

Dynamics of genetic and morphological variability within Neandertals

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Summary - *Paleogenomics may suggest changes to the way anthropologists have discussed the dynamics and morphological diversity among Neandertals. Genetic comparisons show that later Neandertals had relatively low autosomal genetic variation compared to recent humans. The known mitochondrial sample from Neandertals covers a broader geographic and temporal range, and shows greater diversity. This review addresses how genetic data compare to morphological and archaeological evidence about Neandertal variation and dynamics. Traditional views emphasized the morphological differences between western and eastern Neandertal populations, and between early and later Neandertals. Genomes broadly support these groupings, without resolving the outstanding question of the affinities of specimens from southwest Asia. However, the pattern of genetic variation appears to reject a long, in situ transformation of Neandertal groups over time, suggesting instead a more rapid process of regional dispersal and partial population replacement. Archaeological indicators sample dynamics on a much finer timescale than morphological or genetic evidence, and point to dispersal and turnover among Neandertals on a regional scale. In this way, genetic evidence may provide a bridge between the timescales relevant to morphological and archaeological comparisons. New ways of looking at the morphology of Neandertals may yield a better picture of their interactions and movements.*

Keywords - *Ancient DNA, population dynamics, Mousterian, Europe, Central Asia, mtDNA, Vindija, Mezmaiskaya.*

Morphological evidence and archaeological evidence document Neandertal populations at different timescales. Morphology tells us about change over tens of thousands of years, and variation across regions spanning millions of square kilometers. Archaeology can document change in behavior at a single site, among a group of sites in a single region, or between successive industries spanning a few thousand years. Yet few archaeological assemblages are associated with skeletal remains. In some ways, the weakness of each of these kinds of evidence is a strength of the other.

Genetic evidence provides a bridge between the two timescales of morphological and archaeological evidence. At this writing, the genetic data from Neandertal skeletal remains are sparse,

with fewer than two dozen mtDNA sequences (Dalen *et al.*, 2012), and only six specimens with substantial nuclear DNA information (Green *et al.*, 2010). Despite the small sample, these data already may prompt us to revisit the sizes and dynamics of Neandertal populations and their connections or isolation across regions.

Following long precedent, I consider Neandertals as an ancient human population extending across Europe and parts of West and Central Asia between approximately 200,000 and 30,000 years ago. The definition oversimplifies. It excludes skeletal samples before 200,000 years ago that display clear anatomical similarities with later Neandertals. Some ancient populations before 200,000 years ago surely gave rise to

the later Neandertals, and some workers attribute fossils of this antiquity to the Neandertal population (Stringer, 2012), but their variability is not considered here. The definition also excludes Upper Paleolithic people of Europe who followed the Neandertals, and who shared some of their morphological characteristics (Fraye, 1993). Most important, the definition oversimplifies by neglecting the morphological diversity across the geographic range it encompasses.

As described below, the Neandertal population included substantial morphological and behavioral variation. A look within the European and Asian range of Neandertals finds great morphological diversity, which earlier researchers often related to a time axis from early to late, and a geographic axis from east to west. Different parts of this range were the areas of different archaeological industries, which a succession over time in each region that represents a depth of time. Genetic evidence now helps to clarify this distribution while adding new evidence about the movements and population sizes that contributed to it. The groups of specimens that share genetic similarities are not the same as those sharing morphological similarities. Far from a unitary group evolving in isolated glacial conditions, the Neandertals appear to have been a highly dynamic population with the potential for rapid migration and long-distance dispersal. This perspective adds context to the archaeological record of Middle Paleolithic and initial Upper Paleolithic cultural changes.

The context of Neandertal morphological variation

When we describe Neandertals as a “diverse” population, that word demands some context. Anthropologists have often claimed that Neandertals are pointedly *not* diverse, emphasizing the uniformity of Neandertal morphology instead of its diversity. A few discrete traits are indeed relatively uniform in some Neandertal samples, such as the suprainiac fossa (Fraye, 1993). When a skeletal specimen preserves such traits, we can

have some confidence in diagnosing the individual as part of a Neandertal population. But such a diagnosis in most cases depends on a combination of several traits, each individually present in a small fraction of modern humans, but unlikely to occur together outside of Neandertals (Rak *et al.*, 2002). Even when we consider discrete traits, the problem of diagnosing a Neandertal specimen is similar in form to the problem of diagnosing the ancestry of a modern human specimen in a forensic context. No single feature can establish a high confidence in distinguishing whether a specimen is European or African in ancestry today. Traits differ in frequency in these groups, allowing us to use traits in combination as forensic indicators. Nevertheless the frequencies of the traits are the measures of diversity within groups, not the difference in frequencies between groups. When we consider metric traits, the diversity of Neandertal populations is even clearer. By statistical measures such as the coefficient of variation (CV), Neandertal samples do not differ significantly in variation when compared to skeletal samples of later human populations (Hawks & Wolpoff, 2001; Hawks *et al.*, 2000).

