B. Demarsin & M. Otte (dir.). *Neanderthals in Europe*.
Proceedings of the International Conference held in the Gallo-Roman Museum in Tongeren (September 17-19th 2004).
Liège, ERAUL 117 - Tongeren, ATVATVCA 2, 2006, p. 21-34.

THE WRONG QUESTION

Milford H. WOLPOFF
Paleoanthropology Laboratory, Department of Anthropology, University of Michigan, Ann Arbor, Michigan, USA 48109-1092. wolpoff@umich.edu

Abstract: it is hard to believe that opinions about any fossil sample could vary as wildly and completely as opinions about Neandertals and their place in human evolution (compare Wolpoff *et al.* 2004 & Tattersall 2002). The Neandertal sample is more than adequate, and evolutionary theory is the universally held explanatory principle, so there must be more to the story. Part of this is the role Neandertals have come to play in our culture, but even this post-modernist explanation will not suffice. The most compelling explanation of how Neandertal studies landed in so deep a quagmire is that in determining how different Neandertals were from the human condition, the wrong question was being asked.

Key Words: Neandertal, Human Ancestry, Evolution.

Pop Culture

Neandertal is the only word from paleoanthropology commonly found in dictionaries. This is not inconsequential for understanding how we interpret Neandertals; if calling a politician or policy "Neandertal" has meaning, once can imagine the meaning applied to the extinct folks with that name (fig. 1). Alley Oop may present a more benign implication of the "Neandertal" appellation, but the fact is that the word carries baggage from far more than the science involved in discoveries and interpretations of skeletal remains, for these folk have become a part of our culture (Trinkaus & Shipman 1993). Neandertal, moreover, is a *type* of human (Wolpoff & Caspari 1997), playing the role of "other" and used so we can define ourselves as different, and better (Stringer & Gamble 1998).

As European ancestors, the Neandertals' position rose and fell, not because of the advance of scientific discoveries as much as because of the spirit of the times. The first discoveries fit well into the developing evolutionary ideas in Darwin's time. They were the expected savages of the past that fit the needs of Huxley's model of biological evolution and Morgan's model of social evolution. But other discoveries just past the turn of the last century, culminating in Piltdown, seemed to suggest that modern humans were as ancient as or even earlier than Neandertals. It was easier to believe that humans were a degenerate Adam than a perfected ape (Wolpoff & Caspari 1997). Many of the myths about Neandertals had their beginning at this time. Hermann Klaatsch, a Berlin anatomist at the turn of the last century, reconstructed an idealized model of the Neandertal, based on the original faceless Feldhover skullcap, a mandible from Spy, and an isolated upper jaw fragment from Krapina. Pointing to it, he proclaimed (1923) "whenever a well preserved Neandertal skull is discovered, it is sure to look like my reconstruction". Klaatsch thereby originated the "common knowledge" that Neandertals were homogeneous, even before there were significant comparisons to be made.

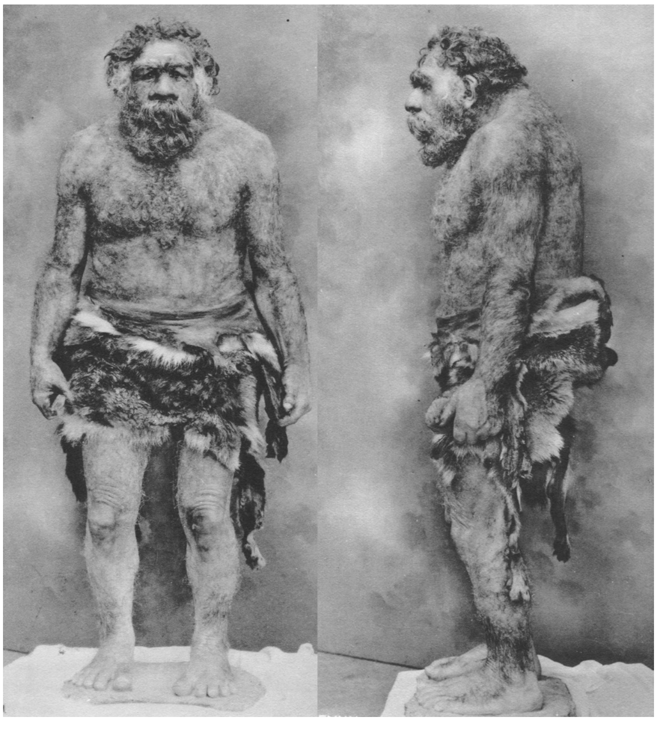


Figure 1. Field Museum of Chicago reconstruction of the old man from La Chapelle. This was in exhibit when this author was a child, and it seemed very impressive!

Klaatsch created another of the long-lasting Neandertal myths with his contention that Neandertals and modern people were contemporaries in Europe. He "found" them together when he was studying the Krapina remains, and he imagined there was a great battle for possession of the Krapina rock shelter (1923). In France he was involved in the discoveries at Le Moustier (a Neandertal youth and an infant) and Combe Capelle (a "modern" specimen) and claimed them to be contemporaries as well. However, his best evidence was from Krapina, where he mistakenly identified juvenile Neandertals as modern humans.

This was part of a concerted effort, especially in Western Europe and America, to remove Neandertals from any ancestral role in the evolution of living Europeans. However then, unlike now, a Neandertal ancestry could be acceptable *as long as it was not for Europeans*; for instance, Boule (1923) wrote: "Whereas the Neandertal man of Europe occupies the position of a type apart, ... which seems according to all the evidence to have vanished without issue, the little we know about this type in Asia shows it as included within a regular evolutionary sequence".

This changed to become a more inclusive rejection when its implicit racism was recognized by the anthropological community as it emerged from and fully rejected the racism of its past (Wolpoff & Caspari 1997). With the exception of a small continuous intellectual thread from scientists of Central and Eastern Europe, the Neandertals were regarded as extinct cousins for *all* humanity by many paleoanthropologists, even as evolutionists such as Dobzhansky and Mayr had come to treat them as a vanished human race, much as earlier Central European scientists such as Gorjanović-Kramberger had (see Radovčić 1988).

The changing scientific perspective is reflected in the many ways Neandertals are depicted in popular literature. For every story sympathetic to Neandertal humanity, as in Asimov's (1959) "Ugly Little Boy", there are various renditions of their low evolutionary stage, lack of human or even primate intelligence, or other limitations (for instance Bisson (2005), recently published and exemplifying many similar interpretations of Neandertal stupidity). Neandertals are also often depicted as human-but-different; without language but telepathic (e.g. Golding 1963), or with very different temperaments and social arrangements as in the parallel Neandertal world described by Sawyer (2003a, 2003b, 2004). Yet Sawyer's description of single-sex Neandertal groups doesn't come from his imagination but from Soffer (1994): even the oddest and most fanciful ideas about Neandertals have a firm basis in paleoanthropological literature

Is it intellectually dead ideas about Neandertals or ideas about intellectually dead Neandertals?

