinereus* s.l., right dentary (ACB-4) in lingual (Q) view, and dorsal vertebra (ACB-4) in dorsal (R) and ventral (S) views. T-U, *Ophisaurus* sp. s.l., left maxilla (ACB-4) in lingual (T) view and osteoderm (ACB-1) in dorsal (U) view. V-Y, *Coronella girondica*, dorsal vertebra (ACB-4) in dorsal (V), lateral (W), ventral (X), and anterior (Y) views. Z-AB, *Zamenis scalaris*, dorsal vertebra (ACB-4) in ventral (Z), anterior (AA), and posterior (AB) views. AC-AE, *Natrix maura*, precaudal vertebra (ACB-4) in lateral (AC), ventral (AD), and anterior (AE) views. AF-AI, *Malpolon monspessulanus*, dorsal vertebra in dorsal (AF), ventral (AG), lateral (AH) and posterior (AI) views. AJ-AK, *Vipera latastei*, precaudal vertebra (ACB-1) in lateral (AJ) and posterior (AK) views. Scale bar equal 1 mm, except for D, E, J, and K, which is 2 mm.

woodlands. Bare rock or rocky soil (Rocky habitat, R) is the preferred habitat of *Timon lepidus* s. l., *Coronella girondica*, and *Vipera latastei*. It seems to lose some relevance in the younger site (in ACB-1: 14.06%), whereas in ACB-4 shows a value of 17.05%; (Fig. 3D). Rocky areas are important since they provide the necessary fissures used by troglophilic species such as *Pelodytes* sp. (Montori and Martínez-Silvestre, 2015). The water-edge habitats (W) are linked to the presence of taxa such as Emydidae indet., and *Natrix maura*, indicating the presence of nearby water bodies in both cases (in ACB-4 13.64%, in ACB-1 17.36%) (Fig. 3D), which could be both permanent or seasonal as indicated by taxa such as *Bufo bufo* s.l., Emydidae indet., and *Natrix maura* for the first type and cf. *Discoglossus* sp., *Pelodytes* cf. *punctatus*, and *Pelodytes* sp. for the second. Water availability, probably favoured the development of Open Humid habitats (OH), which seem to have decreased slightly from

