



Cueva Negra del Estrecho del Río Quípar: a Dated Late Early Pleistocene Palaeolithic Site in Southeastern Spain

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Abstract

Systematic excavation and multidisciplinary research undertaken over three decades have deepened our understanding of the early Palaeolithic archaeology at Cueva Negra del Estrecho del Río Quípar (Caravaca de la Cruz, Murcia, Spain). New results from biochronology and combined ESR and U-series dating corroborate previous magnetostratigraphy, placing the entire excavated sequence between the Jaramillo sub-chron and the Matuyama-Brunhes boundary (i.e. ca. 990–772 thousand years ago (ka)); palaeontological and palynological findings reflect temperate environmental conditions. A bifacially flaked limestone hand axe was excavated 1 m below the top of the Pleistocene sequence. The *Equus* cf. *altidens* tooth that provided the ESR estimate was excavated 1 m below the hand axe. Throughout its 5-m-deep sedimentary sequence, small nodules, fragments and struck flakes make up the bulk of the Palaeolithic assemblage. Stratigraphical analysis points to undisturbed continuous sedimentary deposition above a layer of ashy sediment, encountered 4.5 m below the top of the Pleistocene sequence, which contained thermally altered bone and heat-shattered chert cores and flakes. Cueva Negra is among the earliest European sites with firm evidence of combustion.

Keywords Spain · Late Early Pleistocene · Palaeolithic · ESR-Useries dating · Palaeontology

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Introduction

The Iberian Peninsula offers the most complete record of Early Pleistocene human presence in Western Europe. An important site in the south-east of the peninsula is Cueva Negra del Estrecho del Río Quípar (Fig. 1). Like other well-documented sites, it lies between the Mediterranean coast and a N-S line passing through Madrid (Fig. 2). From N to S, they include not only the Atapuerca Sima del Elefante and Gran Dolina sites (Arsuaga et al. 1999, 2001, 2014; Bermúdez de Castro and Martínón-Torres 2013; Bermudez de Castro et al. 1997, 2011, 2013, 2017; Carbonell et al. 1995, 1999, 2008; de Lombera-Hermida et al. 2015; Duval et al. 2018; Falguères et al. 1999; Huguet et al. 2017; Mallol 1999; Parés et al. 2006, 2013, 2018; Rosas et al. 2006; Terradillos Bernal 2010) but also, closer to the Mediterranean, Vallparadís (Garcia et al. 2011, 2012; Martínez et al. 2010, 2014), Barranc de la Boella (Vallverdú et al. 2014), Alto de las Pícarazas (Vicente Gabarda et al. 2016) and the eastern Andalusian Fuente Nueva-3 and Barranco León-5 sites (Barsky et al. 2015; Fajardo 2009; Gibert et al. 1998; Martínez-Navarro et al. 1997; Toro-Moyano et al. 2003, 2009, 2010; Toro Moyano et al. 2011; Toro-Moyano et al. 2013). Their chronologies show that early Palaeolithic assemblages of pebble tools, choppers and flakes began to include bifacially flaked large cutting tools such as a cleaver (Barranc de la Boella) and a hand axe (Cueva Negra) ca. 0.9–0.8 Ma (i.e. ca. 900–800 ka). These tools are accompanied at Cueva Negra by evidence for the ability to tend fire, hitherto unrecorded in Europe at that time. cursory exploration of the Cueva Negra sediments in 1981 (Martínez-Andreu et al. 1989) paved the way for a programme of systematic excavation that commenced in 1990 since when it has continued annually and provided the abundant finds and data that indicate the antiquity of the site (Walker et al. 2013, 2016a).

Context

Geographical Location

Cueva Negra del Estrecho del Río Quípar is a large, north-facing, rock shelter (ca. 10×10 m in area), in Upper Miocene (Tortonian) biocalcarene rock, lying at 740 m above sea level, a.s.l. ($38^{\circ} 02' 12.5''$ N; $1^{\circ} 53' 5.8''$ W) on the right bank 40 m above the Quípar River where it flows northwards from a 1-km-long gorge (the Estrecho, i.e. “the Narrows”) below the hamlet of La Encarnación in Caravaca de la Cruz municipality (Murcia, Spain) (Fig. 1). The Quípar is a tributary of the Segura River that reaches the Mediterranean Sea 110 km E of Cueva Negra, even though the cave lies only 70 km N of the Murcian coast. Important geological faults determine the alignment of tributaries in the Segura drainage basin. The Estrecho follows the sinistral reverse Quípar Fault, active since the Late Miocene (Messinian). Activity caused uplift of the right bank of the river, thereby saving from riverine erosion the fine-grained fluvial sediments that had accumulated in Cueva Negra under conditions of low transport energy by intermittent overflow of an erstwhile swampy lake fed by the Quípar during the late Early Pleistocene. The Quípar enters the gorge at 725 m a.s.l. and leaves it at 690 m a.s.l. The height of the land above sea level during the Early Pleistocene is unknown. The Upper Miocene (Tortonian) calcarenite formed under the Tethys Sea, arising to become a



Fig. 1 Top left: location of Cueva Negra. Top right: Cueva Negra above the Quípar Gorge. Middle left: fossil equid tooth CN1511. Bottom left: bifacially flaked hand axe. Bottom centre: excavation section showing 1 approximate depth from which CN1511 was dated, and 2 approximate depth from which the hand axe was excavated



Fig. 2 1 Atapuerca Sima del Elefante and Gran Dolina. 2 Vallparadís. 3 Barranc de la Boella. 4 Alto de las Picarrazas. 5 Cueva Negra del Estrecho del Río Quípar. 6 Fuente Nueva and Barranco León. Arrow points north

shoreline surface in the Upper Pliocene. Cueva Negra is a vestige of a trapezoidal endokarstic cavity that likely developed in relation to low-lying lagoons or lakes.

Lithostratigraphy

The fluviatile sediments inside Cueva Negra include clasts eroded from the cave roof and walls. Palaeolithic and faunal remains are present throughout the 5-m depth, implying frequent intervals when the cave was dry, perhaps seasonally. Preliminary microsedimentological analysis shows alternation between archaeological and sterile levels throughout the sequence, suggesting discontinuous Palaeolithic presence at the cave (Fernández et al. 2018). The sedimentary sequence (Fig. 3) shows no significant interruption or disturbance of the successive stratigraphical complexes (Complex 2 - Cx.2, Complex 3 - Cx.3-1 and Cx.3-2; see Fig. 3, column A), perhaps deposited during a relatively short period of geological time by fundamentally uniform, homogeneous alluviation (Angelucci et al. 2013; *pace* Jiménez-Arenas et al. 2011), albeit with a minor interruption at the top of Cx.3-1 in the nature of an incipient palaeosol with erosive traces (Angelucci et al. 2013). Detection of possible discontinuities had led to designation of notional “lithostratigraphical units I–VI” (see Fig. 3, column B) as a precautionary measure during manual excavation; this is carried out in step-wise fashion in a wide trench in order to optimise entry of daylight and facilitate safe access to deep levels whilst maintaining stability of profiles (Walker et al. 2006). Subsequently, detailed sedimentary micromorphological analysis (Angelucci et al. 2013) showed some of these “units” to be superfluous, which is why they are placed between inverted commas wherever they are mentioned in this article. Manual excavation was undertaken in horizontal spits of varying thickness (Fig. 3, column C).

Methodology

Since 1990, manual archaeological excavation has been accompanied by washing the excavated sediment over nested 6 mm, 4 mm and 2 mm, stainless steel sieves, thereby maximising recovery of material > 2 mm in size. Interdisciplinary collaboration has been a priority. Sedimentary components have been the object of palynological, granulometrical, micromorphological and microstratigraphical studies, as well as geochronological investigations that include magnetostratigraphy, optically stimulated luminescence (OSL) and combined uranium-series (U-series) electron spin resonance (ESR). A deeply lying layer of sediment (ca. – 4.5 m; Fig. 3) with undoubted evidence of combustion has been studied using thermoluminescence, Fourier transform infrared spectroscopy (FTIR), ESR palaeothermometry, X-ray fluorescence (XRF), X-ray diffraction (XRD) and thermogravimetric analyses, and taphonomical research involving scanning electron microscopy (SEM) and energy-dispersive (EDS) analyses. Palaeontological and taphonomical research has been carried out on excavated remains of birds, reptiles, amphibians and small and large mammals, and stable-isotope research commenced in 2019. Characterisation of Palaeolithic artefacts includes microscopical studies of use wear or edge damage, and comparison by trace-element characterisation with off-site outcrops of

rock-forming minerals. Attention has been paid also to the hydrogeological evolutionary relationship between the cave and the Quípar valley during the Pleistocene. For various matters referred to in this paragraph, see Angelucci et al. (2013); Carrión et al. (2003; Carrión García et al. 2005); Carrión and Walker (2019); Fernández et al. (2018); López Jiménez et al. (2020); Rhodes et al. (2016); Scott and Gibert (2009); Walker et al. (2004, 2006, 2013, 2016a, b, 2019); and Zack et al. (2013); see also Supplementary Information 2.

Chronology

Magnetostratigraphy

A magnetostratigraphical study of the sedimentary infilling of the rock shelter showed predominantly reverse polarity of the deposits (Scott and Gibert 2009). Consequently, the entire sedimentary sequence was correlated to the reverse polarity Matuyama chron (2.58–0.772 Ma) that preceded the normal Brunhes chron, which provides a minimum age constraint of 0.772 Ma (Okada et al. 2017; Channell et al. 2020) for the sedimentary sequence at Cueva Negra.

U-Series/ESR Dating

An extensive combined U-series/ESR dating study was initiated with the aim of establishing numerical constraints for the sedimentary sequence. Several large-mammal teeth were collected throughout the stratigraphical sequence. Whilst dating analyses are ongoing, we provide the dating results obtained on CN1511, a left maxillary first or second molar tooth of *Equus* cf. *altidens* (site inventory number CN-09152) excavated in archaeological layer 4b of “lithostratigraphical unit IV” within the sedimentary stratigraphical Complex 3-1, approximately half-way down the 5-m-deep sedimentary sequence (Fig. 3).

Two samples (A and B) were collected from CN1511 for dating. They were processed following the same analytical procedure as in Stimpson et al. (2016). The detailed methodology employed is given in the Supplementary Information. Two sets of ages were calculated. The first used the US-ESR model defined by Grün et al. (1988), whilst the second was based on the CSUS-ESR model proposed by Grün (2000). The US-ESR model assumes a gradual U-uptake over time following a one-parameter diffusion equation. In contrast, the CSUS-ESR model is based on the assumption that all of the uranium migrated into the sample at a time given by the closed system U-series age. The CSUS-ESR age corresponds to the maximum age that can be derived from a given U-series and ESR data set. Age calculations using the US-ESR and CSUS-ESR models encompass all possible uptake scenarios. If the dose rates derived from the internal uranium concentrations are low, the differences between the US-ESR and CSUS-ESR models are small. This is not the case when the dose rate of a tooth is dominated by the uranium in the various dental tissues. Data inputs and final age results are displayed in Table 1.