Speth (2005) provides the best review ever of ideas about Neandertal oddness or ineptness, a required reading for any student of the subject. To provide a small taste of this supersized topic: Neandertal morphology shows they suffered from rickets (Ivanhoe 1970), iodine deficiency, dramatic changes in balances of thyroid hormones (Crockford 2003), acromegaly (Ivanhoe 1985) and iodine deficiency (Dobson 1998), and their gestation length was estimated at 11 months or more (Trinkaus 1984, but see Trinkaus & Tompkins 1990); in spite of the slow start Neandertals grew up quickly (Dean, Stringer, & Bromage 1986; Ramirez Rozzi Bermudez De Castro 2004) to be very strong, like the "Incredible Hulk". However, their strength gave them no advantage because Neandertal super-strength: "indicates an adaptation for endurance in prolonged locomotion over irregular terrain. … This locomotion included considerable irregular movement, rather than the more straight-line striding usually employed by recent humans … Their endurance- and strength-related locomotion was thus also poorly directed toward points in the landscape" (Trinkaus 1989:55).

Dare one call this "bumbling"?

Another explanation for their strength is that Neandertals are described as living a life with as much bone-breaking violence as rodeo riders (Berger & Trinkaus 1995), bringing to mind Henri-Martin's (1923) claim that a Mousterian horse tooth from the Mousterian levels at La Quina had bit marks on its labial surface. At least one source of this violence presumably came from the Neandertal hunting technique of wrestling large mammals to the ground with their bare hands (Geist 1981).

Neandertal cultural activities, like their locomotion, have been described as "poorly directed", as Neandertals didn't have the foresight to paint the walls of their caves, the ability to follow knapping rules and make good blades, the insight to invent (their Upper Paleolithic technology and culture is described as "borrowed" – the associations of Upper Paleolithic with Neandertals explained by the possibility that the Neandertals were kept as pets), and their grave goods were actually floor sweepings.

Now, one might think that these various depictions and reconstructions would provide clear evidence of evolution, for they could show how and why modern humans might easily have evolved from the Neandertal condition, for obviously advantageous reasons. But no, they combine to provide an overwhelming case for *denying* evolution by rejecting a Neandertal ancestry, initially because Klaatch's claim of modern populations contemporary with Neandertals, and later because modern populations were thought to precede Neandertals (although this is only relevant to interpreting their evolutionary position if it is assumed Neandertals are a distinct lineage – which happens to be the conclusion drawn from this particular argument). It is as Brace (1964) once quipped about a different Neandertal question; the foundation shifted, but the superstructure remained the same. Apart from the science, this is a logical consequence of treating Neandertals as a type.

Yet we might ask whether the Neandertal contemporaries are actually *modern* humans? Even though they are widely described as modern humans in the secondary literature, the primary sources are more careful. And well they should be, because it is difficult to square the anatomy of some of the "early modern" specimens with the distribution of features in recent or living human populations, broad and varying as this distribution is. For instance the Skhul 2 female (fig. 2) has a frontal with a true supraorbital torus that projects significantly in front of the frontal squama and extends evenly across the middle of the face (including a very broad innerorbital area), only thinning slightly over its most lateral aspect. No recent or living women have a similar upper facial morphology. Sex determination in this individual (McCown & Keith 1939) is uncontested, but her anatomy would be quite exceptional even if "she" were "he".

White and colleagues describe the Herto BOU-VP-16/1 cranium (2003) as part of a population that is "on the verge of anatomical modernity but not yet fully modern" (p. 745). Their multivariate analysis supports this interpretation, placing Herto between modern and Neandertal distributions. This is a description that equally well pertains to subsequent Late Pleistocene African samples at Klasies (Churchill *et al*. 1996; Lam *et al*. 1996; Smith 1992; Wolpoff & Caspari 1996), and Jebel Irhoud (Bräuer 1992). Studying penecontemporary remains from a region very close to Africa, McCown & Keith (1939) regarded the Skhul specimens as a population intermediate between Neandertals and living humans, and the observation (inference) of interbreeding undermines the interpretation of Neandertals as a "type" of hominid, because types to not describe variation within species.

So here is the rub. These "early modern" Neandertal penecontemporaries are not really modern because they differ in meaningful ways from living populations. Well, Neandertals *also* differ in some ways from living populations. Why wouldn't we conclude that for Late Pleistocene populations, differing in some ways from living populations *by itself* is not sufficient to exclude a population from the ancestry of living populations? After all, isn't that difference what evolution is supposed to explain?

The wrong question

So how different are Neandertals? Are they significantly different from living Europeans? This is the issue that most Neandertal studies address, and many of them evidence that significant difference is indeed the case. Such studies have a great antiquity in paleoanthropology's history and were critiqued by Weidenreich more than a half-century ago (1943:44): "It almost became a sport of a certain group of authors to search for the skeletal parts of Neandertal Man for peculiarities which could be claimed as 'specialization', thereby proving the deviating course this form has taken in evolution. … There is not one single peculiarity which has not been taken by some author to represent a unilateral specialization".

The most significant developments in the half-century since Weidenreich wrote these words were not as much in new discoveries as in new approaches to the problem. These were made possible by the continuing evolution of high speed computing. Stringer's (1974, 1978) pioneering early work provides an example (fig. 3).

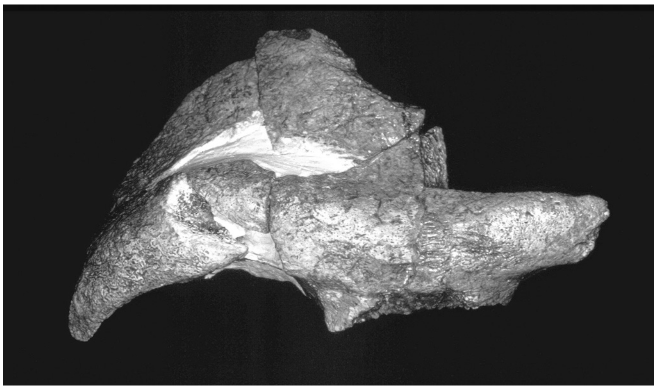


Figure 2. Skhul 2 female frontal bone. The vertical thickness and anterior projection of the true supraorbital torus in this "early modern human" woman is, to the best knowledge of this author, unknown in the women of any living population.

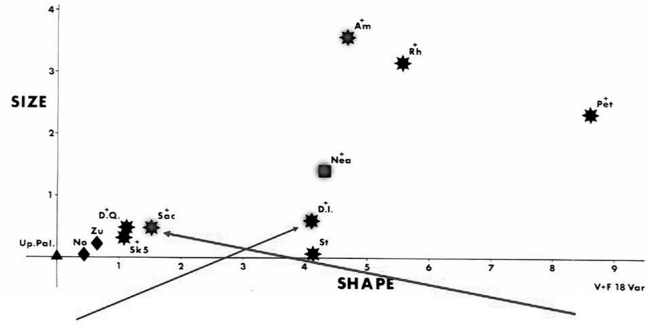


Figure 3. In this figure (modified from Stringer (1978, fig. 17), a number of complete Later Pleistocene crania are compared with Upper Paleolithic Europeans with a Penrose "size and shape" analysis of 18 vault and face measurements. Living peoples such as Norse (No) and Zulu (Zu) are shown to be the most similar to these late Pleisotcene Europeans. The most archaic specimens such as Petralona (Pet) and Kabwe (Rh) are furthest from the European Upper Paleolithic, and the Neandertals (Am=Amud; Sac=Saccopastore 1) are more distant than the several recent populations, although not as distant as the most archaic specimens. D.I. is Djebel Irhoud 1, D.Q. is Qafzeh 6, Sk 5 is Skhul 5, and St is Steinheim. Note that Saccopastore is closer to the European Upper Paleolithic than Djebel Irhoud is.

