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Last Neanderthals and first Anatomically Modern Humans in the NW Iberian Peninsula: Climatic and environmental conditions inferred from the Cova Eirós small-vertebrate assemblage during MIS 3

Iván Rey-Rodríguez [a, b, *], Juan-Manuel López-García [a, b], Maria Bennàsar [a, b], Sandra Bañuls-Cardona [c], Hugues-Alexandre Blain [a, b], Ángel Blanco-Lapaz [d], Xosé-Pedro Rodríguez-Álvarez [a, b], Arturo de Lombera-Hermida [a, b, e], Mikel Díaz-Rodríguez [e], Alicia Ameijenda-Iglesias [e], Jordi Agustí [a, b, f], Ramón Fábregas-Valcarce [e]

[a] IPHES, Institut Català de Paleoecologia Humana i Evolució Social, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain
[b] Area de Prehistòria, Universitat Rovira i Virgili, Fac. de Lletres, Avinguda Catalunya 35, 43002 Tarragona, Spain
[c] Sezione di Scienze Preistoriche e Antropologiche, Dipartimento di Studi Umanistici, Università degli Studi di Ferrara, C.so Ercole I d'Este, 32, 44121 Ferrara, Italy
[d] Institut für Naturwissenschaftliche Archäologie, Universität Tübingen, Rümelinstr. 23, 72070 Tübingen, Germany
[e] Grupo de Estudos para a Prehistoria do Noroeste Ibérico. Arqueoloxía, Antigüidade e Territorio (GEPN-AAT), Dpto de Historia, Universidade de Santiago de Compostela, Praza da Universidade, nº 1, 15782 Santiago de Compostela, Spain
[f] ICREA Research Professor, Spain

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ABSTRACT

Cova Eirós is emerging as a reference site in the northwestern Iberian Peninsula for the study of the development of the last Neanderthal populations and the first populations of Anatomically Modern Humans (AMH) in MIS 3. Cova Eirós is an archaeological site (with Middle and Upper Palaeolithic levels) located in Cancelo, Triacastela (Lugo, northwestern Iberian Peninsula), which has been systematically excavated from 2008 onwards. The small-vertebrate assemblage analysed came from the archaeo-palaeontological field seasons that took place from 2009 to 2014.

At least 18 small-vertebrate taxa have been identified: 1 frog (*Rana temporaria*), 1 snake (*Vipera* sp.), 4 insectivores (*Sorex minutus*, *Sorex* sp., *Talpa* cf. *occidentalis* and *Erinaceus europaeus*), 4 chiropters (*Myotis myotis/blythii*, cf. *Miniopterus* sp., *Myotis* sp. and *Rhinolophus ferrumequinum*) and 8 rodents (*Apodemus sylvaticus*, *Arvicola amphibius*, *Arvicola sapidus*, *Chionomys nivalis*, *Microtus (Terricola) lusitanicus*, *Microtus agrestis*, *Microtus arvalis* and *Microtus oeconomus*).

Using the *Habitat Weighting* method to reconstruct the palaeoenvironment, we reconstruct a landscape for MIS 3 characterized by open woodland formations.

The *Mutual Ecogeographic Range* (MER) method and the *Bioclimatic Model* (BM) used for the palaeoclimatic reconstruction show lower temperatures and higher precipitation than at present in the region.

Our results from Cova Eirós are compared with the data obtained from several other sites in the Iberian Peninsula; it can be said that Neanderthals and AMH were well adapted to the territory that they occupied, as well as to the surrounding environment and the climatic conditions prevalent in the unstable context of MIS 3 in the Iberian Peninsula.

1. Introduction

The history of the climate in the Late Pleistocene is characterized by highly unstable climatic conditions, with alternating cold and warm periods (Sánchez-Goñi and D'Errico, 2005). In the present

* Corresponding author. IPHES, Institut Català de Paleoecologia Humana i Evolució Social, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain.
E-mail address: ivanreyrguez@gmail.com (I. Rey-Rodríguez).

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paper we focus on Marine Isotope Stage (MIS) 3 (ca. 60–30 ka BP), which is characterized by major rapid climatic changes showing high variability, associated with abrupt atmospheric shifts over Greenland (Dansgaard-Oeschger [D-O] events) and episodes of massive iceberg discharge into the North Atlantic. The pollen record from MIS 3 shows a dynamic whereby forest development and semi-desert expansions alternate, linked with the warming and cooling phases of the sea surface, respectively (Fletcher and Sánchez-Goñi, 2008; Fletcher et al., 2010).

Neanderthals and Anatomically Modern Humans (AMH) developed their activities in a context of continuous climatic fluctuations during MIS 3, when the Neanderthals went extinct. There are multiple hypothesis about Neanderthal extinction and is a debate still unresolved; with our data from Cova Eirós we aim at contributing to the discussion about the Neanderthal demise.

In the Iberian Peninsula, the record of Neanderthal human remains and the number of findings have increased over the last few years (Lorenzo et al., 2012). The southern Iberian Peninsula has been considered the last refuge for Neanderthal populations, exemplified by Gorham's Cave (Gibraltar) with an approximate dating of 28 ka BP. These data suggest that Neanderthals held out in those places after the arrival of AMH (Finlayson et al., 2006).

There are a few well-dated sequences in the Iberian Peninsula where Middle and Upper Palaeolithic occupations have been recorded and small-vertebrate studies have been carried out: Cueva del Mirón (Cuenca-Bescós et al., 2009), Cueva del Conde (López-García et al., 2011b), Cova de L'Arbreda (López-García et al., 2015) and Teixoneres Cave (López-García et al., 2012, Talamo et al., 2016). In these sites, Middle to relatively early Upper Palaeolithic assemblages have been reported. We also use the small-mammal study of Gorham's cave (López-García et al., 2011c) with the objective of comparing the environment of this relict Neanderthal population with that of other Middle and Upper Palaeolithic sites (Fig. 1a).

Since the first half of the 1970s several studies of the microvertebrates of the Late Pleistocene of the Iberian Peninsula have been undertaken (compilation in López-García, 2008). In the northwestern Iberian Peninsula, however, we only have the small-vertebrate analyses of Valdavara-1 (López-García, 2008; López-García et al., 2011a) and A Valiña (Fernández-Rodríguez, 1993).

The main objective of this paper is to characterize the palaeoenvironmental and palaeoclimatic conditions that prevailed at the time of the last Neanderthal and the first Anatomically Modern Human populations in the northwestern Iberian Peninsula, and also to integrate our data from Cova Eirós with those from the other Iberian sites. Also, we shall discuss with these new results the multiple factors playing a role in the Neanderthal extinction.

