

Notes

Erik Trinkaus, João Zilhão and Cidália Duarte **O Menino do Lapedo**
Lagar Velho 1 and perceptions of the Neandertals¹

Abstract

The emergence of modern humans during the Late Pleistocene and the phylogenetic fate of the northwestern Eurasian Neandertals have been closely linked to our perceptions of the behavior and abilities of those late archaic humans, the Neandertals. In the past several years, several lines of evidence, including radiometric dating of archeological assemblages, taphonomic analyses of faunal remains, stable isotope analysis of Neandertal remains, the dating of late Neandertal remains, considerations of initial Upper Paleolithic associations and chronologies, and reassessments of Neandertal to early modern human phylogenetic relationships have tended to minimise the perceived behavioral differences between the Neandertals and early modern humans across Europe. Into this context, the discovery of an earlier Upper Paleolithic (Gravettian) early modern human child's skeleton at the Abrigo do Lagar Velho, Lapedo Valley, Portugal with distinctive Neandertal features provides further support for the de-dehumanising of the Neandertals. Its anatomical evidence for population blending when early modern humans spread into southern Iberia after 30,000 B.P. indicates that the behavioral differences between the local Neandertals and in-dispersing early modern humans were subtle and did not preclude them from regarding each other as human.

Keywords

Neandertals; early modern humans; Upper Paleolithic; Late Pleistocene

Introduction

The emergence of modern humans during the Late Pleistocene, from both human paleontological and Paleolithic archeological perspectives, has been a focus of paleoanthropological research and discussion for the past decade. Most of the research has been oriented toward either the phylogenetic relationships between various Late Archaic (including Neandertal) and early modern human populations or the degree to which early modern humans and/or early Upper Paleolithic complexes represented a new plateau in human behavioral evolution. Even though there is no necessary evolutionary or functional relationship between these two issues, they have tended to become combined and views have become polarized into two competing historical scenarios. One scenario invokes significant degrees of regional continuity in human lineages across the Old World combined with modest shifts in behavioral patterns, whereas the other scenario proposes virtually complete population replacement in all but a core area of early modern humans and invokes major changes in behavioral patterns as the mechanism responsible for the dispersal and evolutionary dominance of those early mod-

ern humans. Intermediate versions of the bio-cultural dynamics of modern human emergence have existed at the same time, but they have remained on the periphery of the more animated treatments of these issues.

Into this academic scene an unusual Gravettian child was introduced in 1999, the largely complete Lagar Velho 1 skeleton from the Lapedo Valley, central-western Portugal (Zilhão, Duarte and Araújo 1999; Holden 1999; Trinkaus and Zilhão 1999; Duarte et al. 1999; Trinkaus, Zilhão and Duarte 1999; Zilhão and Trinkaus 1999). The interpretation (Duarte et al. 1999) that it provided evidence of Neandertal-early modern human admixture in Iberia has made it a focus of the debate over the phylogenetic emergence of modern humans. It has also brought to the surface, once again (see Trinkaus and Shipman 1993), the century-and-a-half debate over the nature of the Neandertals and, by extension, what it means to be human.

A Gravettian child from the Abrigo do Lagar Velho

The site of the Abrigo do Lagar Velho was discovered in November 1998 (Zilhão, Duarte and Araújo 1999; Duarte et al. 1999), and it consists of deposits along the base of an east-west limestone cliff on the south side of the Lapedo Valley. It was damaged by earth removal in 1992, and all that was left was a ca 50 cm.-thick remnant of the original deposits, exposed in a fissure running along most of the length of the shelter's back wall, plus the burial isolated at the east end of the shelter and a Gravettian level below the hanging remnant at the west side of the shelter. The remnant corresponds to a section of the original stratigraphic sequence lying between ca 50 and ca 100 cm. below the former ground surface and whose base is now hanging 1.5–2 m. above the surface.

A salvage excavation ensued through the new year, and during July and August 1999 the surface of the site was excavated and extensively screened, recovering many of the missing cranial and dental elements which had been broken and scattered along ca 10 m. of the cliff's base. Deep testing of the preserved deposits under the burial and in the central part of the shelter further documented the stratigraphic and horizontal nature of the sequence, and subsequent excavations (during 2000) have revealed the Gravettian level.

The child, Lagar Velho 1 (figure 1), was on its back parallel to the cliff base, with the head to the east and left side against the cliff. The skeleton and the containing sediment are heavily stained with red ochre, but the alteration of the sediment stopped at the outer border of the skeleton. Analysis of red deer bones found along the edge of the burial pit shows that they are taphonomically distinct from those found in the surrounding and immediately underlying sediments. The latter present eroded surfaces, have a shine that suggests they were chewed and digested by carnivores, often display teeth punctures, and are associated with coprolites. In contrast, the deer bones found by the head and feet of the child's skeleton — two left pelvises, one distal tibia and two tarsal bones — are very well preserved, show no evidence of carnivore activity, were in contact with the body, and have provided radiocarbon dates showing contemporaneity with the burial event. Furthermore, no artifacts or other evidence of human habitation activities were recovered at this level in this part of the shelter.

The simplest explanation for the association is that these bones belonged to parts of deer carcasses deposited with the burial as grave goods. The base of the pit, immediately below and in contact with the child's legs, featured a thin, extensive black lens of charcoal, interpreted as evidence of a fire lit before the deposition of the body. This interpretation is strengthened by the fact that no traces of charcoal were found in the adjacent and underlying deposits.



51

Figure 1. In situ view of Lagar Velho 1 after full exposure and prior to removal of most skeletal elements. The left arm and mandible had been removed prior to the picture, and most of the cranium had been scattered along the shelter wall. © Instituto Português de Arqueologia.

The only diagnostic archeological items in the burial were the charcoal, the red ochre staining and a pierced *Littorina obtusata* shell found near the cervical vertebrae; the last is identical to that from level Jb of the nearby site of Gruta do Caldeirão dated to $26,020 \pm 320$ B.P. (OxA-5542) (Zilhão 1997). In addition, four pierced *Cervus elaphus* canines were discovered during screening of the site, in close association with the cranial fragments scattered by the earth removal. Similar burials with pierced shells and/or teeth and a covering of ochre are known particularly from the Gravettian of Europe, especially from Britain (Paviland), Italy (Arene Candide, Barma Grande, Caviglione, Ostuni) the Czech Republic (Brno-Francouzská, Dolní Věstonice) and Russia (Sunghir) (Svoboda, Ložek and Vlček 1996; Aldhouse-Green and Pettitt 1998; Bader 1998; Giacobini 1999).

Current ground level represents the surface of a sequence whose thickness is estimated to be in excess of 5 m. The uppermost 1.7 m. of the 3 m.-deep test pit excavated in the central part of the shelter contained scarce evidence of human use of the site (heavily burned *C. elaphus* bones) in fine-grained, low-energy fluvial deposits accumulated during the early Upper Paleolithic. The remnant contains a Proto-Solutrean (level 6) through Middle Solutrean (level 9) sequence. In Portugal, Middle Solutrean assemblages with diagnostic laurel-leaf point fragments date to ca 20,000-20,500 B.P. and the Proto-Solutrean dates to ca 21,500 B.P. (Zilhão 1997). Radiocarbon dating of charcoal from level 9 yielded a date of $20,200 \pm 180$ B.P. (OxA-8419) and ones from level 6 yielded results of $21,180 \pm 240$ B.P. (OxA-8420) and $21,380 \pm 810$ B.P. (Sac-1561) (Duarte et al. 1999).