There have been two reasons in recent years why researchers have neglected diversity in favor of uniformity in their description of Neandertals. The first is a concern about whether specialists can diagnose Neandertals from fragmentary specimens. In much of western Europe, the earliest Upper Paleolithic archaeological industry is the early Aurignacian, dating to before 35,000 years ago. In some areas there are “transitional” industries such as Châtelperronian, Uluzzian (Peresani, 2008), or Lincombian-Ranisian-Jerzmanowician (LRJ) (Flas, 2011). These industries combine technical elements found in later Upper Paleolithic industries with raw material procurement and organizational strategies of earlier, Middle Paleolithic traditions. Of these, only the Châtelperronian of southwest France is associated with any relatively complete skeletal specimen, at Saint-Cesaire, France, as well as other fragmentary remains from other sites. Even in this case archaeologists continue to disagree about the strength of association of the skeletal

remains with the tools. Uluzzian and LRJ sites include only less complete specimens: for example, Kent's Cavern (Higham *et al.*, 2011), or Grotta del Cavallo (Benazzi *et al.*, 2011). The problem of skeletal associations extends forward into the early Aurignacian industries in Europe up to 30,000 years ago (Churchill & Smith, 2000). A paramount problem in the anatomical study of Neandertals is to document the biological makers of the earliest Upper Paleolithic industries (e.g., Bailey *et al.*, 2009). Only a small number of skeletal remains have been identified in association with terminal Middle and initial Upper Paleolithic assemblages, nearly all fragmentary. In this context, identifying whether a specimen is "Neandertal" or "modern" may depend very strongly on a single trait. By decomposing Neandertal identity into the morphology of an individual trait, Neandertals are made to look more morphologically homogeneous than if many traits could be considered together.

The second reason for emphasizing Neandertal morphological uniformity has been the widespread assumption that Neandertal traits are a result of long evolution in isolation from other human populations. Earlier workers had discussed the status of Neandertals as a possibly isolated population, but Howell (1952) clearly presented the hypothesis that isolation in glacial Europe gave rise to divergent morphological trends in the Late Pleistocene populations of Europe and West Asia. More recently, Hublin (1998) suggested that long isolation of Neandertals could explain the evolution of their morphological pattern by genetic drift and local selection, both of which would predict a reduction in the variability of this population. The strength of this explanation was that it provided an explanation for the mosaic appearance of Neandertal traits over time within Middle Pleistocene Europeans (Stringer & Hublin, 1999).

These two concerns are interrelated. Both rest on an assumption that Neandertal populations changed relatively slowly, developing specializations that were not shared with contemporary human populations elsewhere in the world. In this model of evolution, when the Neandertals

encountered other human populations after 45,000 years ago, they would have been strongly differentiated in morphology with little overlap in the range of variation. This assumption can be defended in terms of paleoenvironment and cultural dynamics. European Neandertals lived recurrently, if not continuously, in periglacial conditions. Changes in culture, as evidenced by archaeological industries, initially proceeded very slowly, and began to exhibit greater regional diversity and temporal turnover only toward the end of the Neandertals' existence. Their unique anatomical configuration emerged within this context. What could be more natural than to assume that the forces of selection and drift had slowly driven them to greater and greater anatomical specialization within this unique environment?

Yet, our current understanding of the Neandertals shows that they did not experience a slow, plodding march toward anatomical specialization. With more discoveries from extreme eastern Europe and central Asia, it seems that the center of Neandertal evolution may not have been Europe at all. The anatomical record of western Europe lay at one geographic end of a broad distribution, and the few specimens of Neandertals from central Asia show intriguing differences from Neandertals in the west. The Teshik-Tash individual, for example, shows craniometric and mandibular affinities to the Upper Paleolithic sample of Europe (Glantz *et al.*, 2009). This does not eliminate the identification of this specimen as a Neandertal, but it does suggest that the morphological variability of the eastern Neandertals encompassed variation not often found in Europe at the same time.

We can adopt a more nuanced view of the diversity within and among Neandertal populations. The main impediment to understanding Neandertal diversity is the limit on the skeletal record. The Neandertals are the best-known of any human population before 40,000 years ago. However, even with hundreds of known specimens, only a few individuals represent any single part of Neandertal anatomy. Today we can talk about the diversity of Neandertals only at the broadest regional scale.

Early concepts of Neandertal diversity

How can we continue to advance our knowledge of Neandertal diversity in the face of a fragmentary fossil record? An examination of the history of the Neandertal problem adds some perspective on this vital question.

At the beginning, when only a handful of Neandertal specimens were known, anthropologists defined Neandertal “diversity” mostly in terms of obvious differences from humans and other fossil (or purported fossil) specimens. The initial Neandertal discoveries were specimens that represented the later part of the Neandertals’ existence. First to be recognized was Feldhofer, then the specimen from Forbes Quarry, Gibraltar and Engis, Belgium (both discovered earlier) later from Spy, Belgium and the classic French specimens from La Ferrassie (Peyrony & Capitan, 1909) and La Chapelle-aux-Saints (Boule, 1911). This sample of skeletal remains represents the time period between approximately 70,000 and 45,000 years ago. All were found within an area of a million square kilometers of Western Europe, only a small fraction of the area we now recognize as the total Neandertal range. Hence, the initial descriptions of Neandertals were of a biased population: Western European, long after Neandertal origins, and yet well before any possible contact of Neandertals with initial Upper Paleolithic people. Accentuating the morphological difference between this sample and recent humans was very simple.