2. Cova Eirós

Cova Eirós is located in Triacastela (Lugo), northwestern Iberia

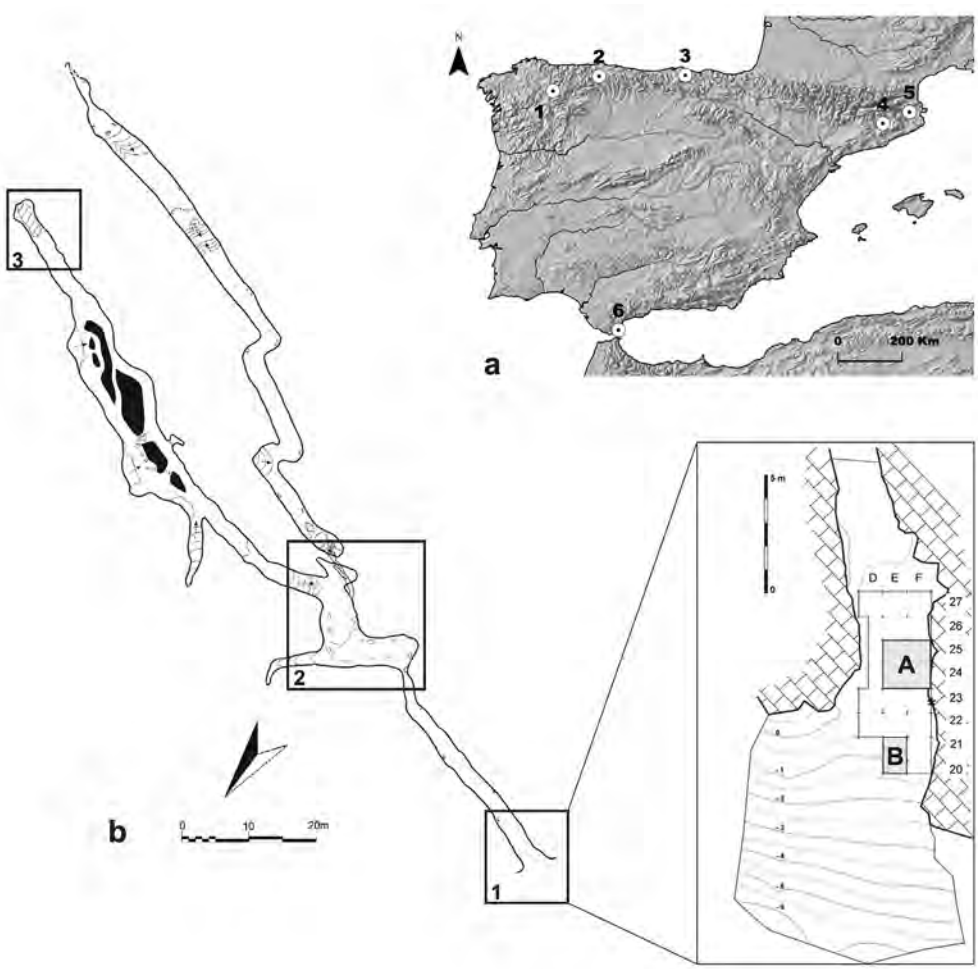

Fig. 1. a) Location of the Middle and Upper Palaeolithic sites mentioned in the text: 1- Cova Eirós, 2- Cueva del Conde, 3- Cueva del Mirón, 4- Teixoneres Cave, 5- Cova de l'Arbreda, 6- Gorham's Cave. b) General plan of Cova Eirós: 1- Location of the current archaeological diggings and the initial test Pit A (A) and test Pit B (B); 2- Location of the Main hall; 3- Location of the paleontological excavations.

(42°46′3″N and 7°12′13″W), at 780 m a.s.l. and at a distance of 25 m from the current bed of the Bezcos stream (Rodríguez-Álvarez et al., 2011). The cave opens onto the NNW-facing slope of Monte Penedo, characterized by Early Cambrian limestones (Calizas de Cándana). The cave has a length of 104 m (Fig. 1b).

The archaeological site to which our sample belongs is at the entrance to the cave, which is 3.5 m wide and 2 m high (Fig. 1b.1). The entrance becomes narrower after the first seven metres, giving way to a small corridor of about 15 m in length. This gives access the largest room in the cave (the "Main Hall" or "Mammoth Hall" indicated in Fig. 1b.2), with a length of 15 m, a maximum width of 6 m and a maximum height of about 5 m, where rock art has been discovered. The cave opens to the NNW and develops into three overlapping levels (de Lombera-Hermida et al., 2014; Rodríguez-Álvarez et al., 2011).

In the 1980s several palaeontological excavations were carried out at the bottom of the cave (indicated in Fig. 1b.3). These yielded around 4000 *Ursus spelaeus* remains, corresponding to a minimum number of individuals (MNI) of 43 (Grandal-D'Anglade, 1993). In 1993 an archaeological intervention was undertaken at the entrance to the cave, and another palaeontological excavation took place at the end of the cave in 1994 (Fábregas-Valcarce et al., 2009; Rodríguez-Álvarez et al., 2011). However, it was not until 2008 that systematic excavations were started. During the 2008 intervention two pits were dug. The first, "Pit A" (2 × 2 m indicated in Fig. 1b.1), was dug about 2 m from the entrance to the cave, incorporating the 1993 pit. The second, "Pit B" (1 × 1.5 m see Fig. 1b.1), was done in the talus outside the cave, with the objective of recording the extension of the human occupations, the stratigraphic sequence and also a possible correlation with the levels of "Pit A".

As a result of the amount of material that was found in the next few seasons, the surface of the excavation area was amplified to reach the current 21 m^2, connecting the two initial pits. To find out the nature and depth of the cave infill we used a ground penetration radar (GPR), which yielded a result of 3.5 m depth along the whole sequence of the entrance (de Lombera-Hermida et al., 2014; Rodríguez-Álvarez et al., 2011).

Up to now we have identified seven main archaeological levels (Fig. 2). From bottom to top these are as follows (Rodríguez-Álvarez et al., 2011):

-Level 4: light brown carbonated clays and fine yellow sands with small limestone and schist gravels, with sub-angular calcareous clasts of small size. The thickness of this level is unknown because it is currently under excavation. The archaeological record of the level is composed of 3261 objects. The lithic assemblage has been ascribed to Mode 3, Mousterian.

-Level 3: the brown clays appear less carbonated and there are small limestone gravels and sand packs with greater compactness and homogeneity than level 2's. The thickness of this level is 20–35 cm. Level 3 has been dated by AMS ^{14}C to 35,100 ± 700 radiocarbon years BP (OxA-30471), from 41,299 to 38,390 cal BP (95.4% probability). The archaeological record for level 3 consists of 2998 elements. The contact with level 2 is sharp and undulating, indicating the existence of an erosive hiatus between the two levels.

The characteristics of the lithic assemblage of level 3 suggest its attribution to Mode 3 (Middle Palaeolithic), defined by the presence of predetermined reduction methods and differential

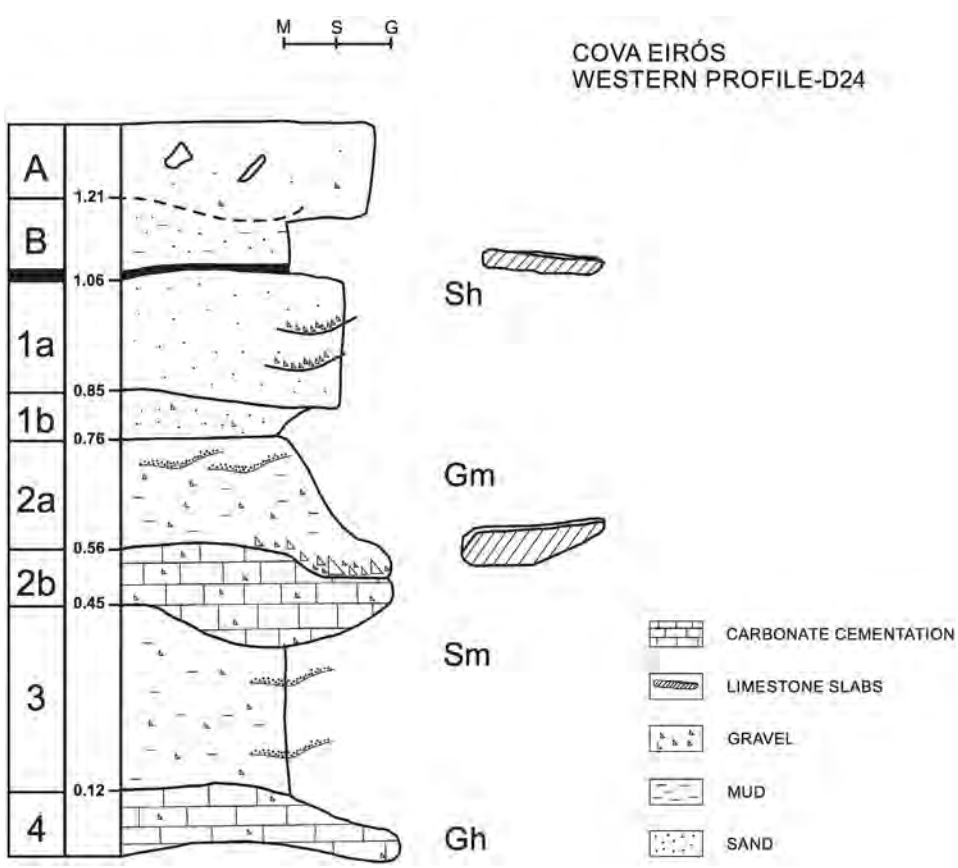

Fig. 2. The stratigraphic sequence of Cova Eirós, Western profile. M) Mud; S) Sand; G) Gravel; Sh) Sand, very fine to very coarse, may be pebbly; Gm) Massive or crudely-bedded gravel; Sm) sand massive; Gh) clast-supported fine gravels. (Miall, 1978).

management of the lithic resources, combining imported resources (fine-grained quartzite) with production on local quartz and quartzite (Fig. 3). A use-wear analysis of this lithic assemblage has identified hunting-related activities (broken spear tips), butchering and hide treatment at the site (Lazúen-Fernández et al., 2011).

