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## CLASSE DE CIÊNCIAS

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**40,000 years later:  
what we know about the presence of Neanderthals in  
Portuguese territory and their extinction.**

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# 40,000 years later: what we know about the presence of Neanderthals in Portuguese territory and their extinction

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## 1 – INTRODUCTION

To understand the human presence in present-day Portuguese territory corresponding to the Mousterian complex—the only cultural complex from the Middle Paleolithic so far recognized and characterized in the Portuguese territory<sup>1</sup>—whose terminus is thought to be at roughly 37 Ka cal BP years, it is important to begin with a brief description of the sites that have been identified up to now that yielded human remains (Fig. 1).

Although some of the caves occupied during the Mousterian period had been excavated in the 19<sup>th</sup> century, as was the case with the Furninha cave, and the materials were carefully recorded according to the levels on which they were found<sup>2</sup>, interest in excavating caves declined during the 20<sup>th</sup> century in favor of the study of open-air sites, usually lacking any stratigraphic indicators. Two main reasons lay behind this: on the one hand, the impossibility of carrying out lengthy and systematic explorations of caves due to the lack of available and suitably qualified archaeologists and, on the other hand, the lack of funding meant that researchers could not be trained who could then, in collaboration with specialists from other countries, establish an area of research, as had been the case in Spain. From the beginning of the 20<sup>th</sup> century until the start of the 1960s, the study of Middle Paleolithic materials in Portugal was therefore restricted to the results of surface collections, involving low investment and a methodology that any amateur could learn in a few hours. This happened with the rich Paleolithic sites on the outskirts of Lisbon, discussed later, which were the object of intensive survey following the discovery of the famous site at Casal do Monte just outside Lisbon, in 1909, by Joaquim Fontes.

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<sup>1</sup> Bicho, 2004.

<sup>2</sup> Delgado, 1884.

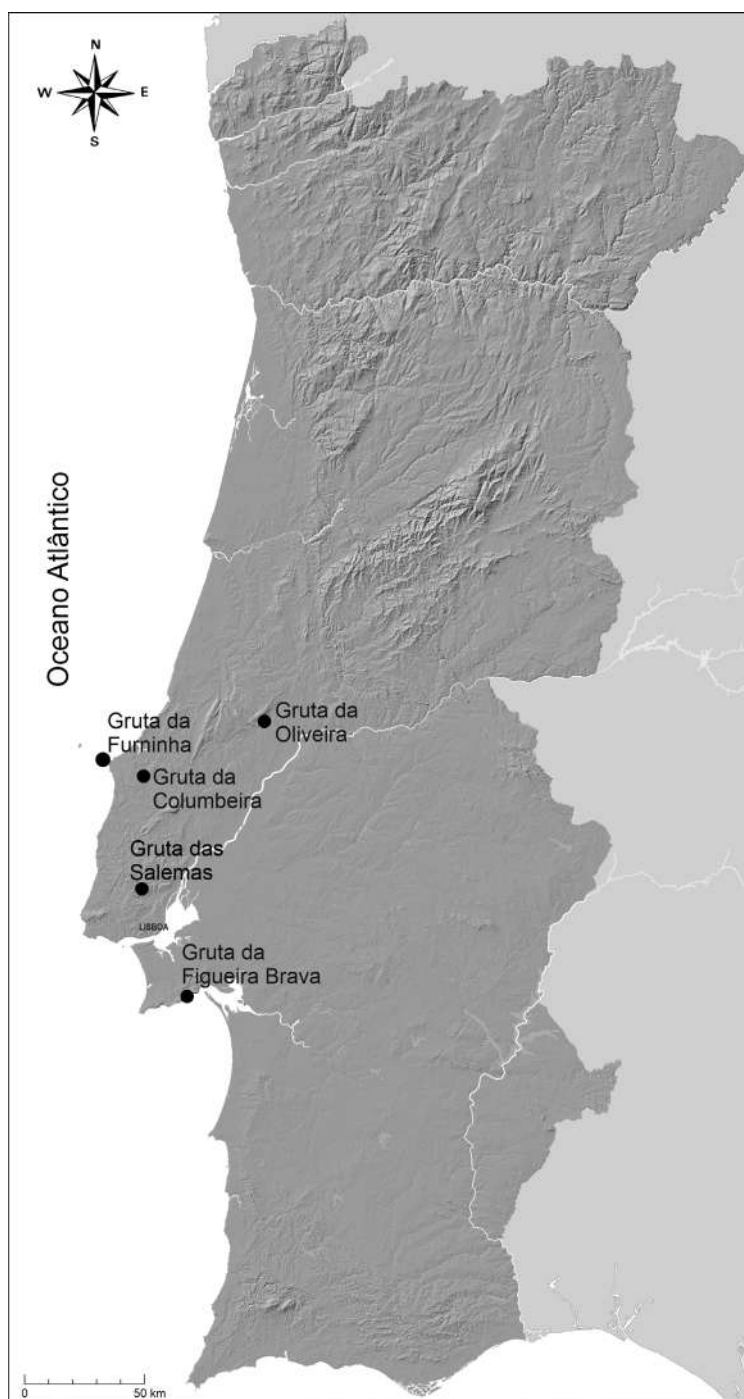


Fig 1 – Portuguese sites that yielded Neanderthal remains.

This approach to studying Paleolithic materials was boosted in the mid-1940s by the presence of H. Breuil in Portugal (between June 1941 and November 1942), legitimizing this form of collecting with the adoption of a method—the so-called ‘series method’—that resolved the limitations arising out of a lack of stratigraphic information, based as much on the typology as on the physical state of the industry. Thus, the greater the surface wear on the artifacts, including the identification of the superimposition of successive forms of erosion (e.g. water, wind), the older the item was, based on the principle that all items were affected by the same conditions since they had been abandoned on the surface. Without wishing to enter into a discussion on the relative merits and limitations of these criteria, which continued to be used in Portugal for the following sixty years due to the work of G. Zbyszewski, a disciple of Breuil, it may be affirmed that it was dominant almost exclusively for the classification of Lower and Middle Paleolithic industry in Portugal until the start of the 1980s, when a small group of researchers emerged who, despite their different academic backgrounds, finally managed in various ways to harness the necessary funding for extensive research into cave and open-air site deposits.

Despite the scarcity of human resources, it was during the end of this long period that some of the most significant advances were made toward understanding the Middle Paleolithic in Portugal, although this has been inseparable from parallel research into the Upper Paleolithic, bearing in mind that the sites were either the same or were located in the same geographical area, particularly the Estremadura Limestone Massif and adjacent areas, where caves are abundant, thus justifying combined research work.

The direct predecessor of the studies currently being undertaken into the Middle Paleolithic period in Portugal was the excavation of the Gruta das Salemas (Loures), followed by that of the Gruta Nova da Columbeira (Bombarral), both carried out by the staff of the Serviços Geológicos de Portugal at the beginning of the 1960s. It was the only official organization that had the necessary resources and technical means to carry out such research, albeit in a circumstantial and limited manner since it was subordinated to geological work. Nevertheless, it was the excavation of these caves due, in particular, to the work of O. da Veiga Ferreira, which inaugurated, with Georges Zbyszewski and José Camarate França the era of modern research into the Middle and Upper Paleolithic in Portugal (Fig. 2).



Fig. 2 – From left to right: Georges Zbyszewski, Octavio da Veiga Ferreira and Luis Pericot García in a lively conversation during the First Archaeological Journeys of Sintra (1958). Photo archive JLC.

The delay in following up the research explains the long period before the appearance of the first summary on the Early and Middle Portuguese Paleolithic<sup>3</sup>. A later and more detailed summary appeared twenty years later (illustrating the rapid evolution of knowledge that had taken place in the interim<sup>4</sup>. Recently, the subject has interested several researchers<sup>5</sup>.

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<sup>3</sup> Zbyszewski, 1974.

<sup>4</sup> Raposo, 1993.

<sup>5</sup> Bicho, 2004; Zilhão, 1992, 2006a, 2006b, 2023; Cardoso, 2002, 2006, 2007.

## 2 – THE ARCHAEOLOGICAL RECORD: PORTUGUESE SITES WITH NEANDERTHAL REMAINS

### 2.1. Gruta da Oliveira (Torres Novas)

The action of water in the river Almonda karst system, which is still being formed, led to the opening up of a series of cavities at decreasingly and successively more recent altitudes in the rocky massif that forms part of the “arrife” area of the Aire mountains, overlooking the vast plain formed by Tertiary and Quaternary sediments to the south.

This cave is still being excavated, under the supervision of João Zilhão (Fig. 15), and no definitive results can be presented at the moment. The first published results refer to a deposit initially attributed to an alluvial cone, the “Mousterian cone”, found in 1989 and corresponding to a secondary sedimentary accumulation within the karst system above the present entrance to the Almonda cave, due to the collapse of a gallery from a higher level where the Gruta de Oliveira cave is situated. This deposit contains a large amount of faunal remains and lithic industry (around 250 artefacts), mainly made of flint (50%), with a high incidence of the Levallois technique and many retouched tools (scrapers, denticulates). The mammal fauna consists exclusively of ungulates (there is only one example of carnivore amongst the 240 fragments of deer, horse, mountain goat, rhinoceros, rabbit, and turtle bones) and may therefore be attributed to the hunting activities of the human group established there, particularly as around 20% of these remains show signs of burning. Two dates have been obtained by U/Th from a horse’s tooth, giving a weighted average result of 61.5 Ka BP, which is compatible with the typological characteristics of the lithic assemblage<sup>6</sup>. The deposit corresponds to an episode of Mousterian occupation of the cave, which, in total, is 6 m deep and is sealed by a thick level of stalagmites (Fig. 3).

The most modern Mousterian occupations of the cave correspond to Levels 8-14, from ca. 71 000–85 000 BP, in the general sequence<sup>7</sup>. In contrast to what was found in the “Mousterian cone”, the tools, which show evidence of the Levallois technique, are mainly quartzite, followed by flint, then quartz. This trend towards

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<sup>6</sup> Zilhão & McKinney, 1995.

<sup>7</sup> Zilhão, 2023.

the underrepresentation of flint is accentuated, in these levels. In Level 9, the radial chipping technology is much more evident in comparison with Level 8, featuring roughly 54% of the total number of items classified. In both levels, it can be seen that the use of raw materials such as quartzite and quartz has not produced items of inferior quality obtained by more expeditious technological means, as is commonly thought to be the case in Peninsular Mousterian contexts<sup>8</sup>.



Fig. 3 – Gruta da Aroeira. View of the entrance. Photo by João Luís Cardoso.

In fact, it is in the finer-grained pieces of quartzite, rather than in the flint, that the application of a refined Levallois technique can be observed (Fig. 4), and this can also be seen indirectly in the fact that the quartzite flakes are not, on average, larger in size than those made of flint. The Oliveira cave therefore

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<sup>8</sup> Marks *et al.*, 2001.

confirms what is already known from previous studies on the Gruta da Figueira Brava and the Gruta Nova da Columbeira, which have always emphasised the important presence of quartz and quartzite in Mousterian associations in Portuguese territory.

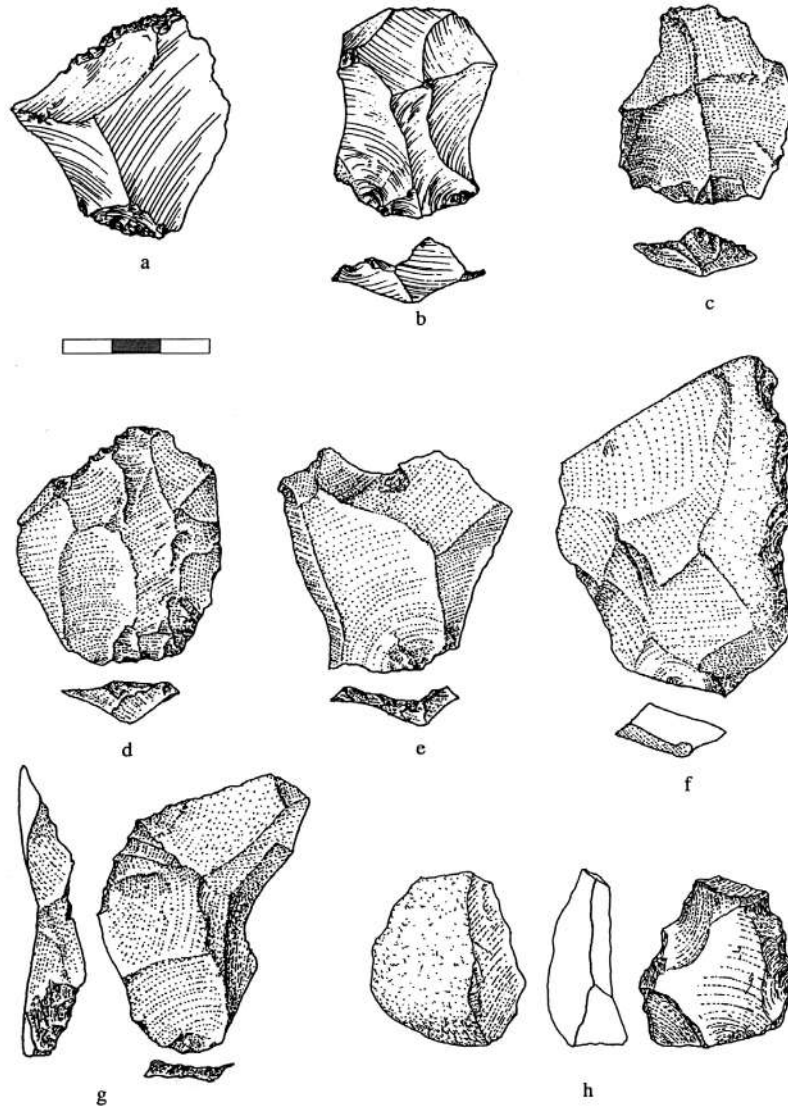


Fig. 4. Industry from Gruta da Oliveira, Level 9: a – retouched flake; b – Levallois flake; d-f – denticulates; g – debordant Levallois flake; h – inversely retouched Tayac point; a, b, flint; c-g, quartzite; h, quartz (after Marks, Monigal & Zilhão, 2001).

The deepest levels (Levels 15-25), chronologically situated between 85 000–92 000 and more than 92 000 BP<sup>9</sup> reveal an abundance of lithic industry. A large quantity of turtle and rabbit remains have been recovered from these older levels, which show signs of burning, an indication that they had been destined for human consumption<sup>10</sup>.

The sedimentation is continuous until Level 9. Between this level and Level 8 there is a stalagmite crust deposit, indicating a significant discontinuity in the sedimentation. This may be linked to climate change since, whilst from Level 10 onwards certain species indicate the existence of open landscapes and a temperate-cold climate (mountain goat, horse, and rhinoceros), these are absent in Level 8, in which red deer are the only large ungulates present out of roughly 300 remains that have been identified<sup>11</sup>. There is also a low incidence of carnivores (fox, leopard, and bear) and, in particular, of a hyena cave. These observations, considered in conjunction with the frequent signs of cutting and burning on the deer remains, suggest that they are connected with human hunting activity. In terms of small mammals, *Apodemus sylvaticus* and *Eliomys quercinus* together make up approximately 96% of the rodents from this period, indicating a Mediterranean climate<sup>12</sup>. Moreover, it is this environment that explains the existence of turtle and rabbit remains, which are particularly abundant in the older levels in the sequence. This evidence indicates the non-selective capture of faunistic resources by humans near the cave.

In addition, the reduction of the territories in which these resources could be captured during the Mousterian period is suggested<sup>13</sup> by a reduction in the use of flint, between the oldest dated occupation, corresponding to the “Mousterian cone”, where, out of the 250 artifacts recovered, around 50% are of flint, 30% quartzite and 20% quartz and the more modern Mousterian occupations, represented by Levels 8 to 12. In support of this theory, the absence of mountain goat in the more modern deposits should be noted, in contrast with its presence in the older levels although its absence may correspond to other causes such as a rise in

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<sup>9</sup> Zilhão, 2023.

<sup>10</sup> Nabais & Zilhão, 2019.

<sup>11</sup> Brugal, *in* Zilhão, 2001.

<sup>12</sup> Zilhão, 2006.

<sup>13</sup> Zilhão, 2001.

temperature after an eventual colder period in around 38-37 Ka calBP, as indicated by the exclusive presence of red deer amongst the fauna hunted at that time.

