

CHAPTER 32 | Phylogenetic Implications¹

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The juvenile Gravettian human skeleton known as Lagar Velho 1 presents a complex mosaic of dental and skeletal characteristics from the perspective of Late Pleistocene European human biology. As a result of this mosaic, and our previous interpretation of it as indicating some degree of Neandertal ancestry in an early modern human European (Duarte et al., 1999), the Lagar Velho child has become more than just an additional Gravettian skeleton from Europe. It has become a significant player in phylogenetic discussions of the evolutionary fate of the Neandertals and of the phylogenetic emergence of modern humans (e.g., Hublin, 2000; Aguirre, 2000; Wolpoff et al., 2001; Adcock et al., 2001; Relethford, 2001a; Zilhão, 2001a, 2001b; Arsuaga et al., 2001b; Jolly, 2001). From the perspective of Late Pleistocene human evolution, it is therefore appropriate to review the phylogenetic implications of the Lagar Velho 1 skeletal and dental morphology.

When the remains were first discovered and during the initial analysis in the laboratory, it was assumed that it merely represented an immature early modern human, a representative of the Gravettian human populations especially well-known from discoveries in northern Italy and Moravia but also known from scattered or incomplete remains across Europe from the Atlantic Ocean to the Russian Plain (see also Chapter 33). This assessment was based on the clear presence of distinctive modern human features such as a prominent chin. Moreover, such an interpretation fit expectations given our knowledge of the skeletal biology of other European Gravettian human remains, all of which are clearly those of early modern humans. It was only subsequently, during a reconsideration of the remains and comparisons of some of the skeletal proportions to other samples, that it occurred to us that this skeleton might provide evidence for some degree of assimilation of Neandertal populations into those of early modern humans dispersing westward across Europe and eventually into Iberia. Once that had occurred to us, we began to investigate the skeleton more carefully, from a phylogenetic perspective as well as from the planned paleobiological perspective.

Apparent evidence for Neandertal assimilation in southwestern Iberia came as a surprise to us, since it was well-documented [in part by one of us (JZ)] that the transition between the Middle Paleolithic and the Upper Paleolithic was relatively late and abrupt in southern Iberia (Vega Toscano, 1990; Villaverde and Fumanal, 1990; Zilhão, 1993, 2001a), and that the archeological transition appeared to be closely associated with the human biological transition between Neandertals and early modern humans (Hublin et al., 1995). We therefore expected there to have been little or no contribution of those late Neandertals in the cul-de-sac of southwestern Europe to the populations of culturally contrasting early modern humans. Indeed, although one of us (ET) had previously supported an interpretation of such assimilation of the Neandertals in central Europe, he had also argued that the western European process was one of replacement of the Neandertals by early modern humans (Smith and Trinkaus, 1991, p. 286; Trinkaus and Shipman, 1993a, p. 415). Similarly, although the other one of us (JZ) had previously argued against simple models of western European Neandertal acculturation (d'Errico et al., 1998; Zilhão and d'Errico, 1999), he had also assumed that the Neandertals had contributed little if at all to those early modern human populations (Zilhão, 1998).

Possible evidence for the assimilation of Iberian Neandertals into early modern human populations, or genetic admixture between the two groups, also came as a surprise to much of the field. Reactions to the initial announcement of it in April 1999 (de Sá, 1999) and the subsequent publication of the formal presentation of the arguments in June 1999 (Duarte et al., 1999) included both enthusiastic acceptance of our interpretation and outright rejection of it, most of them either verbally or in quotes in the public media. Moreover, the global media coverage of the announcement in the spring of 1999 exceeded that of any other Late Pleistocene human paleoanthropological discovery in our memory. Given this attention to our unusual child from the Lapedo Valley, it is appropriate to provide a Late Pleistocene human phylogenetic context and then, in light of the morphological considerations in the previous chapters, assess the position of Lagar Velho 1 within that framework.

The Emergence of Modern Humans in Europe, and the Phylogenetic Fate of the Neandertals

Paleoanthropological discussions of the past two decades have been dominated by considerations, on a pan-Old World basis, of the phylogenetic processes involved in the emergence of early modern humans and the phylogenetic fates of regional late archaic human populations. This has been reflected in journal articles, books and international conferences since 1980 which are simply too numerous to list. Issues of modern human phylogenetic origins have been more or less current since the early twentieth century, when it was recognized that there were archaic humans who preceded modern humans during the Pleistocene (see Trinkaus and Shipman, 1993a). Gradually, particularly during the second half of the twentieth century, the discussion of modern human origins expanded from a Eurocentric view, focused principally on the fate of the Neandertals, to one encompassing most of the Old World. Yet, in part due to the far richer human paleontological record in Europe and the Near East and its associated Paleolithic archeological and geochronological frameworks, the discussions have remained Eurocentric, albeit placed in a broader geographical context.

All of the recent (late twentieth century and initial twenty-first century) serious interpretations of the emergence of modern humans in Europe have invoked some degree of genetic exchange between Europeans and non-Europeans during this time period (i.e., no one has seriously proposed that the Neandertals evolved directly into early modern Europeans in geographic isolation). However, during the past two decades, phylogenetic interpretations have occupied a spectrum of views ranging from one of predominantly local population evolution within Europe in the context of moderate (possibly slightly elevated) levels of gene flow to an interpretation of the absence of local continuity associated with the complete replacement of the Neandertal populations by in-dispersing early modern humans. Although the decade starting about 1987 saw a polarization between the ends of this spectrum of views, with endless (and frequently fruitless) discussions of continuity versus replacement, driven more by reactions and personality conflicts than by constructive research, much of the paleontological field directly concerned with modern human emergence supported some form of an intermediate position, involving some (however large or small) genetic contribution of the Neandertals to early modern European human populations.

Throughout these discussions and arguments, the principal model of dispute has been one in which early modern humans are seen as having emerged first in Africa and subsequently spreading throughout the Old World, absorbing and/or replacing regional archaic human populations, the Replacement Model.² A version of this model, couched in the Pre-

Sapiens paradigm of the first half of the twentieth century (see Vallois, 1958b), was first proposed by Leakey (1935) on the basis of the purported Middle Pleistocene age of the morphologically modern, if robust, human remains from the Kenyan site of Kanjera, and secondarily on the basis of the mandible from the nearby site of Kanam. The former have been shown to post-date the Middle Pleistocene and be most likely of Holocene age (Plummer et al., 1994; Plummer and Potts, 1995), and the latter is pathological and of archaic human morphological affinities (Tobias, 1960).

More recently, a serious Out-of-Africa interpretation of modern human emergence was first proposed on the basis of modern human remains presumed to be associated with South African Middle Stone Age deposits at Border Cave (Beaumont et al., 1978; see also Rightmire, 1979, 1984). A more explicit European version was formulated on the basis of limb segment proportions by one of us (Trinkaus, 1981), although that paper did not name Africa specifically but referred to European early modern humans exhibiting evidence of “gene flow from more equatorial regions” (p. 219), of which Africa was the most likely source. This followed closely on a fictionalized version of such a spread of early modern Africans into Europe (Kurtén, 1980). These two were followed by the cranially-focused arguments of Bräuer (1982, 1984), based in part on the analysis of African late Middle and early Late Pleistocene crania and in part on the purported transitional morphology of the Hahnöfersand frontal bone [the Hahnöfersand specimen has since been shown to be Holocene in age (Terberger et al., 2001)]. Of these early versions of an Out-of-Africa model for modern humans origins (at least for the western Old World), those concerned principally with the African fossil record (Beaumont et al., Rightmire) argued principally for the chronological precedence of early modern humans in Africa, whereas those involving the European fossil record (Kurtén, Trinkaus, Bräuer) argued for modern humans spreading out of Africa and absorbing, to some indeterminate degree, the regional Neandertal populations. Other early 1980s considerations of the issue (e.g., Day and Stringer, 1982; Smith, 1984; Stringer et al., 1984; Stringer, 1984) discussed an Out-of-Africa interpretation but did not reach firm conclusions regarding the role of African populations in the origins of early modern Eurasians. Most other discussions of modern human origins at that time did not place Africa in any special light regarding modern human origins (e.g., chapters in Smith and Spencer, 1984).

Ironically, paleontological evidence for a relatively early (initial Late Pleistocene) age for unquestionably morphologically modern, if robust, human remains had been found in the late 1960s at the KHS site in the Omo-Kibish Formation of southern Ethiopia (Leakey et al., 1969; Butzer et al., 1969). Although the Omo-Kibish 1 remains were explicitly recognized as both early and morphologically modern (Leakey et al., 1969), it was not until a dozen years after their discovery (e.g., Day and Stringer, 1982; Stringer et al., 1984) that they were used as evidence supporting the temporal precedence of modern humans in Africa and even longer before they were used to bolster an explicitly Out-of-Africa model of modern human origins.

In the late 1980s, several results appeared which focused the field on the Out-of-Africa model and began the intense debate of the following decade. This involved the 1987 publication of the first genetically-based explicit Out-of-Africa interpretation (Cann et al., 1987; see Relethford (2001a) for a detailed discussion of the results and subsequent critiques and reanalyses). These living human molecular results were followed by the first explicitly Out-of-Africa Replacement Model of modern human origins based on both the paleontological morphological data and extant human molecular data (Stringer and Andrews, 1988). Together, these articles set the stage for the subsequent arguments and counter-arguments principally with respect to a strict Out-of-Africa with replacement model of modern human origins, in both the paleontological and molecular fields [for a history of the molecular

debate, see Relethford (2001a); no adequate history of the paleontological side exists, but Trinkaus and Shipman (1993a) review the beginning of it, the perspectives of two protagonists are presented in Wolpoff and Caspari (1997) and Stringer and McKie (1996), and an account is presented briefly in Trinkaus et al. (2001)]. In the heat of those arguments, the more moderate Out-of-Africa with admixture models became less visible, even though they were expanded upon and synthesized more globally in the Assimilation Model of Smith et al. (1989) (see also Aiello, 1993).³

The beginning of this debate was also accompanied by the announcement (Valladas et al., 1988) of thermoluminescence dates for the Levantine early modern humans at Qafzeh of ca.90 000 years BP, clearly antedating most of the European (and Near Eastern) Neandertals. This gave strength, along with a growing African record of known or presumed Middle Stone Age modern humans from sub-Saharan Africa pre-dating ca.75 000 years BP, to the arguments that non-European modern humans, sharing the derived characters of European early modern humans, were available to spread across Europe and replace the Neandertals.

Yet, during the subsequent decade, only three forms of paleontological data emerged to support an African (or at least a tropical) origin for early modern Europeans. The first paleontological data consisted of nasal aperture configurations, in which some but not all early modern Europeans were shown to have nasal apertures resembling those of more equatorial human populations (Franciscus, 1995; see Chapter 20). The second was a reanalysis of Late Pleistocene body proportions, building on the earlier work of one of us, which showed a clear tropical body shape among both the Qafzeh-Skhul Levantine early modern humans and the European earlier Upper Paleolithic early modern humans (Holliday, 1995, 1997a; see also Ruff, 1994). Yet, these two analyses provided data to suggest at least some degree of Neandertal genetic contribution to those subsequent European populations.

The third form of paleontological data was the growing accumulation of Levantine and African data to support the temporal precedence of greater African early modern humans relative to those of Europe (Vandermeersch, 1981; Singer and Wymer, 1982; Day and Stringer, 1982; Trinkaus, 1984a, 1995) and their gradual emergence within Africa (Bräuer, 1984, 2001b; Howells, 1988; Hublin, 1991; Stringer, 1992, 1993), both in terms of the fossils and their chronological framework. In this, the Levant is best considered as part of greater Africa, at least temporarily during OIS 5 (Rabinovich and Tchernov, 1995; Stefan and Trinkaus, 1998a; Tchernov, 1998). It should be noted, however, that the temporal precedence of modern humans in Africa is not sufficient by itself to document that early modern Europeans had African ancestry, unless one argues (contrary to most paleontological data) that derived features (however defined) can only emerge once in a geographically dispersed lineage.

Although it has been strongly argued that there are Middle Stone Age early modern humans in southern Africa [e.g., Beaumont et al. (1978), Bräuer (1989), Rightmire and Deacon (1991), and McBrearty and Brooks (2000) and references therein], some of these remains are recent (Sillen and Morris, 1996) and others are morphologically rather archaic (Smith, 1993; Churchill et al., 1996). Others [see list and references in McBrearty and Brooks (2000)] are too fragmentary or anatomically restricted to be diagnostic. It therefore remains debatable to what extent the southern African Middle Stone Age “early modern humans” are in fact “modern,” as opposed to “southern African late archaic.”

The best sample of anatomically clearly “early modern” human remains which substantially predates the disappearance of the European Neandertals are those from northeast Africa (including their temporary OIS 5 expansion into the southern Levant). These include remains from Omo-KHS, Qafzeh and Skhul (Vandermeersch, 1981; Day and Stringer, 1982;

Trinkaus, 1984a, 1995; Holliday, 2000a), all of which appear to date before ca.80 000 years BP (Day and Stringer, 1982; Valladas et al., 1988; Stringer et al., 1989; Mercier et al., 1993). The Taramsa Hill specimen (Vermeersch et al., 1998) may be a more recent Middle Paleolithic member of this lineage.

These paleoanthropological considerations have been joined by a continuous supply of analyses of extant human molecular variation, including analyses of nuclear and mitochondrial DNA [see Relethford (2001a) for a review]. The majority of these molecular studies have claimed to establish an exclusively African origin for modern humanity, usually sometime in the late Middle Pleistocene. However, most of their analyses are limited and can only serve to reject a “candelabra” (Howells, 1959) model (regional continuity without interregional gene flow), a model that has been explicitly rejected by paleoanthropologists concerned with the phylogenetic origins of modern humans (see Wolpoff et al., 2000). Most importantly, as emphasized by Relethford (2001a and elsewhere), analyses of molecular data are frequently taken to establish an African origin of modern humans with replacement elsewhere without testing whether the data reject the logical (and well established) alternative of an African origin with variable amount of population admixture/absorption/assimilation elsewhere (the Assimilation Model). Indeed, in all cases, the data either fail to reject that alternative or are inadequate to test it. Principal among the limitations are the inadequate sample sizes relative to the questions asked, inappropriate quantitative analysis of the data, assumptions of Pleistocene and Holocene human demographic stability, *a priori* assumptions as to the phylogeny involved (which they then fail to reject), and/or assumptions of uniform phylogenetic processes over vast geographic areas and tens of millennia [see Wall (2000) and Relethford (2001a)]. Indeed, given the complex demographical, geographical and phylogenetic histories of human populations over the past 30 millennia, as well as the sample sizes needed for a statistically significant analysis (Wall, 2000), it is unclear to what extent extant human molecular data will ever be able to tell us more than that modern human genetic variation probably emerged to a large extent (but not exclusively) in some part of Africa.

Recently, these Out-of-Africa with full replacement arguments have been supplemented with analyses of fragmentary mitochondrial DNA extracted from at least five Neandertal specimens (Kriings et al., 1997, 1999, 2000; Ovchinnikov et al., 2000; Scholz et al., 2000), three of which have mtDNA sequences and two are based on DNA hybridization. These analyses have documented Neandertal DNA outside of living human ranges of variation, and quantitative treatments of them have been used to argue for the complete phylogenetic demise of the Neandertals. However, it has been shown that the sequence contrasts with those of extant humans do not exclude an interpretation of admixture (Nordborg, 1998), that the magnitude of difference between the Neandertal sequences and those of recent humans are well within the ranges of variation found within other species of living large-bodied hominoids (Gagneux et al., 1999; Relethford, 2001a), and that the lack of affinity to specific extant human regional groups has no bearing on the issue if some degree of admixture is allowed (Relethford, 2001b). In addition, phylogenetic reanalysis of the fossil sequences, using more dynamic assumptions regarding nucleotide substitutions and eliminating possible biases in the reference samples (Gutiérrez et al., 2002), does not support a separation of Neandertal mtDNA from that of recent humans. Indeed, the principal group sequencing DNA from Neandertal fossils has acknowledged that their results can tell us little about the level of admixture between Late Pleistocene human populations (Tschentscher et al., 2000; Serre et al., 2001).

Moreover, the criteria for excluding modern human contaminating DNA after PCR amplification of the extracted DNA [DNA within modern human ranges of variation is by

definition contamination (Krings et al., 2000)] biases any distributional analysis of the fossil DNA. Since almost all individual Neandertal anatomical features are found among modern humans, albeit sometimes in very low frequencies (or vice versa), it would not be surprising to find some overlap between Neandertal and modern human DNA sequences, whatever their phylogenetic relationships were. This technique therefore inappropriately assumes *a priori* complete separation of Neandertal and modern human DNA sequences; such an assumption makes any distributional (and hence evolutionary) analysis of the fossil DNA invalid.

Additionally, this difficulty makes it problematical to establish that one has extracted endogenous DNA from an early modern human unless, as in the case of Mungo 3 (Adcock et al., 2001), the extracted DNA should fall outside of the documented range of variation of extant humanity. It is uncertain whether the DNA hybridization applied to the Aurignacian Vogelherd 3 humerus (Scholz et al., 2000) correctly identified endogenous DNA (Cooper and Poinar, 2000). The other two analyses of earlier Upper Paleolithic human DNA, those of the Paviland 1 and the Sungir 2 and 3 Gravettian specimens (Sykes, 2000; Poltaraus et al., 2000) yielded mtDNA sequences that are common among extant Europeans; given that all three specimens have been handled by numerous individuals since their discoveries and that *a priori* biochemical techniques, especially with the use of PCR, are inadequate to completely exclude the possibility of modern human DNA contamination when the expectation is a sequence within living human ranges of variation (Hagelberg, 2000; Cooper and Poinar, 2000; Serre et al., 2001), these results must be regarded as preliminary [as acknowledged by Sykes (2000) and Poltaraus et al. (2000)].

Consequently, samples of Neandertal DNA will never be sufficient to resolve the replacement versus assimilation debate concerning modern human emergence in Europe (Wall, 2000); they may allow us to say whether some living peoples have Neandertal ancestry, but that is a question of extant human pedigree and of no relevance to assessments of Late Pleistocene human evolution. The issue at stake is *not* whether evidence of Neandertal ancestry can be found in present-day Europeans, but whether such evidence exists among early Upper Paleolithic Europeans. Only if total population continuity in the absence of genetic drift for the last 30,000 years of European prehistory and history is assumed can the two issues be considered as one, and that assumption is completely unwarranted.

Most recently, these biological and paleontological considerations have been joined with reassessments of the chronological relationships between late archaic and early modern humans within Europe. Reconsiderations of key sites across Europe (d'Errico et al., 1998; Zilhão and d'Errico, 1999) indicate that industries securely attributed to the Aurignacian *sensu strictu* (frequently associated *a priori* with early modern humans) spread across most of Europe between ca.36 000 and ca.37 000 years BP (see Chapter 33). However, anatomically diagnostic and well-dated early modern humans in Europe do not appear before ca.34 000 years BP (Smith et al., 1999; Richards et al., 2001; Churchill and Smith, 2000b), and the makers of the Aurignacian prior to that time are known from incomplete remains [arguments that all of the Aurignacian must have been made by the same kind of human, hence early modern humans, are logically unwarranted (Zilhão and Trinkaus, 2001)]. Moreover, as noted by Garralda and Vandermeersch (2002), the fragmentary human remains securely dated prior to ca.33-34 000 BP would fit comfortably within the ranges of variation known for later Middle Paleolithic Neandertals, making it possible that late Neandertals were responsible for much of the pre-34 000 BP Upper Paleolithic.

Furthermore, it is apparent that both the Middle Paleolithic and Neandertals persisted in Iberia south of the Ebro Valley [the Ebro Frontier (Zilhão, 2000); see also Chapter 33] until ca.30 000 BP (Vega Toscano, 1990; Villaverde and Fumanal, 1990; Zilhão, 1993, 2001c; Hublin et al., 1995; Walker, 2001b), and that Neandertals associated with initial Upper Paleolithic industries were present in south-central Europe until ca.28-29 000 BP (Smith et al., 1999) and in France until ca.36 000 BP (Mercier et al., 1991; Hublin et al., 1996; Zilhão and d'Errico, 1999) [the purportedly late date for the Mezmaiskaya 1 Neandertal child (Ovchinnikov et al., 2000) is in contradiction with the stratigraphic context of the burial (Golovanova et al., 1999)]. Therefore, regardless of who were the makers of the earliest Aurignacian, it is apparent that the latest Neandertals and the earliest modern humans in Europe overlapped by several thousand years, both indicating the ability of the Neandertals to persist despite competition from early modern human populations (Hublin et al., 1995; Smith et al., 1999) and providing abundant opportunities for genetic exchanges (Smith et al., 1999; Churchill and Smith, 2000b).

There has also been a growing body of paleontological data (Smith and Trinkaus, 1991; Frayer, 1993; Franciscus, 1995; Holliday, 1997a; Stefan and Trinkaus, 1998b; Wolpoff et al., 2001; Trinkaus, pers. observ.) that supports some degree of morphological continuity between the Neandertals and European early modern humans. These involve aspects of cranial and mandibular shape, nasal aperture morphology, incisor shape, and body proportions, and they generally concern distributions of traits in European early modern humans that place them between the Neandertals and the presumed ancestral form represented by specimens from Qafzeh, Skhul and Omo-KHS in those features, if in most respects closer to the presumed ancestral early modern human form.

The emerging consensus from this brief summary of the relevant aspects of the paleoanthropological and extant human records is that, at least within the western Old World, early modern humans emerged somewhere in northeastern Africa in the early Late Pleistocene or possibly late Middle Pleistocene, and they subsequently dispersed, for reasons poorly understood, through the Near East and across Europe. In the process of that spread, it appears that those dispersing early modern humans variably absorbed or replaced regional populations of Neandertals, in a complex process extending over several millennia. The degree of admixture/assimilation and its temporal and geographic distributions within Europe remain uncertain and debated. However, a significant number of the primary human paleontologists working on this issue have either proposed some degree of Neandertal assimilation into early modern human populations in Europe (e.g., Bräuer, 1989, 2001a; Smith and Trinkaus, 1991; Frayer, 1993; Smith, 1994; Simmons, 1994; Wolpoff et al., 2001) or have acknowledged the possibility of such admixture (e.g., Hublin, 1990, 2000; Stringer, 1989, 1994, 2001; Gambier, 1992; Vandermeersch, 1995; Bräuer and Stringer, 1997). And analyses of both extant and fossil human DNA support and/or do not contradict this interpretation (Nordborg, 1998; Jorde et al. 1998; Harding et al., 2000; Wall, 2000; Relethford, 2001a; Templeton, 2002). Ironically, what has emerged is little more than an Assimilation Model of modern human phylogenetic emergence, one which is primarily more comprehensive, more global and more thoroughly documented than those first proposed two decades earlier.

It is therefore this framework into which the phylogenetic implications of the Lagar Velho 1 morphological mosaic should be placed. More specifically, does Lagar Velho 1 provide additional data to support an Assimilation Model of the early modern human spread in Europe, as has been proposed (Duarte et al., 1999)?

Relevant Comparative Samples

As discussed in Chapter 16, the relevant samples for the assessment of evidence of Neandertal - early modern human admixture in the Lagar Velho 1 remains are: 1) preceding European Neandertals, and 2) roughly contemporaneous European early modern humans. These are the only lineages that could have reasonably been directly ancestral to Lagar Velho 1, given the chronological position of the specimen and geographical constraints in the cul-de-sac of southwestern Europe. No other lineage could have served as its ancestor without leap-frogging in time and/or space over one or the other of these groups.

It is well recognized that the ideal samples for this analysis would be western European, especially southwestern European, Neandertals and early modern humans pre-dating 25 000 years BP from the same region. However, Iberian Neandertal remains are fragmentary and relatively rare, consisting of isolated crania, mandibles, teeth and a few limb bones, only two of which (Devil's Tower 1 and Piñar 3) are juveniles. There are no associated Neandertal skeletons from south of the Pyrenees, and the closest ones in time and space would be those of southwestern France, especially the Châtelperronian Saint-Césaire 1 partial skeleton but also the later Middle Paleolithic ones from La Chapelle-aux-Saints, La Ferrassie, and Roc de Marsal. Early modern humans are even less common and more fragmentary from Iberia, being essentially unknown before the Solutrean; the only pre-Solutrean remains appear to be the lost fragmentary ones from El Castillo (Garralda, 1989; Straus, 1992) and an occipital from Malladetes (Arsuaga et al., 2001a). The closest ones in time and space are the late Aurignacian remains from La Quina and Les Rois, the Aurignacian or Gravettian remains from Cro-Magnon, the unpublished Gravettian remains from Cussac (Aujoulat et al., 2001), Gravettian remains from northwestern Italy, and the partial skeleton from Paviland.