After the first descriptions of Neandertals, some anatomists attempted to accommodate them within human variability by extrapolating from the anatomical patterns of developmental abnormalities or rare morphological correlates of disease. Rudolf Virchow asserted that the Neandertal skeleton was rachitic (Virchow, 1872), while J. Barnard Davis (1867) maintained that the Neandertal skull presented an extreme case of synostosis, accounting for its elongated shape and complete suture closure. In the view of these anatomists, the Neandertals presented a logical extreme of morphological tendencies

already known in contemporary people, allowing their anatomy to be brought within the compass of morphological “laws.” Humans to be compared with Neandertals were pathological variants within populations, not members of very different populations.

By contrast, others attempted to place Neandertals by considering the gradations among human racial groups. For example, Huxley (1864) suggested that human variation was so great that “it is possible to select a series which shall lead by insensible gradations from the Neanderthal skull up to the most ordinary forms”. Quatrefages and Hamy (1882) put the Neandertal skull as part of a primitive race of humans.

The morphology of a large sample of earlier Neandertals represented at Krapina, Croatia, was described only in the first decade of the twentieth century (Gorjanovic-Kramberger, 1906). The Saccopastore specimens from Rome also fall within the early part of the Neandertal range (Bruner & Manzi, 2006), and were described by Sergi (1948a,b). The recovery of these earlier Neandertals, from the Riss-Würm interglacial and earlier, showed anatomical continuity between Neandertals and more ancient human populations. With these samples, the issue of anatomical variation could be conceived in a time dimension. McCown & Keith (1939) conceived the skeletal sample from Skhul and Tabun, in Israel, to have come from a population that may have been a contemporary of the European Neandertals of the last interglacial. In their description, these samples represented a population evolving from a more modern to a more specialized type. The variation across time was related to an evolutionary model of increasing divergence between Neandertal and modern human populations.

Yet, several discoveries from the early twentieth century distracted many anthropologists by appearing to support the argument for an ancient, much more modern “presapiens” form in Europe. Today we appreciate that the supposedly early fossil sample included specimens of questionable or much later provenance, such as Fontéchevade and the infamous Piltown skull.

These did not entirely explain the Presapiens idea, however, which emerged from the alignment of specimens on a morphological axis from modern to Neandertal extremes. For example, Vallois (1954) argued that specimens lacking specific Neandertal characters must therefore represent a distinct group with a phyletic connection to modern humans. Weidenreich (1940) did not accept a presapiens population as specifically distinct from Neandertals, but did categorize samples as *Homo sapiens* based on the absence of Neandertal characteristic morphology irrespective of date (e.g., Swanscombe grouped with Skhul as “*H. sapiens intermediate*”). These examples illustrate a slow trend toward acceptance of two propositions about the evolution of Neandertals and modern humans: “Modern” morphological traits may in many cases be primitive, while the morphological traits of Neandertals may in many cases be derived, or “specialized”.

Neandertal variation and “varieties”

By midcentury, the broad outline of Neandertal variation was visible in the available sample. An early population of Neandertals exhibited the distinctive traits of that population only to a slight degree. These became more accentuated over time, up to the end of the Neandertals’ existence. Howell (1957) considered the variation within the known sample of Neandertals by describing three varieties. His summary helped to crystallize the description of Neandertal change over time and variation across space. In Howell’s description, the varieties were:

Early Neandertals

This group included the Neandertals from Krapina, Saccopastore, and Ehringsdorf. These are European sites (Croatia, Italy, and Germany) representing times from last interglacial (now dated at approximately 120,000 years ago) or earlier. Howell additionally mentioned several Asian specimens, including those from Tabun, Zuttiyeh and Teshik-Tash. This is a motley group, stretching from the Levant (Tabun and

Zuttiyeh) to Uzbekistan (Teshik-Tash). Howell did not assign these Asian fossils explicitly to the early Neandertal group. Howell distinguished the early Neandertals from classic Neandertals by eight cranial features, largely associated with smaller and more compact vaults and less midfacial prognathism. He also claimed that the postcranial skeleton of this early Neandertal sample was “more anatomically modern” than that of later Neandertals.

Classic Neandertals

This group included most of the well-known remains from the Würm glaciation in Europe. In today’s terms, this sample would include specimens as old as 100,000 years and as recent as 40,000 years. Howell characterized this set by cranial features, acknowledging that the sample of Early Neandertal postcrania was not sufficiently numerous to make clear statements about differences with the classic Neandertals. He also pointed out that this set of specimens were known exclusively from southwestern Europe, with western Germany and Italy constituting the easternmost boundaries of the classic Neandertal range.