Following the standard analytical procedure for expectedly “old” (Early Pleistocene or older) samples (e.g. Duval et al. 2012a), laser ablation (LA) U-series analyses were

Fig. 3 Simplified synoptic stratigraphical column (after Angelucci et al. 2013 and Walker et al. 2016a). 1 The approximate depth from which CN1511 was dated. 2 The approximate depth at which the hand axe was excavated. 3 Sediments with evidence of combustion (for details, see Angelucci et al. 2013 and Walker et al. 2016b). A Stratigraphical subdivision based on sedimentological analysis and micromorphology (Angelucci et al. 2013). Key: cx = complex or sub-complex. B Earlier suggested “lithostratigraphical units” (Walker et al. 2006). C Arbitrary labelling of layers and spits during manual excavation. Key: BS = incipient palaeosol. D Stratigraphical column. Key: C = clay; Si = silt; Sa = sand; G = granules and gravel; K = carbonate crusts or flowstones; stones are not represented in the column. E Approximate depth below datum point, in metres. F Stratigraphical position of sedimentary micromorphological samples taken (Angelucci et al. 2013). Key: 1 = silty sand, massive or poorly laminated; 2 = silty sand with flat lamination or cross-bedding; 3 = silt or clayey silt, massive or with flat lamination; 4 = sand; 5 = gravel; 6 = stone lines formed of fine granules; 7 = fine lenses of granules to fine gravel; 8 = calcium carbonate crusts; 9 = main erosive surface between Complex 2 and Complex 3; 10 = minor erosive surfaces

performed first on the tooth cross sections in order to evaluate their suitability for ESR dating. These analyses were carried out following the procedure described in Grün et al. (2014). LA transects performed across the vestibular side of the tooth showed relatively homogeneous U-series data within each tissue (Figs. 4, 5 and S1). Numerical results obtained for each LA spot are given in Supplementary Information Tables S1 and S2. The apparent U-series ages obtained should be regarded as minimum age constraints for the fossils, as uranium uptake may sometimes be delayed significantly after the death of the organism. The enamel tissue in fragments A and B displays an apparent age of 188–213 ka, whilst dentine and cement vary between 308–319 and 242–247 ka, respectively. Consequently, the age results obtained for the dentine tissues suggest that the fossil tooth is at least 320 ka.

Combined US-ESR age calculations performed on the two sub-samples of CN1511 returned age estimates of around 400–410 ka. These close results (within 1.2%) are due to the highly homogeneous U-series and ESR data collected for each dental tissue of the two samples. Consequently, all these data can be merged into one single data set that may be assumed reasonably to be representative of the whole tooth. The resulting US-ESR and CSUS-ESR calculations yielded age estimates of 406 ± 40 and 1446 ± 310 ka, respectively (Table 1). Typically, US and CSUS models are considered to encompass all possible uptake scenarios; thus, the true age of tooth CN1511 should lie somewhere between these two estimates. Given the ESR and U-series data set collected for CN1511, an Early Pleistocene age estimate can be achieved only if the uranium uptake process in dental tissues has been similar to the conditions described by the CSUS model, i.e. a period of little initial U-uptake followed by a rapid uptake around 300 ka. The CSUS-ESR age estimate of 1446 ± 310 ka is the maximum age constraint for CN1511. This supersedes the preliminary CSUS-ESR age result 890 ± 136 ka initially indicated in Walker et al. (2019). Its true age lies somewhere between 406 ± 40 and 1446 ± 310 ka, which is compatible with the independent biochronological and magnetostratigraphical evidence, but also shows the limited value of ESR age estimates on teeth where the total dose rate is dominated by the various U sources in the dental tissues. More fossil herbivore teeth from Cueva Negra are being dated using the same procedure. They should contribute to refine this preliminary ESR chronology. Meanwhile, additional age control is available from the combination of palaeomagnetism and biochronology. A more extensive discussion around the reliability of the dating results and their sensitivity to different sources of uncertainty can be found in the Supplementary Information 1.

Table 1 Data inputs and outputs for the combined U-series/ESR age calculation. Apparent U-series ages are also provided in italics. Key: (1) after Grün and Katzenberger-Apel (1994); (2) A 10% error was assumed; (3) corrected by the long-term water content; Post-Rn equilibrium was assumed in dental tissues and sediment. All errors are given at a 1- σ confidence level. The last column presents the merged dataset: ESR and U-series data collected for each sample have been all combined into one single data set

SAMPLE	CN1511A	CN1511B	Combined
Enamel			
Dose (Gy)	1631 $\pm$ 136	1601 $\pm$ 84	1615 $\pm$ 84
U (ppm)	1.83 $\pm$ 0.09	1.87 $\pm$ 0.10	1.85 $\pm$ 0.09
$^{234}\text{U}/^{238}\text{U}$	1.567 $\pm$ 0.012	1.513 $\pm$ 0.067	1.540 $\pm$ 0.039
$^{230}\text{Th}/^{234}\text{U}$	0.890 $\pm$ 0.016	0.932 $\pm$ 0.094	0.911 $\pm$ 0.050
<i>Apparent U-series age (ka)</i>	<i>213</i>	<i>188</i>	-
Alpha Efficiency ⁽¹⁾	0.13 $\pm$ 0.02	0.13 $\pm$ 0.02	0.13 $\pm$ 0.02
Water content (%)	0	0	0
Initial enamel thickness (μm) ⁽²⁾	1203 $\pm$ 120	1229 $\pm$ 123	1216 $\pm$ 122
Dentine			
U (ppm)	98.4 $\pm$ 3.5	96.7 $\pm$ 3.4	97.7 $\pm$ 3.4
$^{234}\text{U}/^{238}\text{U}$	1.550 $\pm$ 0.004	1.542 $\pm$ 0.004	1.546 $\pm$ 0.004
$^{230}\text{Th}/^{234}\text{U}$	1.048 $\pm$ 0.005	1.055 $\pm$ 0.006	1.052 $\pm$ 0.005
<i>Apparent U-series age (ka)</i>	<i>319</i>	<i>308</i>	-
Water (%)	5 $\pm$ 3	5 $\pm$ 3	5 $\pm$ 3
Removed enamel thickness (μm) ⁽²⁾	54 $\pm$ 5	67 $\pm$ 7	81 $\pm$ 8
Cement			
U (ppm)	82.1 $\pm$ 2.9	83.6 $\pm$ 2.9	81.9 $\pm$ 2.9
$^{234}\text{U}/^{238}\text{U}$	1.615 $\pm$ 0.006	1.600 $\pm$ 0.020	1.608 $\pm$ 0.013
$^{230}\text{Th}/^{234}\text{U}$	0.985 $\pm$ 0.007	0.989 $\pm$ 0.016	0.987 $\pm$ 0.011
<i>Apparent U-series age (ka)</i>	<i>247</i>	<i>242</i>	-
Water (%)	5 $\pm$ 3	5 $\pm$ 3	5 $\pm$ 3
Removed enamel thickness (μm) ⁽²⁾	69 $\pm$ 7	94 $\pm$ 9	81 $\pm$ 8
Sediment			
U (ppm)	1.62 $\pm$ 0.09	1.62 $\pm$ 0.09	1.62 $\pm$ 0.09
Th (ppm)	2.82 $\pm$ 0.13	2.82 $\pm$ 0.13	2.82 $\pm$ 0.13
K (%)	0.64 $\pm$ 0.02	0.64 $\pm$ 0.02	0.64 $\pm$ 0.02
Water (%)	15 $\pm$ 5	15 $\pm$ 5	15 $\pm$ 5
<i>In situ</i> gamma dose rate ($\mu\text{Gy a}^{-1}$) ⁽³⁾	363 $\pm$ 21	363 $\pm$ 21	363 $\pm$ 21
Depth (m)	20 $\pm$ 5	20 $\pm$ 5	20 $\pm$ 5
Combined U-series/ESR age results			
internal dose rate ($\mu\text{Gy a}^{-1}$)	723 $\pm$ 193	825 $\pm$ 172	773 $\pm$ 158
beta dose rate, dentine ($\mu\text{Gy a}^{-1}$)	1690 $\pm$ 451	1631 $\pm$ 340	1667 $\pm$ 341
beta dose rate, sediment or cement ($\mu\text{Gy a}^{-1}$)	1178 $\pm$ 313	1131 $\pm$ 235	1142 $\pm$ 233
Gamma + cosmic dose rate ($\mu\text{Gy a}^{-1}$)	402 $\pm$ 18	402 $\pm$ 18	402 $\pm$ 18
Total dose rate ($\mu\text{Gy a}^{-1}$)	3988 $\pm$ 582	3983 $\pm$ 443	3978 $\pm$ 443
p enamel	-0.55	-0.69	-0.63
p dentine	-0.91	-0.93	-0.92
p cement	-0.80	-0.81	-0.80

Table 1 (continued)

SAMPLE	CN1511A	CN1511B	Combined
Combined US-ESR age (ka)	409 ± 49	402 ± 40	406 ± 40
Combined CSUS-ESR age (ka)			1446 ± 310

Palaeontology Results

Small Vertebrates

Cueva Negra has provided abundant small mammal remains of which 2500 teeth excavated in sedimentary complexes 2 and 3 have undergone detailed taxonomical and metrical analyses (López Jiménez et al. 2020); specimens with the same taxonomical species designation are very similar in the two complexes. Well represented in the rich Cueva Negra assemblage of small mammals (López Jiménez et al. 2020) are *Cricetulus* (*Allocricetus*) *bursae*, *Eliomys quercinus*, *Apodemus* cf. *sylvaticus*, *Sciurus vulgaris*, *Oryctolagus* cf. *giberti*, *Lepus* sp., *Prolagus calpensis*, *Erinaceus europaeus*, *Crocidura kornfeldi*, *Neomys* sp., *Sorex* sp. and *Myotis* cf. *myotis*; latterly, *Hystrix* has been identified also. Absent are some

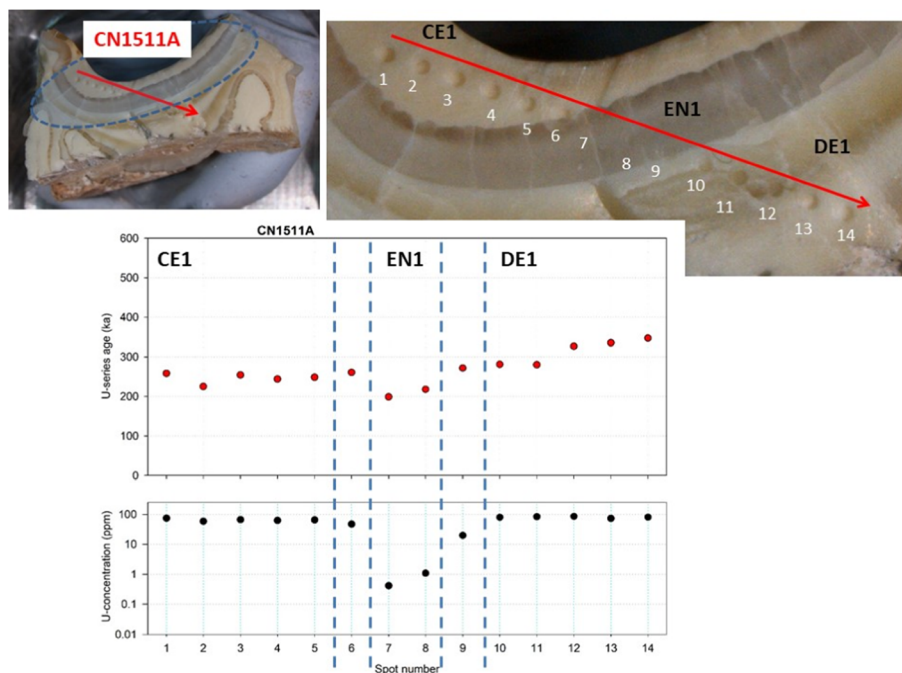


Fig. 4 LA-ICPMS U-series results obtained for transect #1 performed on sample CN1511A. Apparent U-series ages (red circles) and uranium concentration values (black circles) are displayed. The slightly transparent blue domain shows the area sampled for US-ESR dating. Key: CE = cement; EN = enamel; DE = dentine. Numerical values are given in the Supplementary Information 1 (Table S1)