As a result of this paucity of directly relevant human remains, both of these samples can be augmented by including morphologically and temporally similar human remains from across Europe, but it is necessary to restrict the Neandertals to those from the early last glacial (OIS 4 and OIS 3) and the early modern humans to those at least before the last glacial maximum (ca. 20 000 years BP). More distant samples in time and space can be relevant, but only for providing either out-groups or a general comparative framework for morphological patterns and developmental trajectories among robust Pleistocene *Homo*. In this sense, the Qafzeh-Skhul sample, with its large number of immature specimens, becomes particularly appropriate. It also provides a general reference for the probable initial Out-of-Africa ancestral form.

The choice of these potential "ancestral" samples parallels conceptually what would be used reasonably for assessing microevolutionary population relationships within the later Holocene. For example, if one wanted to assess degrees of admixture between Moors and Portuguese during the Islamic period, the reference samples would be preceding Portuguese and their contemporaneous northwestern African populations. Samples from further afield would serve only to provide an out-group framework for assessing the degree of difference between the samples in question.

Consequently, the relevant reference samples for the evaluation of the morphological mosaic of Lagar Velho 1 are the European Neandertals and early modern humans, plus other samples (fossil and recent) to assess aspects of development, normal variation, underlying biology, and integration.

The Lagar Velho 1 remains are those of a juvenile who died approximately during the fifth year postnatal, and most assessments of morphological affinities are based on comparisons of mature individuals from the relevant samples. This has led to comments that it is difficult to assess phylogenetic issues based on an immature specimen, and that any such interpretations are consequently questionable (e.g., Tillier, 2000). However, it should be kept in mind that it is not unusual for immature specimens to provide major amounts of phylogenetic and paleobiological information in hominid paleontology (e.g., Taung 1, Olduvai Hominid 7, KNM-WT 15000, Peking/Modjokerto 1, ATD6-69, Qafzeh specimens). Moreover, and more directly applicable to the issues here, there is an extensive literature documenting the importance of the analysis of both Neandertals and early modern human immature specimens for our assessments of the biological similarities and differences between these two groups (e.g., Fraipont, 1936; de Lumley, 1973; Heim, 1982b; Tillier, 1983a, 1987, 1999; Hublin et al., 1987; Tompkins and Trinkaus, 1987; Minugh-Purvis, 1988, 1998; Madre-Dupouy, 1992; Rak et al., 1994; Mallegni and Trinkaus, 1997; Dodo et al., 1998; Stringer, 1998; Maureille and Bar, 1999; Golovanova et al., 1999; Elyaqine, 1999; Krovitz, 2000; Minugh-Purvis et al., 2000; Ishida and Kondo, 2001; Ponce de León and Zollikofer, 2001).

Yet, it is fully recognized that many aspects of morphology change during growth and development, and that the proportions of structures relative to each other can change markedly during immature life. Indeed, one of us (ET) has previously assessed a variety of aspects of this question in both recent and Pleistocene human remains (e.g., Tompkins and Trinkaus, 1987; Ruff et al., 1994; Tardieu and Trinkaus, 1994; Mallegni and Trinkaus, 1997), extensive literature is available for many of the features in question here, and we have provided in the comparative regional anatomical chapters above a variety of data and references documenting aspects of these developmental changes.

Moreover, each anatomical system needs to be evaluated on its own terms, since different systems develop at contrasting rates; some appear in the mature form (e.g., dental crowns), some achieve their mature form perinatally (e.g., temporal labyrinthine morphology), others change little and in predictable manners during development (e.g., suprainiac morphology, nasal aperture morphology, limb segment proportions, mandibular symphyseal orientation), some change markedly but the contrasts in morphological developmental trajectories appear early in development (e.g., many aspects of the facial skeleton), and others exhibit significant changes during development. This is all part of normal biology and to be expected. There are also other features (e.g., pollical phalangeal lengths and fibular diaphyseal morphology) for which we do not currently know the developmental trajectories in Neandertals and modern humans, and therefore they cannot be employed in phylogenetic assessments.

The assessment of these different patterns of development and the assignment of morphological features to developmental patterns is, and has to be, based on uniformitarian principles. In this, given the phylogenetic proximity of both Neandertals and early modern humans to extant humans, the uniformitarian sample of choice is recent humanity. Therefore, if a developmental pattern can be shown to exist among recent humans, it should be applicable to the Late Pleistocene fossil record unless paleontological data exist to contradict such an application. To date, none of the Late Pleistocene immature remains has been shown to contrast with normal modern human patterns of variation in their *developmental trajectories*, whatever the actual morphological form might be.

Arguments that the samples of immature Late Pleistocene Neandertals and/or early modern humans are inadequate to assess developmental patterns for those human groups

(e.g., Hublin, 2000; Tillier, 2000) are rarely appropriate. Indeed, the normal procedure (e.g., Tompkins and Trinkaus, 1987; Tillier et al., 1995; Mallegni and Trinkaus, 1997; Dodo et al., 1998; Tillier, 1999; Duarte et al., 1999; Cunha, 1999; Kondo and Ishida, 2001; Ponce de León and Zollikofer, 2001; see especially Chapters 17, 22, 25, 29 and 30 above) is to establish a growth pattern based on recent human samples and then to determine where the fossil immature specimens fall relative to that growth trajectory. It is statistically routine to then assess the degree of difference between the fossil specimen(s) and the recent human reference sample. For many, but clearly not all morphological complexes, there is a sufficient number of immature specimens to assess whether the sample in question falls on the same trajectory as the recent human reference sample and the direction of its deviation (if any). Moreover, the use of sufficiently large recent human immature samples increases statistical power and thus allows appropriate analyses of the fossil specimens.

Consequently, as discussed in detail in the preceding chapters for most of the morphological features of concern here, it is possible to assess whether the morphological configurations of Lagar Velho 1 align it more closely with one or the other of these reference samples, or whether there is too large an overlap in the known or expected ranges of variation (in a probabilistic distributional sense) between the reference samples to evaluate the affinities of Lagar Velho 1 for the feature in question.

Pathological Alterations and Development

It is of concern to assess whether the Lagar Velho 1 individual, other than its deceased state, sustained pathological lesions or developmental abnormalities that would have altered its morphological patterns. Although there are lesions on the specimen, all of them are minor. Moreover, there are several indications of normal developmental processes.

The dental remains exhibit no macroscopic developmental defects of the dental enamel (enamel hypoplasia), although there are minor ones at a microscopic level (Chapter 31). None of them indicates more than the most minor of systemic developmental insults. These are associated with minor transverse lines adjacent to the metaphyses of several of the long bones, especially of the lower leg and the feet (Chapter 31). There was a mild periosteal reaction on the external anterolateral mandibular corpus, but the new bone on the surface is thin and has not altered the adjacent contours of the mandible. And the left radius sustained a minor traumatic injury to its lateral midshaft, which altered the immediately adjacent cortical bone endosteally and subperiosteally but did not affect the remainder of the radial diaphysis (Chapter 31). All of these lesions are minor to trivial, and for the only one that altered the adjacent morphology (the radial injury), the morphological assessment can easily correct for the lesion.

There are several aspects of the axial and lower limb skeleton that are developmentally plastic and will reflect any abnormalities in postural or locomotor development. These involve the development of the sinusoidal curve of the iliac crest, of the torsional curvatures of the ribs, and of the angular orientations of the femoral neck, the femoral condylar metaphysis, the tibial condylar metaphysis, the metatarsal heads and the hallucal phalanges. They also include the trabecular patterns of the proximal femora and tibiae. All of them indicate fully normal patterns of development for an active juvenile (Chapters 27 to 29). In addition, the diaphyses of the femora and tibiae exhibit levels of robusticity which are similar to those of other Pleistocene juvenile lower limb bones once they are appropriately scaled for the body and limb segment proportions of the individual (Chapter 29). This is confirmed by the low level of asymmetry of those diaphyses, indicating normal balanced loading of the lower limbs.

The various indications of developmental status, including cranial synchondrosis formation and fusion, epiphysis formation and metaphyseal morphology, are all in agreement with the estimated age-at-death from the dentition of the second half of the fifth year post-natal (Chapter 15). There is a slight delay in the formation of a few of the epiphyses, but all of them appear to be well within normal recent human ranges of variation, especially given the margin of error in the dental age assessment. There is a modest delay relative to early modern humans and most recent humans in the closure of the foramen of Huschke (Chapters 15 and 17), although it remains within the range of variation of the latter.

Consequently, even though Lagar Velho 1 sustained a set of the minor insults that are common to most recent human juveniles and must have been for Pleistocene children, there is nothing in the observable pathological lesions or the indications of postural and locomotor function to indicate anything other than a normally developing child.

Archeological Association

It has also been suggested (e.g., Raposo, 1999; Tattersall and Schwartz, 1999) that the Gravettian age and archeological associations of Lagar Velho 1 should have some bearing on the interpretation that it exhibits a mixture of Neandertal and early modern human ancestry. The similarities of its burial ritual, with abundant ochre and body ornaments, to those of Gravettian early modern humans across Europe have been especially noted. These archeological similarities have been used to argue that the child's social group was fully Upper Paleolithic in its behavior (something with which we agree) and therefore its ancestry must have been fully "modern" (with which we do not agree). This line of reasoning exhibits a profound confusion between human biology and culture, a linking of the two in a manner that was explicitly rejected in sociocultural anthropology a century ago. The archeological context of the child, other than providing a chronological and cultural context for the individual, has no bearing on any interpretations regarding its human phylogenetic significance (see also Chapter 33)

The Morphological Mosaic of Lagar Velho 1

The phylogenetic assessment of the morphological characteristics of Lagar Velho 1 involves dividing characters into those which are distinctively early modern human, those which are distinctively Neandertal, those which occur in higher frequencies among the former, and those which occur in higher frequencies among the latter. There are also a number of features discussed in the preceding chapters which the two reference groups share, either as ancestral traits or as shared derived features relative to earlier Early and Middle Pleistocene presumed common ancestors; those shared traits are not considered here. There is also a number of features for which the morphology is ambiguous, either due to fragmentation or unclear developmental trajectories; these aspects are not considered here although they are discussed in the preceding chapters.

Any such division of traits into these polarities is to a degree artificial, since we know that the individual lived for half a decade as a functioning human. Therefore, the characters must have been biologically integrated and not put together into some form of a chimera. Moreover, it is unlikely that all of these traits were biologically independent, given the constraints of functional and structural integration and forms of pleiotropy. However, except in

a few cases, we do not know these patterns of integration. The traits are therefore presented largely as separate entities, with possible patterns of integration discussed as appropriate. The relative distributions of the traits between the categories will be considered, but it would be fallacious to treat them all as independent characters in any quantitative assessment of the individual's affinities.

It is also difficult to conceptualize these traits in all cases as simply early modern or Neandertal in a European context, if indeed some degree of admixture took place between Neandertals and in-dispersing early modern humans to the north and east of western Iberia. If some degree of assimilation of other European Neandertal populations had taken place, then those early modern human populations dispersing south of the Ebro Frontier already had both early modern human and Neandertal ancestry. If the assimilation was sufficiently large or recent to lead to the presence of some Neandertal traits in those early modern human populations, it may well have obscured the ultimate polarities of some of the traits in question. Such a mixture of "Neandertal" and "early modern human" features in the populations dispersing across the Ebro Frontier would bias the analysis toward minimizing the perceived mix of characters in Lagar Velho 1, since it would reduce the morphological distance between the Neandertals and Gravettian early modern humans and make "Neandertal features" appear less distinctive of the Neandertals. Indeed, for this reason several of the features listed as occurring in higher frequencies among the Neandertals may well have been distinctive Neandertal features had such prior admixture not taken place.

Characteristics Indicating Early Modern Human Ancestry

As previously noted (Trinkaus et al., 1999b), Lagar Velho 1 is principally a "modern human child with genetically-inherited Neandertal traits." Consequently, the majority of the diagnostic traits preserved on the skeleton align it with European early modern humans. These traits include a series of cranial features (Chapters 17 to 20 and 22), mandibular aspects (Chapter 21), a couple of dental ones (Chapters 23 and 24), and a few postcranial aspects (Chapters 28 and 30).

The overall cranial shape, including the relative cranial breadth, are similar to those of early modern humans. The supraorbital region lacks the swelling for the incipient supraorbital torus seen in Neandertal juveniles. The mastoid processes are both large, making them especially similar to European early modern humans, and they project laterally from the coronal contour of the neurocranial vault, rather than rounding inferomedially as do those of the Neandertal immature and mature temporal bones. The auditory meatus is not diagnostic in its oval shape, but the anterosuperior to posteroinferior orientation of the major axis of the meatus is similar to those of recent humans and contrasts with the orientation of the major axis of ovoid Neandertal meatus. The auditory ossicles are modest in size and morphologically similar to those of early and recent modern humans. In the nasal region, the pre-maxillary suture is fully fused and obliterated, and the nasal height and breadth are modest, both of which align it with Upper Paleolithic early modern humans. In addition, the nasal aperture is piriform rather than squared (in contrast with the derived Neandertal pattern), and the inferior nasal aperture margin is convexly rounded anteroposteriorly, providing a sub-nasal gutter, a configuration present in some European early modern humans but absent from the last glacial Neandertals [a rounded margin is present in earlier European and non-European archaic *Homo*, but not in the early last glacial Neandertals (Franciscus, 1995)]. And the interorbital breadth is rather small for all of the samples but closest to the early Upper Paleolithic one.

The Lagar Velho 1 mandible is most notable for its prominent *mentum osseum* with a clearly projecting *tuber symphyseos* and strongly projecting lateral tubercles. Together these form a prominent *trigonum mentale* (*tuberculum laterale* and *tuber symphyseos*). The evolution of the modern human chin is one of the differential development of the portions of the *trigonum mentale* and other associated features of the *mentum osseum*, and not the evolutionary appearance of novel features, since most of these detailed aspects of the “chin” are present in both immature and mature Neandertal mandibles, as well as in some earlier archaic *Homo* specimens (Mallegni and Trinkaus, 1997; Dobson and Trinkaus, 2002). What aligns the Lagar Velho 1 anterior mandibular symphysis with a minority of European early modern humans and especially more recent humans is the *size* and *projection* of these features, and not merely their presence.

In addition, the Lagar Velho 1 mandible exhibits a narrow anterior dental arcade, one which is narrow relative to both those of immature Neandertals and those of juvenile early modern humans. It is likely that this is related to the relative dimensions of the permanent mandibular anterior teeth, since at least the I_2 of Lagar Velho 1 is relatively small and its size relative to the M_1 is well within early modern human ranges of variation and separate from the Neandertal distribution. In addition, the maxillary incisors exhibit moderate double-shoveling, which is relatively rare among European early modern humans and is unknown among the Neandertals with their mesiodistally strongly convex labial maxillary incisors.

The two distinctly early modern human postcranial traits relate to body laterality, clavicular length and pubic breadth. The relatively short clavicle of Lagar Velho 1 distinguishes it from the long ones of Neandertal adults and at least one Neandertal child, and the relatively mediolaterally short superior pubic ramus contrasts with the longer ones of immature Neandertals. The other postcranial similarity to early modern humans and contrast with the Neandertals, femoral robusticity (when scaled only to femoral length), relates to these body proportions, since it reflects habitual baseline load levels on the lower limbs from the body core; a narrow trunk reduces the load levels and hence the femoral robusticity for a given overall level of activity. Since Neandertal and European early modern human adults have similar levels of femoral and tibial diaphyseal robusticity once body proportions are taken into account (Trinkaus et al., 1999c; Ruff et al., 2000), and their neck-shaft angles (reflecting immature locomotor load levels) are the same (Trinkaus, 1993b), it is expected that their juveniles would have had similar activity levels.

Characters Indicating Neandertal Ancestry

There are only a few aspects of the Lagar Velho 1 skeleton which are clearly distinctively Neandertal in their configurations (Chapters 17 and 25). The semispinalis capitis fossae on the occipital bone are strongly marked and clearly separated along the midline; this is in contrast to the early modern human arrangement in which they are both more modest in development and meet along the midsagittal line. In addition, the large projection of the juxtamastoid eminence, when measured from the Frankfurt horizontal and considered separately from the large and bulbous mastoid process, aligns Lagar Velho 1 with the Neandertal juveniles and separate from early modern human juveniles; it is only much older early modern human immature specimens who match the juxtamastoid projection seen in both of the temporal bones of Lagar Velho 1.

The crural proportions, or tibial to femoral length proportions, of Lagar Velho 1 (the first Neandertal feature to be noticed on the remains) are distinctively within the Neandertal

range compared to juvenile specimens of both groups, and its predicted adult value is close to the Neandertal sample mean even though the 95% confidence interval for it overlaps the lower end of the early modern human range of variation. A secondary effect of these limb segment proportions biomechanically, the relative levels of femoral versus tibial robusticity (measured solely relative to bone length), fully aligns Lagar Velho 1 with the Neandertals (Chapter 29).

The short distal limb segment of Lagar Velho 1 lower limb is unlikely to be the result of either developmental plasticity or short-term evolutionary changes. As discussed in Chapter 25, nutritional effects are unlikely to have short-term effects on these limb segment proportions, and short-term climatic stress during development, although it can alter overall body size and proportions, does not produce any consistent effects on limb segment proportions. Moreover, as mentioned in Chapter 25, it is also very unlikely that these crural proportions could have occurred as a result of short-term (genetic) adaptation to last glacial climates in coastal Portugal (*contra* Stringer, 2001). There are immature and mature Gravettian human remains from between 24 000 and 27 000 years BP from coastal Wales (Paviland), the central European plain (Dolní Věstonice) and northern Russia (Sunghir), all of which experienced considerably colder temperatures than western Iberia throughout OIS 3 (van Andel, 2002). Yet, all of the individuals from these sites exhibit high (tropical) crural indices (Holliday, 2000b; Kozlovskaya and Mednikova, 2000; Sládek et al., 2000), indicating little if any adjustments in limb segment proportions (developmental or genetic) to cold stress during the first 10 millennia after the establishment of early modern humans in these regions.

In addition, the “cold adapted” body proportions of Lagar Velho 1 are reflected principally in the relatively short tibiae and fibulae and their diaphyseal robusticity, and to a lesser extent in its brachial proportions (Chapter 25), whereas aspects of the trunk indicate relatively “warm-adapted” proportions; even though some mosaic of changes in these proportions has been documented in other Gravettian remains (principally in trunk breadth in the opposite direction) (Holliday, 1997a, 2000b), none of them has the degree of contrast seen in Lagar Velho 1. It appears unlikely that one portion of the body (the distal legs and to a lesser extent the forearms) would respond to short-term climatic adjustment whereas the rest (body breadth) would not.

There are two other aspects of the skeleton that might be considered as distinctive Neandertal features, the presence of a suprainiac fossa and the retreat of the anterior mandibular profile. The former has been considered to be a uniquely derived Neandertal feature (Santa Luca, 1978; Hublin, 1978b; Stringer and Hublin, 1999), and it is entirely absent from the two European earlier Upper Paleolithic early modern human juvenile occipital bones; however, the presence of similar features in a minority of early modern humans means that it should conservatively be considered among features occurring more commonly among the Neandertals. Similarly, although the anterior symphyseal angle of Lagar Velho 1 is significantly outside of the early modern human range of variation (Chapter 21), it is approached by Předmostí 2 mandible (but see below) and is therefore not considered to be distinctively Neandertal.

Characters Which Occur in Higher Frequencies Among Early Modern Humans

The Lagar Velho 1 remains exhibit several features that occur (or are likely to occur) in both samples but are more common or more strongly expressed in the European early modern human sample (Chapters 17, 21, 23 and 29).

The first of these features is the degree of sagittal, or bregma-lambda, curvature; although both of these Late Pleistocene samples are relatively platycephalic, the early modern human one is less so and Lagar Velho 1 is closer to it. One feature that reflects the relative shortness of the Lagar Velho 1 facial skeleton, maxillary zygomatic root position at the dm^2 , places it closer to the early modern human juveniles but not fully separate from the Neandertals. However, a parallel reflection in the mandible, the mental foramen at the dm_1 , does not distinguish the immature samples (as it does the mature ones) and therefore provides little information on facial projection in these juvenile specimens. The labyrinthine morphology, although close to the Neandertal pattern in some aspects, is more closely aligned with the modern human pattern.

In the mandible, the mandibular notch shape is largely symmetrical, and there is no trace of a distinctive superior medial pterygoid tubercle. Both configurations are known for Neandertals (immature and mature), but they occur more commonly among early modern humans. And the absence of a mid-trigonid ridge on the M_1 is more common among early modern humans, as are the modest shoveling and lingual tubercles of the maxillary incisors.

Two upper limb features place Lagar Velho 1 closer to its early modern human contemporaries but do not completely distinguish it from the Neandertals. These include the anterior rotation of the radial tuberosity and the absence of an opponens pollicis crest on the first metacarpal. Interestingly, one of the Neandertals to exhibit a more anteriorly rotated radial tuberosity is the Saint-Césaire 1 Châtelperronian specimen, suggesting that this feature may not separate late Neandertals from early modern humans. The modest radial lateral curvature of Lagar Velho 1 appears to align it more with more mature early modern humans, but it does not distinguish it from juvenile Neandertals and is therefore not included among these features.

Characters Which Occur in Higher Frequencies Among Neandertals

A similar number of features of Lagar Velho 1 place it closer to, but not exclusively with, the Neandertals (Chapters 17, 21, 25, 29 and 30). In the neurocranium, these include the anteriorly dominant meningeal sulci on the parietal bones, the presence of a suprainiac fossa, and the vertical position of the posterior zygomatic root relative to the auditory meatus. Even though the suprainiac fossa has been considered a distinctive Neandertal feature, it is considered here conservatively as only a Neandertal-like feature given the rare presence of similar features among early modern humans. In the superior facial skeleton, the thickening of the supraorbital margin is close to those of Neandertal juveniles and is at the robust end of the range of variation of early Upper Paleolithic juvenile specimens, whereas the frontal process of the zygomatic bone is strongly built (Chapter 17).

The otherwise modern appearing mandible is exceptional for its degree of anterior symphyseal retreat, a degree that is all the more marked if one takes into account the strongly projecting *mentum osseum*. Were the *mentum osseum* reduced in size, similar to those of Miesslingtal 1 and La Quina 25, as well as of the older Les Rois 1 and Sunghir 2, the anterior angle would be even further from those of the other early Upper Paleolithic early modern Europeans. Yet, it is possible (but not ascertainable) that the Předmostí 2 mandible had a similar degree of retreat, but if so, it would clearly be at the low end of the range of variation otherwise documented for European early modern human juveniles; it is for this reason that this feature is listed here as “Neandertal-like” rather than distinctively “Neandertal” (alternatively, it remains possible that the configuration in the Předmostí 2 mandible indicates

previous admixture in central Europe and that this feature should in fact be considered as a “Neandertal” trait).

In the postcranial remains, three features of the upper limb, the degree of development of the pectoralis major tuberosity on the proximal humeral diaphysis, the modest brachial index, and the pronounced ulnar deviation of the distal pollical phalanx, place Lagar Velho 1 closer to the Neandertals. And in the lower limb, the degree of tibial condylar posterior displacement is marked, as it is in Neandertals and more so than in European early modern humans.

The Nature of the Mosaic

In addition to the polarities of these various traits towards early modern humans or the Neandertals in the Lagar Velho 1 child, the nature of the mosaic for several complexes suggests an unusual combination of its ancestry. For example, the mastoid process is distinctly modern in its size and shape, but the juxtamastoid eminence is close to those of the Neandertals. The general supraorbital configuration is distinctly modern, but the degree of hypertrophy of the superior orbital margin and the frontal process of the zygomatic bones is archaic. The crural index aligns it with the Neandertals, but the indications of body breadth place it among the early modern humans. And the *mentum osseum* is derived in a modern human form, yet the symphyseal retreat aligns it with archaic humans.

These combinations of features, which are expected to generally covary given documented morphological patterns and, in some cases, underlying biology, are unusual. Some of them could be the products of individual variation or mosaic evolution during the European Upper Paleolithic, but to find a suite of disjunctions in expected combinations of associated features suggests more than just individual variation.

The Ancestry of the Lagar Velho 1 Morphological Mosaic

From this complex list of features of Lagar Velho 1 and their affinities to either Neandertals or European earlier Upper Paleolithic early modern humans, it is apparent that the morphological mosaic is real. Moreover, the features derive from various aspects of the skeleton and dentition, such that appropriate functional and structural integration might reduce the number of features, but it would not eliminate the mosaic. The mosaic is sufficiently documented not to be wished away.

