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EVOLUTIONARY SIGNIFICANCE OF THE QUARRY CAVE SPECIMENS FROM MLADEČ

ABSTRACT: The human remains from Mladeč have recently been described in a detailed monograph on the site (Frayer et al. *2005). This material derives from two different caves, the large Dome of the Dead cave and a small, separate side cave discovered during quarrying operations in 1904. Fortunately similar bone tools were found in both localities making archaeological association possible between the two caves. Material from this smaller chamber is less numerous and for the most part has been destroyed or lost since its discovery. However, the two adult crania (Mladeč 5 and 6) represent distinctive specimens with clear morphological links to Neandertals. Here, we review details of the side chamber and test hypotheses concerning the relationship of Mladeč 5 and 6 to earlier populations.*

KEY WORDS: Mladeč Quarry Cave – Early modern humans – Neandertal ancestry

HISTORY

On March 22, 1904, during quarrying operations at the Main Mladeč Cave, in the Moravian village of Lautsch (the Austrian name for Mladeč), an entrance to a second small cave (the "Quarry Cave") was found some 50 meters west of the position of the 1902 entrance to the Main Cave complex. Soon after the discovery of the Quarry Cave, Dr. Jan Smyčka (physician and mayor of the larger nearby town of Litovel – Litau) visited the site (Smyčka 1907). Maška came on August 12th and Josef Szombathy arrived August 25th. These visits focused on the Quarry Cave discoveries; virtually any new human fossil was newsworthy in Austro-Hungary, and of scientific importance throughout the empire at the turn of the century (see also Radovčić 1988). Szombathy (1904) describes this second cave as an isolated triangular chamber with a caved-in ceiling 20 meters long and 6–8 meters broad, oriented in the southeast to northwest direction. Knies subsequently obtained permission to excavate the site. Upon clearing the broken stones it was evident that the ceiling fully covered the sediments including the skeletal remains they contained.

We believe these to belong to three individuals, based on their crania: two adult males (Mladeč 5 and 6, *Figure 1*) and a child (Mladeč 46) (Frayer *et al.* 2005). Numerous additional adult postcranial remains were found together with the two damaged adult crania in the same loam-filled area (Mladeč 61, 65–67, 70–73, 78, 84, 86–87, 93–101). Most of these were listed by Szombathy, who studied them in 1904 and in 1925 in Litovel where they were deposited in 1923 after first being sent to the Fürst Liechtenstein Museum in Úsov Castle. The Quarry Cave remains also included two maxillae (Mladeč 50 and 51), two mandibles (54 and 55), rib fragments (67), a clavicle (65), a scapula (66), a fragmentary ilium (61), two humeri (70 and 71), a radius fragment (72), two "shin bones" (one of these is a femur (Mladeč 78) and the other a misidentified ulna fragment (73)), a tibia (84), a fibula (86) and 12 metacarpals and phalanges (87 and 93). The remainder of the adult remains were later collected by Knies and given to the Moravian Museum in Brno. These were listed by Knies (1905) but never studied by Szombathy, and include a right zygomatic (Mladeč 94), a calcaneus (99), phalanges (98), a scapula (101) and fragments of femur (95), tibia (96), fibula (97), and ribs (100).

In view of the very large number of postcranial remains associated with these three crania and the limited (2 by 3 meter) area of loam the specimens were found in, evidently

FIGURE 1. Three male Mladeč crania: above and below are the Quarry Cave specimens 5 and 6, Mladeč 4 from the Main Cave is between them.

sealed by a rockfall, we believe it is probable that the Quarry Cave skeletons were intentionally buried, possibly at the same time. If so, the remains are unlikely to represent a nuclear family, there are two adult males and a child, and the absence of any body decoration is of some interest (especially in view of the remains of one or more necklaces found in the Main Cave). In that they do not represent a family group and might be three males (certainly the two adults are male), this trio resembles the triple burial from Dolní Věstonice (Vlček 1991).

None of the Quarry Cave specimens were directly dated (Wild *et al*. 2005). The single specimen to survive the Mikulov Castle disaster at the end of the Second World War is Mladeč 5, a cranial vault that was heated and slightly burnt in some areas during the fire. Thus the Quarry Cave specimens can only be related to the Main Cave specimens and their 31 kyr date archaeologically. When the Quarry site was opened in 1904, sediments and other materials from the opening of the small abyss-like cave were initially disposed of, without informing the archaeologists (Knies 1905, Maška 1905, Smyčka 1907). In subsequent visits to the Quarry Cave the museum in Litovel obtained three flat bone points, one 17.8 cm long, another is a fragment of a similar but bigger point, and the third is a smaller fragment, probably not a tool. Knies found another flat bone point consisting of five fragments, totalling about 14 cm in length.

The association of the Quarry Cave remains with those in the Main Cave is unequivocally established through a comparison of these and other artifacts (Bayer 1922, Frayer *et al.* 2005, Svoboda, 2000). Bone tools are the most diagnostic of the Mladeč artifacts, and the most important of the bone tools are found in both the Main and Quarry Caves. These are points with broad bases, or Mladeč type points. Most diagnostically, there is not a single point with a split-base at Mladeč. This is surprising since the thin cross sections that are typical at Mladeč are otherwise generally found with split-bases (Albrecht *et al.* 1972). Unlike so many other sites dug more than one hundred years ago, the Mladeč caves have only a single cultural type and it can be readily identified as Aurignacian. The archaeological remains from the Quarry Cave are clearly and unambiguously related to those of the Main Cave through the common presence of Mladeč points.

NEANDERTALS *AT* MLADEČ?

Ironically, given the tenor of discussions today, Neandertal finds were once reported from Mladeč, although not from the Quarry Cave. In a 1922 article, Smyčka mentioned that the remains discovered by a group of amateurs in 1922 were of "Neanderthal type" (Smyčka 1922). Perhaps for this reason, he believed these to be the earliest of all Mladeč finds. We can no longer be certain which specimens this refers to because, with the exception of Mladeč 4, the 1922 remains were never pictured or described in any detail. It has since been supposed that Szombathy did not mention them for this reason: his paper was about human remains, not Neandertal remains.

It was therefore assumed that some Neandertal remains were destroyed in the Mikulov Castle fire of 1945 before they had been described, and this was reported occasionally by careful readers of the Central European literature (e.g. Leakey, Goodall 1969). Nobody surmised that these were in reality the specimens described by Szombathy (1925: 73–75) as "found after 1903".

