

Vanishing Carnivores: What can the Disappearance of Large Carnivores tell us about the Neanderthal World?

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ABSTRACT This paper examines the relationship between the extinction of carnivores and the disappearance of the Neanderthals. The Iberian Peninsula, as the westernmost point of Eurasia, is the key for an understanding of either the replacement or the continuity of hominids. Cave bear evolutionary history shares some trends with that of the Neanderthals. This means that most of the causes cited to explain the disappearance of Neanderthals have some implications that are linked with this carnivore's history. Some of the causes for the extinction of both are presented together and discussed. We analyse the contrast between the evidence from both central Europe and the Iberian Peninsula, which suggests a cause different from mere climatic stress for the extinction. The problems of the Iberian archaeological record are revised and we stress the need for a large European research programme to verify the data. Copyright © 2004 John Wiley & Sons, Ltd.

Key words: cave bear; carnivores; Neanderthal; Middle Palaeolithic; extinctions; Iberian Peninsula

Vanishing species

Much has been written about *Homo neanderthalensis* (*Hn*) since the first remains were identified. The aim of this literature has been either to illustrate the paradigm of 'primitive man', or to discuss possible reasons for his disappearance. An insistence on stressing differences or similarities has provoked explanations that invoke the themes of continuity or rupture. The disappearance of Neanderthals has been perceived as either the product of biological evolution and social development (new techniques, organization, etc.) or as a result of their catastrophic extinction, elimination and replacement.

All of these explanations are based on sound biological and ecological evidence. Natural (or

social) selection must have eliminated the 'archaic' form in favour of anatomically 'modern' humans (AMH). To summarize (for references, see Burke, 2000a), the same factors which reduced the population of other large mammals and caused their replacement (or succession) have been used to explain the disappearance of *Hn*. These factors include food resources, habitat quality, weather, disease, reduced population density, and lastly, inter-specific competition. In this case, that means the activities of AMH, given that competition from other animals (predators and herbivores) is unlikely.

The replacement hypothesis has used recent dates obtained in the southern and western half of the Iberian Peninsula, associated with Mousterian-type industries and with *Hn* remains, as key evidence. These dates contrast with older ones associated with Upper Palaeolithic industries in Catalonia and Cantabria (Vega *et al.*, 1999; for detailed discussion and references about this

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matter, see Estévez & Vila, 2003). The explanations have postulated, among other things, the existence of an 'ecological' barrier at the level of the River Ebro valley (Zilhao, 1993; D'Errico *et al.*, 1998), a last ecological refuge in the far south (Finlayson, 1999) which would have delayed the arrival of AMH bringing Aurignacian industries from the northeast, or *Hn* resistance in mountain 'strongholds' (Soler & Maroto, 1993). But these *ad hoc* explanations have yet to be satisfactorily matched with existing evidence (Straus, 1997; Cabrera *et al.*, 2001) and this makes Iberia a key point for the explanation of the Neanderthal problem.

The verification of these hypotheses involves palaeoecology and an understanding of the population dynamics of large mammals. It is not possible to make effective use of ecological explanations if questions concerning the hominid ecological context are not answered. In the 'Congrès sur la Chasse de Treignes' in 1997 we posited (Estévez & Martínez, 2000) the existence of indicators in the biostratigraphic dynamics of large mammals which do not adequately support the suggested role of the Peninsula as a climatic refuge. At the congress, we argued that it is possible that the large carnivores were 'collateral victims' of a growing hominid population and of the sliding of *Hn*'s ecological niche towards subsistence strategies that were increasingly characterized by active hunting. This was coherent with the successive extinction in the Peninsula of animals with the greatest biomass (and consequently, the slowest reproductive cycles) starting with elephants (frequently associated with bifacial industries but increasingly rare from the Early Upper Pleistocene onwards), and rhinoceros (which is positively linked with the industries of the Middle Palaeolithic). We linked this dynamic with the successive drastic reduction or virtual disappearance of the hyena, the cave bear and the big felids (beginning with *Felis Panthera spelaea* until *Panthera pardus*). We also linked the apparently more rapid extinction of these animals in the putative refuge areas of the Peninsula (especially in the Mediterranean) compared with central and eastern Europe to a possibly higher population of *Hn* in the Peninsular refuge.