A few of these features are potentially developmentally plastic, and the exact configuration seen in Lagar Velho 1 may well reflect some complex interaction between the individual's genotype and its environment prior to death. However, most of them are minimally altered by the environment except in cases of pathological lesions (not an issue here - see above), and the most plastic of them (femoral and tibial robusticity) must reflect a baseline due to body size and proportions combined with normal posture and locomotion.

Since evolution consists of changing distributions of characters (however delimited), and since such distributions can only be assessed in a probabilistic framework, it is appropriate to view this morphological mosaic in such a probabilistic framework. In other words, if the null hypothesis is that Lagar Velho 1 is simply a European Gravettian early modern human juvenile (i.e., H_0 : Lagar Velho 1 = European Gravettian early modern human juvenile), is it possible to reject this hypothesis?

We do not have (and will never have) adequate paleontological samples to assign precise numerical probabilities to each of the configurations seen in the Lagar Velho 1 remains. However, it is apparent that the probabilities of each set of (presumably) independent traits should multiply to produce the ultimate result. One can therefore assign probabilities to each of the traits listed above. It is fully recognized that there is a degree of arbitrariness in this exercise. However, since the Lagar Velho 1 morphological mosaic must be assessed in a probabilistic framework, any distortion engendered by this exercise is outweighed by the emphasis on the distributional and probabilistic nature of the assessment.

Given the H_0 that Lagar Velho 1 is a normal Gravettian early modern human, the probabilities should be 1.00 for the “early modern human” traits and 0.00 for the “Neandertal” ones. Probabilities of 0.75 and 0.25 can be assigned respectively to the “early modern human like” and “Neandertal like” ones. One can also conservatively condense some of the traits that might be linked (e.g., delete femoral and tibial robusticity since they reflect body proportions, combine dental arcade and anterior-posterior dental proportions, combine supra-orbital margin and zygomatic frontal process thickening, and merge overall cranial shape and relative cranial breadth).

The initial result is as follows. The probability of Lagar Velho 1 representing a normal European Gravettian early modern human juvenile is: 0.00. The presence of any distinctive Neandertal feature is therefore sufficient to exclude Lagar Velho 1 from being expected within the normal distribution of European early modern humans.

However, since one could argue based on the limited sample sizes that the few “Neandertal” features do not have a $P = 0.00$ but rather one somewhat above that, they can then be conservatively assigned a $P = 0.10$. Note that any such adjustments bias the results in favor of accepting the null hypothesis. Yet, using $P = 0.10$ for the Neandertal traits, 0.25 for the Neandertal-like traits and 0.75 for the early modern human traits still provides a highly significant rejection of the null hypothesis, with a $P = 2.86 \times 10^{-10}$.

One could more conservatively only consider those traits that have been classified as “Neandertal” or “Neandertal-like”. This provides a $P = 3.81 \times 10^{-9}$. Or, if one considers that none of the traits is truly unique to the Neandertals and assigns probabilities of 0.25 to each of the “Neandertal” and “Neandertal-like” features and ignores the “early modern human” ones (the same as giving the last all $P = 1.00$), the resultant P-value remains low, at $P = 5.96 \times 10^{-8}$. These values are certainly exaggerated by the number of traits involved, since they are the products of the individual assigned probabilities. However, if one extremely conservatively assigned a probability of 0.50 to each of the “Neandertal” and “Neandertal-like” features, and probabilities of 1.00 to the “early modern human” ones, the resultant P-value is 2.44×10^{-4} . This value is still very low and indicates a clear rejection of the null hypothesis that Lagar Velho 1 represents a normal early modern human. Consequently, adjustments in the assigned probabilities might reduce the level of significance, but they are unlikely to make it other than highly significant.

Lagar Velho 1 is therefore extremely unlikely to be an individual randomly sampled from a representative European Gravettian early modern human population. The same calculation for the null hypothesis that Lagar Velho 1 is a normal Neandertal yields an even lower P-value ($P = 2.86 \times 10^{-23}$), making it also extremely unlikely that this individual represents a normal Neandertal (a conclusion which was rejected from the beginning on the basis of derived modern human features in the skeletal remains).

Obviously these numbers are approximate, but they should be sufficient to demonstrate that both of these null hypotheses can be rejected in a probabilistic framework, and that this skeleton is not just another juvenile from one or the other of these European Late

Pleistocene human populations. The next step is to consider alternative scenarios. The influences of developmental age, abnormalities and short-term adaptation have been addressed above and rejected. The only other alternative of which we are aware is a mosaic of characteristics due to some combination of initial Upper Paleolithic early modern human and Neandertal ancestry in the Lagar Velho 1 individual.

The admixture interpretation of this individual's morphology, based on far less paleontological evidence than has been presented here, has been public for more than three years (de Sá, 1999; Duarte et al., 1999). Our challenge to the field was, in effect, that this is the most reasonable interpretation of which we can conceive: please provide us with testable alternatives that fit the data and human biology. The published responses to date have accepted our interpretation (e.g., Aguirre, 2000; Wolpoff et al., 2001; Adcock et al., 2001; Relethford, 2001a; Kaufman, 2001), equivocated regarding it (e.g., Hublin, 2000; Stringer, 2001), or misrepresented the paleontological data and/or our arguments (e.g., Tattersall and Schwartz, 1999; Cunha, 1999; Tillier, 2000) (we do not include quotes in the public media, since they are frequently incomplete and/or unreliable). No one has proposed an alternative interpretation that conforms to the data and acceptable biology. The admixture hypothesis therefore stands.

The Issue of Admixture

Admixture, interbreeding, population assimilation or (more appropriately in the case of distinct species) hybridization is a common phenomenon when distinct populations (or even subspecies) of a given species meet after long periods of complete isolation or isolation by distance. Whatever behavioral (cultural or non-cultural) differences might exist between the previously separate populations, these are rapidly overshadowed by basic underlying behavioral similarities and some level of admixture takes place. The only documented cases of true human populational separation when distinct groups come into contact with each other are in recent historical cases of complex society human groups in which there are strong rules of endogamy and/or banishment of any offspring of admixture with neighboring groups. Non-human primates and other mammals do not incorporate such social rules.

Morphological analyses of admixture in human populations (e.g., Walter, 1981; Relethford and Lees, 1981; see Chakraborty, 1986) are able to document such admixture up to a millennium after its original occurrence. Indeed, one of the best examples of such admixture, that of the peopling of Iceland (Walter, 1981; Chakraborty, 1986), involves derivation from ancestral populations of northwestern Europe, none of whom differed markedly from each other in the global framework of modern humans. The degree of differentiation of the ancestral populations from Scandinavia and the British Isles was certainly far less than between the Neandertals and Gravettian early modern humans, yet morphologically it has been possible to document the previous populational admixture a millennium later.

Population genetic assessments of human and non-human population admixture (e.g., Walter, 1981; Chakraborty, 1986; Long et al., 1991; Bertorelle and Excoffier, 1998; Parra et al., 1998, 2001) provide more detailed assessments of the original or ongoing patterns of admixture and are able to document the persistence of ancestral population characteristics at least a millennium after the period of initial population contact and admixture, even given continued admixture between culturally defined groups.

At the same time, there is a growing literature on interspecific and intersubspecific hybrids among non-human primates [the issue of specific versus interspecific hybridization

is increasingly a semantic one, since evidence of hybridization with fertile and viable offspring is frequently taken as an indication of conspecific status (the Biological Species definition per Mayr, 1963) and hence a shift of what would have been called interspecific hybridization to labels of intersubspecific hybridization or intraspecific admixture]. Documented cases usually involve contact between previously separate populations as a result of geographical changes in ranges due to natural or humanly-induced processes or as a result of ecological disturbance from either human or natural causes. They also occur along ecological gradients in which two species (or subspecies) remain largely separate but overlap in a “hybrid zone” due to contrasting ecological preferences. Cases in captivity are also documented. The interspecific cases in the wild involve species of *Hylobates* (Brockelman and Srikosamatara, 1984; Marshall and Sugardjito, 1986), *Papio* (Kummer, 1971; Nagel, 1973; Phillips-Conroy and Jolly, 1986), *Macaca* (Bynum et al., 1997; Schillaci and Froehlich, 2001), *Callithrix* (Coimbra-Filho et al., 1993) and *Saguinus* (Coimbra-Filho et al., 1993). Intraspecific, or intersubspecific, hybrids are known in the wild for populations of *Lemur* and *Varecia* (Tattersall, 1993; Vasey and Tattersall, 2002) and *Saguinus* (Cheverud et al., 1993; Peres et al., 1995). In addition, intergeneric and fertile hybrids have been documented for *Papio* and *Theropithecus* (Markarjan et al., 1974; Jolly et al., 1997). This partial list of non-human primate hybrids is sufficient to document that such admixture or hybridization is not uncommon when the appropriate circumstances for its occurrence arise [see Jolly (2001) for an extensive discussion of both primate hybridization and its implications for human evolution].

Among other mammals, hybrids are well documented for species of *Canis* (Kolenosky, 1971; Mengel, 1971; Lehman et al., 1991), *Cervus* (Goodman et al., 1999 and references therein) and *Thomomys* (Patton, 1993), among others. And a variety of avian natural hybrids are known (Gray, 1958; Moore, 1977; Saino et al., 1992). Indeed, natural hybrids and associated hybrid zones are sufficiently common in vertebrates (including eutherian mammals) that their analysis is an important component of ongoing research to understand the processes involved in speciation, species divergence, and species persistence in a dynamic natural world (e.g., Harrison, 1993; Arnold, 1997; Allendorf et al., 2001).

Most of the literature is concerned with the behavioral, reproductive and (increasingly) molecular aspects of such hybrid zones, and relatively little is concerned with morphological characteristics. However, there are sufficient data from these hybrids to document what any cross-breeder of domestic animals or any observer of recently admixed modern human populations knows intuitively; namely, the physical characteristics of the subsequent generations exhibit a complex and usually unpredictable mixture of distinctive characters from both ancestral groups (directional dominance), as well as both intermediate characters (additive) and unique ones (over- or under-dominance) (Mengel, 1971; Nagel, 1973; Markarjan et al., 1974; Cheverud et al., 1993; Coimbra-Filho et al., 1993; Peres et al., 1996; Jolly et al., 1997; Bocheński and Tomek, 2000; Schillaci and Froehlich, 2001; Bynum, 2002). These traits may be in the external (dermal) features, in body proportions, in skull shape, postcranial size and shape, and/or dental proportions, and in most cases the degree of involvement of detailed features of the dentition or skeleton are unknown. However, it has been shown to be possible to distinguish galliform hybrids osteologically using a combination of discrete traits and osteometric values (Bocheński and Tomek, 2000). Moreover, even rare hybridization may result in significant, but apparently random, introgression of genetic alleles into the other population, with most individuals showing evidence of prior hybridization at a limited number of loci (Goodman et al., 1999), apparently thus providing the molecular basis for the observed morphological mosaics (see Jolly, 2001).

What emerges from these examples is that admixture, or hybridization, is rare but by no means exceptional among social primates (and other vertebrates) and that the resultant offspring, whether the F₁ generation or subsequent generations, exhibit a complex and usually unpredictable mixture of features. Given the unusual morphological mosaic of Lagar Velho 1 relative to both Neandertals and European early modern humans, and especially its complex mix of features that resemble one or the other of these potential ancestral groups, it fits closely the expectation (in a general sense) of what would occur should Iberian Neandertals and early modern humans have blended their populations when the latter dispersed south of the Ebro Frontier sometime after 28-30 000 years BP. Indeed, reasonable reconstructions of the human social landscape in Iberia after early modern humans spread into the peninsula suggest that it most likely represented a kind of cultural ecotone, not unlike the kinds of natural ecotones which are the locations of most natural hybrid zones (Moore, 1977; Patton, 1993).

The Implications of Lagar Velho 1 for the Phylogenetic Fate of the Neandertals

From these considerations of current perceptions of the phylogenetic emergence of modern humans in the Late Pleistocene, of the morphological mosaic of the Lagar Velho 1 remains, and from the occurrence and patterns of admixture among non-human primate and some other species, it is apparent that Lagar Velho 1 provides additional evidence for the assimilation of Neandertal populations into those of early modern humans during OIS 3 in Europe. This juvenile's skeleton provides paleontological evidence that, when early modern humans encountered indigenous Neandertal populations in at least one area of Iberia, those Neandertals were seen as potential mates and that offspring ensued.

From the frequent proposals over the past two decades that some degree of admixture occurred, or may well have occurred, when in-dispersing early modern humans encountered Neandertals across Europe, this interpretation should not be surprising. However, Lagar Velho 1 is the first reasonably complete and associated skeleton, providing data on almost all anatomical regions, to provide a clear indication of such admixture.

The primary implication of Lagar Velho 1 for the phylogenetic fate of the Neandertals, therefore, is that those late archaic humans were, to some extent, absorbed into the probably larger populations of early modern humans.

The broader implication of Lagar Velho 1 is a final rejection of the Late Pleistocene Out-of-Africa with complete replacement scenario for modern human emergence. A model of Out-of-Africa with admixture/assimilation, one that reflects the complexities of natural populational processes, appears to be the best and most comprehensive model for at least the emergence of modern humans in Europe.

Lagar Velho 1 also, hopefully, will help us to move beyond the simplistic, categorical and artificial phylogenetic models of modern human emergence that have dominated paleoanthropology for most of the past century, and to see this evolutionary period in the temporal, geographical and populational complexity that undoubtedly existed. Only then will we be able to look at the Neandertals and early modern humans as part of the evolutionary dynamic that led to more recent modern humans, and not merely as "us" versus "them".

ADDENDUM:

What Lagar Velho 1 Does Not Tell Us About Modern Humans and the Neandertals

The Level of Admixture

The Lagar Velho 1 skeleton documents some degree of admixture between Iberian Neandertals and early modern humans. It does not tell us what the frequency of that was within the local populations or the distribution of the admixture across Estremadura, Iberia or Europe. It merely documents its presence at some level greater than zero. As one of us stated a decade and a half ago:

once there is agreement that at least some Neandertals could have contributed to the gene pools of subsequent populations of early anatomically modern humans, it may not be possible to determine from the fossil record to what extent the Neandertals can be included in the ancestry of recent humans. (Trinkaus, 1984a: p. 259)

The Persistence of Neandertal Characteristics

Lagar Velho 1 does not tell us for how long Neandertal characteristics persisted in subsequent lineages of early modern humans in Europe. We know that Lagar Velho 1 had no descendants, unless it suffered from an extreme form of precocious puberty, which would be evident in skeletal abnormalities. The scarcity of distinctive Neandertal features in some regions of Europe five to ten millennia after the appearance of early modern humans in that region suggests that most of the direct evidence of Neandertal ancestry slowly disappeared in those regions. For this reason, we have no knowledge of whether there is direct Neandertal ancestry in extant Europeans. Given the complex population dynamics of even the past few millennia, we would doubt it very much. But this issue, as well as statements concerning it primarily from analyses of Neandertal and recent human DNA, is irrelevant to our understanding of the human population dynamics of Late Pleistocene Europe and the evolutionary processes which led to the disappearance of what we recognize as Neandertals.

Geographic Variation in the Degree of Assimilation

The evidence for Neandertal - early modern human admixture in southwestern Iberia tells us little about the presence/absence or level of such admixture elsewhere in the Neandertal range (or elsewhere in the Old World outside of the presumed northeastern African area of modern human emergence). It merely documents that it may well have occurred. Specifically, it indirectly supports arguments (e.g., Smith, 1984; Bräuer, 1989; Smith and Trinkaus, 1991; Wolpoff et al., 2001) for such Neandertal - modern human admixture in central Europe by showing that it may well have occurred given the opportunity. Indeed, the temporal overlap of late Neandertals and early modern humans in south-central Europe (Smith et al., 1999) presented that possibility.

Yet, even though Lagar Velho 1 makes such central European admixture more plausible, it does not inform us as to the level of such admixture or the persistence of “Neandertal” traits in the subsequent populations of early modern humans. The current evidence for such

Neandertal trait persistence (Smith and Trinkaus, 1991; Frayer, 1993; Holliday, 1997a) tends to be modest and primarily evident in the earliest early modern human remains, those with temporal overlap with the late Neandertals. By the time of Lagar Velho 1 (e.g., Brno-Francouzská, Dolní Věstonice, Pavlov), only a few Neandertal features persist.

Taxonomic Issues

The interpretation of Lagar Velho 1 tells us nothing about the formal taxonomic status of the Neandertals. Whether one chooses to include them within *Homo sapiens* or one resurrects “*Homo neanderthalensis*” for them is a matter of taste. It should ideally be a matter for biological analysis, but its resolution depends upon which characters one chooses to employ (one can always find a set to fall within or outside of the expected ranges of intraspecific variation), which species one chooses to employ for a standard for intraspecific variation, the model/definition of a species (reproductive, phylogenetic, behavioral or morphological) one prefers, whether one’s approach is phenetic or cladistic, and one’s personal tolerance for chaos in the fossil record. All of these are *a priori* criteria that are implicitly or explicitly employed before addressing the issue of *H. sapiens* versus “*H. neanderthalensis*.” The evidence for admixture (or hybridization if two species are represented) in Lagar Velho 1 only documents that interbreeding took place between these groups, not what their taxonomic status might have been. Consequently, *a priori* statements that the admixture interpretation is in error since the Neandertals and modern humans were not conspecific are logically inappropriate, since they decide the conclusion prior to the analysis of the paleontological data.

NOTES

- ¹ We would like to express our gratitude to the other contributors to this volume whose analyses of specific portions of the skeleton have made possible much of this interpretation. In addition, S.W. Hillson, T.W. Holliday, J.H. Relethford, K.R. Rosenberg, F.H. Smith, F. Spoor and C.B. Stringer critically read previous versions of it. However, the contents of the chapter reflect our interpretation of the Late Pleistocene hominid fossil record and the Lagar Velho 1 skeleton, and they do not necessarily reflect the views of the other contributors.
- ² This Replacement Model has metamorphosed for some researchers from an initial one invoking complete replacement of the Eurasian late archaic humans (including the Neandertals) in the Late Pleistocene to one in which there may have been genetic continuity between Neandertals and early modern humans in the Late Pleistocene but all of that Neandertal ancestry was lost prior to the present day. The original formulation was one that addressed human population dynamics in the Late Pleistocene, and it is that Replacement Model which is of concern here. The modified version is indistinguishable from an Assimilation Model with minimal admixture in the context of Late Pleistocene human evolution. In effect, it has transformed a question of Pleistocene human evolution into an issue of living human pedigrees. For this reason, the Replacement Model is treated here as a scenario of extinction of the Neandertals without issue in the Late Pleistocene.
- ³ The Assimilation Model was originally in clear contrast to the Multiregional Model of modern human emergence, in that the initial primary descriptions of multiregional human evolution (e.g. Wolpoff et al., 1984) modeled Pleistocene human evolution as a dynamic reticulating process occurring throughout the humanly inhabited Old World, combining regional differentiation through isolation by distance, genetic drift and selection with the geographically diffuse emergence of those features which characterized general trends in the evolution of the genus *Homo* (see also Trinkaus and Shipman, 1993b). In this, modern human emergence was seen as a continuum of already established processes and patterns. The Multiregional Model was an explicit update of Weidenreich’s (1947) “trellis” model and a rejection of the “candelabra” models of Coon (1962) and Howells (1959) (see Wolpoff and Caspari, 1997; Wolpoff et al., 2000). In recent years, versions of what is here referred to as the Assimilation Model have been labeled as multiregional (e.g., Relethford, 2001a; Wolpoff et al., 2001), focusing on the inferred population processes rather than the interpretation of the historical sequence of Late Pleistocene human population dynamics. Since the term “multiregional” has been employed both to describe a human historical evolutionary sequence and to characterize a process involving a variety of population-based evolutionary mechanisms, it is not employed here to describe what is, in essence, an interpretation of European Late Pleistocene population history.

When the Lagar Velho 1 child was buried in the Lagar Velho rockshelter, some time between ca.25 000 and ca.24 500 BP, the site was not being used for habitation. The same seems to apply both to the preceding period, between ca.27 000 and ca.25 000 BP, and to the subsequent period, between ca.24 500 and ca.23 000 BP (Chapter 3). Throughout these four millennia, human use of the shelter was restricted to funerary purposes but, as argued in Chapter 3, it is quite likely that the only burial found so far represents a single, unique event and that no other interments were placed at the site.

This fact is in apparent contrast with the well-known earlier Upper Paleolithic, principally Gravettian, pattern of repeated burial use of the same location. Based on this pattern, one might be led to infer that, originally, the situation at Lagar Velho would have been akin to, among others, the famous Grimaldi caves (Giacobini, 1999), the Pavlov Hill sites (Dolní Věstonice and Pavlov) (Klíma, 1963, 1995; Svoboda, 1991, 1997; Sládek et al., 2000) or Sunghir (Bader, 1998). Burials of young children, however, are unknown or poorly documented at such funerary sites.

In order to understand the significance of these observations, an investigation of the available data on earlier Upper Paleolithic burials was carried out, suggesting a possible link between the particular situation at Lagar Velho and the overall scarcity of Gravettian child burials. Given that the child's anatomy provides evidence for significant admixture between local Neandertals and modern humans dispersing into Iberia after 30 000 years ago (Chapter 32), the comparative framework includes Middle Paleolithic burials, initially in order to assess whether the ritual practiced at Lagar Velho showed evidence for at least some degree of cultural continuity with the child's Neandertal ancestors. No such evidence was found, but the comparison nonetheless provides insights into the social conditions of children in the Paleolithic (see also Chapter 10) and the mechanisms through which European Neandertals were ultimately replaced by modern humans (see Chapter 34).

Middle and Earlier Upper Paleolithic Burials: A Framework

The assessment of the significance of the Lagar Velho 1 burial requires the establishment of an appropriate comparative framework. Even though several previous attempts have been made to discern patterns in Middle and/or Upper Paleolithic burial patterns (e.g., Harrold, 1980; Binant, 1991b; Defleur, 1993; Riel-Salvatore and Clark, 2001), the data sets contained within those publications are deficient in terms of their completeness, accuracy and agreement with current data on Late Pleistocene human burials. Consequently, we used Riel-Salvatore and Clark's (2001) and Binant's (1991b) lists as a point of departure, correcting for errors in designations or ages-at-death, deleting questionable cases, adding clear omissions, and including associated skeletons whose preservation can only be explained if intentional interment is assumed. Given the nature of the question posed here, the nature of burial practices of young children in the Gravettian, careful consideration of several of the Middle and earlier Upper Paleolithic burial instances and their ages was required.

For the Middle Paleolithic, Dederiyeh 2 (Akazawa and Muhsen, 2002), Mezmaiskaya 1 (Golovanova et al., 1998a, 1998b, 1999), Qafzeh 6, 7, 12, 13, 21 and 22 (Tillier, 1999), Skhul 2, 3 and 10 (McCown and Keith, 1939), Shanidar 9 (Trinkaus, 1983) and the multiple burial in layer III of Zaskalnaya VI (Smirnov, 1991; Pettitt, 1998; Chabai, pers. comm.) were added. For the earlier Upper Paleolithic, Ostuni 2 (Giacobini, 1999; Mussi, 2000), Barma Grande 1, 2, 5 and 6 (Giacobini, 1999; Mussi, 2000), Dolní Věstonice 4 and 36 (Svoboda et al., 1996; Trinkaus et al., 2000b; Sládek et al., 2000), the four individual burials from the Kostenki sites 2, 14, 15 and 18 (Sinitsyn, 1998, pers. comm.), as well as Paviland 1 (Aldhouse-Green, 2000), were added. Malta 1 was also added, based on available contextual and radiometric information (Abramova, 1984; Binant, 1991b; Kuzmin and Orlova, 1998), but it should be borne in mind that two children, not just one, may in fact be represented among the human remains recovered in this burial (Soffer et al., 2001). We did not consider the evidence from Abri Labattut, used in the burial ornaments database of Chapter 10, because of the uncertainties with regard to the age of the individual, the chronology of the event (which is possibly Solutrean), and whether it is indeed a burial (Binant, 1991b). The Balla 1 child (Hillebrand, 1911) was also not included here, since data on its burial context are not available. Ages-at-death for the Předmostí remains are based on Klíma's reconstruction of the "mass grave" (Klíma, 1991; Svoboda et al., 1996: p. 168), with precisions from Matiegka's (1934, 1938) study of these now lost human remains.

