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THE RESEARCH PROBLEM

IN THE ANTHROPOLOGY OF HUMAN ORIGINS, FEW SUBJECTS HAVE STIMULATED AS much research or generated as much controversy as the Neandertals. Most debates have centered on the problem of their affiliation and interaction with early modern humans during the Middle to Upper Paleolithic transition, a period dated roughly between 40 and 30 thousand years ago (kilo-years ago or ka) in western Europe. Important cultural changes are recorded during this episode. Most notable are the emergence of art, personal ornaments, and elaborated bone technology; the diffusion of laminar (blade) and lamellar (bladelet) reduction sequences; the diversification of stone tool types; and the transfers of raw materials over large (>100 km) distances.

Today, it is universally accepted that Neandertals were the only human population present in western Europe during the Mousterian. The faunal evidence indicates that Neandertals primarily hunted large ungulates, with an emphasis on prime-aged individuals (Burke 2000, 2004; Grayson and Delpech 2003; Steele 2004; Morin 2008). The Mousterian Neandertals produced various Levallois-based industries, although several other concepts of core preparation, including blade reduction sequences, are also documented (Delagnes et al. 2007). In contrast, an overwhelming body of data indicates that modern humans were the only occupants of western Europe after the Middle to Upper Paleolithic transition, with the possible exception of Iberia, where Neandertal skeletal features are said to have persisted until ca. 30 ka (Hublin et al. 1995; Churchill and Smith 2000).

Although there is wide agreement on the taxonomy of the human occupants of western Europe before and after the Middle to Upper Paleolithic transition, there is little consensus on the nature of the biological and cultural changes associated with the transition itself. This book reexamines this transition, the study of which has produced contradictory, if intriguing, hypotheses about our relationship to Neandertals. Of special concern in this book is the issue of whether Neandertals and early modern humans differed appreciably in terms of foraging patterns.

Two models, based primarily on biological evidence, have arisen since the 1980s as solutions to the problem of modern human origins. The first, the recent out-of-Africa model or, more simply, the replacement model, asserts that modern humans emerged in Africa at least by 160 ka and spread into Eurasia to replace Neandertals and the other archaic sapiens (Stringer and Andrews 1988; Mellars 1996; Klein 2008). Authors supporting this model generally consider Neandertals to differ biologically and culturally from
early modern humans, many viewing them as different species. A selective advantage favoring modern humans over Neandertals is usually put forward as one of the main causal mechanisms that permitted the replacement of the archaic *H. sapiens* populations.

Replacement scenarios differ from most other archaeological hypotheses because they imply the coexistence of two human species or semi-species, a situation that has no close analogue today. Because Neandertals and early modern humans are extinct populations, hypotheses about their interaction in the Late Pleistocene must be based on indirect evidence, such as human skeletal remains, ancient DNA, lithic assemblages, and archaeofaunas. As a result, linking the static archaeological remains with current observable phenomena is critical to our understanding of the Middle to Upper Paleolithic transition.

The second model, known as the *multiregional model*, posits that Neandertals were connected with early modern humans through gene flow and that they contributed to the gene pool of subsequent populations (Thorne and Wolpoff 1981; Wolpoff 1999). Partisans of this model also assert that Neandertals were a small *H. sapiens* population found at the periphery of the human distribution. In response to local evolutionary pressures, Neandertals are argued to have developed characteristics that distinguished them from other, more centrally located populations with which they exchanged genes.

These two polarized hypotheses about Neandertal and modern human relationships have generated considerable debate and research. Numerous tests of the models just described, including several studies that favor intermediate positions (e.g., Eswaran *et al*. 2005; Trinkaus 2007), have been published in an attempt to shed light on the origins of modern humans in Eurasia. These tests are mostly based on human fossils or genetic evidence (e.g., White *et al*. 2003; Noonan *et al*. 2006). However, many of these tests are unsatisfactory because they do not incorporate the full range of archaeological, skeletal, and genetic data.