The faunal assemblage shows a high fragmentation index, which hinders the taxonomic identification of some remains. Carnivores dominate the faunal representation because of the high representation of *Ursus spelaeus* remains along with *Canis lupus*. As regards ungulates, small and medium-sized taxa are predominant with a highly significant presence of *Cervus elaphus* in the record. The latter is followed at a distance by Rhinocerotidae and *Rupicapra rupicapra* (with only one element identified). Some of the bones show clear-cut marks and fractures, pointing to the anthropic factor as the main agent in butchering-related activities, skinning and bone marrow retrieval, also indicated by the functional studies. We have identified ichthyofaunal remains too, specifically *Salmo trutta*.

Although the excavations are still underway, the archaeological record of level 3 points to short-term, sporadic Neanderthal occupations of the cave. The scarce representation of knapping events, the presence of fragmented "*chaînes operatoires*", curated tools and the relatively high incidence of carnivores in the faunal record point to a logistic settlement model (Rosell et al., 2010; Baena et al., 2012). Human groups would have inhabited the cave as they moved across the territory, maybe in the context of hunting activities (Lazúen-Fernández et al., 2011).

-Level 2: Orange clay-loam layer with greater compactness than the overlying level 1. The uppermost section (2a) is composed of purer sands without concretions, and its lower limit is marked by small limestone slabs. At the bottom of level 2 (2b), there are several sub-angular limestone clasts (3–5 cm), heavily carbonated to the point of forming a crust, and more compacted in the southern part. The thickness of level 2 is between 34 cm and 45 cm. It has been dated by AMS ^{14}C to 31,690 ± 240 radiocarbon years BP (Beta-254280), from 36,136 to 35,032 cal BP (95.4% probability). Level 2 has yielded 1789 archaeological remains.

As regards lithic industry, bladelet production has been identified and some retouched tools have been recovered in level 2. Particularly noticeable is the presence of backed bladelets, truncated tools, denticulates, sidescrapers and burins (Fig. 3). On the basis of its technological features and the radiocarbon date available, this level can be ascribed to the early Upper Palaeolithic (Aurignacian).

The faunal record is dominated by *Ursus spelaeus* (along with cubs), *U. arctos* and other carnivoran taxa (i.e. *Canis lupus, Panthera pardus* and, in a minor degree, *Vulpes Vulpes*). Herbivores are represented by *Capreolus capreolus*, *Cervus elaphus* and *Rupicapra rupicapra*, along with a few rhinocerotid and lagomorph remains, among others. Ichthyofaunal remains (*Salmo trutta*) have been recovered in this level too. The assemblage is defined by its high fragmentation, pointing to the anthropic agent as responsible for the accumulation. Percussion and cut marks were identified on the surfaces of the bones, as well as carnivore marks.

The low density of the lithic assemblage, the expedient lithic reduction strategies (i.e. bipolar-on-anvil knapping), and fragmented reduction sequences (specially on flint and rock crystal elements) point to short-term, sporadic and reiterated human occupations of the cave. The human occupations alternate with those of bears and other carnivores, which use the cave as a den. This kind of opportunistic occupation of caves and high mobility patterns of early Upper Palaeolithic groups is also well attested in other, Cantabrian contexts (Ríos-Garaizar, 2011; Fernández-Rodríguez, 2010).

-Level 1: slightly compact fine yellowish sand with laminar subhorizontal stratification in its upper part and isotropic planar gravels. The upper part of level 1 (1A) is sterile from the archaeological point of view. In the lower part of the level (1B) the sands become orange, more compacted and display a parallel horizontal stratification. The archaeological remains are related to this lower layer. The thickness of level 1 is between 10 cm and 23 cm. The top of level 1 has been dated by OSL to 17,020 ± 1321 BP (MAD-5603BIN). The level disappears in the southern part of line 21–22 between level B and level 2 (Fig. 1b.1).

-Level B: whitish-yellow silty matrix, well compacted, containing angular limestone gravels and sealed by limestone slabs. At the bottom of this level, sealed by limestone slabs and blocks, a thin dark layer is defined (archaeological level B). The thickness of this level is between 12 cm and 37 cm. The remains of this layer were located in a small area of the excavated surface; 612 archaeological items were recovered. Level B has been dated by AMS ^{14}C to 12,040 ± 50 radiocarbon years BP (Beta-308859), 14,045 to 13,755 cal BP (95.4% probability).

-Level C: a heavily compacted clay matrix with gravels and clasts. This level is only identified in the southern part of Pit B. It displays a steep south-facing slope. On the basis of the taphonomic and archaeological features of the record, it has been interpreted as a mixture of levels B, 1, 2, 3 and 4.

-Surface level (level A): Topsoil, very loose and heavily bioturbated organic soil. The thickness is between 10 cm and 45 cm in section.

3. Material and methods

The small-vertebrate fossil remains used in this study are from the archaeo-palaeontological excavation campaigns carried out between 2009 and 2014 in Cova Eirós. In this paper we use all the elements recovered from level 3 and level 2. Analysis of Levels 4 and 1 is still on progress, and we do not yet have a sufficient sample for palaeoenvironmental and palaeoclimatic reconstructions, although the aim is to extend the sample for future reconstructions. The sample comprises disarticulated bones and also isolated teeth that were collected by water screening using superimposed 5 and 0.5-mm mesh screens. In subsequent years, the sediment was sorted and classified at the Institut de Paleoecologia Humana i Evolució Social (IPHES, Tarragona, Spain) and at the Universidade de Santiago de Compostela (USC, A Coruña, Spain).

The sample of small vertebrates has a number of identified specimens (NISP) of 208, which corresponds to a minimum number of individuals (MNI) of 129, representing at least 18 taxa (Table 1, Figs. 4 and 5).

The fossil assemblage was identified following the palaeontological criteria established by Furió (2007) for insectivores, Sevilla (1988) for Chiroptera, López-García et al. (2011a) and López-García et al. (2011b) for rodents, and Blain (2005, 2009) for anurans and snakes. The attribution of each species is based on the cranial and postcranial elements that are diagnostic and allow identification in accordance with systematic palaeontology. The diagnostic elements for bats and shrews are mandible, maxilla and isolated teeth; for Talpidae, isolated teeth and humeri; for Arvicolinae, the first lower molar; and for Muridae, Gliridae and Sciuridae, mandibles and isolated teeth. In addition, the assemblage was grouped on the basis of the minimum number of individuals (MNI).

The taphonomic study of the small mammals is based on the systematic descriptive method that examines the changes resulting from predation (Andrews, 1990; Fernández-Jalvo and Andrews, 1992). Thus, we observe and describe the surface alterations