In this application of multivariate analysis Stringer (1978) demonstrated that modern populations were most similar to the Upper Paleolithic Europeans, and assumed this meant they were most closely related. Neandertals were more distant, and archaic specimens such as Steinheim, Petralona, and Kabwe were found to be more distant yet. Multivariate distance thereby tracked distance of relationship, according to Stringer and many other authors following. This implied to many paleoanthropologists that the European Upper Paleolithic sample had a recent last common ancestor (LCA) with other recent or living groups from Europe and other continents, that the LCA with Neandertals was more ancient, and the LCA with the archaic humans of the Middle Pleistocene even more ancient yet. Neandertals, in this interpretation, were not the ancestors of later Europeans.

While Stringer was one of the earliest to ask this question, and he has continued to do so throughout his career, he has hardly been alone. To cite a much more recent example (but again, hardly a unique one), Havarti (2003) used a generalized procrustes analysis for 17 craniofacial landmarks to examine the differences between humans, chimpanzees, and Neandertal fossils, and analyzed the coordinate configurations of the specimens with principal components. The chimpanzees (*Pan troglodytes* and *P. paniscus*) were clearly separated from each other, and the Neandertals were distinguished from the moderns. This study and a second one (Havarti *et al.* 2004) drew a taxonomic conclusion: Neandertals are more different from modern humans than the closely related chimpanzee species are from each other, and more different than gorilla subspecies. The comparison to chimpanzee species is flawed for several reasons (Ahern *et al*. 2005) and it is the subspecies comparison that is perhaps more relevant. However, the pairwise comparisons of gorilla subspecies and of Europeans from the Mousterian and Upper Paleolithic (fig. 4) do not differ significantly (Havarti *et al.* 2004) even though the difference between the comparisons is exacerbated by the fact that the gorilla comparisons are between mixed-sex samples, while the humans compare a mixed-sex Upper Paleolithic sample with a Neandertal sample that is all male. This result is compatible with genetic comparisons. The ancient DNA variation for Neandertals diverges less from modern humans than chimpanzee subspecies differ from each other (Hawks & Wolpoff 2001).

Yet, like the Stringer example, there is a more fundamental problem with this result – it addresses the wrong question, since surely everybody recognizes that Neandertals are not modern humans.

The right question

These Neandertal analyses can be interpreted quite differently if the right question is asked: instead of questioning how similar Neandertal groups are to recent or modern populations, the *evolutionary* question is *whether Neandertals are among the ancestors of living Europeans.* Similarity is not always a direct reflection of ancestry; if it was, there would be no need for the study of phylogenetics.

There are several ways in which Neandertals may have contributed to the ancestry of the later Europeans:

- through direct descent, with differences between Neandertal folk and later Europeans due to changing selection;
- through mixture in Europe, as populations entering Europe during the interstadials encountered natives;
- through mixture, as European Neandertals dispersing to other regions during stadials contributed to ancestry of ancestral populations evolving outside of Europe (for instance, as in western Asia).

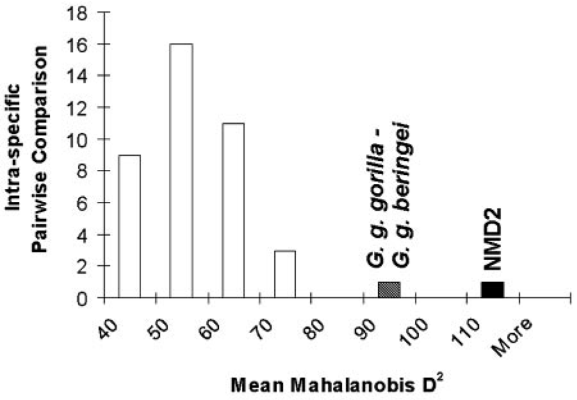


Figure 4. Harvati *et al.* (2004, fig. 2a) show that the pairwise comparison of craniofacial; measurements for Neandertals and Upper Paleolithic Europeans is of greater magnitude than the pairwise comparison of the two gorilla subspecies. However, the difference between the two comparisons is not significant, and this is in spite of the fact that the Upper Paleolithic European sample has males and females while the Neandertal specimens are only male, artificially increasing the difference between the two.

This could be thought of as a genetic or anatomical issue. Genetics addresses it because if all living humans descended from a very small population that lived recently in Africa, none of them descended from Neandertals. On the other hand, if the size of the ancestral human population was not especially small in the Late Pleistocene, Neandertals very well could have been among the ancestors of living populations. Genetic studies in living people can give us important information about the past history of population size as long as we can be sure the genes we study are neural, meaning that natural selection does not play a role in their variation. With neutrality, we can assume that only mutations produce variation in the genes, and only genetic drift, a consequence of small populations, can reduce variation. The amount of variation lost depends only on how small past population size was, and so with the assumption of a known, constant mutation rate we can make estimates of past population size. But the genetic issues are more complex than often supposed. Population subdivision (population structure) significantly effects the estimation of past population size (census size), but not nearly as greatly as the increasing evidence that natural selection plays a large role in our genetic evolution (Bustamante *et al.* 2005; Clark *et al*. 2003; Gillespie 2001; Kamal *et al*. 2006; Wang *et al*. 2006; Wildman *et al* 2003).

There is one clear and testable way in which Neandertals would not be expected to be among the ancestors of living Europeans: if they were a different species. This is a hypothesis of ancestry, with predictions and consequences that can be examined. Stringer's (1978) data inadvertently address this. If Neandertals are a separate lineage, with its own evolutionary tendencies and its unique evolutionary fate, we can expect that Neandertals are more different from living humans than the LCA of Neandertals and living humans is (fig. 5). This is because there is more evolutionary change between Neandertals, the LCA, and living humans than there is between Neandertals and the LCA alone.

This raises the question of common ancestry. Estimating the age of a LCA for a lineage division that this author actually does not believe took place is a risky business. However, many paleoanthropologists accept Krings and colleagues original (1997) divergence estimate of about 600 kyr based

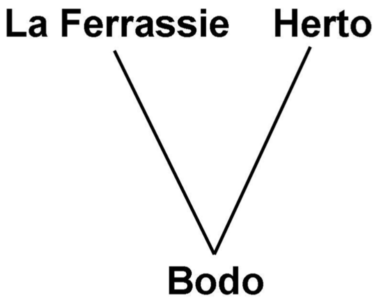


Figure 5. Relations expected from phylogeny of a distinct Neandertal clade. Saccopastore should be far more distant from modern populations than Djebel Irhoud is, in fact Neandertals should be the most distant of all the comparisons. Instead, it is Kabwe and Petralona, much closer to the presumed LCA, that is most distant from the modern populations, and Saccopastore is closer than Djebel Irhoud. Stringer has never questioned the validity of his methods and for more than 30 years he has interpreted the results of this and other studies to mean that Neandertals became extinct with little or no influence on modern populations, because they differ from them. But if we accept this study and others like it, they actually show the opposite. If the Neandertals are more like modern populations than are specimens closer to the LCA of the Neandertals and the modern populations, Neandertals cannot have been a distinct lineage.

on mitochondrial evolution, followed by his error range determination of 317 kyr to 741 kyr (Krings *et al*. 1999). These are supported by/(compatible with) estimates by Hublin (1998) of a bottleneck on the Neandertal lineage at about 480-425 kyr, and those who accept a "*Homo heidelbegensis*" ancestry for the Neandertal species place divergence even further back in time. These divergence estimates would make Bodo a quite credible LCA, and Kabwe and Petralona too late for this, and instead quite credibly on African and European lineages respectively.