Little comparable effort has been made in archaeology, although some have attempted to explain the Middle to Upper Paleolithic transition from the perspective of changes in technology, social organization, ecology, cognitive abilities, or a combination of these (Binford 1982; White 1982; Whallon 1989; Otte 1990; Bar-Yosef 1994; Lieberman and Shea 1994; Mellars 1996; d’Errico *et al*. 1998; Gamble 1999; Conard and Bolus 2003; Klein 2003; Kuhn and Stiner 2006; O’Connell 2006; Zilhão 2007; Stiner and Kuhn 2009). An important issue in several archaeological analyses of the transition concerns similarities in material production. A number of partisans of the replacement model have emphasized processes of emulation and acculturation to explain the similar sets of artifacts found in Neandertal and modern human assemblages (e.g., Demars and Hublin 1989; Mellars 1996). However, this issue remains highly controversial (d’Errico *et al*. 1998; Zilhão *et al*. 2010). This last debate highlights the fact that there is little agreement on what differentiated these groups from a behavioral viewpoint. This includes their dietary patterns.

**FRAMING THE PROBLEM: DID NEANDERTALS AND EARLY MODERN HUMANS DIFFER IN TERMS OF FORAGING BEHAVIORS?**

It is fair to say that despite recent advances in the interpretation of human behavioral and demographic change in the Late Pleistocene, little progress has been made
recently toward a cogent explanation of the Middle to Upper Paleolithic transition. This atmosphere has provided fertile ground for the production of post hoc accommodative arguments. In general, a failure to address basic contradictions in results obtained from sister disciplines (e.g., molecular anthropology versus archaeology) seems to explain this lack of success. To remedy this problem, a reevaluation of our interpretive models concerning the evolution of Neandertals and early modern humans is in order.

This book is a step in this direction. The present study examines the replacement model, which argues for a recent demic expansion of modern humans out of Africa. In this book, *demic expansion* is defined as a group of interbreeding individuals that expands numerically and geographically. More specifically, the next chapters investigate O’Connell’s (2006) proposition that modern humans responded to competition by broadening their diet, in contrast to Neandertals. According to O’Connell (2006), this strategy allowed modern humans to sustain higher population densities than could be maintained by the archaic *sapiens*, which would have provided the former groups with a demographic advantage during the expansion process. Because O’Connell’s model makes unambiguous predictions about diet breadth, it should be possible to test the faunal implications of his proposition using materials derived from the archaeological record. For simplicity, O’Connell’s model is referred to hereafter as the *early Upper Paleolithic intensification hypothesis*, or simply, the *intensification hypothesis*.

The faunal predictions examined in the present analysis build on earlier (e.g., Binford 1978; Speth 1983; O’Connell *et al.* 1988) and more recent (Barlow and Metcalfe 1996; Bird 1997; Broughton 1999; Stiner and Munro 2002; Cannon 2003; Speth and Delpech 2003; Jones 2004a; Nagaoka 2005; O’Connell 2006; Speth and Clark 2006; Bliege Bird and Bird 2008; Wolverton 2008) archaeologically-oriented studies of resource exploitation by human foragers. The dietary implications of O’Connell’s (2006) model are scrutinized here from the standpoint of foraging theory, the strength of which is found in the existence of universals of predator-prey dynamics and a large body of observations on decision making in the context of resource use (MacArthur and Pianka 1966; Charnov 1976; Stephens and Krebs 1986; Danchin *et al.* 2005; Stephens *et al.* 2007). One important quality of this approach is that it can be used to formulate testable theories of human foraging behavior (Winterhalder and Smith 2000; Bird and O’Connell 2006).

A critical implication of the intensification hypothesis is that Neandertals and early modern humans differed in terms of diet breadth. To test this hypothesis, the exceptionally long and detailed sequence of Saint-Césaire, a stratified site in central western France, was selected. This site is well-suited to this task because it contains eight faunal assemblages spanning a significant portion of the Middle to Upper Paleolithic transition. Evidence for changes in diet breadth in the Saint-Césaire assemblages might bring support for O’Connell’s hypothesis. However, interpreting diet breadth in the archaeological record is not a straightforward task because several factors, including climate change, technological innovation, seasonality, group composition, and occupation intensity, may affect its interpretation (Hill *et al.* 1987; Grayson and Cannon 1999; Zeannah 2004). Therefore, these factors must be controlled for. Lastly, it is worth stressing that even though the test is applied to a site from western Europe, the same approach is potentially applicable to other regions as well.
Reassessing Paleolithic Subsistence

ORGANIZATION OF THE BOOK

Before proceeding to the analysis of the Saint-Césaire faunas, it is useful to set the replacement and multiregional models in their historical context, as viewed from the angles of genetics, paleoanthropology, and archaeology. This historical outlook paves the way to a discussion of the theoretical underpinnings of the intensification hypothesis and to how this proposition can be meaningfully applied to the faunal record of Saint-Césaire. These aspects of the research problem are discussed in Chapters 2 and 3.