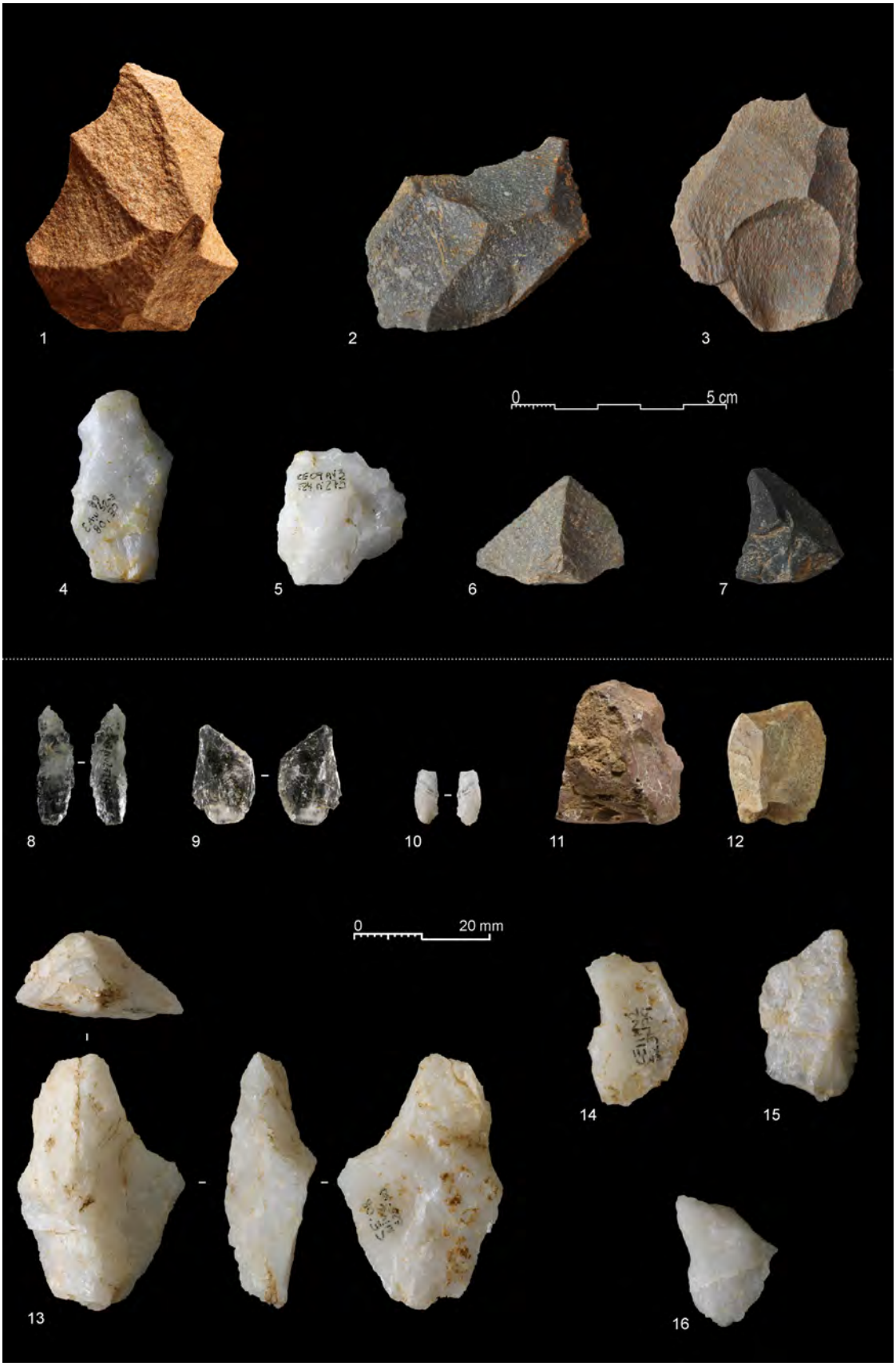

Fig. 3. Lithic industry from Level 3 (1–7) and Level 2 (8–16) of Cova Eirós. Middle Palaeolithic: 1–3: Levallois flakes on fine-grained quartzite. 4: Denticulated tool on quartz. 5: Flake on quartz. 6–7: Discoidal flakes on fine-grained quartzite. Upper Palaeolithic: 8 and 10, bladelets on rock crystal and quartz. 9: Truncated blade on rock crystal. 11: Notched chert. 12: Chert flake. 13: Bipolar-on-anvil product on quartz. 14: Burin on quartz. 15–16: Quartz flakes.

Table 1
Representation of the number of identified specimens (NISP), minimum number of individuals (MNI) and the percentage of the MNI (%) for the small vertebrates of Cova Eirós.

Taxa	Level 2			Level 3		
	NISP	MNI	%	NISP	MNI	%
Rana temporaria	5	5	6.76	2	2	3.64
Vipera sp.	3	1	1.35	0	0	0.00
Rodentia Indet.	5	0	0.00	2	0	0.00
Apodemus sylvaticus	8	4	5.41	3	2	3.64
Arvicola amphibius	12	7	9.46	5	3	5.45
Arvicola sapidus	0	0	0.00	4	3	5.45
Chionomys nivalis	4	3	4.05	3	2	3.64
Microtus (Terricola) lusitanicus	25	16	21.62	12	8	14.55
Microtus agrestis	15	8	10.81	15	8	14.55
Microtus arvalis	33	18	24.32	16	8	14.55
Microtus arvalis-agrestis	5	4	5.41	2	2	3.64
Microtus oeconomus	0	0	0.00	1	1	1.82
Myotis myotis/blythii	0	0	0.00	3	2	3.64
cf. *Miniopterus* sp.	1	1	1.35	0	0	0.00
Myotis sp.	0	0	0.00	1	1	1.82
Chiroptera indet.	1	1	1.35	3	3	5.45
Rhinolophus ferrumequinum	1	1	1.35	1	1	1.82
Sorex minutus	0	0	0.00	3	2	3.64
Sorex sp.	2	2	2.70	7	5	9.09
Talpa cf. *occidentalis*	1	1	1.35	2	2	3.64
Erinaceus europaeus	2	2	2.70	0	0	0.00
Total	**123**	**74**	100.00	**85**	**55**	100.00

present in the small-mammal remains, identifying and recognizing predators on the basis of their interventions. To this end, we analyse the anatomical representation, fracturing and digestion of the remains and compare the results with those obtained from the study of modern pellets known from predators.

3.1. Diversity reconstruction

The biodiversity of a sample helps to reveal the homogeneity of an environment (Magurran and McGill, 2011). We use the Simpson Index (L) to quantify how equal the communities in our archaeological record are. The formula applied is

$$L = s\sum[ni(ni-1)/N(N-1)]$$

where ni is the MNI by taxa; N is total MNI with all the species together; s is number of species for each sample.

The values are between 0 and 1. The lower values (close to 0) indicate that there is a single dominant species, and the higher values indicate a community of different species. The absolute values are standardized, using percentages of the MNI. With this standardization, we can compare samples of different size. The Simpson Index was obtained using PAST software (Paleontological Statistics software) (Hammer et al., 2001).

3.2. Palaeoenvironmental reconstruction

The method used for the palaeoenvironmental reconstruction is the *Habitat Weighting* method (Evans et al., 1981; Andrews, 2006; modified by Blain et al., 2008; López-García et al., 2011a), which is based on the current distribution of each taxon, i.e. the habitat or habitats where it is possible to find each taxon in the Iberian Peninsula nowadays. The habitats are divided into five types (Blain et al., 2008; López-García et al., 2011a, 2010): Open Dry (OD): meadows under seasonal climatic change; Open Humid (OH): evergreen meadows with dense pastures and appropriate topsoils; Woodland (Wo): developed forest, including woodland margins and forest patches; Rocky (Ro): areas with a suitable rocky or stony substratum without vegetation; and Water (Wa): areas along lakes, streams and ponds. The value of 1 is divided between the habitats where it is possible to find the species at present (Table 2).

There are special cases, such as *Microtus oeconomus*, which is currently absent from the Iberian Peninsula and lives in the cold, open environments of northern and central Europe (Markova, 2006). In the Late Glacial this taxon was characteristic of both open humid and woodland habitats (interstadial types) (Cuenca-Bescós et al., 2009). This is the distribution that we use for the *Habitat Weighting* in the present paper.

3.3. Palaeoclimatic reconstruction

In order to reconstruct the palaeoclimatic conditions in Cova Eirós we apply the *Mutual Ecogeographic Range* (MER) method and also the *Bioclimatic Model* (BM). By means of these methods it is possible to quantify the changes in the palaeotemperatures and palaeoprecipitation between the time of the last Neanderthals and the first record of Anatomically Modern Human (AMH) populations in northwestern Iberia.

The *Mutual Ecogeographic Range* (MER) is a quantitative method based on the current distribution of the species (Blain et al., 2016; Blain et al., 2009). We identify the range of species by simply overlapping the geographical areas where the species are present nowadays in the Iberian Peninsula. The atlas (Palombo et al., 2007) used is based on a 10 × 10 km UTM network, and the climatic data that we obtain for these 10 × 10 km squares make it possible to estimate the palaeoclimatic conditions (Font Tullot, 2000). Attention has to be paid to those species whose habitat has been altered by other factors, such as human activity.