In a few cases, specimens listed in Riel-Salvatore and Clark's (2001) paper were not considered. The Staroselje child was excluded, given the evidence (Marks et al., 1997) that this is a late Holocene burial intrusive into the site's upper Mousterian levels. La Ferrassie 4a was excluded on the basis of Maureille's (2002) demonstration that the two bones defining this specimen were in fact part of the rediscovered Le Moustier 2 skeleton. Combe-Capelle and Les Cottés were excluded, since, as stated by Gambier (1989), the latter may well not be Paleolithic and the stratigraphic level of the former is uncertain. Given the description they provide, Riel-Salvatore and Clark's Předmostí 22 individual must correspond to Binant's (1991b) *Sépulture 4*, the partial skull of a 9-10 year old child with fox (not hare) teeth adhering to the forehead. According to Svoboda et al. (1996: pp. 62-64 and 226-229), this fossil is part of an ensemble of human remains belonging to six different individuals recovered by M. Kříž in 1895, one year after K. Maška's excavation of the 18 individuals contained in the site's "mass grave." There is no indication that the ensemble comes from poorly preserved burials, as Binant suggested. However, we did retain the Předmostí 27 adult, found in 1928 by K. Absolon, since it is an associated postcranial skeleton.

Mussi's (2001) list includes three specimens that are not included in the database. The fetus Ostuni 1bis, from the Santa Maria d'Agnano Cave, was found in anatomical position inside its mother's skeleton, so this is not the separate burial of a neonate. According to Gambier (pers. comm.), the "8 year old child" from the Marronnier cave (cf. Onoratini, 1999) includes a small number of remains which, based on dental age, belong to at least two different individuals. Although the site's single cultural level (which, according to Gambier, also contained other scattered, isolated human remains — two juvenile mandible fragments, belonging to individuals with dental ages of 1-3 and 4-6) is indeed Gravettian, the Marronnier remains do not come from burials. The 3 year old child from Le Figuier, by contrast, does come from a burial, which Combier (1967) and Billy (1979) attributed to the Magdalenian, but for which Onoratini (1999) suggests a Gravettian date, based on the identification of a previously unrecognized Noaillian component at the base of the site's sequence. However, the exact stratigraphic provenience of the child is unknown, since it was found during earth removal work to gain access to the site's inner gallery (Combier, 1967: pp. 369-370). Moreover, the single ornament associated with this skeleton — a *Glycymeris violacescens* shell

perforated near the hinge — is characteristic of the site’s Magdalenian levels and rarely found in well-dated Gravettian contexts, as noted by Combier (1967) and Gambier (pers. comm.). Direct dating of this individual may force a revision of its current status, but the evidence provided so far does not support a Gravettian age for the Le Figuier child.

Careful consideration of available contextual evidence also enabled us to go beyond a classification of the different burials into Middle Paleolithic and earlier Upper Paleolithic culture-historical groupings. Our data base is organized in strict chronological terms, irrespective of anatomical form and of any categorization into archeological periods, the latter being used only as a source of information on the time frame to which burials should be assigned. As a result, we ended up with the different individuals, for whom we considered burial being established beyond reasonable doubt, falling into three discrete temporal clusters: an Early Cluster, between ca.120 000 and ca.90 000 BP; an Intermediate Cluster, between ca.70 000 and ca.35 000 BP; and a Late Cluster, between ca.27 000 and ca.20 000 BP (see Tables 33-1, 33-2 and 33-3).

Table 33-1

Burial data, Early Cluster, 120-90 000 BP. List of buried individuals, sorted by age class and then by site, in increasing alphanumeric order (EMH = Early Modern Human).

Individual	Age (years)	Age Class	Physical type	Date (kyr BP)	Basis of dating	Associated culture
Qafzeh 13	neonate	Infant	EMH	120-90	Associated TL	Tabun C-type Mousterian
Shanidar 7	9 months	Infant	Neandertal	120-90	Anatomy	Mousterian
Shanidar 9	9 months	Infant	Neandertal	120-90	Anatomy	Mousterian
Qafzeh 10	6	Child	EMH	120-90	Associated TL	Tabun C-type Mousterian
Qafzeh 12	3-4	Child	EMH	120-90	Associated TL	Tabun C-type Mousterian
Qafzeh 15	8-10	Child	EMH	120-90	Associated TL	Tabun C-type Mousterian
Qafzeh 21	3	Child	EMH	120-90	Associated TL	Tabun C-type Mousterian
Qafzeh 22	4-6	Child	EMH	120-90	Associated TL	Tabun C-type Mousterian
Skhul 1	4-6	Child	EMH	120-90	Associated TL	Tabun C-type Mousterian
Skhul 8	10	Child	EMH	120-90	Associated TL	Tabun C-type Mousterian
Skhul 10	5	Child	EMH	120-90	Associated TL	Tabun C-type Mousterian
Qafzeh 11	12-13	Adolescent	EMH	120-90	Associated TL	Tabun C-type Mousterian
Qafzeh 3	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Qafzeh 6	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Qafzeh 7	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Qafzeh 8	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Qafzeh 9	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Qafzeh 15	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Shanidar 4	–	Adult	Neandertal	120-90	Anatomy	Mousterian
Shanidar 6	–	Adult	Neandertal	120-90	Anatomy	Mousterian
Shanidar 8	–	Adult	Neandertal	120-90	Anatomy	Mousterian
Skhul 2	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Skhul 3	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Skhul 4	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Skhul 5	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Skhul 6	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Skhul 7	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Skhul 9	–	Adult	EMH	120-90	Associated TL	Tabun C-type Mousterian
Tabun 1	–	Adult	Neandertal	120-90	Associated TL	Tabun C-type Mousterian

Table 33-2

Burial data, Intermediate Cluster, 70-35 000 BP. List of buried individuals, sorted by age class and then by site, in increasing alphanumeric order (EMH = Early Modern Human; N = Neandertal).

Individual	Age (years)	Age Class	Physical type	Date (kyr BP)	Basis of dating	Associated culture
La Ferrassie 5	-2 months	Fetus	N	75-60	Chronostratigraphy	Ferrassie Mousterian
Amud 7	10 months	Infant	N	65-55	Associated TL	Tabun B-type Mousterian
Dederiyeh 1	1-3	Infant	N	70-50	Associated TL	Tabun B-type Mousterian
Dederiyeh 2	1-3	Infant	N	70-50	Associated TL	Tabun B-type Mousterian
Kebara 1	7 months	Infant	N	60-50	Associated TL	Tabun B-type Mousterian
Kiik-Koba 2	7 months-1	Infant	N	70-50	Chronostratigraphy	"Kiik-Koba lower level"
La Ferrassie 4b	0-1 month	Infant	N	75-60	Chronostratigraphy	Ferrassie Mousterian
La Ferrassie 8	2	Infant	N	75-60	Chronostratigraphy	Ferrassie Mousterian
Le Moustier 2	0-2	Infant	N	40	Associated TL	Typical Mousterian
Mezmaiskaya 1	<0-3 months	Infant	N	45-40	Associated C-14	Eastern Micoquian
Roc-de-Marsal 1	2-3	Infant	N	ca.70	Chronostratigraphy	Typical Mousterian
Zaskalnaya 1	1	Infant	N	39	Associated C-14	Eastern Micoquian
Zaskalnaya 2	2-3	Infant	N	39	Associated C-14	Eastern Micoquian
La Ferrassie 3	10	Child	N	75-60	Chronostratigraphy	Ferrassie Mousterian
La Ferrassie 6	3-5	Child	N	75-60	Chronostratigraphy	Ferrassie Mousterian
Taramsa 1	8-10	Child	EMH	80-50	Chronostratigraphy	Late Middle Stone Age
Teshik-Tash 1	8-9	Child	N	70-35?	Chronostratigraphy	Asian Typical Mousterian
Zaskalnaya 3	5-6	Child	N	39	Associated C-14	Eastern Micoquian
Le Moustier 1	14-16	Adolescent	N	40	Associated TL	Typical Mousterian
Amud 1	-	Adult	N	65-55	Associated TL	Tabun B-type Mousterian
Feldhofer 1	-	Adult	N	39900±620	Direct date	Micoquian
Kebara 2	-	Adult	N	60-50	Associated TL	Tabun B-type Mousterian
Kiik-Koba 12	-	Adult	N	70-50	Chronostratigraphy	"Kiik-Koba lower level"
La Chapelle-aux-Saints 1	-	Adult	N	65-55	Chronostratigraphy	Quina Mousterian
La Ferrassie 1	-	Adult	N	75-60	Chronostratigraphy	Ferrassie Mousterian
La Ferrassie 2	-	Adult	N	75-60	Chronostratigraphy	Ferrassie Mousterian
La Quina 1	-	Adult	N	65-55	Chronostratigraphy	Quina Mousterian
Le Régourdou 1	-	Adult	N	65-55	Chronostratigraphy	Quina Mousterian
Saint-Césaire 1	-	Adult	N	40-35	Associated TL	Châtelperronian
Shanidar 1	-	Adult	N	70-35	Chronostratigraphy	Mousterian
Shanidar 3	-	Adult	N	70-35	Chronostratigraphy	Mousterian
Spy 1	-	Adult	N	65-55	Chronostratigraphy	Quina Mousterian
Spy 2	-	Adult	N	65-55	Chronostratigraphy	Quina Mousterian

Table 33-3

Burial data, Late Cluster, 27-20 000 BP List of buried individuals, sorted by age class and then by site, in increasing alphanumeric order (EMH = Early Modern Human).

Individual	Age (years)	Age Class	Physical type	Date (kyr BP)	Basis of dating	Associated culture
Cro-Magnon 5	1 month	Infant	EMH	27-21	Stratigraphy	Gravettian?
Dolni Věstonice 36	1-2	Infant	EMH	27.5-26.5	Associated C-14	Pavlovian
Předmostí 6	2-3	Infant	EMH	27-26	Associated C-14	Pavlovian
Předmostí 11	0-3	Infant	EMH	27-26	Associated C-14	Pavlovian
Předmostí 12	0-3	Infant	EMH	27-26	Associated C-14	Pavlovian
Předmostí 13	0-3	Infant	EMH	27-26	Associated C-14	Pavlovian
Dolni Věstonice 4	4-12?	Child	EMH	31-25	Associated C-14	Pavlovian
Kostenki 15 burial	6-7	Child	EMH	32-27	Associated C-14	Gorodtsovian
Kostenki 18 burial	6-7	Child	EMH	21020±180	Direct date	Eastern Gravettian
Lagar Velho 1	4-5	Child	EMH	25-24.5	Associated C-14	Gravettian
Malta 1	>4	Child	EMH	>21	Associated C-14	Eastern Gravettian
Předmostí 2	6-7	Child	EMH	27-26	Associated C-14	Pavlovian
Předmostí 8	3-4	Child	EMH	27-26	Associated C-14	Pavlovian
Předmostí 15	4-12?	Child	EMH	27-26	Associated C-14	Pavlovian
Předmostí 16	4-12?	Child	EMH	27-26	Associated C-14	Pavlovian
Předmostí 17	4-12?	Child	EMH	27-26	Associated C-14	Pavlovian
Sunghir 3	9-10	Child	EMH	24100±240	Direct date	Eastern Gravettian
Arene Candide 1	14-15	Adolescent	EMH	>18540±210	Chronostratigraphy	Gravettian
Baouso da Torre 3	15	Adolescent	EMH	27-21	Chronostratigraphy	Gravettian?
Barma Grande 3	12-13	Adolescent	EMH	27-21	Chronostratigraphy	Gravettian
Barma Grande 4	14-15	Adolescent	EMH	27-21	Chronostratigraphy	Gravettian
Cussac 1	13-15	Adolescent	EMH	25120±120	Direct date	Gravettian
Fanciulli 6	13-15	Adolescent	EMH	27-21	Chronostratigraphy	Gravettian IV
Paglicci 2	12-14	Adolescent	EMH	25.5-24	Associated C-14	Gravettian
Předmostí 7	12-14	Adolescent	EMH	27-26	Associated C-14	Pavlovian
Sunghir 2	13	Adolescent	EMH	23830±220	Direct date	Eastern Gravettian
Baouso da Torre 1	–	Adult	EMH	27-21	Chronostratigraphy	Gravettian?
Baouso da Torre 2	–	Adult	EMH	27-21	Chronostratigraphy	Gravettian?
Barma Grande 1	–	Adult	EMH	27-21	Chronostratigraphy	Gravettian
Barma Grande 2	–	Adult	EMH	27-21	Chronostratigraphy	Gravettian
Barma Grande 5	–	Adult	EMH	27-21	Chronostratigraphy	Gravettian
Barma Grande 6	–	Adult	EMH	27-21	Chronostratigraphy	Gravettian
Brno 2	–	Adult	EMH	23680±200	Direct date	Pavlovian
Brno 3	–	Adult	EMH	27-21	Stratigraphy	Pavlovian
Caviglione 1	–	Adult	EMH	27-21	Chronostratigraphy	Gravettian
Cro-Magnon 1	–	Adult	EMH	27-21	Stratigraphy	Gravettian?
Cro-Magnon 2	–	Adult	EMH	27-21	Stratigraphy	Gravettian?
Cro-Magnon 3	–	Adult	EMH	27-21	Stratigraphy	Gravettian?
Cro-Magnon 4	–	Adult	EMH	27-21	Stratigraphy	Gravettian?
Cussac 2	–	Adult	EMH	25	Associated C-14	Gravettian
Cussac 3	–	Adult	EMH	25	Associated C-14	Gravettian
Cussac 4	–	Adult	EMH	25	Associated C-14	Gravettian
Cussac 5	–	Adult	EMH	25	Associated C-14	Gravettian
Dolni Věstonice 3	–	Adult	EMH	31-25	Associated C-14	Pavlovian
Dolni Věstonice 13	–	Adult	EMH	27-26.5	Associated C-14	Pavlovian
Dolni Věstonice 14	–	Adult	EMH	27-26.5	Associated C-14	Pavlovian
Dolni Věstonice 15	–	Adult	EMH	27-26.5	Associated C-14	Pavlovian

Table 33-3 [cont.]

Individual	Age (years)	Age Class	Physical type	Date (kyr BP)	Basis of dating	Associated culture
Dolni Věstonice 16	–	Adult	EMH	27.5-26.5	Associated C-14	Pavlovian
Fanciulli 4	–	Adult	EMH	27-21	Chronostratigraphy	Gravettian
Fanciulli 5	–	Adult	EMH	27-21	Chronostratigraphy	Gravettian IV
Kostenki 2 burial	–	Adult	EMH	26-20	Associated C-14	Eastern Gravettian
Kostenki 14 burial	–	Adult	EMH	32-27	Associated C-14	Gorodtsovian
Ostuni 1	–	Adult	EMH	25-24	Associated C-14	Gravettian
Ostuni 2	–	Adult	EMH	25-24	Associated C-14	Gravettian
Paglicci 3	–	Adult	EMH	24-22.5	Associated C-14	Gravettian
Paviland 1	–	Adult	EMH	25840±280	Direct date	Gravettian
Pavlov 1	–	Adult	EMH	27-25	Associated C-14	Pavlovian
Předmostí 1	–	Adult	EMH	27-26	Associated C-14	Pavlovian
Předmostí 3	–	Adult	EMH	27-26	Associated C-14	Pavlovian
Předmostí 4	–	Adult	EMH	27-26	Associated C-14	Pavlovian
Předmostí 5	–	Adult	EMH	27-26	Associated C-14	Pavlovian
Předmostí 9	–	Adult	EMH	27-26	Associated C-14	Pavlovian
Předmostí 10	–	Adult	EMH	27-26	Associated C-14	Pavlovian
Předmostí 14	–	Adult	EMH	27-26	Associated C-14	Pavlovian
Předmostí 18	–	Adult	EMH	27-26	Associated C-14	Pavlovian
Předmostí 27	–	Adult	EMH	27-26	Associated C-14	Pavlovian
Sungir 1	–	Adult	EMH	22930±200	Direct date	Eastern Gravettian
Veneri Parabita 1	–	Adult	EMH	ca.22	Chronostratigraphy	Gravettian
Veneri Parabita 2	–	Adult	EMH	ca.22	Chronostratigraphy	Gravettian

For the Middle Paleolithic and the earliest Upper Paleolithic, chronological assignment was based on several considerations. First, the Tabun 1 adult female burial is inferred to be from layer C and, therefore, dates to OIS 5 or earlier, although a case has been made that this burial relates instead to the human activity recorded in layer B, in which case it would belong to the Intermediate, not the Early, Cluster (for a discussion of the issue, cf. Bar-Yosef, 1998, 2000; Quam and Smith, 1998). However, Grün and Stringer's (2000) revision of the ESR and U-series chronology of the site, including direct dating of dental material from the Tabun 1 specimen, for which they estimated a chronology with interval limits all contained between 110 000 and 150 000 BP, depending on different sets of assumptions, suggests that this fossil most likely belongs in the Early Cluster. Second, as suggested by several anatomical features (Trinkaus, 1983), the earlier sample of the Shanidar Neandertals (Shanidar 2, 4 and 6 to 9) probably dates to the earliest Late Pleistocene, not to the mid-Late Pleistocene; the later sample (Shanidar 1, 3 and 5) probably dates to the later Middle Paleolithic, as suggested by radiocarbon dating of the site (Bar-Yosef, 2000). Two of these individuals, Shanidar 2 and 5, are not included in the burial sample, since they probably were preserved as a result of rockfalls and not intentional burials (Trinkaus, 1983). Third, it is assumed that the TL dates obtained for the levels containing the Skhul and Qafzeh burials also date those burials, even if a) by definition, the burials must post-date the levels, b) some U-Th dates on animal bones from Skhul indicate the presence of components which may be significantly more recent than the TL-dated flints (McDermott et al., 1993), and c) Stringer (1998) has argued that morphological variability in the Qafzeh-Skhul sample argues in favor of deposition over a time span significantly larger than is indicated by the range of TL results.

Assignment of the specimens in Table 33-2 was based on the radiometric dates available for the deposits containing the burials (bearing in mind the above mentioned reserva-

tions and uncertainties concerning Qafzeh and Skhul), coupled with chronostratigraphic correlation. For the other Near Eastern sites (Amud, Dederyieh and Kebara), we followed the chronology proposed by Bar-Yosef (1998). The Taramsa specimen was included in this group on the basis of an OIS 4 age for the burial, inferred from OSL dates ranging between ca.80 000 and ca.50 000 BP for the late Middle Paleolithic context with which the skeleton was associated (Vermeersch et al., 1998). For the French and Belgian sites (La Chapelle-aux-Saints, La Ferrassie, La Quina, Le Moustier, Régourdou, Roc-de-Marsal, Saint-Césaire and Spy), we followed Mellars' (1996) suggestions of the chronological boundaries for the different Mousterian variants of the Aquitaine basin, his summary of the available TL dating results, and his evaluations of the positions of specific levels in the regional sequence. The Neandertal type-specimen from the "small Feldhofer cave", directly dated to ca.40 000 BP (Schmitz et al., 2002), is included given the recovery of a high percentage of this individual's original skeletal elements, even though its burial status cannot be ascertained.

No reliable information exists on the chronology of the Teshik-Tash burial or the lithic assemblage associated with it, the "Asian typical Mousterian" (Ranov, 1978; Smirnov, 1991). It is assumed, therefore, that it dates to the same time period as all other Neandertal burials known in Europe, i. e., to between 70 000 and 35 000 BP, an assumption which is supported by its craniofacial morphology (Ullrich, 1955). The date suggested for Kiik-Koba is based on information provided by Gladilin (1971, 1979) and Chabai (pers. comm.). Gladilin demonstrated that the infant burial belonged to the occupation documented in lower Level VI, as did the adult, not to that in upper Level IV, as had been suggested by the excavator, Bonch-Osmolovski (1940). The industry contained in Level VI has no parallels and, hence, is simply known as "Kiik-Koba, lower level industry" (Kolosov et al., 1993). The arctic-boreal fauna recovered in the level (including *Rangifer tarandus* and *Vulpes corsac*) suggests an OIS 4 age for this context, including the Neandertal burials.

Mezmaiskaya was also placed in the Intermediate Cluster, in spite of the direct date of $29\ 195 \pm 965$ BP (Ua-14512) reported by Ovchinnikov et al. (2000). Given the stratigraphic situation reported by the excavators, the burial must date to more than 40 000 years ago, since the associated skeleton was found at the base of Level 3, C-14 dated to $> 45\ 000$ BP (LE-3841). Moreover, the hiatus between level 3 and Holocene Level 1 that exists at the front of the cave, where the skeleton was recovered, corresponds to the deposition of Levels 2B and 2A inside the cave, for which there are three coherent C-14 determinations: $40\ 660 \pm 1600$ BP (LE-3599) for Level 2B; $36\ 280 \pm 540$ BP (Beta-53897/ETH-9817) and $35\ 760 \pm 400$ BP (Beta-53896/CAMS-2999) for Level 2A (Golovanova et al., 1998a, 1998b, 1999). This suggests that the Mezmaiskaya infant is contemporary with the infants and child buried in Level III of Zaskalnaya VI, in Crimea (and also found in an Eastern Micoquian context), for which a tripeptide bone date on horse bone collected in the burial pit is available: $39\ 100 \pm 1500$ BP (OxA-4773) (Pettitt, 1998).

Since it falls within the range of radiocarbon dating, the Late Cluster is less problematic. Still, the dates or date ranges assigned to the specimens listed in Table 33-3 also rest on a number of interpretations. The Kostenki material, in particular, was included on the basis of Sinitsyn's (1998) review of the chronology of this complex of sites, which makes it clear that an important proportion of available radiocarbon determinations are significantly rejuvenated. Reliable results, coupled with stratigraphic correlation based on the position of the different levels in relation to the two humic horizons identified at the site, indicate that occupations and features in the middle chronological group (estimated to date between 32 000 and 27 000 BP) and in the recent chronological group (estimated to date between 26 000 and 20 000 BP) fit for the most part in the time frame occupied by the Pavlovian and the

Gravettian. The same applies to the child burial found at Malta, a Siberian site for which the first radiocarbon measurements suggested an age of ca.15 000 BP but which is now securely dated to ca.20 000-21 000 BP (Kuzmin and Orlova, 1998; Richards et al., 2001).

Where the Baouso da Torre 3 individual is concerned, we followed Giacobini's (1999) and Mussi's (2000) assignment to the Gravettian and consider the association with a split-base bone point reported by Binant (1991b) to be spurious. Following Bouchud (1966), the Cro-Magnon burials (Lartet, 1868) are also considered to be Gravettian, and not Aurignacian, in age, because a) they were recovered from the upper part of the site's stratigraphic sequence and b) until the mid-20th century, the "Aurignacian" chronostratigraphic unit encompassed an "*Aurignacien supérieur*," only subsequently recognized as a separate entity, the Gravettian. Moreover, the associated ornaments — some 300 perforated shell beads mixed with the human bones, as well as several pierced teeth (Binant, 1991b) — fit comfortably within the range of variation of known Gravettian grave goods. The funerary use of the Cro-Magnon shelter may well be contemporaneous, therefore, with that in the inner galleries of the recently found parietal art site of Cussac (Aujoulat et al., 2001, 2002), where five individuals have been identified: one adolescent, directly dated to 25 120 ± 120 BP (Beta-156643), in locus 1; one adult whose direct date failed, in locus 2; and three other adults, possibly a multiple burial, in locus 3.

The attribution to the Gravettian of the Cro-Magnon and Baouso da Torre burials finds additional support in the fact that no uncontroversial evidence for intentional burial is known from the Aurignacian. In fact, virtually all of the human remains so far found in levels dated to the corresponding time period are isolated finds. Such is the case, in particular, with the Kostenki 1 material directly dated to 32 600 ± 1100 BP (OxA-7073) (Richards et al., 2001), which was sampled from a tibia and fibula recovered in close proximity inside that site's stratigraphic Level III (Sinitsyn, 1998, pers. comm.). The probably Aurignacian human remains from Mladeč include multiple skeletal elements of an adolescent male and a young adult (Szombathy, 1925; Trinkaus et al., n.d.), but it is likely that these and the other Mladeč human remains accumulated in a talus cone within the karstic cave system (Svoboda, 2000a) and therefore cannot be strictly considered as burials. This suggests that burial may not have been practiced in the Aurignacian, as may also have been the case, at least in western Europe, during the period between 20 000 and 16 000 BP. The latter may explain the dearth of human remains from the Solutrean, Solutreo-Gravettian, Salpétrian, Early Epigravettian and Badegoulian. That the cultural practice of body interment immediately after death was not universally shared, in time or space, during the Upper Paleolithic, lends further consistency to the hypothesis that the three temporal clusters into which our sample falls are a realistic rendering of when this behavior was in use in the time periods following its emergence in OIS 5 or slightly earlier.