The focal points of Chapters 4 through 7 consist of a presentation of archaeological research at Saint-Césaire and of a description of the faunal samples. This includes an overview of the site’s stratigraphy and chronology, as well as an in-depth analysis of the taphonomic processes that modified the composition of the faunal samples. These chapters also address the issue of the respective contribution of humans and carnivores to the faunal accumulations and the problem of occupational mixing. Lastly, these chapters investigate seasonality patterns in the assemblages, a factor that can affect the interpretation of diet breadth. The methods employed for that purpose, some of which are new, are used to identify the modal seasons of prey procurement throughout the sequence.

The last set of chapters (8–12) begins with an investigation of transport decisions at Saint-Césaire and is followed by a confrontation of the dietary predictions of the intensification hypothesis with the faunal assemblages. The results from this test lay the ground for an extensive literature review, which is carried out in Chapter 10, of the evidence for dietary change in coeval sequences from Europe and Southwest Asia. In contrast, Chapter 11 switches from a spatial to a temporal perspective and examines factors that appear to have mediated variations in diet breadth in western France throughout the Late Pleistocene. In the final chapter, the conclusions that emerged from these analyses of foraging patterns are evaluated in light of current debates about biological and cultural changes during the Middle to Upper Paleolithic transition.
HUMAN ORIGINS AND THE PROBLEM OF NEANDERTALS

THE “NEANDERTAL PROBLEM” HAS LONG FASCINATED BOTH THE SCIENTIFIC community and the public. To satisfy this insatiable interest, excellent historical reviews of ideas about modern human evolution have appeared over the years, the most comprehensive ones being those of Grayson (1983) and Trinkaus and Shipman (1993). Because the goal of this book is not to provide a detailed historiographic analysis of the Neandertal problem but rather to test key ideas about dietary change across the Middle to Upper Paleolithic transition, only a cursory examination of the development of this research is provided. The reader is invited to consult the foregoing references for additional information. Specifically, this chapter provides a discussion on the historical development of the demic expansion model and synthesizes recent information collected by anthropologists and geneticists about the nature of the presumed interactions between Neandertals and early modern humans. This review highlights contradictions between the models and the data that lay the ground for the formulation of an archaeological test of the demic expansion hypothesis. This test is presented at the end of this chapter.

TWENTIETH-CENTURY THOUGHT AND THE EMERGENCE OF THE REPLACEMENT MODEL

The idea that Neandertals were replaced as a result of a dispersal event can be traced back at least to the beginning of the twentieth century and the work of scholars such as Boule (1908, 1923), Sollas (1911), Verneau (1913), Peyrony (1933, 1934), Garrod (1938), and Breuil and Lantier (1951). Despite differences in interpretation, propositions made by these scholars were similar in relying heavily on diffusion and migration to explain the demise of Neandertals. These concepts were then widely, and often abusively, used in anthropology (Trigger 1989). As noted by Trigger (1989), the belief that cultural behavior was biologically determined, combined with disenchantedness about the benefits of industrial development, generated overall skepticism about human creativeness during the early twentieth century. The assumption was that humans are innately resistant to change and that independent evolution of particular cultural features was unlikely in the past. In this framework, Paleolithic “cultures” were perceived as relatively stable constructs. Consequently, industrial sequences were generally interpreted as reflecting the replacement of one “culture” by another at a more “advanced” stage of development (e.g., Sollas 1911; Breuil and Lantier 1951). A brief example taken from one of the most
respected Paleolithic experts of his times, Denis Peyrony, will illustrate the view that permeated many of these early studies.

Peyrony (1933, 1934) attributed changes during the Middle to Upper Paleolithic transition to two episodes of migration. For him, the Châtelperronian (ca. 39–36 ka), the earliest Upper Paleolithic industry in France, coincided with a westward expansion of oriental modern humans who replaced the local Mousterian Neandertals. In contrast, Peyrony (1934) saw both similarities and differences between the Châtelperronian and the Aurignacian, which he interpreted as reflecting “contacts” between a recently arrived *Homo sapiens* population and a novel population of migrants from the same species. Indeed, his observations led him to wonder “whether the men from La Ferrassie (the ‘Châtelperronians’) had contacts with the first Cro-Magnons (the ‘Aurignacians’) who arrived in the Vézère valley, and whether these contacts could not have been a cause for the relatively rapid transformation of the toolkit” (Peyrony 1934:42; translation by the author). Although this short excerpt does not do justice to the diversity of views that were expressed during that period (some, such as Hrdlička [1927] and Weidenreich [1947], were more favorable to a gradual evolution of Neandertals into modern humans), Peyrony’s view of the early Upper Paleolithic was typical in that it downplayed local processes of change.