Southwest Asian Neandertals

This group included the entire known fossil record of the Levant to the Zagros, including Skhul, Tabun, Zuttiyeh, and Qafzeh (all in the Levant) and Shanidar, Iraq. Howell noted the divergent opinions of anthropologists about the evolutionary scenario that generated this sample. He offered the opinion that the initial population of the Levant represented by Tabun had affinities with Early Neandertal people, and that the region had undergone a trend of “sapiensization” explaining the Skhul sample.

Howell identified these varieties of Neandertals to clarify his position on the Neandertal ancestry of recent humans. In his view, several previous authors had been too categorical in their insistence that Neandertals could not have been ancestors of modern peoples. He allowed that the classic Neandertals may have been too specialized to have given rise to later populations within Europe. But the early Neandertals were

less anatomically specialized and may have been ancestral to modern humans in some other, non-European, region. Moreover, the Southwest Asian Neandertals appeared to provide evidence of an evolutionary trend toward modern humans.

Emerging problems with Neandertal varieties

Howell's (1957) paper was fundamental to the definition of Neandertal variation. His groupings have in later years been widely repeated. In the abstract, Howell's scheme differentiated Neandertals along two axes: east (in particular the Levant) versus west, and early versus late. Both these axes help to organize the morphological comparison of Neandertal samples. In addition, some workers have emphasized a north-south axis of variation within Europe.

The differences between classic Neandertals and early Neandertals, such as the Krapina and Saccopastore samples, have repeatedly been observed, as reviewed by Hawks & Wolpoff (2001). The distinction between early and classic Neandertals emerged from the work of Gorjanovic-Kramberger (1906), Weidenreich (1928, 1943), Weinert (1936) and Sergi (1948). Many workers have pursued the hypothesis that classic Neandertals represent a specialized population evolving in partial isolation from other ancient people. Under such a hypothesis, the early Neandertals are expected to exhibit fewer of the distinct Neandertals characteristics compared to later, classic Neandertals.

The east-west axis of variation has been frequently recognized in morphological comparisons (Voisin, 2006). However, the east-west axis within Neandertals today presents much more potential complexity than in Howell's time. If the populations of Central Asia before 40,000 years ago were Neandertals, and if the Shanidar and Levantine sites also represent Neandertals, the eastern "pole" of Neandertals was bifurcated to the north and south of the Black Sea-Caspian Sea corridor. There is no reason to expect that these two areas would have aligned along the same morphological axis. At

present the skeletal evidence from the Central Asian Neandertal sites is insufficient to test whether these represent a similar population those further south.

There is reason to suspect greater complexity. Howell's "Southwest Asian Neandertal" sample has been a focus of repeated debate. At the time he wrote, McCown & Keith's (1939) description of the Skhul and Tabun remains had grouped these as representatives of a single population, anatomically intermediate between classic Neandertals and modern humans. Howell advocated this combined sample as a single undifferentiated population. Some recent authors have followed this position (Arensburg & Belfer-Cohen, 1998; Kidder *et al.*, 1992), while others have preferred to separate the Levantine skeletal sample into at least two different groups: Neandertals (generally Amud and Kebara, sometimes Tabun B), and modern humans (generally Skhul, Qafzeh, sometimes Tabun C).

A problematic aspect of the idea of Levantine Neandertals is that the very features that distinguish them from European Neandertals tend to align them with modern humans. For example, the Amud skeleton has stature and limb proportions that set it apart from European Neandertals, but that fall within the range of variability of the Skhul and Qafzeh skeletal remains. Trinkaus (1995) considered the Near East, including Shanidar and the Levantine samples, to include two forms of hominins: "late archaic" and "modern" forms. He argued that the late archaic forms in the Near East have no close connection to European Neandertals, and that similar features reflect mosaicism or generalized archaic morphology in both evolving populations.

Several workers after Howell added the concept of a north-south axis of Neandertal diversification within Europe. Rosas and colleagues (2006) noted that southern Neandertals tend to have increased heights of the lower face and broader faces than the northern sample of Neandertals within Europe. Because the line separating north and south must run along the very long east-west axis of Europe, there are many possible ways to divide the continent into northern and southern samples.

Paleogenetics

The data from paleogenetics of Neandertals have rapidly changed during the past few years. As a result, descriptions of the state of the evidence from as recently as 2005 are now obsolete. In that time, the synthesis of Neandertal DNA evidence has proceeded from a very simple model to one involving more complicated population interactions and movements.

