

# The assimilation model, modern human origins in Europe, and the extinction of Neandertals

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## Abstract

Debate continues concerning the role of the Neandertals in the emergence of early modern Europeans. This paper presents one assessment of aspects of the morphological data, chronological patterns, genetic information and archaeology relevant to the debate. It is clear that none of these unequivocally support any of the models offered to explain modern human origins. In fact despite various claims to the contrary, there continues to be valid scientific debate about the interpretation of patterns from all of these disciplinary domains and which models they are more commensurate with. The assessment presented here concludes that the assimilation model is the best explanation for the origin of anatomically modern humans in Europe. If Neandertals are assimilated into in-migrating populations of modern people in Europe, then Neandertals do not go extinct in the classical sense of the word. © 2004 Elsevier Ltd and INQUA. All rights reserved.

## 1. Introduction

In the aftermath of the recognition of the original Neandertal specimen in 1856, three major perspectives emerged to explain the “Neandertaler’s” distinctive anatomical pattern and phylogenetic relationship to modern people (see detailed reviews in Brace, 1964; Spencer and Smith, 1981; Spencer, 1984; Bowler, 1986; Smith, 1997). Mainly under the influence of Rudolf Virchow (1872), one perspective held that the Neandertal was nothing more than a pathologically deformed member of a “civilized” European race. Others, including Hermann Schaaffhausen and T.H. Huxley, supported a second view, in which the specimen derived from an archaic, aboriginal race that occupied Europe prior to historically documented European peoples. The third interpretation emerged from the assessment of William King (1864) that the specimen was so distinctive that it must be recognized as a distinct species, which King named *Homo neanderthalensis*. In fact, King noted that

the “Neandertaler” was so distinctive that erection of a new genus might be necessary. Even those who favored the third view (at least in terms of taxonomy), during the late 19th and early 20th centuries did not agree on the role of a Neandertal species in human biological history. Some believed that Neandertals were logical ancestors for modern humans (e.g. Schwalbe, 1904, 1906; Gorjanović-Kramberger, 1906; Hrdlička, 1927), while others argued they were too distinctive to play such an ancestral role and thus must represent an extinct side branch of the human family tree (e.g. Keith, 1915; Boule, 1911/1913, 1921).

Virchow’s perspective clearly has not stood the test of time. Neandertals as a group are certainly not pathological, although individual cases of pathology have strongly influenced some interpretations of their paleobiology (Trinkaus, 1985). Virchow’s explanation was possibly plausible when only a single Neandertal skeleton (along with a few other fragments) was known. However, its plausibility weakened as each additional Neandertal specimen was discovered during the late 19th and early 20th centuries (Bowler, 1986; Smith, 1997). The other arguments posited by Virchow in

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support of his view was systematically refuted at the beginning of the 20th century (Schwalbe, 1901). On the other hand, the interrelated issues of whether Neandertals comprise a species separate from *Homo sapiens*, and whether they have any ancestral role in the history of our species, have formed the crux of the “Neandertal debate” throughout the 20th and into the 21st century.

This paper presents one assessment of the state of this debate and focuses on four specific sets of information. The first and most obvious of these sources of information derives from various analyses of the fossil human record. The second comprises the accumulating information from both pertinent ancient DNA studies and analyses of extant modern human genetic variation. The third source of information is the archaeological record spanning the late Mousterian, Initial Upper Paleolithic, and Aurignacian cultural periods of the European Paleolithic. Finally, the fourth data set is the pattern of late Neandertal and early modern human-associated chronometric dates in Europe and other pertinent regions of the Western Old World. In fact, one of us has argued previously that the most influential factor in altering perspectives on late Pleistocene human evolutionary history has been this “chronological revolution” (Smith, 1991; Smith et al., 1989). Each of these data sets is critical to current discussions of Neandertal extinction.

## 2. Neandertals as a species

During much of the 20th century, Neandertals were commonly placed in their own species—usually in *H. neanderthalensis*—by some researchers but were maintained in *H. sapiens* by others (see the review in Smith, 2002). For example, Gorjanović-Kramberger originally considered the Krapina remains to be a form of *H. sapiens* (Radović, 1988). He later changed his mind and classified them as “*Homo primigenius*”, the taxon used for Neandertals in German-speaking Europe at the time (Gorjanović-Kramberger, 1906), probably based on the influence of Schwalbe (1904, 1906). However, despite the change in taxonomy, Gorjanović-Kramberger never wavered in his belief that Neandertals were the direct lineal ancestors of modern humans (Radović, 1988). By the 1960s it was common to attribute Neandertals and other archaic post-*Homo erectus* groups to geographically and temporally defined subspecific categories, such as *H. sapiens neanderthalensis* or *H. sapiens rhodensiensis* (Campbell, 1963, 1965), or just to refer to them as archaic *H. sapiens* (e.g. Wolpoff, 1980; Smith, 1985). However, there was always at least an undercurrent of dissatisfaction with this approach (Howells, 1974, 1976; Stringer et al., 1979; Eldredge and Tattersall, 1982). Beginning particularly from the mid-1980s (e.g. Tattersall, 1986, 1992), this undercurrent has grown into a

powerful call to recognize Neandertals as a distinct species.