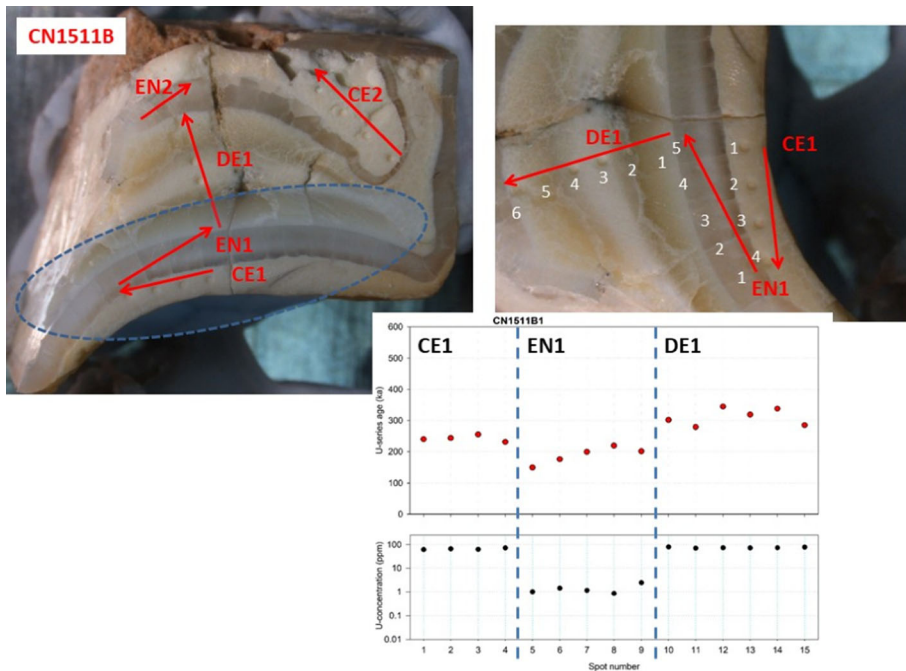


Fig. 5 LA-ICPMS U-series results obtained for transect #1 performed on sample CN1511B. Apparent U-series ages (red circles) and uranium concentration values (black circles) are displayed. The slightly transparent blue domain shows the area sampled for US-ESR dating. Key: CE = cement; EN = enamel; DE = dentine. Numerical values are given in the Supplementary Information 1 (Table S2)

taxa (e.g. *Castillomys rivas*) identified in Jaramillo sub-chron sediments in Murcia at Quibas-Sima near Fortuna (Piñero et al. 2020). Particularly significant at Cueva Negra are the lower first molar teeth of the extinct Arvicoline voles *Victoriamys chalinei* ($n = 155$), *Mimomys savini* ($n = 34$), *Iberomys huescarensis* ($n = 191$), *Pliomys episcopalis* ($n = 11$), *Stenocranius gregaloides* ($n = 3$) and *Terricola arvalidens* ($n = 2$). *Mimomys savini* was a characteristic Biharian species (Fejfar et al. 1998) that existed in Europe from middle Early Pleistocene to early Middle Pleistocene times (ca. 1.8–ca. 0.6 Ma). *Victoriamys chalinei*, *Iberomys huescarensis*, *Stenocranius gregaloides* and *Terricola arvalidens* are well-known in Spain during the late Early Pleistocene (Cuenca-Bescós et al. 2010), when *Terricola* and *Stenocranius* arose (Van Kolfschoten and Markova 2005), whilst the last appearances in Spain of *Victoriamys chalinei*, *Iberomys huescarensis*, *Stenocranius gregaloides*, *Terricola arvalidens* and *Pliomys episcopalis* are during the early Middle Pleistocene (Agustí et al. 2015; Cuenca-Bescós et al. 2010).

The association at Cueva Negra of *Mimomys savini*, *Iberomys huescarensis* and *Stenocranius gregaloides* has parallels in northern Spain in layers TD3-TD8 at Atapuerca (Cuenca Bescós et al. 1995, 1999), and layers D5 at Cal Guardiola and Vallparadís EVT7, at Terrassa in Catalonia (Minwer-Barakat et al. 2011); at Atapuerca, the *Allophaiomys* (*Victoriamys*) *chalinei* biozone falls between ca. 0.9 and ca. 0.6 Ma (Cuenca-Bescós et al. 2010). In southeastern Spain, Cueva Victoria near Cartagena in Murcia has given its name to the many specimens of *Victoriamys chalinei* (Martin

2015) from sediments for which $^{230}\text{Th}/\text{U}$ and palaeomagnetic analyses of flowstone imply an age of ca. 0.9–0.85 Ma (Budsky et al. 2015; Gibert and Scott 2015; Gibert et al. 2016). In Granada, *Iberomys huescarensis* and *Mimomys savini* come from the Huéscar 1 site (Mazo et al. 1985; Agustí et al. 2010). Extended-range luminescence dating using a suite of different cutting-edge approaches (OSL dating of quartz “supergrains”, multi-grain and single-grain thermally transferred (TT) OSL of quartz and post-infrared infrared (pIR-IR) stimulated luminescence of K-feldspars) yielded internally consistent ages of ca. 0.45 Ma (Demuro et al. 2015) for the site, i.e. much younger than the pre-Brunhes chronology (>0.77 Ma) derived earlier by magnetostratigraphical correlation with the nearby locality of Puerto Lobo (Gibert et al. 2007). Additionally, biochronological inference based on the abundant presence of *Mimomys* and absence of *Arvicola* suggests a time no later than the initial Middle Pleistocene (0.77–ca.0.6 Ma). The *I. huescarensis* biozone defined in the Granada Guadix-Baza Basin (Agustí et al. 2015) between 1.07 and ca. 0.8 Ma (perhaps reaching a slightly younger age), and the following *T. arvalidens* biozone there, after the Matuyama-Brunhes boundary, afford an appropriate chronological context for Cueva Negra which has provided two *T. arvalidens* teeth and lies 50 km away from the northern rim of the Guadix-Baza Basin. In western Andalusia, in Cadiz, the late Early Pleistocene site of El Chaparral offers a range of arvicoline species comparable with those at Cueva Negra (López-García et al. 2012).

The initial study of excavated bones of 66 bird taxa (by avian palaeontologist A. Eastham in Walker et al. 2004, 2006) is being extended currently (2019–2020) by A. Rufà Bonache. Hermann’s tortoise is represented by abundant remains identified as *Testudo* (*Eurotestudo*) *hermanni* (X. Murelaga Bereicua, pers. comm., 2007–2008; and see comment in Morales Pérez and Sanchis Serra 2009, 1156; for definition of *Eurotestudo*, see de Lapparent de Broin et al. 2006a, b, c). Latterly, following Bour and Ohler (2008), it has been argued by Pérez-García et al. (2015) that Hermann’s tortoise at Cueva Victoria in Murcia should be classified as *Chersinne hermanni*, which may have consequences for further investigation of the Cueva Negra specimens, given that both sites are of similar age. Intriguing taphonomical research suggests that early humans consumed tortoise before 1 Ma at the Atapuerca Sima del Elefante (Blasco et al. 2011). Remains of reptiles and amphibians corresponding to thirteen taxa, all present in Spain today, indicate summer and winter temperatures similar to those nowadays at Cueva Negra though precipitation was greater (H-A. Blain, pers. comm., unpublished report October 2019). Compilation of the complete faunal list is at an advanced stage of progress. The small vertebrates are consistent with palynological evidence of benign environmental conditions and overlapping biotopes including temperate gallery woodland with deciduous trees identified by palynology (Carrión et al. 2003; Carrión García et al. 2005; Carrión and Walker 2019). Nearby presence of a lake is indicated by eight species of waterfowl, including diving pochards that reflect the existence of an erstwhile lake near the cave (of the eight, only the mallard exists in the neighbourhood today). The faunal taxa identified at the site indicate the presence of other biotopes nearby, namely, open mixed woodland, open grassland and moorland and craggy mountainsides. The biodiversity manifested by the excavated remains is undoubted evidence of the importance of the habitat that the rock shelter afforded to several species that frequented it. Flora and fauna are appropriate for a warm marine isotope stage, plausibly MIS21 (0.87–0.81 Ma),

though other contenders could be MIS 25 (after ca. 1 Ma; cf., Lisiecki and Raymo 2005) or the somewhat cooler MIS23 (ca. 0.9 Ma). These are not, however, the only possibilities, because, during glacial periods, the Iberian Peninsula was often a refugium for “interglacial” fauna (“glacial species” of such large mammals as reindeer, woolly rhinoceros and mammoths first appeared in Spain perhaps as late as MIS 6); moreover, before MIS 16, glaciations seem to have been less severe; therefore, the presence of temperate-adapted fauna need not altogether rule out a glacial period.

Large Mammals

Revision of remains of the large mammals excavated at Cueva Negra demonstrates presence of *Macaca* sp., Proboscidea indet., *Ursus* sp., Mustelidae, *Crocota*, *Lynx* sp., *Equus* cf. *altidens*, *Stephanorhinus etruscus*, *Sus scrofa*, *Capreolus*, *Dama* cf. *vallonnetensis*, *Megaloceros novocarthaginiensis*, Caprini indet. and *Bison* sp. There are some differences with previously published faunal lists (e.g. Walker 2009), where *Equus* cf. *suessenbornensis*, *Bos primigenius*, *Cervus* cf. *elaphus* and *Capra* cf. *ibex* were included; as explained elsewhere (Walker et al. 2016a), small fragments of large mammals, recovered during the 1981 prospection, when the assemblage was regarded as early Late or late Middle Pleistocene in age, understandably were assigned provisional taxonomical identifications appropriate for that period by J. Estévez Escalera, which continued to influence excavators after 1990 until much earlier extinct taxa began to be identified by J. Gibert i Clois whose death in 2007 unfortunately delayed the process of taxonomical revision. None of the available caprine remains favours an assignation to *Capra* over *Hemitragus*. The only horn core belongs to *Bison* and bovine dental remains also fit that taxon. Large deer and horse are discussed below. Some specimens of biochronological relevance are discussed here. Detailed analysis is in progress of the numerous large-mammal fossils. A preliminary conclusion is that *Crocota* and *Bison* imply an open landscape away from the river valley, whilst deer, bear and boar point to more closed conditions, probably in the river valley. *Equus* cf. *altidens* suggests an open, dry landscape nearby. The caprine and perhaps the macaque suggest the rocky environment of the surrounding steep valley sides. The deer, boar and macaque imply temperate environments, either during an interglacial period or maybe even in a glacial one with limited effect in terms of temperature at this latitude.