Mitochondrial DNA

The complete mitochondrial genomes of more than a dozen Neandertals have been described and small fractions of the mitochondrial sequences are known for many more. These extend from as far to the east as Okladnikov Cave in the low Altai (Krause *et al.*, 2007), and as far west as El Sidrón in Spain (Lalueza-Fox *et al.*, 2012). The distance between those two sites encompasses nearly the entire east-west range known for the Neandertals. The north-south extent of data is much more restricted, as none of the sites from present-day Israel or Iraq have yet yielded genetic evidence. Dalén and colleagues (2012) have recently reviewed the mtDNA evidence from Neandertals, including a full list of those specimens that have yielded mtDNA sequences. These include specimens from El Sidrón (Lalueza-Fox *et al.*, 2012) and Valdegoba, Spain (Dalén *et al.*, 2012), Scladina, Belgium (Orlando *et al.*, 2006), Feldhofer, Germany (Krings *et al.*, 1999), Monti Lessini, Italy (Caramelli *et al.*, 2008), Vindija, Croatia (Green *et al.*, 2008), Mezmaiskaya (Ovchinnikov *et al.*, 2000) and Okladnikov, Russia (Krause *et al.*, 2007) and Teshik-Tash, Uzbekistan (Krause *et al.*, 2007). All these specimens can be connected by a phylogenetic tree that does not include any sequences from other known samples of living humans or ancient DNA from modern human specimens.

No known living people have mtDNA sequences that belong to the clade shared by all known Neandertals, a fact that strongly influenced many researchers to believe that Neandertals had become extinct without issue

(e.g., Serre *et al.*, 2004; Currat & Excoffier, 2004). Additionally, no ancient specimens of modern humans have been found to share a Neandertal-like mtDNA type (Serre *et al.*, 2004; Caramelli *et al.*, 2003). As discussed below, the hypothesis of no Neandertal ancestry for living people has been contradicted by nuclear DNA evidence (Green *et al.*, 2010). Yet the lack of mtDNA sharing between Neandertal and later human populations is not consistent with a neutral explanation rooted in Upper Paleolithic demographic growth (Manderscheid and Rogers, 1996; Ghiretto *et al.*, 2011). One hypothesis that would reconcile the mtDNA and nuclear genetic data is that the mtDNA of Neandertals was subject to negative selection in competition with mtDNA clades present in modern humans (Hawks, 2006). Another possibility is repeated demographic turnover.

The pattern of mtDNA evolution within Neandertals suggests that repeated turnover of the population of European Neandertals did happen. When considering the entire sample of mtDNA, the amount of variation within the Neandertal sample is approximately equal to the variation within living people across the same geographic range, from Spain to Central Asia (Caramelli *et al.*, 2008; Krause *et al.*, 2007). The common ancestor of all Neandertal mtDNA sequences lived approximately 200,000 years ago, around the same time as the modern human mtDNA last common ancestor (Dalen *et al.*, 2012). Taken by themselves, these comparisons are consistent with the hypothesis that Neandertals had approximately the same population structure and demographic history as modern Eurasians. However, when we compare earlier and later Neandertals, the picture is more complex. The sample of Neandertal mtDNA taken from European specimens after 50,000 years ago is depauperate in variation compared to the full sample (Lalueza-Fox *et al.*, 2008). The lack of variation in later European Neandertals is not consistent with these being a sample drawn from a small geographic area of a larger distribution, without demographic turnover (Dalen *et al.*, 2012). Instead, it appears that the western part of the

Neandertal range underwent at least one episode of large-scale migration and partial population replacement. A tightly related clade of sequences includes the specimens from Vindija, El Sidrón and Feldhofer, seven specimens in all. These are all among the latest Neandertals in the west. The Central Asian or eastern European portion of the Neandertal range retained greater mtDNA variation in this later time period, possibly indicating that this area was a source for later Neandertals in Western Europe. Dalen and colleagues suggested that a mass dispersal of Neandertals from the eastern into the western part of their range would be consistent with the mtDNA phylogeography. An alternative hypothesis is that natural selection on Neandertal mtDNA affected the frequency of clades in Western Europe.

Fabre and colleagues (2009) also emphasized a biogeographic division of mtDNA into eastern and western groups. They used a different methodology, focused upon whether the geographic range of Neandertals could be divided into replicable subsamples. In addition to the division into Central Asian and European groups, the study also suggested that the Italian and Croatian specimens might belong to a “southern” group. This study did not consider the times represented by different sites, and adding the dynamic reflected by time would likely change the groupings. By testing *a priori* models, the study avoided some of the problems attendant upon the tree-based approaches described above.

Nuclear DNA

Three Neandertals from Vindija have been represented by substantial sequencing of the nuclear genome, averaging nearly 1x coverage for each of them. Much smaller fractions of the nuclear genome have been recovered from Neandertal specimens from Feldhofer Cave, El Sidrón, and Mezmaiskaya (Green *et al.*, 2010). All of these except for Mezmaiskaya are among the group of later Western European Neandertals discussed above, all of which fall into a single mtDNA clade. This is therefore a highly constrained set of Neandertals in space and time. The full set of mtDNA extends includes an

eastern range with greater diversity and much earlier specimens in Western Europe.