The *Bioclimatic Model* (BM) was developed by Hernández-Fernández (2001) in order to reconstruct palaeoclimatic conditions. According to Hernández-Fernández (Hernández-Fernández, 2001; Hernández-Fernández et al., 2007), small- and large-mammal species can be ascribed to ten different climates. Taking into account the rodent assemblage, six of those different climates are present in the sample from Cova Eirós: IV, *Subtropical* with winter rains and summer droughts; V, *Warm temperate* with not very severe winters but high humidity; VI, *Typical temperate* with winters that are cold but not very long, but summers that are cool; VII, *Arid-temperate* with large temperature contrasts between winter and summer; VIII, *Cold-temperate* with cool summers and long cold winters (boreal); and IX, *Polar* with very low temperatures and very short summers (Table 3). Previously, it is necessary to calculate the Climatic Restriction Index ($CRIi = 1/n$, where i is the climatic zone where the species appear and n is the number of zones where the species is present) and the Bioclimatic Component ($BCi = (\Sigma\ CRIi)\ 100/S$, where i is the climatic zone; S is the number of species). From the BC a mathematical model has been developed as a regression that allows us to calculate climatic parameters (see Appendix 1).

By means of the MER and BM we are able to estimate the mean annual temperature (MAT), the mean temperature of the coldest month (MTC), the mean temperature of the warmest month (MTW) and the mean annual precipitation (MAP). These data may then be compared with the values from the meteorological research station of Lugo, which has a MAT of 11.1 °C; a MTC (January) of 5.9 °C; a MTW (July) of 17.1 °C; and a MAP of 1033 mm (Font Tullot, 2000).

4. Results and discussion

4.1. Taphonomic remarks

In level 3, 70% of the incisors are digested, reaching severe levels; 72% of the molars are digested, reaching moderate levels.

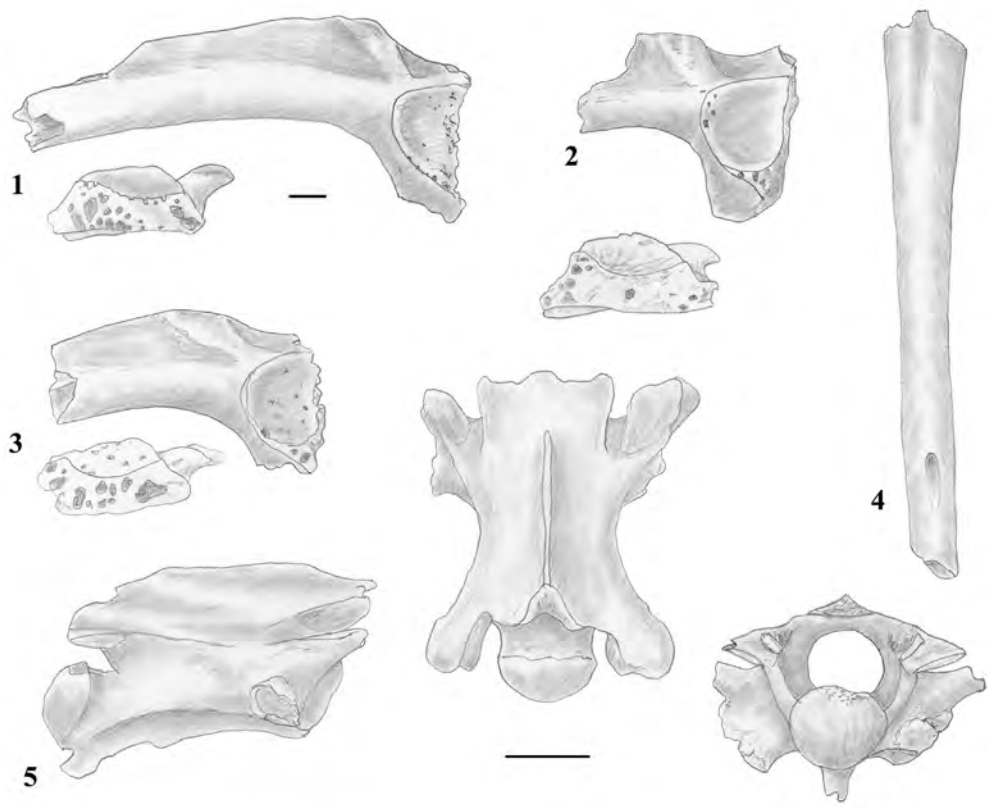

Fig. 4. Amphibian and reptile fossil remains identified in Cova Eirós. 1–3) Left ilia of *Rana temporaria* (lateral and distal views); 4) Tibio fibula of *Rana temporaria* (lateral view); 5) Trunk vertebra of *Vipera* sp. (dorsal, posterior and right lateral views). Scales 2mm.

These data point to a moderate level of modification, or to predator category 3, i.e. a diurnal raptor (Andrews, 1990). While the postcranial elements looked unaltered by digestion (Table 4). For this reason, is necessary to expand the sample level 3, so this should be regarded as just a preliminary study. The digestion in level 2 reaches extreme degrees on incisors and molars, affecting 82% and 67% respectively (Table 4), indicating the presence of a canid predator, the maximum category in terms of bone fracture (Andrews, 1990). In addition, small bites are reported,a high fracture level (no maxilla or mandible complete, 80% teeth out of its jaws, 45.9% and 10% incisors and molars broken respectively, 99% of postcranial remains broken) and very low representation of the identifiable remains, which would reinforce our hypothesis. All these points would consistent with a small carnivore such as the fox (*Vulpes vulpes*).

The fox (*Vulpes vulpes*) is a carnivoran species with high ecological plasticity, found in all types of natural habitat, from semiarid deserts to tundra and forests. In general, fragmented and heterogeneous habitats and ecotones at the margins of forest and scrub habitats are more suitable than homogeneous environments (Harris and Smith, 1987; Gloor et al., 2000). A similar point applies to its dietary preferences: the wide distribution of the fox and the diversity of habitats where it lives, in conjunction with its general behaviour in prey selection, result in a long list of preyed-upon species. As a consequence, the fox is generally classified as omnivorous and opportunistic (Macdonald, 1997). Studies of the diet of the fox in the Iberian Peninsula have shown that small mammals and lagomorphs make a larger part, with a higher consumption of rabbit in the Mediterranean region and more small rodents in the north. Other food and prey, including fruit, reptiles, insects, earthworms, crayfish and fish, complement the fox diet, depending on the type of habitat and the time of the year (Artois and Stahl, 1990; Weber, 1996; Macdonald, 1997; Fernandez and Ruiz-de Azua, 2005) and in some cases making good use of overabundant population episodes.

Accordingly, the fox does not exhibit preferential criteria in selecting the taxa it consumes, and the assemblage can be seen as a reflection of the local living community. Palaeoecological interpretations based on the relative abundances of taxa are thus a reliable indication of the mammal habitat in which the hunting predators consumed their prey.

4.2. The microvertebrate assemblage of Cova Eirós

There are no significant differences between level 3 and level 2 regarding the small vertebrates; in general, there is continuity between the species found in both levels, the assemblage being composed by 18 taxa (Figs. 4 and 5).

Some species that are represented only in one level, such as *Arvicola sapidus*, *Microtus oeconomus*, *Myotis myotis/blythii*, *Myotis* sp. and *Sorex minutus* in the case of level 3, and *Vipera* sp., cf. *Miniopterus* sp. and *Erinaceus europaeus* for level 2.

The most abundant species are the common vole (*Microtus arvalis*; 14.55%$_{\text{level 3}}$ and 24.32%$_{\text{level 2}}$), the Lusitanian pine vole (*Microtus (Terricola) lusitanicus*; 14.55%$_{\text{level 3}}$ and 21.62%$_{\text{level 2}}$), the field vole (*Microtus agrestis*; 14.55%$_{\text{level 3}}$ and 10.81%$_{\text{level 2}}$) and the northern water vole (*Arvicola amphibius*; 5.45%$_{\text{level 3}}$ and 9.46%$_{\text{level 2}}$).