Burial Behavior in Relation to Age-at-Death

The individuals were classified into five groups on the basis of their ages-at-death: fetuses, infants, children, adolescents and adults. Boundaries between each category were based on human biological and ethnographic evidence relating to where, on average, major thresholds are crossed in human development. Birth separates fetuses from infants, even if all fetuses or fetuses-to-newborns in our database had passed the seventh month of pregnancy and, therefore, must correspond to stillborn prematures. The end of breastfeeding separates infants from children, and we used an age of three years as the boundary between the two categories, based on data from the !Kung San, one of the best studied examples of

hunter-gatherer cultures; according to Stuart-Macadam (1995), following Konner, in a sample of 78 infants and children, 58% were weaned by two years of age, 76% by three years, and 90% by four years. Stuart-Macadam also mentions data from Wickes indicating a similar pattern for Native Australians but providing evidence for breastfeeding lasting longer among subarctic populations, with Greenlanders weaning between three and four years, and Inuit around seven years. The initial stages of puberty occur, on average, around age 12, and 12 years was therefore selected as the boundary separating children from adolescents. Individuals above the age of 15 were classified as adults, since, even though full skeletal maturity had not yet been attained, healthy females usually become fertile around that age, past which, therefore, they are eligible for marriage. Moreover, in most hunter-gatherer cultures, females and males above 15 are active participants in most if not all aspects of the group's social and economic life (Bogin, 1998).

This step was required in order to investigate possible differences between immature individuals (or categories of immature individuals) and adults, or between different categories of immature individuals. The second step was the identification of the sources of information to exploit in order to achieve that purpose. In an archeological situation, such sources are of two kinds: a) on a short-time scale, possible differences in the ritual treatment given to individuals of the different age classes buried in the same site, or in sites that are sufficiently close in space and time for cultural homogeneity to be assumed, and b) on a long-time scale, the frequency with which burial, as well as the different components of burial ritual, affects the different age classes.

The first approach was followed by Vanhaeren and d'Errico (2001) in their comparative study of the Terminal Magdalenian, Epigravettian or Azilian child burials from France and Italy dated to between 10 000 and 11 000 BP. They showed that the shell beads decorating the clothes with which these young children were dressed at the time of interment a) were smaller, or cut to smaller sizes, than those naturally available, and b) were smaller than those from habitation contexts presumably lost by individuals belonging to the different age classes, including adults. Such a miniaturisation indicates that the shell beads were manufactured on purpose for the children in question, and, hence, that either these children specifically, or children in general, had a defined social status in these human groups.

Vanhaeren and d'Errico also noted that their findings are consistent with White's (1999) observation that the 10 000 ivory beads found in the Sunghir double burial of a 9-10 year old child and a 12-14 year old adolescent are one third smaller than those found with the single adult burial from the same site. This observation hints at juveniles having their own social status in the Gravettian as well, and it prompted us to extend the analysis of the issue to other burials of the period, following both strategies outlined above to the extent permitted by available data.

The Compositions of Multiple Burials

The two Sunghir burials are separated by 1000 years, which means that we cannot disregard the possibility that the reported difference between the adult and the juveniles in the average size of the associated ivory beads is due to changes in manufacturing techniques or cultural fashion occurring over the millenium in question. This difficulty may be overcome by the investigation of possible differences between individuals of different age classes found in multiple burials, that is, in a situation where diachronic variation can be excluded.

There are two instances of possible multiple burials in the Middle Paleolithic. The earliest is the feature containing the Shanidar individuals 4, 6, 8 and 9. However, it is not clear whether this association represents a single burial event or four different burial events in the same location. Given the progressively greater disturbance of the deeper burials, the latter is more likely to be correct (Trinkaus, 1983). In any case, none of these individuals was associated with grave goods or other evidence of ritual behavior beyond interment itself [the purported flowers with the burial (Solecki, 1975; Leroi-Gourhan, 1999) is most likely the result of rodent burrowing (Sommer, 1999)], so no evidence exists that the nine month old Shanidar 9 infant was treated at death differently from the three adults. The other instance is the pit in Level III of Zaskalnaya VI containing two infants and one child, where, however, a similar uncertainty pertains (Smirnov, 1991; Chabai, pers. comm.).

Table 33-4 lists all multiple burials currently known for the earlier Upper Paleolithic. Apart from the 9-10 year child in the Sunghir double burial, infants and children are present only in the Předmostí mass grave containing individuals 1 to 18. In all other instances of multiple burials, only adults or adults and adolescents are represented. Provided that reasonable explanations can be given for the Sunghir and Předmostí exceptions, this pattern suggests that, in the Gravettian, pre-puberty children were socially recognized as a separate age class and, accordingly, treated separately at death.

The ages of the two immature individuals in the Sunghir double burial are consistent with the hypothesis that they were close relatives who met a simultaneous death and were given a simultaneous interment, as is the particular disposition of the bodies, extending in opposite directions from the point of contact between their two skulls and sharing as a common grave good, extending for the combined length of the two bodies, the longest of the several ivory spears placed alongside them. This may explain why the younger individual was given the same treatment as the older one or that the boundary between childhood and adolescence was placed, at the time, around age 10-12. It is also possible that the extraordinary, unique richness of this double burial is an indication of a hereditary high social status, a factor that always needs to be considered when generalizing about the social condition of children.

Table 33-4
Paleolithic multiple burials.

Burial	Fetuses	Infants	Children	Adolescents	Adults	Observations
Early Cluster						
Shanidar 4, 6, 8 and 9	–	1	–	–	3	Consecutive, not simultaneous interments
Intermediate Cluster						
Zaskalnaya 1, 2 and 3	–	2	1	–	–	Consecutive, not simultaneous interments
Late Cluster						
Barma Grande 2, 3 and 4	–	–	–	2	1	
Cussac 3, 4 and 5	–	–	–	–	3	
Dolni Věstonice 13, 14 and 15	–	–	–	–	3	
Fanciulli 5 and 6	–	–	–	1	1	
Předmostí mass grave	–	4	2	4	8	Catastrophic event
Sunghir 2 and 3	–	–	1	1	–	Simultaneous death of two siblings?
Veneri Parabita 1 and 2	–	–	–	–	2	

The Předmostí “Mass Grave”

One of the unique burial features of the earlier Upper Paleolithic is the Předmostí “mass grave,” excavated by Maška in 1894 and containing the remains of eighteen individuals. The burial complex was never described in detail by Maška. However, his field diary survives (Svoboda, 2000b), and, on the basis of Maška’s notes and drawings and a set of assumptions regarding the sequence with which Maška excavated the burial, Klíma (1991) undertook a reconstruction of the distribution of the remains within the mass grave. Our consideration of the Předmostí grave complex is based on Klíma’s interpretation, supplemented by observations and photographs of the human remains provided by Matiegka (1934).

Klíma’s (1991) reconstruction of the Předmostí multiple burial, adapted to visually enhance the information supporting our interpretation of it, is reproduced in Fig. 33-1. According to Maška (Svoboda et al., 1996: p. 226), the grave was found under an accumulation of sharp-edged limestone blocks of various sizes, forming a 40 cm thick cairn that extended beyond the feature to the north and east but left its southern part uncovered. Scattered human remains were present outside of the feature, to the south and southeast, suggesting some post-depositional disturbance of at least this part of the grave.

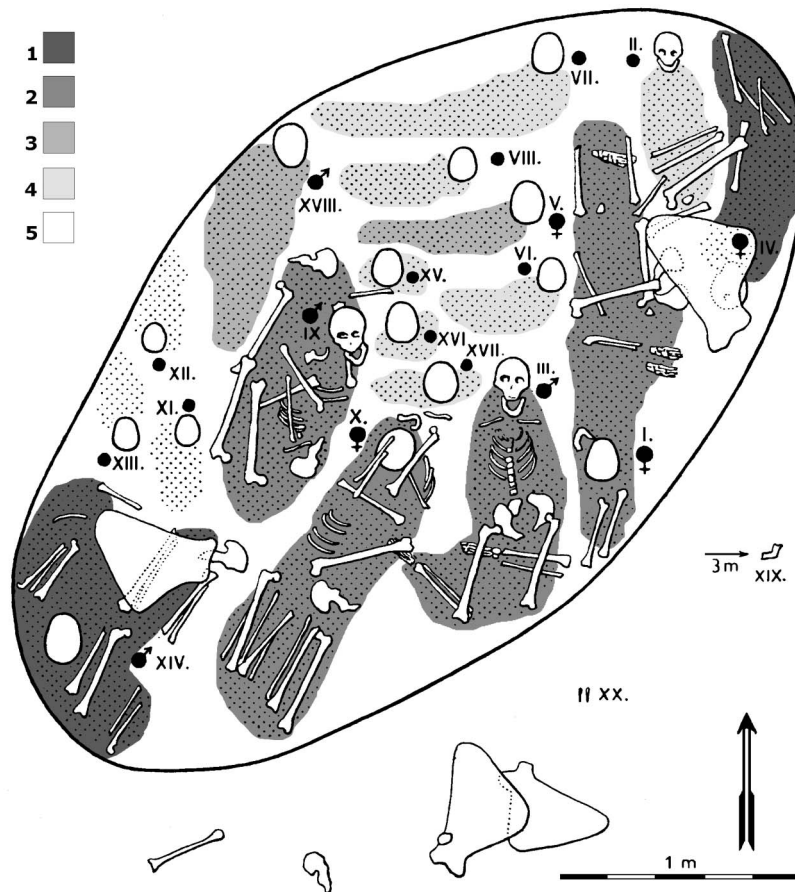


Fig. 33-1 – Klíma’s spatial reconstruction of the Předmostí “mass grave,” reproduced from Klíma (1991), with adaptations. The dotted areas denote the probable position of the postcranial skeletons of the different individuals. Ages-at-death were corrected according to Matiegka (1934, 1938). Shading codes visually enhance our interpretation of the pattern underlying age and space distributions: 1. the two elder individuals; 2. the two prime adult male-female couples; 3. the two young adults; 4. the “children” (ages 2-3 to 12-14); 5. the “babies.”

No evidence of red ochre was observed in the grave or on the bones. Binant (1991b) stated that a string of 14 ivory beads was recovered in the grave, but Klíma noted that no mention of such items exists in Maška's documentation and field notes, that Maška himself explicitly remarked on the total absence of ornaments in the burial context, and, therefore, that the string is probably a composition made with scattered beads found in the adjacent habitation levels, not in the grave. According to Svoboda et al.'s (1996) rendering of Maška's field notes, the only possible grave goods are a fox skull placed on one of the skeletons, scattered flint debris and burnt bone fragments. Since the presence of these items can be explained through post-depositional animal burrowing and/or the inheritance of anthropic components present in the sediments used to re-fill the pit, the only evidence of ritual behavior other than interment itself is the two mammoth shoulder blades covering the individuals placed at the northeastern and southwestern ends of the feature.

Eighteen individuals are reported from the grave: eight are adults, four men and four women, and ten are immature. The latter are described by Maška as "mostly children, the youngest of them only half a year old" and, according to Klíma's Fig. 2, three are "babies," four are "children," and three are "young individuals." Using the information provided by Matiegka (1934, 1938), however, one of Klíma's "children," Předmostí 6, would be two to three years old at death and, therefore, falls into our "infant" age class. Notwithstanding, the age difference between this individual and the three infants Předmostí 11, 12 and 13 must have been significant and readily apparent, because Klíma's refers to the latter as "nursing" while using the word "child" for Předmostí 6. Předmostí 7, on the other hand, would have been 12 to 14 years old at death and, therefore, falls into our "adolescent" age class. Where the three "young individuals" Předmostí 15, 16 and 17 are concerned, it would seem, from Matiegka's monograph, that they corresponded to incomplete skull pieces whose ages-at-death were difficult to evaluate. Klíma's differentiation of these as "young individuals," considered, in his illustrated reconstruction of the grave, as a category separate from that of the "children," might be taken to suggest that they were adolescents. In the text, however, Klíma explicitly describes these finds as "child skeletons."

Therefore, in terms of the age classes considered in this study, the number of infants, children and adolescents in the Předmostí mass grave is, respectively, of three, six and one, or of four, five and one, depending on how Předmostí 6 is defined. This level of uncertainty, however, does not affect the characterization of the multiple burial as presenting a catastrophic mortality profile. This suggests that its composition accurately portrays the age structure of a complete or near-complete social unit and that the grave corresponds to the simultaneous death of all its members. This inference is further supported by the spatial arrangement of the bodies and the preservation of the anatomical association of many of the skeletons, neither of which is easily explained in a framework of consecutive interments in the same place, with successive reopenings and closings of the grave, which would create greater disturbance of the remains from previous burial episodes. One must always bear in mind, however, that Klíma's reconstruction is tentative and conditioned by many uncertainties and sources of possible error: incorrect correspondence between individuals in the fossil catalogue and individuals in the grave plan, margins of error inherent in the assignment of ages-at-death, postdepositional disturbance of the burial context, the relatively arbitrary nature of the boundaries between stages of development, etc.

Nonetheless, the fact that both older and younger individuals are represented among the adults of both sexes lends further credence to the interpretation of the mass grave as recording a single death event and, hence, the simultaneous perishing of individuals

linked by close social and biological ties. In fact, the ages assigned by Matiegka to the four females (15-16 for Předmostí 5, 20-25 for Předmostí 1, 20-30 for Předmostí 10, and 30-35 for Předmostí 4) show that all the immature individuals could well be their children, and the age difference between the youngest and the oldest female also makes it possible that the former was the latter's daughter. This point is made by Table 33-5, which assumes that a) women had their first child at 16, b) they gave birth at four year intervals, and c) they lived until an age in the mid-point of their estimated age-at-death intervals. Under such assumptions, the three older women would have generated 10 descendants: three infants, five children, one adolescent, and one adult. Decreasing the birth interval or the lifetime of these females produces variation of these figures in opposite directions, and mortality in early developmental stages implies that the number of surviving children must have been smaller than the potential maximum. Given this, the ages-at-death for the different immature skeletons provided by Klíma and Matiegka fit the model's predictions extremely well.

Matiegka only assigned ages-at-death to two of the four adult males (20-25 for Předmostí 9, and 35-40 for Předmostí 3), but the dental wear of Předmostí 14 suggests he was a middle aged adult, and Klíma noted that he was the oldest person in the grave. Given the data for the females, it is clear that the fourth adult male, Předmostí 18, can only have been the son of any of the females in the grave if his mother was the older woman Předmostí 4. In that case, given the 15-16 years of age of the Předmostí 5 female, whose only potential mother in the grave is also Předmostí 4, Předmostí 18 could have been the older brother of Předmostí 5. Under the assumptions of the model in Table 33-5, admitting this possibility carries the following implications: a) that the age-at-death of Předmostí 18 was between 17 and 19; b) that the age-at-death of his putative mother was 35, i. e., the upper limit of the estimated interval; c) that his putative mother gave birth to two successful children, a boy and a girl, between ages 16 and 19. Matiegka was unable to assign a definite age to Předmostí 18, but Klíma referred to him as a boy. However, even if he seems to have been a young adult, the possibility that he could have been Předmostí 5's older brother remains weak, given the demographic requirements of the hypothesis.

Table 33-5

Model of the reproductive potential of the Předmostí females.

Female individual	Age	Ages they gave birth					Ages of their children when they died				Total
		16	20	24	28	32	Infants	Children	Adolescents	Young adults	
Předmostí 5	15-16	-	-	-	-	-	-	-	-	-	0
Předmostí 1	20-25	+	+	-	-	-	1	1	-	-	2
Předmostí 10	20-30	+	+	+	-	-	1	2	-	-	3
Předmostí 4	30-35	+	+	+	+	+	1	2	1	1	5
Total descendants		3	3	2	1	1	3	5	1	1	10
Immatures and young adults in grave (Klíma and Matiegka)							4	5	1	2	12

The adult individuals buried in the mass grave at Předmostí are, therefore: two prime adult females (individuals 1 and 10), two prime adult males (individuals 3 and 9), one older female (individual 4), one "middle aged" male, the oldest person in the burial (individual 14), and two young adults (individuals 5 and 18). Hence, these individuals may have formed husband-wife couples, and this seems quite likely at least where the six older people are concerned, the locations of their bodies in the burial pit being consistent with this hypothesis.

Individuals 1 and 3 lie next to each other, and so do 10 and 9, forming at death the two prime-age adult couples they may have been in life. Moreover, they occupy the central area of the grave, much as they must have played a central role in organizing and leading the group's daily life. Individuals 4 and 14 are separated, but in a special way, one at each of the two extremities of the grave, and each covered by a mammoth shoulder blade, a distinction enjoyed by none of the others. This distinction may be related to the fact that, in these groups, elderly people enjoyed a high social status, their location in the collective burial meaning that they were supposed to "envelop" the rest of the group in death much as they would have "protected" them in life, with their wisdom and experience. Conversely, the peripheral location of individuals 5 and 18 may be related to their younger age, to their being unwed, or to their being wed but still without children.

A number of plausible explanations can be invoked for what may have caused the catastrophe recorded in the collective burial of these individuals (starvation, unpredicted severe weather, etc.) and, simultaneously, for the fact that other people (neighboring bands, the rest of the band, etc.) could come to the place in time to bury their kin or allies before scavengers consumed the corpses. The lack of evidence for personal ornamentation in all of the Předmostí individuals, contrasting with the important grave construction, may also be related to the exceptional nature of the event.

In this context, the most reasonable explanation for the sex and age structure of the Předmostí "mass grave", therefore, is that it corresponds to a complete or near complete social unit, the core of which are three couples and the descendants of the adult women. Moreover, the different individuals are not distributed at random (Fig. 33-1), and the spatial arrangement of the bodies presents a problem that, as Klíma (1991) pointed out, begs for a social explanation. Regardless of the validity of our own particular solution for the problem, that spatial pattern quite clearly shows at least that a) the specific emplacement of each individual obeyed certain rules and b) such rules required that mature and immature individuals occupied separate areas of the grave. This carries the implication that, at death, the age class to which immature individuals belonged carried more weight than close kinship, i. e., that infants and children were not buried alongside their mothers, even if the whole family died together, and the mothers were buried alongside their mates. Infants, in particular, seem to have formed a separate category and, in this regard, the possible anomaly to the pattern represented by Předmostí 6 may well be more apparent than real. Although possibly under three years, it was buried with the group's children and adolescents, not in the well defined cluster of "babies." This suggests that it may have been significantly older than the latter, and socially perceived as such — in its third year of life, it is conceivable that it was weaned and, hence, that it was already viewed as a "very young child."

In the framework of the social model outlined above, the placement of Předmostí 5 and 18 also makes sense. On the one hand, they are close to the other adults and, therefore, their position is not anomalous. On the other hand, if they were unmarried siblings, their placement with the group's children and adolescents would make sense if marrying, or having children, represented a major threshold in life. This may well hold for Předmostí 5 who, in the model presented in Table 33-5, would be too young to have been the mother of any of the group's infants and children. A number of alternative plausible explanations can also be offered for Předmostí 18 if, as it seems quite likely, he wasn't the son of any of the women in the grave: the unmarried brother of one of the males, a visiting ally, Předmostí 5's groom, etc. In any of these cases, his social condition may have been distinct from that of the other males in the three core couples of the group, explaining his peripheral position in the grave.

In sum, the evidence reviewed above suggests that we can safely infer from Předmostí:

- that age classes were socially recognized in the Gravettian;
- that “adults” and “infants” formed two such age classes, and that children formed a third, intermediate category;
- that each individual’s age-at-death influenced the kind of mortuary treatment received.

Where the issue of possible distinctions in social status between adolescents and children, i. e., between pre- and post-puberty individuals, is concerned, however, Předmostí is inconclusive. Children are separated from the adults, but at least one adolescent was buried among them in a second example (after the double burial of Sunghir) of association between children and adolescents.

These findings are consistent with the evidence provided by multiple burials. As in the latter, infants and children are separated from the adults, although children may be associated with adolescents and adolescents with adults. When cemeteries (defined hereafter as sites that, in a given period, were used for funerary purposes at least once, even if settlement activities are also documented therein) are considered, this pattern remains unchanged (see below).

Open-Air Cemeteries

At open air sites, the association of burials with other features — activity areas, habitation areas, other burials — is difficult to evaluate. Each individual burial episode may have taken place long after any signs of previous occupations of the same place had become covered by vegetation or sediments, or long after the tradition relating that particular spot with a certain individual, or with individuals of a particular social condition, had been lost. Sunghir is a good example of this, because, even if apparently spatially associated, the habitation levels date to 27-28 000 BP, whereas the burials date to 23 000 (single adult burial) and 24 000 (double child-adolescent burial) BP (Pettitt and Bader, 2000). Svoboda et al. (1996: p. 214) also argue that the Dolní Věstonice burials are more recent than the settlement levels into which the burial pits were excavated.

Thus, in such open air contexts, what archeologically may appear as the multifunctional use of the same place, in all likelihood represents the opposite, that is, the use as a cemetery of an area peripheral to or distant from the contemporary habitations. In some instances, such an area may coincide or overlap with the location of older (or later) settlements, but there is no evidence that such a coincidence was deliberate. By the same token, the fact that individual burials have been recovered from the area archeologically defined as a single open air site does not necessarily mean that all of the burials were contemporary or that it was considered socially appropriate for the individuals concerned to be buried together.

Table 33-6 presents the data for open air cemeteries of the Late Cluster (in the Middle Paleolithic there is only one individual buried in the open, the Taramsa child). Apart from Sunghir and Předmostí, the infant and child burials at such sites are those from Dolní Věstonice and Kostenki, where adult burials are also known. Given the above, and given the following information on these funerary features, such a general spatial coincidence does not contradict the hypotheses concerning the particular status of infants and children derived from the analysis of the multiple burials.

Table 33-6

Paleolithic open air cemeteries and age classes of the individuals buried in them.

Burial	Fetuses	Infants	Children	Adolescents	Adults	Observations
Intermediate Cluster						
Taramsa	–	–	1	–	–	
Late Cluster						
Brno	–	–	–	–	2	
Dolní Věstonice I	–	–	1	–	1	Child = DV4, with no context
Dolní Věstonice II	–	1	–	–	4	Infant = DV36, identified among DVII faunal remains
Kostenki 2	–	–	1	–	–	
Kostenki 14	–	–	–	–	1	
Kostenki 15	–	–	1	–	–	Isolated below habitat level
Kostenki 18	–	–	–	–	1	Far from any habitat level
Malta	–	–	1	–	–	
Pavlov	–	–	–	–	1	
Předmostí	–	4	5	1	9	Except for one adult, all in “mass grave”
Sunghir	–	–	1	1	1	Child in double burial with adolescent

The Dolní Věstonice 4 child comes from area I of the site, which also contained the burial of the Dolní Věstonice 3 female, but there is no indication that the two burial events were related to what, at the time, may have been conceived as the same place. Moreover, the child comes from Absolon's 1927 excavations, whereas the woman was found by Klíma in 1949 (Svoboda et al., 1996: p. 64), which indicates that they cannot have been spatially close. The Dolní Věstonice 36 infant is a set of teeth identified among the faunal remains from area II of the site (Trinkaus et al., 2000b). It is inferred to have come from a burial because of the otherwise taphonomically unusual anatomical association. No such feature, however, was recognized in the field, so there is no basis to consider that this infant was in any way associated with the adults recovered in the same general area (the triple burial of Dolní Věstonice 13-15 and the single burial of Dolní Věstonice 16).

As for the child buried at Kostenki 18, it was found “in the middle of the fields, away from any occupation feature” (Binant, 1991b). According to Sinitsyn (1998, pers. comm.), the child buried at Kostenki 15 was placed at the edge of a bone concentration interpreted as the possible remains of a dwelling. Geological contemporaneity between the burial pit and the cultural layer containing this problematic feature seems clear, but synchronicity between the two occupation episodes (habitation and burial) cannot be ascertained and, stratigraphically, the burial is below the cultural layer. The two adults come from other parts of this complex of sites. The stratigraphic situation described by Abramova (1984) for Malta evokes that of the child buried at Kostenki 15, i. e., below an intact cultural layer, indicating that the burial event preceded the habitation and is unrelated to the latter.

Cave or Rockshelter Cemeteries

Unlike open air sites, caves and rockshelters are places easily identifiable as discrete spots on the landscape and whose identification with social traditions is, therefore, easier to maintain across generations. In light of this, the simultaneous presence in this type of cemetery of individuals belonging to age classes that, on the basis of the evidence from

multiple burials, should not have shared the same burial emplacement, could be taken as a significant obstacle to the inferences concerning the differential treatment of infants and children.

Table 33-7

Cave and Rockshelter cemeteries, per time cluster, and age classes of the individuals buried in them.