Regarding the hominid problem, the most interesting case (Kurten, 1976) of the disappear-

ance of a carnivore species is without a doubt that of *Ursus spelaeus* (*Us*). The parallels that can be established between the evolutionary trends of the cave bear and *Hn* are particularly interesting: both species undergo a phyletic evolution from a European form (*H. heidelbergensis* and *U. deningeri*, respectively) whose evolutionary trends from the Middle to the Upper Pleistocene have been documented and differ from the form/species that replaced them by having 'shorter distal limb segments, expanded shaft and articular head sizes' (Wolpoff, 1989: 121–122), and especially, a stronger scapula and proximal humerus articulation, stronger phalanges, clumsier bodies, heavier cheekteeth and higher frontal bone (cf. Stringer & Gamble, 1996; de Torres, 1988; Fosse *et al.*, 2001; Argant & Philippe, 2002).

Biogeographically, the ancestor species *H. heidelbergensis* and *U. deningeri* already occupied the same areas. *U. deningeri* is present on either side of the Straits of Gibraltar, as are contemporary human industries with much-quoted similarities. *Hn* was present from Gibraltar through Palestine to Uzbekistan. *Us* was found from Reguerillo (Madrid) and A Valinha (Galicia) through Turkey and as far as the Urals. Their distribution maps, therefore, overlap except for a few hundred kilometres in the south. It has also been observed that *U. deningeri* and Middle Pleistocene humans did not occupy high mountains areas, while *Us* (Fosse *et al.*, 2001) and *Hn* succeeded in penetrating high into the mountains. At both ends of this range we find another closely related form/species (*H. sapiens (sapiens)* and *U. arctos* respectively) which had separated phylogenetically during the late Lower or early Middle Pleistocene and which would finally replace *Hs* and *Us*. Both ancient species (forms) met the same fate: they were replaced by the more lightly built animals, *H. sapiens (sapiens)* and *U. arctos* respectively, which were perhaps more active hunters.

These common evolutionary trends, the spatial and time ranges and its ultimate fate make the study of the 'cave bear's story' especially interesting, or at least offer food for thought regarding the real possibility of finding satisfactory answers based on the existing Neanderthal record. Most of the issues discussed (for instance by Trinkaus, 1989) have a number of implications that may be resolved by putting the Neanderthal evidence in

context with the much larger palaeontological record. In the following paragraphs I highlight some aspects of this issue and try to explain how we can orient our research by comparing the study of *Hn* with that of the other species which disappeared in the Upper Pleistocene. In other words, I propose to use the problems that have arisen in the study of *Us* to orient the research of *Hn*.

Evolutionary palaeontology and taxonomy

Hundreds of thousands of skeletal remains of *Us* have been found dating to the Upper Pleistocene. Nevertheless, it is still difficult to chart the phyletic and taxonomic evolution of the species in detail (see: de Torres, 1988 versus Argant & Philippe, 2002). The possible presence of more than one single *Ursus* species (de Torres, 1988 or Fosse *et al.*, 2001 versus Tillet & Binford, 2002: 68–69) illustrates the possibility that a number of very similar *K* reproduction species could have shared territory in the Iberian Peninsula. There has also been speculation about an evolutionary leap (Nagel & Rabeder, 2002) or the influence of a number of population movements on the genetic flow of populations of *Us* which may have taken place between the middle/late and Upper Würm periods (<34 ky). If this phenomenon could be extrapolated to human groups, it would favor continuist explanations (for instance Straus, 1997: 239).

It has been said (de Torres, 1975) that climatic changes stimulated variability between *demos* (breeding communities), but that isolation reduced internal variability. In short, *Us* was probably a polytypical species with many local varieties. If *Hn* had to face similar survival conditions, they may have been subject to the same kind of selective pressures and variability may have been expressed in a similar way. The possibility that different groups of *Hn* inhabited small, stable territories has already been pointed out by several classic authors (e.g. de Lumley-Woodyear, 1969–1971). The evolutionary consequences of this isolation for *Hn* could have been similar for *Us*. Finally, the surprising results of molecular biology and studies of the DNA of bears, which claim that very distant geographical

forms are closely linked genetically, are very difficult to match with the traditional taxonomy (see: Waits & Taberlet, 2002). This illustrates the serious difficulties facing those who wish to understand evolutionary processes or evaluate the meaning of these results when they are applied to humans.