AMS radiocarbon dating of charcoal ($24,860 \pm 200$ B.P. (GrA-13310)) and *C. elaphus* remains ($24,660 \pm 260$ B.P. (OxA-8421), $24,520 \pm 240$ B.P. (OxA-8423)) directly associated with the burial and of a vertebra from a semi-articulated section of a *Oryctolagus cuniculus* vertebral column ($23,920 \pm 220$ B.P. (OxA-8422)) immediately overlying the legs (Duarte et al. 1999) confirm the slightly older age suggested by the stratigraphy. The dates for the rabbit vertebra and the charcoal lens effectively bracket the burial between ca 24,000 and ca 25,000 B.P., with the date for the charcoal being that which is most closely related to the archeological event, placing it between ca 24,500 and ca 25,300 B.P.

Paleontological interpretation of the Lagar Velho 1 child

During excavation and the initial cleaning and reassembly of the Lagar Velho 1 human remains, it was assumed that this represented a juvenile of the European late Aurignacian / Gravettian human population (figure 2). This lineage is well documented from Britain (Paviland), France (Cro-Magnon), Italy (Arene Candide, Barma Grande, Baouso da Torre, Caviglione, Grotta dei Fanciulli, Paglicci, Parabita, Ostuni), Austria (Willendorf), the Czech Republic (Brno-Francouzská, Dolní Věstonice, Pavlov, Předměstí), Russia (Sunghir) and elsewhere, but it was previously unknown in Iberia. Moreover, with the destruction of the Předměstí remains in 1945, juveniles (except for fragmentary mandibles and teeth from sites such as Isturitz, Miesslingtal and La Quina, plus the older late juveniles / early adolescents from Les Rois and Sunghir) were largely unknown for this group.

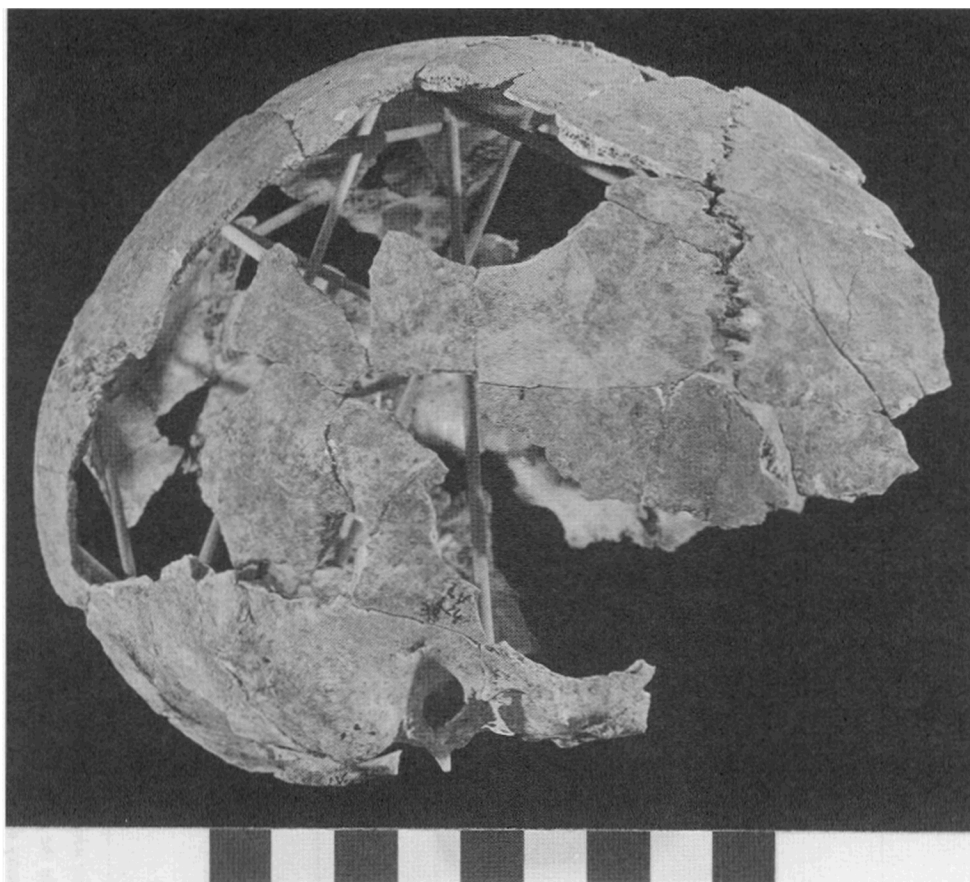


Figure 2. Lateral right view of the reassembled neurocranium of Lagar Velho 1. Scale in centimeters.
© Instituto Português de Arqueologia.

The attribution of the skeleton to this early modern human sample was based on both expectations from its archeological context (only early modern humans were known from this time period in Europe) and the clear, prominent *mentum osseum* (chin) on the mandible, one of the first elements excavated of the burial and a distinctive morphological feature of modern humans (figure 3). However, during excavation and early in the paleontological analysis of the human remains, it was noticed that it presented a curious mosaic of features, most of which aligned it with contemporaneous early modern humans and others which were reminiscent or even distinctive of the Neandertals (Trinkaus and Zilhão 1999; Duarte et al. 1999; Trinkaus, Zilhão and Duarte 1999).

53

Given its geographical and chronological provenance, and normal patterns of Late Pleistocene hunter-gatherer terrestrial mobility patterns, only European early modern humans or Neandertals are likely to have been ancestral to this child's population. It is remotely possible that humans dispersed across the Straits of Gibraltar from northwest Africa at this time, given the early Upper Paleolithic occupation of mediterranean islands requiring maritime dispersal at least over short distances (Chilardi et al. 1996), but it is unlikely that this was ever a significant contribution to the Pleistocene populations of Iberia. Moreover, what

	'Neandertal'	'Neandertal-like'	'Early Upper Paleolithic-like'	'Early Upper Paleolithic'	Intermediate
<i>Cranio-facial</i>	semispinalis capitis fossae	bregma-lambda curvature zygomatic frontal process breadth meningeal sulci supraorbital fossa juxtamasroid eminence supraorbital margin thickening foramen of Huschke posterior zygomatic root vertical position symphyseal retreat	maxillary zygomatic root position labyrinthine morphology auditory ossicle size sigmoid notch shape medial pterygoid tubercle absent	supraorbital shape mastoid size and shape nasal height and breadth pre-maxillary suture fusion sub-nasal gutter auditory meatus orientation mentum osseum narrow anterior dental arcade interorbital breadth	interorbital breadth
<i>Dental</i>	I ₂ shoveling			anterior-posterior dental proportions I ¹ and I ² double shoveling	I ¹ , I ² shoveling I ¹ lingual tubercle
<i>Postcranial</i>	crural proportions tibio-femoral robusticity	pectoralis major tuberosity ulnar deviation of distal thumb tibial condyle displacement	brachial proportions scapula axillary border radial lateral curvature radial tuberosity opponens pollicis	clavicular length relative pubic breadth femoral robusticity	tibial robusticity

Table 1. Preliminary assessment of morphological features of Lagar Velho 1, providing those which occur virtually only in the Neandertal or European early Upper Paleolithic human samples ('Neandertal' and 'Early Upper Paleolithic') and those which occur in higher frequencies in the Neandertal or European early Upper Paleolithic human samples ('Neandertal-like' and 'Early Upper Paleolithic-like' respectively). Features for which the two reference samples overlap in frequency distributions, whether ancestral or derived relative to earlier human samples, are not included. All features which change through development are adjusted, to the extent currently possible, for the developmental age of Lagar Velho 1.

little is known of contemporaneous early modern human populations in northern Africa (Ferembach 1976; Thoma 1984) suggests that they did not differ markedly from the pattern well-documented for European early modern humans. Consequently, the observed mosaic was interpreted to indicate that when early modern humans dispersed south of the Ebro frontier (Zilhão 1993; 1997; 1998; 2000) after 30,000 BP, they reproductively intermingled with the resident Neandertal populations.