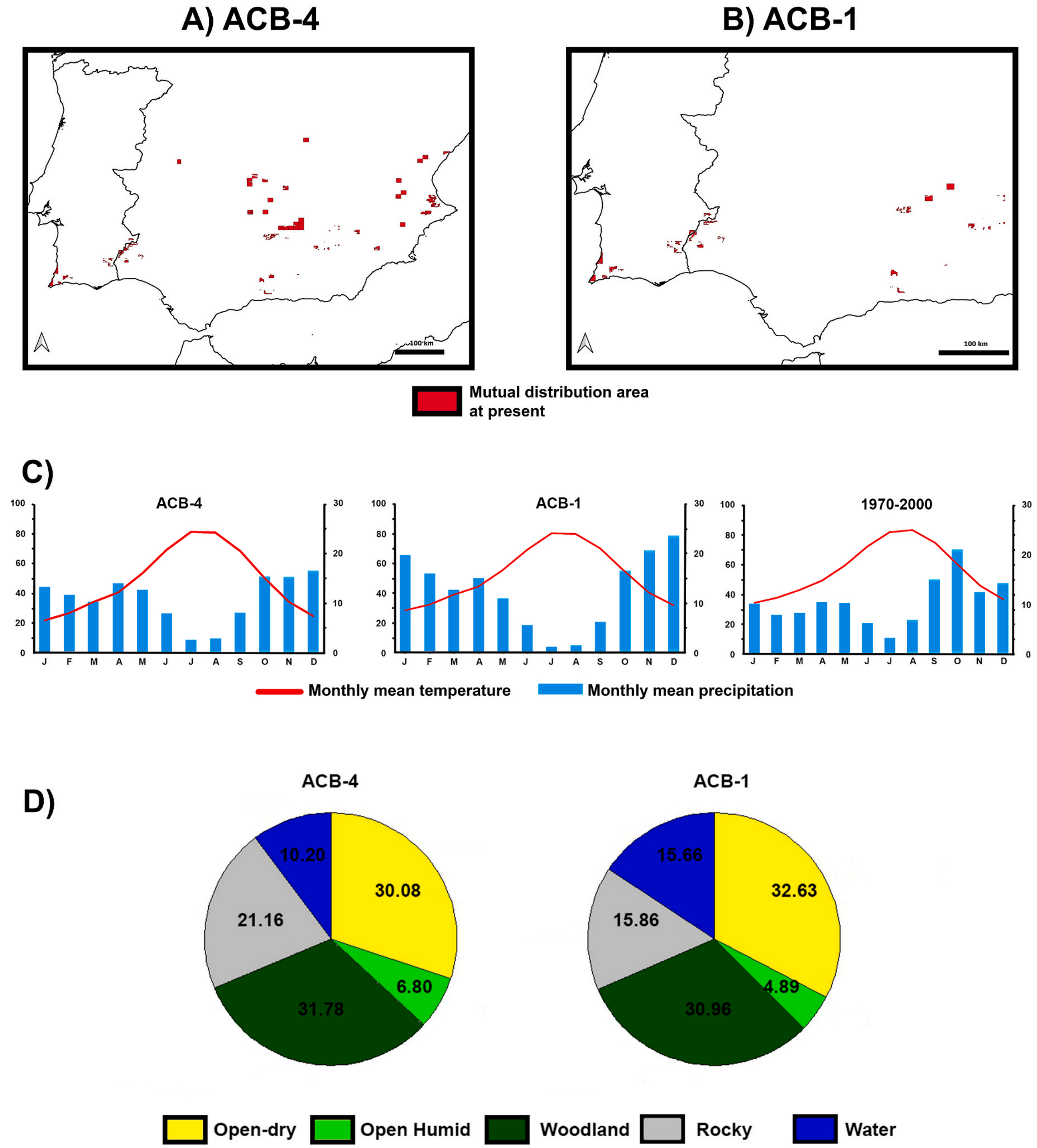

Fig. 3. A-B) Mutual distribution area for the whole amphibian and reptile assemblages determined in the latest Pliocene and earliest Pleistocene Almenara-Casablanca (ACB) 4 and 1 palaeontological sites (Almenara, Castellón, Spain). The distribution area is represented by 10 × 10 km UTM grids. Data extracted from Loureiro et al. (2008) and AHE (2021). C) Climatograms showing the quantitative climate reconstructions of ACB-4 and ACB-1, applying the scale P = 2 x T. Abbreviations: P = precipitation, T = temperature, MAT = mean annual temperature, and MAP = mean annual precipitation. D) Palaeoenvironmental reconstruction (%) based on fossil herpetofauna from the ACB-4 and ACB-1.

ACB-4 (9.09%) to ACB-1 (6.08%) (Fig. 3D).

4.4. Species diversity

Statistical analyses following the rarefaction and extrapolation with Hill numbers method allow testing sample completeness and compare biodiversity between assemblages (see Supplementary Data 2). The selected base sample size (m) is 49, being the maximum reference sample size of the analysed sites (ACB-1).

Comparing diversity among sites based on sample-size (Fig. SP2A), two groups in terms of species richness ($q = 0$) are observed. The first one is composed by ACB-4 site, being the richest of the three assemblages (26.19), and the second one is composed by ACB-1 and ACB-3 sites, both showing similar values (17.00 and 16.96, respectively). Despite the species richness differences observed between both groups, these are not statistically significant (95% confidence intervals overlap). According to Shannon and Simpsons indices ($q = 1$ and $q = 2$, respectively; Fig. SP2A), ACB-1 and ACB-3 sites are less diverse in terms of evenness than ACB-4. This is due to the fact that ACB-1 assemblage is dominated by *Tarentola mauritanica* and ACB-3 by *Blanus cinereus* s.l., in ACB-4 the species more equally distributed.

The results were compared with coverage-based rarefaction and extrapolation curves (Fig. SP2B), which confirm the order and significance of the biodiversity indices between the analysed assemblages

Table 2
Annual and monthly climatic values calculated for the studied sites and present-day Almenara region (1970–2000). MAT, mean annual temperature (°C); MAP, mean annual precipitation (mm); N, number of pixels used in the calculation; σ, standard deviation of obtained values; Δ, difference between the values obtained from the different fossil assemblages and current values in Almenara for the period 1970–2000). Data obtained from WorldClim 2.1 (Fick and Hijmans, 2017).