Three human remains recovered from the deeper levels have been classified as Neanderthal, given that the associated lithic technology is clearly Mousterian. These are remains recovered in 2006 and later, from the deepest levels of the stratigraphic sequence (Layers 9, 10, 17, 18, 19 and 22). A review of the absolute chronology of the occupation of this cave carried out after 2006, led to the conclusion that, contrary to the conclusions previously presented, it took place between around 71,000 years ago (beginning of MIS 4) and around 106,000 years ago (end of MIS 5 d), based on the combined application of the U-Th and OSL methods<sup>14</sup>, so the chronology of the human remains found is closer to the lower chronological limit indicated.

## 2.2. Gruta da Furninha (Peniche)

The formation of this cave, which nowadays overlooks the sea, is related to a platform caused by marine abrasion of approximately 15 m above sea level. The filling in of a vertical aven approximately 10 m high inside the cave is therefore more recent than the marine episode which, using altimetric criteria, correlates with the last interglacial period<sup>15</sup>. Excavations carried out in 1879 by J. F. Nery Delgado<sup>16</sup> were undertaken in compliance with the best scientific standards of the time, and careful records were kept of the stratigraphy and positions of all the lithic industries and bones recovered, which are still preserved today in the Geological Museum in Lisbon. The Pleistocene sequence consisted of a conglomerate at the bottom, containing few faunal remains, followed by a thick sedimentary complex separated from the former by a stalagmite crust, revealing discontinuity in the sedimentation. This succession consisted of seven fossiliferous bone levels, separated by abandonment episodes consisting of eolic sands.

The largest lithic and faunistic assemblage comes from the third and second fossiliferous levels. The typology of the associated flint items lies mainly within the Mousterian period, revealing mixtures caused by circulation currents within

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<sup>14</sup> Zilhão, 2023, p. 44.

<sup>15</sup> Breuil & Zbyszewski, 1942.

<sup>16</sup> Delgado, 1884.

the cave. These mixtures were noted by Nery Delgado and later assessed by Joaquim Fontes, who carried out a review of the lithic materials and identified some Mousterian items<sup>17</sup>, later confirmed by Breuil and Zbyszewski (1942).

The existence of Mousterian tools in this cave along the stratigraphic Pleistocene sequence<sup>18</sup>, mixed with faunal remains can be explained by the aforementioned mixtures, given that the coexistence of humans with large carnivores, essentially represented by the striped hyena (*Hyaena hyaena prisca*) and a small wolf (*Canis lupus lunellensis*), is not plausible. Proof of this lies in the fact, Joaquim Fontes emphasized that half a *Canis lupus* radius did not appear to have been transported to any significant distance and was recovered from the second level whilst the other half was recovered 1.30 m above it from another level. Although it is certain that movement occurred, there are no doubts that this Mousterian cave is contemporary with the striped hyena, a species that became extinct in Europe beyond the Pyrenees at the beginning of the Riss glaciation<sup>19</sup>, whose coexistence with the equally archaic small wolf that also occurs there in abundance, underlines the refuge-area character of Portuguese territory in late Pleistocene times. Assuming that the formation of the cave corresponds to that of the marine abrasion platform outside it, connected to the 5-8 m level, the opening of the well excavated by Nery Delgado inside it and the basal gravel preserved in it must correspond to a regressive moment, which can be connected to the regressive movement preceding the beginning of the last glaciation, between MIS 5e and MIS 5d, between 123 000 and 109 000 years BP, and the filling of the well must have started immediately afterward. In fact, as Nery Delgado had already concluded, the essentially aeolian nature of the sands deposited inside this well is compatible with a regressive stage in which dune feeding was ensured by the vast platform that emerged at the time, extending as far as the Berlengas, swept by the cold Atlantic winds. It is interesting to note that in the basal detrital fill, some of the pebbles are pinkish granite from Berlengas, evidence of the direct transportation of clastic elements between the two sites during the periglacial period, either by man or naturally through watercourses.

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<sup>17</sup> Fontes, 1916, pp. l.1.

<sup>18</sup> Bicho & Cardoso, 2010.

<sup>19</sup> Cardoso, 1993.



Fig. 5. Gruta da Furninha seen from the sea. Photo by J. L. Cardoso.



Fig. 6. Gruta da Furninha. Entrance. Photo by J. L. Cardoso.



Fig. 7. Gruta da Furninha. Two mousterian artifacts top: denticulate; bottom: scraper. LNEG Geological Museum. Photo by J. L. Cardoso.

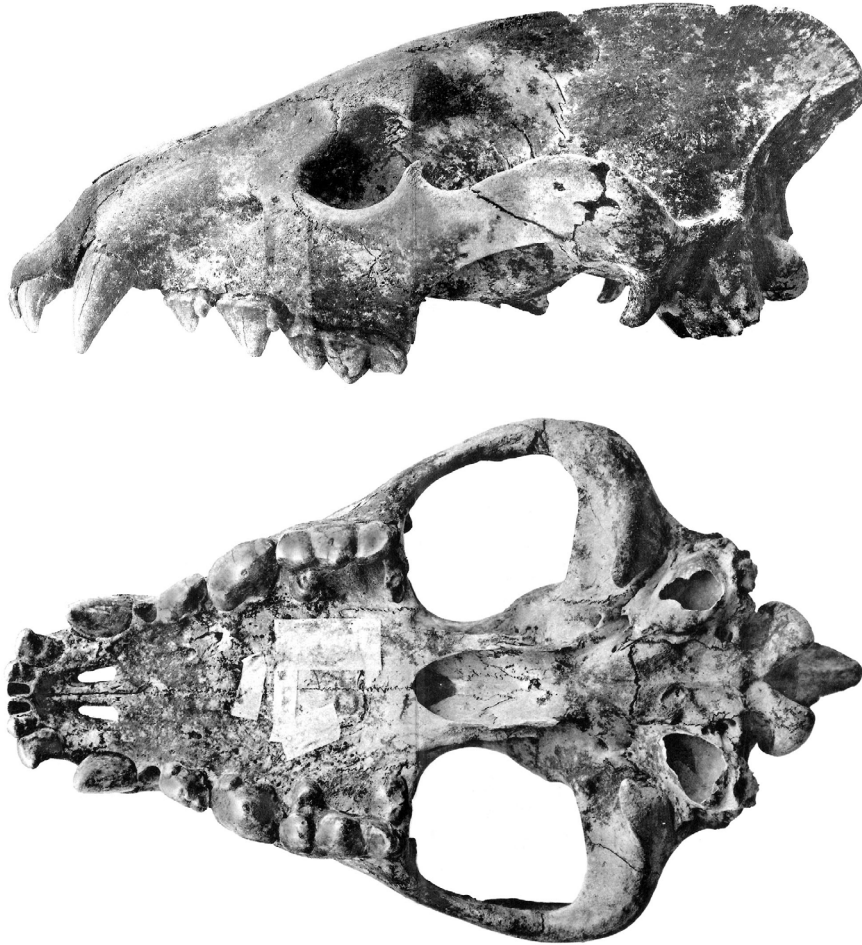


Fig. 8. Skull of *Hyaena hyaena prisca* (according to Harlé, 1910/1911, modified).

In this context, a U/Th date obtained suggests the formation of this sequence c. 80.88 Ka BP (+42.42; -31.26 Ka)<sup>20</sup>. Despite a high level of uncertainty, this result is compatible with the end of the last interglacial when the cave was formed; it is also compatible with the Mousterian industry recovered from it.

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<sup>20</sup> Cardoso, 1993.

From the third ossiferous level comes a fragment of a human hemimandible from a juvenile individual, which was given due prominence at the time<sup>21</sup>, corresponding to a Neanderthal remnant due to its stratigraphic position, being the first to have been identified in Portugal.

### **2.3. Gruta Nova da Columbeira (Bombarral)**

Explored in 1962 by O. da Veiga Ferreira with the assistance of G. Zbyszewski and J. Camarate França, this constitutes one of the most complete and rich Mousterian stratigraphic successions ever identified in Portugal. The stratigraphic sequence and the associated artefacts from each of the levels identified are clearly defined<sup>22</sup>.

The cave, surrounded by a landscape of Jurassic limestone, is set halfway up the left-hand slope of the Roto valley, which is cut deeply into the karst landscape. It consists of a high thin gallery, approximately 20 m long, on average 3 to 4 m wide and roughly 10 m high. The stratigraphy observed in successive vertical cuts consists of a maximum of 10 levels (Fig. 18) which are almost always separated by a fine stalagmite film, indicating a possible halt in sedimentation and in occupation<sup>23</sup>. The last campaign in 1971, under the direction of J. Roche, aimed to record a more detailed stratigraphic succession. An attempt to correlate the two stratigraphic sequences, as well as to articulate and discuss the various absolute dates obtained, which were dubitatively associated with various limitations, led to a review of all the available information. As it was not possible to obtain radiocarbon dates on bones, due to the lack of collagen, and bearing in mind the published stratigraphic information, we resorted to the direct dating of a triero-type instrument, made from a robust rhinoceros' bone, collected in layer 8 using the U-Th method<sup>24</sup>. The reason for this choice was that it was an unquestionably carved piece and that it came from the layer that provided the first Neanderthal tooth collected in Portuguese territory. It is a left lower first molar germ from the top of Level 9 (Level 10 is sterile), in contact with Level 7 in a sector where Level 8 is missing<sup>25</sup>.

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<sup>21</sup> Delgado, 1884, Pl. 1 A, no. 1.

<sup>22</sup> Cardoso, Raposo & Ferreira, 2002.

<sup>23</sup> Zbyszewski, 1963; Ferreira, 1966, 1984.

<sup>24</sup> Zilhão *et al.*, 2010.

<sup>25</sup> Ferreira, 1966; Ferembach, 1964/1965; Antunes *et al.*, 2000.

First studied by Ferembach (1964/1965), who attributed it with reservations to a Neanderthal, it was later restudied and attributed with certainty to a juvenile Neanderthal<sup>26</sup>. Since the dating of the bone piece used indicates a date of around 87 000 years, which can be found in MIS 5b, it is to this period that this individual should be reported, associated with the most important occupation found in the cave.

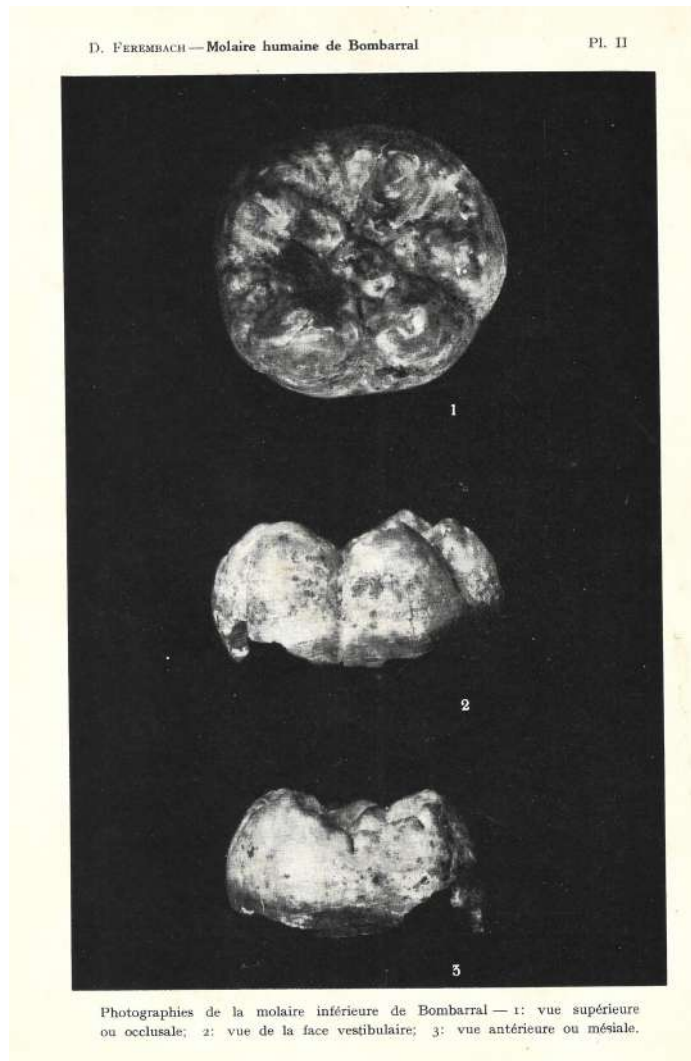


Fig. 9. Gruta Nova da Columbeira. Neanderthal lower left first molar germ (seg Ferembach, 1964/1965).

<sup>26</sup> Antunes *et al.*, 2000.



Fig. 10. Gruta Nova da Columbeira. Entrance. Photo taken in 1962 during the excavations. J. L. Cardoso/O. da Veiga Ferreira Archive.



Fig. 11. Gruta Nova da Columbeira. View of the interior of the cave during the excavations carried out in 1962, showing the dark and carbonaceous layer (C. 8) corresponding to the most important moment of the Neanderthal occupation of the cave. J. L. Cardoso/O. da Veiga Ferreira Archive.

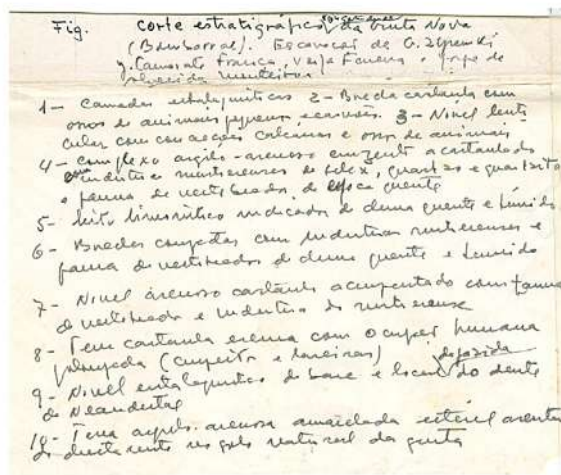
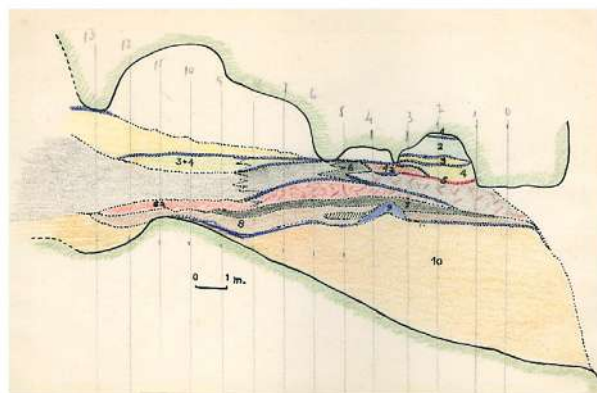


Fig. 12. Gruta Nova da Columbeira. Longitudinal cross-section. Original stratigraphical description by O. da Veiga Ferreira. J. L. Cardoso/O. da Veiga Ferreira Archive.

In fact, Level 8, containing 2433 artifacts, is followed by Level 7 which has 1,880; Level 6 contains only 677 artifacts 56 and 107 respectively in Levels 5 and 4, the most modern in the sequence containing lithic industries, indicating the possibility that it continued to be occupied sporadically over a period that is impossible to determine but cannot have lasted longer than a few centuries. Level 7 corresponds to the most modern effective human occupation of the cave. Level 6 corresponds to the establishment in the cave of a hyena den indicated by the presence of numerous coprolites, and the amount of artifacts decreases abruptly—a situation which can be observed even more clearly in the two more modern levels.

Six deciduous rhinoceros teeth (*D. hemitoechus*) were recovered from Level 6 of the Gruta Nova da Columbeira; however, as the human presence is slight in this level, the presence of this species may be attributed to the activities of large predators and the same may be true of a fragment of jawbone containing two molars worn to the roots at Gruta da Figueira Brava, corresponding to an old individual. This was also the pattern witnessed in Lorga de Dine, where there is no evidence of any compatible human occupation<sup>27</sup>.

In conclusion, Levels 8 and 7 correspond to the “main levels of human occupation of the cave and the only ones in which it is possible to accept the hypothesis of consistent occupations involving continuous residence”<sup>28</sup>.

The lithic industries of the Gruta Nova de Columbeira were attributed to the techno-typological group known as “Mousterian with denticulates”, with Levallois debitage and Levallois facies (Fig. 13).

Given the rarity and the controversy surrounding similar occurrences, it is also worth noting the presence of certain bones which had been broken deliberately and used as tools, as can be deduced by the marks that remain on them<sup>29</sup>, which one of the best examples is precisely the piece dated by U-Th.