Giant Deer *Megaloceros novocarthaginiensis*

A species of large deer is represented by a skull fragment, teeth and dental and bone fragments (some of these remains previously had been regarded as *Cervus*). What remains of the brow tines shows that they were palmate (Fig. 7 (1)). European large deer form two groups (Azzaroli 1952). The genus *Megaloceros* has palmate brow tines, whilst various other genera have brow tines that are cylindrical in cross section.

The species of *Megaloceros* includes *M. giganteus*, *M. novocarthaginiensis*, *M. savini* and *M. matritensis*. These differ in the morphology and proportions of their antlers, mandible, dentition and the bones of the skeleton, as well as in dental enamel thickness and absolute size (Van der Made and Tong 2008; Van der Made 2015a, 2019; Van der Made et al. 2017). The adults of *Megaloceros giganteus* have palmate

brow tines that dip laterally, whilst in the other species, they dip medially (Van der Made and Tong 2008). In the large deer from Cueva Negra, the plane of palmation dips medially, in contrast to *M. giganteus*. The antero-posterior diameter of the antler above the burr (DAPb) and the height of the bifurcation between brow tine and main beam (Hext) are indicated in the bivariate diagram (Fig. 7) where different species of *Megaloceros* occupy separate fields in terms of differential proportions and size of their antlers. *Megaloceros novocarthaginiensis* is represented by two specimens that show some damage; hence, real values were slightly larger than those measured (see arrows in Fig. 7). The Cueva Negra antler affords high values for both Hext and DAPb, as in *M. novocarthaginiensis*. General size, as indicated by dentition, accords with this identification.

This identification has biochronological implications. The giant deer *M. novocarthaginiensis*, *M. savini* and *M. matritensis* share features, which are interpreted as shared derived features, including a palmate brow tine that dips medially, a middle tine and moderately robust mandibles (Van der Made 2015a, 2019; Van der Made et al. 2017). These three species show, in this order, a cline in decreasing size and the progressive development of morphological features, including a lowering of the origin of the brow tine, increased relative premolar size (particularly P₂), and an increase in enamel thickness. *Megaloceros novocarthaginiensis* is described at Cueva Victoria near Cartagena in Murcia (Van der Made 2015a). The age of Cueva Victoria was interpreted initially as ca. 1.2–1.4 Ma (Agustí et al. 2015), though subsequent palaeomagnetic and ²³⁰Th/U analyses of flowstones point towards ca. 0.9–0.85 Ma, possibly correlated to MIS22 (Gibert et al. 2016 and references therein). *Megaloceros savini* is believed to be of early Middle Pleistocene age and is known from a series of localities in the Cromer Forest Bed (UK), including Pakefield (Lister 1993) as well as from Voigtstedt and Süssenborn in Germany (Kahlke 1965, 1969). Pakefield is probably the oldest of these localities and is correlated to MIS17, ca. 0.68 Ma, or MIS19, ca. 0.75 Ma (Parfitt et al. 2005). *Megaloceros matritensis* is known from 10 localities or levels, which are all younger than all known localities with *M. savini*. These three species form an evolutionary lineage, because (1) they share derived features, showing them to be closely related; (2) they have different ages; and (3) there is a gradual change in size and morphology from the older to the younger species (Van der Made 2015a, 2019; Van der Made et al. 2017). Being ancestral to *M. savini*, presence of *Megaloceros novocarthaginiensis* at Cueva Negra indicates an older age than that of any site with *M. savini* (Figs. 6 and 7). Even though the earliest *M. savini* might not be from MIS19, but instead from MIS17, some time is needed in order to evolve a different morphology and size from *M. novocarthaginiensis*, suggesting a final Early Pleistocene age for Cueva Negra.

Rhinoceros *Stephanorhinus etruscus*

Cueva Negra has provided over 30 Rhinocerotid fossils, nearly all of them tooth fragments. The enamel of the teeth is smooth as in *Stephanorhinus*, unlike the rugose enamel of *Coelodonta*. The four European *Stephanorhinus* species differ in size, tooth proportions and morphology of the skull, teeth and postcranial skeleton. Whereas *Stephanorhinus kirchbergensis* was a large species, the Cueva Negra teeth are more similar in size to those of the remaining species. These species differ in hypsodonty,

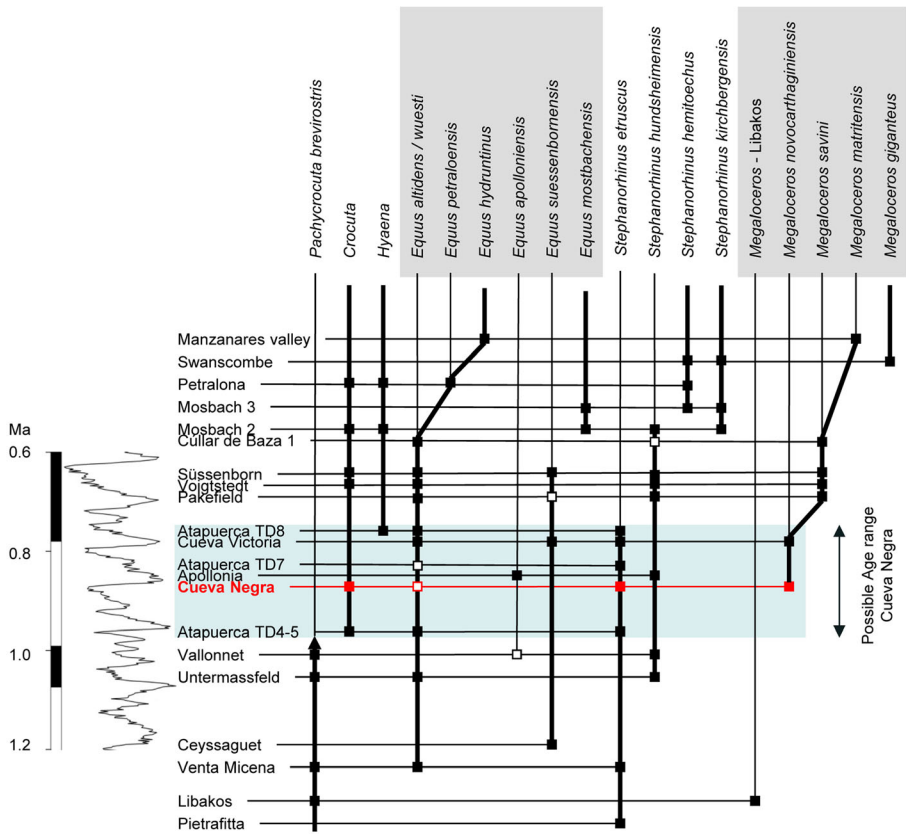


Fig. 6 Stratigraphical distribution of taxa discussed in the text (after Van der Made et al. 2017). Solid squares indicate presence, and open squares indicate possible presence or presence of a similar species that is not exactly known (conventionally indicated by: cf., aff., ?, sp.). Localities older than 1.2 Ma and younger than 0.6 Ma shown in approximate order of age (old below, young top)

which is well seen in the molars, of which there are bigger samples, but the pattern is similar in the premolars. P_3 and P_4 are from the same tooth row and both are unworn at the junction of the anterior wing of the hypoconid and the metalophid, which is where crown height is measured (Van der Made 2010). The Cueva Negra P_4 (Fig. 8) is more hypsodont than its homologue in *S. hundsheimensis*. The M_3 has a posterior valley, which in lingual view is U-shaped, whilst that of *S. hemitoechus* has a V-shape. Therefore, the rhinoceros from Cueva Negra is not *S. hemitoechus*. The teeth from Cueva Negra are most similar to those of *S. etruscus*. The later samples of *S. etruscus* have been considered, variously, to be small and more closely related to *S. hundsheimensis* (Mazza et al. 1993), to belong to that species (Lacombat 2006), or to be more closely related or identical to *S. etruscus* (Cerdeño 1993; Van der Made 1999, 2010, 2015b; Pandolfi et al. 2017). The material from Cueva Negra belongs to this small rhinoceros.

The late appearances of *S. etruscus* (Pandolfi et al. 2017) at Cueva Victoria (Van der Made 2015b) and Atapuerca TD4-7 (Van der Made 1999) are both below the Matuyama-Brunhes boundary and above the Jaramillo sub-chron (Gibert et al. 2016;

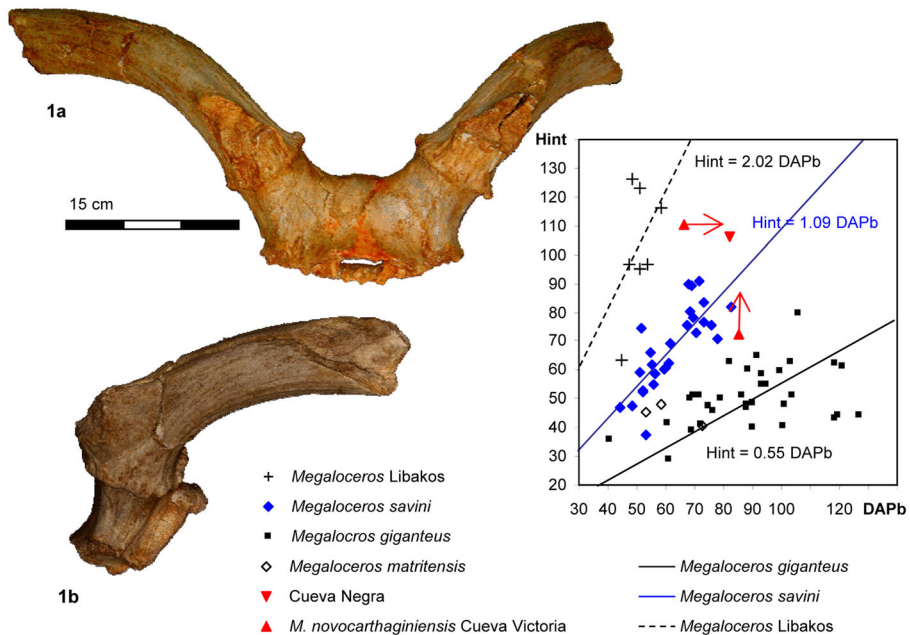


Fig. 7 *Megaloceros novocarthaginiensis* from Cueva Negra (squares C2b, C2c; layers 3k, 3l): skull fragment with bases of right and left antlers, in (1a) frontal and (1b) left lateral views. Right: bivariate diagram comparing DAPb and Hext of the antlers of various species of *Megaloceros*. DAPb = antero-posterior diameter of the antler, taken just above the burr. Hext = distance from just below the burr to the bifurcation between the brow tine and main beam, measured on the lateral side. Measurements as by Van der Made and Tong 2008, Fig. 4. Arrows indicate approximate measurements. Specimens: *Megaloceros* sp. from Libakos (material studied in TUC - see Supplementary Information 2 for acronyms of collections); *M. novocarthaginiensis* from Cueva Victoria (IPS, MAC; Van der Made 2015a) and Cueva Negra (MAM); *M. savini* from Ponte Galeria (MPUR), Süssenborn (IQW) and Cúllar de Baza 1 (MNCN); *M. matritensis* from Transfesa (MNCN; Van der Made et al. 2017) and Arenero los Pinos/km 5 carretera de San Martín de la Vega - both in terraces of the Manzanares in Madrid (MSI; Van der Made et al. 2017); *M. giganteus* from Swanscombe (NHM), Steinheim (SMNS), Neumark Nord (LVH), Bisnik Cave (ZPALUWr), Late Pleistocene Rhine sediments (SMNS; IPRFWUB), Botro Maspino (IGF) and “Altai” (IAMM)