Neandertals are clearly distinctive in terms of their overall morphology (total morphological pattern) compared to modern humans. This fact has been established by numerous comparative analyses going back to the above-mentioned work of Gorjanović-Kramberger, Boule, Schwalbe, Keith and others. It has been reaffirmed by numerous more recent morphometric monographs on Neandertals (e.g. Suzuki and Takai, 1970; Heim, 1976; Smith, 1976; Trinkaus, 1983; Condemni, 1992), as well as countless studies on specific aspects of Neandertal anatomy. Noteworthy among these latter types of studies is work by Santa Luca (1978), which ushered in the modern, cladistically influenced search for derived discrete traits that would uniquely characterize Neandertals. Subsequent work by Hublin (1978, 1980), Rak (1986, 1998); Rak et al., 1994, 2002), Bailey (2002) and Schwartz and Tattersall (1996, 2000), among others, has continued this approach and lead to claims for autapomorphic Neandertal features in the dentition, face, internal nose, cranial vault and mandible. Similar post-cranial features have also been suggested (see review in Pearson, 2000) but are beyond the scope of this paper. It has also been suggested that the pattern of Neandertal ontogeny differs from that of modern humans (Ponce de Léon and Zollikofer, 2001; Lieberman, 1998; Lieberman et al., 2000) and that this constitutes yet another strong piece of evidence that Neandertals are a distinct species. Finally, various multivariate metric assessments have emphasized the difference in overall morphological form between the crania of Neandertals and modern humans, including some early modern specimens from the European Paleolithic (e.g. Stringer, 1974, 1978; Howells, 1989; Lahr, 1994, 1996, Harvati et al., 2004). The recent study by Harvati et al. (2004, p. 1152) sums up the general consensus resulting from all of these studies: “(w)e interpret the evidence presented here as supporting the view that Neanderthals represent an extinct human species and therefore refute the regional continuity model for Europe.”

This interpretation appears all the more robust in light of genetic data, both mitochondrial and nuclear, that indicate a recent African origin for all modern humans (Nei and Roychoudhury, 1982; Cann et al., 1987; Cavalli-Sforza et al., 1994; Ingram et al., 2000; see also the review in Relethford, 2001). In addition, several ancient DNA analyses that suggest Neandertals cluster at the periphery or outside the modern human range, while Aurignacian and Gravettian-associated humans fall well within that range (Krings et al., 1997, 2000; Scholz et al., 2000; Schmitz et al., 2002; Caramelli et al., 2003). Furthermore, the Aurignacian is viewed as being uniquely associated with modern humans (Mellars, 1996a, 2002; Klein, 1999), and both are widely held to

represent migrants into Europe, proximally from the Near East. Finally available chronometric frameworks suggest that modern humans enter Europe relatively late, long after modern humans appear in Africa and western Asia, and experience some degree of overlap with late Neandertals (see reviews in Churchill and Smith, 2000; Smith, 2002). Taken together with the morphometrics and genetics, these patterns form a convincing case for separation of Neandertals into a separate species, *H. neanderthalensis*.

In the face of such a compelling case, why even question a separate specific status for the Neandertals? Despite all of the evidence cited above, some late European Neandertal populations exhibit morphological patterns that approach early modern human anatomical patterns somewhat more than “typical” European Neandertals do (Wolpoff et al., 1981; Smith, 1984, 1994; Wolpoff, 1989, 1999; Trinkaus et al., 1999). Furthermore, the earliest modern Europeans exhibit certain morphological features that might well suggest some Neandertal contribution to their ancestry (Fruyer, 1992, 1993, 1997; Fruyer et al., 1993; Smith, 1984; Smith et al., 1989; Wolpoff, 1999). Certainly both of these claims have been questioned (e.g. Stringer and Bräuer, 1994; Lieberman, 1995; Bräuer and Stringer, 1997; Bräuer and Broeg, 1998; Lieberman et al., 2000). But even if the claims are true, does it necessarily invalidate placement of Neandertals in a separate species?

The most novel recent approach to addressing this issue has been provided by Jolly’s (2001) assessment of “hybridization” and the question of how to define species in cercopithecine monkeys, specifically the subtribe Papionina (baboons, mangabeys, and mandrills). Jolly notes that, despite genetic and morphometric data on nearly 1000 animals in the major Ethiopian and Kenyan hybrid zones between *Papio* species, there is still only a very general conception of the degree of gene flow taking place and how this is reflected in the genotypes and phenotypes of the baboons involved. Basically, Jolly concludes that “(t)he baboon analogy does not...inspire confidence that the detailed dynamics of ‘archaic’—‘modern’ interactions will ever be determined” (2001, p. 198). He believes that the complexity of the population dynamics in these hominins is more complex than is likely determinable from fossils. Jolly suggests that debating the species question with respect to Neandertals and modern humans is not likely to be a useful endeavor, and using the *Papio* analogy, he recommends recognizing Neandertals and early moderns as allotaxa. Allotaxa are phylogenetically close but biologically distinctive groups, whose ranges normally do not overlap geographically but often form hybrid zones of various extents (Grubb, 1999). Taking this approach removes the impetus for debating the species question, but it still leaves the

question as to whether early modern humans have any Neandertal ancestry.