TEMPERATURE													
ACB-4	**MAT**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Mean	14.75	6.61	8.05	10.42	12.29	16.09	20.84	24.55	24.31	20.69	15.18	10.42	7.54
σ	1.13	1.93	1.72	1.45	1.27	0.96	1.01	1.37	1.19	1.02	1.38	1.8	1.98
Min	11.26	2.30	3.60	6.20	8.45	12.85	18.2	20.35	20.7	17.5	11.45	6.35	3.4
Max	17.06	12.27	12.81	13.98	14.95	18.4	23.4	27.33	26.9	23	18.15	15.22	13.48
N	4996	4996	4996	4996	4996	4996	4996	4996	4996	4996	4996	4996	4996
Δ	−2.29												
ACB-1	**MAT**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Mean	15.72	8.56	9.73	11.77	13.4	16.68	20.89	24.17	24.04	21.2	16.46	12.21	9.57
σ	1.25	2.65	2.31	1.86	1.5	0.91	1.14	1.9	1.65	1.07	1.7	2.41	2.74
Min	11.26	2.3	3.6	6.2	8.45	12.85	18.2	20.38	20.77	17.5	11.45	6.35	3.4
Max	17.06	12.27	12.81	13.97	14.95	17.76	22.63	26.58	26.14	22.52	18.15	15.22	13.48
N	1133	1133	1133	1133	1133	1133	1133	1133	1133	1133	1133	1133	1133
Δ	−1.32												
Almenara (1970–2000)	**MAT**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Mean	17.04	10.35	11.39	13.01	14.86	17.93	21.72	24.60	24.99	22.46	18.13	13.84	11.15
σ	0.26	0.30	0.31	0.29	0.31	0.25	0.19	0.14	0.16	0.24	0.30	0.34	0.30
Min	16.02	9.10	10.20	11.90	13.70	17.00	21.00	24.10	24.30	21.50	17.00	12.50	9.90
Max	17.24	10.60	11.60	13.20	15.10	18.10	21.90	24.70	25.10	22.60	18.40	14.10	11.40
N	43	43	43	43	43	43	43	43	43	43	43	43	43
PRECIPITATION													
ACB-4	**MAP**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Mean	438.74	45.49	39.24	34.34	46.6	42.32	26.25	8.58	9.52	26.78	51.58	51.45	56.57
σ	52.18	17	12.06	6.54	4.12	5.74	6.42	4.43	6.53	8.2	4.43	14.43	19.26
Min	360.91	22.4	21.53	24.94	38.66	23.03	11.29	1	3	17.61	44.68	31.33	29.55
Max	553.11	78.36	67.07	57.83	57.22	52.22	37.01	20.34	30.41	57.94	69.59	85.25	99.14
N	4996	4996	4996	4996	4996	4996	4996	4996	4996	4996	4996	4996	4996
Δ	+17.25												
ACB-1	**MAP**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Mean	500.26	65.89	53.47	42.34	50.11	36.82	18.92	4.15	4.77	20.6	55.29	68.82	79.06
σ	42.85	12.5	9.45	5.68	3.92	6.89	5.51	2.45	1.25	1.53	4.28	13.17	14.76
Min	425.33	43	41.06	34.16	42.35	23.03	11.29	1	3	17.61	48.67	49	52.33
Max	553.11	78.36	67.07	56.62	57.22	52.22	30.82	9.94	8	25.88	63.22	85.25	99.14
N	1133	1133	1133	1133	1133	1133	1133	1133	1133	1133	1133	1133	1133
Δ	+78.77												
Almenara (1970–2000)	**MAP**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Mean	421.49	33.84	26.19	27.86	34.93	34.40	21.02	10.79	22.70	50.35	70.14	41.56	47.72
σ	5.25	0.43	0.39	0.41	1.40	1.79	1.53	1.07	0.90	0.57	0.93	0.58	0.62
Min	412	32.00	26.00	27.00	33.00	33.00	19.00	9.00	21.00	49.00	66.00	40.00	45.00
Max	432	34.00	27.00	29.00	39.00	40.00	26.00	14.00	25.00	51.00	71.00	42.00	48.00
N	43	43	43	43	43	43	43	43	43	43	43	43	43

detected in the sample-size based curves (Fig. SP2A). Both curves were linked with the construction of a sample completeness curve (Fig. SP2C), which allows us to examine how the sample completeness varies with the sample size. When the sample size is standardized small differences in terms of sample coverage are observed between the analysed assemblages. ACB-4 shows lower value (0.677) than ACB-1 and ACB-3, both with similar sample coverage values (0.818 and 0.840, respectively). Despite this, these differences are not statistically significant given that 95% confidence intervals overlap, showing that all the assemblages have been equally sampled. There is therefore a correspondence between the conclusions regarding the values of biodiversity estimators drawn based on both curve types.