Szombathy's visit to Litovel and to Mladeč in 1925 was evidently very brief and his description of the material "after 1903" was superficial (1925). Some of his contemporaries repeated Fürst's assertion (1923–24) that bones were found of at least five individuals, of a male, of a female and of three children. This did not agree with the description of specimens Szombathy designated as discovered "after 1903" so it was generally accepted that Szombathy described only some of the specimens discovered after 1903.

Scholars who consulted the 1925 monograph questioned why Szombathy did not describe the human remains found in 1922, when it was evident that he must have seen them in Litovel, concluding that he must have left out the Neandertals. We now recognize that indeed he did see them, and that he described them as well, emphasizing that the most important discovery was cranium 4 (*Figure 1*) and the remains associated with it. This is clearly mentioned by Blekta (1932), and so it is completely obvious now that there was only one period of major discoveries in the Main Cave after 1903. These were the 1922 finds, discovered by amateurs under the chimney. What was most misleading was the title of the section of the 1925 monograph in which Szombathy described these remains: "Die Menschlichen Skelettreste der Fürst-Johanns-Höhle von den Grabungen seit 1903" (Szombathy 1922: 73). "Since 1903," for the most part, meant "in 1922."

Thus the 1922 material, its provenience, and even the circumstances of discovery can be identified. Smyčka was wrong to assert (1922) that these finds are the earliest of all, are more primitive, and are of Neandertal type. The morphology we can discern from the published photograph of Mladeč 4 does show a prominent supraorbital region, but while its supraorbital morphology may be more prominently developed than in the Mladeč 6 it is not as projecting or thick as Mladeč 5, and the size of structure as seen in lateral view was the only basis for Smyčka's description of Mladeč 4 as a Neandertal. We do not believe it is sufficient. Moreover, Mladeč 4 was evidently not earlier than the other finds. The 1922 remains were associated with Aurignacian tools, as we describe above, and the human bone fragments are in exactly the same state of fossilization as the other human skeletal material from the Main Cave (e.g. Mladeč 1) and the Upper Pleistocene faunal remains.

NEANDERTAL ANCESTRY *FOR* MLADEČ?

We do not believe the Mladeč Quarry Cave males are Neandertals either. Our interest is in how these males might be related to Neandertals through ancestry. We assume the phylogeny of the Mladeč Quarry Cave adult male crania reflects the phylogeny of the population from which they came, but we are limited to male comparisons because only adult males are known from the Quarry Cave. Adult males have a more dramatic or pronounced expression of many characteristics than females or juveniles (Krogman, Işcan 1986), and there is an exceptionally poor representation of females in the Skhul/Qafzeh cranial sample (the only potential non-Neandertal ancestral sample), which makes the male-male comparisons necessary in any event.

The issue of relationships can be expressed in three hypotheses about the ancestry of the Mladeč Quarry Cave males: unique Neandertal ancestry, unique African ancestry, combined Neandertal and African ancestry. We reject out-of-hand the notion that the European Neandertals are the sole ancestors of the Mladeč Quarry Cave males. This is a polygenic interpretation that would mean the Mladeč population evolved its modern features independently, in parallel with similar changes that were taking place in other regions. Such a perspective requires a very unlikely number of homoplasies. If Neandertals were a different species than modern humans, such a theory would also require that the Mladeč population was part of this species.

Let us, then, consider the other two hypotheses about the ancestry of the Mladeč Quarry Cave male crania:

1. They are descendants of Skhul and Qafzeh populations and not of Neandertals (Eve replacement theory);
2. They are descendants of both European Neandertal populations and the penecontemporary Skhul and Qafzeh populations (Multiregional evolution).

The second of these involves some degree of Neandertal ancestry. This means more ancestry than a drop of cream in a cup of coffee, as one author put it, or slight leakage across a species boundary, as another author would have it, because this expectation is not about the *possibility* of Neandertal ancestry, but about the *evidence* for ancestry, sufficient ancestry to have visible consequences in the distribution of traits in post-Neandertal Europeans. This means there was enough ancestry for Neandertal genes to persist if they were under selection or disappear of they were selected against, in other words evolution by normal processes. Gene changes are not necessarily the results of complete population replacements, and in any event the great majority of all genetic changes, almost certainly the ones we are dealing with here, are changes in allele frequencies and not the replacements of one gene by another.

"Out of Africa" versus complete replacement

According to the "Out of Africa" theory of total replacement the first hypothesis is the expected one. Supporters of this theory have been strong in their contentions about the ancestry issue, especially those who regard the Neandertals as a different species. The testable claim is that since Neandertals are a different species from contemporary *Homo sapiens* populations, there can be no Neandertal ancestry of the earliest post-Neandertal Europeans such as Pestera cu Oase (Trinkaus *et al*. 2003), Lagar Vehlo (Zilhao, Trinkaus 2002), and of interest here, Mladeč (Frayer 1986, Frayer *et al*. 2005, Jelínek 1983, 1987). The "Out of Africa" total replacement theory requires that Neandertal features should disappear with Neandertal populations, and we would not expect them to persist into subsequent European populations. This Eve replacement theory is based on the proposition that evolutionary change occurs as one species replaces another.

"Out of Africa" began as a replacement theory. It was first published by Protsch (1975), who argued that since modern humans were dated earlier in Africa than anywhere else, they must have evolved there and replaced other populations as they dispersed. The key question distinguishing various versions of the "Out of African" theory is whether replacement was complete – was there mixing during this time of replacement? When Stringer and Andrews reviewed the issue (1988: 1263), they considered *Homo sapiens* a distinct species (meaning modern *Homo sapiens* because they wrote: "throughout this article the use of the term *Homo sapiens* will be restricted to anatomically modern humans"). Stringer and Andrews (1988: 1267) contended that this species appeared first in Africa: "we feel that an African origin for *Homo sapiens* is highly probable". Mitochondrial DNA, initially, seemed to strongly support the replacement theory. The interpretation of a unique recent ancestry for mtDNA accounted for its limited variation under the assumption of neutrality, and workers such as Stoneking and Cann quickly concluded that the complete replacement of existing mtDNA lines by Eve's descendents required that there was a speciation (Stoneking, Cann, 1989). These papers further developed the theory that modern humans appeared as a new species, and that the evolutionary process was one of species replacement. Although workers such as Bräuer (1992) have called this a "test theory" and complained that all the focus of "Out of Africa" critics seemed to be on trying to disprove it, there was a reason for this – it is one of the "Out of Africa" formulations that can be clearly disproved.