Since the initial description of this pattern (Duarte et al. 1999), additional remains of Lagar Velho 1 have been recovered and further analysis has been carried out on the skeleton. The additional information has refined and expanded the documented nature of the mosaic, although many of the assessments of the affinities of various features *must remain preliminary* at this stage, given the dearth of detailed assessments of the biology, developmental patterns and the Late Pleistocene European distributions of many of these features. It is nonetheless possible to put together lists of features that can be considered as Neandertal features, Neandertal-like features (occurring in higher frequencies among them), early modern human-like features (occurring in higher frequencies among them), early modern human features, and intermediate features (table 1), bearing in mind that the details of this list *will be revised* as more paleontological analysis is carried out.

Regardless of the final list of characteristics that are used to assess the implications of Lagar Velho 1, it is apparent that the individual's remains exhibit both individual features that clearly align it with Neandertals or European early modern humans and features that occur in higher frequencies in one or the other group. Moreover, the summed probability of all of these diverse features occurring in one European early modern human individual is exceedingly low, thereby demanding explanation. The trivial developmental lesions and normal growth patterns of developmentally plastic aspects of the skeleton indicate that developmental abnormalities cannot account for the pattern. Admixture between Neandertals and early

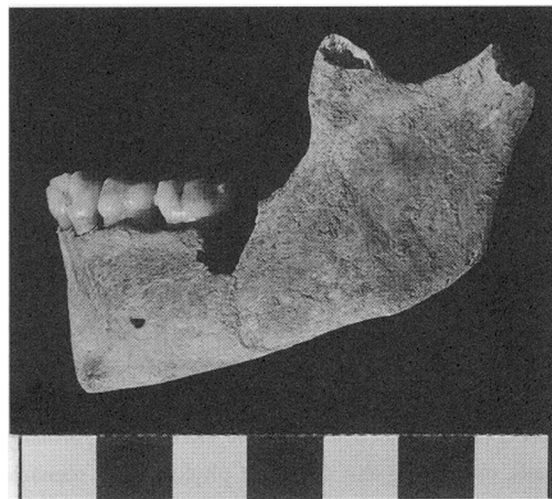


Figure 3. The Lagar Velho 1 mandible in norma lateralis left, oriented relative to the alveolar plane. Scale in centimeters. © Instituto Português de Arqueologia.

modern humans is the only explanation proposed which conforms to the empirical evidence of Lagar Velho 1, the relevant Late Pleistocene human fossil record, and current knowledge of human developmental biology.

When the admixture interpretation of Lagar Velho 1 first appeared in April 1999 (at professional meetings and in the media) and subsequent to its publication (Duarte et al. 1999) in June 1999, there was an excessive academic and public media reaction to the idea that Neandertals and early modern humans may have successfully interbred in southwestern Europe. The coverage in the media was largely favorable, but it was apparent that the high level of interest was provoked by the idea of Neandertals and modern humans being close enough to join in biologically and socially productive unions; it clearly struck at perceptions of what it meant to be human and of how special we, as modern humans, might actually be. The academic reaction, unfortunately, consisted largely of uncritical rejection or acceptance of the interpretation in line with the individual's previous views of the population dynamics of modern human emergence, with little consideration of the paleontological realities of the Lagar Velho 1 remains. Considered assessment came principally from the small number of human paleontologists who have been directly involved in the scientific evaluation of the Late Pleistocene hominid fossil record, of which only one (Hublin 2000) has so far been published.

An historical framework

Paleoanthropological concerns with the emergence of modern humans and the role of the Neandertals in that process date back to the late nineteenth century (see Trinkaus and Shipman (1993) for historical details). Early in the twentieth century the Neandertals became identified as a late derived group of archaic humans, with the dominant view (e.g. Boule 1911; 1912; 1913; Keith 1915) emphasising their apparent functional and behavioral contrasts with modern humans and placing them phylogenetically distant from ourselves. This view was reinforced by reassessments of the Late Pleistocene Paleolithic archeological record (e.g. Breuil 1912), which portrayed the early Upper Paleolithic industries as indicating a major advance in human behaviors relative to the Neandertal-associated Middle Paleolithic. The phylogenetic implications of this approach for the Neandertals have remained dominant (if somewhat muted) in subsequent considerations of later Pleistocene hominid evolution, although there have been several shifts in the perceptions of the behavioral attributes of these late archaic humans and their associated archeological remains.

56

In the mid-twentieth century, concern with the Neandertals and modern human origins focused on a) correcting the previous functional anatomical misinterpretations, b) seeing the Neandertals as phylogenetically and taxonomically much closer to ourselves given the by-then-available and accepted perspective of *Homo erectus* and *Australopithecus* as earlier and more archaic hominids, c) refining the details of phylogenetic scenarios given an improved fossil record and especially the expansion of the geological, archeological, paleoecological and geochronological contexts, and d) establishing a rigorous methodology for evaluating Paleolithic technologies. These trends continued through the 1960s with little changing

despite impressive discoveries at sites such as Amud, Arcy-sur-Cure, Combe Grenal, Régourdou and Shanidar. During this time period, the novel and interesting work on the Neandertals was largely on their archeological remains, with the widespread use of standardized approaches to lithic technology and the growing use of behavioral models to understand Middle Paleolithic variability.

The later 1960s and especially the 1970s were dominated by interest in Pliocene and Early Pleistocene hominid evolution, bracketed by the naming of *Homo habilis* in 1964 and *Australopithecus afarensis* in 1978. Paleoanthropological attention was focused on the diversity of early hominids of eastern Africa and on complex issues regarding early hominid phylogeny, taxonomy and functional anatomy. This focus was combined with the acceptance of the Oldowan as the earliest hominid technology and concern as to its adaptive significance. The Late Pleistocene hominids were largely forgotten, the prevailing view being that the Neandertals were well understood and that early modern humans were, well, just modern humans.

In the context of this focus on the early phases of hominid evolution, research did continue during the 1970s on Late Pleistocene archeological sites and human remains. Paleontologically, it refocused on Neandertal, early modern human and recent human patterns of morphological variation, redefining the appropriate samples, proposing revised (and alternative) phylogenetic scenarios, and investigating aspects of functional morphology beyond the basics of posture and locomotion (e.g. Stringer 1974a; 1974b; Trinkaus 1975; 1983a; Smith 1976; Heim 1976; 1982; Frayer 1978; Hublin 1978; Vandermeersch 1981), much of which came together in the early 1980s (see Smith and Spencer 1984). This research was done almost entirely out of the limelight.

The resultant new synthesis tended to increasingly define the Neandertals in terms of their derived morphology, relative to both their Middle Pleistocene predecessors and modern humans. At the same time, this research documented the morphological patterns of European and Near Eastern early modern humans, noting both contrasts with and similarities to those of the Neandertals. Even though the resultant phylogenetic scenarios embraced a spectrum of views, from complete replacement of the Neandertals by in-dispersing early modern humans to predominantly local continuity and including scenarios involving varying degrees of and geographical variation in admixture between these two groups, most of these (and other) paleoanthropologists agreed that there was a significant degree of morphological contrast between Neandertals and early modern humans across Europe and the Near East, however much one or another morphological complex might indicate affinities between them. This was combined with the redating of the African later Pleistocene sequence (Beaumont and Vogel 1972; Wendorf et al. 1975), considerations of northwest Eurasian limb proportions (Trinkaus 1981), and renewed analysis of later Pleistocene African fossil human remains (Day and Stringer 1982; Bräuer 1984), all of which coalesced into the first formulations of out-of-Africa models of western Old World modern human emergence involving either admixture (Trinkaus 1981; Bräuer 1984) or replacement (Stringer and Andrews 1988).