There is a marked diversity in the use of raw materials throughout the entire sequence, revealing a trend towards an increase in the use of flint and a corresponding reduction in the use of quartz and stable levels for quartzite. However, this does not mean that this increase of flint can be attributed to an extension of the territories from which resources were gathered. The geology of the surrounding area shows that flint could have been obtained in the form of nodules or smoothed pebbles from the limestone outcrops, including the massif in which the cave itself is set, whilst quartz and quartzite were plentiful in the lowlands nearby that extended to the sea. Moreover, this increasing demand for flint is not accompanied by any increase in its use; the rate at which it was processed into tools decreased, in contrast to the use made of quartz and particularly quartzite. Thus, the greater demand for flint did not compromise but, in fact, stimulated the use made of the other raw materials and did not correspond to an evolutionary pattern that heralded the Upper Paleolithic.

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<sup>27</sup> Cardoso, 1993.

<sup>28</sup> Cardoso, Raposo & Ferreira, 2002, p. 50.

<sup>29</sup> Barandiarán & Ferreira, 1971; Cardoso, Raposo & Ferreira, 2002.

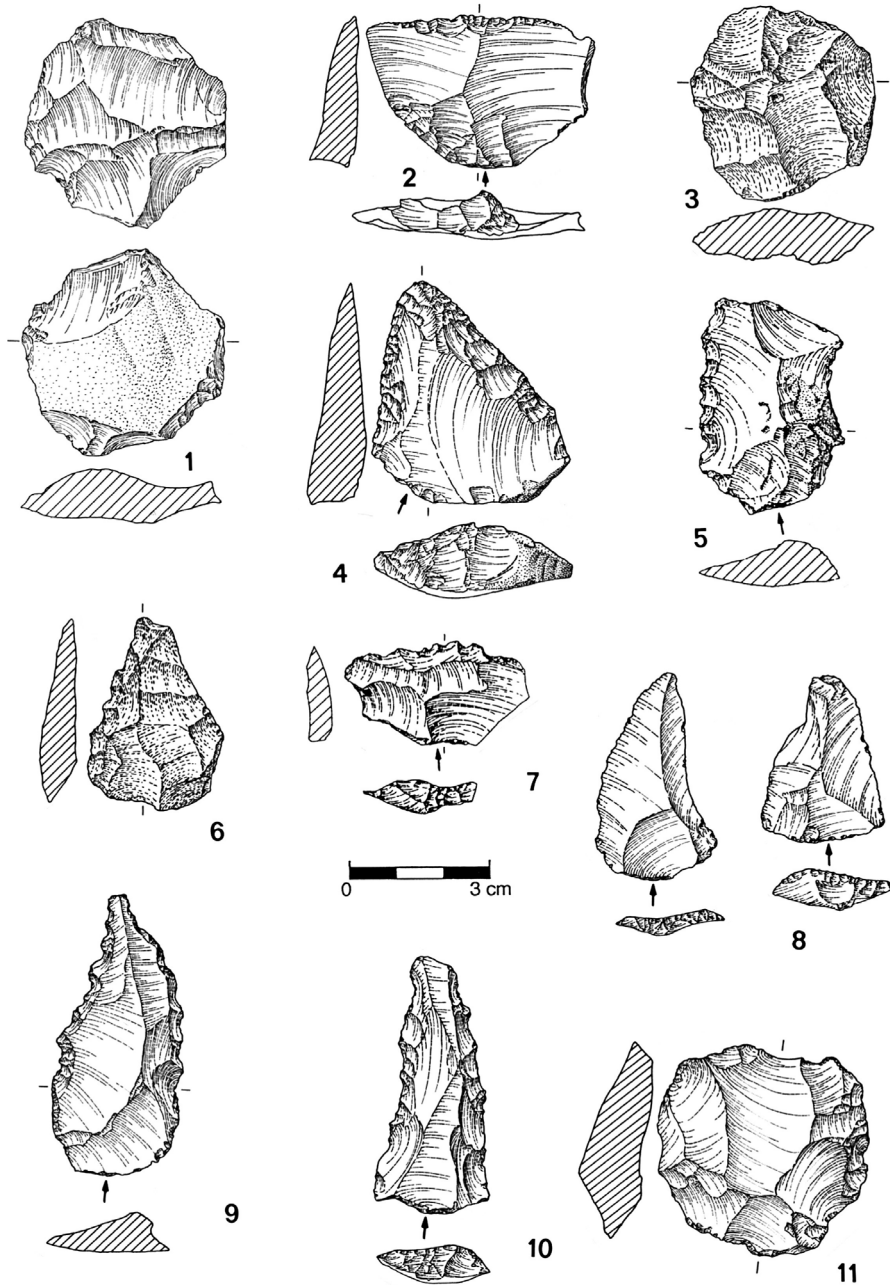


Fig. 13. Industry from Gruta Nova da Columbeira. Level 6a: 2 – denticulate; 4 – deviated sidescraper. Level 7: 1, 3 – cores; 5 – denticulate. Level 8: 6, 7 – denticulates; 8 – Levallois flakes; 9, 10 – Tayac points; 11 – core. All of flint, except 3, 6, of quartzite (after Cardoso, Raposo & Ferreira, 2002, modified).

Evidently alternating use was made of the cave by humans and predators and the levels which reveal the most intensive human occupation are also those which contain the smallest amount of carnivore remains. In Level 8, which has a high concentration of carbon resulting from prolonged burning, only one wolf radius was recovered and in Level 7, three sets of hyena, in contrast with the abundance of lithic industry already mentioned. Conversely, the levels containing the largest collection of carnivore remains in the central part of the fill contained very little lithic industry. Lastly, the upper levels, bearing no traces of human presence, are characterised by the presence of birds, including birds of prey and the remains of the prey with which they are normally associated.

The composition of the large mammal fauna<sup>30</sup> suggests temperate climatic conditions, with some cold and dry spells, favourable for the presence of *Capra pyrenaica* (mountain goat) which was also well-adapted to the surrounding stony landscape that forms part of the Estremadura environment of low mountain outcrops under a strong ocean climatic influence. The existence of several rhinoceros (*Dicerorhinus hemitoechus*) milk teeth indicates opportunistic hunting involving the capture of younger and weaker animals. However, as all the examples of this species are restricted to Level 6<sup>31</sup>, which corresponds to the hyena den, these remains may be linked to the activities of this carnivore.

The most interesting of the faunal elements is the terrestrial turtle (*Chersine hermanni*) since this is the Portuguese site that contains the largest amount of remains of this species<sup>32</sup>. This species prefers coastal areas at altitudes of no more than 500–600 m and a Mediterranean environment. Nowadays its circum-Mediterranean distribution seems to be influenced in particular by a need for summer, rather than winter, heat, and rain. Although the adults can withstand temperatures of up to 10° or even 20° below zero, embryo development requires high temperatures, with an optimum of around 30 °C but never below 20 °C. As the turtles reproduce in summer and incubation lasts roughly 2.5 months, between June and August/September they need temperatures that remain close to this optimum. It is without doubt due to the lack of these conditions that the species

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<sup>30</sup> Cardoso, 1993.

<sup>31</sup> *Ibidem*.

<sup>32</sup> Jiménez Fuentes, Cardoso & Crespo, 1998.

became extinct in Portuguese territory long before the end of the last glaciation, as it had been unable to support the climatic deterioration that took place soon after the cave was occupied. Of the 349 remains identified, 338 came from Level 8, which contains the greatest amount of evidence of human presence. There is no doubt that they had been caught by humans and that this had been easy to accomplish, a fact that also may explain the rapid extinction of the species. There is no Upper Paleolithic site in the region where their presence was maintained. A re-examination of the entire collection of chelonians found in this cave was recently published<sup>33</sup>, and showed that two species were consumed, *Chersine hermanni* and *Emys orbicularis*, the latter corresponding to the terrapin, which is still common in Portuguese inland waters today.

The frequent presence of the terrestrial turtle (Fig. 14), which is the largest in terms of amount in Level 8 of Gruta Nova da Columbeira indicates a higher anthropic incidence. The same conclusion may be extended to the remains of this species originating in the deeper levels of the Gruta da Oliveira, which are carbonized like the rabbit remains associated with them. Both species are plentiful in most of the caves showing human Mousterian occupation—and also marked in the Gruta de Ibn Amar<sup>34</sup>—although they differ in quantity, indicating a practice of the hunting of small animals, which seems to have been common throughout the Late Mousterian period.

It is important to emphasize the lack of sea mollusks, explained by the distance from the shoreline, more than 10 km, having in attention the opportunistic, occasional, and non-specialized type of recollection. In conclusion, although the chronometric information merits additional efforts in terms of revision/conformity, the abundance of lithic industry attributed exclusively to the Mousterian, the abundance of faunal associations that have been recovered, and the relationship that may be established between the two assemblages throughout the stratigraphic sequence, one of the most complete in the Mousterian, and finally, the discovery of a neandertal tooth are all factors which make this cave an important site in the Late Iberian Mousterian<sup>35</sup>.

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<sup>33</sup> Boneta Jiménez; Cardoso & Pérez-García, 2023.

<sup>34</sup> Bicho, 2004.

<sup>35</sup> Raposo & Cardoso, 1998b; Cardoso, Raposo & Ferreira, 2002, figs. 15-17.



Fig. 14. Gruta Nova da Columbeira. Fragments of the shell of a land tortoise (*Chersine hermanni*) consumed by Neanderthals. Notice in one of the fragments the intentional sub-parallel incisions produced by a flint cutting instrument (above) Photo by J. L. Cardoso.

#### 2.4. The Salemas cave (Loures)

The former, which was explored in 1961, became famous as a result of the Upper Paleolithic sequence that was identified there. At the base of the fill, an archaeological level from the Middle Paleolithic period was observed, containing some fairly untypical materials geologically associated with a faunal assemblage also resulting from remobilisations within the cave lasting for an undetermined period of time.

A second lower left deciduous molar was found in the basal layer of the Salemas cave, in a Mustierian context. Denise Ferembach's studies (1962; 1964/1965) were inconclusive. When it was restudied later by Antunes *et al.* (2000), its attribution to a young Neanderthal left no room for doubt. Therefore, the absolute chronology remains open and new dating attempts are justified, possibly using other methods.

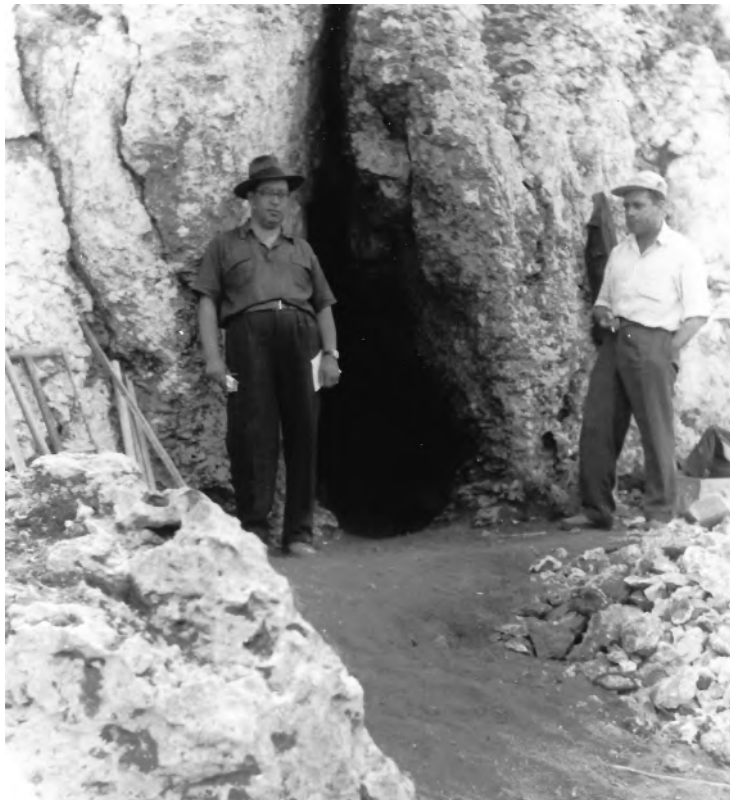


Fig. 15. Entrance to the Salemas Cave, corresponding to an enlarged vertical diaclase in the pinewood limestones of the upper Cenomanian in the Lisbon region. Photo from the time of the excavations, with José Camarate França on the left and O. da Veiga Ferreira on the right. J. L. Cardoso/O. da Veiga Ferreira Archive.

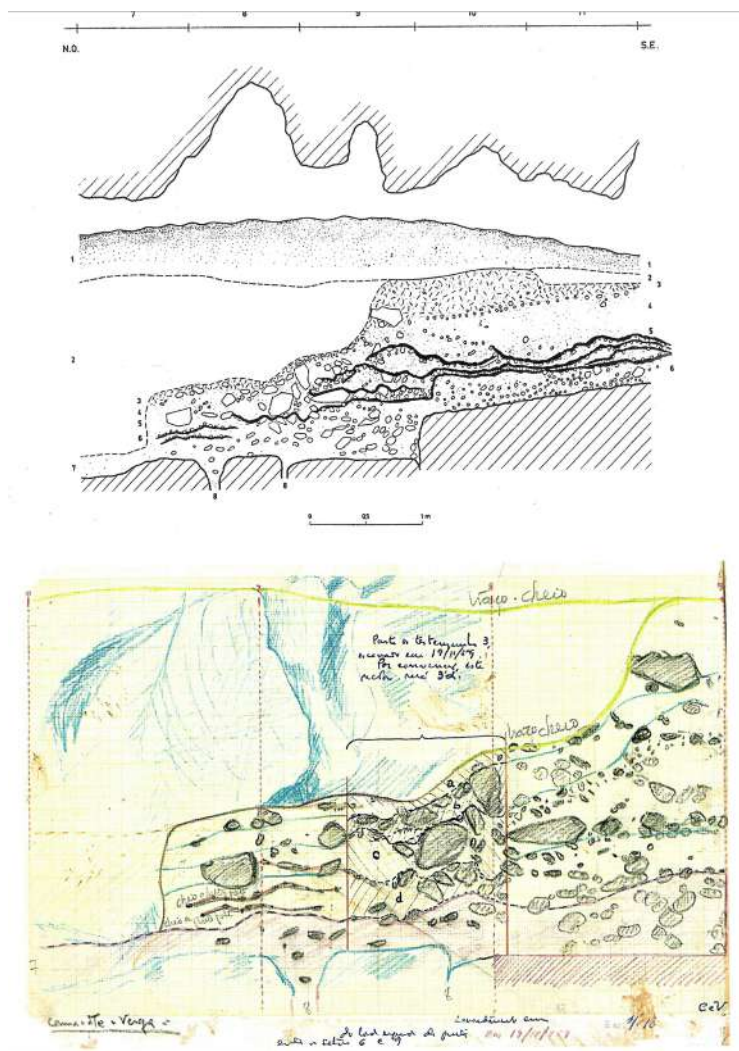
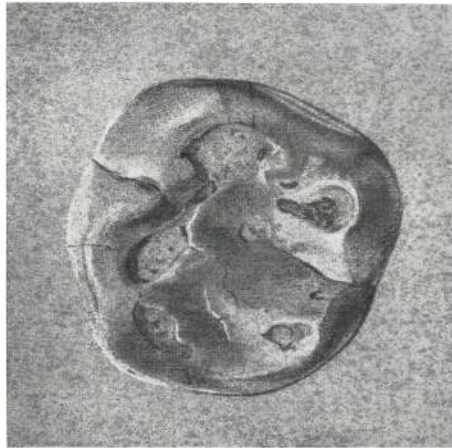


Fig. 16. Gruta das Salemas. Longitudinal stratigraphic section of the Salemas Cave fill, executed at the end of the work by O. da Veiga Ferreira and J. Camarate França, with the Middle Paleolithic levels at the base of the sequence. J. L. Cardoso/O. da Veiga Ferreira Archive.

D. FEREMBACH

Molaire de Salemas

PL. I



La dent de Salemas. En haut vue mésiale, en bas vue occlusale (grossie environ 6 fois).

Fig. 17. Gruta das Salemas. Second left deciduous molar of a Neanderthal collected in the Middle Paleolithic levels (seg. Ferembach, 1964/1965, modified).

## 2.5. Gruta da Figueira Brava (Setúbal)

Directly overlooking the sea and set in a miocenic calcarenite massif on the south side of the Arrábida mountains to the west of Portinho da Arrábida, various excavation campaigns were carried out in this cave at the end of the 1980s<sup>36</sup>. The entrance to the former shelter was gradually filled in by calcium carbonate precipitates (Fig. 18). Only a small part of the interior has been explored but the stratigraphic,

<sup>36</sup> Antunes & Cardoso, 2000.

faunal, and archaeological records emphasize the importance of this site. The stratigraphic sequence in the area excavated consists of materials that have been remobilized from other parts of the interior of the cave.