"Out of Africa" without complete replacement

There are other "Out of Africa" formulations, because not everybody with an "Out of Africa" position thinks Neandertals are a different species. Some such as Bräuer (1992) assert that Neandertals could have interbred with Upper Paleolithic Europeans but just did not do it very often, while others contend that interbreeding was common and significant (Smith *et al*. 2005). Whatever the case, this process can no longer be described as "replacement" because it involves mixture between two populations. Bräuer, in early versions of his "Afro-European *sapiens* hypothesis (e.g. 1984: 158), argued for mixture: "During the Würm glaciation, anatomically modern humans expanded further … in both the Near East and Northern African there followed a period of mixing, after which these forms cause the disappearance of the Neandertaloid populations … during the next millennia – in what was probable (sic) a relatively slow process of hybridization and replacement – they also superseded the European Neandertals." Bräuer considers himself an adherent to the "Out of Africa" position (Bräuer, Stringer 1997) but his is not a complete replacement theory and observers such as Relethford (1999, 2001, Relethford, Jorde 1999) correctly note that Bräuer's position is actually a variant of Multiregional evolution.

Similarly, Eswaran's Wave theory (2002) is a variant of Multiregional evolution (Wolpoff 2002), as is the Assimilation theory proposed by Smith *et al.* (2005). This raises the interesting question of how "Out of Africa" replacementists can maintain a distinct position once *complete* replacement is rejected. The simple answer seems to be that *they redefine Multiregional evolution* (some of these attempts are detailed in Wolpoff *et al.* 2000), not because the alternative to Multiregional evolution is unthinkable, but because the alternative is undefinable. If one chooses to accept an "Out of Africa" theory that is based on mixtures of invading Africans with native populations, what would the lowest proportion be for this theory to become Multiregional evolution? One answer is to restrict Multiregional evolution to only describe the situation of *no* African contribution (Collard, Franchino 2002). A more satisfying answer is that the question is absurd.

Collard and Franchino (2002: 324) assert that: "the multiregional evolution model not only argues that non-African archaic hominids made a significant contribution to the gene pool of living humans, but also *discounts migration of recently evolved Africans as a significant factor in the emergence of modern humans outside of Africa*" (our italics). The later claim is surprising, because the contention that Multiregional evolution discounts significant African contribution to human evolution is not only contradicted by the first publication on the topic (Wolpoff *et al.* 1984) that based the model on the contention that most gene flow was expected from the Centre (Africa) to the edge (*sensu* Thorne 1981), it flies in the face of all subsequent publications including the papers Collard and Franchino review in their publication. These authors may agree or disagree with the contention of a significant African contribution to human evolution, but they have no grounds for denying the centrality of gene flow from the centre to the edge of the human species to Multiregional evolution, from its very beginning. Models including population mixing are reticular and, although differing in detail, all describe the evolutionary process within a subdivided species (Templeton 1997).

"Out of Africa" and Neandertal ancestry

The contention that modern humans came out of Africa can only impact the question of Neandertal ancestry for the Quarry Cave males if the Neandertals were replaced without mixture. Mixture of moderns with Neandertals – enough mixture to be discernable in fossil anatomy – is sufficient to disprove complete replacement. A more interesting question is how much mixture is required to account for the distribution of features in the Quarry Cave males under an "Out of Africa" theory.

Some Out of Africanists describe the European replacement as not quite complete but it has never been clear what this means, and it certainly means different things to different authors. Minimal mixture proposed by replacement theorists responds to the need to posit just enough mixture with Neandertals to account for the similarities of early Upper Paleolithic Europeans to Neandertals after the replacement (Bräuer 1992). Stringer (1982, 1992) asserts that the amount of mixture required is not sufficient to show that Neandertals are the same species as the humans with whom they are mixing. But how much mixture does this require? It must be enough to be compatible with Hawks' (1997) estimate that at least 25% of the ancestors of Upper Paleolithic people would have to be Neandertals, to account for the preservation of Neandertal "autapomorphies" documented by Frayer (1993). The key point is that mixture reflects the process of evolution *within* the human species and provides the possibility for Neandertal genetic material to continue to be promoted by selection in subsequent populations. This is why any reticular model that fits this description is just a restatement of Multiregional evolution (Relethford 2001).

As a side note, once such mixture is admitted to, as overwhelming evidence suggests it should be, it is time to stop referring to the intrusive group as "moderns". Surely if two human groups can and do have offspring when they are in contact, regularly enough to leave sufficient influence on subsequent generations to be found in their spotty and irregularly preserved fossil remains, it is not correct to call or think of one as being more modern than the other.

EQUAL ANCESTRY HYPOTHESIS

If we assume an "Out of Africa" interpretation of Multiregional evolution, it is possible to examine hypotheses of ancestry for the Quarry Cave males. If we are not willing to make such an assumption, or if we contend that the populations entering Europe were from both Africa and other sources, this question is much more difficult to answer because the source of the non-European ancestral populations can no longer be specified. While we are more sympathetic with the later, especially given the anatomical details of the Oase cranium, which appears to be earlier than the Quarry Cave remains, investigating the Quarry Cave question from the "Out of Africa" perspective is of some interest and we will do this here.

Unique ancestry in one of these source populations does not mean we would expect all the resemblances of the Mladeč Quarry Cave crania be with the source population in question because we assume that sampling error and other sources of variation would insure this not be the case. If under the complete replacement model we do not necessarily expect all the resemblances to be in a single direction, it is difficult to specify exactly how many resemblances to one potentially ancestral population would be enough to refute the hypothesis of complete replacement by the other. A hypothesis of replacement with limited mixture is even more difficult to specify. On the other hand, since the Multiregional model does not limit the possible patterns of multiple ancestry, its refutation must be accomplished with a demonstration that the complete replacement model is correct.

The conservative hypothesis addressing an "Out of Africa" interpretation of Multiregional evolution is that the Quarry Cave males have equal ancestry in the earlier Neandertals and African source population. We must assume that the equal ancestry hypothesis and the complete replacement hypotheses have predictions about metric and non-metric similarity that do not overlap, because if their predictions cannot be distinguished, it would mean that the Neandertal and African source population samples are so similar that their phylogeny cannot be resolved. It follows from this assumption that:

- if the equal ancestry hypothesis cannot be disproved, the complete replacement theory must be incorrect;
- the complete replacement theory is also rejected if analysis reveals a preponderance of resemblances between Mladeč and the Neandertals;
- the complete replacement theory will be supported if analysis disproves the equal ancestry hypothesis and reveals a preponderance of resemblances between Mladeč and the African source population.

If the equal ancestry hypothesis cannot be disproved, we note that this result implies much more mixture than the "Out of Africa" interpretation of Multiregional evolution would predict. One reason for this is that the results of gene flow between unequal sized populations is the predominance of genes from the larger population, and estimated population size differences alone would predict that Skhul/Qafzeh would more greatly affect the Mladeč gene pool than the Neandertals would, if gene flow alone were the cause of change (Relethford 2001).