The morphological contrasts between the Neandertals and early modern humans were interpreted in functional terms as indicating a significant adaptive shift between the two

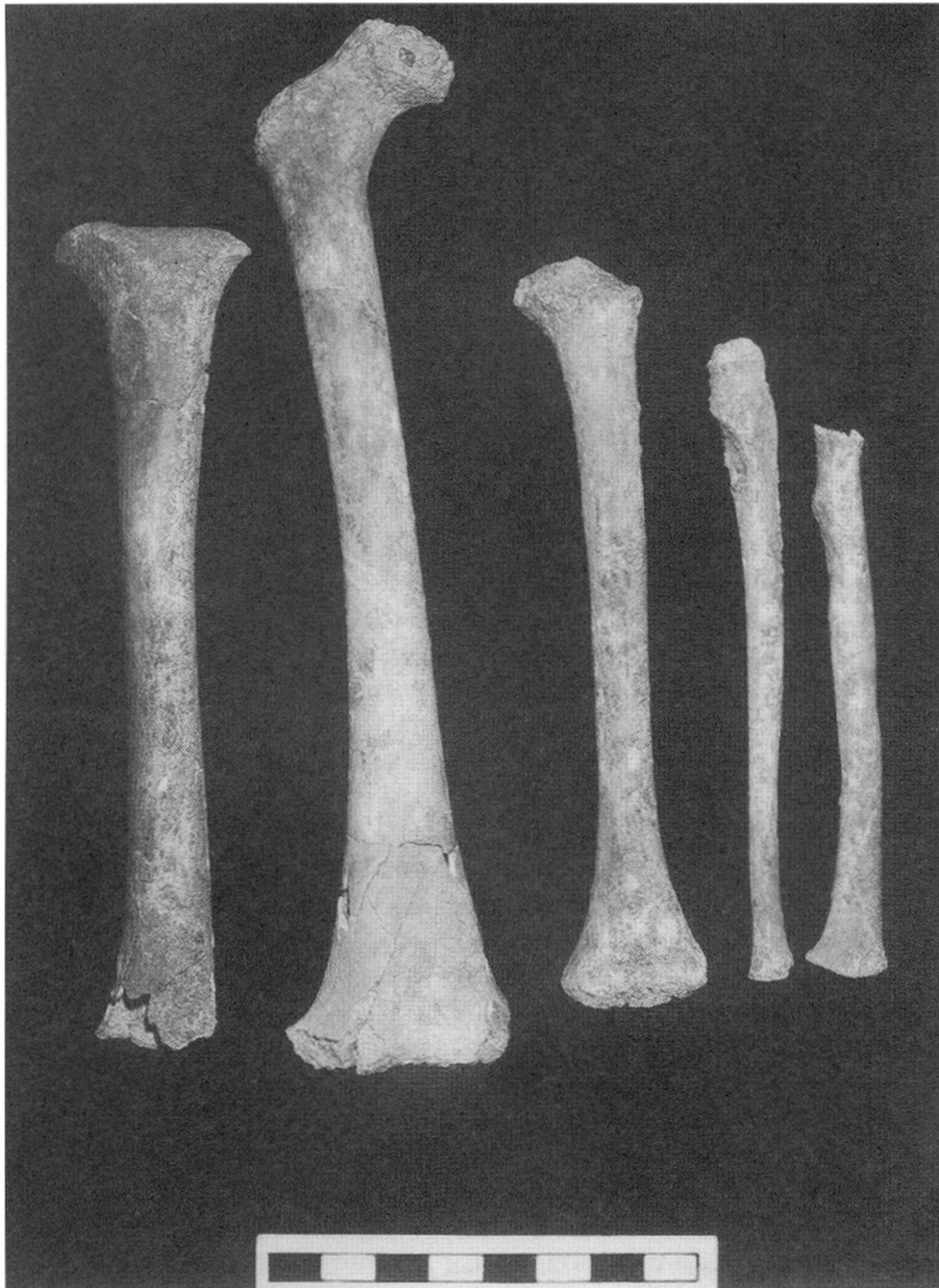


Figure 4. Anterior views of the more complete long bones of Lagar Velho 1, without their preserved but separate epiphyses. From left to right, the left tibia, the right femur, the left humerus, the left ulna and the left radius. Only the radius does not preserve both metaphyseal surfaces. Scale in centimeters.
© Instituto Português de Arqueologia.

groups, as a means of explaining the evolutionary dominance of the early modern human pattern after a relatively short period of time (Trinkaus 1983b; 1986). Ironically, these views coalesced (along lines of agreement and disagreement) despite the almost universal recognition that the Levantine Skhul and Qafzeh remains represented cranio-facially robust early modern humans associated with Middle Paleolithic assemblages (Vandermeersch 1981; Trinkaus 1984) and the 1979 discovery of a Neandertal skeleton associated with an initial Upper Paleolithic (Châtelperronian) industry at Saint-Césaire in France (Lévêque and Vandermeersch 1980). These biobehavioral discrepancies were either mentioned only in passing or integrated into existing models (Trinkaus and Shipman 1993).

In contrast with the low profile of paleontological research on the Neandertals, the Mousterian debate, involving inferences about Neandertal behavior derived from lithic assemblages and faunal remains left behind at Middle Paleolithic sites, was unquestionably one of the major issues of the 1970s and into the 1980s. Binford (1989) and Gamble (1986), among others, eventually suggested that significant differences existed between the Lower and Middle Paleolithic, on one hand, and the Upper Paleolithic, on the other hand, with respect to patterns of site organisation and group mobility. It was only in the latter period that one could clearly see the planning and tactical depth and the technology maintenance behavior (curation) found in every hunter-gatherer society of the ethnographic present. Different revisions of the archaeological record tended to agree in recognising that the appearance of these novel features represented a threshold indicating the appearance of language and that they were invariably associated with fully modern humans. The implications were that Neandertals probably lacked language, that they were intellectually and behaviorally inferior to modern humans, and that such an inferiority explained their demise and ultimate replacement by early modern humans. This view made it into the 1990s as an orthodoxy challenged by only a minority of researchers and was combined with the anatomical evidence of clear separation between the two groups to produce a powerful synthesis, epitomised in volumes such as those by Stringer and Gamble (1993) and Mellars (1996).

In the late 1980s and initial 1990s, four 'events' occurred to increasingly distance the Neandertals from modern humanity and especially from early modern humans and to strengthen this orthodox view of the biological and cultural separation of Neandertals as a different, extinct species of human. The first was the dating by TL and ESR of archeological materials, from the levels into which the Levantine Qafzeh and Skhul early modern humans had been buried, to the later portion of oxygen isotope stage 5 (ca 90,000 years B.P.). This established, for the first time, the chronological priority of early modern humans over the Neandertals in one geographical region. The second was the introduction of extant human molecular data into the phylogenetic debate over modern human origins, interpretations of which championed an out-of-Africa scenario with total replacement of all non-African late archaic humans (Cann, Stoneking and Wilson 1987; Stringer and Andrews 1988). The third event was the AMS radiocarbon dating of early Aurignacian levels in northern Spain, and hence at the western edge of the Neandertal range and of the European cul-de-sac, to ca 40,000 years B.P. (Bischoff et al. 1989; Cabrera and Bischoff 1989). This dating was taken to indicate (despite the lack of associated diagnostic human remains) that early modern humans overlapped in time with Châtelperronian-associated Neandertals (at Saint-Césaire and sub-

sequently at Arcy-sur-Cure – Grotte du Renne (Lévêque and Vandermeersch 1980; Hublin et al. 1996)) and eventually replaced them, and that the Upper Paleolithic characteristics of the Châtelperronian were the result of Neandertal acculturation. The last of these ‘events’ was the growing recognition that the Middle Paleolithic and the Neandertals survived relatively late in Iberia south of the Ebro Valley, to at least 30,000 years B.P., apparently isolated from both the biological and cultural dynamics in the Pyrenees and beyond (Vega Toscano 1990; Villaverde and Fumal 1990; Zilhão 1993; Hublin et al. 1995).