Burial	Fetuses	Infants	Children	Adolescents	Adults	Observations
Early Cluster						
Qafzeh	–	1	5	1	6	
Shanidar	–	2	–	–	3	
Tabun	–	–	–	–	1	
Skhul	–	–	3	–	7	
Intermediate Cluster						
Amud	–	1	–	–	1	
Dederiyeh	–	2	–	–	–	
Feldhofer	–	–	–	–	1	
Kebara	–	1	–	–	1	
Kiik-Koba	–	1	–	–	1	
La Chapelle-aux-Saints	–	–	–	–	1	
La Ferrassie	1	2	2	–	2	
La Quina	–	–	–	1	–	
Le Moustier	–	1	–	1	–	
Le Régourdou	–	–	–	1	–	
Mezmaiskaya	–	1	–	–	–	
Roc-de-Marsal	–	1	–	–	–	
Teshik-Tash	–	–	1	–	–	
Saint-Césaire	–	–	–	1	–	
Shanidar	–	–	–	–	2	
Spy	–	–	–	–	2	
Zaskalnaya VI	–	2	1	–	–	
Late Cluster						
Arene Candide	–	–	–	1	–	
Baouso da Torre	–	–	–	1	2	
Barma Grande	–	–	–	2	4	
Caviglione	–	–	–	–	1	
Cro-Magnon	–	1	–	–	4	Infant = newborn/fetus in mother?
Cussac	–	–	–	1	3	
Fanciulli	–	–	–	1	2	
Lagar Velho	–	–	1	–	–	
Ostuni	–	–	–	–	2	
Paglicci	–	–	–	1	1	
Paviland	–	–	–	–	1	
Veneri Parabita	–	–	–	–	2	

Table 33-7 lists all the caves and rockshelters known to have been used as funerary sites in the three time clusters considered in our analysis. The most striking feature of this table is that, in the Late Cluster, only one infant, Cro-Magnon 5, and one child, Lagar Velho 1, were buried in a cemetery of this kind. Lagar Velho 1 seems to have been alone, whereas Cro-Magnon 5 was associated with four adults. Given how the site was excavated, it cannot be excluded that this was a late fetus or newborn perinatally dead with its mother and buried with her. If so, this would have been the burial of its dead mother, not the infant's *per se*, a situa-

tion similar to that of the Ostuni 1 pregnant woman. Cro-Magnon 2, an adult female, could have been Cro-Magnon 5's mother. Another possible example of late fetuses or newborns associated with their mothers is that reported by Binant (1991b) for the Proto-Magdalenian (late Gravettian, ca. 22 000 BP) level of the Abri Pataud. The human skeletal material found therein may have been derived from disturbed burials and included the remains of a young adult female (20-25 years old) found "intimately" mixed with those of a newborn infant. This evidence indicates that Cro-Magnon 5 is not necessarily an exception to the pattern revealed by Table 33-7: that, in the Gravettian, as a rule, pre-adolescent individuals were not buried in cemetery sites used for adolescents and adults.

Table 33-8

Evidence for ritual other than interment itself, for individuals under 13, listed per time cluster in increasing numeric order of estimated age-at-death.

Individual	Age (years)	Age Class	Features	Use of ochre	Ritual
Early Cluster					
Qafzeh 13	neonate	Infant			
Shanidar 7	9 months	Infant	Hearth	No	
Shanidar 9	9 months	Infant		No	Multiple burial
Qafzeh 21	3	Infant			
Qafzeh 12	3-4	Child			
Qafzeh 22	4-6	Child			
Skhul 1	4-6	Child	Pit	No	
Skhul 10	4-6	Child			
Qafzeh 10	6	Child	Pit	No	
Qafzeh 15	8-10	Child	Pit	No	
Skhul 8	10	Child			
Intermediate Cluster					
La Ferrassie 5	-2 months	Fetus	Pit; Mound	No	
Mezmaiskaya 1	<0-3 months	Infant		No	
La Ferrassie 4b	0-1 month	Infant	Pit	No	
Kebara 1	7 months	Infant		No	
Kiik-Koba 2	7 months-1	Infant	Pit	No	
Amud 7	10 months	Infant	Pit	No	Deer maxilla on pelvis
Le Moustier 2	0-2	Infant	Pit	No	
Zaskalnaya 1	1	Infant	Pit	No	Multiple burial
Dederiyeh 1	1-3	Infant	Pit	No	Slab on head, flake on thorax
Dederiyeh 2	1-3	Infant		No	
La Ferrassie 8	2	Infant		No	
Roc-de-Marsal 1	2-3	Infant	Pit	No	
Zaskalnaya 2	2-3	Infant	Pit	No	Multiple burial
La Ferrassie 6	3-5	Child	Pit	No	Slab with cupholes on bottom face over grave
Zaskalnaya 3	5-6	Child	Pit	No	Multiple burial
Teshik-Tash 1	8-9	Child	Pit	No	Grave inside circle of goat horns
Taramsa 1	8-10	Child	Pit; Mound	No	
La Ferrassie 3	10	Child	Pit	No	
Late Cluster					
Cro-Magnon 5	1 month	Infant		No	
Dolni Věstonice 36	1-2	Infant		No	
Předmostí 11	0-3	Infant	"Mass grave"	No	
Předmostí 12	0-3	Infant	"Mass grave"	No	
Předmostí 13	0-3	Infant	"Mass grave"	No	
Předmostí 6	2-3?	Infant	"Mass grave"	No	

Table 33-8 [cont.]

Individual	Age (years)	Age Class	Features	Use of ochre	Ritual
Late Cluster					
Předmostí 8	3-4	Child	“Mass grave”	No	
Malta 1	>4	Child	Stone coffin in pit	Yes	Ornaments, ivory tools, stone tools
Lagar Velho 1	4-5	Child	Pit	Yes	Fire, shroud, ornaments, rabbit, deer parts
Kostenki 15 burial	6-7	Child	Pit	Yes	Seated; pierced fox teeth; bone and stone tools
Kostenki 18 burial	6-7	Child	Pit	No	Bones, arranged as three beds, covered body
Předmostí 2	6-7?	Child	“Mass grave”	No	
Předmostí 15	4-12?	Child	“Mass grave”	No	
Předmostí 16	4-12?	Child	“Mass grave”	No	
Předmostí 17	4-12?	Child	“Mass grave”	No	
Dolní Věstonice 4	4-12?	Child	Mammoth scapula	Yes	Pierced fox teeth; some bones burnt
Sunghir 3	9-10	Child	Pit	Yes	Double burial; weapons, ornaments, beads

When data on other ritual behaviors associated with interment are considered (Table 33-8), it becomes apparent, however, that a significant difference also seems to exist between infants and children. In the Late Cluster, no instances of formal burial features containing individualized late fetuses, newborns or infants are known, and no ritual behaviors other than interment, or inferred interment, are documented for skeletons belonging to these age classes; none displayed any evidence that red ochre was used in its burial, and none was associated with personal ornaments clearly its own. In contrast, children between the ages of 3 and 12 years, as exemplified by Lagar Velho 1, are buried in features, are associated with ochre, and bear personal ornaments. Even if Lagar Velho 1 is the single example from a cave or rockshelter site, it shares such a treatment with those from the open air cemeteries of Dolní Věstonice I, Kostenki 15, Kostenki 18 and Malta, even if ochre does not seem to have been used in Kostenki 18. The Předmostí children are exceptions to the ornaments rule but, in this wholly exceptional case, adults were deprived of them too.

Diachronic Variation

The evidence reviewed above suggests that, in the Gravettian, pre-adolescents were treated at death differently from adolescents and adults. Children were buried separately, but with similar rituals. Infants were buried separately from all others and with no ritual. Where the latter are concerned, however, even the evidence for interment is remarkably thin, if Předmostí is not considered. Two instances remain, Cro-Magnon 5 and Dolní Věstonice 36, but the former may have been part of its mother’s burial, and whether the latter was buried is based on taphonomic inference, not field observation. In fact, one may speculate from these data whether, in normal conditions, Gravettian people buried nursing infants at all, or, alternatively, whether Gravettian people considered that an individual existed as an independent person and, hence, worthy of burial at its death, only after becoming independent, in terms of subsistence, from its mother.

It is nonetheless clear that taphonomic factors cannot explain the dearth of Gravettian infant burials and the absence of ornaments in them. Where the latter are concerned, the

fact that Dolní Věstonice 36 is only a set of associated teeth does suggest preservation problems. However, if so, one would expect ornaments made on teeth (present in all of the site's other burials) to be preserved. Since such was not the case, the absence of evidence may well be evidence of absence.

Tables 33-2, 33-7 and 33-8 also make it clear that the pattern revealed by the Intermediate Cluster is an almost reverse image of the Late Cluster's. In the Intermediate Cluster, the number of fetuses' and infants' burials is equal to that of adults, matching an expected mortality distribution for immature individuals (Trinkaus, 1995b) and suggesting that there was little discrimination on the basis of age. Moreover, the evidence for ritual other than interment is as strong among the youngest individuals as among older children (or as weak, depending on how one chooses to look at the evidence for Middle Paleolithic burial rituals — see Chapter 10 for the rationale behind our acceptance of the evidence for ritual presented in Table 33-8). Besides the decoration on the lower surface of the slab covering the La Ferrassie 6 child, and the controversial circle of goat horns associated with Teshik-Tash 1, the Amud 7 and Dederiyeh 1 infants are both associated with variably convincing evidence of ritual. This is all the more significant since, in the Intermediate Cluster, such evidence is remarkably more faint where adults are concerned. A comparison with the Intermediate Cluster also makes it clear that the “mutual avoidance” of children and adults documented for the Gravettian does not apply to the later Middle Paleolithic. This is well exemplified by the situation which is the closest to a true cemetery, that in the Ferrassie-type Mousterian level CD of the type-site, which contained several contiguous burial pits at broadly the same elevation and containing fetuses, infants, children and adults.

Table 33-9

Age class structure of the populations of buried individuals from the beginning of the Middle Paleolithic to the end of the Gravettian.

	Fetuses		Infants		Children		Adolescents		Adults		Total	
	N	%	N	%	N	%	N	%	N	%	N	%
Early Cluster	—	0	3	10	8	28	1	3	17	59	29	100
Intermediate Cluster	1	3	12	36	5	15	1	3	14	42	33	100
Late Cluster	—	0	6	9	11	16	9	13	43	62	69	100
TOTAL	1		21		24		11		74		131	

A diachronic analysis of the variation in the age structure of the populations of buried individuals from the three temporal clusters recognized (Table 33-9) confirms the existence of significant differences between them that cannot be attributed to taphonomic, evolutionary or biobehavioral factors, and, therefore, can only have a cultural explanation. In the Early Cluster, immature individuals are 41%, in the Intermediate they are 58%, and in the Late they are 39%. The structure is therefore very similar in the earlier and later periods, i. e., no fetuses, few infants. Relative to adults, however, adolescents are underrepresented in the earlier: 1 adolescent (6% of all past-puberty individuals) against 17 adults in the Early Cluster, versus 9 adolescents (17% of all past-puberty individuals) and 43 adults in the Late Cluster. The Intermediate Cluster features the same underrepresentation of adolescents seen in the Early Cluster — 1 adolescent (7% of all past-puberty individuals) versus 14 adults — but it stands out in the comparisons mainly because fetuses and infants correspond, here, to 41% of the total sample, against only 10% and 9%, respectively, in the Early and the Late Clusters. If fetuses are grouped with infants, and adolescents with adults, in order to avoid the zeros and low numbers in the contingency table, it becomes possible to evaluate statistically the signif-

ificance of differences between the three periods in the representation of the three age groups so formed, where nursing and puberty are the dividing developmental thresholds. Using Microsoft Excel's chi-square test function, the results presented in Table 33-10 are obtained.

Table 33-10

Chi-square testing of the significance of the differences in age class structure between populations of buried individuals from the beginning of the Middle Paleolithic to the end of the Gravettian. Individuals are grouped in three classes: fetuses and infants, post-lactating pre-puberty juveniles, adolescents and adults. Significance levels adjusted with a sequentially reductive multiple comparison correction.

Comparison (3 age classes)	P value	Significance	Confidence level
Early vs Intermediate vs Late	0.001	Different	99%
Early vs Intermediate	0.030	Not different	–
Intermediate vs Late	<0.001	Different	99%
Early vs Late	0.369	Not different	–
Early + Intermediate vs Late	0.014	Different	95%

If, in order to avoid possible biases introduced by any errors related to the ascription of sites to either the Early or the Intermediate Cluster, or to their different geographic distributions (the former is entirely western Asian, and the latter contains no burials from central Europe), those two clusters are combined, the specificity of the Gravettian pattern does not disappear. Since the percentage of children is similar in the two samples thus obtained (21% and 16%, respectively), that specificity is related to the fact that, in the earlier, fetuses and infants are 26% of the total, and post-puberty individuals 53%, whereas in the later the corresponding figures are 9% and 75%, respectively. These differences remain significant at the 95% confidence level ($P = 0.014$).

Assuming that it is correct to discriminate within the pre-35 000 BP sample between an Early and an Intermediate Cluster with the compositions given in Tables 33-1 and 33-2, Table 33-10 also shows that the Early Cluster's structure approaches a significant difference relative to the Intermediate Cluster, but it cannot be distinguished statistically from the Late Cluster. This moderate contrast is not explained by the fact that the Late Cluster is entirely made up of early modern humans, which also predominate in the Early Cluster, in contrast with the almost exclusively Neandertal composition of the Intermediate Cluster. When the age class structure of buried Neandertals and buried early modern humans from the Early Cluster is compared, contrasting the frequencies for pre-puberty and post-puberty individuals (a compaction of the sample into these two groups is required for the chi-square test to be possible) gives a P-value of 0.794, that is, the two samples are identical.

It would seem, therefore, that fetuses and infants were “worthy” of burial in the late Middle Paleolithic, but that such was not the case, or only rarely was the case, either before or after. Moreover, since they are found on their own, the “fetuses” in question (La Ferrassie 4a and 5, as well as, possibly, Mezmaiskaya 1) must correspond to bodies that somehow “came out” of their mothers' wombs, i.e., they are either premature or dead-at-birth babies. Therefore, if their mothers too died as a result of perinatal complications, they must have been buried somewhere else. This hypothesis, however, is not consistent with the evidence contradicting any spatial discrimination between individuals belonging to different age classes in the Intermediate Cluster. Hence, it seems more logical to admit that their mothers survived, which highlights another contrast with the Late Cluster, where the only fetuses known (Ostuni 1bis, certainly; Abri Pataud, almost certainly; and Cro-Magnon 5, quite possibly) were in their dead mothers.

It is in any case clear that, by comparison with the Early and especially the Late Clusters, the frequency of fetuses and infants among buried individuals appears to be anomalously high in the Intermediate Cluster, as noted by Defleur (1993: p. 275) for the Mousterian as a whole. Moreover, there is some evidence that, in the burials from this cluster, ritual behavior is better documented in association with such individuals than with the other age classes. This may reflect that society placed more significance in the loss of very young lives than in the loss of older children (there is a gap between ages-at-death of 3 and 9 in the Intermediate Cluster), adolescents and adults. Alternatively, as noted above, the mortality pattern in the Intermediate Cluster, except for the dearth of older adults, is remarkably close to what would be expected from normal demographic patterns (Trinkaus, 1995b). If anything, there are too few infants preserved given normal recent human rates of infant mortality [20% to 50%; available figures for the !Kung and the Hadza, for instance, are 44% and 39% respectively (Bogin, 1998)], which is probably explainable as a result of the poor preservation of neonatal skeletal remains and the absence of excavations until the late twentieth century capable of routinely recognizing such fragmented human remains.

There is no reason to assume that such preservation and excavation issues affect Intermediate Cluster burials less than Early and Late Cluster ones. In fact, therefore, it is the frequency of fetuses and infants among buried individuals in these clusters that is anomalously low, not that in the Intermediate Cluster that is anomalously high. This implies that the real difference between the Intermediate and Late Clusters of burials, or between primarily later Middle Paleolithic people (mostly Neandertals) and Gravettian people (all early modern humans), is the emergence of age-related criteria for the differential burial of members of a social group. The data for the Early Cluster, however, do not preclude that similar criteria were already in use by OIS 5 times. Therefore, this cultural trait may well have varied non-directionally, and the hypothesis that what we may be seeing in the Gravettian is its re-emergence more than its first emergence cannot be rejected at present.

Conclusions on Middle and Earlier Upper Paleolithic Burials

In the Gravettian, the end of breastfeeding and the onset of puberty seem to have been socially significant developmental thresholds. The patterns derived from multiple burials are consistent with those derived from the analysis of sites with single or accretional episodes of burying in indicating that fetuses and infants did not receive ritualized interment. The presence of infants in the Předmostí “mass grave” is an apparent exception that can be explained by the unusual situation pertaining there. Moreover, the three nursing individuals were placed together, in their own spatial cluster, separated from the other members of the group and, more importantly, separated from their putative mothers. Gravettian pre-puberty children did receive a ritualized burial, but in localities different from those appropriate for post-puberty adolescents and adults. The fact that children are present, together with adolescents and adults, in the Předmostí “mass grave”, is again only an apparent exception. Those children clustered together spatially, and they were separated from their putative mothers. The placement of pre-puberty individuals in this collective tomb was based on their ages-at-death, not their parental ties.

In the later Middle Paleolithic, by contrast, no difference between developmental stages as defined using weaning and puberty as thresholds is apparent, at least as far as burial is concerned. It remains possible that age classes were recognized at the time, but such a recognition was not reflected in archeologically-preserved manifestations of material cul-

ture. The fact that fetuses and infants represent 39% of the sample of buried individuals in this time range makes it abundantly clear that the dearth of such individuals in Gravettian burials cannot be explained by taphonomy or preservation, and it must be considered as the manifestation of a cultural practice. Such a dearth is all the more striking if we consider that, in hunter-gatherer societies, many offspring die in infancy.

From this perspective, the Lagar Velho 1 child, with a secure chronology (ca. 24 500 BP) and age-at-death (4.5 years old), represents unequivocal evidence that, in the mid-Upper Paleolithic, young children became socially part of the world of living humans past the age of about four, that is, past weaning. Much the same can probably be said for the Malta 1 child. Among the rituals elsewhere associated with Gravettian adolescents and young adults that are documented in the Lagar Velho child burial, the most striking is the fire at the bottom of the burial pit, described in the double burial of one adolescent and one adult at Grotta dei Fanciulli, as well as in the single burial of the Sunghir 1 adult. The use of red ochre, as well as the presence of ornaments on the forehead or around the neck, are commonplace in adult burials of the period (Chapter 10).

The immature dead rabbit placed across the child's lower legs and the possible meat offerings represented by the red deer pelvis recovered in contact with the child's feet and right shoulder have less well documented counterparts in the Middle Paleolithic and are the kinds of grave goods which are not uncommon in Gravettian burials. These faunal elements may be used to support notions of cultural continuity between the Middle and the Upper Paleolithic. To a certain degree, and at a broad scale of analysis, such a continuity is to be expected in the first place, but such elements cannot be interpreted as signaling the survival in the Gravettian of Portugal of features of culture that would have been characteristic of the preceding late Mousterian.

In Chapter 32, we argued that the only possible explanation for the anatomical mosaic apparent in the Lagar Velho child's skeleton is that, at least in the western periphery of the peninsula, the dispersal of early modern Europeans into Iberia involved extensive biological admixture with local Neandertals; sufficiently extensive that, a few millennia later, the evidence for such an admixture was present in different aspects of the morphology of the people then living in Portugal. No such evidence, however, is apparent in the realm of culture; burial ritual, lithic technology and typology, ornament types, art styles and habitat features of the Portuguese early Upper Paleolithic all link it to contemporary western European technocomplexes and provide no unambiguous clues to a putative survival of cultural traditions typical of the latest Mousterian (see below and Chapters 10 and 33). Therefore, there are no known cultural correlates of the process of biological admixture inferred from the child's anatomy. Such an absence has been used by some to oppose that interpretation, but their arguments are logically and empirically inconsistent (see Chapter 32).

The Middle-to-Upper Paleolithic Transition in Portugal

Technologically and typologically, the lithic industries from Estremadura (the region of Portugal where the Lagar Velho site is located) that are well dated to the period between 27 000 and 20 000 years ago fit comfortably within broader western European frameworks (Zilhão, 1995, 1997). The late Aurignacian and early Gravettian assemblages resemble what is known from the Aquitaine basin in terms of both the workshop facies (such as Vale de Porcos) and the lithic components recovered in highly specialized, ephemeral logistic sites (such as Pego do Diabo). Font-Robert points are unknown, and no assemblages can be securely assigned to the period between ca.25 000 and ca.23 000 BP. Such might be the appropriate chronostratigraphical slot for the *Fontesantense* industry, but this industry has been TL-dated to ca.38 000 BP at the eponymous site of Fonte Santa, and the issue of its true chronology remains unsettled (Zilhão, 2001d). Technological developments again follow a strikingly parallel track throughout the period coinciding with the onset of the Last Glacial Maximum, between ca.23 000 and ca.20 000 BP — the succession of “Proto-Magdalenian”, Terminal Gravettian (“Aurignacian V”), Proto-Solutrean, Lower Solutrean and Middle Solutrean industries has been recognized in both Estremadura and Aquitaine. Close correspondence between naming and definition, both typological and technological, exists between the two regions, and there is also strict synchronicity between them in the timing of the passage from one stage to the next (Zilhão, 1995, 1997, 2000a; Zilhão and Aubry, 1995; Zilhão et al., 1997, 1999).

As discussed in Chapter 10, the use of fox canines separates eastern and central Europe from southern Europe, where red deer canines are the only animal teeth in Gravettian burials and tend to be arranged in headdresses, as has also been inferred for the Lagar Velho child. The kinds of shells used enable further differentiation of the world of Gravettian burials into three “ornament provinces”: a central and eastern European province (characterized by beads,

bracelets and other items of body decoration made of mammoth ivory, by *Dentalium* fossil shells and by perforated fox canines), a southern, Mediterranean province (with *Cyclope* shells and perforated red deer canines), and a western, Atlantic province (with the same perforated red deer canines but this time associated with *Littorina* shells). Where Portugal is concerned, this pattern is strengthened by the fact that the ornament types associated with the Lagar Velho 1 child have counterparts in isolated finds from Gravettian habitation levels in such cave sites as Caldeirão (Zilhão, 1995, 1997) and Buraca Escura (Aubry et al., 2001).

A significant level of cultural uniformity across Atlantic Europe, consistent with the evidence from lithic technology, ornaments and burial ritual, is also indicated by the striking stylistic parallels between animal figures attributed to the Gravettian in the rock art of the Côa Valley, in northeastern Portugal, and in the cave art of the Pyrenees, Aquitaine and Ardèche areas of France (Guy, 1998). Moreover, campsites excavated in the Côa Valley have yielded TL dates for Gravettian levels that indicate broad contemporaneity with the Lagar Velho child burial (Mercier et al., 2001). At Olga Grande 4, for instance, the average of five dates on burnt quartzites from Gravettian level 3 is $27\,800 \pm 1800$ BP, a result that is consistent with the calibrated age of the burial. That level contained colorants that may have been related to the artistic activity in the valley, as well as quartzite picks used to peck the outlines of the animal figures engraved on the schist panels, as was established by use-wear analysis (Aubry, 2001). These items were associated with abundant lithic remains, including typical Gravettian microliths, organized around a very large hearth. A similar spatial organization of the habitat around extensive fire features is documented at another Gravettian site in the area, Salto do Boi (Cardina). Close parallels for these features and camp types are found in the Gravettian open air sites from the Rhône valley, notably Vigne Brun, at Villerest (Loire), radiocarbon dated to ca. 23 000 BP (Desbrosses and Kozłowski, 1994: p. 50).

These patterns in no way contradict the hypothesis of extensive population admixture at the time of contact derived from the particular anatomy of the Lagar Velho child. In fact, assuming that, in the framework of admixture, the resulting population should be expected to inherit from the different ancestral groups in the realm of culture as well as in the realm of biology overlooks the fundamental difference that exists between the two realms in terms of the mechanisms regulating the generational transmission of traits. The transmission of cultural traits is a Lamarckian process (characters acquired in one generation are passed on to the next), whereas the transmission of biological traits is a Darwinian process (adaptive characters randomly evolved in certain individuals eventually become predominant in the whole population over the long term because they are adaptive, i. e., because they favor the differential reproductive success of their offspring or become fixed through genetic drift in small populations). Consequently, whether a given technology or behavior is maintained and taught to the next generation or abandoned and replaced by something new is a matter decided upon by individuals and social groups. In contrast, whether a given anatomical trait will or will not be transmitted is determined by differential reproduction and is the domain of natural selection and drift, which is largely independent of human volition and whose scale of operation is the long-term, not the short-term. That is why, ultimately, population admixture and interbreeding are issues that must be decided upon the biological evidence, genetical and skeletal, not upon the archeological evidence, particularly when such evidence is scant and the order of magnitude of the chronological resolution of the data is the millennium, not the generation.