The biggest problem is to identify the African source population. Herto, Omo Kibbish, and Jebel Irhoud comprise the most relevant African cranial sample for comparison, and four of these may be male (Herto, Omo 1 and 2, Jebel Irhoud 2), but Skhul and Qafzeh comprise a *more recent* sample of "early modern" males, with sex determination based on both postcranial and cranial features. Our comparisons with the Skhul/Qafzeh sample are as much dictated by necessity as by the position of the sample in time and space because we do not have access to Herto, or its cast, and any comparisons with this important, complete African would necessarily be incomplete. Klein (2001) notes that for much of the late Middle and early Upper Pleistocene the Levant can be considered an ecological part of Africa. Here we treat the Skhul/Qafzeh sample as representing Africans, as others have.

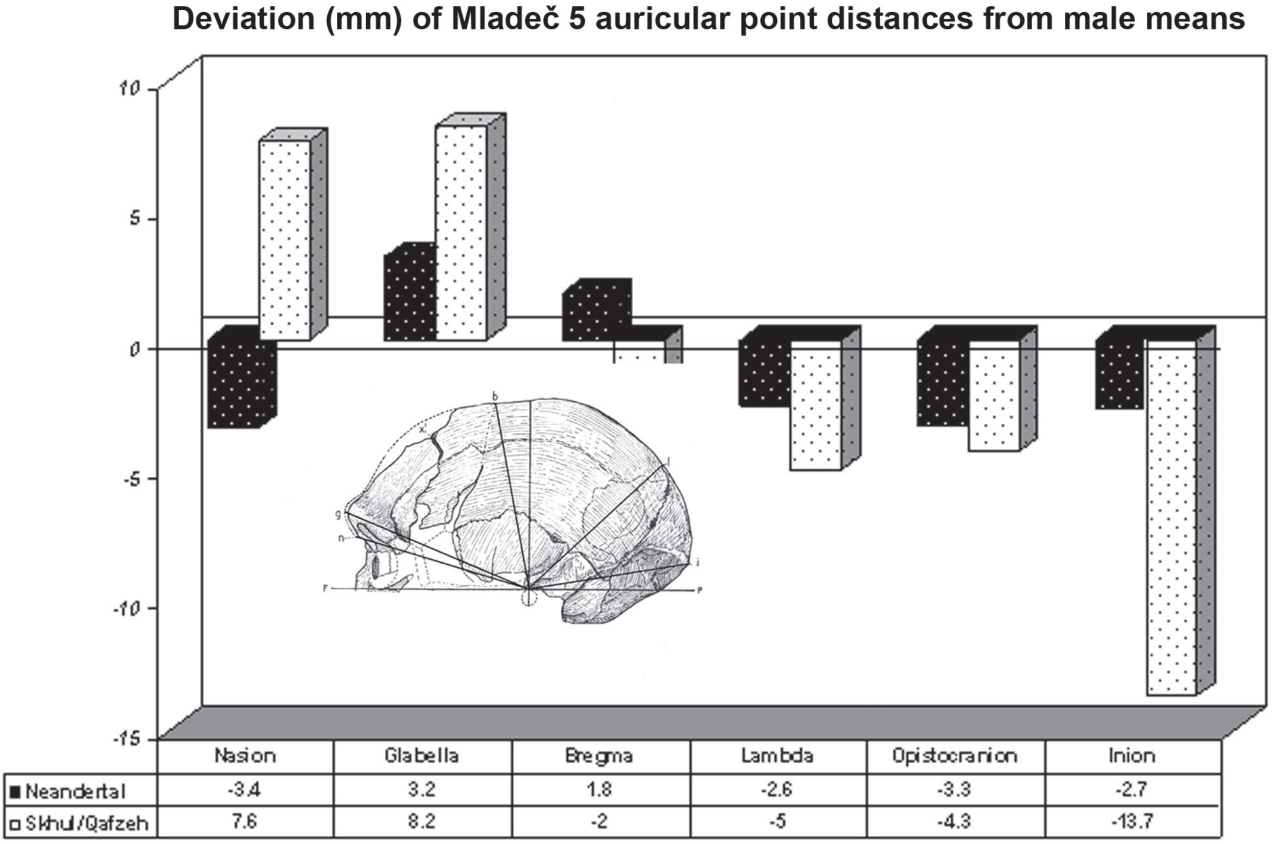
Metric approaches

White observes (2000: 375): "the skull is the only part of the skeleton that is widely used in estimating geographic ancestry," and the fact is that the Mladeč 5 cranium closely approximates several European Neandertals in overall lateral profile (*Figure 2* and Wolpoff *et al.* 2001). However, the *prima fascia* case for examining a hypothesis of mixed ancestry for the Quarry Cave males is that their size and shape resemble earlier Neandertal males at least as well as they resemble Skhul/Qafzeh males. We quantified this observation with a comparison of means for measurements that reflect the sagittal profile (*Figure 3*). In a series of measurements from the auricular point, projected into the sagittal plane, we found that Mladeč 5 is invariably closer to

FIGURE 2. The Mladeč 5 male (centre) compared with Qafzeh 9 (left) and Spy 2 (right) in lateral profile. While this paper examines a hypothesis of equal ancestry for the Mladeč Quarry Cave males, this profile shows a closer and more detailed resemblance to the Neandertal condition.

the Neandertal males than it is to males from Skhul/Qafzeh (measurements from the auricular point are not possible for Mladeč 6). The conservative hypothesis is that the Quarry Cave males have equal ancestry in the earlier Neandertal and Skhul/Qafzeh hominids. It is this equal ancestry hypothesis that we further examine below.

More general metric comparisons are of interest for issues of size and shape. We examined these in detail, using a large number of systematic metric comparisons that were compiled as part of the descriptions and analysis of the Quarry Cave crania presented by Frayer *et al.* (2005). One way to abstract pattern from a large number of individual



Deviation (mm) of Mladeč 5 auricular point distances from male means

	Nasion	Glabella	Bregma	Lambda	Opistocranion	Inion
■ Neandertal	-3.4	3.2	1.8	-2.6	-3.3	-2.7
□ Skhul/Qafzeh	7.6	8.2	-2	-5	-4.3	-13.7

FIGURE 3. Comparison of sagittal auricular distances for Mladeč 5 and male cranial sample means, shown as the deviation (in millimetres) of the Mladeč male from the potentially ancestral Neandertal sample (n=5) and Skhul/Qafzeh sample (n ranges from 2 to 4). These distances are shown on the drawing of the Skhul 9 vault, modified from McCown and Keith (1939). For example, the figure shows the sagittal projection of the nasion-auricular distance in Mladeč 5 is 3.4 mm less than the male Neandertal mean, and 7.6 mm greater than the male Skhul/Qafzeh mean. In *every* comparison Mladeč 5 is closer to the Neandertal mean.