Biogeography

As far as their range is concerned, both species (*Hn* and *Us*) share most of the same biotope. *Us* has been described as a very adaptable species which favoured temperate forest areas. Some authors maintain that it would have preferred a temperate oceanic climate without extreme temperatures and open areas of high grassland rather than dense woodland and it is not associated with cold fauna (Fosse, *et al.*, 2001). But in terms of the Iberian Peninsula it has been said that *Us* was 'a species that was adapted to harsh climatic conditions' (Castaños 1988: 53) and associated at some sites with the species indicators of the lowest temperatures in the Peninsula. So its range may have included cold steppe lands and it could therefore have tolerated a wide climatic spectrum. In fact, we have associations in which it shares taphocenosis with *Capreolus*, *Rangifer* and even *Saiga* (Enloe *et al.*, 2000). It is found in caves at sea level and at sites above 2000 m. In the Peninsula, *Us* (de Torres, 1988) was restricted to the Cantabrian coast (as far as Galicia, the furthest western site being Valinha), as far south as Reguerillo near Madrid and in the northern part of Catalonia on the Mediterranean basin. The bears of Portugal associated with the industries of the Middle Palaeolithic or the Upper Palaeolithic were classified as *U. arctos*, as are those found in Andalusia.

There appears, therefore, to have been an ecological barrier which prevented the expansion of *Us* southwards. It is curious that this seems to largely coincide with that which (according to the Ebro frontier hypothesis) presumably obstructed the movement of AMH towards the south. In short, if some kind of ecological element restricted *Hn* to the south and west, why did the same thing not happen to *Us*? On the other

hand, in the Upper Palaeolithic one observes the slow expansion or increasing presence of *U. arctos* at sites formerly occupied by *Us*. Obviously, a biogeographic divergence in the ultimate fate of two species as ecologically similar as *Hn* and *Us* is difficult to justify on climatic and ecological grounds.

Diet

It is clearly important to make an analysis of diet if we wish to understand the coexistence of hominids, *Us* and *U. arctos*. Dental morphology has shown that, unlike *U. arctos*, *Us* was hypocarnivorous and must have gradually increased its vegetarian diet throughout its evolution. Despite the fact that studies of stable isotopes would appear to confirm this hypothesis, there are some contradictory results (Bocherens, 2002 or Stiner, 2002 versus Hilderbrand *et al.*, 1996). In this case it is probably not simply a case of improving the technique, but of understanding the significance of the sample. One might ask whether a sufficiently representative spectrum of variability has been analysed. Apart from geographical and chronological vectors, one should also include those related to sex and age. Another important problem is that we are analysing the remains of animals which died for different reasons, one of which may well have been a deficient diet.

The fact that *Us* has on many occasions been found only with the remains of artiodactyls (*Capra* and *Rupicapra*) in caves of the Cantabrian basin has led scholars to state over and over again that the cave bear must have supplemented its diet with meat (Altuna & Merino, 1984: 222; Castaños, 1990) while in the south of Germany and Italy there is evidence that *Us* was not in the habit of taking fauna back to the cave (Hahn & Kind, 1991; Stiner, 2002). An identical line of questioning is used for *Hn* (Madella *et al.*, 2002 versus Shea, 1998). Recent analysis of a large sample indicates that although the diet of hominids of the Upper Pleistocene is less abrasive (more carnivorous) than that of the Middle Pleistocene, Neanderthal samples show a very varied omnivorous diet although they seem to be more carnivorous during the interglacial periods

than during the coldest periods (Pérez *et al.*, 2003).

Those arguing against continuity (e.g. Mellars, 1973) also stressed the contrast between the supposed feeding strategies of *Hn* and those of the Upper Palaeolithic. Later detailed revision has shown as far as the French evidence is concerned (Brugal & Jaubert, 1991), that there was a development from open-air scavenging to more active and territorial food procurement including the entry into caves and the use of natural traps, culminating with active, controlled hunting during the Middle Palaeolithic (in the strict sense of the term). In concordance with this hypothesis, analysis of remains from sites such as Lezetxiki and Pendo on the Cantabrian coast showed that the ungulates found there had been brought by humans and there is little evidence of the activity of carnivores (J. Martinez, unpublished doctoral dissertation, 1998: 488). Recent studies also show an unbroken human hunting dynamic from the Middle to Upper Palaeolithic in Castillo (Pike-Tay *et al.*, 1999).