Fig. 18. Gruta da Figueira Brava seen from the sea. Photo by J. L. Cardoso.

The base of the sequence corresponds to a conglomerate related to the raised, level beach measuring 5-8 m, which is well preserved in the outer part of the cave, as in the whole of the Arrábida southern coast<sup>37</sup> and can be attributed to an interstadial form at the beginning of the last glaciation period. Two recent radiometric dates on shells from the Forte da Baralha conglomerate deposit to the west of Sesimbra indicate a much more recent chronology of ca. 37 Ka calBP and 38 Ka calBP<sup>38</sup> that is not compatible with the geological regional record<sup>39</sup>.

The results of the faunal studies<sup>40</sup> show the presence of large mammals such as elephant/mammoth, aurochs, rhinoceros, and horses, incompatible with the mountain land overlooking the cave. These species could only have been caught on the vast coastal plain if it was exposed and extended to the east to the estuary of the river Sado<sup>41</sup>.

<sup>37</sup> Teixeira & Zbyszewski, 1949.

<sup>38</sup> Pereira & Angelucci, 2004.

<sup>39</sup> Cardoso, 2006.

<sup>40</sup> Cardoso, 1993.

<sup>41</sup> Antunes & Cardoso, 2000.



Fig. 19. Gruta da Figueira Brava. Stratigraphic section of the trench excavated in 1988, with a sandy reddish main level dated between ca. 86 000 and 90 000 years. Photo by J. Pais (*in* Antunes & Cardoso, 2000, modified).

The conglomerate level, which mainly consists of Jurassic limestone pebbles, was identified inside the cave, lying directly on the miocenic substrate. This conglomerate is followed by a series of fine carbon beds, resulting from the lixiviation and transport of the products of combustion from fireplaces in other areas of the cave, which can also be observed presently in the exterior of the cave.

The cave was originally a vast room opened up by marine abrasion, the ceiling of which later collapsed. A similar situation can be observed today along the coast, with the opening of other caves at low-water level. Later, the entrance to the cave was progressively filled in by heavy precipitation of calcium carbonate, leading to the present situation of a main entrance, determined by an important vertical diacalse in the Miocene calcarenites, and two other entrances.

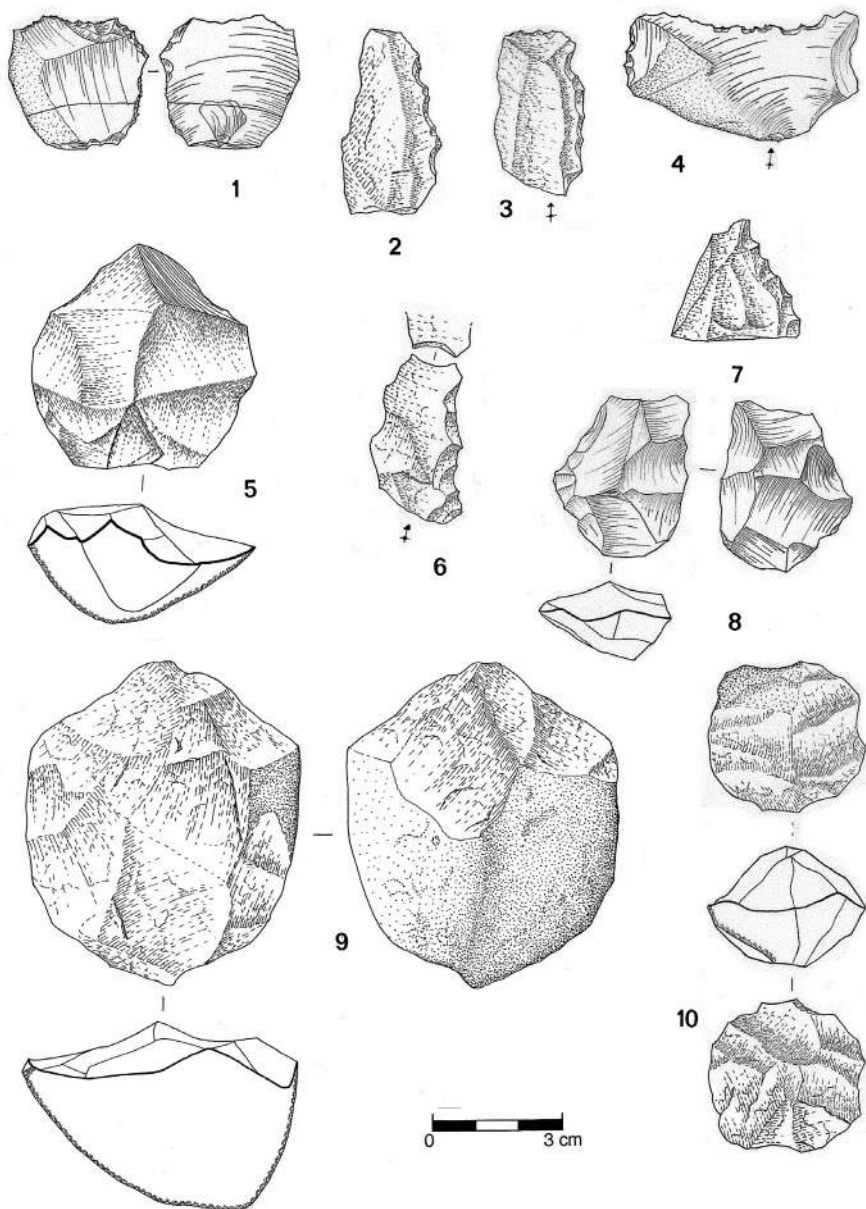


Fig. 20. Industry from Gruta da Figueira Brava. 1, 4 – transverse sidescrapers; 2, 3, 6 – single sidescrapers; 7 – perforating point; 5, 8, 9, 10 – cores. All of quartz, except 1, 4, 8, of flint (after Raposo & Cardoso, 2000).

The first series of excavations in the cave was carried out between 1986 and 1990 by a team led by Miguel Telles Antunes and João Luís Cardoso. The intervention focused on the first room, in a gallery that extends laterally, communicating with the second room. A basal detrital layer is followed by a red, fossiliferous level containing an abundant lithic industry resulting from a similar process, crossed by irregular whitish veins of calcium carbonate (Level 2). The upper part of this level contains Roman and Islamic materials mixed with the remains of domestic mammals, shells, and birds, and the series is sealed from above by a stalagmite bed which is still forming today<sup>42</sup>. From an archaeological point of view, approximately four thousand artifacts have been studied, or approximately two and a half thousand if the splinters from chipping are excluded<sup>43</sup>. Within this assemblage, the lithic industry appears to be expeditious, with no artifacts displaying any notable typological outlines due to the poor quality of the raw material, dominated by quartz pebbles of local origin. Some rare flint items occur, probably originating from the S. Luís mountains 10 kilometers away. Chipping from Mousterian centripetal disc cores predominates; amongst the retouched tools there is a prevalence of scrapers, followed by denticulates and notches. According to the traditional typological diagnostic criteria applied to Middle Paleolithic assemblages, the Figueira Brava industry corresponds to a Typical Mousterian, rich in denticulates of non-Levallois debitage and facies (Fig. 19).

The significant invertebrate marine fauna confirms a strong aquatic element in the diet of the Neanderthal populations based on what was, at the time, a large shelter.

The stratigraphic evidence of this is now easily seen in the open, in the former vestibular area of the old cave, where a real lemachelic level has been identified, corresponding to an old shell mound, based on the Miocene substrate, part of the oldest phase of the Neanderthal occupation of the cave (Fig. 21).

In addition to molluscs (indicating waters that were, in general, slightly cooler) (Fig. 22) there was also included crustaceans such as *Maja squinado* and *Cancer pagurus*, whose pincers have been deliberately broken to enable the soft flesh to be extracted<sup>44</sup> (Fig. 23).

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<sup>42</sup> *Ibidem*.

<sup>43</sup> Cardoso & Raposo, 1995; Raposo & Cardoso, 2000a, b.

<sup>44</sup> Callapez, 2000.



Fig. 21. Gruta da Figueira Brava. Lumachelic level currently open air, observed along the old entrance to the cave, based on the Miocene biocalcarenic substrate. Photo by J. L. Cardoso.

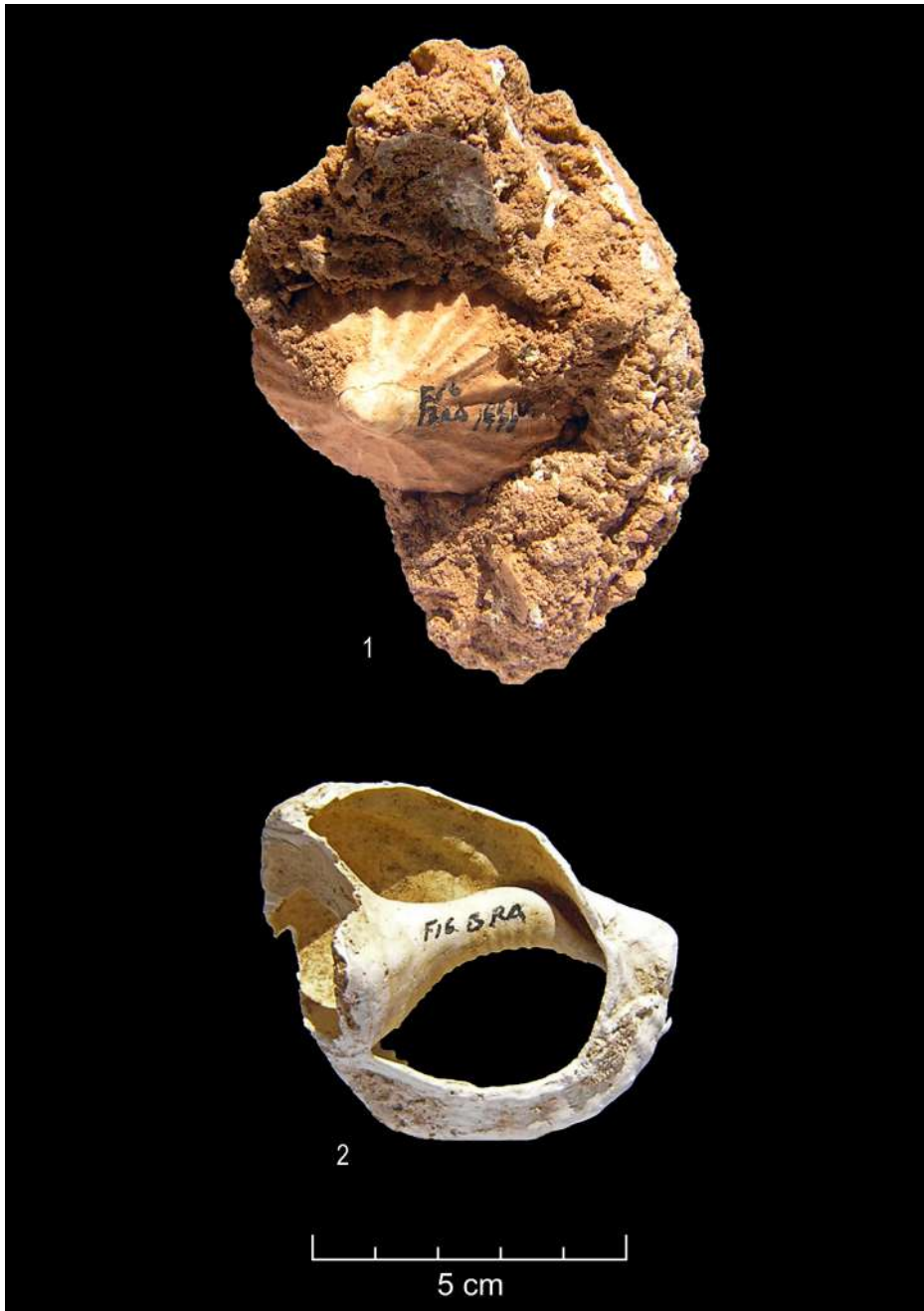


Fig. 22. Gruta da Figueira Brava – Evidence of the exploitation of marine resources: top: *Patella* sp. shell embedded in the hardened sediment inside the cave; bottom: fragmented shell of *Charonia lampas*. Photo by J. L. Cardoso.



Fig. 23. Gruta da Figueira Brava. *Cancer pagurus* (crab) claws, intentionally broken by Neanderthals to extract meat. Excavations by M. Telles Antunes and J. L. Cardoso. Photo by J. L. Cardoso.

Between 2011 and 2013, another team, led by João Zilhão and in which one of us (J.L.C.) participated, carried out investigations in the inner room of the cave, which had not yet been excavated, as well as in the corresponding front area, open onto the sea. It was then possible to confirm the results of the previously published investigations, namely the intense and systematic exploration of aquatic resources, with the identification of a varied set of species of mollusks, mammals, and fish, some of which had not yet been identified, although the general conclusions obtained previously remained unchanged, with the difference that they were published in a worldwide journal<sup>45</sup>, thus being much better known internationally. The extension of the excavated and sampled area to obtain reliable absolute dates, using the dating of stalagmitic crusts collected both inside and outside the cave, made it possible to establish a sequence of four episodes of human occupation, all Mousterian. The episode corresponding to the excavations of the 1980s, which provided the most numerous collections of archaeological and paleontological remains, was located between 86 000 and 90 000 years ago (MIS 5b). It was from here that the only human remains came, corresponding to an upper premolar, whose characteristics relate to an adult Neanderthal<sup>46</sup>. It comes from layer 2 (pinkish in color), dated by the uranium series method from stalagmitic crusts identified in the 2010 / 2013 excavations, between 86.9 - 88.1; 85.4 - 89.8; and 86.7 - 92.7 Ka<sup>47</sup>. (Fig. 24).

The study of the faunal remains recovered, seen together, led to the conclusion of the association of Mediterranean with nordic elements, indicating a climate colder than nowadays and a fairly substantial amount of forest and rocky terrain. The faunal record therefore indicates that, as the cave overlooked the coastal plain at the time, it was here that the majority of the animals were caught, including the elephant or even the mammoth<sup>48</sup>, both by humans and by other predators from the cave, such as the leopard, cave lion, hyena, wolf and grizzly bear, alternating with humans in their use. However, unlike the Gruta Nova da Columbeira, it was not possible to demonstrate clearly how this human occupation alternated with that of the carnivores, given the characteristics of the stratigraphic record.

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<sup>45</sup> Zilhão *et al.*, 2020.

<sup>46</sup> Antunes *et al.*, 2000.

<sup>47</sup> Zilhão *et al.*, 2020.

<sup>48</sup> Antunes & Cardoso, 1991.

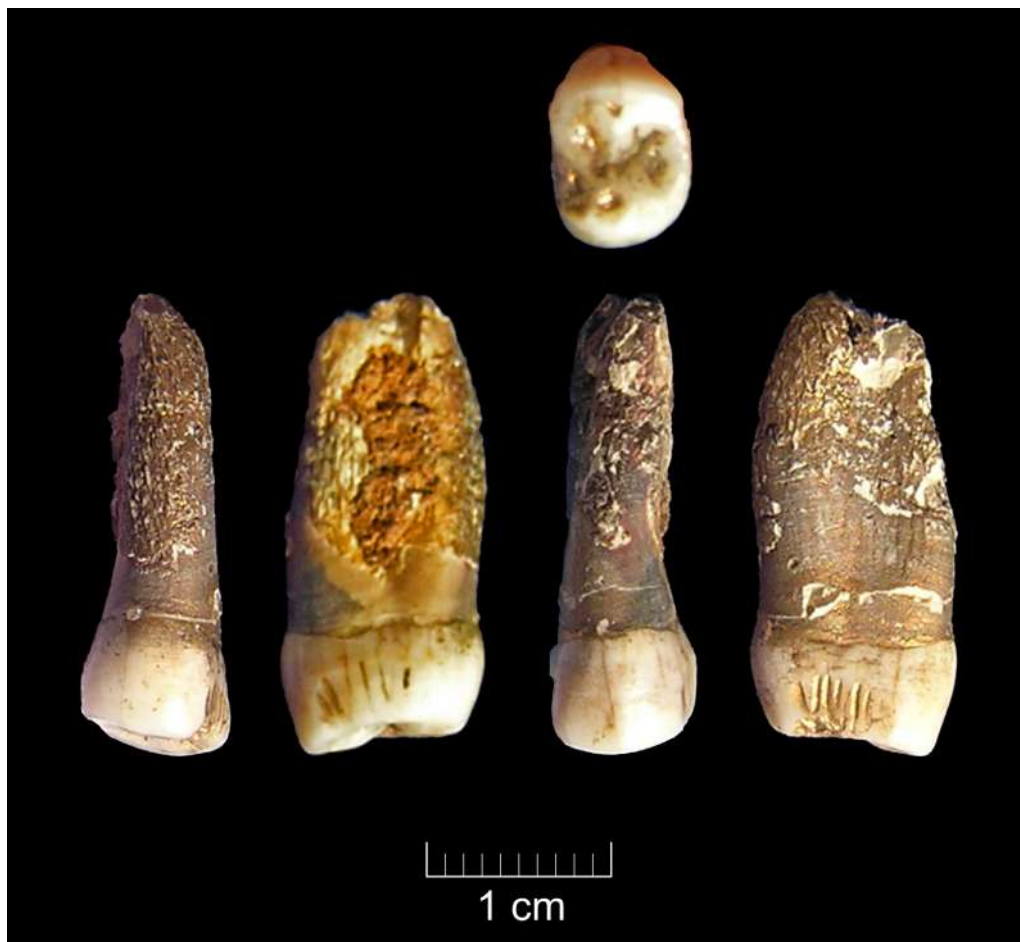


Fig. 24. Gruta da Figueira Brava. Upper premolar from an adult Neanderthal. Excavations of M. Telles Antunes & J. L. Cardoso. Photo by J.L. Cardoso.