### 3. Morphology and chronology

As late as the mid-1980s, it could be argued that the appearance of modern human morphology during the Pleistocene occurred essentially contemporaneously in various areas of the Old World (e.g. Smith, 1985; Wolpoff, 1980). However, application of thermoluminescence (TL) and electron spin resonance (ESR) dating to selected fossil human remains beginning in the late 1980s demonstrated that modern human morphology was established in the Near East and Africa long before it was established in Europe (Valladas et al., 1988; Grün and Stringer, 1991). Most recently, dates for the Omo Kibish 1 (Fleagle et al., 2003) and Herto (White et al., 2003) human specimens from Ethiopia indicate that modern human cranial form was present in East Africa as early as 160 ka and certainly by 130 ka. Next this cranial form occurs in the Levant at maximally just over 100 ka (Bar-Yosef, 1998, 2000). In Europe, however, the earliest-known dates for early modern human remains are 34–36 ka, direct AMS radiocarbon dates on a modern human mandible from Peștera cu Oase, Romania (Trinkaus et al., 2003), and 34.2–34.9 ka, standard and AMS radiocarbon-dated carbonates associated with the remains from Mladeč, Czech Republic (Svoboda et al., 2002). Assuming the dating is close to correct, this pattern of appearance of modern cranial form can be cited as support for an African origin of modern human morphology, followed by a spread into the Near East and then, considerably later, into Europe.

Howells (1974, 1976, 1989) has argued that the fundamental homogeneity of modern human cranial form is one of the strongest indications that modern people have a recent, single region of origin. The crania of early modern humans in Africa and the Near East certainly exhibit some archaic features (Corruccini, 1992; Fruyer et al., 1993; Wolpoff, 1999), but their overall form is certainly more modern than that of the Neandertals as Howells and others (Bräuer, 1984, 1989; Stringer and Andrews, 1988; Lahr, 1994, 1997; Bräuer and Broeg, 1998) have shown. Given the fact that the early modern Europeans basically conform to a similar pattern (Kidder et al., 1992; Lahr, 1996), the most logical interpretation is that they are derived from early modern populations already established in the Near East. The remaining question concerns just what happens when these early modern groups encounter Neandertal populations in the Near East and Europe. For the most part, this is where the current controversy concerning the role of Neandertals in the evolutionary history of modern Europeans focuses. Did the Neandertals contribute to early modern European

populations or did they go extinct in the strict sense of the word?

While the overall gestalt of cranial form in early modern Europeans is generally different from Neandertals, there are exceptions. For example, the cranium of Mladeč 5 exhibits strong similarity to Neandertals in lateral view, and this specimen does not cluster with other moderns in vault form (Kidder et al., 1992). But even this specimen lacks the characteristic oval shape of Neandertals when viewed from the rear and exhibits an overall morphology that conforms to the modern human pattern. For example, although the specimen's brow ridge is very robust, its shape conforms to the pattern seen in early modern humans, and the same applies to the specimen's mastoid region (Smith, 1984). Thus, when the total morphological pattern of the cranium is considered, Mladeč 5 falls within the early modern pattern, not the Neandertal one. Other early modern European crania are even less obviously Neandertal like in basic shape and morphology.

On the other hand, there are some details of early modern European anatomy that may reflect Neandertal influence. Many of these features have been discussed by Frayer (1992, 1993, 1997), as well as in other contexts (Smith et al., 1989; Frayer et al., 1993; Wolpoff, 1999). Generally, these features exhibit higher frequencies in Neandertals and early modern Europeans than in later European or non-European Pleistocene human samples, and this pattern is suggested to demonstrate a Neandertal contribution to early modern Europeans. For example, Frayer (1993, p. 17) notes that the projection of nasion forward of the lateral face (bi-fmt line) is marked in Neandertals, reflecting the mid-sagittal facial prognathism characteristic of them. Frayer demonstrates that while the earliest modern Europeans (early Upper Paleolithic) exhibit significant reduction in this dimension compared to Neandertals, they have markedly more upper midfacial prognathism than do the Skhul/Qafzeh sample of early moderns from the Near East (Table 1). Thus, the early modern Europeans exhibit a distinct feature that it not marked in their presumed Near Eastern ancestors and thus seems to reflect some degree of Neandertal ancestry.

The rear of the cranium exhibits two features that further reflect continuity in morphological details of late Pleistocene Europeans. First, European Neandertals have a high frequency of occipital buns, a distinctively

Table 1  
Nasion projection from the bi-fmt line. Data in mm from Frayer (1993)

	Mean (N)	Range
European Neandertals	29.3 (11)	26.5–35.8
Skhul/Qafzeh	12.4 (3)	6.6–21.7
Early Upper Paleolithic	21.9 (16)	14.6–31.9
Later Upper Paleolithic	19.3 (23)	10.4–30.7

Table 2  
Incidence of occipital bone features discussed

	Suprainiac fossa	Occipital buns
European Neandertals	100 (24/24)1	80 (8/10)
Skhul/Qafzeh	14.3 (1/7)2	0 (0/5)
African Early Moderns	0 (0/3)3	0 (0/3)
African Archaics	20.0 (1/5)3	33.3 (2/6)
Early Upper Paleolithic	38.5 (10/26)	68.4 (13/19)
Late Upper Paleolithic	23.7 (9/38)	—

Values represent the % of specimens in which the feature is present. Figures in ( ) indicate the number of individuals exhibiting the feature followed by the sample size. Except where indicated the data on suprainiac fossae are taken from Frayer (1993). Data on occipital buns were collected by FHS.