Therefore, in a scenario of admixture between Neandertals and early modern humans in Iberia, which, if any, cultural traits from the latest Mousterian survive in the generations immediately following the time of contact is an issue of historical contingency. The ethno-

historical record shows that a whole continuum of possibilities exists between the two conceivable poles of 1) admixture resulting in early modern humans fully adopting the culture of the local Neandertals and 2) admixture resulting in Neandertals fully adopting the culture of the incoming early modern humans. What exactly happened is a matter for empirical investigation and cannot be predicted from the fact of admixture itself, as revealed in an independent manner by features identified in the empirically independent realm of human biology. This said, the particular combination of anatomical features borne by the Lagar Velho individual is such that, taxonomically, he is best defined as “a modern human child with genetically-inherited Neandertal traits” (Trinkaus et al., 1999b). The fact that, anatomically, the child is principally a modern human, suggests an imbalanced interaction, with Neandertal populations being essentially absorbed and genetically swamped, with particular features characteristic of such populations being still present a few millennia after contact but disappearing subsequently. In such a scenario of absorption as is suggested by the biological data, it is not surprising, particularly given the much faster pace of change permitted by Lamarckian mechanisms of cultural transmission, that no specifically Mousterian traits of culture are to be found in the archeological record of Portugal ca.25 000 years ago.

That none are found either in the preceding time period, between 28 000 and 25 000 BP, i. e., that period which immediately followed the time of contact, is also not inconsistent with the admixture hypothesis. Where this particular time frame is concerned, our knowledge of the record is slim and essentially limited to stone tools. In the Caldeirão sequence (Zilhão, 1995, 1997), the stratigraphic succession shows that the blade/bladelet assemblage associated with ornaments made on marine shells recovered in layer Jb, dated to ca.26 000 BP, directly overlies the strictly Middle Paleolithic flake assemblage with no evidence for ornaments found at the top of layer K, dated to ca.27 600 BP. But the physical appearance of people in the periods immediately before and after 28 000 BP remains unknown, as do their burial and ritual traditions.

The pierced *Littorina* shells recovered in level Jb of Caldeirão are nonetheless suggestive of continuity with the subsequent time period of the Lagar Velho child and of discontinuity with the preceding Mousterian in aspects of culture other than lithic technology. This is consistent with an interpretation of the general hypothesis of admixture inferred from the child’s skeletal mosaic as a more concrete model of interaction where the last Neandertals of Portugal were absorbed by incoming modern humans resulting, in the domain of culture, in a swift loss of specifically Mousterian traditions, and, in the domain of biology, in genetic swamping with short-term (in an evolutionary perspective) survival of some specifically Neandertal anatomical traits. Where the issue of survival of cultural traits is concerned, however, one must always bear in mind that only a very small part of past behavioral repertoires survives until the present. Put another way, the fact that the Aurignacian and the earliest Gravettian of Portugal show no Mousterian influence only tells us that the lithic technology of post-contact times is that which was brought into the region by early modern humans. But this tells us very little about the nature, intensity and immediate outcome of the interaction with Neandertals in the realms of myths, beliefs, usages or perishable material culture, all of which remain inaccessible to us.

The Middle-to-Upper Paleolithic Transition in Europe

When the archeological, paleontological and paleogenetical evidence pertaining to the Middle-to-Upper Paleolithic transition in Europe is considered, the phylogenetic interpretation of the child’s mosaic anatomy not only makes sense, it matches expectations.

Arguments to the contrary have essentially been that admixture between Neandertals and early modern humans is simply inconceivable and, hence, cannot even be contemplated in the Lagar Velho case. Such arguments are as logically and empirically inconsistent as the objections discussed above and are of two kinds. The first is that Neandertals and early modern humans were different species and, hence, interbreeding would have been impossible by definition. The second is that the contrast in intellectual and behavioral capabilities between the two species must have been such that, even if possible from a biological-mechanical perspective, culturally, subjectively, interbreeding would in practice have been a taboo outcome in any instance of contact between individuals of the two species.

The fallacious nature of the first kind of arguments was discussed in Chapter 32. Where the second is concerned, it is essentially based on the notion that the “Upper Paleolithic” or “symbolic” revolution is a threshold separating full-blown humanity from preceding and contemporary biologically and culturally archaic, not-fully-human populations of the genus, and that such a revolution only occurred in the modern human lineage. Therefore, following this line of thought, when early modern humans spread into Europe, they encountered people (the Neandertals) who not only were not quite human, but were also perceived as such. Based on his view of a long-term contemporaneity between Châtelperronian Neandertals living in western and central France and Aurignacian modern humans living in northern Spain, Mellars (1999), for instance, suggested that “some fundamental barrier must have existed to prevent the total integration and assimilation of the two populations over this impressive time span of 5000-6000 years,” particularly given “the possibility of some occasional, short-term interpenetration between the two territories... of the kind apparently reflected in the reported interstratifications at Roc-de-Combe, Le Piage and El Pendo.” The fact that “the Châtelperronian and the Aurignacian remain clearly identifiable and sharply separated technological traditions over this prolonged span of time,” in spite of “the archaeological evidence for various forms of ‘acculturation’ or technology transfer between the two groups,” was then used to infer a “fundamental barrier to integration between the final Neandertal and earliest anatomically modern populations;” otherwise, that is, if “close social interaction and interbreeding between the two populations had occurred, then the Châtelperronian would surely have ceased to exist as a clearly distinct archaeological entity over a much shorter time span.” This, in turn, is said “to reinforce the view that we are dealing with two populations sharply separated biologically and behaviorally, possibly of different species and conceivably with some other basic social, cognitive, or psychological barriers to communication.”

Recent work (d’Errico et al., 1998; Zilhão and d’Errico, 1999; Zilhão, 2001a; Bordes, 2002) has shown that the empirical basis of Mellars’s view is flawed. The Châtelperronian predates the Aurignacian in all of the Franco-Cantabrian region, and the reported instances of interstratification are artifacts of post-depositional processes, not genuine evidence for long-term contemporaneity between the two technocomplexes. This in itself makes “acculturation”, “technology transfer” or “imitation without understanding” invalid explanations for the Upper Paleolithic features of the Châtelperronian, which include the production of symbolic items of material culture such as personal ornaments and decorated bone and ivory tools. If the early Aurignacian is indeed a proxy for early modern humans (and the currently available evidence does not preclude that Neandertals may have been its authors, at least in part), then, in the Franco-Cantabrian region, the contact between Neandertals and early modern humans was one between populations having achieved a similar stage of cultural development and, hence, between populations for which the null hypothesis that their cognitive capacities and behavior were equivalent cannot be refuted. A case can be made that much the same pertains across most of central Europe, given the technological continuity

between the Bohunician, the Szeletian and equivalent pre-Aurignacian early Upper Paleolithic technocomplexes and their regional Middle Paleolithic antecedents.

Mellars's view of a fundamental barrier preventing interbreeding and assimilation could be vindicated only if Neandertals and early modern humans had lived side by side for several millennia inside the same regions, with interpenetrating territories, but maintaining separate, independent, cultural identities. When analyzed from an adequate taphonomic perspective, however, the stratigraphic and chronometric data do not support such a notion in any region of Europe and, in particular, in Mellars's case study, the Franco-Cantabrian region. Those data do not support either the notion that, in the latter, such coexistence occurred across segregated territories with stable but fluctuating boundaries, such a fluctuation explaining the reported instances of interstratification. But they do suggest that, once Aurignacian early modern humans had replaced Châtelperronian Neandertals in the Franco-Cantabrian region, a stable frontier emerged that separated them from the Mousterian Neandertals who continued to thrive in Iberian regions to the south of the Ebro basin for at least five millennia (Zilhão, 1993, 2000b). Numerous analogies exist in the archeological and ethnohistorical records to show that such major geographical or ecological divides may function as long-lasting lines of separation between populations that are all fully modern both cognitively and behaviorally and, therefore, this "Ebro frontier" pattern does not support Mellars's view either. For instance, a much longer-lasting cultural barrier existed between New Guinea and Australia throughout the Holocene. Against the background of the occupation of the Pacific islands, the expanse of sea separating the two landmasses can only be considered as trivial. Nevertheless, agriculture never became established south of the Torres Strait until Europeans arrived, in spite of the fact that environments in Arnhem Land and elsewhere in northern Australia were no different from those in coastal New Guinea. The explanation for the "Ebro frontier", therefore, needs be no different from the explanation of the "Torres Strait frontier", i. e., historical and ecological, not biological or cognitive.

In this framework, the argument put forward by Mellars becomes nothing more than an iteration in archeology of the view discussed in Chapter 32 that a barrier preventing interbreeding and cultural assimilation must have existed simply because we are dealing with two different biological species. Not only is there no direct, one-to-one correlation between biology and behavior, not only is taxonomic separation at this level in any case irrelevant when it comes to assessing the possibility of admixture, but Mellars's line of reasoning also overlooks major biological and psychological evidence.

The diagnosis that Neandertals are a different species rests essentially on the morphological and genetic data, i. e., on the amount of difference with present-day humans recognized in the fossil anatomy and the mtDNA extracted from the bones of a few Neandertal individuals. In the use of mtDNA for phylogenetic purposes, however, the comparisons are restricted to the non-coding, hypervariable regions, so that only drift from a common maternal ancestor, not change brought about by adaptation, is measured. The anatomical comparisons, while providing abundant evidence for two distinctive groups of humans, have never been shown to reflect fundamental differences in behavioral capabilities (as opposed to shifts in the frequencies of habitual behaviors). Consequently, the data available have, by definition, no bearing on the issue of assessing the social, adaptive and reproductive capabilities of the compared groups.

Notwithstanding, the case could be made that differences in physical appearance between Neandertals and early modern humans were such that admixture would have been psychologically inconceivable, even if no significant differences in cognitive potential and levels of cultural achievement existed. Empirical data and experiments (see Kurzban et al.,

2001, for discussion and references) have been used to claim that, among humans, “encountering a new individual activates three ‘primitive’ or ‘primary’ dimensions — race, sex and age — which the mind encodes in an automatic and mandatory fashion (i. e., across all social contexts and with equal strength).” If categorizing people by race is a universal feature of human behavior, and if such a categorization predisposes one to discriminate between *us* and *them*, then “ingroup favoritism paired with outgroup indifference or hostility” is to be expected to a much greater extent when modeling interactions between individuals which differ not just in race but in species.

Psychology, however, suggests (Kurzban et al., 2001) that “although selection would plausibly have favored neurocomputational machinery that automatically encodes an individual’s sex and age, ‘race’ is a very implausible candidate for a conceptual primitive to have been built into our evolved cognitive machinery.” This is because “ancestral hunter-gatherers traveled primarily by foot and, consequently, residential moves of greater than 40 miles would have been rare. Given the breeding structure inherent in such a world, the typical individual would almost never have encountered people sampled from populations genetically distant enough to qualify as belonging to a different ‘race.’ If individuals typically would not have encountered members of other races, then there could have been no selection for cognitive adaptations designed to encode such a dimension, much less encode it in an automatic and mandatory fashion.” Thus, “the (apparently) automatic and mandatory encoding of race” must be instead “a byproduct of adaptations that evolved for an alternative function that was a regular part of the lives of our foraging ancestors: detecting coalitions and alliances.” In this context, a neurocognitive machinery designed to track shifting alliances would have been adaptive. Because “the actions that reveal coalitional dispositions are usually transitory, and so are frequently unavailable for inspection by others when decisions relevant to coalitional affiliation need to be made,” “alliance-tracking machinery should be designed to note these rare revelatory behaviors when they occur, and then use them to isolate further cues that happen to correlate with coalition.” Race gets involved at this stage; because of the correspondences detected between allegiance and appearance, “stable dimensions of shared appearance ... emerge in the cognitive system as markers of social categories.” In this regard, race is no different from dress, dialect or ethnic badges: a readily observable, rather arbitrary feature that “acquires social significance and cognitive efficacy when it validly cues patterns of alliance.” This hypothesis was tested by different experiments conducted with subjects that “had experienced a lifetime in which ethnicity (including race) was an ecologically valid predictor of people’s social alliances and coalitional affiliations. Yet less than 4 minutes of exposure to an alternative social world in which race was irrelevant to the prevailing system of alliance caused a dramatic decrease in the extent to which they categorized the others by race.” Kurzban et al. (2001) concluded from this that “coalition, and hence race, is a volatile, dynamically updated cognitive variable, easily overwritten by new circumstances.”

In order to better grasp the European situation between ca.40 000 and ca.30 000 BP, this evidence needs to be compounded with realistic evaluations of the extent to which Neandertals could have been represented as *them* on the basis of their physical appearance alone. It is in this regard significant that it is to one of the most prominent advocates of the fundamental separateness of Neandertals, Carleton Coon (1939: p.24), that we owe the observation that, in reference to an artist’s reconstruction of a Neandertal man in modern western clothing, “our impressions of racial differences between groups of mankind are often largely influenced by modes of hair dressing, the presence or absence of a beard and clothing.” Two decades later Straus and Cave (1957: p.359) stated that if the La Chapelle-aux-Saints Neandertal “could be reincarnated and placed in a New York subway — provided that he were

bathed, shaved, and dressed in modern clothing — it is doubtful whether he would attract any more attention than some of its other denizens.” Indeed, several more recent anatomically accurate reconstructions of Neandertals (by Anderson and Trinkaus, Daynès, the Neanderthal Museum, etc.), have highlighted the issue reflected in the quotes from Coon and Straus and Cave; those features which, under a cladistic perspective, lead to the classification of Neandertals as a different species correspond to anatomical particulars which would have been inaccessible to a Paleolithic observer. In any concrete situation of contact, for example, no early modern human would have been capable of assessing whether the other did or did not have a suprainiac fossa, if his labyrinth had a proper orientation, or if his bregma-lambda curvature was sufficiently high (Fig. 34-1). And, in those features of the Neandertals that would have been accessible for observation — stature, skin, eye and hair color, shape of the face and forehead — those *other* people would not have fallen outside the casually perceived range of variation which may well have existed among early modern humans (given the large superciliary arches and low frontal profiles of a number of them).

Therefore, using the fact that Neandertals and early modern humans *might* have been different species to argue against the possibility of interbreeding in fact amounts to a fundamental misunderstanding of the relation between scientific categories and empirical reality and to a reification of the former as if they were reality itself. Ethnobotany and ethnozoology are full of examples of taxonomic systems which differ from those of modern science simply because

they are designed for action in daily life and hence are based on different, utilitarian parameters. Our knowledge of what actually happened at this time is reduced, but it nonetheless allows us to reject the possibility that early modern humans dispersing into Europe categorized the human landscape they encountered along the lines of present-day paleontology.

Understanding what happened at the time of contact between Neandertals and early modern humans in Europe, therefore, requires that we move away from the *a priori* categorization of them as different hominid taxa and picture the situation in terms of individuals and social groups operating in real time and in real geography, in a world of small bands, of travel by foot, and of low population densities. The perception that, to us, with the benefit of being able to sample across whole continents and tens of thousand of years, they were different races, or different species, does not mean that the concrete actors on the ground behaved in the framework of assumed identities of *us* moderns versus *them* Neandertals. An early modern human camping at Isturitz, in the French Basque country, 35 000 years ago, would not have been aware that his ances-

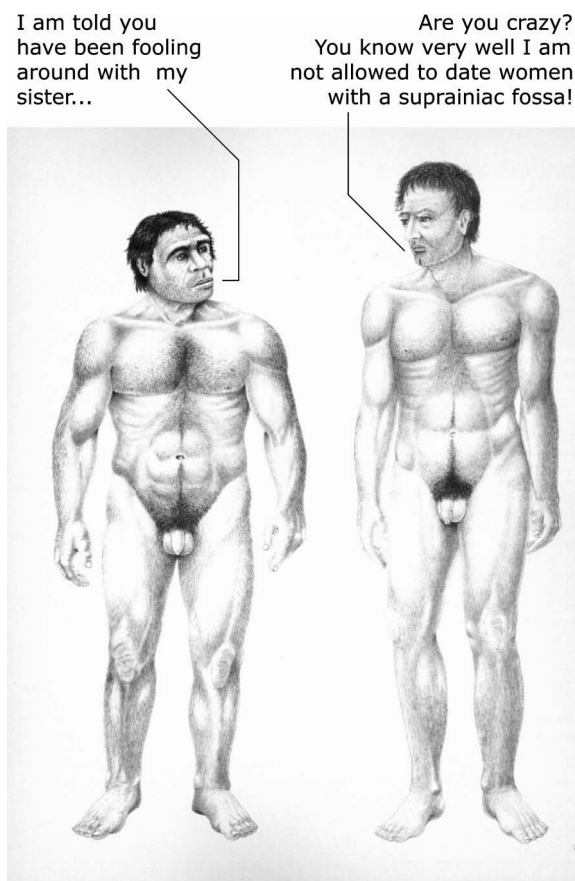


FIG. 34-1 – A conversation between a Neandertal and a modern human that we can be sure never actually took place ... and not because of language problems! [modified after a drawing by Carles Puche in Arsuaga et al., 2001b, p. 325]. With permission of the editor.

tors had come from Africa, would not even be aware that people like him occupied all available land to the east, across the great European plain and southern Siberia. In fact, he would not be aware that such things as the continents of Europe, Asia and Africa existed in the first place, much less that his biological, individual and social identity could be based on the fact that he shared with people living in those continents a common ancestry and a number of physical traits separating them from the people living to the south and southwest.

The decisions that our hypothetical Isturitzian had to make when it came to dealing with meridional neighbors must have been decisions on issues of coalition and alliance, and the questions being asked most certainly were of the kind “is this person healthy?”, “is this person good-looking?”, “is this young person old enough to be a suitable mate?”, “can those people be trusted as allies?”, “if we have to fight those people, can we win?”, “is access to those people’s land and its resources worth the trouble of having to deal with them?” Physical appearance, as well as differences in culture, must have played a role as cues to the categorization of the actors involved, so that, in the above list of questions, one could conceivably replace “those people” with something like “those stocky fair-skinned folk who paint their bodies and hunt their deer with spears instead of javelins.” We know that the ultimate outcome of the infinite number of such decisions made by the real people on the ground in Europe at the time was the disappearance of the Neandertal phenotype sometime after 30 000 BP. In a long-term, evolutionary perspective, therefore, it is appropriate to say that Neandertals were replaced by early modern humans. But this tells us nothing about the concrete historical features of the short-term processes whose cumulative consequences led to such an outcome.

It is at that scale of analysis that the mosaic anatomy of the Lagar Velho child becomes relevant, particularly in its contrast with contemporary Gravettian skeletons from central and eastern Europe which lack clear Neandertal features. Such skeletons, however, date to 10 000 years after the time of contact, as opposed to only 3000 years in the Portuguese case. Therefore, the absence of such traits may have at least two different interpretations (Zilhão, 2001a, 2001b; Zilhão and Trinkaus, 2001; see also Chapter 32). In the core areas of continental Europe, mutual avoidance may have been the rule and interbreeding rare or insignificant, with short-term Neandertal extinction coming about as a result of differential fertility, of the fragmentation of social territories and of the demographic side effects of such factors. Alternatively, interbreeding also occurred at the time of contact but the anatomical traits inherited from Neandertals vanished after only a few thousand years, through the operation of demographic or genetic processes that remain to be modeled. This second hypothesis is consistent with the fact that archaic traits have been diagnosed on the early modern human skeletal material from Mladeč (Wolpoff et al., 2001), possibly of early Aurignacian age, as well as with Smith’s (1984) suggestion that a genetic input from early modern humans explains the gracile features of the Neandertal remains from Vindija Level G₁, radiocarbon dated to ca.29 000 BP (Smith et al., 1999).

These data also highlight that, even if Mellars’s long-term contemporaneity across a rather stable frontier separating Aurignacian early modern humans in northern Spain from Châtelperronian Neandertals in southern France can no longer be retained as a valid hypothesis, such situations did indeed exist not only in the Iberian case but also in other parts of Europe (Zilhão 2001a). Much the same may have occurred with regions around the Black Sea, in the Crimea and northern Caucasus, where Middle Paleolithic Neandertals seem to have survived until ca.30 000 BP (Marks and Chabai, 1998), whereas early modern humans with an early Upper Paleolithic tool-kit are known to have settled the Russian plain at least since ca.33 000 BP, given the direct date for the human remains in Level III of Kostenki 1 (Richards et al., 2001). The Neandertal populations of the Slovenian and Croatian karst, in particular,

seem to have survived for several thousand years after the loess plains of Moravia and southern Germany were first settled by early modern humans some time after 36 000 BP. In this case, the contemporaneity seems to have been between archeologically Upper Paleolithic people (Szeletian or Olchevian and Aurignacian) on both sides. The same may obtain where the now flooded plains of the British Channel are concerned, since they quite likely stably separated for a few millennia the early modern humans of Aurignacian France from the Lincombian Neandertals who may have survived in southern England until ca.30 000 BP, no evidence for modern humans being known in the region before about that time (Aldhouse-Green and Pettitt, 1998). As argued above, these situations do not vindicate assertions that they imply some fundamental barrier to assimilation and interbreeding between the populations living on each side of the frontier. What they do is present us with a challenge to explain why the spread of early modern humans was punctuated by such moments of stability, to explain how that pattern may relate to the nature of their cultural adaptations and to ecological competition with Neandertals, to find out when, why and how such frontiers eventually disappeared, and, in each concrete instance of such a disappearance, what was the outcome in terms of the culture and biology of the human groups living in those regions in subsequent times. Where Iberia is concerned, and in the light of the biological evidence provided by the Lagar Velho child, we take up that challenge in the following section.

Establishment and Disappearance of the Ebro frontier

In the period between ca.36 000 and ca.30 000 BP, two technocomplexes are documented in the Iberian Peninsula, the Aurignacian and the Mousterian. In the Cantabrian strip, in the Basque country and along the southern flank of the Pyrenees, in Aragón and northern Catalonia, all archeological contexts securely dated to that period are Aurignacian. Conversely, south of the Ebro basin, along the Mediterranean coast of Spain, and in Andalucía, Portugal and the Meseta, all archeological contexts securely dated to that period are Mousterian, and dates for the Aurignacian are no earlier than ca.30 000 BP. Such late dates for the Aurignacian of these regions are consistent with the fact that, typologically, the bone and lithic assemblages found therein do not contain split-base bone points and lithic types characteristic of the Aurignacian I, whereas such items are commonly found in the chronometrically earlier assemblages (such as those excavated in the sites of La Viña, Isturitz or l'Arbreda) from regions to the north. The Ebro frontier model suggests that this distribution reflects a real and lasting spatial segregation between the two technocomplexes and, given their known associations with different hominid forms, between early modern humans to the north and Neandertals to the south.

The model also hypothesizes that this episode of stasis in the westward spread of early modern humans must have been somehow related to the fact that the Ebro basin represents a major biogeographical divide between the Iberian and Eurosiberian domains. During later OIS 3 times, peninsular environments to the south of the Ebro basin would have been predominantly temperate, contrasting with the more open, steppe-like landscapes to which early modern humans dispersing across the central European plain would have become culturally adapted. Iberian Neandertals would have survived largely in isolation from early modern humans established to the north because, as the climatic conditions of later OIS 3 gradually set in, they had been able to develop successful adaptations to the kinds of environments created by such conditions, whereas those environments were unattractive to the steppe-adapted early modern humans. Hence, competition between the two populations for

the territories of Iberia did not develop until climatic deterioration began to favor the southward expansion of the kinds of environments preferred by southwestern European early modern humans, who expanded with them. In global records, the first signs of this deterioration coincide with the first appearance of the Aurignacian in eastern and southern Spain and in Portugal and, under the model's assumptions, with early modern humans taking over those regions previously occupied by Neandertal groups.

In spite of some claims to the contrary, results of research carried out since the original formulation of the model in the early 1990s (Zilhão, 1993; for a concurring view of the process see also Arsuaga, 2000, p. 354-355) have been consistent with its basic tenets or, at least, have not refuted them. The very late survival of the Mousterian in Portugal documented at such sites as Foz do Enxarrique, Gruta do Caldeirão and Gruta da Figueira Brava has been confirmed by the dates of $31\ 900 \pm 200$ BP (GrA-10200) and $32\ 740 \pm 420$ BP (OxA-8671) obtained on burnt bone samples from Level 8 of the long and rich Middle Paleolithic sequence currently under excavation in the Gruta da Oliveira, Almonda karstic system (Zilhão, 2000b). Even if doubts have arisen concerning the real age of the Zafarraya mandible (Barroso Ruiz, 2001), the late dates for the Zafarraya Neandertals based on stratigraphically secure samples (Hublin et al., 1995) have not been entirely refuted. Moreover, the association of Neandertals with the latest Iberian Mousterian has been established at Cabezo Gordo, Murcia (Walker 2001a, 2001b), where levels containing diagnostic Neandertal remains and overlain by ca. 2 m of deposits also containing Mousterian lithics have been dated to $34\ 450 \pm 600$ BP (OxA-10666). Furthermore, Garralda and Vandermeersch (2002) have pointed out the non-diagnostic nature of all human remains associated with the earliest Aurignacian of southwestern Europe, which means that it cannot be decided at present whether early modern humans were indeed responsible for the manufacture of such assemblages, although this is still quite possible (Zilhão and Trinkaus, 2001).