Examining figure 17 from Stringer's 1978 publication, we can see (fig. 3) that a Neandertal, Saccopastore, is actually more like modern Europeans (and other modern humans) than Kabwe or Petralona are, even though these two are closer to the LCA. Saccopastore is even more similar to Djebel Irhoud, equally unexpected under a divergence hypothesis. If Neandertals were a separate lineage *we would expect Saccopastore to be least like these samples* (fig. 5). The Neandertal mean Stringer determined (Nea) is clearly more like the moderns than Petralona or Kabwe. Stringer's data, addressing the right question, reject the hypothesis that Neandertals are a distinct lineage.

How we may examine the hypothesis of Neandertal ancestry

Considering the question of Neandertal ancestry anatomically, we may address three aspects:

- Can all Neandertals be distinguished from contemporary non-Neandertals?
- Is there a unique Neandertal lineage with its own evolutionary tendencies?
- Do post-Neandertal Europeans retain Neandertal features?

Can all Neandertals be distinguished from contemporary non-Neandertals?

One place where there are Neandertals and penecontemporary non-Neandertals is in Western Asia. Amud and Tabun may well span the entire range for this sample (Tabun earliest, Amud latest). Arranged in order reflecting the seriation of virtually any feature, the two Neandertals never stand out at the extreme. figure 6 shows lateral views of the crania arranged by forehead flattening; Qafzeh 5 has the most extreme expression of this feature. This mixture of the two samples was reported and detailed by McCown & Keith (1939) and is well known. For instance, in their systematic analysis of Amud's postcranial remains, Endo & Kimura (1970) systematically compared the features of the fragmentary Amud skeleton to European Neandertals and Skhul 4. They found Amud intermediate, but, in their words, slightly closer to Skhul in the comparisons. Examining their data shows that the preponderance of closest postcranial resemblances are between the two Levantines, when only unique similarities are examined. To wit:

- 24 characters link Amud with Skhul 4 but do not appear in European Neandertals;
- 14 characters link Amud with European Neandertals but do not appear in Skhul 4;
- 8 characters link Skhul 4 with European Neandertals but do not appear in Amud.

In a more formal way to approach this question, Kramer and colleagues (2001) employed a cladistic analysis to examine the Levant cranial sample for anatomical clusters. The hypothesis of taxonomic distinction for the Neandertals predicts that they should cluster together if derived features are examined. The most complete Levantine cranial specimens were employed in these analyses in order to maximize trait coverage across all regions of the skull. The Levantine Neandertals are represented by Amud and Tabun, while the "moderns" include Skhul 4, 5 and 9, and Qafzeh 3, 6, and 9. Males and females are represented in both samples. ER 3733 was used as an outgroup to define character states for the 12 nonmetric features examined (there were no missing data). The three cladistic analyses were performed using PAUP. Because of the limited size of the data sets, PAUP was able to complete exhaustive searches for all possible trees for each analysis.

Using the same characters, this approach was first applied to the sequential samples of European Neandertals and early Upper Paleolithic crania, basically to see if it worked with the low level taxonomic distinctions involved. Figure 7 depicts one of the seven most parsimonious trees reported by Kramer and colleagues. Of the nearly 1000 trees, ranging in length from 19 to 29 steps, evaluated by PAUP, the seven most parsimonious cladograms all displayed a Neandertal clade distinct from an Upper Paleolithic human clade. This result is similar to those reported above; early Upper Paleolithic folk are not Neandertals.

With this success, over 10,000 trees were constructed from the Levantine sample using PAUP, ranging in length from 26

Figure 6. The 9 most complete adult Levant crania, shown in lateral views to the same approximate size and reversed when necessary to face in the same direction. From the upper left corner, naming each row left to right, the specimens are: Qafzeh 3, Skhul 4 (a cast of the Mario Cech reconstruction), Qafzeh 9, Skhul 9, Qafzeh 6, Skhul 5, Tabun 1, Amud 1, Qafzeh V. Qafzeh specimens 3 and 5 are at the extremes for forehead rounding, occipital angulation, supraorbital prominence, mastoid size, and a number of other features. This illustrates what the PAUP analysis (fig. 8) shows: the Levant hominids do not form two distinct anatomical clusters, Neandertals and "moderns".

to 35 steps. Of the 17 most parsimonious trees (length=26), Kramer and colleagues note that not one revealed a "Neandertal" clade of Tabun and Amud distinct from the early moderns from Skhul and Qafzeh (the majority consensus tree is shown in figure 8). In addition, of the next 24 most parsimonious cladograms (length=23), only two grouped Tabun and Amud to the exclusion of the Skhul/Qafzeh remains. These results cannot be due to the inability of PAUP to distinguish Neandertal from modern human morphology. Kramer and colleagues interpreted them as a failure to reject the null hypothesis that these specimens all belong to a single species. They certainly show that all Neandertals cannot be distinguished from contemporary non-Neandertals.

Is there a unique Neandertal lineage with its own evolutionary tendencies?

There are many ways to approach this question, but an excellent unexpected opportunity to examine it came with the discovery of the Herto cranium (BOU-VP-16/1), a large and robust Ethiopian male about 165 kyr old (White *et al*. 2003). In fact, Herto was specifically used by the authors to address questions about both the origin of modern humans and the fate of the Neandertals.

The Herto specimens were said to "exclud[e] Neandertals from a significant contribution to the ancestry of modern humans" (White *et al*. 2003) because they look more like modern humans than Neandertals do. This interpretation of the Herto taxonomy starts with an implicit assumption about whether modern humans are a distinct entity and that Neandertals fall on a different lineage. For it to be a valid interpretation of phylogeny there would have to be a monophyletic group composed of Herto and all recent and living humans, but excluding Neandertals and their European ancestors (and by inference also excluding Middle Pleistocene Asians). Otherwise, the contributions of Neandertals to later Europeans could not be addressed by examining the character states in penecontemporary or older populations in Africa.