In the 1950s and 1960s, scholars became increasingly discontented with diffusion and migration as explanatory mechanisms for change (Trigger 1989). The postulates that cultural behavior is determined by biology and that specific innovations rarely emerged more than once in prehistory were severely criticized and challenged. Under the impulse of the *new physical anthropology* of Sherwood Washburn (1951) and the *new archaeology* of Lewis Binford (1962), the focus shifted from the documentation of “culture” diffusion and population replacement to systemic explanations based on quantitative methods, deductive reasoning, and evolutionary thinking (Bettinger 1991; Trinkaus and Shipman 1993). In Paleolithic research, these new perspectives prefaced the emergence of gradualist views of modern human evolution (Brace 1964; Brose and Wolpoff 1971) and of more sophisticated versions of the replacement model (Stringer 1974; Howells 1976). This last camp included an influential archaeologist: François Bordes.

Bordes, Peyrony’s pupil, spent a considerable portion of his career working on Neandertal stone tool productions. His views on biological and cultural evolution in the Late Pleistocene are laid out in a volume that he edited after a symposium on human origins held in Paris (Bordes 1972a, 1972b). Although he rejected the hyper-diffusionism of Breuil and Garrod, approaches that he attributed to a lack of empirical data and to an inappropriate use of historical analogies, Bordes did not completely dismiss population replacement as a cause of change. Bordes firmly believed that two distinct biological populations, the Neandertals and the Pre-*sapiens* (ancestral modern humans), occupied France throughout the Mousterian, a view also held by a few biological anthropologists (e.g., Vallois 1949). With respect to the early Upper Paleolithic, Bordes assumed that the Pre-*sapiens* were the makers of the Châtelperronian and that a foreign population of modern humans was the author of the Aurignacian.

Bordes (1961:808) described the Aurignacians as “oriental” modern humans who migrated to France with a “well-developed culture” that allowed them to replace the “occidental” modern humans associated with the Châtelperronian. Bordes thought that the purported “inter-stratifications” of Châtelperronian and Aurignacian industries at
Le Piage, Roc de Combe, and El Pendo brought support to his replacement model (Bordes and Labrot 1967; Champagne and Espitalié 1967; Bordes 1984). These inter-stratifications, including those recently reported at the Châtelperron type-site (Gravina et al. 2005), are now known to be based on incorrect observations and redeposited materials (d’Errico et al. 1998; Bordes 2002; Zilhão et al. 2007). However, it was a discovery made in 1979 in Charente-Maritimes, France, that first cast strong doubts on Bordes’s proposition.

SAINT-CÉSaire AND THE UPPER PALEOLITHIC NEANDERTALS

In the seventies, modern humans were nearly universally considered the sole makers of Upper Paleolithic industries in Europe, including the Châtelperronian. Indeed, few scholars believed that Neandertals contributed to innovations such as the production of personal ornaments or the emergence of bone tool technology, which were regarded as hallmarks of the Aurignacian expansion (Trinkaus and Shipman 1993). This view was, in part, discredited in July 1979 when a Neandertal skeleton was uncovered associated with a number of Châtelperronian objects in a site locally known as “la Roche à Pierrot” near the city of Saint-Césaire (Figure 2.1) in western France (Lévêque and Vandermeersch...
1980). This association, unanticipated at the time of the discovery, profoundly modified the then-prevailing views about the advent of the early Upper Paleolithic.

The Saint-Césaire discovery caused a paradigm shift by changing the identity of the Châtelperronians from modern humans to Neandertals, which constituted a fatal blow to the Pre-sapiens hypothesis (Trinkaus and Shipman 1993). The implication of this new identity was far-reaching: Neandertals did contribute to the Upper Paleolithic. For many, this finding forced a reappraisal of Neandertal cognitive abilities and made claims for behavioral differences between archaic sapiens and early modern humans less compelling. Some supporters of the replacement model took a different perspective on the problem and argued for a Neandertal “acculturation” to explain similarities in cultural behavior between the Châtelperronian and the Early Aurignacian, not unlike Peyrony had done sixty years earlier (Demars and Hublin 1989; Mellars 1996). As pointed out earlier, this interpretation is highly debated (d’Errico et al. 1998; Mellars et al. 1999; Conard and Bolus 2003).