Notes: 1. Frayer recognizes one specimen from Krapina (Kr 11.5) as lacking a suprainiac fossa. We believe the specimen is not preserved medially enough to make this judgment. 2. Frayer recognizes a suprainiac fossa in Qafzeh 6 and Skhul 9. We identified a fossa only in Skhul 9. 3. Data collected by FHS.

shaped posterior vault characterized by paralambdoidal flattening and a distinct shelf below the nuchal torus. This distinctive morphology was first described as an occipital bun by Boule (1911/1913). As Table 2 shows, early modern Europeans also have a high incidence of this feature, while neither the Skhul/Qafzeh nor early modern African samples exhibit this feature at all. Since the Skhul/Qafzeh and African early moderns presumably represent the ancestors of the early modern Europeans, the absence of bunning in the former two samples raises the question of the source of the high incidence of bunning in the latter sample. Basically, there are three possible explanations for this. First, the bunning in the early modern Europeans could still be derived from earlier African or West Asian samples. Second, the bunning in European Neandertals may not be homologous to that in the European early moderns. Third, the bunning in the early modern Europeans reflects a contribution by European Neandertals.

The first possibility, that bunning entered Europe with the in-migrating moderns, depends on establishing the presence of the feature in West Asian or African archaic populations. West Asian Neandertals lack any indication of occipital bunning, and earlier hominins, like Zuttiyeh, do not preserve this region of the cranium. In the African Transitional Group, the later archaic humans from Africa (Bräuer, 1984, 1989, 2001) occipital buns are found in both cranial specimens from Jebel Irhoud in Morocco. Lateral contours of the Ngaloba cranium suggest some bunning, but close inspection of the specimen shows that there is distortion around the lambdoidal suture. It is this distortion that results in the suggestive lateral contour, which has been used to argue for bunning in this specimen. The buns in the Jebel Irhoud specimens are not in question. But here there is

yet another possible explanation. Jebel Irhoud's geographic location places these humans in close proximity to Western Europe, across the Strait of Gibraltar. It has been noted that other aspects of the Jebel Irhoud morphological pattern approaches the European Neandertal condition and thus that they may well show the effects of gene flow from European archaic populations from the North (Simmons and Smith, 1991). This also may explain the presence of occipital buns in the one African Transitional Group site that might have experienced some biological interaction with European Neandertals. Certainly, this explanation cannot be ignored, particularly since the Irhoud specimens are the only ones in West Asia and Africa to exhibit occipital bunning.

The second possible explanation is that bunning in early modern Europeans is not homologous to the condition in European Neandertals (Lieberman, 1995; Lieberman et al., 2000). This is certainly possible, for as Lieberman (1995) aptly points out, we do not really know the genetic basis of such traits as occipital bunning. Furthermore, the shape and form of bunning is different in Neandertals compared to that in early modern Europeans, a fact emphasized by Lieberman et al., 2000. For instance, in Neandertals, the buns extend laterally on the cranial rear, while in early moderns the buns are restricted generally to the medial portion of the bone. However, this likely can be explained by the fact that the overall shape of the vault in moderns is altered from the oval "en bombe" shape of the Neandertals. The modern vault is higher with a more parallel-sided shape. Assuming that buns are formed as Trinkaus and Le May (1982) hypothesized, that is by a posteriorly directed growth spurt in the brain late in childhood, the same process might well result in a Neandertal-like bun in a low, oval vault form and a more centrally restricted extension in a higher, narrower vault. While this is difficult to prove, it is a more logical explanation than one suggesting that a separate process resulted in early modern European buns. This is particularly true when the frequencies of bunning in late Pleistocene populations are considered. As Table 2 shows, the highest frequencies of bunning during this period are in European Neandertals and the sample that immediately followed them in Europe. It is hard to imagine why this pattern would occur in exactly the same region but from different processes.

When all three explanations are considered, the most logical is that the high frequency of bunning in early modern Europeans reflects Neandertal influence in the former's gene pool. However, it is important to bear in mind that the other explanations are not necessarily excluded by the available data. A similar explanation is also the most reasonable one for other such features, including the second occipital feature mentioned above—the suprainiac fossa. However, a consideration

of the suprainiac fossa is a bit more complicated since a clearer functional argument can be made for the presence of this feature (Hublin, 1978, Caspari, 1991) than for occipital bunning.

The suprainiac fossa in Neandertals is generally an oval depression located just above the nuchal torus with the long axis of the structure running horizontally. While there is considerable variation in the expression of this feature in Neandertals (Hublin, 1978), the surface bone of the fossa tends to present a distinctive pot-marked or pitted appearance that Caspari (1991) has suggested reflects resorptive activity. Some form of a fossa is present in all known Neandertal occipitals. Similar structures are found in several pre- and post-Neandertal samples, but a particularly high frequency of this feature is found in early modern Europeans (Table 2). While these structures are similar to the Neandertal condition, they are certainly not identical. In modern crania, the fossa tends to be much less marked and restricted to the midline region. Also the structure tends either to be more rounded in shape or distinctly triangular with the apex of the triangle pointing in an inferior direction. As both Caspari (1991) and Frayer (1993) have discussed, the structure in moderns is generally related to the form of the external occipital protuberance, and the protuberance is, in turn, related to the attachment of the nuchal ligament. Thus the form of the fossa may well relate to the pattern of loading along the nuchal torus (Caspari, 1991) including the role of the nuchal ligament in this pattern.