The similarity of the sample coverage values also ensures that the palaeoclimatic and palaeoenvironmental differences observed between the three analysed sites (ACB-4, ACB-1 and ACB-3) are not caused by differences of sample sizes.

5. Discussion

On the basis of the palaeoecological reconstruction obtained from ACB-4 and 1 sites, the following points are discussed: (i) a comparison with other proxies and previous palaeoclimatic and palaeoenvironmental recontructions from these sites; (ii) contextualization of our results in the Plio-Pleistocene climate variability; (iii) palaeoecological context at Iberian level during this chronology, and (iv) integration of our results into the palaeoenvironmental evolution in the region.

5.1. Comparison with other proxies from ACB-4 and ACB-1 sites

In previous research the MER method has been applied to the palaeoherpetofaunal assemblage from ACB-4 and ACB-1 at different geographical scales, i.e., provincial level (Blain, 2005, 2009) or within the limits of the Iberian Peninsula (Agustí et al., 2009). After the application of the UDA/ODA Discrimination Methodology and the MCR method to these assemblages, the obtained values are lower in both MAP and MAT (Supplementary Data 3). Moreover, the σ is slightly lower in all the cases in our results than those published by Agustí et al. (2009).

According to our reconstructions, based on the updated faunal composition of ACB-4 and ACB-1, the latest Pliocene was somewhat cooler and drier than the earliest Pleistocene. These results differ from other interpretations given for the Pliocene-Pleistocene transition in

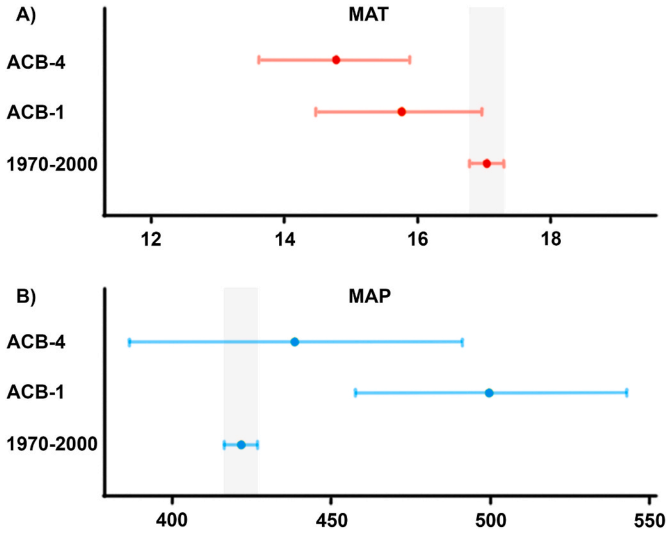

Fig. 4. Dispersion of the annual climatic values calculated for the studied sites and present-day Almenara region (1970–2000). A) MAT, Mean Annual Temperature (°C). B) MAP, Mean Annual Precipitation (mm). Central dot denotes mean value, and horizontal bars indicates the standard deviation of the values.

other European areas and with other proxies (i.e., isotopic record, small mammals, pollen) in which the Early Pleistocene was cooler and drier than the Late Pliocene (Hernández Fernández et al., 2007; Popescu et al., 2010; Domingo et al., 2013; Szabó et al., 2017). For instance, Ezquerro et al. (2022) reconstructed the climate evolution in the Teruel Basin from the Late Miocene to the Early Pleistocene (9.8–1.8 Ma) based on lacustrine calcite oxygen isotope composition (δ^{18}Oc). According to these authors, climate was characterised by being occasionally cooler in certain moments of the latest Pliocene (i. e., MIS G4, G2 and 104), and warmer periods in other moments of the earliest Pleistocene (as in MIS 95) (Ezquerro et al., 2022).

The landscape surrounding of Almenara-Casablanca during the Pliocene-Pleistocene transition was dominated by a mixture of forests/scrubs formations with open habitats, mainly meadows that undergo cyclic changes in response to seasonal variations in climatic and rainfall patterns. Moreover, the sum of OD and OH (36.87% and 37.53% in ACB-4 and ACB-1, respectively) slightly exceeds the forest habitat in the sites studied (31.78% in ACB-4 and 30.96% in ACB-1). In broad terms the obtained habitat values are similar between the two sites, but some considerations can be pointed out.