Life, death and extinction

One of the most interesting subjects in evolutionary palaeontology is that regarding extinctions, and those of the Quaternary have obviously attracted most attention due to the presence of hominids (Martin & Klein, 1984; Martin & Wright, 1967; Nitecki, 1984; etc.). In the case of *Us*, after its frequency peak in deposits during the OIS3 (65–34 ky BP), its presence decreases and it is extremely doubtful that it was present during the Magdalenian. The only direct date after 22 ky BP is that from Oillascoa (Fosse *et al.*, 2002). Many of the remains in the west that have been dated to after 30 ka BP are problematical. It is necessary to carry out detailed analysis of each and every one of the cases and, of course, conduct a series of direct datings of the osteological material. The evidence for the other big carnivores in the Basque Country shows a similar pattern. There are no hyena remains after OIS2 (Altuna & Mariezkurrena, 1988; Altuna 1992; Castaños, 1990). In the case of felines, it is even difficult to establish their taxonomy due to the fact that even fewer remains are available.

It has been suggested (Altuna, 1994) that *F. (P.) spelaea* was replaced by *F. P. leo* in the latter part of the Quaternary. *P. pardus* may even have survived until the Late glacial in the Basque Country. In the Mediterranean area all the large carnivores seem to disappear before OIS2. The hyena survives only until Early Würm, *Us* until 36 ky BP and the big felines do not go beyond 18 ky BP.

The extinction of the carnivores and its effect on the *Hn* problem

Endogenous causes

Internal causes have been put forward for the extinction of the cave bear. Among them is traumatic extinction due to processes of genetical degeneration, although some authors reject this hypothesis (i.e. de Torres, 1975, 1988). Genetic 'suicide' through isolation, would fit in with the last dates of presence, which are like a mosaic. It is interesting to observe that a simulation of an isolation of felines in the Italian Peninsula leads to their extinction (O'Regan *et al.*, 2002). If this could be extrapolated to the hominid population, it would fit with other suggestions regarding hominid depopulation in this area before the arrival of AMH (Finlayson, 1999). But it would be necessary to carry out studies to simulate this possible dynamic on a continental scale and show the genetic isolation of each area.

External causes: climate

It has been suggested that the colder climate of the OIS2 pleniglacial may have contributed to their extinction. But the real question is: why did *Us* disappear from northeast Spain if the environmental conditions at the most critical moment are not as harsh as those in central Europe when the animal is most abundant in that area?

At odds with the strict climatic hypothesis is the same wide spectrum of accompanying fauna from the Crimea or the Urals to the Italian Peninsula or Galicia (i.e. Fernández Rodríguez, 1993; Burke, 1999, 2000b). Neither is there a significant change (in terms of climate indicators)

in the list of species present between the moment when the carnivores are most plentiful and when they decrease and disappear. On the other hand, it has been possible to detect vegetation changes in the stratigraphic sequences throughout the OIS5 until OIS3 periods before 30 ka BP, when carnivores are abundant (cf. Piqué, 1998). A comparison of the palaeoclimatic curve with the frequencies of *Us* (i.e. Fosse *et al.*, 2001) shows clearly that the species was not dramatically affected by climatic change.

A significant increase in the number of remains of *Us* has been detected in caves just before the decline of the species. Although this can be broadly synchronized with just before or at the beginning of the Upper Palaeolithic industries, this event is not totally synchronized climatically, or by the industrial manifestations that accompany it (Estévez, 1980; Klein & Cruz Uribe, 1994; Hahn & Kind, 1991; Weinstock, 2000). There are representations of large carnivores (felines, bears) in the oldest cave art (33–30 ka) in the centre of France (Clottes, 2001) and south Germany (Hahn, 1986). No such equivalence has been found in the art of the Iberian Peninsula. The climatic cause on its own, directly or through indirect repercussions does not appear to be sufficiently supported. Nor should isolation and the local and sedentary nature of populations be considered a characteristic provoked by an increasingly harsh climate. Throughout the evolutionary process (Argant & Philippe, 2002) *Us* had to survive pronounced climatic Dansgaard-Oeschger and Heinrich events.

Interspecific competition: competition for food

Competition for food with hominids may be another critical issue in the analysis of the disappearance of the large carnivores. The careful analysis of the remains of herbivores and especially dens are crucial elements in the evaluation of the importance of this possible form of competition (Fosse, 1997). If from the Crimea to Portugal hominids started to hunt (especially equids, deer and bovines) and to scavenge other prey, they must have competed mainly with hyenas. It has been postulated that some caves served as human hunting camps for goats and it

has also been suggested that *Us* could have included the meat of animals such as *Capra* and *Rupicapra* in their diet. It is difficult to calculate competition because, as we have stated, the question of the contribution of meat to the diet of *Us* is unresolved, and we are also unable to evaluate the true vegetable contribution to the diet of *Hn*. Competition between *Hn* and *Us* which could have been definitively unfavourable to the latter on the basis of a vegetarian diet is very unlikely.