TABLE 1. Distribution of metric data, summarizing how often measurements of the Mladeč Quarry Cave crania lie closer to the Neandertal or Skhul/Qafzeh male means (reported in Frayer *et al*. 2005). The question of which mean the Quarry Cave specimens more closely approach is examined in all cases, and in only those cases when the Mladeč data lie between the means of the comparative samples. For instance, of all the cranial comparisons made for Mladeč 5, the Mladeč specimen was between the means for the Neandertal and Skhul/Qafzeh males 33 times. Thirteen of these times Mladeč 5 was closer to the Neandertal male mean, it was closer to the Skhul/Qafzeh males 20 times. In total Mladeč specimen was compared with the Neandertal and Skhul/Qafzeh males 112 times (the additional comparisons where cases when the Mladeč specimen did not lie between these means). It was more similar to the Neandertal males 62 times and Skhul/Qafzeh males 50 times.

	Mladeč values lying between means		**Mladeč values anywhere (between the means, or above/below them)**	
Closer to ➔	**Neandertal**	**Skhul/Qafzeh**	**Neandertal**	**Skhul/Qafzeh**
Mladeč 5	13	20	62	50
Mladeč 6	9	9	30	29

comparisons is to determine how often they result in greater similarity to one group as compared to another. In *Table 1* we examine the question of how often the Mladeč Quarry Cave specimens are more similar to Neandertal males and how often they are more similar to Skhul/Qafzeh males. Overall, in less than half (45%) the metric comparisons the Skhul/Qafzeh sample was more similar for Mladeč 5, whereas in Mladeč 6 the total comparisons were about equally divided between the two possible ancestral groups. In the more restricted comparison, when the only Mladeč cranial metrics considered were those cases that fell between the Neandertal and Skhul/Qafzeh means, the values were closer to the Skhul/Qafzeh mean in 60% of the comparisons for Mladeč 5 and in 50% of the comparisons for Mladeč 6.

The distribution for Mladeč 6 clearly cannot be distinguished from the equal ancestry hypothesis, as it is equally similar to both samples, in either comparison. Mladeč 5 is more often closer to Skhul/Qafzeh for values lying between the means of the comparative samples, but is more often closer to the Neandertals considering all comparisons. This means that the Mladeč 5 values far more often lay beyond the Neandertal average than beyond the Skhul/Qafzeh average, "beyond" being defined by the direction of difference between the two comparative samples. Because we are interested in the probability of one out of two possible outcomes, and since we can specify the underlying distribution as reflecting equal ancestry, we used the normal approximation of the binomial distribution for examining the probability that these comparisons could be found in a distribution where the expected relationship is the same for each comparative sample (Siegel 1956). In the comparisons where Mladeč 5 is between the means of the comparative samples, the probability of 13 or fewer out of 33 (13+20) traits resembling Neandertals is 0.15. Examining the distribution that includes all comparisons, whether the Mladeč 5 values lie between the means or not, the probability of 62 or more out of 112 traits resembling Neandertals is 0.11. Therefore, we cannot reject the equal ancestry hypothesis at the 0.05 level.

Of course, these results indicate that the Skhul/Qafzeh sample cannot be the unique ancestor, the requirement of the Eve replacement theory.

Non-metric approaches

There are several ways to approach the question of equal ancestry non-metrically, and thereby avoid questions raised by size variation (Hauser, DeStefano 1989), although there are admittedly few size differences between the male samples. The great differences in morphology between the overall shape between the Mladeč males and some specimens in the Skhul/Qafzeh sample are readily observable (*Figure 2*). The Mladeč crania can be forensically identified as European, whereas using standard forensic techniques (e.g. Gill, Gilbert 1990), the crania from Skhul and Qafzeh are not identified as Europeans: some of these specimens resemble Africans, some East Asians, and others cannot be unambiguously placed.

What is interesting is that some of the features that identify the Quarry Cave males as Europeans are shared with Neandertals (*Figure 4*), and there are other common Neandertal features in these remains (Frayer 1993). For instance, the small mastoid process of Mladeč 5 (*Figure 1*) and elliptical suprainiac fossa on Mladeč 6 (*Figure 5*) exemplify anatomy said to be unique in the Neandertals (Hublin 1998), but clearly are not uniquely Neandertal because they are found in these post Neandertal Europeans.

However, while showing the persistence of Neandertal features in the Mladeč remains addresses the ancestry issue (Frayer 1993, 1997), it is not a direct test of the equal ancestry hypothesis. To make such a test and transform these and similar comparisons into statements with statistical meaning requires overcoming some formidable obstacles; with a sample size of 2 for the Quarry Cave adult males, and comparative samples that are extremely small. The comparisons are not systematically constituted, in that different comparisons can have different sample sizes and some observations compare different specimens than others. Finally, while we know that many of the non-metric comparisons involve observations that are not independent of each other, just as the metric comparisons do, and we know we cannot specify the pattern of dependence, or for that matter the underlying variance/covariance matrix of the samples (Ahern *et al.* 2005). For these reasons, we proceed with caution, and focus on some simple tactics that make as few assumptions as possible.

FIGURE 4. Superior view of Mladeč 5 (centre) compared with Spy 1 (left) and Spy 2 (right). Some regionally common similarities of the Mladeč specimen to these crania that can be seen in this view include the flattened cranial rear, and the lateral angulation of the lateral superior orbital border. The position of maximum cranial breadth is anterior as it is in Spy 1, not the more common Neandertal posterior position seen in Spy 2. However, the general cranial dimensions and many specifics such as the postorbital constriction more closely resemble Spy 2.

We use pairwise analysis here for hypothesis testing, to examine the relationship of the Mladeč Quarry Cave crania to the individuals in our two comparative samples of potential ancestors. Questions have been raised about whether it is valid to use pairwise analysis this way, for hypothesis testing, even though it has become normal to do so in genetic analysis. One paper (Collard, Franchino 2002) collected osteological and soft tissue data for *Gorilla, Homo, Hylobates*, and *Pan*, to further examine this issue. The pairwise differences that were calculated were used to construct phylogenetic trees which were then rejected because they did not conform to the widely accepted molecular tree for these genera. The authors concluded (p. 333): "Pairwise difference analysis cannot be relied on to recover phylogenetic information from all primate morphological datasets."