However, even assuming some functional basis for the trait and the recognition that the form of the fossa is different in Neandertals and later populations, the fact is that the fossa is always positioned the same relative to the superior and supreme nuchal lines, and it has the same surface appearance. Thus, while there are certainly some troublesome uncertainties (Frayer, 1993; Lieberman, 1995), it is possible to make a strong argument that the fossa represents a homologous structure in all of these samples. With that assumption, the data in Table 2 show that early modern humans in Europe have a very high frequency of a trait that has its highest frequency in European Neandertals. While the trait is certainly found outside of Europe (Trinkaus, 2004), it is not common in potentially ancestral populations to early modern Europeans from Africa and the Near East. Of course, given the potential functional aspects of the fossa, it could be argued that high frequencies of the feature in European Neandertals and early modern Europeans reflect some common functional adaptation. While that possibility cannot be totally excluded, it is difficult to conceive of what that adaptation would be, particularly since it does not seem to be significant in other parts of the late Pleistocene western Old World. As was true for occipital bunning, the most logical interpretation is that the high frequencies of this feature in Europe reflect

some genetic continuity on that continent. In other words, Neandertals are contributing to some extent to the gene pool of the early modern European population. As noted above, however, these contributions appear to be reflected in anatomical details, rather than in the basic gestalt of cranial form. Such an interpretation is commensurate with the view that populations bearing modern morphology did enter Europe and were the primary basis of the modern people of the European Upper Paleolithic. But data like those discussed above suggest that they were not the exclusive contributors to the biological makeup of early modern Europeans.

#### 4. Ancient and modern DNA

Beginning particularly with the publication of the pivotal paper on living human mitochondrial DNA variation by [Cann et al. \(1987\)](#), the analysis of numerous aspects of both nuclear and mitochondrial DNA have had massive impact on the interpretation of modern human origins. Indeed this and other genetic analyses on living humans formed the basis of the emergence of the recent African origin perspective on the emergence of modern humans as laid out by [Stringer and Andrews \(1988\)](#). Recent analyses of extant human mitochondrial (mt) DNA using the most up-to-date approaches strongly support the original suggestion that Africa is the homeland of all modern humans ([Ingram et al., 2000](#)). This conclusion is supported by studies on various other genetic systems, including Y-chromosomes, alu insertions, microsatellites, and numerous nuclear polymorphisms (see [Hammer and Zegura, 1997](#); [Jorde et al., 2000](#); [Relethford, 2001](#); [Pääbo, 2003](#); [Carroll, 2003](#), for reviews). The influence of such studies has been to promote the view that all modern human variation derives from Africa within a relatively recent time framework. It is fair to state that this view has become increasingly embraced by the media and, because of this, by the interested public in general.

Of course, there are genetic assessments that do not so unequivocally support a recent African origin model. Noteworthy among these are those of [Relethford \(2001\)](#), who notes that the same genetic patterns might occur if Africa had certain levels of higher effective population size during the appropriate periods of the late Pleistocene. [Relethford's](#) view is that current data do not allow for unequivocal support for either the recent African origins model or a multiregional approach to modern human emergence. Furthermore, some genetic polymorphisms suggest considerable time depth outside Africa (e.g. [Harding, 1997](#); [Harding et al., 1997, 2000](#); [Yu et al., 2001](#)) a fact which is not consistent with a recent African origin for all recent human genetic variation. [Templeton's \(2002\)](#) analysis of ten human

genetic systems presents the view that the distribution of the coalescence ages of these systems indicate that modern human genetic variation results from several waves of migration out of Africa extending back into the Middle Pleistocene. Thus, according to [Templeton](#), the modern human gene pool is not totally the result of a single, late set of migration from Africa. Rather, it can be explained by admixture between the later populations migrating out of Africa and populations already established in portions of Eurasia.

It is not the purpose of this paper to review all of the genetic evidence pertinent to modern human origins but simply to point out one important fact. Not all analyses of the genetic data support a recent origin of the entire modern human gene pool in Africa. In this regard, one additional recent study bears mention. This is the recent work by [Eswaran \(2002\)](#) which presents a model that suggests modern human populations from Africa could certainly have ultimately replaced archaic human populations in Eurasia and yet have assimilated genetic material and even morphological features from those populations. However, this diffusion wave model posits that, given a slight reproductive advantage for individuals with a full set of modern genes over individuals with a combination of archaic and modern elements, these modern individuals would quickly constitute the overwhelming majority of the population. Yet despite the dominance of the modern people and their genetic pattern, there would always be the possibility for significant archaic genes to be present in the gene pool. These archaic genes likely do not affect the overall modern form of the individuals but perhaps could control such features as those discussed in the previous section.