In this study we have analysed small mammals, squamate reptiles and amphibians. In the archaeological record of Cova Eirós, there are at least 16 small-mammal species represented. For the squamate reptiles and amphibians, however, we only have two

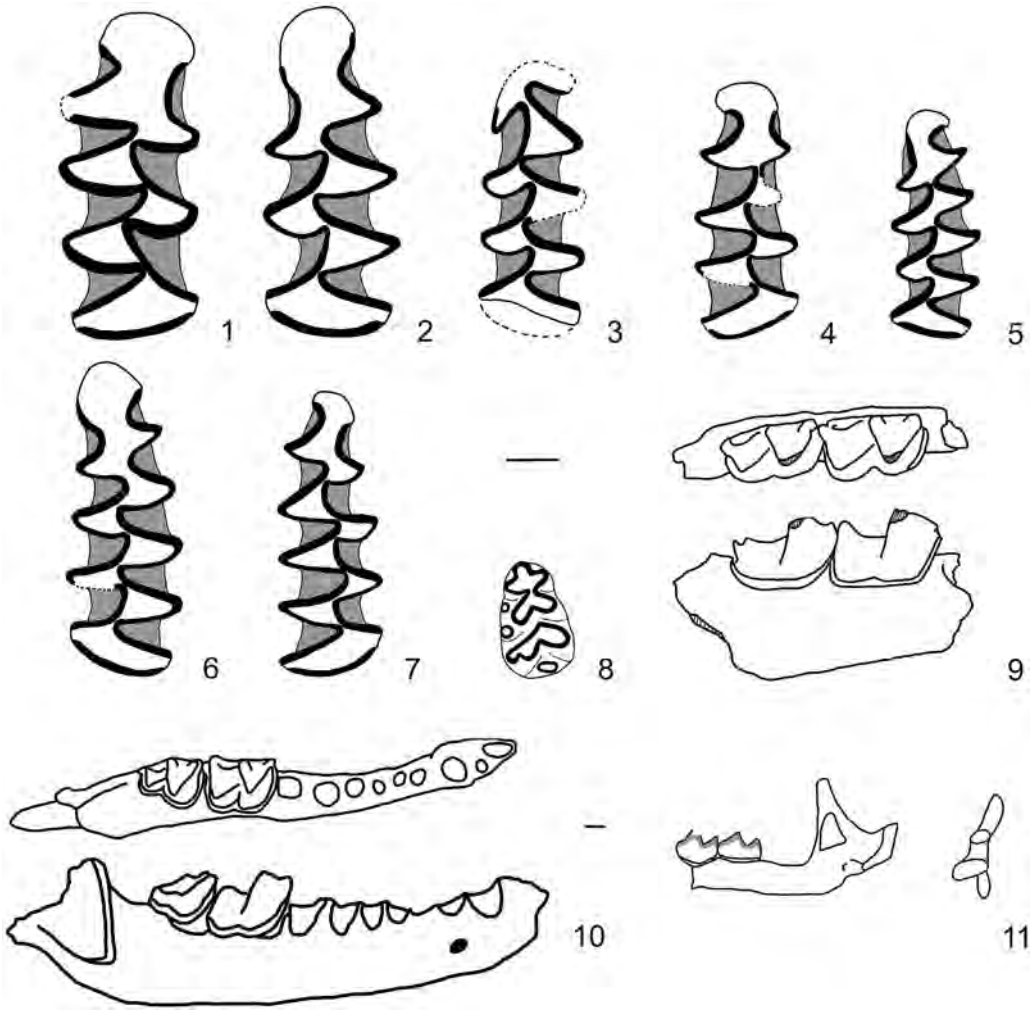

Fig. 5. Small-mammal fossil remains identified in Cova Eirós. 1) Right m1 of *Arvicola sapidus* (occlusal view); 2) Left m1 of *Arvicola amphibius* (occlusal view); 3) Left m1 of *Chionomys nivalis* (occlusal view); 4) Right m1 of *Microtus oeconomus* (occlusal view); 5) Left m1 of *Microtus (Terricola) lusitanicus* (occlusal view); 6) Left m1 of *Microtus arvalis* (occlusal view); 7) Right m1 of *Microtus agrestis* (occlusal view); 8) Left m1 of *Apodemus sylvaticus* (occlusal view); 9) Right mandible of *Rhinolophus ferrumequinun* (occlusal and lingual view); 10) Right mandible of *Myotis myotis/blythii* (occlusal and buccal view); 11) Right mandible of *Sorex minutus* (posterior and lingual view). Scales 1 mm.

Table 2
The species scores according to the distribution for the *Habitat Weighting*: OD (Open Dry); OH (Open Humid); Wo (Woodland); Ro (Rocky) and Wa (Water).

Taxa	Habitat weighting				
	OD	OH	Wo	Ro	Wa
Rana temporaria		0.4	0.4		0.2
Vipera sp.	0.25	0.25	0.25	0.25	
Apodemus sylvaticus			1		
Arvicola amphibius		1			
Arvicola sapidus					1
Chionomys nivalis				1	
Microtus (Terricola) lusitanicus		0.5	0.5		
Microtus agrestis		0.5	0.5		
Microtus arvalis	0.5		0.5		
Microtus oeconomus		0.5	0.5		
Myotis myotis/blythii			0.75	0.25	
cf. *Miniopterus* sp.			0.75	0.25	
Myotis sp.			0.5		0.5
Rhinolophus ferrumequinum			0.75	0.25	
Sorex minutus			0.5	0.5	
Sorex sp.		0.5	0.5		
Talpa cf. *occidentalis*		0.5	0.5		
Erinaceus europaeus		0.5	0.5		

Table 3
Distribution of species scores for the *Bioclimatic Model* (according to Hernández Fernández, 2001; Hernández-Fernández et al., 2007): IV *Subtropical*; V *Warm temperate*; VI *Typical temperate*; VII *Arid-temperate*; VIII *Cold-temperate* and IX *Polar*.

Taxa	Bioclimatic model					
	IV	V	VI	VII	VIII	IX
Apodemus sylvaticus	0.50	0	0.50	0	0	0
Arvicola amphibius	0.25	0	0.25	0.25	0.25	0
Arvicola sapidus	0.50	0	0.50	0	0	0
Chionomys nivalis	0.25	0	0.25	0	0.25	0
Microtus (Terricola) lusitanicus	0	1	0	0	0	0
Microtus agrestis	0	0	0.50	0	0.50	0
Microtus arvalis	0	0	1	0	0	0
Microtus oeconomus	0	0	0.33	0	0.33	0.33

species. We do not compare thus our archaeological data for the herpetofauna with the current values of these species because we consider that the sample of squamate reptiles and amphibians is not representative enough. However, we include these taxa in the palaeoenvironmental and palaeoclimatic reconstructions.

The current autochthonous small-mammal fauna of Galicia is

Table 4
Intensity of digestion of dental and postcranial elements of small mammals of Cova Eirós level 2 and level 3.

Digestion of elements	Level	
	2	3
Incisors		
Absent	18.5	30
Light	39.7	25
Moderate	15.3	15
Heavy	11.1	10
Extreme	2.6	0
Molars		
Absent	32.8	27.9
Light	40.9	34.9
Moderate	16	30.2
Heavy	5.6	7
Extreme	3.4	0
Postcranial		
Absent	63.6	100
Light	22.7	0
Moderate	9.1	0
Heavy	0	0
Extreme	0	0

made up of 43 species (10 insectivores, 17 chiropters and 16 rodents), seven of which are endemic to the Iberian Peninsula: *Talpa occidentalis*, *Galemys pyrenaicus*, *Sorex granarius*, *Arvicola sapidus*, *Microtus (Terricola) lusitanicus*, *Microtus (Terricola) duodecimcostatus* and *Mus spretus* (Palombo et al., 2007). If we compare this with the small vertebrates from the Iberian Peninsula as a whole, Galicia contains 71.4% of the insectivore species, 68% of the chiropter species, 76.2% of the rodent species, and 71.7% of the total micromammals species represented in the Peninsula (López-García et al., 2011a).

The number of small-mammal species currently found in the region of Cova Eirós consists of 23 taxa. Particularly noteworthy is the presence of *Rattus rattus*, *Rattus norvegicus*, *Eliomys quernicus*, *Mus domesticus*, *Pipistrellus pipistrellus*, *Rhinolophus hipposideros*, *Myotis nattererii*, *Crocidura suaveolens*, *Sorex coronatus*, *Sorex granarius* and *Neomys anomalus* (Díaz-d'a Silva and Cartelle, 2007) because these species are not represented in the archaeological record of the northwestern Iberian Peninsula (Rey-Salgado, 2011).

In level 3 and level 2 of Cova Eirós, 16 species have been recorded, representing 69.6% of the number of species currently documented in the region, and mainly consisting of rodents.