The most celebrated result from the nuclear DNA evidence is the finding that non-African populations today derive a proportion of their ancestry from Neandertals (Green *et al.*, 2010). The fraction of ancestry represented by such introgression from Neandertals is between 1 and 4 percent of the genealogical ancestry of individuals with European, Asian or other non-African origins. Some of the similarity of non-Africans to Neandertals may be attributable to the ancient Middle Pleistocene structure of African populations (Eriksson & Manica, 2012), but this effect alone cannot explain the pattern of similarities, which therefore require substantial introgression (Yang *et al.*, 2012). It is possible that some similarities of living people and Neandertals resulted from gene flow between Neandertals and African contemporaries before the Late Pleistocene dispersal of modern populations. At present, there is no indication that Europeans have substantially more Neandertal ancestry than Asians or other peoples outside Africa (Green *et al.*, 2010). The Denisova genome represents a population with substantial genetic separation from Neandertals (Reich *et al.*, 2010). This population is represented only by three individuals from Denisova Cave, in the Altai Mountains. However, the population was among the ancestors of native Aboriginal Australians and related peoples of New Guinea and Oceania (Reich *et al.*, 2011). The introgression from these ancient populations into recent humans is not a focus of this paper, which is about the dynamics of Neandertal populations.

Nuclear DNA variation among the known Neandertal genomes is very limited compared to that found in living human populations. By using the genome of the Denisova specimen as an out-group, Reich and colleagues (2010) showed that the variation across the Neandertal geographic range, from Mezmaiskaya to El Sidrón, is very low compared to the variation within humans today, or between Neandertals and the Denisova genome. They interpreted this low variation within Neandertals as evidence for a bottleneck in the population history of Neandertal groups.

If we add the Denisova genome, which is quite genetically divergent from Neandertals, the total variation of the archaic human sample is only slightly greater than the variation among the most distant human populations today.

The low nuclear DNA diversity of these late, mostly Western European Neandertals more or less matches the low mtDNA diversity found in the same sample. This reduces the probability that natural selection specific to mtDNA can explain the mtDNA phylogeography of Neandertals. In the absence of selection, neither geography nor time considered alone would be sufficient to explain the grouping of the later, western subset of Neandertals into a tight mtDNA genealogical arrangement. One possible explanation is a movement of Neandertals from the eastern to western part of their range sometime after the origin of this clade, some 60,000 years ago. This movement would have to have replaced a large fraction of the mtDNA gene pool of earlier Neandertals in western Europe; otherwise, clades shared by earlier Neandertals such as Scladina would still be found among the later Neandertals. The replacement of earlier, more diverse mtDNA clades would be easier if the effective number of Neandertals in western Europe was very small. A small effective size does not necessarily imply a very small census population size (Hawks, 2008), and might point to a way to uncover population dynamics of this population, as discussed below.

The reduced variation of nuclear and mtDNA in the late western Neandertals reflects high genetic drift in this component of the Neandertal population. Genetic drift may reflect many different demographic phenomena, including small population size, recurrent movement, extinction and recolonization of small subpopulations (Eller *et al.*, 2004), or selection-migration interaction. We do not have nuclear genetic data from earlier Neandertals, and so we cannot directly test the hypothesis of a population bottleneck in the classic or later Neandertals. Nuclear genetic sampling of a broader range of Neandertals, including eastern and earlier specimens, might uncover substantially more variation.

Reconciling paleogenomics and morphology

The discussion of genetic diversity among these Neandertals has not yet attempted to reconcile their genealogical arrangement with morphological classification schemes. The later Western European Neandertals that share a close mtDNA genealogical connection (Vindija-Feldhofer-El Sidrón) are not synonymous with “classic Neandertals”. The well-known classic Neandertals include specimens such as La Chapelle-aux-Saints (France), La Ferrassie 1, Monte Circeo 1 (Guattari) as well as Feldhofer 1. This classic Neandertal sample includes specimens earlier than 70,000 years old and some as recent as 45,000 years ago. The classic Neandertals flank both the earlier and later sides of the 50,000-year-old dispersal of Neandertals proposed by Dalen and colleagues (Dalen *et al.*, 2012).

Meanwhile, the clade that connects late European Neandertal mtDNA into a tight cluster includes great morphological diversity. The two Vindija mtDNA sequences included by Dalén and colleagues (Dalen *et al.*, 2012) are both from layer G3 of the site, perhaps 40,000 years old. Both are derived from postcranial fragments without diagnostic morphological traits. The other material from G3 includes cranial, mandibular and dental remains that are not synonymous with classic Neandertal morphology (Ahern, 2004). These late Neandertals from Vindija display less pronounced morphology than classic Neandertals and lack traits that are common in the earlier classic Neandertals (Smith, 1992). These specimens are connected to Feldhofer and El Sidrón not only by mtDNA relationships but also their very low nuclear DNA diversification. If the Vindija specimens can be lumped together in mtDNA and nuclear DNA diversity with the remains from El Sidrón and Feldhofer, it seems possible that traditional morphological groupings will fail to capture real biological differences among Neandertal populations.