[Relethford \(2001\)](#) has suggested that the genetic data are most consistent with a “mostly out of Africa” model, in which the majority of the modern human gene pool stems from Africa. However, variable amounts of Eurasia “indigenous” genes are assimilated into local modern gene pools. This perspective also would seem to the view of several other geneticists cited above. For example, [Jorde et al. \(1997, p. 134\)](#) state that “(a)n African origin, with some mixing of populations, appears to be the most likely possibility.” [Avice \(2000, p. 134\)](#) notes that available data do not clearly support either replacement of indigenous by expanding modern gene pools or intermixture thereof, but that “...preliminary indications are that an intermediate level of mixing and replacement may have been involved.” Finally, [Templeton \(2002, p. 50\)](#) recognizes a major genetic impact from the latest (and earlier) migration waves identified in his analyses, but points out that selected traits “...are difficult to reconcile with a population replacement, but is compatible with this most recent out-of-Africa expansion event being characterized by interbreeding.”

In 1997, a short (378 base pair) segment of mt DNA was isolated from the right humerus of the original Neandertal skeleton recovered in 1856 (Krings et al., 1997). Subsequent comparison of the sequence derived from the Feldhofer 1 specimen to a series of 994 recent humans from around the world yielded an average of 27 DNA differences between the Neandertal and recent human sequences. Pairwise comparisons result in an average of only 8 differences when recent human sequences were compared with those of other recent humans. It was further calculated that Neandertals diverged from the line leading to modern humans between 550 and 690 ka (Krings et al., 1997), a date range that fits well with the idea that Neandertals emerged as a distinct species in the European Middle Pleistocene (see also Krings et al., 1999). Subsequent extraction of similar-sized segments of mt DNA has been made in three other specimens: an infant from Mezmaiskaya in Russia (Ovchinnikov et al., 2000), a specimen from level G3 at Vindija in Croatia (Krings et al., 2000), and a second individual from the Feldhofer site in Germany (Schmitz et al., 2002). All four of the ancient DNA sequences from these Neandertals cluster rather close together and fall at the extreme periphery of recent human variation. The latter observation stems from the fact that 0.002% of pairwise comparisons among recent sequences are larger than the smallest Neandertal-recent human difference, based on the Feldhofer 1 sequence (Krings et al., 1997).

These results have certainly added to the impression that Neandertals were distinctly different from modern humans. This view has been significantly enhanced by the isolation of mt DNA sequences from two 24 ka early modern humans from Paglicci, Italy (Caramelli et al., 2003). These sequences fall well within the range of living humans. Caramelli and colleagues argue that this discontinuity from the Neandertal condition is difficult to reconcile with a Neandertal contribution to the early modern European gene pool. But that conclusion is, at best, an overstatement. As important as the Paglicci sequences are, a sample size of two is completely insufficient to make any meaningful statement concerning the possibility of some degree of Neandertal contribution to the early modern gene pool. The only way the Italian specimens would have provided a clear answer to the admixture issue is if they had Neandertal-like sequences. Furthermore, we have no idea what the mt DNA sequences of archaic people from Africa or Asia were. Thus it is possible that Neandertals are no more divergent from modern humans than all archaic people are, including those from Africa. Again, while the importance of the ancient DNA data currently available for late Pleistocene hominins are, they do not provide compelling evidence for totally excluding Neandertals from the ancestry of early modern Europeans.

## 5. Archaeology and chronology

While a detailed review of Paleolithic archaeology pertinent to the question of modern European origins is beyond the scope of this paper, a number of general issues bear brief mention. These include the dating of and hominin associations with late Mousterian and early Upper Paleolithic cultural manifestations, the origin of the Initial Upper Paleolithic and of the Aurignacian, and the possibilities for contact between the cultures of the Neandertals and early modern people in Europe. The Initial Upper Paleolithic (IUP) is used here to designate those early Upper Paleolithic complexes that appear to have technological and typological connections to the Mousterian, including the Châtelperronian, Uluzzian, and Szeletian (see Klein, 1999). It should also be kept in mind that the time period under consideration here, the Interpleniglacial of oxygen isotope stage 3-extending from ~39 to ~29 ka, was a dynamic period. It was a relatively warm and wet period during which sediments in rock shelters were as likely to wash away as to accumulate (Cabrera Valdés and Bischoff, 1989; Laville et al., 1980). This means that much of the crucial evidence pertinent to the issues under discussion here is likely to be largely missing from many important depositional sequences. As recent reviews have reaffirmed (Gamble, 1986; Mellars, 1996b; Klein, 1999; Churchill and Smith, 2000), the Mousterian in Europe gives every indication of being the sole product of Neandertals. The IUP has produced few associated fossil human remains, and only the Châtelperronian is associated with truly diagnostic remains. These remains, from the sites of St. Césaire and Arcy-sur-Cure (Grotte du Renne) in France, are certainly Neandertals (Lévêque and Vandermeersch, 1980; Hublin et al., 1996; Trinkaus et al., 1999). The remains associated with the other IUP variants basically comprise isolated teeth. While they show some affinities with Neandertals, they are too few and fragmentary to allow any conclusion about the identity of the makers of these cultures (Churchill and Smith, 2000). Hominin remains associated with cultural remains that may represent a different IUP expression at Vindija cave in Croatia are also Neandertals (Wolpoff et al., 1981; Smith, 1984; Karavanić, 1995; Karavanić and Smith, 1998).