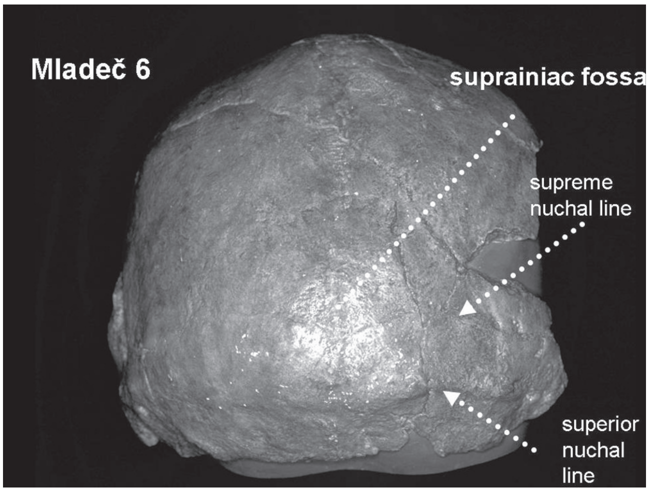


FIGURE 5. Posterior view of the Mladeč 6 cranium (cast) showing the elliptically shaped suprainiac fossa above the supreme nuchal line. The lower border of the fossa is formed by this line, which is the top of the bilaterally arched nuchal torus. Because this is claimed to be a homologous structure to the Neandertal condition, some authors deny it exists (Stringer, Bräuer 1994), or attribute its description to incompetence on the part of the researchers (Bräuer *et al.* 2004). These instances of theory used to refute data reverse the normal relation of cause and effect in science.

We do not see this as a valid criticism of pairwise analysis but as an example of how hypothesis testing differs from inductionist fishing. If we had no idea what the phylogeny of these primates might be, it could be sensible to look at trees developed from pairwise comparisons to develop hypotheses about their relationship. But hypothesis testing brings all the available knowledge to the question. After all, we actually do accept the molecular tree that Collard and colleagues provide, and those who question it (Marks 1992) raise only the issue of the African hominoid branching sequence, arguing that there are insufficient molecular data to resolve it (Marks 1992 and elsewhere). Collard and Franchino (2002) inadvertently demonstrate the fragility of their indictivist approach that ignores what is already known by reworking their analyses to include *Colobus*; they "show" *Colobus* has fewer pairwise differences from *Homo* than any of the other taxa do. This result should have been quite enough reason to stop, but does not provide a reason for throwing out the pairwise baby with the indictivist bathwater.

Since hypothesis testing brings together the known information to develop the hypothesis to be tested, we suggest an example using the data Collard and Franchino (2002) provide: the African hominoid branching sequence. Their data address hypotheses concerning the sister group of *Homo*. Prior knowledge restricts the possibilities to *Pan* and *Gorilla*, or both of these apes. In the four tables that summarize pairwise comparisons of *Homo* to *Pan* and *Gorilla* (Collard, Franchino 2002), there are invariably fewer pairwise difference between *Homo* and *Pan* than any other comparison. Although unrecognized by the authors, this is the most convincing anatomical basis for a *Homo-Pan* sister grouping published thus far, and a compelling reason to accept the validity of pairwise analysis for hypothesis testing.

For our pairwise analysis we examined 30 non-metric traits from all parts of the cranium, as described in *Table 2*. These non-metric traits are unrelated to the concocted "observations" analysed by Bräuer and Broeg (1998). Our traits were scored as present or absent, so that the differences could be validly combined without weighing one more than another. Three of the non-metric variables completely separated the Neandertal and Skhul/Qafzeh samples. Of them, the Mladeč crania were like the Neandertals in two, and like Skhul/Qafzeh in one. Seven additional traits almost completely separated the comparative samples; meaning that all of one sample were the same for the character state, and only one specimen in the other sample differed from the opposite character state. Of these, the Mladeč crania were like the Neandertals in four and like Skhul/Qafzeh in two. For the seventh trait, one Mladeč cranium was like each comparative sample. In spite of the predominance of Neandertal resemblances for this subset of 10 traits, the normal approximation of the binomial distribution shows the equal ancestry hypothesis cannot be rejected at the 0.05 level.

Because this analysis and the metric one were based on characteristics of the groups themselves, for a third analysis we addressed the relationship of individuals in a way that ignored group assignments. We calculated the pairwise differences between each of the two Mladeč crania and the 8 other specimens from the non-metric traits. These are shown in *Figures 6* and *7*. Pairwise difference analysis is commonly applied to DNA sequence data to derive information about past population demography. It has also been applied to sequence data to investigate the closeness of relationship that a single ancient individual has to samples of living humans from different regions of the world (Krings *et al*. 1997), and has been used to examine anatomical similarity by other authors besides ourselves (Harvati *et al*. 2004, among others). In these genetic analyses, the number of nucleotide differences between all possible pairs of individual DNA sequences is counted, and the results are presented as the frequency distribution of the number of differences. The assumptions are that each difference represents a mutation and that individuals who share fewer pairwise differences are more closely related because fewer mutations separate them. An equivalent assumption underlies all phenetic clustering techniques, where similarity is assumed to reflect relationship. Such procedures consider individuals who cluster more closely to be more closely related to each other. They do not necessarily assume a full independence of the traits, just as independence cannot be assumed for nucleotide differences in the non-recombining mtDNA molecule. The required assumption is that traits more closely linked are randomly distributed throughout the data set. The procedure is conservative, in that the absence of data for a specimen is considered the absence of difference. Missing data in our comparative samples are not randomly distributed.

TABLE 2. Characteristics used in the pairwise difference analyses summarized in *Figures 6* and *7*. In compiling these features we attempted to score structures on various parts of the cranium and maximize the size of the comparative sample. We chose observations that could be unambiguously and repetitively scored with accuracy.

Whole cranium
„teardrop“ shape (seen from top)
cranial rear rounded (seen from back)
occipital bun
asterionic parietal thickness (>9 mm)
lambdoidal occipital thickness (>8 mm)*
Occipital
vertical occipital face short
sagittal groove along vault posterior
occipital plane long (>60 mm)
suprainiac fossa, elliptical form
paramastoid crest prominent
occipitomastoid crest prominent*
broad occiput (>120 mm)
retromastoid process prominent
nuchal torus extends across occiput
Temporal
mastoid-supramastoid crests well separated
mastoid process projects minimally*
glenoid articular surface flattened
supraglenoid gutter long*
external auditory meatus leans forward*
mastoid tubercle*
Frontal
glabellar depression
frontonasal suture arched
supraorbital centre dips downward
broad frontal (>125 mm)
central frontal boss
frontal long (gl-br>113)
frontal keel
anterior temporal fossa border angled*
lateral supraorbital central thinning*
medial height of supraorbital large (>19 mm)

* not preserved in Mladeč 6 and therefore not used in Mladeč 6 analysis *(Figure 7)*.