So, Herto provides the basis of a test for the hypothesis of a separate Neandertal lineage, because if this hypothesis is

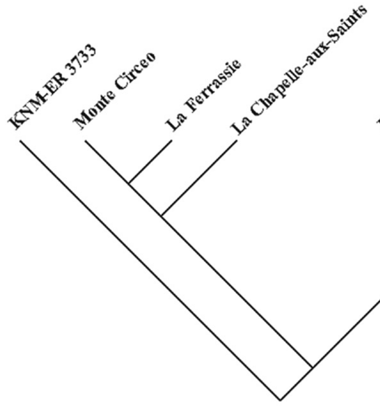


Figure 7. Comparison of European Neandertal males and earlier Upper Paleolithic males. One of the seven most parsimonious cladograms (length=19) shown here, generated by PAUP, demonstrating that "Classic" western European Neandertal males are all distinguished from succeeding Earlier Upper Paleolithic males using the anatomical criteria and approach also applied to the Levant sample (fig. 8). In fact, all seven of the shortest trees placed these Neandertals on a clade distinct from that occupied by the earlier Upper Paleolithic males. This verifies the accuracy of the approach used to ask whether the same Neandertal vs. "modern" division can be shown in the Levant hominids.

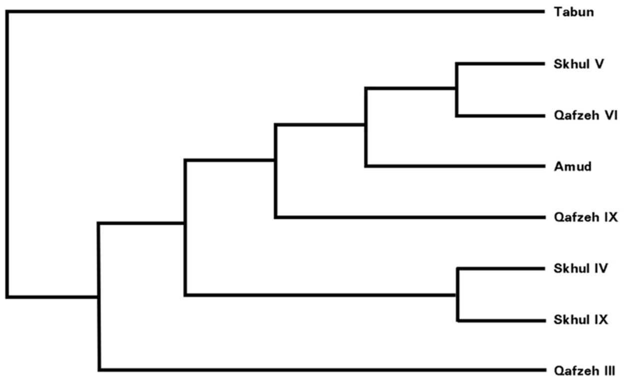


Figure 8. Levantine "Neandertals" and Levantine "early modern humans". The 50% consensus tree for the 17 most parsimonious cladograms (length=26) generated by PAUP is shown here. Tabun and Amud (the "Neandertals") do not cluster apart from the "early moderns" from Skhul/Qafzeh. None of the 7 shortest trees displayed a Tabun/Amud clade separate from that of Skhul/Qafzeh. By themselves, the Skhul individuals run the gamut from most plesiomorphic (Skhul 4) to most derived (Skhul 5).

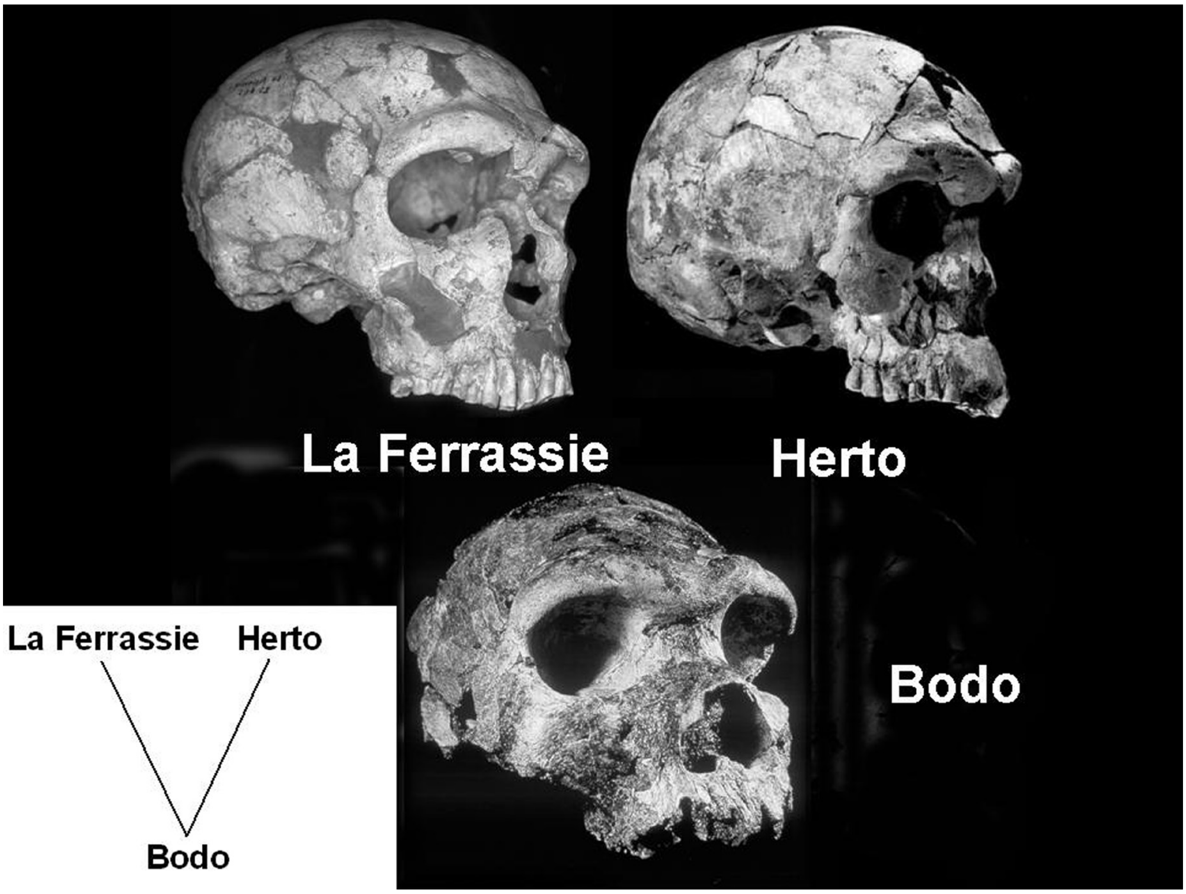


Figure 9. The question of a unique Neandertal lineage is addressed by comparisons with the Herto cranium (adapted from White *et al*. 2003), a specimen widely considered an ancestor of living humans. If there is a unique Neandertal lineage, it should increasingly separate from this human linage over time, and we would expect Herto to be more different from La Ferrassie than either differs from their LCA, perhaps Bodo or something like it (Bodo is a credible LCA because if one believes Neandertals are a separate lineage, one might also believe the mtDNA based estimate of 600-700 kyr for the separation). It appears that La Ferrassie is more similar to Herto than the LCA, which either requires an explanation of parallel evolution, or far more probably means that there was reoccurring gene flow (sensu Templeton (2005) between the populations. This indicates they are not on separate lineages (see fig. 12 for a more formal assessment).

valid, we can expect the Neandertal line to become more and more different from the Neandertal/human LCA. This prediction is the same as that discussed above over the issue of how to interpret Stringer's work in an evolutionary context. Herto should differ from the LCA, but differ even more from the Neandertals that evolved from it, presumably as part of a separate lineage (fig. 9).