All four of these ‘events’, combined with the increasing use of cladistic methodology (and its emphasis on identifying uniquely derived – autapomorphic, ‘divergent,’ ‘specialized’ – traits) in Pleistocene hominid paleontology (Stringer, Hublin and Vandermeersch 1984; Stringer 1987; Condemi 1991; Rak, Kimbel and Hovers 1994), tended to peripheralize the Neandertals in hominid evolution. This was augmented with emphasis archeologically and paleontologically on the apparent or presumed behavioral contrasts between the Neandertals and early modern humans (e.g., Trinkaus 1986; Binford 1989; Klein 1989; Stringer and Gamble 1993; Mellars 1996).

It should be emphasised that these trends of the late 1980s and early 1990s were by no means universal among paleoanthropologists. However, the most frequently portrayed scenario of modern human emergence in the Near East and Europe was one of adaptively superior early modern humans spreading north through the Levant and then westward across Europe, out-competing and displacing most of the Neandertal populations and acculturating the remaining fragmented Neandertal groups, with only a few peripheral Neandertal populations surviving in the cul-de-sac of Atlantic Europe. This was presumed by many to be confirmed by the announcement (Krings et al. 1997) that mitochondrial DNA extracted from the original 1856 Neandertal fossil lay significantly outside of living human ranges of variation.

Even though phylogenetic arguments, both paleontological and molecular, supporting this scenario have continued during the past decade, there has been an abundance of critiques of the extreme replacement model of modern humans origins, and positions (at least among those researchers with some perspective on the hominid fossil record and population biology) have tended to soften. Much the same can be said for extreme models of regional continuity.

Even the divergent nature of the Neandertal 1 mtDNA has become less important, given the application of populational (as opposed to cladistic) models to its interpretation, and the recognition that we have known since the 1880s that the Neandertals, biologically speaking, fall outside the range of variation of living humanity. In particular, despite the sequencing of additional Neandertal mtDNA from Mezmaiskaya and Vindija (Ovchinnikov et al. 2000; Krings et al. 2000) that is similar to the Neandertal 1 mtDNA, it has been demonstrated that the data are compatible with both replacement and admixture models of modern human emergence (Nordborg 1998), that the ranges of variation in intraspecific chimpanzee mtDNA far exceed the living human plus Neandertal variation (Gagneux et al. 1999), and that the lack of affinities between Neandertal and recent European mtDNA tells us little about Neandertal genetic contributions to early modern human populations (Relethford 2001b). The interpretations of the Neandertal mtDNA have been further compromised by the analysis of divergent mtDNA from a Late Pleistocene early modern Australian (Adcock et al. 2001).

In addition, whereas analyses of living human DNA continue to appear in print arguing for a strictly African origin of all modern humans, it is becoming apparent that their conclusions are highly sensitive to the sample size analysed (many have <100 individuals globally), the number of (presumably independent) loci considered (for many $N = 1$), the demographic models assumed (most generated without cognizance of known parameters of Pleistocene human biogeography and population instability), the level of admixture between early modern and late archaic humans assumed, and the particular algorithms employed for analysis (many use inappropriate cladistic approaches: see Hawks et al. 2000; Wall 2000; Relethford 2001a). Most importantly, it is now evident (Wall 2000) that analyses of extant human DNA, with or without Neandertal DNA, will probably never be able to distinguish between replacement and admixture scenarios of Neandertal / early modern human population dynamics. At best, with vastly more data, they may be able to assess the frequency of 'Neandertal genes' in living human populations. The application of DNA technology to modern human origins therefore can address solely a philosophical and sociopolitical issue regarding the integrity of living human gene pools. It is irrelevant to our understanding of the evolutionary dynamics of modern human emergence.

From these reassessments of the human paleontological and molecular data pertinent to modern human emergence, there has been a subtle but perceptible drifting away from the phylogenetic schemes of the late 1980s. Whereas 'multiregionalism' was originally construed to argue for intraregional continuity, with interregional gene flow, between late archaic and early modern humans (Wolpoff, Wu and Thorne 1984; Frayer et al. 1993), it is now associated with an out-of-Africa emergence of modern humans with a high level of gene flow, including admixture with, or absorption of, regional Neandertal and other late archaic human populations (Wolpoff et al. 2001). At the same time, strict replacement models (e.g. Stringer and Andrews 1988, Cann, Stoneking and Wilson 1987) have been frequently replaced by arguments accepting some assimilation of local Neandertal groups, initially among paleontologists (e.g. Hublin 1990; Smith and Trinkaus 1991; Vandermeersch 1995) and subsequently among molecular biologists (e.g. Ovchinnikov et al. 2000; Krings et al. 2000).

As noted a decade ago and increasingly apparent today, the paleoanthropological debate is no longer between 'replacement' versus 'continuity', but between trivial versus major gene flow, or assimilation, between the Neandertals and early modern humans. Moreover, whereas the out-of-Africa with replacement scenario was originally formulated in terms of the human population dynamics during the Late Pleistocene, it is increasingly being stated in terms of the degree of persistence of Neandertal 'genes' in living human populations – it has thereby been transformed by its proponents from a paleoanthropological and evolutionary discussion into one concerned solely with the pedigree of living humanity.

61

Also during the 1990s, increasingly appropriate analyses of Neandertal and early modern human functional anatomy have concluded that many of the behaviorally significant changes were more subtle than previously proposed. This began to emerge from efforts to appropriately biologically scale the features in question (Ruff et al. 1993). The result was a more complex mosaic of biobehavioral changes (Trinkaus 1995; 2000; Trinkaus et al. 1999), especially around the time of this Late Pleistocene transition (Trinkaus et al. 1998). This was combined

with assessments of Neandertal-associated faunal remains (e.g., Jaubert et al. 1990; Patou-Mathis 1993; Farizy, David and Jaubert 1994; Stiner 1994; Speth and Tchernov 1998; Marean and Kim 1998; Gaudzinski and Roebroeks 2000), indicating less of a contrast in animal exploitation than had been inferred previously. In addition, the late survival of Neandertals in southern Iberia, not far from presumed contemporaneous early modern humans in the Pyrenees, was used by Hublin and colleagues (1995, 936) to argue against 'an overwhelming superiority of modern groups' given the inferred ability of the Iberian Neandertals to resist competition from early modern humans on their northern frontier for many millennia.

The chronological and technological reassessment of the Châtelperronian and initial Aurignacian (d'Errico et al. 1998; Zilhão and d'Errico 1999) demonstrating the chronological priority of the Châtelperronian, and hence the independent development of an 'Upper Paleolithic' behavioral complex by the Neandertals, has served to confirm this changing view. This is combined with the growing realisation (Smith et al. 1999; Churchill and Smith 2000) that the earliest well-dated diagnostically modern human remains in Europe are <33,000 years old, and that the biological affinities of the makers of the earliest phases of the Aurignacian are simply unknown.

Recently, the documentation that Neandertals survived after 30,000 years B.P. in central Europe and possibly in the Caucasus (as opposed to merely in the peripheries of Atlantic Europe), several millennia after the appearance of modern humans in Europe (Smith et al. 1999; Ovchinnikov et al. 2000), has reinforced the idea that they were able to compete successfully with early modern human populations for an extended period of time. And growing evidence from stable isotopes of Neandertals (Fizet et al. 1995; Bocherens et al. 1999; Richards et al. 2000) has shown that at least in Europe they behaved as top-level carnivores, a niche that must have included significant active predation of the mammals whose remains they processed.

From this has emerged over the last decade, but especially in the past two years, a perception of the Neandertal to early modern human transition as one between behaviorally similar groups of humans. However much they may have contrasted in their anatomies, the adaptive differences between them were apparently subtle, permitting at least their co-existence for extended periods of time and, as had been previously proposed at least for central Europe (Smith and Trinkaus 1991; Bräuer 1984; Holliday 1997), some degree of genetic exchange.

62 **The implications of Lagar Velho 1**

It is therefore in this context that the announcement of the morphological mosaic of Lagar Velho 1 appeared. As mentioned, all too many of the reactions to the interpretation of Lagar Velho 1 followed predictable patterns based on the scholars' previous positions regarding modern human origins.