Parés et al. 2013, 2018; Álvarez-Posada et al. 2018). Palaeomagnetic and $^{230}\text{Th}/\text{U}$ analyses of flowstones imply an MIS22 age ca. 0.9–0.85 Ma for the Cueva Victoria faunal assemblage (Budsky et al. 2015; Gibert and Scott 2015; Gibert et al. 2016). The Atapuerca Gran Dolina TD4-7 levels have been dated by a multi-technique dating approach including magnetostratigraphy, US-ESR, TL, pIR-IR and TT-OSL methods (Álvarez-Posada et al. 2018; Arnold et al. 2014; Berger et al. 2008; Falguères et al. 1999). More recently, direct combined U-series/ESR dating of a *Homo antecessor* tooth from TD6 provided a constrained age of 0.95–0.77 Ma (Duval et al. 2018). The only known Middle Pleistocene occurrence of *S. etruscus* is at Atapuerca TD8 (Van der Made et al. 2017) immediately above the Matuyama-Brunhes boundary (Parés et al. 2013) and dated variously to around 0.6 Ma (Falguères et al. 1999) and 0.816 ± 0.140 Ma (Berger et al. 2008). The site was correlated to MIS19 on the basis of these methods and fauna (Van der Made et al. 2017). The presence of a small rhinoceros, identified as *S. etruscus*, suggests an age for Cueva Negra, not later than TD8 or MIS19.

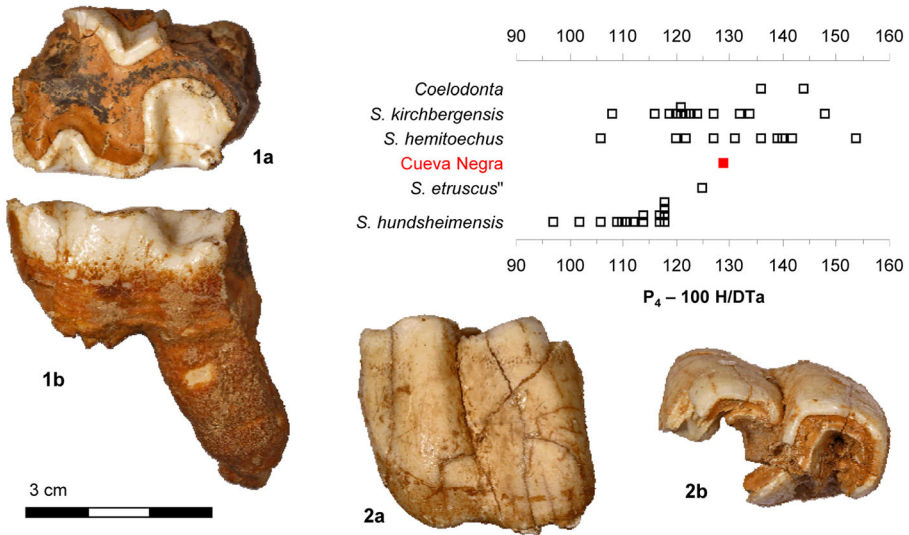


Fig. 8 *Stephanorhinus etruscus* from Cueva Negra: (1) right M_3 in (1a) occlusal and (1b) lingual views (square C2a, layer 6e; ID = H03-016); and (2) left P_4 in (2a) buccal and (2b) occlusal views (ID = H00-015). Top right: comparison of the hypsodonty indices of this P_4 with various species of European Pleistocene rhinoceroses. Specimens: *S. hundsheimensis* from West Runton (NHM), Voigtstedt (IQW), Süssenborn (IQW), Mosbach (NMM); “small *S. etruscus*” from Atapuerca TD-base (MB), Cueva Negra (UMu); *S. hemitoechus* from Bilzingsleben (FBFSUJ), Ehringsdorf (IQW) and Late Pleistocene Rhine sediments (NMM); *S. kirchbergensis* from: Mosbach (NMM), Bilzingsleben (FBFSUJ), Ehringsdorf (IQW) and Late Pleistocene Rhine sediments (NMM); *Coelodonta* from Late Pleistocene Rhine sediments (NMM). The hypsodonty index is $100 H/DTa$, where H = crown height and DTa = transverse diameter of the anterior lobe (measurements as in Van der Made 2010, Fig. 5/3)

Horse *Equus* cf. *altidens*

Many horse fossils, mostly teeth, were recovered from Cueva Negra. The lower cheek teeth have V-shaped linguaflexids (or entoflexids; Fig. 9 (1)) and the upper cheek teeth have short protocones (Fig. 9 (2)), as in the stenonid horses and unlike the caballoid horses (Forstén 1988). Therefore, they do not represent a caballoid horse such as *E. caballus*. The stenonid horse *E. suessenbornensis* is very large and has many plications in the upper cheek teeth (Musil 1969), whereas Cueva Negra horse teeth are smaller with few plications (Fig. 9 (2)). Another large horse was *E. apolloniensis* (Koufos et al. 1997). The remaining stenonid horses of the late Early to Late Pleistocene of Europe are small, present fewer plications in the upper cheek teeth and have slender metapodials. Horses of this group from the latest Early Pleistocene were slightly larger than the earlier and later *E. altidens* and currently are assigned to other species, such as *E. wuesti* (Musil 2001), though the exact relationship with *E. altidens* is unclear (Van der Made et al. 2017). From the earliest Middle Pleistocene onwards, these horses plausibly formed an evolutionary lineage *E. altidens* - *E. petralonensis* - *E. hydruntinus* (Van der Made et al. 2017), characterised by decrease in postcranial size. This is less clear in the teeth, no doubt because their very hypsodont teeth show a wide range of variation. At Cueva Negra, the teeth fall within an overlapping range between *E. altidens* and *E. petralonensis* (Musil 1969; Tsoukala 1989), though sparsity of

postcranial remains precludes further precision. The horse fossils from Cueva Negra are assigned to *Equus* cf. *altidens*.

Caballoid horses appeared first with *E. mosbachensis* and maybe *E. ferus* (or *E. ferus torralbae*) ca. 0.6–0.5 Ma and replaced the large stenorid horse *E. suessenbornensis*. The smaller *E. altidens* survived this event and coexisted with the caballoid horses, giving rise to the smaller *E. petralonensis* (Van der Made et al. 2017). The horse from Cueva Negra belongs to one of those species. This imprecision limits the biochronological value. However, a left maxillary $M^{1/2}$ of *Equus* cf. *altidens* from Cueva Negra (ID = CN-09152) was used for ESR dating (CN1511) (Figs. 1, 4 and 5).

Spotted Hyaena *Crocota*

A hyaena mandible (Fig. 10) came from disturbed sediment that filled a small pit dug into the Pleistocene sediments after the Spanish Civil War. The specimen likely came from the upper part of the sediments of Cueva Negra (in 2019, more hyaenid fossils were excavated in them). Its teeth are damaged, but its P_4 length is measurable. Originally, its M_1 length exceeded that of the existing tooth fragment which nevertheless is as long as in *Crocota*. The genus *Crocota* has elongated M_1 that are longer with

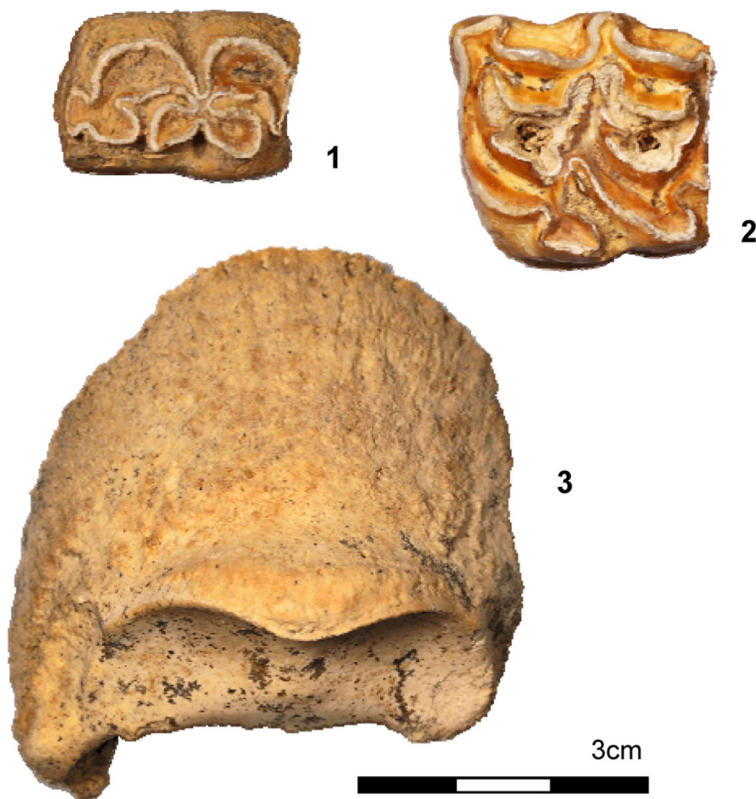


Fig. 9 *Equus* cf. *altidens* specimens from Cueva Negra: (1) left $M_{1/2}$ (ID = H93-007) in occlusal view; (2) left $P_{3/4}$ (ID = H05-021) in occlusal view; (3) third phalanx in dorsal view

respect both to their width and to the length of the other cheek teeth than was the case in *Hyaena* and *Pachycrocuta*; the specimen from Cueva Negra clusters with *Crocota* (Fig. 10).