According to our analysis, in ACB-4, woodland and bushland were slightly more developed than open grasslands. Interpretations based on other faunal proxies such as rodents or chiropterans equally indicate a relevant representation of forests and scrublands, at the time (Agustí et al., 2011). Moreover, the habitat preferences of the extant representatives of the forest taxa found in ACB-4, suggest a greater variety of forest types. Small mammal taxa with OD requirements are present at this site, i.e., *Stephanomys* gr. *minor* (Agustí et al., 2011). The presence of wetland areas is supported by the presence of the lagomorph *Prolagus calpensis* and the talpid *Desmana inflata* (Furió, 2007; Agustí et al., 2011). *Blanus cinereus* s.l. and *Talpa* cf. *fossilis* indicate loose, moist soil.

In ACB-1, the dominant habitat changes, with OD slightly higher than WO (32.63% and 30.96%). Both the small and large mammal assemblages are composed by a mixture of taxa linked with open habitats (i.e., *Stephanomys progressus* or *Equus stenonis*) and tree and shrub formations, such as *Eliomys quercinus* and Sciurinae indet. (Gil and Sesé, 1984; Soto and Morales, 1985; Agustí et al., 2011). In this locality, the water-related habitats recorded the highest values of the all sites studied. This result is reinforced by the presence of other taxa linked to aquatic habitats, such as gastropods (i.e., *Galba truncata*) and bivalves (i. e., *Pisidium personatum*) (Bech et al., 1997), birds (i.e., *Geronticus eremita*) (Sánchez Marco, 1996), and mammals (i.e., *Prolagus capensis* and *Desmana inflata*) (Gil and Sesé, 1984; Furió, 2007).

The rainfall values obtained from the analyses of the ACB-4 and ACB-1 assemblages may appear to be in disagreement with the dominant type of habitats inferred for each of them (slightly major representation of open habitats in ACB-1). However, this could be related with a decrement of summer rainfall in ACB-1 respect to ACB-4. In the latter, the precipitation seems to be more uniform during the year; whereas in ACB-1 this parameter occurred mainly during the autumn/winter (Fig. 3C). In fact, although the difference between the obtained results in each locality are small, the seasonality of the annual rainfall is slightly higher in ACB-1 than the ACB-4, as is indicated by the Precipitation Concentration Index (PCI) (Table 3). This index reflects the seasonality of rainfall (Oliver, 1980). According to the latter author, a PCI value below 10 indicates uniformity in precipitation distribution throughout the year (i.e., the same amount of rainfall occurs each month). PCI values between 10 and 15 denote a moderate seasonal distribution of the rainfall, while values between 15 and 20 are associated with an irregular annual distribution of precipitation. When the index exceeds 20, the seasonal differences of the annual rainfall distribution are pronounced. Naturally, higher values indicate an increase of monthly concentration. Thus, the obtained PCI for ACB-4 (9.78) denotes that rainfall was relatively uniform during the year. However, ACB-1 recorded higher PCI than ACB-4 (11.08), indicating major seasonality in the latest Early Pleistocene than in the earliest Late Pliocene in the region of Almenara.

In modern Mediterranean ecosystems, the precipitation that takes place during the early spring months is the major driver of annual primary production (Allard et al., 2008; Bartsch et al., 2020). The importance of spring rainfall in a Mediterranean climate has not only to do with triggering plant growth and moistening the soil before the extremely dry and hot summer months but is of major importance for the recharge of aquifers thanks to the low evaporation rates in early spring. Although the summer rain combined with warm temperatures are

Table 3
Climatic interpretation of the climatograms obtained for ACB-4 and ACB-1, and the present-day Almenara region (1970–2000). Abbreviations: MAT = mean annual temperature, MAP = mean annual precipitation, PCI= Precipitation Concentration Index.

	ACB-4		ACB-1		1970–2000	
MAT	14.75	Temperate	15.72	Warm	17.04	Warm
Atmospheric temperature range	12.37	Medium	11.64	Low	9.94	Low
Summer temperature	24.55	Warm	24.17	Warm	24.99	Warm
Winter temperature	6.61	Temperate	8.56	Temperate	10.35	Mild
MAP	438.74	Low	500.26	Low	421.49	Low
Rainfall distribution	Irregular	Mediterranean	Irregular	Mediterranean	Irregular	Mediterranean
Type of precipitation	Rain		Rain		Rain	
Gaussen Index	4	Mediterranean	4	Mediterranean	4	Mediterranean
Lautensach-Meyer Index	4	semi-arid	4	semi-arid	5	semi-arid
Dantin-Revenga Index	3.36	Arid	3.14	Arid	4.04	Arid
De Martonne Index	17.73	semi-arid	19.45	semi-arid	15.59	semi-arid
PCI	9.78		11.08		9.87	

important favouring the development of some types of scrub and forest formations in Western Europe (Bartsch et al., 2020), it is also known that there seems to be a positive correlation between annual rainfall and the development of Mediterranean grassland (Jongen et al., 2011). Thus, the degree of seasonality in precipitation is determinant in the type of floral formation in Mediterranean regions. Although the differences between the woodland and open habitats are minimal, our results indicate stronger seasonality in precipitation values for ACB-1. This could partially explain the shift towards a higher presence of open-dry habitats compared to ACB-4.