From a palaeoecologial point of view, the high diversity is a result of stable climatic conditions. The vegetation is heterogeneous and complex on account of this biodiversity (Margalef, 1974).

4.3. Palaeoenvironmental and palaeoclimatic conditions during the Middle-Upper Palaeolithic in Cova Eirós

According to the MD95-2043 pollen record from the Alborán Sea core (ca. 48.1 to 26.8 ka BP), MIS 3 is characterized by alternating phases of forest development and semi-desert expansion in phase with the warming and cooling of sea surface temperatures, respectively (Fletcher and Sánchez-Goñi, 2008). Along this period the expansion of mixed oak forest (deciduous and evergreen *Quercus*) during interstadials alternated with the expansion of semi-desert vegetation (*Artemisia*, Chenopodiaceae and *Ephedra distachya* type) during stadials and Heinrich Events (HE) (Fletcher and Sánchez-Goñi, 2008; Harrison and Sánchez-Goñi, 2010; Sánchez-Goñi and D'Errico, 2005; Sánchez-Goñi et al., 2008).

The results obtained for biodiversity by means of the Simpson Index are the value of 0.888 for level 3 and 0.837 for level 2. These values indicate high diversity on both levels and the presence of a community, for there is no dominant species. There is a higher diversity on level 3 than level 2 but there is little change between the two levels.

Table 5
Values of temperature and precipitation for the Cova Eirós sequence obtained by the Mutual Climatic Range method and the Bioclimatic Model. MAT (mean annual temperature); MTC (mean temperature of coldest month); MTW (mean temperature of warmest month); MAP (mean annual precipitation); Max (maximum of values obtained); Min (minimum of values obtained); SD (standard deviation of values obtained); **Δ** (difference between the values obtained by analysing the small mammals from Cova Eirós and current values).

	Mutual ecogeographic range		Bioclimatic model	
	Level 2	Level 3	Level 2	Level 3
MAT	7.69	8.18	8.58	9.16
SD	1.60	1.17	3.39	3.39
MAX	10	10	–	–
MIN	5	7	–	–
Δ	−3.41	−2.92	−2.52	−1.94
MTW	16.08	15.82	18.13	18.37
SD	1.04	0.98	4.77	4.77
MAX	18	18	–	–
MIN	15	15	–	–
Δ	−1.02	−1.28	1.03	1.27
MTC	1.15	1.36	−0.3	0.66
SD	1.34	1.36	4.66	4.66
MAX	4	4	–	–
MIN	0	0	–	–
Δ	−4.75	−4.54	−6.2	−5.24
MAP	1738	1827	1332	1322
SD	444	480	533	533
MAX	2500	2500	–	–
MIN	800	800	–	–
Δ	705	794	299	289

Simpson index for the Mousterian sites commented in this paper is between 0.71 (the lower value comes from Cueva del Conde level 20a, López-García et al., 2011c) and 0.84 (the higher value for Arbreda Cave level I, López-García et al., 2015); for the Aurignacian levels we have values between 0.74 (the lower value for Arbreda Cave level H, López-García et al., 2015) and 0.85 (for Cueva del Conde level 20b, López-García et al., 2011c).

On the other hand, regarding the palaeoclimatic conditions, *Mutual Ecogeographic Range* (MER) and the *Bioclimatic Model* (BM), yield results suggesting that the precipitation was higher and the temperatures lower than at present. The results in the two cases are consistent with each other, taking into account the standard deviation (SD) (Table 5).

Our data show a palaeoenvironment composed mainly of woodland and open humid habitats, but there is also a significant proportion of rocky habitat found in both levels (Table 6). The Mousterian level has a habitat dominated by woodland (46%), associated with species such as *Apodemus sylvaticus* and *Myotis myotis/blythii*. The proportion of open humid habitat (26%) is also noticeable, due to the presence of taxa such as *Rana temporaria*, *Microtus (Terricola) lusitanicus* and *Arvicola amphibius*. *Arvicola sapidus* is only present in this level, which is important because this taxon is always associated with stable water sources in the vicinity

Table 6
Percentage of the palaeoenvironmental reconstruction for level 3 and level 2. OD (Open Dry); OH (Open Humid); Wo (Woodland); Ro (Rocky) and (Wa) Water.

	OD	OH	Wo	Ro	Wa
Level 3	3.33	26.00	46.00	13.33	11.33
Level 2	5.77	31.92	47.31	13.46	1.54

of the cave. This explains the percentage of watery environments (11%) found in level 3.

Also relevant is the presence of the taxon *Chionomys nivalis*, with middle European requirements (3.64%$_{level\ 3}$ and 4.05%$_{level\ 2}$), and *Microtus oeconomus* (1.82%$_{level\ 3}$). The snow vole (*Chionomys nivalis*) is associated with high mountains, and the presence of this taxon in the Iberian Peninsula is restricted to rocky areas (Palombo et al., 2007). *Microtus oeconomus*, as said before, lives in open, cool environments (Cuenca-Bescós et al., 2009).

According to the new data obtained from Cova Eirós small vertebrates, level 2, which is related with the AMH populations, has similar paleoenvironmental and paleoclimatic conditions as found in level 3: the main types of habitats are woodland (47%) followed by open humid (32%), reflecting the species found in this level, such as *Microtus arvalis*, *Microtus agrestis* and *Microtus (Terricola) lusitanicus*.

The faunal assemblage is composed of species such as *Cervus elaphus*, *Capreolus capreolus* and *Rupicapra rupicapra*, among others, species whose preferential habitats are woodland and open humid habitats (Mateos-Quesada, 2005). The small vertebrates on levels 3 and 2 also indicate an open woodland environment.

The palaeoenvironmental and palaeoclimatic conditions in conjunction with the chronological data suggest an interstadial between H4 and IS10 for the Mousterian level and between IS6–IS7 for level 2 (Fig. 6).

4.4. Comparison with other Middle-Upper Palaeolithic Iberian sites

MIS 3 is characterized by unstable climatic conditions with alternating warm and cold periods, as commented above. In this unstable context, we have two human species, Neanderthals and AMH. In the Iberian Peninsula there are several sites where Middle-Upper Palaeolithic sites have available small-vertebrate studies (Figs. 1 and 6).

In general, the data obtained through the *Habitat Weighting* method show that the landscape was dominated by open forest formations in all the Iberian Peninsula sites analysed, which is the same pattern as that found in both levels of Cova Eirós.

Palaeoclimatic conditions have been ascertained using the *Mutual Ecogeographical Range* method. The data for the north-eastern Iberian Peninsula during MIS 3 (López-García et al., 2014; López-García et al., 2015) show temperatures between −7.7 °C and −2.8 °C colder and precipitation between 75 and 350 mm higher than at present. The Mousterian level of Cueva del Conde (López-García et al., 2011b) has temperatures between −3.8 °C and −1.1 °C lower and precipitation 527 mm higher, while level 3 of Cova Eirós yields temperatures −2.9 °C lower and precipitation 794 mm higher.

It is thought that the last refuge for Neanderthal populations was Gorham's Cave (Finlayson et al., 2006). The palaeotemperatures at this cave (López-García et al., 2011c) were between −10 °C and −3.7 °C lower than at present, whereas the values for the precipitation were 23 mm higher.

For the Upper Palaeolithic, with its AMH populations, we focus on the sites with small-vertebrate studies where Aurignacian industries have been recovered: Cova de l'Arbreda (López-García et al., 2015) and Cueva del Conde (López-García et al., 2011b).

In the case of Cova de l'Arbreda the temperatures were between −6.7 °C and −5.8 °C lower than nowadays, whereas the precipitation values are 142 mm higher. The palaeotemperatures at Cueva del Conde were between −2.1 °C and −0.3 °C lower, and the precipitation was 465 mm higher than currently. In the case of level 2 of Cova Eirós, we have found the temperatures to be −3.4 °C lower and precipitation 705 mm higher.

To sum up, these data suggest that the palaeoenvironment during MIS 3 in the Iberian Peninsula as a whole was dominated by open woodland formations, with the highest proportion of woodland in Gorham's Cave. Regarding the palaeotemperatures and the palaeoprecipitation, we have found that the temperatures were lower and the precipitation higher that at present for both Neanderthal and AMH populations.