Crocota was common in Western Europe and the oldest site with certain presence of *Crocota* is Atapuerca Trinchera Dolina TD4 (García and Arsuaga 2001; Fig. 3), shown by palaeomagnetism to be slightly younger than the Jaramillo sub-chron (Álvarez-

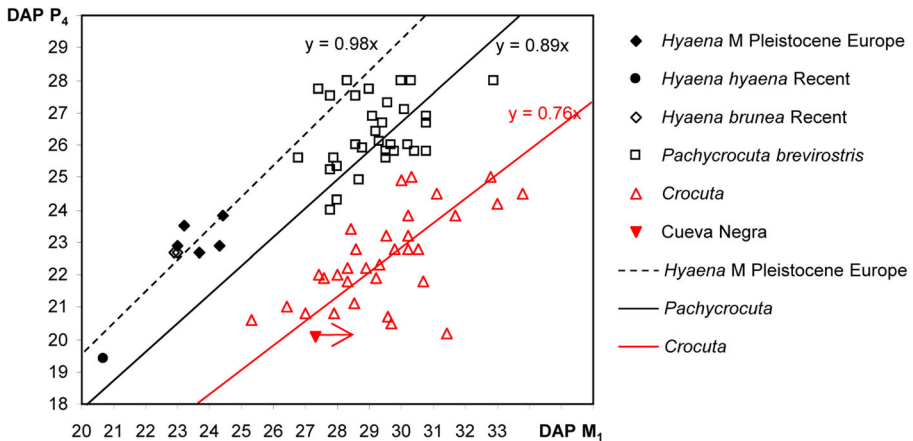


Fig. 10 *Crocota* from Cueva Negra (squares C2a/2b, ID=HM0001): right mandible with P₂-M₁, in (1a) occlusal and (1b) lingual views. Bivariate diagram comparing antero-posterior diameters (DAP) of M₁ and P₄ of different Hyaenidae. Specimens: recent *Hyaena hyaena* from Khorramabad (Iran); recent *Hyaena brunnea* (NBC); Middle Pleistocene *Hyaena* sp. from Atapuerca TD8 (IPHES), Mosbach (NMM), St. Estève and Lunel Viel (Bonifay 1971); *Pachycrocuta brevirostris* from Valdarno, Sainzelles, Kromdraai, Venta Micena, Untermaassfeld, Vallonnet, Gombaszög, Incarcari I, Lakhuti, Zasuhino, Stránská Skála, Manastirec, Siwaliks Volga R, and Zhoukoudian (data from Turner and Antón 1996); *Crocota* from Tighennif (MNHN), Lunel Viel, Châtillon-St.-Jean, Grotte de la Baume Longue and Rigabe (Bonifay 1971) and Abric Romani (MMPC), as well as from Cueva Negra

Posada et al. 2018; Parés et al. 2018). The presence of this taxon, probably at the top of the sequence of Cueva Negra, suggests an age not older than TD4.

Bear *Ursus* Sp.

Isolated anterior teeth, disconcertingly similar in size and shape to some isolated first and second mandibular Neanderthal incisors published from the Grotte d'Hortus (de Lumley-Woodyear 1973), were found in superficial loose sediment and compared with Neanderthal examples (Walker et al. 2006) at a time when the Cueva Negra deposits were considered to be no earlier than the late Middle Pleistocene, but acceptance of their greater antiquity now renders untenable any such comparison. Subsequent morphological considerations imply that those specimens very likely belong to *Ursus* sp., in support of which a characteristically ursid lateral (third) incisor was identified during the 2019 excavation in the uppermost sediments of a hitherto unexcavated area at the rear of the cave; levels excavated previously at the site had provided one or two bone fragments tentatively regarded as ursid also.

Discussion

The late Early Pleistocene age of the Cueva Negra assemblage is supported by presence of the giant cervid *Megaloceros novocarthaginiensis* in sediments that magnetostratigraphy assigns to the Matuyama chron. *Megaloceros novocarthaginiensis* is known only from the late Early Pleistocene. The rhinoceros *Stephanorhinus etruscus* is an Early Pleistocene taxon that is recorded at only one early Middle Pleistocene site. Palaeontological considerations of Cueva Negra imply a time after the Jaramillo sub-chron (1.07–0.99 Ma: Channell et al. 2020). Consequently, the sedimentary sequence must have been laid down between the end (0.99 Ma) of that sub-chron and the Matuyama-Brunhes boundary at 0.772 Ma. The palaeontological and magnetostratigraphical constraints of 0.99–0.772 Ma are compatible with the age range given by the CSUS-ESR and US-ESR age results of 1446 ± 310 ka and 406 ± 40 ka (i.e. 1.45 ± 0.31 Ma and 0.41 ± 0.04 Ma), respectively.

At the rear of the cave, at a depth of 4.5 m (Fig. 3), well below the level dated by ESR sample CN1511, undoubted evidence of combustion has been exposed to date over a 4-m² area in a layer of ashy sediment containing diverse, thermally affected elements including bone fragments, chert (flint) nodules and struck flakes (Walker et al. 2016b). Chert had been heated to >400–450 °C according to TL and ESR palaeothermometry determinations, though higher temperatures are implied by >100 heat-shattered chert spalls <2 mm in size, and by both low- and high-power microscopy of thermally altered chert (Walker et al. 2016b). Bone had been heated to >400–450 °C according to FTIR. The effects of combustion are supported by (1) SEM-EDS, (2) contrasts with bones in overlying layers involving colorimetric and taphonomical analyses of small-mammal remains (Rhodes et al. 2016; Walker et al. 2016b) and (3) the significant component of hydroxyapatite in the combusted sediment in contrast to overlying and underlying sediments, the chemical and mineral composition of all of which have been compared using thermogravimetric analysis with mass spectrometry and granulometry by laser diffraction, and XRF and XRD methods (Walker et al.

2016b). The deeply lying combustion feature is of great interest because the high temperature that was reached suggests fire was tended deliberately at the rear of the rock shelter (Walker et al. 2016b). It is plausible, therefore, that at Cueva Negra, fire was tended inside the cave, causing temperatures above those usually reached by bush fires outdoors. Absence of hearth stones or a fire pit implies uncontrolled heat. However, unless provision of suitable fuel had been made inside the cave, it is unlikely that sparks from a bush fire outside could have set alight brushwood, by chance lying inside, such as to produce a roaring fire. Maybe a bush fire outside left embers that were taken inside, where fire could be tended away from rain or wind. Plausibly, whoever frequented the cave was less afraid of fires than were animals fleeing from them. A blazing fire tended in a cave could fulfil several purposes: keeping fierce animals away, providing warmth and light and roasting food in its embers. Fire implies human cognitive capability at Cueva Negra comparable with that at other sites with combustion and hand axe remains such as Wonderwerk Cave ca. 1 Ma in South Africa (Berna et al. 2012) and Gesher Benot Ya'aqov ca. 0.78 Ma in Israel (Alpersen-Afil 2012; Alpersen-Afil and Goren Inbar 2010; Goren-Inbar et al. 2004).

The Cueva Negra artefact assemblage demonstrates presence of technological diversity and utilisation of a variety of raw materials. A bifacially flaked hand axe on limestone was excavated (in "lithostratigraphical unit II_{ii}", spit 3h: Fig. 3) approximately 1 m above the dated equid tooth CN-1511. It was fashioned by removal of no more than 30 flakes from a hard limestone cobble that still bears some cortex (Walker et al. 2006, Figs. 8 and 9; 2013, Fig. 6; 2016a, Fig. 1). It had lost its tip in antiquity; its edges are sharp and fresh, neither rolled nor water-worn, and its horizontal transverse cross section shows an S-twist (which is seen often in "Acheulian" hand axes). A chopping tool with sharp, fresh edges, formed by unidirectional removal of 15 flakes from a flat limestone cobble, was excavated in the same layer. The hand axe and chopping tool were examined by XRD analysis and petrological microscopy. They had been fashioned on flat, hard cobbles that probably came from a fluvio-lacustrine gravel formed by erosion of mountainsides containing Mesozoic Jurassic Middle Lias beds of limestone containing a quartz component that rendered it particularly hard. By contrast, quartz was not detected in limestone cobbles that likely had been eroded from Middle Jurassic Dogger beds of Mesozoic limestone containing less quartz, and that, in the Cenozoic era, were incorporated into an Upper Miocene (Tortonian) conglomerate from which cobbles of limestone, quartzite and chert have been sampled at an outcrop 0.8 km east of Cueva Negra, and where artefacts resembling some excavated at the cave have been collected (Walker et al. 2006), as well as a small discoidal core, fashioned from chert, which was discarded after centripetal working had removed the last flake from it, as evidenced by the resulting flake scar (Walker et al. 2016a, Fig. 3b). Notwithstanding the predominant presence of chipped artefacts of chert (flint) in the Palaeolithic assemblage at Cueva Negra (Walker et al. 2016a, Table 4c), attention is drawn to the fact that it was not chert but a particularly hard type of limestone on which the hand axe and chopping tool were fashioned, though several small artefacts in the excavated Palaeolithic assemblage also are of limestone. A small discoidal limestone core with a central scar corresponding to the last flake removed from it was found on the surface beside the mouth of the cave (Walker et al. 2016a, Fig. 3a); the core itself seems to have been fashioned from a very large flake of limestone rock.

In relation to the 5-m depth of sedimentary complexes Cx2, Cx3-1 and Cx3-2 (Fig. 3), the small artefacts excavated in these are fundamentally similar throughout, both as regards technological aspects and rock types (Walker et al. 2016a, Tables 4c, d), and the latter includes chert, limestone, marble, quartzite, quartz and a single example of radiolarite. Laser-ablation inductively coupled plasma mass spectrometry enabled analysis of trace elements for “finger-printing” cherts, such that a sample from Cueva Negra could be compared and contrasted with samples obtained at several outcrops in and around the upper Quípar valley: 56 chert samples were analysed for 19 lanthanide and rare-earth trace elements, all of which afforded detectable values in those items (Zack et al. 2013). Factor analysis, applied to the values, differentiated between sources, and corroborated the plausible inference from field work that an Upper Miocene (Tortonian) conglomerate outcrop 0.8 km east of the cave was the likely source of most of the excavated chert, though a small proportion (ca. 15%) could have come from sources up to 30 km away (Zack et al. 2013). High-power microscopical inspection by one of us (I. M-L.) is underway of the steep and abrupt secondary knapping (“retouch”) of “scraper” edges at Cueva Negra, with the detection of polish (cf., Keeley 1980; Gutiérrez Sáez 1996; Márquez et al. 2001; Martín-Lerma 2015) and striae (cf., Del Bene 1979; Mansur-Franchomme 1980) typical of those caused by application to animal skin or flesh (cf., Peretto 1994; Ollé 2003; Bello et al. 2009; Cristiani 2009; Lemorini et al. 2014, 2019; Viala et al. 2020). Plausibly, they may well have been caused by the defleshing of herbivores and ruminants, such as those excavated at the cave, and initial inspection of polish and striae on other pieces (e.g. Fig. 11) suggests their use on harder materials such as wood, bone or antler (cf., Crovetto et al. 1994a, b; Pedergrana and Ollé 2017). Small artefacts often referred to in the Palaeolithic literature as beaks (*becs*) rarely show microscopical signs of use wear or edge damage at Cueva Negra and probably were small cores from which very small flakes were removed for use as tools without secondary knapping, as has been proposed for similar pieces at the Italian site of Isernia La Pineta (Crovetto 1994; Crovetto et al. 1994a; Longo et al. 1997; Peretto 1994; Peretto et al. 2004), and unretouched microflakes 5–15 mm in size abound in the Cueva Negra débitage. Occasionally, artefacts at Cueva Negra show evidence of re-use after patina had developed over earlier secondary knapping (cf., Parush et al. 2015).

With very few exceptions indeed, the chipped stone elements are < 60 mm in size (Walker et al. 2016a). Secondary knapping, i.e. edge-“retouch”, on struck flakes (that are defined by having a striking platform and bulb of percussion) was reported in 3% of an excavated sample of 3500 chipped stone pieces (Walker et al. 2016a, Table 4d), including on “microlithic” flakes < 30 mm in size (e.g. Walker et al. 2016a, Fig. 5d, p). Among chert (flint) flakes struck by repetitive or recurrent removal from cores are some that were excavated in “lithostratigraphical unit III” (which lies *below* “unit II_{ii}” that contained the hand axe), including one with a faceted striking platform suggestive of preparation beforehand of the core for its hierarchical reduction (Walker et al. 2016a, Fig. 2a), and another with the triangular shape that often characterises flakes that are removed when cores are reduced by centripetal flaking (Walker et al. 2016a, Fig. 2b); in both cases, negative flake scars on the dorsal surface of these flakes indicate recurrent flaking of the cores.