5.2. Pliocene-Pleistocene climatic variability

The latest Pliocene reflects a progressive climatic deterioration and a gradual expansion of the Northern Hemisphere ice sheets, but the first pronounced glacial cycle is not recognized until the Pliocene-Pleistocene transition, about 2.7 Ma (Abrantes et al., 2012; De Schepper et al., 2014). This climatic change took place in pulses, giving place to the alternation of steppes during cold and dry events and more forested habitats during warm and humid periods (de Beaulieu et al., 2005).

The rich record of the Teruel Basin has provided interesting insights into the climate of the Late Pliocene at regional level (Ezquerro et al., 2022). A trend toward a more humid and cooler climate has been observed during the Late Pliocene with, however, some events related with the climatic variability recorded at this chronology. Between 2.7 and 2.6 Ma, three wet and cool peaks occurred, the MIS G4 (∼2.69 Ma), G2 (∼2.64 Ma), and 104 (∼2.60 Ma), with other three warm and dry minor events, MIS G5 (∼2.70 Ma), G3 (∼2.67 Ma), and G1 (∼2.63 Ma) (Shackleton et al., 1995; Hennissen et al., 2014). Our results thus seem to suggest that ACB-4 was formed during a temperate moment.

Thereafter, for the period encompassing from 2.6 to 2.4 Ma, at least four warm and dry phases are recorded: MIS 101, 99, 97, and 95, which took place at ∼2.54, ∼2.49, ∼2.45, and ∼2.41 ka, respectively (Friedrich et al., 2013; Donders et al., 2018). The climate reconstruction of ACB-1 may represent one of these warm peaks.

As mentioned above, several works (Hernández Fernández et al., 2007; Popescu et al., 2010; Domingo et al., 2013; Szabó et al., 2017) pointed out an inverse scenario (Early Pleistocene was cooler and drier than the Late Pliocene) than our results. These differences are related to the current mutual distribution area obtained in each case, which is clearly biased for the used species. In the case of the assemblage from ACB-1 site, we have used the only current autochtonous species of discoglossid in the Iberian Peninsula (Speybroeck et al., 2016), *Discoglossus galganoi*, for cf. *Discoglossus* sp. *D. galganoi* inhabits mainly Western Iberian Peninsula, with few localities in the Eastern region (Martínez-Solano, 2014). Thus, this distribution area is geographically limited to the southern and western Iberia. Regarding to ACB-4, the assemblage draws a wide distribution of the common area, formed by three great areas located at southern Portugal and centre and east of Spain. Nowadays, 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. The concentration of the mutual area of the ACB-1 assemblage in Western Iberia provides high values linked to the precipitation than those obtained with the taxa described in ACB-4. The explanation for the results related to temperature is more complex, but it must be related to the inclusion of MAT values in the climate database that are lower and come from the central and eastern regions of the peninsula, compared to those obtained in the southwestern quadrant of Iberia.

5.3. Comparison with other Iberian sites

The scarcity of sites of similar chronology to ACB-4 in the Iberian Peninsula makes the task of comparing results difficult. Huélago 4 site (Guadix-Baza Basin; Granada, southern Spain) is slightly younger than ACB-4, but in a setting quite different to that of ACB-4. In this sense, Huélago 4 site is located in an inner mainland basin in southernmost Spain much further away from the sea than Almenara. As a result, this locality experiences higher temperatures due to its more southerly location and increased continentality resulting from the absence of a moderating effect from proximity to the sea. Moreover, a trend towards decreasing annual rainfall from west to east, as currently observed in the Iberian Peninsula (Ninyerola et al., 2005), is expected. Besides the larger fauna, only the small mammals from this locality have been described. According to the assemblage, the surrounding area of the site consisted of a mixed landscape with open habitats (indicated by the presence of *Stephanomys* cf. *balcellsi* and *Castillomys crusafonti*), scrubland/woodland (inferred from cf. *Oryctolagus* sp. and *Apodemus* sp.) and some water bodies (indicated by *Prolagus* sp.). The slightly older site of Tollo de Chiclana 13, also in the Guadix-Baza Basin, is considered as having been formed under warm and humid conditions due to its insectivore assemblage, particularly considering the presence of *Asoriculus gibberodon* (Minwer-Barakat et al., 2010). According to Reumer (1984) this fossil species had a mainly aquatic life style or at least a clear preference for humid habitats based on an actualistic interpretation of its paleoecology. As in Huélago 4, during the Late Pliocene the area around Tollo de Chiclana 13 consisted of a mosaic of open habitats with some interspersed tree and shrub patches (Minwer-Barakat et al., 2012).