Another suggested cause of the extinction of *Us* was the possible inability of its genotype to adapt to new selective pressures and above all its low level of competitiveness in relation to other herbivores. However, it is difficult to imagine why this lack of competitiveness should suddenly take on catastrophic proportions when these sympatric species had evolved side by side throughout all the climatic oscillations of the Pleistocene.

Competition for living space: the use of caves

Traditionally, *Hn* has been associated with an increasingly intense and regular occupation of caves. *Us* was a hibernating animal which needed these spaces. It would therefore seem logical to think that a more intense occupation by humans could have increased this pressure. Although available data do not indicate permanent human occupation, it is believed that in many cases *Us* occupied the same dens on a regular basis over periods of hundreds of years, and thus any intrusion, albeit occasional, would have caused considerable disturbance.

Direct human action: hunting

This is another of the most frequently discussed causes, especially in relation to *Us* (see comments in Tillet & Binford, 2002). The subject is not without its ideological baggage (Pacher, 2002). The literature is full of examples of *a priori* and subjective conclusions being drawn regarding the non-hunting of certain species because of their alleged dangerousness. This kind of subjectivity, whilst it may represent a good suggestion, cannot

be demonstrated coherently. Anthropogenic marks are the only proof that a species was hunted. The case documented in Germany (Münzel *et al.*, 2001) was probably an example of winter hunting in dens, which is the type of hunting that would have provoked the greatest disturbance. Moreover, there are quite a number of signs of the subsequent removal of flesh and not only in German caves but also in Spain (J. Martinez, unpublished doctoral dissertation, 1998), France (David, 2002) and Belgium (Germonpré & Sablin, 2001), and of course at key sites such as Biache St Vaast and Regourdou, albeit involving *U. arctos* (Bonifay, 1989).

The interpretation of the 'cult of the bear' (which was at the heart of the controversy) could be discussed today from a perspective with less religious contamination and in relation to sculpted and painted figures and bear skulls which were broken in order to pull out the teeth, although all these manifestations are associated with the Upper Palaeolithic (Clottes & Begouen, 1981; Fosse *et al.*, 2001; Rouzard, 2002).

To summarize, it is clear that if we accept the dates that we have at the moment, the last refuges of *Us* almost coincide geographically with those inhabited in the last century by *U. arctos* (mountain areas of Asturias, León and Galicia, the Basque Country, the Pyrenees—Oillascoa at over 1000 m altitude, the Alps—Nixloch at more than 700 m altitude, and Slovenia). If we also accept that both the climatic conditions of the Upper Pleistocene and the Holocene and the ecological requirements of the two species of bears were different, we must conclude that there was perhaps a similar cause for their disappearance, but that it was not ecologically triggered. In the extinction process of *U. arctos*, the one we know the most about, this was brought about by human persecution and the anthropogenic destruction of its biotope.

Discussion

All these suggestions come up against a number of problems, at least in the Iberian Peninsula, that must be overcome before an attempt can be made to verify the implications that arise.

The old excavations

In the Iberian Peninsula some critical sites (Bolinkoba, Santimamiñe, Altamira, Carihüela or Cova Negra), where *Hn* or *Us* has a recent date attribution, were excavated before the 1930s. Recent re-excavations are only partially documented. The results therefore refer mainly to the old stratigraphic cuts.

Shortage of sedimentary studies

Sedimentological and palynological analyses carried out at sites have frequently failed to give precise results (Altuna & Mariezkurrena, 1988: 182). There are many sites where sedimentary scars (or hiatuses) exist and have been verified (Arbreda, Corb, Labeko Koba, Abauntz, Peña Miel, Casares, Amalda, Lezetxiki, Cova Negra...). In a number of important cases a stratigraphic inversion or a removal may have occurred (i.e. Lezetxiki III, after Baldeón, 1993; or Zafarraya, see Cortes *et al.*, 1996). This may also have disturbed bone material from lower levels. At some sites this removal may have been carried out by humans in ancient times. Hominids sometimes had direct access to unsedimented skeletons of carnivores thousands of years old and in some cases they were manipulated, made use of, and moved (Garma and Abauntz sites in Spain, and in the French caves of Chauvet, Tuc d'Audobert, Trois Freres, Isturitz, etc.).