Although the epithets “Acheulian”, “Levalloisian” and “Mousteroid” had been applied at Cueva Negra (Walker et al. 2013), they have been replaced since (Walker

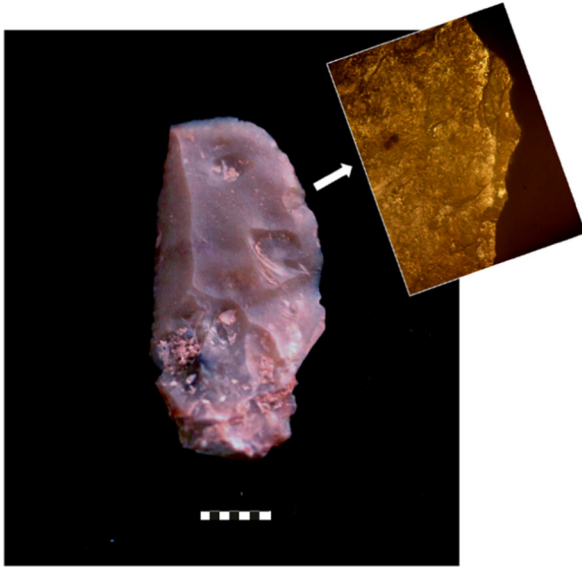


Fig. 11 Flake from Cueva Negra with traces of use-wear characteristic of application to wood and subsequent secondary knapping indicating re-use ($\times 200$). Photo: I. Martín Lerma

et al. 2016a) by Shea's A-I modal descriptors (Shea 2013, 2016). Shea's modal approach relies on the same exclusionary principle and process of elimination that underpin "differential diagnosis" by medical practitioners, working backwards from the objects of study in order to whittle down mutually exclusive categories. An early archaeological practitioner was Yale's Irving Rouse (Rouse 1960; cf., Rouse 1939) who deployed it in the service of differential diagnosis of ceramic types by attribute discrimination. Modal analysis is helpful for analysing the differential composition of a lithic assemblage and defining it from the standpoint of the several technical modes represented in it. Such appreciation goes beyond regarding a prehistoric lithic assemblage as characterisable solely, or even mainly, in terms of the identification in it of a particular forward sequence of core reduction (perhaps detected by lithic refitting) or a particular operational sequence or *chaîne opératoire* (perhaps inferred from diacritical inspection of lithics). Shea's scheme is clinically aseptic, in so far as it avoids contamination from preconceived notions imbued with determinism, whether about essentialist mental concepts underpinning technical behaviour (e.g. Boëda 1994; Boëda et al. 1990; Geneste 1985), essentialist quasi-biological presumptions about Palaeolithic technology having evolved in homotaxial relation to evolution of different hominid species (e.g. "modes 1–5" of Clark 1969, or "1–6" of Clark 1970) or the ecological determinism that tinges some interpretations of lithic reduction sequence studies (for discussion of interactions between different standpoints, see Bar-Yosef and Van Peer 2009; Bleed 2001; Shott 2003; Tostevin 2011). Shea's approach can lead to a consideration of how far it is helpful or useful to embrace particular Palaeolithic assemblages with labels such as "Oldowan", "Acheulian", "Mousterian", "Levalloisian" or Grahame Clark's "modes 1, 2, 3". They raise methodological and epistemological problems. Foremost among them is how far it is useful to speak of *the Acheulian* in general, or, more specifically, an Acheulian *tradition* (Lycett and Gowlett 2008), an Acheulian

identity (Butzer 1971, p. 448) or an Acheulian *techno-complex* (Sharon and Barsky 2016). The unhyphenated term *technocomplex* was coined (Clarke 1968, p. 331) for assemblages with spatio-temporal spreads of ≤ 5000 km in radius and $\leq 20,000$ years (e.g. Solutrian, Magdalenian), in contrast to more circumscribed *culture groups* on the one hand, and, on the other, wide-ranging *industries* regarded (Clarke 1968, p. 667) as sets “of single-material artefact-type assemblages from a continuous space-time area, taxonomically linked by mutual technological affinities. Frequently, a single material aspect from a technocomplex entity” (e.g. Oldowan, Acheulian, Mousterian). Vast differences of temporal scale during the Pleistocene (cf., Bailey 1983) raise substantive questions about the commensurability of various assemblages and “type fossils” indiscriminately assigned to *the Acheulian*. The problem with type-fossil approaches is that “Types are not groups of objects, but classes whose significata consist of sets of modes, stating the necessary and sufficient conditions of membership” (Dunnell 1971, p. 159). A neurobiological propensity in *Homo* for flexible cognitive relationships could have arisen, spontaneously and independently, at widely separated times and places, enabling manual dexterity to advance differential aptitudes for technical innovation, albeit sporadically. Bifacial working of stone has appeared, disappeared and re-appeared, from the mid-Early Pleistocene to the Holocene in Africa and Eurasia, and from the Late Pleistocene to the Holocene in Australia and the Americas (Brumm and Moore 2012). An isolated appearance can be a sufficient rational conjecture for interpreting the Cueva Negra hand axe parsimoniously, without requiring it *also* to exemplify a preconception of “the first Acheulean technology” in southern Spain, supposedly introduced from Africa by a conjectural “MIS 22 human dispersal associated with Acheulean tools” (Gibert et al. 2016); moreover, the Cueva Negra faunal assemblage lacks specifically African faunal taxa.

Because, to date, no more than one hand axe has been excavated at Cueva Negra, by classifying it as a “mode E1 elongated cutting tool” (Shea 2013, 2016), the matter is avoided of how many such tools need be present before labelling an assemblage “Acheulian” or “mode 2”. In drawing attention to the problems that can arise from using a type-fossil name to label a Palaeolithic assemblage comprising diverse forms, Kleindienst (Kleindienst 1961; cf., Kleindienst 1962) proposed reserving the label “Acheulian” for those, mainly later, assemblages in which 40–60% of artefacts were bifacially flaked hand axes or cleavers, as Mary Leakey (1975) recalled though she did not refrain from using it at Olduvai (Leakey 1971; Leakey and Roe 1995). Nevertheless, “Oldowan” (or “mode 1”) is unsuitable also for labelling the Cueva Negra assemblage, because, as at several early European sites, most artefacts at the cave (apart from a C1 unidirectionally flaked chopping tool > 60 mm in size) are smaller than very many Oldowan artefacts from Olduvai (cf., Leakey 1971; Leakey and Roe 1995). By side-stepping unhelpful labels, time-honoured may they be, Shea’s scheme of modes A–I embraces a range of flexible cognitive relationships between stone workers and possibilities afforded by stones (“lithic affordances”). The Cueva Negra Palaeolithic assemblage has examples of Shea’s technical modes A, B, C, D, E and F (and even perhaps sub-mode G1). Modification of Shea’s modal descriptors appropriate for Cueva Negra may have to be entertained in the light of his forthcoming publication about the modal application to African stone artefacts (Shea 2020). In correspondence with Shea, we have indicated (cf., Walker et al. 2016a) that at Cueva Negra, his mode C of pebble cores and non-hierarchical cores (Shea 2013, 158 Table 2)

comprises four distinct groups, as follows: C1 > 60 mm, unidirectionally flaked chopper; C1 < 60 mm, stubby or keeled non-hierarchically worked pieces (small cores and nodules); C2 < 60 mm, showing both large non-hierarchical flake scars and diminutive ones at the bevelled or chamfered tip of an elongated narrow spur that is defined by the large flake scars on a stubby or keeled piece (e.g. Walker et al. 2016a, Figs. 4f-4m; cf., so-called awls, borers, microperforators, beaks, *becs*); C2 < 60 mm, keeled plano-convex pieces the side and extremities of which bear non-hierarchical flake scars (e.g. Walker et al. 2016a, Figs. 4b-4e; cf., so-called slugs, *limaces*, proto-*limaces*, planes, spokeshaves). Although there is evidence of bipolar working at Cueva Negra, the small size of most pieces can render its identification uncertain; nor is it always possible to tell whether a flaked artefact had its origin in a small pebble core or in part of a big flake or fragment detached from a large block (analogous problems exist in other Palaeolithic assemblages, cf., Debénath and Dibble 1994, 10).

The majority of artefacts excavated at Cueva Negra lack formal shape, which is unsurprising because raw materials most often available near Cueva Negra include relatively intractable cobbles of limestone, quartzite and frangible, sub-parallelepiped pieces of tabular chert that, when struck, rarely affords conchoidal fractures or provides feathered flakes with convex bulbs of percussion and well-marked striking platforms. Most chert nodules are *fissural* (Stein 1981, 537: “Fissural” [adj.], entered under “Fissure”; cf., “fissilità” Crovetto et al. 1994b, 87). They shatter often when struck, leaving only tiny chips and fragments. Sometimes, however, striking splits them apart along fissures or *fissural* flat planes, defined by the internal structure and impurities, resulting in flattish, sub-rectangular laminar pieces (Walker et al. 2013, Fig. 17; Walker et al. 2016a, Fig. 5s). Some of these underwent secondary knapping that modified a perpendicular margin by steep “retouch” to give it an acute angle (sub-mode D1) suitable for firm scraping and cutting (e.g. Walker et al. 2013, Fig. 8; Walker et al. 2016a, Fig. 5a and c right-hand piece). Although steep “retouch” applied to the edge of thin, feathered flakes can reduce the risk of snapping during use, well-formed feathered lakes are uncommon at Cueva Negra. Erosion of nearby escarpments caused displacement from Jurassic Mesozoic rock strata of chert (flint) nodules (where some weigh as much as five kilogrammes, 5 kg) that in the Cenozoic era often underwent Miocene, Pliocene and Early Pleistocene rolling and battering, during processes, first, of marine, and, subsequently, continental erosion, followed by deposition in conglomerates or gravels (Walker et al. 2013). In consequence, readily available chert blanks and nodules are mostly small (< 100 mm in size, < 0.5 kg in weight).

The Cueva Negra Palaeolithic assemblage bears comparison with finds from the Spanish Catalanian sites of Barranc de la Boella near Tarragona, where a bifacially flaked schist cleaver, trihedral “pick”, and small chert flakes and denticulates date from between 1 and 0.870 Ma (Vallverdú et al. 2014), and Vallparadís at Terrassa, where ESR and magnetostratigraphy indicate an age of 0.830 ± 0.070 Ma for an assemblage of small artefacts (some prepared by bipolar core reduction), which included *becs*, denticulate and notched pieces, “a few examples of centripetal cores and débordant flakes” and a chopping tool fashioned on a cobble (Barsky et al. 2013; Duval et al. 2012a; Garcia et al. 2011, 2012; Martínez et al. 2010). It is pertinent to remark here that centripetal reduction has been detected in the Italian Pirro Nord 13 assemblage possibly dating from ca. 1.3 Ma (Arzarello and Peretto 2010; Arzarello et al. 2012, 2015), considerably earlier than its appearance at Vallparadís and Cueva Negra. Furthermore,

in East Africa, ca. 1.6–1.4 Ma at Peninj (Tanzania), there were not only hand axes but also discoidal cores fashioned for “obtaining pre-determined flakes” (de la Torre et al. 2003; cf., de la Torre 2009; de la Torre and Mora 2008) though prior hierarchical core preparation has been disputed (Díez Martín and Sánchez Yustos 2012; Díez Martín et al. 2012, 2015).