The Iberian earliest Early Pleistocene is also poor in sites with small vertebrate record to compare with ACB-1 (see López-García et al., 2024). Nevertheless, some comparisons can be made based on the small mammal record of ACB-1. As previously mentioned, during the MN17 the small mammal assemblages are typically dominated by arvicoline rodents in a context of low diversity of insectivores and rodents. This dominance of arvicolines evidences the predominance of open herbaceous biotopes, seldom accompanied by taxa related to woody vegetation. This is the type of landscape inferred for Tollo de Chiclana 10 and 10B (Minwer-Barakat et al., 2005) and for El Rincón-1 (Júcar Basin; Motilleja, Albacete, south-central Spain) (Montuire, 1999). In the latter site the author applied the cenogram method (Valverde, 1968; Legendre, 1986) as an alternative for the environmental reconstruction which is based on the ranking of mammal species in a community (excluding carnivores and bats) in relation to their weight and size. The slope and the continuity/discontinuity of the graph obtained representing the body mass of the taxa present in a community is related to the type of environment (open or closed) and climatic conditions (dry or wet), and can be used in well represented fossil mammal assemblages. However, an assemblage dominated by forest taxa with a similar age as ACB-1 has been described coming from the Pedrera del Corral d'en Bruach (Garraf Massif, Castelldefels, Barcelona, northeastern Spain) in which two rodent taxa (*Apodemus atavus* and *Apodemus jeanteti*) account for 73.70% of the NISP and 50.91% of the NMI of the material (López-García et al., 2024).

Therefore, in basis of the small-vertebrate assemblages, the landscape during the Iberian latest Late Pliocene was dominated by open forest formations, independently of the location of the site (i.e., inner basin vs coastal area). But during the earliest Early Pleistocene, an apparent ecological zonation probably existed. Thus, in the coastal areas (i.e., ACB-1 and Pedrera del Corral d'en Bruach), the woodland habitat was apparently dominant or at least had a high value. At the contrary, open habitats seem to have been more developped in inner mainland. Such a difference could be related with the climate-moderating effect of the sea. Several authors pointed out that the proximity or distance to the sea is a key factor that explain the local climate of a region (Grosrey, 1974; Hernández et al., 1977; Vidal-Abarca et al., 1987; Stonevicius et al., 2018). Moreover, Mediterranean-type ecosystems are considered as highly resilient, understood as its capacity to absorb disturbance and reorganize (Folke et al., 2014). This property has been put in relation with their evolutionary history and, probably, their high ecological diversity (Lavorel, 1999). Albeit southern Europe saw a general decline in forests and a rise in herbaceous and steppe environments during the

Pliocene-Pleistocene, vegetation patterns varied significantly from a region to another, due to geographical and climatic factors. Floral extinctions are known to have occurred at different periods across the European regions, reflecting complex vegetation dynamics (Magri et al., 2017). Although in the case of the Iberian Peninsula the available information is limited (Carrión et al., 2022), flora was apparently not affected during the Pliocene-Pleistocene transition. However, it is only later, during the Early Pleistocene, that *Brumelia*, *Cupressus*, and, probably, *Zelkova* disappeared from the Iberian Peninsula (Postigo-Mijarra et al., 2010).

Regarding to animals, the Pliocene-Pleistocene transition did not had an apparent great impact on the Iberian assemblages. At around 2.6 Ma, Erycinae (even if this taxon was present in Central Europe during the Early Pleistocene; Böhme, 2020), and Scolecophidia disappeared from Western Europe, whereas some temperate taxa, as Agamidae, Gekkota, Scincidae, and Blanidae, underwent a southward withdrawal (Bailon, 1991; Bailon and Blain, 2007). At Iberian context, these groups were restricted to coastal areas in eastern Spain (Blain et al., 2016a), which could be an indicative of the probable above mentioned ecological zonation. Between the two sites (ACB-4 and ACB-1), no significant changes have been detected in the herpetofaunal associations studied. Likewise, small mammal faunas were not significantly affected during the Pliocene-Pleistocene transition (Agustí et al., 2001). At the contrary, this boundary seems to have influenced large mammal communities, as evidenced by the dispersion of the first representatives of *Equus* in the region—a phenomenon referred to as the *Equus*-Event—which has been linked to the expansion of open environments (Iannucci and Sardella, 2023).