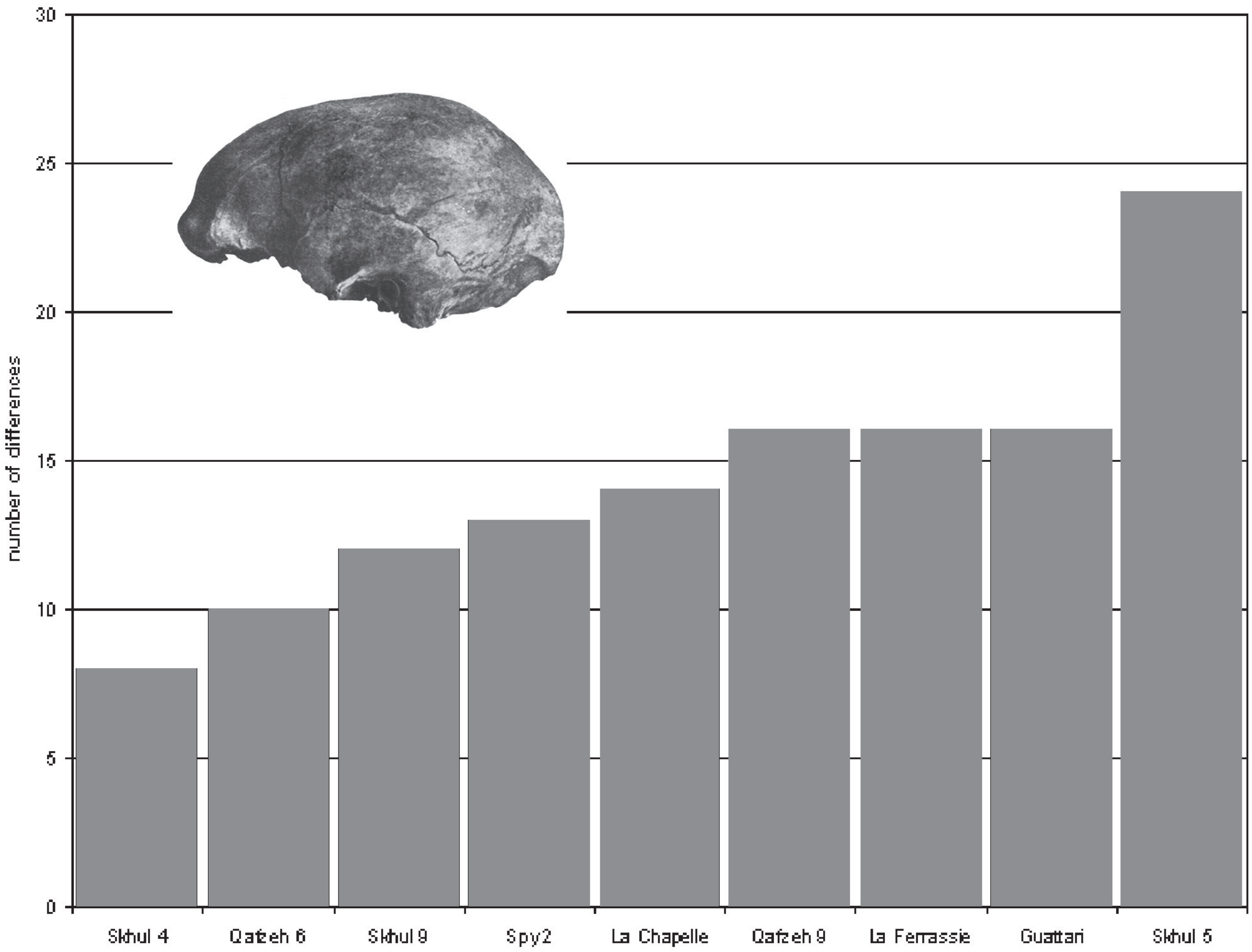


FIGURE 6. Pairwise differences between Mladeč 5 and the most complete Neandertal and Skhul/Qafzeh males. 30 non-metric traits (*Table 2*) are used in this analysis.

The Skhul/Qafzeh crania have more missing data than the Neandertals do. This means that in this specific analysis, the results will be weighed to show more similarities with the Skhul/Qafzeh remains.

The number of differences between each Mladeč cranium and the others were tallied, and the figures aligned the specimens in order of increasing difference. The average pairwise difference between Mladeč 5 and the Neandertal sample is 14.8, and between it and the Skhul/Qafzeh sample is 14.0, virtually the same. For Mladeč 6 the corresponding comparisons are 7.8 and 11.6 differences, so it is closer to the Neandertal sample. A Sample Runs test (Swed, Eisenhart 1943) was used to examine whether the ordering of Neandertal and Skhul/Qafzeh crania, based on the number of pairwise differences from the Mladeč crania, is random (the null hypothesis). Randomness can be rejected at the $p = 0.05$ level when there are 2 or less, or 9 or more runs from the same site, for a sample of this size. There are 5 runs for Mladeč 5 and 3 runs for Mladeč 6 – randomness in the order of pairwise similarities cannot be rejected. Again, these data fail to reject the equal ancestry hypothesis, and thereby disprove the notion that the Mladeč crania are uniquely related to Skhul/Qafzeh.

Our analyses are limited by the small sample sizes and ignorance of the underlying variance/covariance matrices for the data. The significance tests we used above are the ones we believe are valid for the metric and non-metric comparisons we could make. As we noted, these fail to disprove the hypothesis of equal ancestry for the Mladeč male crania. On this basis, and because of other similarities and comparisons reviewed in the text, we firmly conclude it is very unlikely that the Skhul/Qafzeh remains are the sole or unique ancestors of Mladeč. Replacement hypotheses for the origin of these Europeans, whether complete replacement or mostly complete replacement, can be ruled out.