The dating of the late Mousterian and IUP, which at the present time appear to be the handiwork of Neandertals, is a matter of some debate. Late dates for Mousterian, all ~28 ka, have been reported on the Iberian Peninsula (Hublin et al., 1996; Straus, 1997), Croatia (Smith et al., 1999), and the Caucasus region (Ovchinnikov et al., 2000). These are all based on radiocarbon dating, and each has been questioned on various grounds (see D'Errico et al., 1998; Zilhão and D'Errico, 1999; and the review in Churchill and Smith,

2000). Recently, Conard and Bolus (2003) have argued that all of the radiocarbon dates in this age range are likely to be too young. They point to peaks in the production of specific radioisotopes during the period between 50 and 30 ka (and particularly between 40 and 30 ka) that would lead to complications in radiocarbon dates from this range. Essentially, Conard and Bolus suggest that  $^{14}\text{C}$  dates from this period may well be underestimates of 6–10 ka. If this idea is correct, the dates for late Neandertals would fall back to a range of ~40–35 ka.

In recent years, the Upper Paleolithic cultural expression taken as the hallmark of early modern humans has been the Aurignacian. Indeed, the dominant idea has been that the Aurignacian represented the migration of modern humans into Europe. In fact in the 1920s, Boule (1921) opined that the European Neandertals were replaced by modern Aurignacian peoples, who had developed their distinctive anatomy and superior culture somewhere outside of Europe. More recently, a similar view has been expressed by a number of archaeologists (e.g. Mellars, 1996a, 2002, 1998; Klein, 1999; McBrearty and Brooks, 2000; Conard and Bolus, 2003) in various forms. These view the Aurignacian as emerging somewhere east of Europe and entering and spreading throughout Europe on the feet of early modern invaders. As has been noted, however, (see reviews in Straus, 1995, 1997, 2003; Clark, 1997; Karavanić and Smith, 1998; Churchill and Smith, 2000):

- (1) there is no convincing precursor of the Aurignacian itself outside of Europe; and
- (2) the Aurignacian is not nearly as uniform throughout its range as is often suggested. In fact, it is suggested that the Aurignacian was likely strongly influenced by regional variants of the Middle Paleolithic. Even Kozłowski and Otte (2000), who support the idea that the Aurignacian spreads across Europe in migrating waves, also believe that local manifestations of the Aurignacian are characterized by varying degrees of assimilation of local Middle Paleolithic influences.

Regardless of its origin, there are two other problems with the Aurignacian that are pertinent here. First, there is a distinct debate as to how early the Aurignacian appears in Europe. Dates around 40 ka or older have been published for Aurignacian (or Aurignacian-like) components in northern Spain and the Balkans (see Straus, 1997), but these have been challenged (D'Errico et al., 1998; Zilhão and D'Errico, 1999). If the conservative view is taken, the Aurignacian seems to post-date 36.5 ka (Zilhão and D'Errico, 1999). However, there is certainly not full agreement on the chronology of the early Aurignacian, just as is the case with the late Mousterian. Second, there is increasing question regard-

ing who made the early Aurignacian. Again the assumption has always been that early modern humans were the responsible parties. Recent assessments demonstrate that much of the best evidence for this association is disappearing. For example, recent reanalysis and dating of the Cro-Magnon remains from France have shown them to be 27.7 ka and likely to be associated with Gravettian rather than Aurignacian (Henry-Gambier, 2002). Several other prominent associations have either already been shown to be erroneous (Smith et al., 1999) or soon will be published as erroneous. The specimens left, with the exception of the aforementioned Mladeč remains, are not very compelling on the basis of context, diagnostic morphology or both (Churchill and Smith, 2000). While it is clear that Upper Paleolithic components post-dating 30 ka are associated with modern humans, it is increasingly less clear that this is unequivocally the case prior to this date. The 35 ka date for the Peștera cu Oase mandible strongly suggests that modern people were in Europe prior to 30 ka (Trinkaus et al., 2003), but any association between these people and the early Aurignacian will have to be reestablished. The point here is that the idea that modern people entered Europe outfitted with the Aurignacian and then spread throughout Europe in tandem is not unequivocally supported by the available evidence.

Finally, there is the question of the origin of the IUP. Since at least some aspects of typology and technology in the IUP show some similarities to the later Upper Paleolithic, it has been suggested that the IUP reflects some degree of acculturation on the part of Neandertal groups under the influence of the presence of modern humans and their culture (Hublin et al., 1996; Karavanić and Smith, 1998; Klein, 1999). In addition to the cultural issues, evidence that Neandertals and early modern humans overlapped chronologically has been cited. This includes evidence from overlapping chronometric dates (see Churchill and Smith, 2000) and evidence of interstratification of Châtelperronian and early Aurignacian at three sites in southwestern Europe (Laville et al., 1980; Klein, 1999). However, D'Errico et al. (1998) and Zilhão and D'Errico (1999) have challenged both the interstratification evidence and the overlap of chronometric dates. They argue that all Châtelperronian components actually predate the Aurignacian and that Neandertals developed cultural similarities to later Upper Paleolithic independently of any external influence. Thus, like the origin of the Aurignacian, the explanation for the IUP and related expressions is far from clear.