5.4. Comparison with Almenara-Casablanca 3 (late Early Pleistocene)

Finally, even if out of the chronological range of this paper, the comparison with the late Early Pleistocene site of Almenara-Casablanca 3 (ACB-3) is of interest. ACB-3 is the youngest locality (Early Pleistocene) in the Almenara-Casablanca karstic complex (see Supplementary Data 1). Similar revision of its palaeoherpetofaunal assemblage (Table SP1) and the application of the same protocol than for ACB-1 and ACB-4 have been done (Table SP2; Figure SP1A). When compared, the value of MAT for ACB-3 (15.76 °C) is strongly similar to those obtained in ACB-1 (15.72 °C). On its behalf, MAP is slightly lower than in ACB-1 (491.64 mm and 500.26 mm, respectively). Moreover, the IPC indicates also a similar seasonality of the rainfall (11.08 for ACB-1 and 11.03 for ACB-3) (Table SP3).

The palaeoenvironmental reconstruction records a slight dominance of the open habitats over (48.80%, which is the result of the sum of Open Dry and Open Humid habitats) the WO (30.65%) ones (Figure SP1C in Supplementary Data 1). Thus, the highest values for OD and OH environments of the all studied sites are recorded in ACB-3, coinciding with the lowest extension for forest and scrubland. Therefore, it seems that during the latest Early Pleistocene, the evolution towards the settlement of a landscape dominated by increasingly opened forests continued.

6. Conclusions

Our study sheds light on the ecological changes that took place during the Pliocene-Pleistocene transition on the eastern coast of the Iberian Peninsula, inferred from the results obtained using palaeoclimatic and palaeoecological proxies based on the herpetofaunal assemblages from ACB-4 (MN16, Late Pliocene) and ACB-1 (MN 17, earliest Pleistocene). The review of the material has enabled to add two taxa (Testudines indet. and *Tarentola mauritanica*) to the previous faunal lists for ACB-4 site, contributing to a more precise palaeoenvironmental reconstruction.

According to habitat preferences and distribution patterns of the extant or closely related taxa recorded in the studied assemblages, the landscape was composed by forest and/or scrubland with interspersed open areas around Almenara-Casablanca during the late Pliocene at the time the infilling of the karstic fissure ACB-4 took place. This landscape had changed into a predominantly open landscape by the time the ACB-1 filling was formed, in the earliest Pleistocene. The change between both habitat types is probably evidencing the reinforcement of the modern Mediterranean climate in the region, in which summer is a dry season which records the lowest annual rainfall of the year.

The palaeoclimatic reconstruction gives a relatively stable pattern, but cooler (−2.29 °C to −1.32 °C) and more humid (+17.25 mm to +78.77 mm) than the current climate in the area. According to our results, the transition between the Pliocene and Pleistocene in the region involved a rise in mean annual temperatures accompanied by an increase in precipitation which acquired a more seasonal character, undoubtedly influencing the changes detected in vegetation and habitat types.

When the late Early Pleistocene site ACB-3 is considered, the interpretation that open habitats gained importance compared to forests and rainfall acquired a more seasonal pattern is confirmed. This reduction in tree cover is supported by the presence in ACB-4 and ACB-1 of taxa clearly related with forest habitats, as *Ophisaurus* sp. s. l., which has not been evidenced in ACB-3.

CRediT authorship contribution statement

Rafael Marquina-Blasco: Conceptualization, Methodology, Formal analysis, Writing – original draft. **Christian Sánchez-Bandera:** Methodology, Formal analysis, Writing – review & editing. **Juan Manuel López-García:** Writing – original draft. **Alberto Martínez-Ortí:** Writing – review & editing. **Paloma Sevilla:** Writing – review & editing. **Francisco Javier Ruiz-Sánchez:** Supervision, Writing – review & editing. **Hugues-Alexandre Blain:** Conceptualization, Supervision, Writing – original draft.

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.quascirev.2024.109154.

Data availability

Data will be made available on request.

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