To examine this prediction, it is reasonable to use a measure of phenetic similarity (Wolpoff & Lee 2001). A more formal phylogenetic approach is problematic because the closeness of relationship of the putative lineages assures that no phylogenetic hypothesis could be adequately tested with the information available to us (Hawks 2004). It is also problematic because the Herto variables that can be compared are limited to those reported in Nature. One author of the Herto paper describes the Nature publications as "announcements" (White 2003), but the information published in this difficult to get into high impact journal is often the only source of data for years if not decades, and thereby is the basis for scientific discussion. This is neither an isolated opinion nor a minor inconvenience - some museums now consider publication in *Nature* and *Science* insufficient for access to the specimens they possess. Finally, a phylogenetic approach is difficult because while Bodo, by morphology and by age, provides a reasonable idea of what a LCA for the lineages could be like, not enough of the vault preserved for a valid systematic comparisons, and these are even more circumscribed by the small number of measurements and observations published for both Bodo and Herto.

Working with Sang-Hee Lee, we developed a phenetic approach to the question of similarity (Wolpoff & Lee 2001) that was based on the comparison of all available homologous measurements between pairs of specimens. The dispersion of the data around a linear regression through these points, which we call STET (fig. 10), is a measure of similarity that takes both size and shape into account (Lee & Wolpoff 2005). STET values clearly and unambiguously distinguish variation within species (pairs of specimens within the same species) from the higher magnitudes of STET values for pairs of specimens from different species (fig. 11).

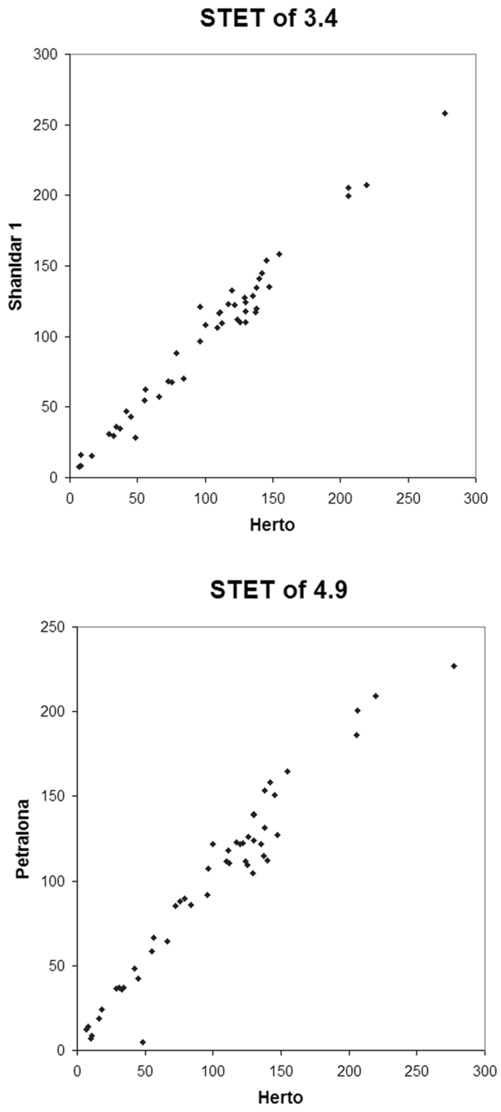


Figure 10. STET values determined from bivariate plots of Herto (BOU-VP-16/1) and two specimens from the European deme: Petralona (earlier) and Shanidar 1 (later). If there is a European deme that is reproductively isolated from the African deme, we would expect divergence to increase for its more recent members. This is not the case.

A serration of STET values can be used to test the hypothesis of lineage difference (Lee & Wolpoff 2006), because if Neandertals are a distinct lineage, they should be more different from Herto than a earlier member of the European lineage such as Petralona is (fig. 9). This is not the case (fig. 12). Neandertals are more similar to Herto than Neandertal ancestors are.

The large, robust Herto male cranium affords the first opportunity to compare the Europeans to an African specimen of Neandertal age clearly related to modern populations, and evaluate whether the Europeans fit the model of a distinct line, evolving in a different direction, without confusing the evaluation with issues of size and robustness. These comparisons quite clearly show the Europeans are *not* evolving in a different direction from the rest of humanity. Whatever the causes of Neandertal variation, and there are sure to be many, lineage distinction does not seem to be one of them.

Do post-Neandertal Europeans retain Neandertal features?

Some Neandertal features certainly appear to persist until modern times in Europe (fig. 13), where for the most part they comprise part of the set of characteristics used to identify Europeans in a forensic context (Gill & Gilbert 1990). The earliest post Neandertal European crania are from the Romanian site of Peştera cu Oase (Trinkaus 2005; Trinkaus *et al*. 2003) and the Moravian site of Mladeč (Wild *et al*. 2005). While the former is not yet fully published, the later remains are well analyzed (Frayer 1986; Jelínek 1983; Jelínek *et al*. 2006; Wolpoff *et al*. 2001). Some of the features that identify the Mladeč males as Europeans are among those shared

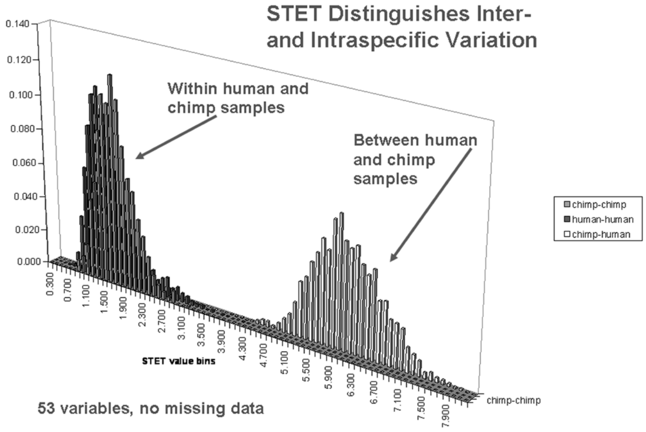
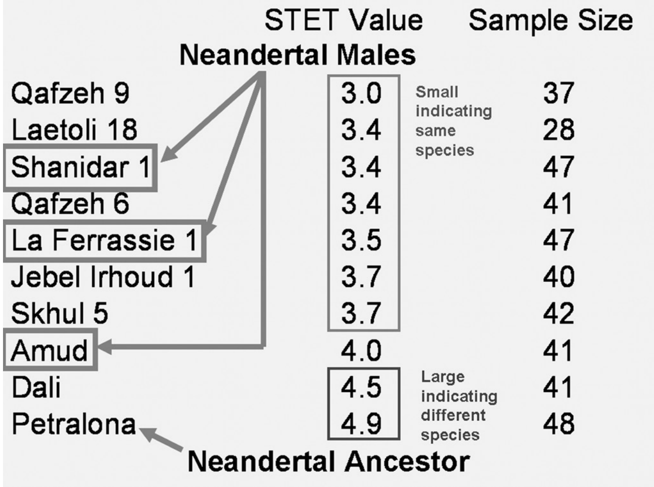


Figure 11. STET values for interspecies and intraspecies comparisons of chimpanzee and human samples, courtesy of Sang-Hee Lee.



Neandertal Males	STET Value		Sample Size
Qafzeh 9	3.0	Small indicating same species	37
Laetoli 18	3.4		28
Shanidar 1	3.4		47
Qafzeh 6	3.4		41
La Ferrassie 1	3.5		47
Jebel Irhoud 1	3.7		40
Skhul 5	3.7		42
Amud	4.0		41
Dali	4.5	Large indicating different species	41
Petralona	4.9		48

Neandertal Ancestor

Figure 12. STET values for Herto compared with Neandertals and a Neandertal ancestor, Petralona. All specimens in this comparison are males.

with Neandertals, and there are other common Neandertal features in these remains (Frayer 1992). For instance, the small mastoid process of Mladeč 5 and elliptical suprainiac fossa on Mladeč 6 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. The issue of uniqueness would only be important in the context of a separate Neandertal lineage.