## 6. Conclusion

While many discussions of modern human origins in Europe suggest that the question have been solved in



favor of one perspective or another, we show here that there are many unanswered questions. Often, claims that the issue has been resolved seem to be based on what might be termed a modified domino theory. In other words, the argument is that the domains of genetics, anatomy, and archaeology all support each other, particularly when it comes to total replacement models. Generally one gets the impression that even if there might be a minor point in one of these domains that does not support a particular perspective, the other areas make up for this by their “unequivocal” support of the perspective. We believe that, when each domain is carefully considered, none unequivocally supports any particular model. This includes the Assimilation Model, the model we believe is the best explanation for modern human origins in general and the origin of modern Europeans in particular.

The assimilation model (AM) was first proposed in the late 1980s (Smith et al., 1989), although aspects of it were certainly discussed earlier (e.g. Smith, 1985; Trinkaus and Smith, 1985). Basically, this model posits that anatomically modern humans emerged in Africa and radiated from there into West Asia and later into the remainder of Eurasia. However, rather than totally replacing the archaic peoples they encountered in Eurasia, we believe that genetic exchange occurred between the expanding moderns and the indigenous archaics. This model differs from the recent African origin (RAO) model in that the AM holds that the genetic exchange was more than “incidental.” While RAO has accepted that some “hybridization” may have occurred between Neandertals and early moderns, it is clear that the extent of the Neandertal genetic input is considered essentially insignificant (e.g. Stringer and Bräuer, 1994; Bräuer and Stringer, 1997; Bräuer and Broeg, 1998; Klein, 1999; Bräuer, 2001). Furthermore, the AM holds that the more modern-like features seen in some late Neandertals, such as Vindija (Wolpoff et al., 1981; Smith, 1984) or St. Césaire (Trinkaus et al., 1999; Wolpoff, 1999), are the result of assimilation of early moderns into late Neandertal populations. Proponents of RAO see these as homoplasies (e.g. Stringer and Bräuer, 1994). On the other hand, AM strongly supports the perspective of the multiregional evolution (MRE) model (e.g., Frayer et al., 1993; Wolpoff, 1999) that gene flow plays a vital role in the emergence of modern humans throughout Eurasia. It differs from MRE in that AM recognizes Africa as the likely source of the basic modern human anatomical form and that the modern humans radiating out of Africa have the major, catalytic effect on the emergence moderns in Europe and Asia (Smith et al., 1989; Smith, 2002). The AM also emphasizes that the evidence for assimilation stems from anatomical details rather than overall morphological gestalt of the earliest modern Europeans. Similarly, we view the AM as the best explanation for the mosaic

morphology of the Lagar Velho child (Zilhão and Trinkaus, 2002), a basically modern child with some Neandertal-reminiscent anatomical details.

In our opinion, the morphological evidence in Europe and the temporal trends discussed previously are most commensurate with the AM and not a model focused on virtually total replacement. Furthermore, we believe the AM is the best fit for the mostly out of Africa genetic perspective reflected in the work of Haprending and Rogers (2000) and others, Relethford (2001), Templeton (2002), and others; and we see the AM being eminently logical in light of the pertinent archaeological evidence. However, we also recognize that we are making a likelihood statement here. The available data do not reject the other models, and there are certainly uncertainties that are critical. As discussed previously, these uncertainties are found in the morphological, genetic and archaeological interpretations on which the AM is based. While fully admitting this, we continue to consider the AM to be the most logical explanation for modern human origins in Eurasia as we understand the phenomenon at the current time. We are convinced that the population dynamics characterizing this phenomenon were very complex. In fact, while Klein (1999, p. 518) argues that “...the Cro-Magnon invasion of Europe would have differed fundamentally from the historic European invasion of the Americas or Australia...”, we think that this is likely to be a good model for the dynamics of interaction between the indigenous European Neandertals and the “Cro-Magnon” invaders.

It is clearly the case that the Neandertal physical type disappears from the European scene soon after 30 ka, and only limited examples for the survival of Neandertal anatomical features exist after 25 ka. But this does not mean that Neandertals necessarily went extinct in the total biological sense. As Zubrow (1989) showed many years ago, a slight reproductive advantage of moderns would lead to “replacement” of Neandertals in a short time span. If this is added to the probability that incoming moderns were numerically superior to the indigenous Neandertals, populational and genetic swamping of the latter by the former populations is eminently likely. As was discussed above, we believe that there is sufficient evidence from details of morphology to hold that Neandertals were assimilated into early modern European populations, and that this interpretation is commensurate with some interpretations of the pertinent genetic data. We feel that these features and other Neandertal genetic contributions were quickly swamped and were likely present in European populations for only a few thousand years at most. But if Neandertals did contribute to these early modern populations, their “extinction” consisted, at least in part, of assimilation and not biological annihilation.

D. Serre et al. (2004) provide an addition four Neandertal and three early modern European mt

DNA sequence. These follow the pattern indicated by us in the text. Serre and colleagues show that a Neandertal contribution of  $\leq 25\%$  to early modern European gene pools cannot be excluded based on currently available data.

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