For those who accept the emerging view of the Neandertals as similar to, although certainly not identical to, early modern humans in their behavioral repertoires, and that the contrasts are principally differences of degree and not of kind, some degree of admixture

between the populations would not be surprising. Indeed, increasingly discussions of modern human origins that are predisposed to accept some level of gene flow (however high or low) between late archaic and early modern humans (e.g. Hublin 2000; Adcock et al. 2001; Wolpoff et al. 2001) are willing to accept Lagar Velho 1 as a piece of that scenario.

For those who continue to perceive a major adaptive and biological gulf between these two, albeit morphologically distinct, groups of Late Pleistocene hominids, multiple reasons for rejecting the admixture interpretation of Lagar Velho 1 continue to be raised.² These reasons, most of which have been addressed (Trinkaus and Zilhão 1999), involve 1) refusal to accept body proportions as a population marker, despite the fact that they are a form of principal European paleontological evidence supporting an out-of-Africa scenario, 2) arguments for short term changes in body proportions, when contemporaneous Gravettian individuals in much colder climates (Dolní Věstonice, Paviland and Sungir) show no such change in adults or late juveniles, 3) confusion between the potential ancestors of Lagar Velho 1 (Neandertals and pre-24,000 BP early modern humans) and living humanity, 4) a failure to perceive the degree and patterning of human biological evolution and diversity in space and during the past 25–30,000 years, 5) the application of typological and cladistic frameworks which are scientifically inappropriate, 6) the rejection of arguments based on a juvenile specimen, when abundant research (see Tillier (1999) and references therein) has documented a multitude of contrasts between Neandertal and early modern human immature specimens and the developmentally early appearance of 'Neandertal features' has been used to argue for their distinctiveness, 7) a lack of appreciation for the developmental trajectories of skeletal features, and/or 8) a failure to place the mosaic of features of Lagar Velho 1 into an appropriate probabilistic framework, thereby taking into account both distinctive features of the reference samples and the frequency distributions of variable features found in both groups.

Most disturbing in this debate has been the tenacity with which the critiques of the admixture interpretations have maintained some of the above fallacious arguments. It is apparent that the idea of admixture must be unacceptable to some, an aberration of the normal order. Moreover, the idea of Neandertal and early modern human populations blending socially and biologically tends to negate the perception of modern humans as special, descendant from creatures less human than ourselves but somehow sufficiently distant from them to avoid the pollution associated with such connections.

Yet, however much the current assessments of the morphological affinities of Lagar Velho 1 are expanded as more data are collected, contracted as the biological interrelationships between features are analysed, integrated into a more comprehensive developmental framework, and adjusted as the comparative framework is refined, the morphological mosaic is unlikely to go away. The ultimate reception of the current interpretation, however, will depend as much on changing perceptions of who the Neandertals were as people as on the paleontological and archeological evidence Lagar Velho 1 provides for Late Pleistocene human evolution.

Notes

- ¹ The Lagar Velho 1 project has been conducted through the auspices of the Instituto Português de Arqueologia, and additional support has been provided by the L.S.B. Leakey Fdn., the Wenner-Gren Foundation, Washington University and the University of Iowa. We thank A.C. Araújo, S.E. Bailey, A. Coppa, F. d'Errico, R.G. Franciscus, S.W. Hillson, T.W. Holliday, J.J. Hublin, B. Maureille, M. Ponce de Leon, C.B. Ruff, F.H. Smith, F. Spoor, C.B. Stringer, B. Vandermeersch and C. Zollikofer for productive discussions regarding the Lagar Velho remains and their implications.
- ² The scientific criticisms of the admixture interpretation (with the exception of Hublin 2000) are known from personal communications, discussions at conferences and quotes in the public media. For this reason, none of the arguments mentioned are referenced to individuals.

Editorial note

The editors intend to publish a discussion on this article in the next issue.

References

- Adcock, G.J., E.S. Dennis, S. Easteal, G.A. Huttley, L.S. Jermiin, J. Peacock and A. Thorne, 2001: Mitochondrial DNA sequences in ancient Australians. Implications for modern human origins, *Proceedings of the National Academy of Sciences USA* 98, 537-542.
- Aldhouse-Green, S. and P.B. Pettitt, 1998: Paviland Cave. Contextualizing the 'Red Lady,' *Antiquity* 72, 756-772.
- Bader, O., 1998: *Upper Palaeolithic site Sungir (graves and environment)*, Moscow.
- Beaumont, P.B. and J.C. Vogel, 1972: On a new radiocarbon chronology for Africa south of the equator, *African studies* 31, 65-89, 155-182.
- Binford, L.R., 1989: Isolating the transition to cultural adaptations. An organizational approach, in L.R. Binford (ed.), *Debating archaeology*, New York, 464-481.
- Bischoff, J.L., N. Soler, J. Maroto and R. Julià, 1989: Abrupt Mousterian/Aurignacian boundary at c.40 ka B.P. Accelerator C-14 dates from l'Abreda Cave (Catalunya, Spain), *Journal of archaeological science* 16, 563-576.
- 64 Bocherens, H., D. Billiou, A. Mariotti, M. Patou-Mathias, M. Otte, D. Bonjean and M. Toussaint, 1999: Palaeoenvironmental and palaeodietary implications of isotopic biogeochemistry of last interglacial Neanderthal and mammal bones in Scladina Cave (Belgium), *Journal of archaeological science* 26, 99-607.
- Boule, M., 1911: L'homme fossile de La Chapelle-aux-Saints, *Annales de paléontologie* 6, 111-172.
- Boule, M., 1912: L'homme fossile de La Chapelle-aux-Saints, *Annales de paléontologie* 7, 21-56, 85-192.
- Boule, M., 1913: L'homme fossile de La Chapelle-aux-Saints, *Annales de paléontologie* 8, 1-70.

- Bräuer, G., 1984: A craniological approach to the origin of anatomically modern *Homo sapiens* in Africa and implications for the appearance of modern Europeans, in F.H. Smith and F. Spencer (eds.), *The origins of modern humans*, New York, 327–410.
- Breuil, H., 1912: Les subdivisions du Paléolithique supérieur et leur signification, *Congrès international d'anthropologie et d'archéologie préhistoriques* 14, 1–238.
- Cabrera, V. and J.L. Bischoff, 1989: Accelerator C-14 dates for Early Upper Paleolithic (Basal Aurignacian) at El Castillo Cave (Spain), *Journal of archaeological science* 16, 577–584.
- Cann, R.L., M. Stoneking and A.C. Wilson, 1987: Mitochondrial DNA and human evolution, *Nature* 325, 31–36.
- Chilardi, S., D.W. Frayer, P. Giola, R. Macchiarelli and M. Mussi, 1996: Fontana Nuova di Ragusa (Sicily, Italy). Southernmost Aurignacian site in Europe, *Antiquity* 70, 553–563.
- Churchill, S.E. and F.H. Smith, 2000: Makers of the early Aurignacian of Europe, *Yearbook of physical anthropology* 43, 61–115.
- Condemi, S., 1991: Some considerations concerning Neandertal features and the presence of Neandertals in the Near East, *Rivista di antropologia* 69, 27–38.
- Day, M.H. and C.B. Stringer, 1982: A reconsideration of the Omo Kibish remains and the erectus-sapiens transition, in H. de Lumley (ed.), *L'Homo erectus et la place de l'homme de Tautavel parmi les hominidés*, Paris, 814–846.
- d'Errico, F., J. Zilhão, M. Julien, D. Baffier and J. Pelegrin, 1998: Neanderthal acculturation in western Europe? A critical review of the evidence and its interpretation, *Current anthropology* 39, 1–44.
- Duarte, C., J. Maurício, P.B. Pettitt, P. Souto, E. Trinkaus, H. van der Plicht and J. Zilhão, 1999: The early Upper Paleolithic human skeleton from the Abrigo do Lagar Velho (Portugal) and modern human emergence in Iberia, *Proceedings of the National Academy of Science USA* 96, 7604–7609.
- Farizy, C., F. David and J. Jaubert, 1994: *Hommes et bisons du Paléolithique moyen à Mauran (Haute-Garonne)*, Paris.
- Ferembach, D., 1976: Les restes humains de la Grotte de Dar-es-Soltane 2 (Maroc) Campagne 1975, *Bulletin et mémoires de la Société d'Anthropologie de Paris* 13(3), 183–193.
- Fizet, M., A. Mariotti, H. Bocherens, B. Lange-Badré, B. Vandermeersch, J. Borel and G. Bellon, 1995: Effect of diet, physiology and climate on carbon and nitrogen stable isotopes of collagen in late Pleistocene anthropic palaeoecosystem: Marillac, Charente, France, *Journal of archaeological science* 22, 67–79.
- Fraye, D.W., 1978: Evolution of the dentition in Upper Paleolithic and Mesolithic Europe, *University of Kansas publications in anthropology* 10, 1–201.
- Fraye, D.W., M.H. Wolpoff, F.H. Smith, A.G. Thorne and G.G. Pope, 1993: The fossil evidence for modern human origins, *American anthropologist* 95, 14–50.
- Gagneux, P., C. Wills, U. Gerloff, D. Tautz, P.A. Morin, C. Boesch, B. Fruth, G. Hohmann, O.A. Ryder and D.S. Woodruff, 1999: Mitochondrial sequences show diverse evolutionary histories of African hominoids, *Proceedings of the National Academy of Sciences USA* 96, 5077–5082.
- Gamble, C., 1986: *The Paleolithic settlement of Europe*, Cambridge.
- Gaudzinski, S. and W. Roebroeks, 2000: Adults only: Reindeer hunting at the Middle