Problems with biostratigraphic correlations

At many sites in the Peninsula most work has been done within the classical alpine sequence system. This has resulted in an excessively simplified chronological attribution to the Würm I, Würm II and the intermediate interstadial that depends upon the more or less cold character of the fauna set. In several significant cases (Lezetxiki, Carihüela, Zafarraya) the sequence can be reinterpreted with relative ease. When there have been no absolute datings or when these have produced contradictory results, the chronology has been extrapolated from the accompanying industry. But in this case dubious criteria have been applied because of the low degree of typological expressivity (formal stan-

dardization) of the ancient industries. Consequently, it is possible to reinterpret the chronology of the stratigraphy (Estévez & Vila, 2003).

The problem of the smaller oscillations of the OIS5 and OIS4

We may ask if fast climatic variation in a short sequence can be documented satisfactorily in stratigraphies. Nor do we know what might have been the consequences in a refugium environment such as the Peninsula of such rapid changes as the shorter ones documented during OIS5 to OIS3.

The lack of direct absolute datings

One of the problems facing us is the lack of direct datings for both *Hn* and carnivores. For this critical period of >30ky there are problems regarding the reliability of the traditional system of radiocarbon dating and isotopic instability during key periods (Beck *et al.*, 2001; Kitagawa & van der Plicht, 1998). Regardless of all these difficulties, the problematic datings have been the basis for all the speculation about the late north-south movement of AMH (Raposo, 1995; Estévez & Vila, 2003).

Problems of taphonomic resolution

Since the first archaeozoological papers concerning the Peninsula were written (J. Altuna, unpublished doctoral dissertation, 1972; J. Estevez, unpublished doctoral dissertation, 1979; Davidson, 1972; Straus, 1982) a whole range of literature and taphonomic methodologies has been developed to establish the agents for the taphonomic processes. One mechanical conclusion that has frequently been used is that of synchronizing the population maximum with the maximum number of remains recovered. This principle might be valid if we supposed that thanatocenoses occur randomly or equally spaced in time from a living population. However, we must realize that the-more-dead-bodies-the-larger-the-population assumption would perhaps be a little hasty in the case of carnivores and humans. Moreover, it has been suggested that an increase in the number of remains in the caves may well be the consequence of stress.

Problems with the visibility of the sample

The same doubts and problems of randomness that we suggested for the datings of the last bears should be extended to the chronostratigraphical attributions of the remains of *Hn* (Estévez & Vila, 1999, 2003). If we accept the survival of *Us* (attested by very few remains out of a large sample of cave bear bones) at least 20 ky after its maximum presence, we might think that (extrapolating these relative proportions to the small human bone sample) the discovery of hominids with Neanderthal features beyond 30 ky is more a question of chance than of their real absence (see Zilhao & Trinkaus, 2002).

Conclusion

The striking similarities in the range, evolutionary story, fate and time of decline of *Hn* and *Us* force one to link the explanation for both phenomena. The Iberian Peninsula is the key area in the search for the causes. It is the western-most limit of the range of both species and at the same time one of the places where their range did not overlap. It could have been the last refuge for *Hn* but one of the first places where big game, as well as carnivores and cave bear, declined. It is very difficult to explain the disappearance of both species directly by climatic causes and, if we consider the very different ecological niches of both (*Us* more herbivorous, *Hn* more meat-oriented) we need to look for another explanation. If *Us* had found refugia in which it could survive until the Last Termination, why not *Hn*? The strategies in reproduction, hunting and settlement of *H. sapiens* could possibly provide such an explanation. But, quoting Burke (2000b: 333): 'more research into late Middle Palaeolithic occupation of Western Europe is necessary to enable us to tackle those issues related to the advent of the Upper Palaeolithic in the region.' It would be necessary to closely examine the implications of the hypotheses regarding the ultimate fate of *Hn* in relation to the ecology and the population dynamics in order to verify them, instead of trying to resolve this problem from the 'unifacial' perspectives of the stone industries, bioanthropology or palaeogenetics. This will not be possible without a wide-ranging multinational and

interdisciplinary programme to obtain, de-subjectivize, balance and study the required data.

Acknowledgements

The research for this paper was partially supported by the project PB088 Ministerio de Ciencia y Tecnología. The English translation was by Mike Gates, Diptrans (Institute of Linguists, London).

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