In the rocky and more mountainous area of the Arrábida range, *Capra pyrenaica* remains were also recognised in the faunal assemblage, representing the second most frequent species of large mammal to be identified (ca. 22%) after the red deer (*Cervus elaphus*)<sup>49</sup>. This situation indicates the exploitation of various biotopes near the cave, a situation that appears identical to that which has been observed in the other Estremadura caves with significant Mousterian occupations. The human occupation is therefore residential in type, associated

<sup>49</sup> Cardoso, 1993.

with the systematic and non-specialised use of the various food resources available in the surrounding area, from the shore to the mountain area, including the coastal plain.

Underlying this proposition is the abundance of marine species, whose importance in the diet of the Neanderthals had already been duly highlighted, based on the testimonies collected in the excavations carried out between 1986 and 1990 under the direction of M. Telles Antunes and João Luís Cardoso, indicating a systematic collection from along the rocky or sandy shore, both in the intertidal and infralitoral areas including crustaceans<sup>50</sup>, a reality that was later confirmed<sup>51</sup>.

The area in which the food resources were obtained would not extend beyond the area surrounding the site. The exception is the whitish or sometimes streaked flint, which came from the São Luís mountains roughly 10 km away in a straight line. However, the scarcity of this raw material (161 cores and debitage products out of a total of 3,848 items and 21 tools out of a total of 358)<sup>52</sup> is clear proof of the infrequent use made of this resource, despite its obvious advantages given the poor quality of the local rock, and it reinforces the local, though prolonged, nature of the human occupation.

### 3 – NEANDERTHAL SETTLEMENT AND SUBSISTENCE

The importance of the stratigraphic sequences of some of the caves, such as the Gruta da Oliveira and the Gruta Nova da Columbeira indicate residential types of sites, with prolonged and recurrent characteristics. The Gruta da Figueira Brava also appears to indicate this type of occupation, although clearly, it is not possible in any of these cases to determine the duration of human presence nor, in most cases, any possible seasonal occupation. However, certain sites indicate short-term occupation due to the scarcity of the artifacts found and the poor stratigraphic record—as in the case of Lapa dos Furos, where only seven artifacts were identified, corresponding to a date of 40 Ka calBP as a terminus post quem

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<sup>50</sup> Callapez, 2000.

<sup>51</sup> Zilhão *et al.*, 2020.

<sup>52</sup> Raposo & Cardoso, 2000.

for the Mousterian occupation<sup>53</sup>—the Gruta da Figueira Brava was certainly occupied in spring and summer, given the abundance of young rabbits that had been caught by humans<sup>54</sup>. The occupation of the cave alternated with that of carnivores, as observed in other caves dating from the same period (Gruta do Caldeirão, Gruta do Escoural, Gruta Nova da Columbeira).



Fig. 25. Figueira Brava Cave. Dagger made on a proximal radius of auroch. Photo by J. L. Cardoso.

<sup>53</sup> Zilhão, 2006.

<sup>54</sup> Mein & Antunes, 2000.

The area in which resources were gathered—including raw materials for manufacturing artifacts—was always restricted to the area surrounding each site. Medium-sized mammals, such as red deer and horse, were common at the time in their respective biotopes and indicative of open land or corresponding more to forest areas.

The hunting of very large mammals is documented in Figueira Brava Cave by the presence of aurochs (and eventually by elephants and mammoths), some deliberately broken aurochs' bones had been transformed into various tools, as the dagger made on a proximal radius of auroch (Fig. 25), or bones of rhinoceros, such as the trihedral tool found in Level 8 of Gruta Nova da Columbeira (Fig. 26).



Fig. 26. Gruta Nova da Columbeira. Trihedral tool made on a massive bone of rhinoceros. Photo by J. P. Ruas (in Zilhão *et al.*, 2010).

The hunting of small and medium-sized prey is documented in Gruta da Oliveira, Gruta Nova da Columbeira, and Gruta da Figueira Brava. Besides the presence of rabbits, most of the remains consisted of deer whilst other species such as horse and mountain goat were also present but in differing amounts due to the nature of their respective biotopes. In addition to meat, bone marrow was also systematically used by fracturing long bones or other anatomical segments rich in bone marrow, as evidenced by two horse hemi-mandibles fractured longitudinally along their lower edge for this purpose (Fig. 27). The contribution made by carnivores cannot be quantified but would have been much lower, bearing in mind the number of remains preserved, particularly in Levels 8 and 9 of the Gruta Nova da Columbeira.

In addition, the importance of gathering mollusks from the shore should also be stressed in the areas nearest to the coast, such as Gruta da Figueira Brava and Gruta de Ibn Amar, where fishing has also been recorded. In the former, the marine prey also extended to crustaceans (*Maja squinado*, *Cancer pagurus*), whose pincers were found deliberately broken<sup>55</sup>, and marine mammals such as the common dolphin (*Delphinus delphis*) and the ringed seal (*Pusa hispida*)<sup>56</sup>. These may correspond to the secondary exploitation of animals washed up on the shore (or captured on it, in the case of the seal), with the latter species indicating a colder climate than nowadays. This is a clear indication of the importance of the marine resources gathered and consumed in the cave, at present unique evidence in Portuguese territory in terms of the variety and abundance of the remains preserved.

The practice of recollection was extended to other species easily captured, such as the terrestrial European tortoise, very well documented in Gruta Nova da Columbeira and Gruta da Oliveira.

In the Algarve, the sites discovered so far are located no more than 10 km away from the present coastline<sup>57</sup>, meaning that most of the inland Algarve area would have been covered at the time by dense maquis and forests, making traveling and hunting in that area difficult. The exceptions would have been the water

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<sup>55</sup> Callapez, 2000.

<sup>56</sup> Antunes, 2000; Zilhão *et al.*, 2020.

<sup>57</sup> Bicho, 2004.

courses which, as in the case of Estremadura, would have been a good means of penetrating and traveling into the area, favoring hunting and, therefore, open-air establishments of groups of people, a situation that is particularly well evidenced by finds recovered in the Tejo valley and its tributaries or sub-tributaries, such as the River Nabão in the Tomar area or the River Almansor in the Benavente/Santo Estevão area.

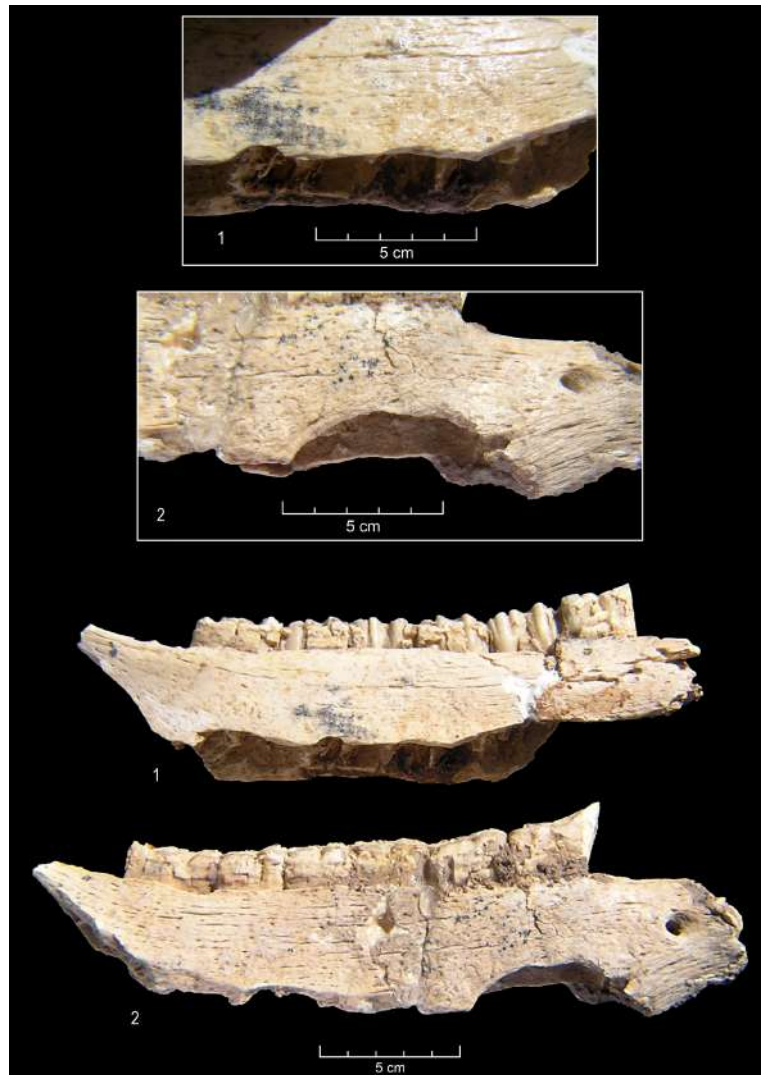


Fig. 27 – Gruta da Figueira Brava. Two horse (*Equus caballus*) hemimandibles whose lower edge has been intentionally removed by multiple percussions, allowing the bone marrow to be extracted for food purposes. Photo by J. L. Cardoso.

#### 4 – THE PORTUGUESE RECORD IN THE CONTEXT OF THE WESTERNMOST DISAPPEARANCE OF NEANDERTHALS

Until very recently, the fact that the first anatomically modern human populations did not occupy the center, south, and west of the Iberian Peninsula until around 34 Ka calBP was generally accepted. This fact was justified by the combined effects of two factors: the possible difficulty of adapting to the respective natural environments and, above all, the fact that these environments were occupied by Neanderthals. In this context, it would be expected that the size of the respective territories would have played a decisive role: the smaller and geographically more accessible territories would have generated all the phenomena of acculturation and/or a rapid decrease in population and the extinction of the less well-equipped population. The less geographically accessible territories would have led to the preservation of cultural traits and a longer survival of the older populations who could make use of sufficiently large areas for reproduction. This would have been the case in the east (Greece and Italy) and the west (Portugal and Mediterranean Spain) respectively.

Moreover, the role played by the present-day Portuguese territory as an area of refuge originates in much earlier times. In this context, it is important to remember the abundant presence of *Hyaena hyaena prisca* (the antecedent of the present-day African striped hyena), as well as the ancient subspecies of small wolf (*Canis lupus lunellensis*) in the Furninha cave (Peniche) at the start of the last Ice Age (around 80 Ka BP), whilst in the areas of Europe beyond the Pyrenees records only exist up to the Mindel-Riss interglacial period, as they were unable to survive the rigors of the Rissian cold that began around 250 Ka calBP.

The past decade and the beginning of this one contributed with theoretical models to explain the late survival of the last Neanderthals in the south and southwest of Iberia. This situation may at least be partly explained by ecological reasons and the behavioral preferences of the two human groups, which has been called the “Ebro frontier”, an imaginary geographical line that would act as a stable barrier between the region to the north and the rest of the Iberian territory inhabited by the last Iberian Neanderthals<sup>58</sup>.

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<sup>58</sup> Zilhão & Trinkaus, 2002, p. 567.

However, this demographic model based on a lasting and stable separation between two populations has also been frequently questioned. Jöris *et al.* (2003), for example, verify that (1) there is a clear discrepancy between the radiocarbon dates obtained for bones and charcoal of sites used to justify the model, with the latter being several thousands of years more modern; 2) as a consequence, they conclude that there is no proof of the duration of Middle Paleolithic industries in the southwest of the Iberian Peninsula during the oldest phases of the Aurignacian, a conclusion which contradicts the “Ebro frontier” model which, as previously stated, distinguished between the Late Mousterian industries of the southwest and those of the Early Aurignacian in the northeast; 3) in fact, the available dates imply a model of population dynamics which shrank during the most intensely arid and cold phases and expanded during the warmer interstadial phases, giving rise to the idea of regional development during the Aurignacian in south-east Europe based on Late Mousterian industries produced by Neanderthals. These transitional industries are, however, completely absent from Portuguese territory.

The absence of transitional industries that have been attributed to Neanderthal/Modern Human cultural contacts<sup>59</sup>, as are found in northern Iberia and France (i.e., the Chatelperronian), seem to add weight to the view of limited contact between Neanderthals and modern humans in southern and western Iberia Straus (2021), despite the occurrence of the hybrid skeleton of the “Lapedo child” in central Portugal<sup>60</sup>.

Following the issues raised by Jöris *et al.* (2003), most of the dates for late Neanderthal occupations in southern and western Iberia have been, over the last decade, questioned by other authors<sup>61</sup> due to possible age underestimations related to problems with site integrity, contamination with younger carbon, or poor preservation of collagen in bone samples. In fact, several sites yielding absolute dating results for Neanderthal occupations after 40 Ka calBP, including the Portuguese sites of Gruta da Figueira Brava, Gruta Nova da Columbeira,

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<sup>59</sup> Hublin, 2015; Hublin *et al.*, 2020; Mellars, 2004; Ruebens *et al.*, 2015.

<sup>60</sup> Zilhão & Trinkaus, 2002.

<sup>61</sup> Higham *et al.*, 2014; Maroto *et al.*, 2012; Wood *et al.*, 2013.

Foz do Enxarrique, Gruta da Oliveira, and the Spanish sites of Zafarraya<sup>62</sup>, and Jarama VI<sup>63</sup>, have been recently reassessed, with the new results indicating either considerable underestimations of the original dates<sup>64</sup> or a lack of solid evidence for the association of dates and stratigraphy<sup>65</sup>. On the other hand, the Spanish sites of Cueva Antón<sup>66</sup>, Higueral de Valleja<sup>67</sup>, Carihuela<sup>68</sup>, as well as Gorham's cave in Gibraltar<sup>69</sup>, are still strong contenders for a late persistence of Neanderthals in southern Iberia. With a few exceptions, these occupations are composed of small lithic assemblages, including very few, undiagnostic retouched stone tools<sup>70</sup>. In this regard, some authors have highlighted that until actual hominin fossils or sediments with human aDNA are found in unquestionable association with the stone tools, the authorship of those assemblages cannot be confirmed<sup>71</sup>. In Portugal, for example, and as shown above, the presence of Neanderthal bones is only restricted to a limited number of sites, most of them without any possibility of new archaeological interventions.

The location of some of those very late Neanderthal sites seems, however, to support the idea that any persistence of Neanderthals until 37 Ka calBP was mostly restricted to the near-coastal areas<sup>72</sup> and, possibly, that the lack of a more substantial number of Neanderthal cave occupations between c. 42 Ka calBP and 37 Ka calBP is due to a preference for open-air settings along rivers, lake margins and the seaside<sup>73</sup>. Alternatively, the lack of archaeological and fossil evidence for this interval has also been related to climatic and landscape instability that either erased the archaeological record or prevented its formation<sup>74</sup>. Some researchers have also advocated that a climate-induced chain reaction of habitat fragmentation, diminished social networks and low fertility rates were the triggers for

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<sup>62</sup> Hublin *et al.*, 1995.

<sup>63</sup> Lorenzo *et al.*, 2012.

<sup>64</sup> Cunha *et al.*, 2019; Kehl *et al.*, 2013; Wood *et al.*, 2013; Zilhão *et al.*, 2020, 2021.

<sup>65</sup> Zilhão *et al.*, 2011.

<sup>66</sup> Zilhão *et al.*, 2017.