Wolpoff and his collaborators (Thorne and Wolpoff 1981; Wolpoff et al. 1984) saw in the Saint-Césaire finding evidence for the local evolution of Neandertals into modern humans. This view became known as the multiregional model, a proposition that finds its roots in the gradualist models of Weidenreich (1947) and Brace (1964). Gene flow is presented in the multiregional model as the principal mechanism that maintained unity between African and Eurasian populations throughout the Middle and Late Pleistocene:

Multiregional Model posits that humans evolved as an interconnected polytypic species from a single origin in Africa some 2 myr ago. The small population effects during initial colonizations as humans expanded out of Africa helped establish regional differences, some of which were subsequently maintained through isolation-by-distance and adaptive variation. Advantageous changes spread widely because of genic exchanges across the interconnected network of populations. (Wolpoff 1999:543)

The multiregional model attributes the maintenance of regional differences between the interconnected human populations to a “center-and-edge” effect (Thorne 1981). According to this hypothesis, early modern human groups from Africa – a region then located at the center of the human range – were associated with patterns of gene flow, drift, and local selection that differed from those encountered by populations at the periphery. Indeed, because the center of a range usually provides optimal habitat conditions, more variation can be tolerated. Central populations will therefore tend to be larger and in more frequent contact with each other, conditions that promote gene flow and counter genetic drift. In contrast, at the periphery, less-than-ideal ecological conditions increase selective pressures on variation. In addition, the presumably small population sizes of colonizer groups at the fringes of the range are conducive to partial isolation, which favors the loss of variation and the emergence of novel adaptive features as new habitat conditions are encountered. As a result, the multiregional model predicts that skeletal homogeneity will be greater in peripheral than in central populations. Data from central Europe, and more particularly southeastern Asia and Australia, were argued to be in agreement with these views (Smith 1982; Wolpoff et al. 1984; Hawks et al. 2000).

At the same time that these propositions were being made, a new player – human genetics – came to the forefront of the debates on modern human origins. Brown (1980) performed one of the first genetic analyses focusing on this problem. He argued that
variation in the mitochondrial DNA (mtDNA, an organelle in the cell membrane that contains a short sequence of DNA) of living humans indicates that modern populations went through a severe “population constriction” around 180 to 360 ka, a scenario that became known as the garden of Eden hypothesis. Following Brown’s lead, Cann and her associates proposed, in 1987, a second model of modern human origins. These authors stated that current mtDNA diversity reflects a severe bottleneck in population size around 200 ka and concluded that this phenomenon was accompanied by the replacement of archaic populations by a newly emerged and rapidly expanding African population: anatomically modern Homo sapiens (Cann et al. 1987:35–36). This model, dubbed the mitochondrial Eve hypothesis, was claimed to provide strong support for the replacement model.

In the Near East, the early dates (≈100 ka) that were then being published for some Mousterian assemblages containing modern human skeletons were received with a good deal of skepticism by supporters of the multiregional model because they were not consistent with a gradual model of Homo sapiens emergence (Valladas et al. 1988). Building on these and the molecular findings, Stringer and Andrews (1988) gave new impetus to the replacement model by positing that modern humans arose early in Africa and later spread to Eurasia where they supplanted the local populations. Importantly, these authors argued that the replacement process occurred without significant interbreeding. Several empirical predictions were derived from these propositions:

The model of a recent African origin . . . predicts different patterns of variation comparing African populations and those from elsewhere. Variation should be greatest within African populations (based on their earlier divergence, and assuming predominantly neutral genetic change), and they should be sharply distinguished in gene frequencies from non-African populations. Transitional fossils would not occur outside the African area of origin, and population replacement would represent the mode of establishment of Homo sapiens in other areas. The earliest record of Homo sapiens fossils should occur in the continent of origin of the species (Africa), and the youngest records at the peripheries of the radiation. Population relationships in Europe, Asia, and Australasia would approximate those of the Holocene only in the later Pleistocene. (Stringer and Andrews 1988:1264)

The approximately 160,000-year-old early modern human remains found in 1997 at Herto in the Middle Awash in Ethiopia (White et al. 2003) are important in this respect because they were said to corroborate this view (Stringer 2003).