Wolpoff and colleagues (2001) examined the question of what the Neandertal features in these earliest modern Moravians reveals about their ancestry; in particular, could the hypothesis of a half Neandertal-half Skhul/Qafzeh ancestry be rejected? They calculated the pairwise differences between each of the two Mladeč crania and the most complete Neandertal and Skhul/Qafzeh crania. These comparisons were based on observations for 30 non-metric traits (the non-metric traits are specified in the figures titles and are unrelated to the concocted "observations" analyzed by Bräuer & Broeg (1998)). The results of the pairwise comparisons are shown in figures 14 and 15.

Pairwise difference analysis is applied to DNA 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). 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 (see also Harvati and colleagues (2004), who use the same technique). 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. 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 Mladeč 5 and 6 and each of the others was tallied, and the figures aligned the specimens in order of increasing difference. The average pairwise difference between Mladeč 5 and the Neandertal sample (fig. 14) is 14.8, and between it and the Skhul/Qafzeh sample is 14.0, virtually the same. For Mladeč 6 (fig. 15) the corresponding comparisons are 7.8 and 11.6 differences, so this Aurignacian European is closer to the Neandertal sample. A Sample Runs Test 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 in the order of pairwise similarities cannot be rejected by these data; the pairwise comparisons fail to reject the equal ancestry hypothesis, and thereby disprove the notion that the Mladeč crania are uniquely related to Skhul/Qafzeh.

This non-metric analysis is 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. These limitations affect the resolution of our analysis, but it is clear that we have failed to disprove the hypothesis of equal ancestry for the Mladeč male crania. This fact, and the persistence of some Neandertal features in Europe until recent, even modern times, combines to show that Europeans retain Neandertal features. Of course, it is also true that some Neandertal features have spreads to other populations, and many European features show descent from other populations, and/or are the consequences of natural selection. These are the consequences of the breeding structure of human populations (Lasker & Crews 1996; Moore 1994).

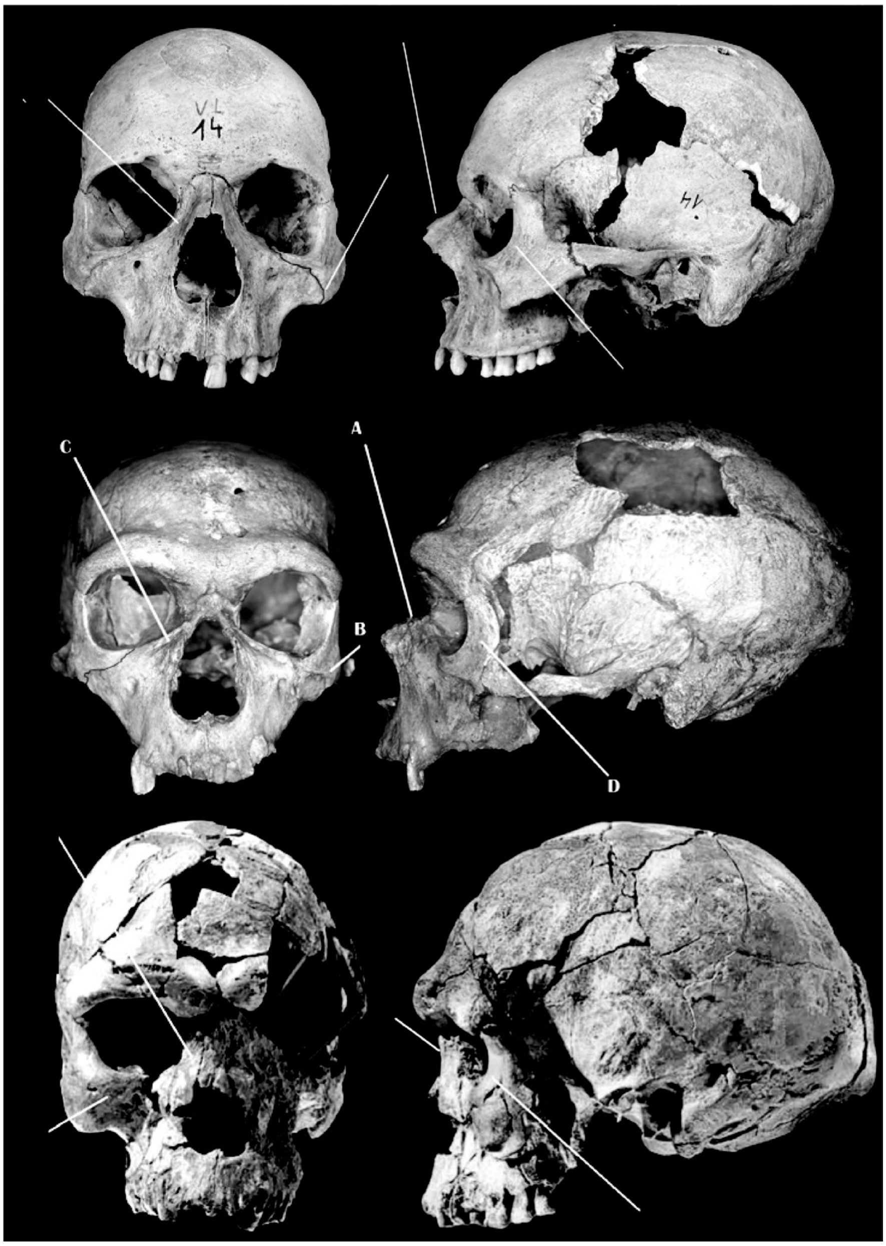


Figure 13. Some distinctive Neandertal features remain common in Europe today. Features showing sufficient geographic variation to be useful in forensic analysis are often found in the midface (Gill & Gilbert 1990). Here, four features of the midface in La Chapelle (center) are compared with similar anatomy in the modern specimen above, a Copper Age male from a 8-10 century Croatian site - Lijeva Bara (Vukovar, Croatia) - shown above, and contrasting anatomy in the Herto Ethiopian below (from White *et al*. 2003). Crania are shown to the same approximate size. European regional characteristics illustrated are:

A: the high nasal angle defined by the slope of the lofty nasal bridge as it rises up between the orbits and incorporates the frontal processes of the maxillae as well as the nasal bones themselves (not preserved in La Chapelle, the view shows the nasal process of the maxilla);
B: the course of the zygomaxillary suture (enhanced) that turns inward at its most inferior aspect;
C: the maxillary expansion at the lateral nasal borders, resulting in a "pinching" of the region so that these borders are laterally oriented;
D: the lateral orientation of the zygomatic bone.