Claims of a long-term contemporaneity between Mousterian or Châtelperronian Neandertals and Aurignacian early modern humans have also been made for northern Catalonia, and they are taken to imply that the Ebro frontier never existed, the Middle-to-Upper Paleolithic transition and the replacement of Neandertals by early modern humans having been a mosaic process across the whole of Iberia (e.g. García et al., 2001). This is based on chronometric results obtained at two sites, Fuentes San Cristóbal (Huesca) and Ermitons Level IV (Girona). In the first site, a Mousterian point is the only artifact recovered in an archeological level dated to ca. 36 000 BP, a result that in no way is inconsistent with the hypothesis that there is no Mousterian in the region after the arrival of the Aurignacian, which, as exhaustively argued elsewhere (Zilhão and d'Errico, 1999), takes place no earlier than ca. 36 500 BP (in spite of claims to the contrary based on earlier interpretations of the Aurignacian of l'Arbreda and Reclau Viver). At Ermitons, Level IV yielded two dates, $36\ 430 \pm 1800$ BP (CSIC-197) and $33\ 190 \pm 660$ BP (OxA-3725). Maroto et al. (1996) have argued that the second date, from an unidentified bone sample collected in the stratigraphic profile and obtained through AMS, is more reliable than the first, conventional result and would prove a survival of the Mousterian in the region until well after the arrival of the Aurignacian. That level, however, is a cave bear den, and the most parsimonious interpretation of the evidence is that cave bear lived at the site ca. 33 000 BP, long after it was abandoned by the human group who discarded the few Mousterian lithics (69 pieces in all, including unflaked pebbles and chunks — Ortega and Maroto, 2001) recovered in the level.

Where the age of the Aurignacian south of the Ebro basin is concerned, the $29\ 940 \pm 150$ BP date for Level IV of Sector I of Cova Foradada (Alicante) (Casabó, 2001) is identical to that of $29\ 690 \pm 560$ BP (KN-1/926) for Level XII of the nearby site of Cueva de Mallaetes

(Valencia) (Fortea and Jordá, 1976). A significantly earlier result of $33\,900 \pm 1100$ BP (AA-1388) has been published for Level 4 of Cova Beneito (Alicante), but the level lacks stratigraphic integrity and the association between the dated sample and the Upper Paleolithic items found therein is far from demonstrated (Villaverde et al., 1998). Two AMS results of ca. $33\,000$ BP have been reported for charcoal samples collected in Aurignacian Level 11 of Cueva Bajondillo (Málaga), but these results are in contradiction with TL dates of ca. $28\,000$ BP for underlying Levels 13 and 14, the former Aurignacian and the latter Mousterian (Baldomero et al., 2001). At Gorham's Cave (Gibraltar), the earliest Upper Paleolithic in Context 9 yielded four AMS charcoal dates comprised between $29\,250 \pm 650$ BP (OxA-7077) and $30\,250 \pm 700$ BP (OxA-7076), and the date of $32\,280 \pm 420$ BP (OxA-7587) for the charcoal lens defined as Context 24 provides a *terminus ante quem* for the site's Middle Paleolithic sequence (Pettitt and Bailey, 2000). Thus, although it cannot be excluded that Bajondillo will eventually provide sounder evidence for an arrival of the Aurignacian in southern Spain significantly earlier than is postulated by the Ebro frontier model, the fact is that, so far, the earliest Upper Paleolithic is still dated to no earlier than ca. $30\,000$ BP everywhere else along the coasts of Valencia, Murcia and Andalucía. And, in the Meseta, the Aurignacian is still unknown, whereas Mousterian assemblages have been shown to survive until $32\,600 \pm 1860$ BP (Beta-56639) and $29\,500 \pm 2700$ BP (Beta-56638) in upper Level 2 of the Jarama VI cave (Guadalajara) (Jordá, 2001).

Therefore, regardless of which were the causes, biogeographical or other, behind its establishment and ultimate disappearance, the Ebro frontier still stands as a descriptive model of the Middle-to-Upper Paleolithic transition in Iberia and the ultimate replacement of peninsular Neandertals by early modern humans dispersing into it from regions further to the north (Fig. 34-2). Therefore, assuming that the "when" question is pretty much set-

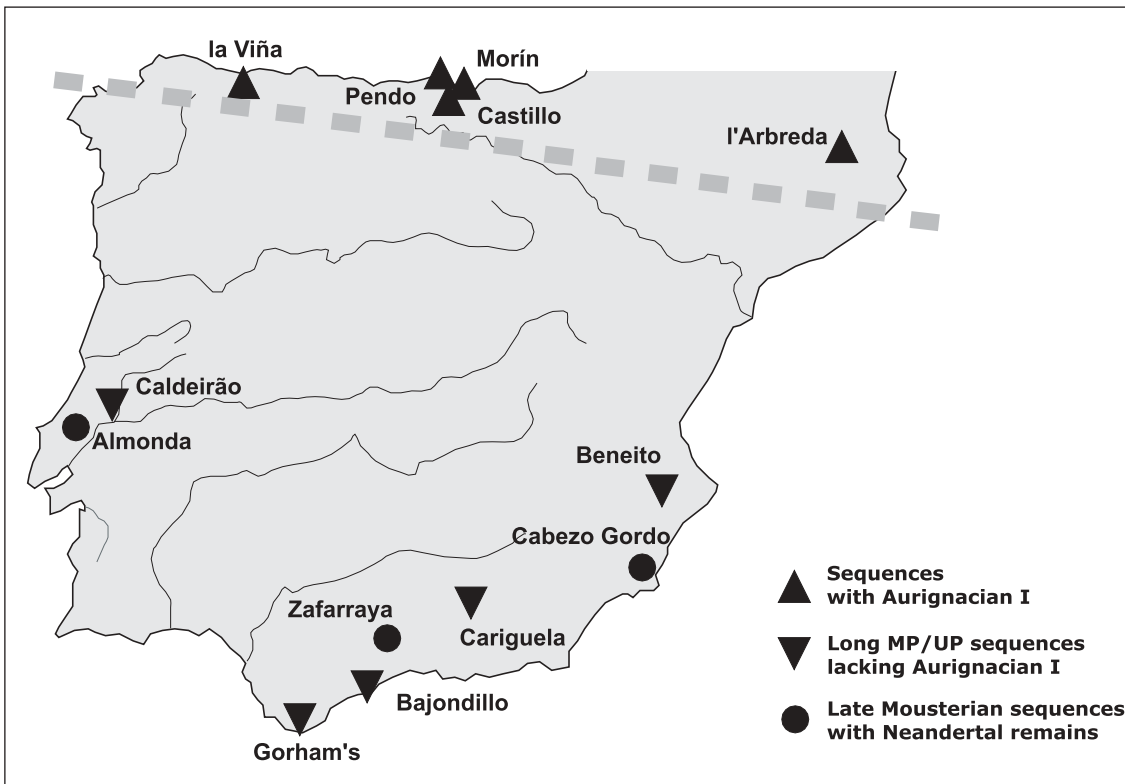


FIG. 34-2 – The Ebro frontier model.

tled, and leaving aside for the moment the “why” question, the interpretation of the Lagar Velho child as evidence for admixture inevitably raises the “how” question and creates the need to use the available data to discuss the nature of the different mechanisms conceivably involved. As an introduction to such modeling work, which requires extensive simulation yet to be carried out, and in order to allow for a better definition of the issues and assumptions at stake, we provide openly simplified graphical illustrations of the different variations of what the process might have been in Figs. 34-3 to 34-5.

Modeling assumptions are that bands are evenly distributed across the Iberian landscape, that each band is made up of 25 individuals, that the population density is $0.01/\text{km}^2$, and that the area of Iberia available for occupation at the time was of $ca.500\ 000\ \text{km}^2$. Hence, the peninsula would have been inhabited by 200 bands for a total of 5000 people, and each band exploited territories of $ca.2500\ \text{km}^2$. Initially, $ca.36\ 000\ \text{BP}$, 35 such bands (875 people) would be composed of “pure” modern humans inhabiting regions to the north of the Ebro, and the remainder 165 (4125 people) would be composed of “pure” Neandertals inhabiting regions to the south of that divide (Fig. 34-3a).

Fig. 34-3b illustrates what the situation might have been $ca.30\ 000\ \text{BP}$, some time after early modern humans had begun to disperse into previously Neandertal territory, and it assumes that no significant gene flow occurred across the Ebro for the $ca.6000$ years of stable geographical segregation between the two populations. The assumptions under the pattern in Fig. 34-3b are that there still is no interbreeding and that, as a result, a frontier is maintained, and such a frontier moves westward and southward in a gradual, linear way, as in Ammerman and Cavalli-Sforza (1973)’s “wave of advance” model of the spread of farming across Europe. The 175 bands of early modern humans in Fig. 34-3b are therefore made up of 4375 biologically “pure” people, as are the 25 remaining bands of Neandertals. Given the fixed nature of the westernmost territorial boundary (the Atlantic seaboard), in a mutual avoidance scenario (i. e., one in which Neandertals retreat as early modern humans advance) and in order to accommodate all 4125 Neandertals that lived in the peninsula before early modern humans started to spill across the Ebro, each of those 25 band territories would now have to accommodate 165 persons, or 165 band territories would now divide between them an area previously occupied by only 25 such territories. In either case, population density among Neandertals would have increased to 0.066 persons per km^2 . Further reduction to only half the area but maintaining population size would bring those numbers up to 0.132 , 13 times higher than in the original modeling assumptions. In the end, when only one territory of $2500\ \text{km}^2$ is left, those 4125 Neandertals would be packed at an impossible density of $1.65/\text{km}^2$. Clearly, mutual avoidance with Neandertals retreating elsewhere as early modern humans advance is simply not a realistic scenario. However, if Neandertals go extinct locally as the wave of advance moves on, then Fig. 34-3b can be read as displaying a situation where the Neandertal population is down to only 625 individuals. If there is no interbreeding with early modern humans, given the spatial distribution of the bands on the ground, finding mates at the peripheries becomes more and more difficult and extinction is now imminent. Within very few generations, an early modern human on the ground in the Lisbon area might be able to tell and retell his folk gathered at night around the fireplace the fascinating story of “Ishi (Kroeber, 1961), the last Neandertal” (Fig. 34-3c).

In Fig. 34-4a, the wave of advance spread of early modern humans is modified to incorporate interbreeding. As a result, a hybrid zone (Jolly, 2001) between “pure” Neandertals and “pure early modern humans” is formed. If gene flow from the east is constant, the hybrid zone will display a cline in the weight of Neandertal features, with groups closer to the Pyrenees being “hybrid moderns”, i.e., closer to “pure” early modern humans,

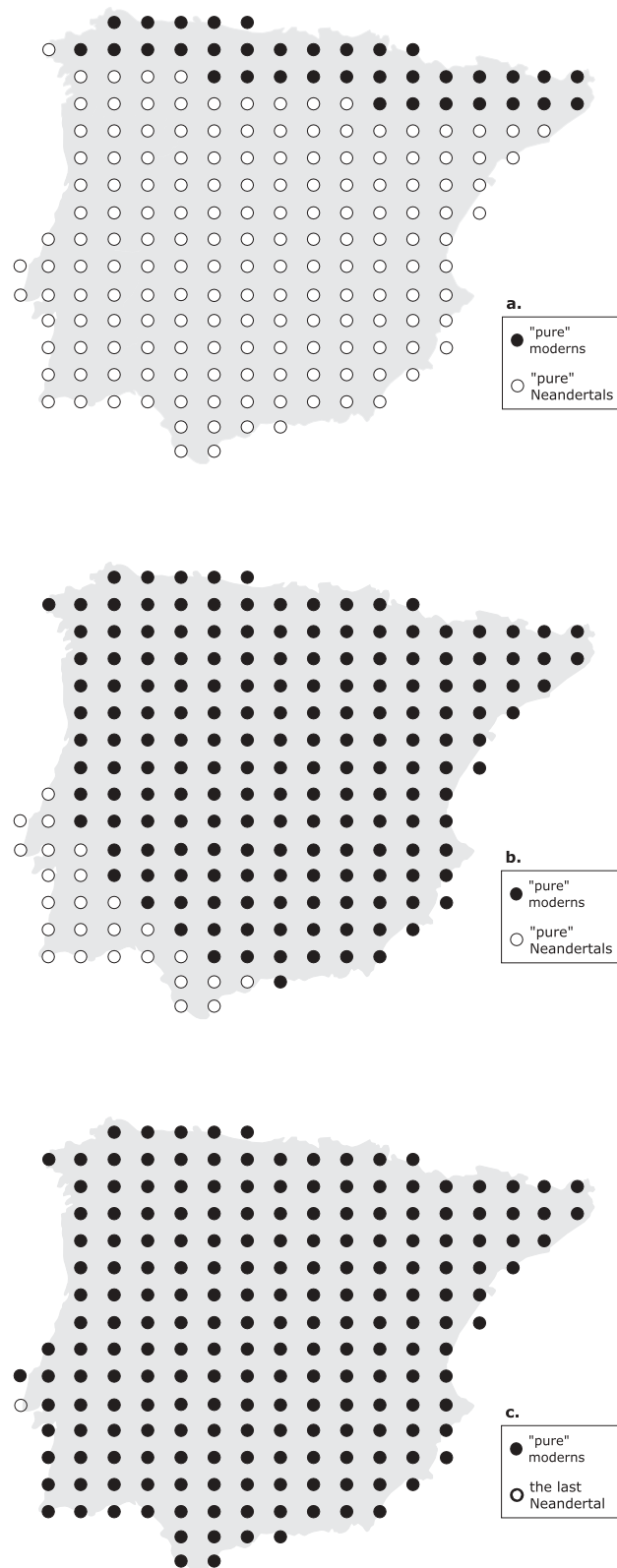


FIG. 343 – Disappearance of the Ebro frontier through a gradual, linear, wave of advance expansion of modern humans, with no interbreeding. a) step 1: the initial situation, some time between ca.36 000 and ca.30 000 BP; b) step 2: ca.30 000 BP moderns occupy most of the Iberia and Neandertals are restricted to the southwestern periphery of the Peninsula; c) step 3: “Ishi, the last Neandertal” dies with no offspring somewhere near Lisbon.



FIG. 34-4 – Disappearance of the Ebro frontier through a gradual, linear, wave of advance expansion of modern humans, with interbreeding. a) step 1: a hybrid zone is established displaying a northeast-southwest gradient of increasing of weight of Neandertal features; b) step 2: with continuing gene flow from the east, the “pure” Neandertal phenotype disappears; c) step 3: modern humans with genetically-inherited Neandertal traits occupy the southwestern periphery of Iberia, a “pure” modern phenotype prevails everywhere else.

and groups closer to the western and southern Atlantic coasts being “hybrid Neandertals”, i. e., closer to “pure” Neandertals. Several generations later (Fig. 34-4b), continued gene flow from the east would have eliminated the “pure” Neandertal phenotype, and individual Neandertal features all but disappear among groups occupying the northeastern half of the peninsula, although they are still present, albeit in lower frequencies, among the descendants of people living in parts of the hybrid zone of the previous stage. Given some more time (Fig. 34-4c), such features will only survive among people inhabiting southern Portugal and western Andalucía. Taxonomically, if their remains were ever found, those people would have to be classified as “modern humans with genetically-inherited Neandertal traits” — i. e., the Lagar Velho child. At that time, everybody else in Iberia is now “pure” modern.

A different scenario is modeled in Fig. 34-5. Bands of early modern humans are assumed to penetrate rapidly and deeply into areas beyond the Ebro divide situated along the coastal plains and the major rivers valleys that drain the Meseta. In doing so, they may have been occupying territory uninhabited by Neandertals or from where Neandertals retreated as early modern humans expanded. Among low density populations of hunter-gatherers, conditions to find mates are generally that one is guaranteed to be available in a universe of ca.400 people defined in such a way that residential moves of more than 200 km are not required (Smith, 1992), i. e., a universe such as that defined by the hexagons linking bands A and B in Fig. 34-6 with their 16 closest neighbors. If interbreeding does not take place, the model’s assumption of a population density of 0.01/km² implies that an individual in a band at the head of the early modern humans’ expansion front would need a mating network extending over some 500 km. The same would be true of individual Neandertals in groups surviving in the westernmost outposts of their world. Under these circumstances, therefore, interbreeding makes ecological sense and is likely to have been subjectively considered desirable and adaptive from the perspective of both sides. Thus, if a scenario of mosaic deformation of the frontier is assumed, mating networks must incorporate both Neandertal and early modern human bands, a hybrid zone exists as in Fig. 34-4 and, consequently, the different settlement nodes of that zone coded in Fig. 34-5 as “modern” and “Neandertal” should in fact be read as “predominantly modern” and “predominantly Neandertal”. Ultimately, with continued gene flow from the east, the general biological outcome of the process is as in Fig. 34-4c, even if its concrete historical features were significantly different in cultural detail.

These examples suffice to show that, against the current empirical and theoretical background, the only viable way to explain the replacement of Neandertals by early modern humans without assuming extensive interbreeding is the “Ishi, the last Neandertal” model outlined in Fig. 34-3. One must bear in mind, however, that the historical analog of that model was entirely exceptional, occurred in a situation of overwhelming technological disparity and demographic disadvantage (bow and arrow Native American hunters of California against industrial age European settlers), none of which can be realistically assumed for Late Pleistocene Iberia. Moreover, the extreme concealment strategy followed by Ishi’s people (the Yahi, a subgroup of the Yana tribe) in the latter part of the nineteenth century was the rather idiosyncratic and desperate reaction of an uncommonly spirited and resilient group to their recognized failure in opposing the progressive penetration and encroachment of their territories by the California goldrush prospectors and their descendants. Rather than the rule, such a mode of resistance to, or denial of change, was in fact exceptional among Native Americans.

This strategy was adopted in 1870, at a time when Ishi was a little boy, after three women from the group were captured into the “white world.” This episode was the last in a

string of losses of lives and reproductive potential, mainly through a number of massacres carried out by white vigilante groups, that brought the number of Yahi down from the 300-400 inferred to have been alive in 1865 to the only 15-16 who went into concealment. When he surrendered in August, 29, 1911, Ishi was the last survivor of the group, and he had been living in complete human loneliness in a territory of no more than 5 km² since the death of his old mother, in November of 1908. He left no direct descendants, but his people's genes were nonetheless transmitted to the following generations by one of the women abducted in 1870, to whom a child was born in the winter of 1870-1871. The subsequent history of this child is unknown, but he is likely to have blended into the California frontier. Instances of survival and blending of individuals of the Yahi's close neighbors and members of the same language group, the Yana, are in any case well documented. The bottom line is that interbreeding occurs even in such extreme cases.

Therefore, the phylogenetic interpretation of the Lagar Velho child presented in Chapter 32 not only is that which best fits available paleontological and paleogenetical data. It also matches logical expectations given the concrete geographical and historical features of the process, i. e., when the hypothesis is evaluated against the human landscape of Iberia between ca.36 000 and ca.30 000 years ago and realistic models of hunter-gatherer behavior are used.

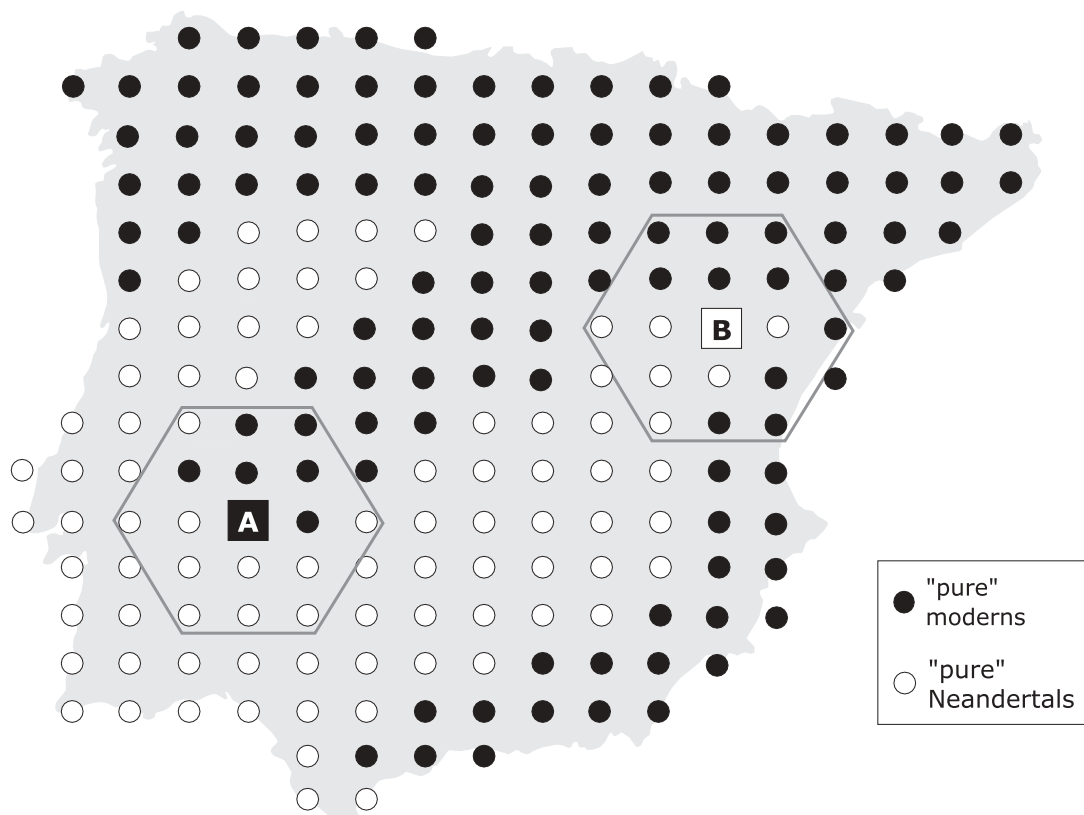


FIG. 34-5 – Disappearance of the Ebro frontier through mosaic expansion of early modern human groups penetrating deep into Neandertal territory, southward along the Atlantic and the Mediterranean coasts, westward along the Tagus Valley. Interbreeding is required for the normal operation of mating networks.

Conclusion

Binford (1983) has argued that, among mammals, including humans, fertility is higher among tropical populations than among subarctic ones. This is consistent with, and may be largely the product of, longer birth intervals produced by later weaning among high latitude human populations. Assuming that this applies to the European Neandertals, compared to their African contemporaries, it may help to explain some of the dynamics of the Neandertal to early modern human transition across Europe.

During the cold phases of the Late Pleistocene, principally much of OIS 4 to 2, most of Eurasia was uninhabitable. The northernmost areas were covered by ice sheets and barren tundras, and population densities in the settled areas must have been much lower than in equatorial areas such as much of Africa. Consequently, it is quite likely that, between 100 000 and 45 000 years ago, a large majority of the planet's human beings lived in Africa, where modern morphology evolved.

Given these two circumstances, it may be possible to explain why that early modern human morphology prevailed across the whole of the Old World after ca.30 000 BP. When adaptive success brought about population increase approaching the continent's carrying capacity, African groups started to disperse into the neighboring regions, a process that may have been enhanced by the OIS 3 climate warming. Given enough time, even a very small difference in fertility would put the smaller, scattered and demographically unstable populations of Neandertals at a demographic disadvantage, especially if interbreeding was common (Zubrow, 1989). In fact, if the relation between Africa and Europe between ca.45 000 and ca.35 000 BP is modelled after that outlined above for the relation between Europe and Iberia between ca.36 000 and ca.30 000 BP, then continuous gene flow from Africa must ultimately predict the extinction of the Neandertal phenotype, as is documented in the archaeological and paleontological records.

What such models cannot predict, however, is exactly how such an extinction occurred in the many different time-space landscape units involved. That is exactly where the Lagar Velho child becomes of relevance; it provides a precious window of visibility into the nature of the replacement-through-admixture process in one such unit. Moreover, it shows eloquently that we can learn as much about the expansion of early modern humans by studying the process in the different ends-of-the-world where morphologically archaic humans survived longest as by studying it in their core area of origin, Africa.

The child's anatomy suggests that, biologically, the early Upper Paleolithic people of Portugal descended from a process of extensive admixture occurring at the time of contact between early modern humans dispersing into Iberia and the last Neandertals. Culturally, the most salient cultural achievement of those early Upper Paleolithic people is the open-air rock art of the Côa valley (Baptista, 1999). Thus, the fact that it contributed to the clarification of many issues of modern human emergence in Europe should not overshadow the Lagar Velho find's broader significance for Iberian archeology: that it brought to us a "portrait of the artist as a young child".