The assimilation model, a variant of the earlier hybridization model (Bräuer 1981), incorporates elements from the replacement and multiregional positions in suggesting that the demic expansion of modern humans into Eurasia was accompanied by admixture with archaic sapiens (Smith et al. 1989; Eswaran et al. 2005; Trinkaus 2005, 2007). In general, the assimilation model is similar to the replacement model, with which it differs only relative to the extent of gene flow inferred to have taken place (virtually none in the replacement model, some in the hybridization model). The discovery of “hybrid” specimens in Romania (Trinkaus et al. 2003; Soficaru et al. 2006, 2007; Rougier et al. 2007) and at Lagar Velho in Portugal (Duarte et al. 1999), as well as molecular evidence for gene flow between archaic sapiens and early modern humans (e.g., Garrigan et al. 2005b; Evans et al. 2006; Garrigan and Hammer 2006; Hayakawa et al. 2006; Green et al. 2010), have been presented in support of this model.
CURRENT ISSUES IN THE MODERN HUMAN ORIGINS DEBATE

As we have seen, before the rise of the new archaeology, major changes in the archaeological record of western Europe – for instance, between the Châtelperronian and the Aurignacian or the Gravettian and the Solutrean – were generally perceived as evidence for large-scale migrations and physical replacement of local populations. In the sixties, many of these hypotheses were substituted by models emphasizing local continuity. However, the assumption that the Aurignacian constitutes a migration and replacement event has been, and still is, widely accepted. Critics of this position have been few (Clark 1992; Straus 1997). However, new interpretations of the data are sometimes at odds with this hypothesis. These conflicting interpretations are considered in this section.

Early Modern Human Fossils in Europe

Although most scholars consider the Aurignacian to be the first industry produced by early modern humans in western Europe, this assumption is not shared by all (e.g., Bar-Yosef 2002). Likewise, some doubts have recently been raised concerning the association of Neandertals with the Châtelperronian (Bar-Yosef and Bordes 2010). At the moment, human remains attributed with some degree of certainty to the Early Aurignacian are limited to a few cranial fragments and isolated teeth that are not easily diagnosed (Churchill and Smith 2000; Henry-Gambier et al. 2004; Bailey and Hublin 2005; Bailey et al. 2009; Ramirez Rozzi et al. 2009). With a date of \( \approx 35 \) ka, the modern human specimens (a mandible as well as a complete cranium from a second individual) from Peștera cu Oase in Romania may be considered coeval with the Early Aurignacian. Unfortunately, these specimens have no associated artifacts (Trinkaus et al. 2003; Rougier et al. 2007). Concerning the cranium, Rougier and colleagues (2007:1170) noted that “Oase 2 is ‘modern’ in its abundance of derived modern human features, but it remains ‘nonmodern’ in its complex constellation of archaic and modern features.” Another early specimen, sometimes attributed to modern humans, consists of a 35,000- to 37,000-year-old maxilla from Kent’s Cavern in England (Jacobi et al. 2006). However, the taxonomic affinities of this maxilla are uncertain because some scholars question, given its fragmentary nature, whether it is possible to attribute it to a specific morphotype (Higham et al. 2006).

Scarce information is available for the later Aurignacian. The human fossil assemblage from Mladeč, Czech Republic, dated at \( \approx 31 \) ka, and therefore, postdating the Early Aurignacian, provides evidence for anatomically modern morphology in the later Aurignacian (Wild et al. 2005). However, some authors see archaic characteristics in this assemblage as possibly indicative of a Neandertal ancestry, a claim that is debated (Bräuer et al. 2004). In Romania, human remains from Peștera Muierii, dated to \( \approx 30 \) ka, as well as a slightly later (\( \approx 29 \) ka) cranium from Cioclovina, have been argued to indicate admixture between Neandertals and early modern humans (Soficaru et al. 2006, 2007). In France, modern human specimens from La Crouzade are also attributed to this period (Henry-Gambier and Sacchi 2008).

In this chronological framework, the 32- to 33-ka age obtained for the Vindija G1 remains (a right mandible fragment and a parietal fragment) from Croatia is intriguing, given the geographic origin of the specimens. This is because if one accepts the demic