Prudence counsels against regarding the appearance in Africa and western Eurasia of a variety of analagous techniques for reducing stone cores as representing more than a general propensity in early *Homo*, from the middle of the Early Pleistocene onwards, for manual dexterity, technical capability and cognitive versatility (cf., de la Torre et al. 2003). In terms of natural selection, adaptive value could have been conferred by a general propensity underpinned by neurogenetics and neuroepigenetics (Manrique and Walker 2017; Walker 2016, 2017). Involvement of *epigenetics* carries implications for human biological reproduction that (a) transmission from progenitor to progeny was neither an inevitable nor a necessary outcome, and (b) that neurobiological evolution of the propensity could be non-linear and stall, with “snakes-and-ladders” consequences of appearances, disappearances and re-appearances in the spatio-temporal spread of behavioural aptitudes (moreover, fragile, tiny, human groups can become extinct from extraneous circumstances beyond their control). Such implications complicate proposals based on solely *genetic* co-evolution of dual inheritance (e.g. Boyd and Richerson 1985; Durham 1991; Richerson and Christiansen 2013) which could underpin transmission of hand axe reproducibility (Boyd and Richerson 2005 pp. 54–57, Fig. 3.1; Lycett and Gowlett 2008). The notion of neurobiological propensity is compatible with sporadic appearance of hand axes in an otherwise different lithic assemblage, as at Cueva Negra. It is also compatible with their notoriously variable Pleistocene distribution across the Old World. This underlies long-standing disputes about Hallam Movius’ “Line” (Movius 1948) and the appropriateness of using a common Old World (“Acheulian”) terminology that includes elongated cutting tools bearing flake scars on two opposite faces which exist in eastern Asia (Brumm and Moore 2012; Corvinus 2004; Dennell 2015; Lycett and Bae 2010; Lycett and Chauhan 2010; Lycett and Norton 2010; Norton and Braun 2010; Petraglia and Shipton 2008, 2009).

Fire implies human cognitive capability at Cueva Negra, comparable with that at the Old World sites with combustion and hand axes which are Wonderwerk Cave ca. 1 Ma in South Africa (Berna et al. 2012) and Gesher Benot Ya’aqov ca. 0.78 Ma in Israel (Alpersen-Afil 2012; Alpersen-Afil and Goren Inbar 2010; Goren-Inbar et al. 2004). The small and “microlithic” components of the Cueva Negra assemblage resemble some in the Early Pleistocene assemblage from Bizat Ruhama in Israel (Zaidner 2013) within the Matuyama chron (Laukhin et al. 2001), and small flakes produced by pebble-core reduction were present ca. 1.6–1.4 Ma at ‘Ubeidiya (Bar-Yosef and Goren-Inbar 1993; Shea and Bar-Yosef 1999; Tchernov 1988) where hand axes were present ca. 1.4–1.2 Ma. Earlier examples of hand axes in Israel were reported from Nahal Zihor ca. 1.6 Ma (Grosman et al. 2011). Hand axes were present in India at Attirampakkan ca. 1.5 Ma (Pappu et al. 2011) and Isampur ca. 1.27 Ma (Paddayya et al. 2002). However, only “Oldowan” chopping tools accompanied the small-brain *H. erectus ergaster georgicus* at Dmanisi in Georgia ca. 1.8 Ma (Baena et al. 2010; Celiberti et al. 2004; de Lumley et al. 2005; Džaparidze et al. 1992; Gabounia and Vekua 1995; Gabunia et al. 1999; Garcia et al. 2010; Lordkipanidze et al. 2013; Rightmire et al. 2006). As mentioned in the “Introduction” section, there are

Palaeolithic assemblages without bifacial artefacts in Spain before 1 Ma, e.g. the Atapuerca Sima del Elefante where artefacts and fragmentary *Homo* sp. fossils were excavated in sediments dated to ca. 1.2–1.1 Ma (Bermúdez de Castro et al. 2011; Carbonell et al. 2008; de Lombera-Hermida et al. 2015; Huguet et al. 2017; Parés et al. 2006; Rosas et al. 2006), and at the eastern Andalusian sites of Barranco León-5, where tooth fragments assigned to *Homo* sp. were found, and Fuente Nueva-3, which dated from 1.4 to 1.2 Ma (Álvarez et al. 2015; Barsky et al. 2015; Carbonell and Rodríguez 2006; de Lumley et al. 2009; Duval et al. 2012a, b; Fajardo 2009; Gibert et al. 1998; Gibert et al. 1999a, b; Gibert et al. 2001; Martínez-Navarro et al. 1997; Oms et al. 2000; Ribot et al. 2015; Toro-Moyano et al. 2003, 2009, 2010; Toro Moyano et al. 2011; Toro-Moyano et al. 2013). Different conjectures have been put forward about how often Early Pleistocene *Homo* was present in Western Europe, about possibly available routes of access from Africa, and about what were the corresponding technological behaviours (Bar-Yosef and Belfer-Cohen 2001; Carrión and Walker 2019; Galliotti and Mussi 2018; Gibert et al. 2016; Goren-Inbar and Gonen 2006; Goren-Inbar et al. 2000; Hovers and Braun 2009; Ollé et al. 2016; Sharon and Barsky 2016; Shea 2013, 2016; Vallverdú et al. 2014; Walker 2017). Detailed analysis of the various conjectures falls out with the scope of this discussion.

Suffice it to say that self-justifying conjectures must be eschewed about notional palaeoanthropological and palaeodemographical associations with Palaeolithic technologies, let alone about their conjectural long-distance or inter-continental displacements. It is enough here to indicate that comparable with several Cueva Negra items are some small chert artefacts, excavated together with larger pieces at Fuente Nueva-3 and Barranco León-5 which are near Orce in the northern part of the Guadix-Baza Basin in Granada, barely 50 km from Cueva Negra. The lithic diversity of the Cueva Negra assemblage reflects cognitive capacity for technical competence, and underlines the pertinence of reflexions by others that have taken note of the lithic diversity and variability of European Early Pleistocene assemblages (Barsky 2009; Barsky et al. 2013, 2015; Carbonell et al. 2009). It has to be remarked, nevertheless, that the Cueva Negra Palaeolithic assemblage shows scant resemblance either to the assemblages of ca. 1.2–1.1 Ma from the Atapuerca Sima del Elefante, or those from layers TD6-TD4 of the Atapuerca Gran Dolina (Carbonell et al. 1995, 1999; Mallol 1999; Terradillos Bernal 2010) attributable to *H. antecessor* that dates from 949 to 772 ka (Duval et al. 2018) and therefore was contemporary with Cueva Negra. An accommodative conjecture might be that whereas possible demographical displacements in western Eurasian latitudes of low relief could have occurred in response to palaeoenvironmental fluctuations during the Pleistocene (Hosfield 2016), nevertheless the high topographical relief of regions around the northern shore of the Mediterranean Sea could have favoured a variety of idiosyncratically local responses by small, environmentally restricted, human communities (Carrión and Walker 2019; Walker 2017). Of plausible relevance here is the likelihood of the adaptability of later Early Pleistocene humans with regard to availability of resources and their seasonal variability in northern Mediterranean landscapes (Carrión and Walker 2019; Walker 2017). Microstratigraphical analysis shows that Palaeolithic activity at Cueva Negra was discontinuous (Fernández et al. 2018), doubtless on account of sporadical incursions of water, overflowing (perhaps seasonally) from the erstwhile lake nearby, fed by the Quípar River, and responsible for the alluvial sediments deposited in the rock shelter. Conceivably, human absences

favoured accumulation in the rock shelter of remnants of small vertebrates that had succumbed to foxes, lynxes and birds of prey (non-human impingement is implied by taphonomical considerations: Rhodes et al. 2016; Walker et al. 2016b). Currently, the objects of doctoral research by G. Linares-Matás at Oxford University are bones showing cut-marks and others with signs of gnawing which have been excavated in several levels that contained Palaeolithic artefacts. In particular, excavation in 2019 of the uppermost sediments at the rear of the rock shelter, hitherto unexplored, uncovered bones of large carnivores, including hyaena and bear, and large herbivores, including giant deer and horse. Moreover, in the 1990s, remains of bison, rhinoceros and a Proboscidean were found in the uppermost sediments, adjacent to the 2019 excavation, which were near the mouth of the cave, and preliminary taphonomical observations from the uppermost sediments imply that the cave may have become a haunt of carnivores after humans had ceased to frequent it. In any case, the biodiversity manifested by the excavated remains throughout the sedimentary sequence is undoubted testimony to the importance of the habitat that the rock shelter afforded to several species that frequented it, though the complex stratigraphical palimpsest, to which they contributed, renders it hard to disentangle, with accuracy and precision, the part played by its Palaeolithic visitors. It is opportune, with a view to suggesting a possible analogy, to offer brief remarks on a contemporaneous site in Spain where research is further advanced and suggests an appropriate direction for future scientific inquiry at Cueva Negra. The principal site of reference is, of course, the Atapuerca Gran Dolina level TD6 where primary human utilisation of animal carcasses is implied by a cut-mark on bone interrupted by a later tooth-mark attributed to gnawing by a scavenging animal (Blasco and Rosell 2009). The size of most gnaw-marks from TD6 implies teeth of small carnivores such as foxes; moreover, cut-marks and other traces of human intervention there are similar on skeletal parts of both large and small prey, which would have been unexpected were large carnivores to have gained prior access (Carbonell and Rosell 2004). Intervention by early humans is not unthinkable (Díez and Rosell 1998; Díez et al. 1999) and given credence both by a range of impingements on carcasses that implicates human agency (Saladié et al. 2011, 2014), and by mathematical modelling of plausible environmental carrying capacity (Rodríguez-Gómez et al. 2013). Although taphonomical research at Cueva Negra is at an early stage, comparability with other Spanish Early Pleistocene sites can be entertained as a possible expectation.

Conclusion

The Cueva Negra del Estrecho del Río Quípar offers evidence of intermittent Palaeolithic activity after the close of the Jaramillo sub-chron ca. 0.99 Ma and before the Matuyama-Brunhes boundary of 0.772 Ma, which period is demonstrated in particular by presence of *Megaloceros novocarthaginiensis* in the magnetostratigraphical context of reverse magnetic polarity. ESR chronology and other palaeontological data from the site are compatible with the aforementioned period, to which the sedimentary sequence is assigned, as are comparable aspects of Palaeolithic activities recorded at other contemporaneous Spanish sites. Likewise, evidence of combustion at Cueva Negra is broadly commensurable in time with that, from the Matuyama-Brunhes boundary, at

Gesher Benot Ya'aqov at the eastern end of the circum-Mediterranean region. A reasonable palaeobiological inference is that cognitive versatility facilitated human survivability in the extended geographical and ecological ranges of the genus *Homo* towards the close of the Early Pleistocene.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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