- Palaeolithic site Salzgitter-Lebenstedt, northern Germany, *Journal of human evolution* 38, 497-521.
- Giacobini, G., 1999: Les sépultures du Paléolithique supérieur d'Italie, in D. Sacchi (ed.), *Les faciès leptolithiques du nord-ouest méditerranéen: milieux naturels et culturels*, Carcassonne, 29-39.
- Hawks, J., K. Hunley, S.H. Lee and M. Wolpoff, 2000: Population bottlenecks and Pleistocene human evolution, *Molecular biology and evolution* 17, 2-22.
- Heim, J.L., 1976: Les hommes fossiles de La Ferrassie I, *Archives de l'Institut de Paléontologie Humaine* 35, 1-331.
- Heim, J.L., 1982: Les hommes fossiles de La Ferrassie II, *Archives de l'Institut de Paléontologie Humaine* 38, 1-272.
- Holden, C., 1999: Ancient child burial uncovered in Portugal, *Science* 283, 169.
- Holliday, T.W., 1997: Body proportions in Late Pleistocene Europe and modern human origins, *Journal of human evolution* 32, 423-447.
- Hublin, J.J., 1978: Le Torus occipital transverse et les structures associées. Évolution dans le genre *Homo*, Thèse de Docteur de Troisième Cycle, Université de Paris VI.
- Hublin, J.J., 1990: Les peuplements paléolithiques de l'Europe. Un point de vue paléobioéographique, in C. Farizy (ed.), *Paléolithique moyen récent et paléolithique supérieur ancien en Europe, mémoires du Musée de Préhistoire de l'Île de France* 3, 29-37.
- Hublin, J.J., 2000: Modern-nonmodern hominid interactions. A Mediterranean perspective, in O. Bar-Yosef and D. Pilbeam (eds), *The geography of Neandertals and modern humans in Europe and the greater Mediterranean. Peabody Museum bulletin* 8, 157-182.
- Hublin, J.J., C. Barroso Ruiz, P. Medina Lara, M. Fontugne and J.L. Reyss, 1995: The Mousterian site of Zafarraya (Andalucia, Spain). Dating and implications on the Palaeolithic peopling process of western Europe, *Comptes rendus de l'Académie des Sciences de Paris* 321, 931-937.
- Hublin, J.J., F. Spoor, M. Braun, F. Zonneveld and S. Condemi, 1996: A late Neanderthal associated with Upper Palaeolithic artefacts, *Nature* 381, 224-226.
- Jaubert, J., M. Lorblanchet, H. Laville, R. Slott-Moller, A. Turq and J.P. Brugal, 1990: *Les chasseurs d'Aurochs de La Borde. Un site du Paléolithique Moyen (Livernon, Lot)*, Paris.
- Keith, A., 1915: *The antiquity of man*, London.
- Klein, R.G., 1989: *The human career*, Chicago.
- Krings, M., C. Capelli, F. Tschentscher, H. Geisert, S. Meyer, A. von Haeseler, K. Grossschmidt, G. Possnert, M. Paunović and S. Pääbo, 2000: A view of Neandertal genetic diversity, *Nature genetics* 26, 144-146.
- Krings, M., A. Stone, R. Schmitz, H. Krainitzki, M. Stoneking and S. Pääbo, 1997: Neandertal DNA sequences and the origin of modern humans, *Cell* 90, 19-30.
- Lévêque, F. and B. Vandermeersch, 1980: Découverte de restes humains dans un niveau castelperronien à Saint-Césaire (Charente-Maritime), *Comptes rendus de l'Académie des Sciences de Paris* 291, 187-189.
- Marean, C.W. and S.Y. Kim, 1998: Mousterian large-mammal remains from Kobeh Cave. Behavioral implications for Neanderthals and early modern humans, *Current anthropology* 39, 79-113.

- Mellars, P., 1996: *The Neanderthal legacy*, Princeton.
- Nordborg, M., 1998: On the probability of Neanderthal ancestry, *American journal of human genetics* 63, 1237-1240.
- Ovchinnikov, I., A. Götherström, G.P. Romanova, V.M. Kharitonov, K. Lidén and W. Goodwin, 2000: Molecular analysis of Neanderthal DNA from the northern Caucasus, *Nature* 404, 490-493.
- Patou-Mathis, M., 1993: Etude taphonomique et palethnographique de la faune de l'abri des Canalettes, in L. Meignan (ed.), *L'abri des Canalettes. Un habitat moustérien sur les grands Causses (Nant, Aveyron)*, Paris, 199-237.
- Rak, Y., W.H. Kimbel and E. Hovers, 1994: A Neanderthal infant from Amud Cave, Israel, *Journal of human evolution* 26, 313-324.
- Relethford, J.H., 2001a: Ancient DNA and the origin of modern humans, *Proceedings of the national academy of sciences USA* 98, 390-391.
- Relethford, J.H., 2001b: Regional affinities of Neanderthal DNA with living humans do not reject multiregional evolution, *American journal of physical anthropology* 115, 95-98.
- Richards, M.P., P.B. Pettitt, E. Trinkaus, F.H. Smith, M. Paunović and I. Karavanić, 2000: Neanderthal diet at Vindija and Neanderthal predation. The evidence from stable isotopes, *Proceedings of the National Academy of Sciences USA* 97, 7663-7666.
- Ruff, C.B., E. Trinkaus, A. Walker and C.S. Larsen, 1993: Postcranial robusticity in *Homo*, I. Temporal trends and mechanical interpretations, *American journal of physical anthropology* 91, 21-53.
- Smith, F.H., 1976: The Neanderthal remains from Krapina, *Department of anthropology, University of Tennessee, report of investigations* 15, 1-359.
- Smith, F.H., and F. Spencer (eds), 1984: *The origins of modern humans*, New York.
- Smith, F.H., and E. Trinkaus, 1991: Les origines de l'homme moderne en Europe centrale. Un cas de continuité, in J.J. Hublin and A.M. Tillier (eds), *Aux origines d'Homo sapiens. Nouvelle encyclopédie Diderot*, Paris, 251-290.
- Smith, F.H., E. Trinkaus, P.B. Pettitt, I. Karavanić and M. Paunović, 1999: Direct radiocarbon dates for Vindija G₁ and Velika Pećina Late Pleistocene hominid remains, *Proceedings of the National Academy of Science USA* 96, 12281-12286.
- Speth, J.D. and I. Tchernov, 1998: The role of hunting and scavenging in Neanderthal procurement strategies, in T. Akazawa, K. Aoki and O. Bar-Yosef (eds), *Neandertals and modern humans in western Asia*, New York, 223-239.
- Stiner, M.C., 1994: *Honour among thieves. A zooarchaeological study of Neanderthal ecology*, Princeton.
- Stringer, C.B., 1974a: A multivariate study of cranial variation in middle and Upper Pleistocene human populations, Ph.D. Thesis, University of Bristol.
- Stringer, C.B., 1974b: Population relationships of later Pleistocene hominids. A multivariate study of available crania, *Journal of archaeological science* 1, 317-342.
- Stringer, C.B., 1987: A numerical cladistic analysis for the genus *Homo*, *Journal of human evolution* 16, 135-146.
- Stringer, C.B. and P. Andrews, 1988: Genetics and the fossil evidence for the origin of modern humans, *Science* 239, 1263-1268.