Two avenues of evidence will provide more insights about Neandertal population dynamics. Obviously, uncovering more nuclear genomes

from Neandertals or early Upper Paleolithic humans would advance our knowledge greatly. Tempering this expectation is that the later western Neandertals, with lower genetic diversity, are the ones most likely to provide more genetic data. Earlier Neandertals, and the Neandertals from central Asia, would be most useful to uncover new knowledge about the population dynamics of this ancient group. A second source of evidence may come from the introgression of Neandertal genes into later human populations. As we begin to uncover the genes in living people that came from Neandertals, we face the possibility that these genes may represent different ancient Neandertal groups to greater or lesser degrees. The initial work on Neandertal genetics suggested that most of the population mixture with Neandertals may have happened in west Asia (Green *et al.*, 2010). That would suggest that European Neandertals are themselves somewhat genetically distinct from the population that gave rise to most Neandertal genes in recent populations. Comparing different Neandertals with each other will help us uncover the structure of the population that gave rise to Neandertal ancestry in living people. By doing so, we may gain an additional genetic probe into the period before 60,000 years ago, as Neandertal populations had differentiated before the large-scale encounters with dispersing people from Africa.

Population dynamics

During the 1950s, as anthropologists began to acknowledge the morphological diversity of Neandertal populations, they became increasingly concerned with the Neandertal potential for individual dispersal and population movement. The attention to “early” Neandertals as a group dating to the last interglacial brought with it the understanding that Neandertals had persisted through at least one entire glacial cycle. Howell (1952) proposed that glacial cycles provided the isolation that enabled classic Neandertals to evolve their specialized anatomy. Weckler (1954) argued that isolation was one consequence of

glaciations, but that long-distance migrations and recolonizations of formerly periglacial habitat was an important cause of population change in Neandertals and the modern humans who encountered them.

Today, our knowledge of the geographic range of the Neandertals confirms their existence across a broad range of climate regimes. From the Altai to Spain, the known geographic range of Neandertals covered more than 7000 kilometers east to west. On the longitudinal range is little doubt, because of the mtDNA evidence European Neandertal specimens to Okladnikov Cave (Krause *et al.*, 2007). Okladnikov is at present the easternmost site to produce skeletal remains attributable to Neandertals, although other sites with similar archaeology are found in the Altai. The Neandertals also covered a substantial range in latitude. The northernmost Neandertal site may be Byzovaya, which does not present skeletal remains but does include a Late Mousterian assemblage with some technical links to central European Neandertal sites (Slimak *et al.*, 2011). The earliest faunal evidence from Mamontovaya Kurya is earlier than the Byzovaya evidence and also contemporary with late Neandertals. However, these sites are at the end of the Neandertals’ timespan, and possibly represent the activity of subsequent people. The paleoecological reconstruction of Mousterian sites encompasses almost the entire range of European ecological contexts, except for Alpine and Arctic biomes (Banks *et al.*, 2008). Although the European climatic conditions oscillated considerably during the Late Pleistocene, the Neandertals seem likely to have been capable of adapting to changing conditions, either by tracking ecotones as climate shifted or by changing their subsistence strategies to meet new requirements. In other words, the archaeological record by itself is sufficient to show us that Neandertal populations were highly dynamic in areas where habitation was possible only during intermittent climatic periods.

Archaeological evidence alone gives us some indications that Neandertals rapidly colonized new regions when they became suitable

for habitation. The possible excursions of Late Mousterian people north of the Arctic Circle to Byzvyaya and Mamontovaya Kurya are strong indicators of such a potential, if these sites truly represent Neandertal activity. Bar-Yosef (1992) suggested that later Neandertal sites in the Levant, including Amud and Kebara, may represent the recolonization of this area from Europe as cold conditions intensified during the Würm glaciation. Shea (2008) considered the record of modern and Neandertal activity in the Levant to represent multiple cases of population turnover, as climate shifts caused successive populations of Paleolithic humans to abandon the area or become locally extinct.

Across northwestern Europe, from Britain to Poland, an area of more than a million square kilometers was abandoned by Neandertals during the early stages of the last glaciation and not re-inhabited until after approximately 60,000 years ago. The intermittent occupation of these parts of Europe was likely not a function of “habitat tracking” by Neandertals, but instead a record of regional expansions and partial extinctions when climatic conditions deteriorated (Hublin & Roebroeks, 2009). White & Pettitt (2011) suggested a very small Neandertal population size in northwestern Europe during the late Middle Paleolithic, and considered the possibility that the occupation of Britain was maintained as seasonal hunting camps rather than permanent settlement. This kind of occupation would put movements of several hundred kilometers into the ordinary behavioral pattern of individual Neandertals. At an extreme, the survival of Neandertals on the northwestern tier of Europe may have been precarious (White, 2006). From the perspective of population dynamics, this does not suggest a dense, stable population, but instead one of great mobility and repeated ability to colonize and exploit new opportunities.