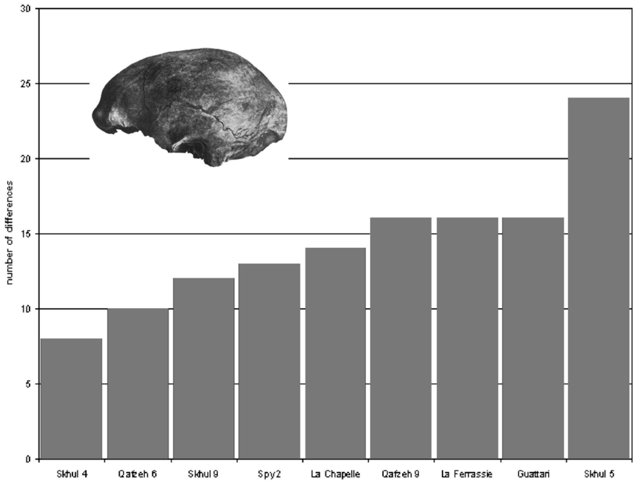


Figure 14. Pairwise differences between Mladeč 5 and the most complete Neandertal and Skhul/Qafzeh males. 30 non-metric traits are used in this analysis: "teardrop" shape (seen from top), cranial rear rounded (seen from back), occipital bun, asterionic parietal thickness (>9 mm), lambdoidal occipital thickness (>8 mm), vertical occipital face short, sagittal groove along vault posterior, occipital plane long (>60 mm), suprainiac fossa of elliptical form, paramastoid crest prominent, occipitomastoid crest prominent, broad occiput (>120 mm), retromastoid process prominent, nuchal torus extends across occiput, mastoid-supramastoid crests well separated, mastoid process projects minimally, glenoid articular surface flattened, supraglenoid gutter long, external auditory meatus leans forward, mastoid tubercle, glabellar depression, frontonasal suture arched, supraorbital center 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).

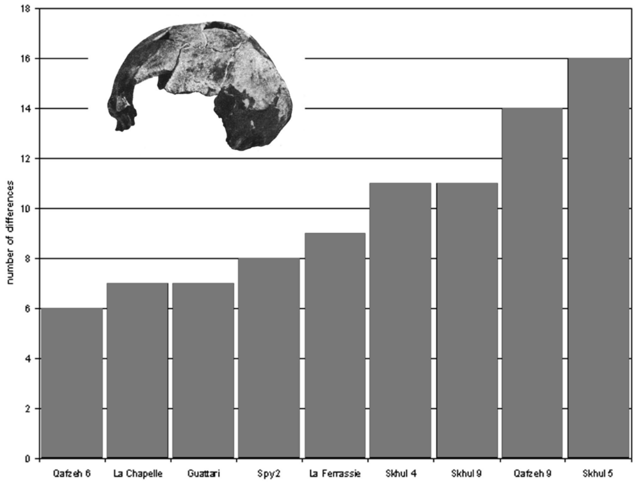


Figure 15. Pairwise differences between Mladeč 6 and the most complete Neandertal and Skhul/Qafzeh males. 22 non-metric traits are used in this analysis, less than the number for Mladeč 5 because the vault is less complete: "teardrop" shape (seen from top), cranial rear rounded (seen from back), occipital bun, asterionic parietal thickness (>9 mm), vertical occipital face short, sagittal groove along vault posterior, occipital plane long (>60 mm), suprainiac fossa elliptical, paramastoid crest prominent, broad occiput (>120 mm), retromastoid process prominent, nuchal torus extends across occiput, mastoid-supramastoid crests well separated, glenoid articular surface flattened, glabellar depression, frontonasal suture arched, supraorbital center dips downward, broad frontal (>125 mm), central frontal boss, frontal long (gl-br>113), frontal keel, medial height of supraorbital large (>19 mm).

Neandertal species, clade, or hybrid

Whether Neandertals are regarded as a species, clade, or hybrid population, such an interpretation would reflect an essentialist view of variation where distinct types mix. Yet, Neandertals need not be any of these but still could be different: Neandertals are not necessarily a type of human. Without question, Neandertals reflect geographic variation, and the fact is that geographic variation regularly evolves and persists within species, without the necessity of reproductive isolation (Bossart & Prowell 1998; Laporte & Charlesworth 2002; Pannell & Charlesworth 1999; Ptak & Przeworski 2002; Templeton 1998; Templeton *et al*. 1995; Wijsman & Cavalli-Sforza 1984; Wilkinson-Herbots 1998).

Variation can arise from differences in selection acting on adaptive traits, isolation by distance and unequal reciprocal gene flow in the absence of selection, and clinal distributions created by balances of gene flow (mostly from the center to the edges of the human range) and selection. It probably cannot be repeated too often that gene flow refers to the movements of genes, which may or may not involve the movements of peoples (Lasker & Crews 1996), but in either case gene flow is reciprocal and requires interbreeding between people from different groups, which is varyingly been called mixture, admixture, assimilation, or hybridization (as in the case of the so-called "love child"), depending on how different the author regards the mixing populations. One cannot overestimates the effects of restricted gene flow because of isolation by distance (Eller 1999; Hanson 1966; Templeton 1997, 2002; Wright 1943).

Yet, it is the fact of human mixture itself that continues to be unexpected and surprising. Consider Sládek and colleagues' (2002) analysis of the Šala frontal bone. Even though they conclude it is most similar to the Skhul frontals, it does not occur to these authors that this similarity could reflect recurrent gene flow between Europe and Western Asia. For many authors, it seems that gene flow, if it happened at all, only happened at the time Neandertals disappeared and therefore played a role in their disappearance. Before this time, the underlying assumption is one of Neandertal isolation and separation; how else could Neandertals have evolved their distinct features? This is a powerful argument, even standing as an explanation for cases when the features turn out not to be distinct. But the world view that differences must evolve under isolation flies in the face of modern evolutionary biology that considers the role of population structure in creating diversity within widespread species.

If there was mixture between Neandertals and other populations, it was at this time when changing selection associated with climatic change and emerging (or entering) cultural innovations were important causes of evolutionary change (d'Errico 2003; Zilhão 2001). It might be that selection within Neandertal populations promoted key adaptations introduced by the new populations, but it would also be the case that Neandertal cold adaptations would be of significant selective advantage to populations adapted to other climates. We would expect gene flow to be multidimensional, and this makes the populations more similar to each other. This process has been likened to the Tasmanian situation, but it is quite different. Population replacement, intermixture, and swamping in Tasmania took 150 years, the interactions in Europe were over a period estimated as 40 times as long (Mellars 2006). It is unreasonable to suppose the same mechanisms were at work.

Conclusions

It often seems as though the Neandertal issues will never be resolved, but I do not believe this will be the case. One promising direction is to ask the right question and not the wrong question about their relationship to us. While Neandertals are clearly different from living populations, more different than living populations are from each other (wrong question), the best available evidence is that Neandertals are among the ancestors of living populations, and that some of their features remain, especially but not uniquely in Europe (right question).

Acknowledgements

I am deeply grateful to Demarsin Bart and the Gallo-Romeins Museum in Tongeren for inviting me to the "Neandertals in Europe" Congress, held in Tongeren, Belgium, and arranging funding for my visit and presentation. I thank the curators of the Neandertal and other Late Pleistocene European fossils reported in this paper, for permission to study the remains in their care.

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