- Stringer, C.B. and C. Gamble, 1993: *In search of the Neanderthals*, London.
- Stringer, C.B., J.J. Hublin and B. Vandermeersch, 1984: The origin of anatomically modern humans in western Europe, in F.H. Smith and F. Spencer (eds), *The origins of modern humans*, New York, 51-135.
- Svoboda, J., V. Ložek and E. Vlček, 1996: *Hunters between east and west*, New York.
- Thoma, A., 1984: Morphology and affinities of the Nazlet Khater man, *Journal of human evolution* 13, 287-296.
- Tillier, A.M., 1999: *Les enfants moustériens de Qafzeh*, Paris.
- Trinkaus, E., 1975: A functional analysis of the Neandertal foot, Ph.D. Thesis, University of Pennsylvania.
- Trinkaus, E., 1981: Neandertal limb proportions and cold adaptation, in C.B. Stringer (ed.), *Aspects of human evolution*, London, 187-224.
- Trinkaus, E., 1983a: *The Shanidar Neandertals*, New York.
- Trinkaus, E., 1983b: Neandertal postcrania and the adaptive shift to modern humans, in E. Trinkaus (ed.), *The Mousterian legacy. Human biocultural change in the Upper Pleistocene*, Oxford (BAR International Series 164), 165-200.
- Trinkaus, E., 1984: Western Asia, in F.H. Smith and F. Spencer (eds.), *The origins of modern humans*, New York, 251-293.
- Trinkaus, E., 1986: The Neandertals and modern human origins, *Annual review of anthropology* 15, 193-218.
- Trinkaus, E., 1995: Near Eastern late archaic humans, *Paléorient* 21, 9-23.
- Trinkaus, E., 2000: The 'robusticity transition' revisited, in C. Stringer, R.N.E. Barton, and J.C. Finlayson (eds), *Neanderthals on the edge*, Oxford, 227-236.
- Trinkaus, E., C.B. Ruff, S.E. Churchill and B. Vandermeersch, 1998: Locomotion and body proportions of the Saint-Césaire 1 Châtelperronian Neandertal, *Proceedings of the National Academy of Sciences USA* 95, 5836-5840.
- Trinkaus, E., and P. Shipman, 1993: *The Neandertals. Changing the image of mankind*, New York.
- Trinkaus, E., C.B. Stringer, C.B. Ruff, R.J. Hennessy, M.B. Roberts and S.A. Parfitt, 1999: Diaphyseal cross-sectional geometry of the Boxgrove 1 Middle Pleistocene human tibia, *Journal of human evolution* 37, 1-25.
- Trinkaus, E. and J. Zilhão, 1999: Lagar Velho FAQs (Frequently asked questions regarding the Lagar Velho 1 human skeleton) <http://www.ipa.min-cultura.pt/news/noticias/lapedo/lapedofaq>, Instituto Português de Arqueologia.
- Trinkaus, E., J. Zilhão and C. Duarte, 1999: The Lapedo child. Lagar Velho 1 and our perceptions of the Neandertals, *Mediterranean prehistory online* (<http://www.med.abaco-mac.it/articles/doc/013.htm>).
- Vandermeersch, B., 1981: *Les hommes fossiles de Qafzeh (Israël)*, Paris.
- Vandermeersch, B., 1995: *Homo sapiens sapiens*: ce que disent les fossiles. *La recherche* 26, 614-620.
- Vega Toscano, L.G., 1990: La fin du Paléolithique moyen au sud de l'Espagne: Ses implications, in C. Farizy (ed.), *Paléolithique moyen récent et Paléolithique supérieur ancien en Europe*, Nemours, *mémoires du Musée de Préhistoire de l'Ile de France* 3, 169-176.
- Villaverde, V. and M.P. Fumanal, 1990: Relations entre le Paléolithique moyen et le

- Paléolithique supérieur dans le versant Méditerranéen espagnol, in C. Farizy (ed.), *Paléolithique moyen récent et Paléolithique supérieur ancien en Europe, mémoires du Musée de Préhistoire de l'Île de France* 3, 177-183.
- Wall, J.D., 2000: Detecting ancient admixture in humans using sequence polymorphism data, *Genetics* 154, 1271-1279.
- Wendorf, F., R.L. Laury, C.C. Albritton, R. Schild, C.V. Haynes, P.E. Damon, M. Shafiqullah and R. Scarborough, 1975: Dates for the Middle Stone Age of east Africa, *Science* 187, 740-742.
- Wolpoff, M.H., J. Hawks, D.W. Frayer and K. Hunley, 2001: Modern human ancestry at the peripheries. A test of the replacement theory, *Science* 291, 293-297.
- Wolpoff, M.H., Wu X.Z. and A.G. Thorne, 1984: Modern *Homo sapiens* origins. A general theory of hominid evolution involving the fossil evidence from east Asia, in F.H. Smith and F. Spencer (eds), *The origins of modern humans*, New York, 411-483.
- Zilhão, J., 1993: Le passage du Paléolithique moyen au Paléolithique supérieur dans le Portugal, in V. Cabrera (ed.), *El origen del hombre moderno en el Suroeste de Europa*, Madrid, 127-145.
- Zilhão, J., 1997: *O Paleolítico Superior da Estremadura Portuguesa*, Lisboa.
- Zilhão, J., 1998: The extinction of Iberian Neandertals and its implications for the origins of modern humans in Europe, in F. Facchini, A. Palma di Cesnola, M. Piperno, and C. Peretto (eds), *XIII International congress of prehistoric and protohistoric sciences* 2, 299-312.
- Zilhão, J., 2000: The Ebro frontier. A model for the late extinction of Iberian Neanderthals, in C. Stringer, R.N.E. Barton, and J.C. Finlayson (eds), *Neanderthals on the edge*, Oxford, 111-121.
- Zilhão, J., C. Duarte and A.C. Araújo, 1999: A sepultura infantil do Paleolítico superior inicial do Abrigo do Lagar Velho (Lapedo, Leiria) <http://www.ipa.min-cultura.pt/news/noticias/lapedo/lagarvelho>, Instituto Português de Arqueologia.
- Zilhão, J. and F. d'Errico, 1999: The chronology and taphonomy of the earliest Aurignacian and its implications for the understanding of Neandertal extinction, *Journal of world pre-history* 13, 1-68.
- Zilhão, J. and E. Trinkaus, 1999: An early Upper Paleolithic burial from the Abrigo do Lagar Velho, Portugal, *Anthropologie (Brno)* 37, 98.