<sup>67</sup> Jennings *et al.*, 2009.

<sup>68</sup> Carrión *et al.*, 2019. Andalusia, Spain

<sup>69</sup> Finlayson *et al.*, 2006.

<sup>70</sup> Vaquero & Romagnoli, 2017.

<sup>71</sup> Straus, 2021.

<sup>72</sup> Wolf *et al.*, 2018.

<sup>73</sup> Zilhão, 2021; Zilhão *et al.*, 2011.

<sup>74</sup> Aubry *et al.*, 2011; Mallol *et al.*, 2012.

Neanderthal demise in Iberia<sup>75</sup>, possibly resulting in independent disappearance of regional groups well before the arrival of modern humans, likely during the climate deterioration thought to have been provoked by the Heinrich Event 5<sup>76</sup>.

The physical separation between Neanderthals and modern humans proposed by the “Ebro Frontier” seems also not compatible with recent evidence for the presence of Early Aurignacian materials in Bajondillo (southern Iberia) c. 43 Ka calBP<sup>77</sup> and those found at Lapa do Picareiro (Portuguese Estremadura) dated to c. 40 Ka calBP<sup>78</sup>. Together, these studies provide critical insights into the timing and pathways of early modern human dispersal into Europe. They highlight a rapid expansion of modern humans across Eurasia, challenging previous assumptions about the pace and nature of this process (Fig. 28).



Fig. 28. Location of sites south of the Ebro basin with Middle Paleolithic occupations possibly dating to after 40 Ka calBP (black dots) – according to Zilhão (2021); and Upper Paleolithic sites possibly dating to 40 Ka calBP or before (red dots) – according to Haws et al., (2020) and Cortés-Sánchez et al. (2019).

<sup>75</sup> Dalén *et al.*, 2012; Melchionna, 2018.

<sup>76</sup> Galván *et al.*, 2014, previously considered as one of the last refuge zones of the Neanderthals. Evidence of Neanderthal occupation in Iberia after 42 ka is now very scarce and open to debate on chronological and technological grounds. Here we report thermoluminescence (TL

<sup>77</sup> Cortés-Sánchez *et al.*, 2019.

<sup>78</sup> Haws *et al.*, 2020, 2021.

Both sequences, however, have been recently criticized. The Bajondillo lithic assemblage has been argued to be a mixed collection of artifacts from younger and older occupations as lacking typological traits of the Proto or Early Aurignacian phases<sup>79</sup>. While the association between dates and the Aurignacian bladelet component detected in levels GG-HH-II at Lapa do Picareiro has also been put into question by Zilhão (2021, 2022), arguing that those materials should probably be of a later stage of the Aurignacian technocomplex.

Overall, as elsewhere in Eurasia, currently available data from Iberia seems to indicate that a rather complex mosaic of processes might have occurred during the thousands of years preceding the ultimate disappearance of the Neanderthals. Most of the identified patterns are still very tentative and contingent on more dating and taphonomic analyses of existing key sites and the further excavation and study of new ones<sup>80</sup>. Particularly relevant is the fact that as recently observed by Cascalheira et al.<sup>81</sup>, very little is known about the eco-cultural dynamics occurring between the apparently stable and resilient conditions of MIS 5 Neanderthals—as revealed by the outstanding discoveries in southwestern Iberia of recurrent use of coastal resources<sup>82</sup>, production of art<sup>83</sup>, use of personal ornaments<sup>84</sup>, and rapid technological pace<sup>85</sup>—and the later parts of the MIS 3 when Neanderthals are likely to have completely disappeared from the archaeological record.

After close to 400 000 years of evolutionary success across Eurasia<sup>86</sup>, Neanderthals disappeared from the archaeological record sometime between c. 45 000 and 30 000 years ago, being replaced by modern humans<sup>87</sup>. At least three different categories of hypotheses have been advanced to explain the disappearance of the Neanderthals<sup>88</sup>. First, the event has been causally related to the migration of modern humans into territories occupied by Neanderthals, with both groups competing for the same resources. Inter-specific differences in skeleton

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<sup>79</sup> de la Peña, 2019

<sup>80</sup> Straus, 2021

<sup>81</sup> Cascalheira et al., 2022.

<sup>82</sup> Zilhão et al., 2020.

<sup>83</sup> Hoffmann, Standish et al., 2018.

<sup>84</sup> Hoffmann, Angelucci et al., 2018.

<sup>85</sup> Zilhão et al., 2021.

<sup>86</sup> Arsuaga et al., 2014.

<sup>87</sup> Benazzi et al., 2011; Higham et al., 2011; J.-J. Hublin, 2015.

<sup>88</sup> Vaesen et al., 2021.

morphology<sup>89</sup>, cognition<sup>90</sup>, technology<sup>91</sup>, social<sup>92</sup> or economic patterns<sup>93</sup>, would have given modern humans significant advantages. Second, environmental change, including general climatic instability<sup>94</sup>, extreme climatic conditions<sup>95</sup> or the introduction of pathogens by modern humans<sup>96</sup>, have been suggested to led Neanderthals to extinction. Finally, due to the presumed small size and limited interconnectedness of Neanderthal populations, internal demographic dynamics, such as inbreeding, Allee effects, or stochastic fluctuations, have been pointed as potential independent factors impeding Neanderthals to persist in the long run<sup>97</sup>.

Many of these hypotheses are based on single-cause models, investigated through mathematical estimations, whose results are hard to test against the complexity present in the archaeological record. In fact, for the most part, studies based on mathematical models have been theoretical, with minimal use of archaeological data<sup>98</sup>.

Currently, different hypotheses remain open to debate, and many explanations appear to have more opponents than proponents<sup>99</sup>, particularly the ones supporting cognitive “superiority” of modern humans, who had evolved in Africa, developing complex cultural traditions that allowed them to expand and replace all other hominins<sup>100</sup>. A series of discoveries on Neanderthal production of art and personal ornaments<sup>101</sup>, reliance on coastal resources and diverse subsistence practices<sup>102</sup>, and the production of specialized/complex tools and rapid technological change<sup>103</sup> across Europe, have provided important evidence to

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<sup>89</sup> Bastir *et al.*, 2020; Sorensen & Leonard, 2001; Steudel-Numbers & Tilkens, 2004; Stewart *et al.*, 2019.

<sup>90</sup> Berwick & Chomsky, 2017; Bolhuis *et al.*, 2014; Burke, 2012; Kochiyama *et al.*, 2018; Mellars, 2004; Mithen, 1996, 1997; Pearce *et al.*, 2013; Wynn & Coolidge, 2004.

<sup>91</sup> Bar-Yosef & Kuhn, 1999; Chu, 2009; Collard *et al.*, 2016; Dibble *et al.*, 2018; Kolen, 2000; Muller & Clarkson, 2016; Shea & Sisk, 2010.

<sup>92</sup> Gamble, 1999; Horan *et al.*, 2005.

<sup>93</sup> Marean, 2014; Richards *et al.*, 2001; Shipman, 2015; Stiner & Kuhn, 2006; Timmermann, 2020.

<sup>94</sup> Finlayson, 2008; Jiménez-Espejo *et al.*, 2007; Müller *et al.*, 2011; Tzedakis *et al.*, 2007.

<sup>95</sup> Golovanova *et al.*, 2010.

<sup>96</sup> Greenbaum *et al.*, 2019; Houldcroft & Underdown, 2015; Wolff & Greenwood, 2010.

<sup>97</sup> Finlayson, 2004; French, 2016; Kolodny & Feldman, 2017; Vaesen *et al.*, 2019.

<sup>98</sup> Roberts & Bricher, 2018.

<sup>99</sup> Vaesen *et al.*, 2021.

<sup>100</sup> McBrearty & Brooks, 2000.

<sup>101</sup> Hoffmann, Angelucci *et al.*, 2018; Hoffmann, Standish *et al.*, 2018; Rodríguez-Vidal *et al.*, 2014; Zilhão *et al.*, 2010.

<sup>102</sup> Blasco *et al.*, 2014; Sistiaga *et al.*, 2014; Zilhão *et al.*, 2020.

<sup>103</sup> Hardy *et al.*, 2020; Soressi *et al.*, 2013; Zilhão *et al.*, 2021.

question if the Neanderthal archaeological record is different enough to explain their demise in terms of “inferiority”<sup>104</sup>. These data contradict the classic idea that the Middle Paleolithic was a period of stasis<sup>105</sup>, with few behavioral changes occurring across time and space. On the contrary, it indicates that specific spatial and chronological tendencies exist amongst Neanderthal stone tool assemblages<sup>106</sup>, subsistence patterns<sup>107</sup>, and that geographical patterning is supported by variation in skeletal features<sup>108</sup> and genetics<sup>109</sup>.

COMUNICAÇÃO APRESENTADA À CLASSE DE CIÊNCIAS  
NA SESSÃO DE 2 DE FEVEREIRO DE 2023

COMUNICAÇÃO RECEBIDA A 31 DE MARÇO DE 2024

### References

- Antunes, M. T. (ed.), *Últimos Neandertais em Portugal – evidência, odontológica e outra*. Lisboa, Academia das Ciências de Lisboa, 2000.
- Antunes, M. T. & Cardoso, J. L., Quaternary elephants in Portugal: new data. *Ciências da Terra*, 1992. Lisboa, 11, pp. 17-37.
- Antunes, M. T. & Cardoso, J. L., Gruta Nova da Columbeira, Gruta das Salemas and Gruta da Figueira Brava: stratigraphy, and chronology of the pleistocene deposits. In Antunes, M. T. (ed.): *Últimos Neandertais em Portugal – evidência, odontológica e outra*. Memórias da Academia das Ciências de Lisboa. Classe de Ciências. Lisboa, 38, pp. 23-67, 2000.
- Antunes, M. T., Cunha, A. S., Schwartz, J. & Tattersall, I., The latest Neanderthals: evidence from Portugal. In Antunes, M. T. (ed.): *Últimos Neandertais em Portugal – evidência, odontológica e outra*. Memórias da Academia das Ciências de Lisboa. Classe de Ciências. Lisboa, 38, pp. 283-318, 2000.
- Arsuaga, J. L., Martínez, I., Arnold, L. J., Aranburu, A., Gracia-Téllez, A., Sharp, W. D., Quam, R. M., Falguères, C., Pantoja-Pérez, A., & Bischoff, J., Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. *Science*, 344(6190), pp. 1358-1363, 2014.

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<sup>104</sup> d’Errico & Banks, 2013; Villa & Roebroeks, 2014; Zilhão, 2006.

<sup>105</sup> de la Torre *et al.*, 2013.

<sup>106</sup> Hovers & Kuhn, 2007; Ruebens, 2013; Sykes, 2012.

<sup>107</sup> Hardy & Moncel, 2011.

<sup>108</sup> Rosas *et al.*, 2006.

<sup>109</sup> Dalén *et al.*, 2012.

- Aubry, T., Dimuccio, L. A., Almeida, M., Neves, M. J., Angelucci, D. E., & Cunha, L., Palaeoenvironmental forcing during the Middle–Upper Palaeolithic transition in central-western Portugal. *Quaternary Research*, 75, pp. 66-79 2011. <https://doi.org/10.1016/j.yqres.2010.11.002>
- Barandiarán, I. & Ferreira, O. da Veiga, Huesos labrados en el Paleolítico Antíguo y Médio de Portugal. *Arqueologia e História, Série IX*, 3, Lisboa. pp. 31-54, 1971.
- Bar-Yosef, O., & Kuhn, S. L., The Big Deal about Blades: Laminar Technologies and Human Evolution. *American Anthropologist*, 101, pp. 322-338, 1999.
- Bastir, M., García-Martínez, D., Torres-Tamayo, N., Palancar, C. A., Beyer, B., Barash, A., Villa, C., Sanchis-Gimeno, J. A., Riesco-López, A., & Nalla, S., Rib cage anatomy in *Homo erectus* suggests a recent evolutionary origin of modern human body shape. *Nature Ecology & Evolution*, 4(9), pp. 1178-1187, 2020.
- Benazzi, S., Douka, K., Fornai, C., Bauer, C. C., Kullmer, O., Svoboda, J., Pap, I., Mallegni, F., Bayle, P., Coquerelle, M., Condemi, S., Ronchitelli, A., Harvati, K., & Weber, G. W., Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. *Nature*, 479(7374), Article 7374, 2011. <https://doi.org/10.1038/nature10617>
- Berwick, R. C. & Chomsky, N., Why only us: Recent questions and answers. *Journal of Neurolinguistics*, 43, pp. 166-177, 2017. <https://doi.org/10.1016/j.jneuroling.2016.12.002>
- Bicho, N., The Middle Paleolithic occupation of Southern Portugal. In Connard, N. J. (ed.) *Settlement dynamics of the Middle Paleolithic and Middle Stone Age*, 2. Tübingen: Kerns Verlag, pp. 513-531, 2004.
- Bicho, N. F. & Cardoso, J. L., Paleolithic occupations and lithic assemblages from Furninha cave, Peniche (Portugal). *Zephyrus*. Salamanca, 66, p. 17-37, 2010.
- Blasco, R., Finlayson, C., Rosell, J., Marco, A. S., Finlayson, S., Finlayson, G., Negro, J. J., Pacheco, F. G., & Vidal, J. R., The earliest pigeon fanciers. *Scientific Reports*, 4, p. 5971, 2014.
- Bolhuis, J. J., Tattersall, I., Chomsky, N., & Berwick, R. C., How could language have evolved? *PLoS Biol*, 12(8), e1001934, 2014.
- Boneta Jiménez, I., Cardoso, J. L. & Pérez-García, A., The turtles from the middle Paleolithic site of Gruta Nova da Columbeira (Bomarral, Portugal): Update through an archaeozoological perspective. *The Anatomical Record – Wiley, Special Issue Article* (Glendale, Arizona, 29 maio 2023), pp 1-15, 2023. De col. com Iratxe Boneta Jiménez e Adán Pérez-García. <https://doi.org/10.1002/ar.25229>
- Breuil, H. & Zbyszewski, G., *Contribution à l'étude des industries paléolithiques du Portugal et de leurs rapports avec la géologie du Quaternaire. Les principaux gisements des deux rives de l'ancien estuaire du Tage*, *Comunicações dos Serviços Geológicos de Portugal*, 23, Lisboa, pp. 3-328, 1942.
- Burke, A., Spatial abilities, cognition and the pattern of Neanderthal and modern human dispersals. *Quaternary International*, 247, pp. 230-235, 2012. <https://doi.org/10.1016/j.quaint.2010.10.029>
- Callapez, P., Upper Pleistocene marine invertebrates from Gruta da Figueira Brava (Arrábida, Portugal). In Antunes, M. T. (ed.): *Últimos Neandertais em Portugal – evidência, odontológica e outra*. Lisboa, Academia das Ciências de Lisboa, pp. 83-103, 2000.