DISCUSSION AND CONCLUSIONS

The exact details of ancestry for the Mladeč Quarry Cave males may never be worked out, but we may address the

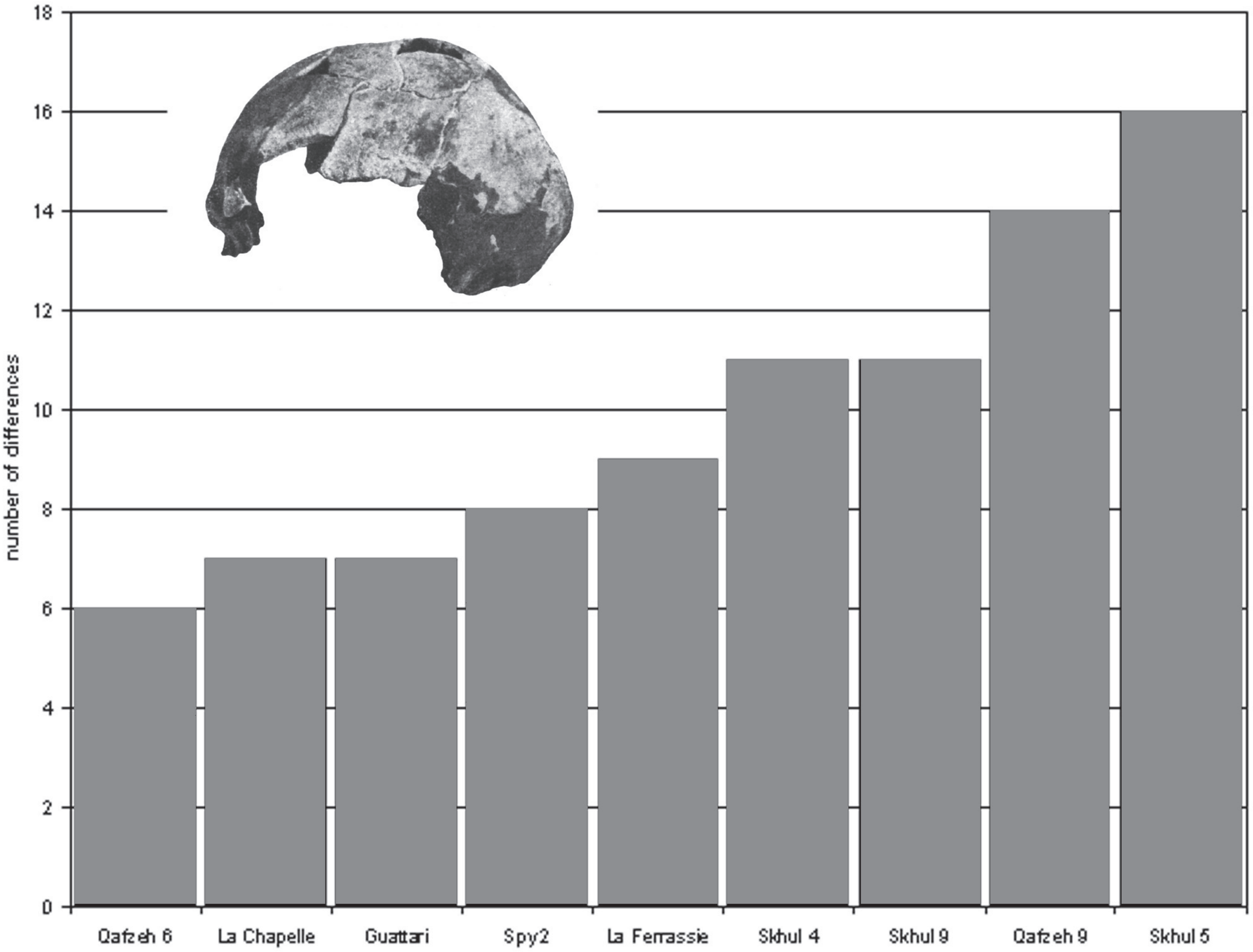


FIGURE 7. Pairwise differences between Mladeč 6 and the most complete Neandertal and Skhul/Qafzeh males. 22 non-metric traits are used in this analysis (*Table 2*), less than the number for Mladeč 5 because the vault is less complete.

boundary conditions, the limits within which such details must lie. The evolutionary changes in Europe very often resulted in the same anatomical consequences that genetic exchange with other populations could have created. And why shouldn't they? European populations were never isolated from the rest of the world for long periods of time. Both ideas and genes, especially useful ideas and successful genes, were exchanged throughout the Pleistocene and there is little wonder that both the causes of selection and their genetic consequences were broadly similar across large parts of the world. How, in principle, could the effects of gene flow and local selection ever be clearly separated? How might we distinguish anterior dental reduction due to selection from reduction introduced to Europe with incoming populations from anterior dental reduction taking place in situ as is evident at late Neandertal sites such as Hortus (Lumley 1972) and Vindija (Wolpoff *et al.* 1981)? Changes such these might make gracile populations appear more similar to each other than their phylogenies would imply. But in this analysis, as much as possible we rely on traits that are not simple reflections of gracility or robustness. In any event, the fact is that we cannot disprove a hypothesis of equal ancestry for the Mladeč Quarry Cave males, and these considerations help make this hypothesis conservative in that the process of change would be expected to produce more similarities between Mladeč and Skhul/Qafzeh.

In broad outline, there is no doubt that some populations entered the very sparsely populated European region during Würm interstadials, and mixed with the indigenous natives. We have no direct evidence for the magnitude of these population movements, and migration is only one of the mechanisms promoting the exchange of genes. However, there is no reason, biological or cultural, to suppose that the genes of small local populations were swamped out by such a process and that the African contribution to later Europeans could be described as a flood, as some have asserted. Direct evidence contradicts this. Nor can this properly be described as "assimilation". The dates for specimens that some describe as "hybrids" range over 10,000 years, from the 36,000–34,000 year age of Pestera cu Oase (Trinkaus *et al.* 2003), to the 24,500 year old Lagar

Velho child from Portugal (Duarte *et al*. 1999), a rather long period for a flood.

All human populations are admixed populations. Multiregional evolution rests on the contention that human populations have been systematically exchanging genes throughout their evolution and thereby incorporates the ethnogenic tenet that populations eventually become extinct, split apart, or merge with other populations (Moore 1994, 1995). Mladeč, indeed all Europeans, are an example of this, mixed populations living at the western periphery of the Eurasian range, at lower number and with more susceptibility to environmental changes than more centrally located human groups. But the process of mixture spread fully across Europe, and took place over thousands of years. Models of Neandertal evolution based on the fate of natives in colonized regions such as Tasmania, which took place on an isolated island over no more than a handful of generations, do not inform this process.

The human story, as far as we understand it, is a constant record of population splits, competitions, replacements, and mergers. When people meet, whether for the first time or yearly or seasonally, friendly or not, biological and cultural information is exchanged. In the last two European interstadials, peoples were in contact and exchanged ideas and mates. Some groups died out and were replaced by their neighbours, others mixed culturally and biologically, to varying degrees, while retaining some local, regional continuity in both culture and genes. The Mladeč remains are one of the earliest post-Neandertal examples of this ethnogenic process in Europe.

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