4.5. Cova Eirós and the context for Neanderthals and Anatomically Modern Humans

In Western Europe MIS 3 has been well studied with a view to reconstructing the impact of climatic fluctuations and the arrival of AMH, associated with the replacement of the Neanderthals. We

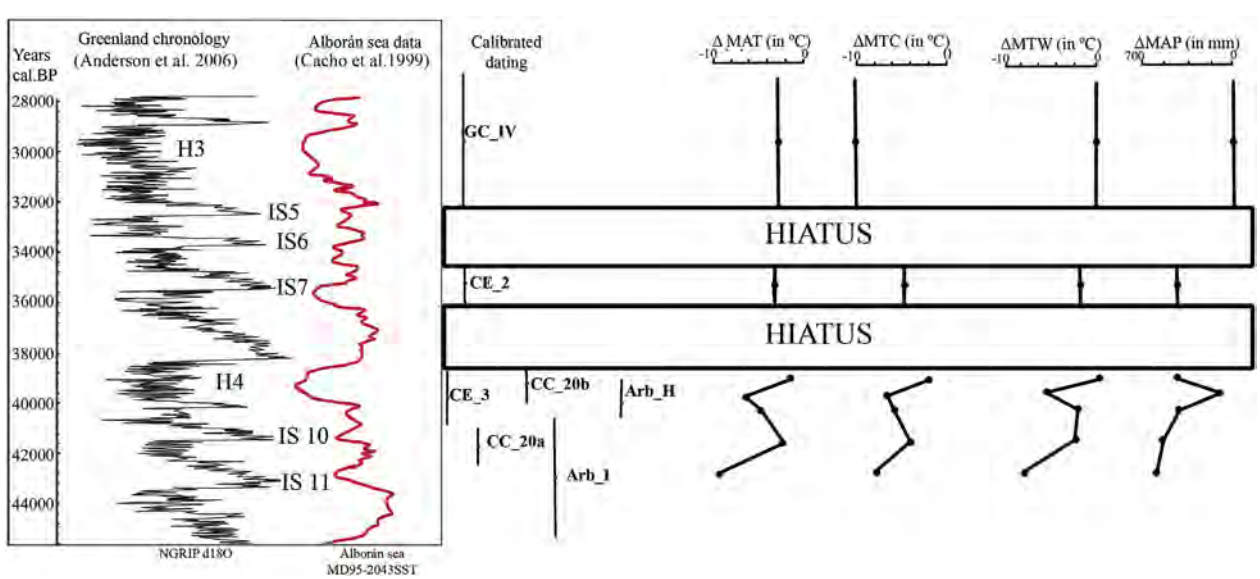

Fig. 6. Correlation between the average of the mean annual temperatures (MAT), mean temperature of the coldest month (MTC), mean temperature of the warmest month (MTW) and mean annual precipitation (MAP) obtained by the Mutual Ecogeographical Range (MER) method used for the studies of small-vertebrate assemblages. These results are compared with the oxygen isotope curve from 45,000 to 28,000 years cal BP and the Alborán sea surface. H) Heinrich events; IS) Interstadials; Arb) Cova de l'Arbreda; CC) Cueva del Conde; CE) Cova Eirós; GC) Gorham's Cave (Anderson et al., 2006; Cacho et al., 1999).

would like to connect our results with the debate on the disappearance of the Neanderthals from the fossil record during MIS 3, which is one of the most widely debated issues in European prehistory. In Cova Eirós we have found the last Neanderthals and the first AMH populations in the northwestern Iberian Peninsula, until now a region aloof of this debate.

The two main hypotheses for the disappearance of the Neanderthals are on the one hand competition between AMH and Neanderthals: in this view, the latter went extinct because they were replaced by the AMH that arrived from Africa via the Near East (Hockett and Haws, 2005).

Another hypothesis is that AMH had no substantial role in the extinction of the Neanderthals whereas the main cause was climate change and its effects on the environment (Bradtmöller et al., 2012; Mallol et al., 2012; Stewart, 2007). However, this proposal has not been widely accepted because Neanderthals had previously been able to adapt successfully to climatic fluctuations for 300 kyr (Jiménez-Espejo et al., 2007).

Other authors have argued for a combination of climate with the competition from modern humans (Banks et al., 2008). The late survival of the Neanderthals in Gibraltar (Finlayson et al., 2006) shows that they were contemporary with modern humans in Europe for several millennia (Higham et al., 2014; Maroto et al., 2012).

We have already seen that the Neanderthals had proved their ability to adapt to various climatic fluctuations. With the data obtained from the small vertebrates of Cova Eirós, we might say that the palaeoenvironmental and palaeoclimatic conditions where Neanderthals and AMH developed their activities in the northwestern Iberian Peninsula do not exhibit any climatic change that could be specifically linked with the Neanderthal extinction. Taking into account the small-mammal assemblage analysed, we have observed that there are no significant differences between the taxa found on level 3 and level 2, even though these species are sensitive to climatic fluctuations. No big shifts in the taxonomical association have been reported for both levels; the changes are in the presence of certain taxa and the percentage representation of the taxa. The palaeoclimatic and palaeoenvironmental conditions thus provide no evidence for a major climatic change that would have explained the substitution of Neanderthals by AMH. We also see the same pattern in other sites with small-vertebrate studies in the Iberian Peninsula, such as Cova de l'Arbreda (López-García et al., 2015), Cueva del Conde (López-García et al., 2011c) and Teixoneres Cave (López-García et al., 2012).

Thus, the small-vertebrates studies in the Iberian Peninsula suggest that the climate change by itself can be ruled out as the main and unique factor involving the Neanderthal demise.

Nevertheless, the climatic instability during MIS 3 caused changes in the vegetation and mammal communities of the territories of Western Europe that negatively impacted the Neanderthal populations (d'Errico and Sánchez-Goñi, 2003). Consequently, Neanderthals have adapted their subsistence and territory exploitation strategies as it is shown by the intensification in the processing and profiting of the faunal remains and calories (Hodgkins et al., 2016), the change to high logistic mobility patterns and the occupation of uplands and peripheral areas (Baena et al., 2012; Baena-Preysler and Carrión-Santafé, 2013; Vaquero-Rodríguez et al., 2006), as it seems to be the case of the Neanderthal occupations at level 3 of Cova Eirós. These changes may have caused nutritional stress and the fragmentation of Neanderthal populations (i.e. Finlayson and Carrion, 2007; Hublin and Roebroeks, 2009). In that context of adaptation, environmental and population stress we could also take into account other cultural behaviours such as cannibalism. According to this hypothesis, Neanderthal cannibalism was a common behaviour at moments of environmental or population stress; this had an obviously negative impact on these populations and in the end they became extinct (Agustí and Rubio-Campillo, 2016). The appearence of AMH may have triggered the pressure and cause instability in the Neanderthals groups, whether these two species had direct contact or not.

Thus, the environment could have played an important role at increasing the stress on the Neanderthal populations, but was probably not a decisive factor; the arrival of AMH could have also been partially responsible for their extinction.

5. Conclusions

The analysis of the small vertebrates from Cova Eirós has led to the identification of 215 specimens (NISP) with a minimum number of individuals (MNI) of 129. The palaeoclimatic conditions, as inferred from the small vertebrates, suggest lower temperatures and higher precipitation than nowadays and an environment dominated by open forest.

At Cova Eirós, we find the last Neanderthal populations of Northwestern Iberia, with Mousterian industries dating 41,299–38,390 cal BP, as well as the first Anatomically Modern Humans in this region, dating to 36,136–35,032 cal BP and with Aurignacian technology. It should be borne in mind that at Cova Eirós there is a chronological gap and an erosive hiatus between the occupations of levels 3 and 2.

According to the data obtained elsewhere in the Iberian Peninsula, Neanderthals and AMH lived in different environmental and climatic conditions during MIS 3, showing that they were adapted to the surrounding environment, although that implied some changes in the subsistence strategies of the Neanderthal groups.

What we propose is that the extinction of the Neanderthal populations resulted from a combination of different factors, and cannot be explained by palaeoenvironmental and palaeoclimatic conditions alone. In a context of changing environmental and subsistence strategies, the presence of a new rival population in their territories may have triggered the pressure and instability among Late Neanderthal populations.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2016.08.030.

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