- Cardoso, J. L., *Contribuição para o conhecimento dos grandes mamíferos do Plistocénico Superior de Portugal*. Oeiras, Câmara Municipal de Oeiras, 1993.
- Cardoso, J. L., *Pré-História de Portugal*. Lisboa, Editorial Verbo, 2002.
- Cardoso, J. L., The Mousterian Complex in Portugal. *Zephyrus*. Salamanca, 59, pp. 21-50, 2006.
- Cardoso, J. L., *Pré-História de Portugal*. Lisboa, Universidade Aberta, 2007.
- Cardoso, J. L. & Raposo, L., As indústrias paleolíticas da Gruta da Figueira Brava (Setúbal). In 3.<sup>a</sup> Reunião do Quaternário Ibérico. Coimbra, 1995, pp. 451-456.
- Cardoso, J. L.; Raposo, L. & Ferreira, O. da Veiga, *A Gruta Nova da Columbeira – Bombarral*. Câmara Municipal do Bombarral, 2002.
- Carrión, J. S., Fernández, S., Jiménez-Arenas, J. M., Munuera, M., Ochando, J., Amorós, G., Ponce De León, M., Zollikofer, C., Martín-Lerma, I., Toro-Moyano, I., Hajdas, I., & Walker, M. J., The sequence at Carhuela Cave and its potential for research into Neanderthal ecology and the Mousterian in southern Spain. *Quaternary Science Reviews*, S027737911930188X, 2019.  
<https://doi.org/10.1016/j.quascirev.2019.04.012>
- Cascalheira, J., Gonçalves, C., & Maio, D., The spatial patterning of Middle Palaeolithic human settlement in westernmost Iberia. *Journal of Quaternary Science*, 37(2), 291-299, 2022. <https://doi.org/10.1002/jqs.3286>
- Chu, W., A functional approach to Paleolithic open-air habitation structures. *World Archaeology*, 41(3), 348-362, 2009.
- Collard, M., Tarle, L., Sandgathe, D., & Allan, A., Faunal evidence for a difference in clothing use between Neanderthals and early modern humans in Europe. *Journal of Anthropological Archaeology*, 44, 235–246, 2016. <https://doi.org/10.1016/j.jaa.2016.07.010>
- Cortés-Sánchez, M., Jiménez-Espejo, F. J., Simón-Vallejo, M. D., Stringer, C., Lozano Francisco, M. C., García-Alix, A., Vera Peláez, J. L., Odriozola, C. P., Riquelme-Cantal, J. A., Parrilla Giráldez, R., Maestro González, A., Ohkouchi, N., & Morales-Muñiz, A., An early Aurignacian arrival in southwestern Europe. *Nature Ecology & Evolution*, 3, pp. 207-212, 2019. <https://doi.org/10.1038/s41559-018-0753-6>
- Cunha, P., Martins, A., Buylaert, J.-P., Murray, A., Gouveia, M., Font, E., Pereira, T., Figueiredo, S., Ferreira, C., Bridgland, D., Yang, P., Stevaux, J., & Mota, R., The Lowermost Tejo River Terrace at Foz do Enxarrique, Portugal: A Palaeoenvironmental Archive from c. 60–35 ka and Its Implications for the Last Neanderthals in Westernmost Iberia. *Quaternary*, 2(1), 3, 2019. <https://doi.org/10.3390/quat2010003>
- Dalén, L., Orlando, L., Shapiro, B., Brandström-Durling, M., Quam, R., Gilbert, M. T. P., Díez Fernández-Lomana, J. C., Willerslev, E., Arsuaga, J. L., & Götherström, A., Partial genetic turnover in neandertals: Continuity in the east and population replacement in the west. *Molecular Biology and Evolution*, 29(8), pp. 1893-1897, 2012.
- de la Peña, P., Dating on its own cannot resolve hominin occupation patterns. *Nature Ecology & Evolution*, 3, p. 712, 2019. <https://doi.org/10.1038/s41559-019-0886-2>

- de la Torre, I., Martínez-Moreno, J., & Mora, R., Change and Stasis in the Iberian Middle Paleolithic: Considerations on the Significance of Mousterian Technological Variability. *Current Anthropology*, 54(S8), S320-S336, 2013. <https://doi.org/10.1086/673861>
- Delgado, J. F. N., La grotte de Furninha a Peniche. In *Congrès Internationale d'Anthropologie et d'Archéologie Préhistoriques. IX Session. Lisboa, 1884*, pp. 207-278.
- D'Errico, F., & Banks, W. E., Identifying Mechanisms behind Middle Paleolithic and Middle Stone Age Cultural Trajectories. *Current Anthropology*, 54(S8), S371-S387, 2013. <https://doi.org/10.1086/673388>
- Dibble, H. L., Sandgathe, D., Goldberg, P., McPherron, S., & Aldeias, V., Were Western European Neandertals Able to Make Fire? *Journal of Paleolithic Archaeology*. 1(1), pp. 54-79, 2018. <https://doi.org/10.1007/s41982-017-0002-6>
- Ferembach, D., La deuxième molaire déciduale inférieure de la grotte de Salemas (Portugal). *Comunicações dos Serviços Geológicos de Portugal*. Lisboa, 46, pp. 177-187, 1962.
- Ferembach, D., La molaire humaine inférieure moustérienne de Bombarral (Portugal), *Comunicações dos Serviços Geológicos de Portugal*, 48, Lisboa, pp. 185-190 (1964/1965).
- Ferreira, O. da V., Acerca dos primeiros restos de Homo neanderthalensis encontrados no Mustierense de Portugal, *Lucerna*, 5, Porto, pp. 361-375, 1966.
- Ferreira, O. da V., O mais importante nível de ocupação do caçador Neandertal da Gruta Nova da Columbeira (Bombarral). In *Volume d'Homage au géologues G. Zbyszewski*. Paris, Éditions Recherche sur les Civilisations, pp. 365-370, 1984.
- Finlayson, C., *Neanderthals and modern humans: An ecological and evolutionary perspective* (Vol. 38). Cambridge University Press, 2004.
- Finlayson, C., On the importance of coastal areas in the survival of Neanderthal populations during the Late Pleistocene. *Quaternary Science Reviews*, 27(23-24), pp. 2246-2252, 2008. <https://doi.org/10.1016/j.quascirev.2008.08.033>
- Finlayson, C., Pacheco, F. G., Rodríguez-Vidal, J., Fa, D. A., López, J.M. G., Pérez, A. S., Finlayson, G., Allue, E., Preysler, J. B., Cáceres, I., Carrión, J. S., Jalvo, Y. F., Glead-Owen, C. P., Jimenez Espejo, F. J., López, P., Sáez, J. A. L., Cantal, J. A. R., Marco, A. S., Guzman, F. G., Brown, K., Fuentes, N., Valarino, C. A., Villalpando, A., Stringer, C. B., Ruiz, F. M. & Sakamoto, T., Late survival of Neanderthals at the southernmost extreme of Europe. *Nature*, 443(7113), pp. 850-853, 2006. <https://doi.org/10.1038/nature05195>
- Fontes, J., Instruments paléolithiques dans la collection de préhistoire du Service Géologique, *Comunicações do Serviço Geológico de Portugal*, 12, Lisboa, pp. 1-16, 1916.
- French, J. C., Demography and the Palaeolithic Archaeological Record. *Journal of Archaeological Method and Theory*, 23(1), pp. 150-199, 2016. <https://doi.org/10.1007/s10816-014-9237-4>
- Galván, B., Hernández, C. M., Mallol, C., Mercier, N., Sistiaga, A., & Soler, V., New evidence of early Neanderthal disappearance in the Iberian Peninsula. *Journal of Human Evolution*, 75, pp. 16-27, 2014. <https://doi.org/10.1016/j.jhevol.2014.06.002>
- Gamble, C., *The palaeolithic societies of Europe*. Cambridge University Press, 1999.

- Golovanova, L. V., Doronichev, V. B., Cleghorn, N. E., Koulikova, M. A., Sapelko, T. V., & Shackley, M. S., Significance of Ecological Factors in the Middle to Upper Paleolithic Transition. *Current Anthropology*, 51(5), pp. 655-691, 2010. <https://doi.org/10.1086/656185>
- Greenbaum, G., Getz, W. M., Rosenberg, N. A., Feldman, M. W., Hovers, E., & Kolodny, O., Disease transmission and introgression can explain the long-lasting contact zone of modern humans and Neanderthals. *Nature Communications*, 10(1), Article 1, 2019. <https://doi.org/10.1038/s41467-019-12862-7>
- Hardy, B. L., & Moncel, M.-H., Neanderthal Use of Fish, Mammals, Birds, Starchy Plants and Wood 125-250,000 Years Ago. *PLOS ONE*, 6(8), p. e23768, 2011. <https://doi.org/10.1371/journal.pone.0023768>
- Hardy, B. L., Moncel, M.-H., Kerfant, C., Lebon, M., Bellot-Gurlet, L., & Mélard, N., Direct evidence of Neanderthal fibre technology and its cognitive and behavioral implications. *Scientific Reports*, 10(1), Article 1, 2020. <https://doi.org/10.1038/s41598-020-61839-w>
- Harlé, E., Les mammifères et oiseaux quaternaires connus jusqu'ici en Portugal. *Comunicações da Comissão do Serviço Geológico de Portugal*. Lisboa, 8, p. 22-85, 1910/1911.
- Haws, J. A., Benedetti, M. M., Bicho, N. F., Cascalheira, J., Ellis, M. G., Carvalho, M. M., Friedl, L., Pereira, T., & Talamo, S., The early Aurignacian at Lapa do Picareiro really is that old: A comment on 'The late persistence of the Middle Palaeolithic and Neandertals in Iberia: A review of the evidence for and against the "Ebro Frontier" model.' *Quaternary Science Reviews*, 274, p. 107261, 2021. <https://doi.org/10.1016/j.quascirev.2021.107261>
- Haws, J. A., Benedetti, M. M., Talamo, S., Bicho, N., Cascalheira, J., Ellis, M. G., Carvalho, M. M., Friedl, L., Pereira, T., & Zinsious, B. K., The early Aurignacian dispersal of modern humans into westernmost Eurasia. *Proceedings of the National Academy of Sciences*, 117, pp 25414-25422, 2020. <https://doi.org/10.1073/pnas.2016062117>
- Higham, T., Compton, T., Stringer, C., Jacobi, R., Shapiro, B., Trinkaus, E., Chandler, B., Gröning, F., Collins, C., Hillson, S., O'higgins, P., Fitzgerald, C., & Fagan, M., The earliest evidence for anatomically modern humans in northwestern Europe. *Nature*, 479(7374), pp. 521-524, 2011. <https://doi.org/10.1038/nature10484>
- Higham, T., Douka, K., Wood, R., Ramsey, C. B., Brock, F., Basell, L., Camps, M., Arrizabalaga, A., Baena, J., Barroso-Ruiz, C., Bergman, C., Boitard, C., Boscato, P., Caparrós, M., Conard, N. J., Drazil, C., Froment, A., Galván, B., Gambassini, P., ..., Jacobi, R., The timing and spatiotemporal patterning of Neanderthal disappearance. *Nature*, 512(7514), pp. 306-309, 2014. <https://doi.org/10.1038/nature13621>
- Hoffmann, D. L., Angelucci, D. E., Villaverde, V., Zapata, J., & Zilhão, J., Symbolic use of marine shells and mineral pigments by Iberian Neandertals 115,000 years ago. *Science Advances*, 4(2), eaar5255, 2018. <https://doi.org/10.1126/sciadv.aar5255>
- Hoffmann, D. L., Standish, C. D., García-Diez, M., Pettitt, P. B., Milton, J. A., Zilhão, J., Alcolea-González, J. J., Cantalejo-Duarte, P., Collado, H., Balbín, R. de, Lorblanchet, M., Ramos-Muñoz,

- J., Weniger, G.-C., & Pike, A. W. G., U-Th dating of carbonate crusts reveals Neanderthal origin of Iberian cave art. *Science*, 359(6378), p. 912-915, 2018. <https://doi.org/10.1126/science.aap7778>
- Horan, R. D., Bulte, E., & Shogren, J. F., How trade saved humanity from biological exclusion: An economic theory of Neanderthal extinction. *Journal of Economic Behavior & Organization*, 58(1), pp. 1-29, 2005.
- Houldcroft, C. J., & Underdown, S. J., Neanderthal Genomics Suggests a Pleistocene Time Frame for the First Epidemiologic Transition. *bioRxiv*, 017343, 2015. <https://doi.org/10.1101/017343>
- Hovers, E. & Kuhn, S., *Transitions before the transition: Evolution and stability in the Middle Paleolithic and Middle Stone Age*. Springer Science & Business Media, 2007.
- Hublin, J. J., Barroso, C., Medina, P., Fontugne, M., & Reyss, J. L., The Mousterian Site of Zafarraya (Andalucia, Spain): Dating and Implications on the Paleolithic Peopling Processes of Western Europe, vol. 321, *Comptes-Rendus de l'Académie des Sciences de Paris*. pp. 931-937, 1995.
- Hublin, J.-J., The modern human colonization of western Eurasia: When and where? *Quaternary Science Reviews*, 118, pp. 194-210, 2015. <https://doi.org/10.1016/j.quascirev.2014.08.011>
- Hublin, J.-J., Sirakov, N., Aldeias, V., Bailey, S., Bard, E., Delvigne, V., Endarova, E., Fagault, Y., Fewlass, H., Hajdinjak, M., Kromer, B., Krumov, I., Marreiros, J., Martisius, N. L., Paskulin, L., Sinet-Mathiot, V., Meyer, M., Pääbo, S., Popov, V., ... Tsanova, T., Initial Upper Palaeolithic Homo sapiens from Bacho Kiro Cave, Bulgaria. *Nature*, 581(7808), Article 7808, 2020. <https://doi.org/10.1038/s41586-020-2259-z>
- Jennings, R. P., Giles Pacheco, F., Barton, R. N. E., Collcutt, S. N., Gale, R., Gleed-Owen, C. P., Gutiérrez López, J. M., Higham, T. F. G., Parker, A., & Price, C., New dates and palaeoenvironmental evidence for the Middle to Upper Palaeolithic occupation of Higueral de Valleja Cave, southern Spain. *Quaternary Science Reviews*, 28, pp. 830-839, 2009. <https://doi.org/10.1016/j.quascirev.2008.11.014>
- Jiménez-Espejo, F. J., Martínez-Ruiz, F., Finlayson, C., Paytan, A., Sakamoto, T., Ortega-Huertas, M., Finlayson, G., Iijima, K., Gallego-Torres, D., & Fa, D., Climate forcing and Neanderthal extinction in Southern Iberia: Insights from a multiproxy marine record. *Quaternary Science Reviews*, 26, pp. 836-852, 2007. <https://doi.org/10.1016/j.quascirev.2006.12.013>
- Jiménez Fuentes, E., Cardoso, J. L. & Crespo, E. G., Presencia de *Agryonemis* (=Testudo) hermanni (Gmelin, 1789) en el Paleolítico Medio de la Gruta Nova de Columbeira (Bombarral, provincia de Estremadura, Portugal), *Studia Geológica Salmanticensia*, 34, Salamanca, pp. 123-139, 1998.
- Jöris, O., Álvarez, E. & Weninger, B., Radiocarbon evidence of the Middle to Upper Paleolithic transition in Southwestern Europe, *Trabajos de Prehistoria*, 60 (2), Madrid, pp. 15-38, 2003.
- Kehl, M., Burow, C., Hilgers, A., Navazo, M., Pastoors, A., Weniger, G.-C., Wood, R., & Jordá Pardo, J. F., Late Neanderthals at Jarama VI (central Iberia)? *Quaternary Research*, 80(2), pp. 218-234, 2013. <https://doi.org/10.1016/j.yqres.2013.06.010>
- Kochiyama, T., Ogihara, N., Tanabe, H. C., Kondo, O., Amano, H., Hasegawa, K., Suzuki, H., Ponce De León, M. S., Zollikofer, C. P. E., Bastir, M., Stringer, C., Sadato, N., & Akazawa, T.,

- Reconstructing the Neanderthal brain using computational anatomy. *Scientific Reports*, 8(1), Article 1, 2018. <https://doi.org/10.1038/s41598-018-24331-0>
- Kolen, J., Hominids without Homes. On the nature of Middle Palaeolithic settlement in Europe. In W. Roebroeks & C. Gamble (Eds.), *The Middle Palaeolithic Occupation of Europe*, Leiden, Leiden University/European Science Foundation, pp. 139-177, 1999.
- Kolodny, O. & Feldman, M. W., A parsimonious neutral model suggests Neanderthal replacement was determined by migration and random species drift. *Nature Communications*, 8(1), Article 1, 2017. <https://doi.org/10.1038/s41467-017-01043-z>
- Lorenzo, C., Navazo, M., Díez, J. C., Sesé, C., Arceredillo, D., & Pardo, J. F. J., New human fossil to the last Neanderthals in central Spain (Jarama VI, Valdesotos, Guadalajara, Spain). *Journal of Human Evolution*, 62(6), pp. 720-725, 2012.
- Mallol, C., Hernández, C. M., & Machado, J., The significance of stratigraphic discontinuities in Iberian Middle-to-Upper Palaeolithic transitional sites. *Quaternary International*, 275, pp. 4-13, 2012. <https://doi.org/10.1016/j.quaint.2011.07.026>
- Marean, C. W., The origins and significance of coastal resource use in Africa and Western Eurasia. *J. Hum. Evol.*, 77, pp. 17-40, 2014. <https://doi.org/10.1016/j.jhevol.2014.02.025>
- Marks, A., Monigal, K. & Zilhão, J., The lithic assemblages of the Late Mousterian at Gruta da Oliveira, Almonda, Portugal. In Zilhão, J.; Aubry, T. & Carvalho, A. F. (eds.): *Les premiers homes modernes de la Péninsule Ibérique*. Lisboa: Instituto Português de Arqueologia, pp. 145-154, 2001.
- Maroto, J., Vaquero, M., Arrizabalaga, Á., Baena, J., Baquedano, E., Jordá, J., Julià, R., Montes, R., Van Der Plicht, J., Rasines, P., & Wood, R., Current issues in late Middle Palaeolithic chronology: New assessments from Northern Iberia. *Quaternary International*, 247, pp. 15-25, 2012. <https://doi.org/10.1016/j.quaint.2011.07.007>
- Mcbrearty, S., & Brooks, A. S., (2000) – The revolution that wasn't: A new interpretation of the origin of modern human behavior. *J. Hum. Evol.*, 39, pp. 453-563. <https://doi.org/10.1006/jhev.2000.0435>
- Mein, P. & Antunes, M. T., Gruta da Figueira Brava: petits mammifères – Insectívora, Chiroptera, Lagomorpha. In ANTUNES, M. T. (ed.): *Últimos Neandertais em Portugal – evidência, odontológica e outra*. Lisboa: Academia das Ciências de Lisboa, pp. 163-177, 2000.
- Melchionna, M., Small and isolated: Ecology and fragmentation of Neanderthals. *Fossilias – Reports in Palaeontology*, pp. 53-56, 2018. <https://doi.org/10.32774/FosRepPal.20.1810.075356>
- Mellars, P., Neanderthals and the modern human colonization of Europe. *Nature*, 432(7016), pp. 461-465, 2004. <https://doi.org/10.1038/nature03103>
- Mithen, S., *Domain-specific intelligence and the Neanderthal mind. Modelling the Early Human Mind*, McDonald Institute, Cambridge, pp. 217-229, 1996.
- Mithen, S., The prehistory of the mind. *Cambridge Archaeological Journal*, 7, pp. 269-269, 1997.
- Muller, A., & Clarkson, C., Identifying major transitions in the evolution of lithic cutting edge production rates. *PLoS One*, 11(12), e0167244, 2016.

- Müller, U. C., Pross, J., Tzedakis, P. C., Gamble, C., Kotthoff, U., Schmiedl, G., Wulf, S. & Christanis, K., The role of climate in the spread of modern humans into Europe. *Quaternary Science Reviews*, 30(3), pp. 273-279, 2011. <https://doi.org/10.1016/j.quascirev.2010.11.016>
- Nabais, M. & Zilhão, J., The consumption of tortoise among Last Interglacial Iberian Neanderthals. *Quaternary Science Reviews*, S0277379118310217 (2019). <https://doi.org/10.1016/j.quascirev.2019.03.024>
- Pearce, E., Stringer, C. & Dunbar, R. I. M., New insights into differences in brain organization between Neanderthals and anatomically modern humans. *Proceedings of the Royal Society B: Biological Sciences*, 280(1758), 20130168, 2013. <https://doi.org/10.1098/rspb.2013.0168>
- Pereira, A. R. & Angelucci, D. E., Formações dunares no litoral português, do final do Plistocénico e inícios do Holocénico, como indicadores paleoclimáticos e paleogeográficos. In Tavares, A. A.; Tavares, M. J. F. & Cardoso, J. L. (eds.): *Evolução geohistórica do litoral português e fenómenos correlativos*. Lisboa, Universidade Aberta, pp. 221-256, 2004.
- Raposo, L., O Paleolítico Médio. In Carvalho, G. S.; Ferreira, A. B. & Senna-Martinez, J. C. (Eds.): *O Quaternário em Portugal. Balanço e perspectivas*. Lisboa, Colibri, pp. 147-161, 1993.
- Raposo, L. & Cardoso, J. L., Las industrias líticas de la Gruta Nova da Columbeira (Bombarral, Portugal) en el contexto del Musteriense Final de la Península Ibérica, *Trabajos de Prehistoria*, Madrid, 55 (1), pp. 39-6, 1998.
- Raposo, L. & Cardoso, J. L., A Gruta da Figueira Brava no contexto do Paleolítico Médio final do sul e ocidente ibéricos. In *Encontro sobre a Arrábida*, Lisboa, Instituto Português de Arqueologia, pp. 7-19, 2000.
- Raposo, L. & Cardoso, J. L., Mousterian industries of the Gruta da Figueira Brava. In Antunes, M. T. (ed.): *Últimos Neandertais em Portugal – evidência, odontológica e outra*. Lisboa, Academia das Ciências de Lisboa, pp. 319-337, 2000.
- Richards, M. P., Pettitt, P. B., Stiner, M. C., & Trinkaus, E., Stable isotope evidence for increasing dietary breadth in the European mid-Upper Paleolithic. *Proceedings of the National Academy of Sciences*, 98(11), pp. 6528-6532, 2001.
- Roberts, M. F., & Bricher, S. E., Modeling the disappearance of the Neanderthals using principles of population dynamics and ecology. *Journal of Archaeological Science*, 100, pp. 16-31, 2018. <https://doi.org/10.1016/j.jas.2018.09.012>
- Rodríguez-Vidal, J., D'errico, F., Pacheco, F. G., Blasco, R., Rosell, J., Jennings, R. P., Queffelec, A., Finlayson, G., Fa, D. A., & López, J. M. G., A rock engraving made by Neanderthals in Gibraltar. *Proceedings of the National Academy of Sciences*, 111(37), pp. 13301-13306, 2014.
- Rosas, A., Martínez-Maza, C., Bastir, M., García-Taberner, A., Lalueza-Fox, C., Huguet, R., Ortiz, J. E., Julia, R., Soler, V. & De Torres, T., Paleobiology and comparative morphology of a late Neanderthal sample from El Sidrón, Asturias, Spain, *Proceedings of the National Academy of Sciences*, 103(51), pp. 19266-19271, 2006.
- Ruebens, K., Regional behaviour among late Neanderthal groups in Western Europe: A comparative assessment of late Middle Palaeolithic bifacial tool variability. *J. Hum. Evol.*, 65, pp. 341-362, 2013. <https://doi.org/10.1016/j.jhevol.2013.06.009>

- Ruebens, K., Mcpherron, S. J. P. & Hublin, J.-J., On the local Mousterian origin of the Châtelperronian: Integrating typo-technological, chronostratigraphic and contextual data. *J. Hum. Evol.*, 86, pp. 55-91, 2015. <https://doi.org/10.1016/j.jhevol.2015.06.011>
- Shea, J. J. & Sisk, M. L., Complex projectile technology and Homo sapiens dispersal into western Eurasia. *PaleoAnthropology*, 2010, pp. 100-122, 2010.
- Shipman, P., *The invaders: How humans and their dogs drove Neanderthals to extinction*. Harvard University Press, 2015.
- Sistiaga, A., Mallol, C., Galván, B., & Summons, R. E., The Neanderthal Meal: A New Perspective Using Faecal Biomarkers. *PLOS ONE*, 9(6), e101045, 2014. <https://doi.org/10.1371/journal.pone.0101045>
- Sorensen, M. V., & Leonard, W. R., Neandertal energetics and foraging efficiency. *J. Hum. Evol.*, 40(6), pp. 483-495, 2001.
- Soressi, M., Mcpherron, S. P., Lenoir, M., Dogandzic, T., Goldberg, P., Jacobs, Z., Maigrot, Y., Martisius, N. L., Miller, C. E., Rendu, W., Richards, M., Skinner, M. M., Steele, T. E., Talamo, S. & Texier, J. P., Neandertals made the first specialized bone tools in Europe. *Proc Natl Acad Sci U S A*, 110, pp. 14186-14190, 2013. <https://doi.org/10.1073/pnas.1302730110>
- Studel-Numbers, K. L., & Tilkens, M. J., The effect of lower limb length on the energetic cost of locomotion: Implications for fossil hominins. *J. Hum. Evol.*, 47(1-2), pp. 95-109, 2004.
- Stewart, J. R., García-Rodríguez, O., Knul, M. V., Sewell, L., Montgomery, H., Thomas, M. G., & Diekmann, Y., Palaeoecological and genetic evidence for Neanderthal power locomotion as an adaptation to a woodland environment. *Quaternary Science Reviews*, S027737911830831X, 2019. <https://doi.org/10.1016/j.quascirev.2018.12.023>
- Stiner, M. C., & Kuhn, S. L., Changes in the 'Connectedness' and Resilience of Paleolithic Societies in Mediterranean Ecosystems. *Human Ecology*, 34, pp. 693-712, 2006. <https://doi.org/10.1007/s10745-006-9041-1>
- Straus, L. G., Neanderthal last stand? Thoughts on Iberian refugia in late MIS 3. *Journal of Quaternary Science*, 2021. <https://doi.org/10.1002/jqs.3252>
- Sykes, R. M. W., Neanderthals 2.0? Evidence for expanded social networks, ethnic diversity and encultured landscapes in the Late Middle Palaeolithic. In *Unravelling the Palaeolithic—10 Years of Research at the Centre for the Archaeology of Human Origins, CAHO*, University of Southampton, pp. 73–84, 2012.
- Teixeira, C. & Zbyszewski, G., Le niveau quaternaire marin de 5-8 m au Portugal, *Boletim da Sociedade Geológica de Portugal*, 8 (1/2), pp. 1-6, 1949.
- Timmermann, A., Quantifying the potential causes of Neanderthal extinction: Abrupt climate change versus competition and interbreeding. *Quaternary Science Reviews*, 238, 106331, 2020. <https://doi.org/10.1016/j.quascirev.2020.106331>
- Tzedakis, P. C., Hughen, K. A., Cacho, I., & Harvati, K., Placing late Neanderthals in a climatic context. *Nature*, 449(7159), Article 7159, 2007. <https://doi.org/10.1038/nature06117>

- Vaesen, K., Dusseldorp, G. L., & Brandt, M. J., An emerging consensus in palaeoanthropology: Demography was the main factor responsible for the disappearance of Neanderthals. *Scientific Reports*, 11(1), Article 1, 2021. <https://doi.org/10.1038/s41598-021-84410-7>
- Vaesen, K., Scherjon, F., Hemerik, L., & Verpoorte, A., Inbreeding, Allee effects and stochasticity might be sufficient to account for Neanderthal extinction. *PLOS ONE*, 14(11), e0225117, 2019. <https://doi.org/10.1371/journal.pone.0225117>
- Vaquero, M., & Romagnoli, F., Searching for Lazy People: The Significance of Expedient Behavior in the Interpretation of Paleolithic Assemblages. *Journal of Archaeological Method and Theory*, 25(2), pp. 1-34, 2017. <https://doi.org/10.1007/s10816-017-9339-x>
- Villa, P., & Roebroeks, W., Neandertal Demise: An Archaeological Analysis of the Modern Human Superiority Complex. *PLOS ONE*, 9(4), e96424, 2014. <https://doi.org/10.1371/journal.pone.0096424>
- Wolf, D., Kolb, T., Alcaraz-Castaño, M., Heinrich, S., Baumgart, P., Calvo, R., Sánchez, J., Ryborz, K., Schäfer, I., & Bliedtner, M., Climate deteriorations and Neanderthal demise in interior Iberia. *Scientific Reports*, 8(1), pp. 1-10, 2018.
- Wolff, H., & Greenwood, A. D., Did viral disease of humans wipe out the Neandertals? *Medical Hypotheses*, 75(1), pp. 99-105, 2010. <https://doi.org/10.1016/j.mehy.2010.01.048>
- Wood, R. E., Barroso-Ruiz, C., Caparros, M., Jorda Pardo, J. F., Galvan Santos, B., & Higham, T. F., Radiocarbon dating casts doubt on the late chronology of the Middle to Upper Palaeolithic transition in southern Iberia. *Proc. Natl. Acad. Sci. USA*, 110, pp. 2781-2786, 2013. <https://doi.org/10.1073/pnas.1207656110>
- Wynn, T. & Coolidge, F. L., The expert Neandertal mind. *J. Hum. Evol.*, 46, pp. 467-487, 2004. <https://doi.org/10.1016/j.jhevol.2004.01.005>
- Zbyszewski, G., Jazidas quaternárias de Salemas (Loures) e de Columbeira (Bombarral), *Boletim da Academia das Ciências de Lisboa*, N. S., 35, Lisboa, pp. 137-147, 1963.
- Zbyszewski, G., L'Âge de la pierre taillée au Portugal, *Les Dossiers de l'Archéologie*, 4, Dijon, pp. 19-30, 1974.
- Zilhão, J., Estratégias de povoamento e subsistência no Paleolítico e no Mesolítico de Portugal. In Moure Romanillo, A. (ed.): *Elefantes, Ciervos y ovicaprinos. Economía y aprovechamiento del medio en la prehistoria de España y Portugal*. Santander, Universidad de Cantabria, pp. 149-162, 1992.
- Zilhão, J., Middle Paleolithic settlement patterns in Portugal. In CONARD, N. (ed.): *Settlement dynamics of the Middle Paleolithic and Middle Stone Age*. Tübingen, Kerns Verlag, pp. 597-608, 2001.
- Zilhão, J., Chronostratigraphy of the Middle-to-Upper Paleolithic Transition in the Iberian Peninsula, *Pyrenae*, 37 (1), 2006.
- Zilhão, J., Neandertals and moderns mixed, and it matters. *Evolutionary Anthropology: Issues, News, and Reviews*, 15(5), pp. 183-195, 2006. <https://doi.org/10.1002/evan.20110>
- Zilhão, J., The late persistence of the Middle Palaeolithic and Neandertals in Iberia: A review of the evidence for and against the "Ebro Frontier" model. *Quaternary Science Reviews*, 270, 107098, 2021. <https://doi.org/10.1016/j.quascirev.2021.107098>

- Zilhão, J., Everything you always wanted to ask about the Lapa do Picareiro Aurignacian and should not be afraid to know: A reply to 'The early Aurignacian at Lapa do Picareiro really is that old.' *Quaternary Science Reviews*, 277, 107296, 2022. <https://doi.org/10.1016/j.quascirev.2021.107296>
- Zilhão, J., *Portugal na Idade do Gelo*. Lisboa, Fundação Francisco Manuel dos Santos, 2023.
- Zilhão, J., Anesin, D., Aubry, T., Badal, E., Cabanes, D., Kehl, M., Klasen, N., Lucena, A., Martín-Lerma, I. & Martínez, S., Precise dating of the Middle-to-Upper Paleolithic transition in Murcia (Spain) supports late Neandertal persistence in Iberia. *Heliyon*, 3(11), e00435, 2017.
- Zilhão, J., Angelucci, D. E., Arnold, L. J., Demuro, M., Hoffmann, D. L., & Pike, A. W. G., A revised, Last Interglacial chronology for the Middle Palaeolithic sequence of Gruta da Oliveira (Almonda karst system, Torres Novas, Portugal). *Quaternary Science Reviews*, 258, 106885, 2021. <https://doi.org/10.1016/j.quascirev.2021.106885>
- Zilhão, J., Angelucci, D. E., Badal-García, E., D'errico, F., Daniel, F., Dayet, L., Douka, K., Higham, T. F. G., Martínez-Sánchez, M. J., Montes-Bernárdez, R., Murcia-Mascarós, S., Pérez-Sirvent, C., Roldán-García, C., Vanhaeren, M., Villaverde, V., Wood, R., & Zapata, J., Symbolic use of marine shells and mineral pigments by Iberian Neandertals. *Proceedings of the National Academy of Sciences*, 107(3), pp. 1023-1028, 2010. <https://doi.org/10.1073/pnas.0914088107>
- Zilhão, J., Angelucci, D. E., Igreja, M. A., Arnold, L. J., Badal, E., Callapez, P., Cardoso, J. L., D'errico, F., Daura, J., Demuro, M., Deschamps, M., Dupont, C., Gabriel, S., Hoffmann, D. L., Legoinha, P., Matias, H., Monge Soares, A. M., Nabais, M., Portela, P., Queffelec, A., Rodrigues, F. & Souto, P., Last Interglacial Iberian Neandertals as fisher-hunter-gatherers. *Science*, 367(6485), eaaz7943, 2020. <https://doi.org/10.1126/science.aaz7943>
- Zilhão, J., Cardoso, J. L., Pike, A. W. G. & Weninger, B., Gruta Nova da Columbeira (Bombarral, Portugal): Site stratigraphy, age of the Mousterian sequence, and implications for the timing of Neanderthal extinction in Iberia. *Quartär*, 24, pp. 93-112, 2011.
- Zilhão, J. & Mckinney, C., Uranium-Thorium dating of Lower and Middle Paleolithic sites in the Almonda karstic system (Torres Novas, Portugal). In 3.<sup>a</sup> Reunião do Quaternário Ibérico. Coimbra, pp. 513-516, 1995.
- Zilhão, J. & Trinkaus, E., Historical implications. In Zilhão, J. & Trinkaus, E. (eds.) *Portrait of the artista as a child. The gravettian human skeleton from the Abrigo do Lagar Velho and its archeological context*. Lisboa, Instituto Português de Arqueologia, pp. 542-558, 2002.