We cannot consider Neandertal population dynamics without discussing the probable effects of small population numbers on their distribution. The estimation of population numbers from archaeological site densities is imprecise with many sources of error. Nevertheless, some

estimates of the total number of Neandertals representing traditions such as the Mousterian of Acheulean Tradition (MTA) are as low as a few hundred individuals total (Richter, 2006). Across peninsular Europe, there may have been fewer than 10,000 Neandertals living at any given time, an indication of the census population size. Certainly, the genetic variation of Neandertals is consistent with a very small effective population size. Many factors reduce genetic variation relative to census population size (Hawks, 2008), including two of particular relevance to Neandertal population structure: extinction and recolonization of groups (Eller *et al.*, 2004), and broader regional-scale cultural replacement in the presence of selection (Premo & Hublin, 2009). Such small groups and regional populations would have very little genetic “inertia” against the long-term effect of gene flow. Genetic continuity in this scenario could never persist for long against even a moderate amount of immigration acting over many generations.

Genetics now leads us to a picture of a highly dynamic Neandertal population. This should not be a surprise in the context of the archaeological record, which shows abundant evidence for regional-scale population movement and rapid changes to cultures and adaptive strategies. But it is not clear that the genetic and archaeological data actually converge on a single picture of population dynamics.

Archaeological and genetic evidence: a case study

A close look at a single archaeological example helps to demonstrate the difficulty of reconciling archaeological and genetic observations into a single population model. The Quina Mousterian in southwestern France appears to represent a regional Neandertal adaptive pattern. As climate conditions gave rise to a mix of steppe and boreal forest, Neandertals specialized on reindeer, and to a lesser extent horse, replacing an earlier strategy using a broader mix of large fauna. The accompanying toolkit has been

recovered from many sites in the region, consistently overlying earlier Denticulate and Typical Mousterian assemblages (Guerin *et al.*, 2012).

As we consider this kind of technical transition, it is not obvious how the earlier and later Neandertals of southwestern France were related to each other. The transition in this area, around 60,000 years ago, is a temporal boundary between traditions each of which lasted for thousands of years. Certainly it is possible that the earlier population underwent cultural adaptive evolution, suiting it better to the changing ecology, and resulting in the later cultural tradition. But it is also possible that ideas spread when people themselves spread.

Cultural change and spatial dispersal were likely interlinked. An effective faunal procurement strategy may open up habitat that earlier Neandertals had less success exploiting. The colder parts of Germany seem to have seen the spread of reindeer hunters during MIS 4, in an occupation that may have been thin on the ground but potentially occupied a broad area (Uthmeier *et al.*, 2011). As different Neandertal groups used different adaptive strategies, some would have expanded in geographic range, sometimes into new previously unoccupied territory but often into territories formerly occupied by groups with different cultural strategies. Could northern Neandertal reindeer hunters have followed their herds right down into the heartland of France, as conditions grew colder, replacing their cousins to the south?

Despite the evidence for cultural change, as far as we know the morphological variation across this cultural transition was continuous. Before 60,000 years ago, southwestern France was inhabited by people we call classic Neandertals. Skeletal associations with Quina Mousterian, for example from Les Pradelles (Mussini, 2011) and Combe Grenal, present no obvious appearance of morphological discontinuity with other classic Neandertals. Condemi and colleagues (2010) considered the dental sample from the Rhône valley of southeastern France, including the well-known classic and late Neandertal sites of Hortus, Tournal and Le

Portel and the older sites of Genay and Payre. Their comparisons were necessarily limited but showed a lack of regional differentiation between this set of Neandertals and the remainder of the Neandertal sample from across Europe. Within Spain, Rosas and colleagues (2006) described the mandibular remains from El Sidrón, including them in several comparisons of regional samples of Neandertals. They found evidence for a significant difference in mandibular morphology between “northern” and “southern” samples, which they attribute to a smaller dentition and degree of midfacial prognathism in the southern sample. However, these “northern” and “southern” sets each include specimens known to be part of the “late western Neandertals” that preserve low genetic variability. To the extent that there is a morphological difference here, it does not match the genetic pattern.

In short, morphological comparisons across the relevant time span in France and Spain are insufficient to support the hypothesis of a large-scale migration bringing in a new mtDNA type. Yet it is difficult to imagine that a widespread movement of Neandertals could reach northern Spain by around 50,000 years ago without passing through southwestern France or affecting the skeletal sample of Spain. Possibly the very small sample of physical remains will simply be insufficient to test hypotheses of population dynamics on this scale.

If the Neandertals of southwestern France, for example, were fewer than 1000 individuals, how could they have maintained identifiable traditions of stone technology for thousands of years? If their gene pool was constantly in flux due to immigration and long-distance movement of individuals, how could their cultures not have rapidly changed beyond recognition? In this scenario it seems necessary to assume very strong reinforcement of technology by learning biases, probably mediated by the observed utility of stone tool choices within the local ecology (Henrich, 2001). Learning and cognition may have supported a dynamic Neandertal population, enabling their persistence in a tenuous paleoclimatic regime.

Conclusion

A synthetic view of Neandertal population dynamics must incorporate morphological, genetic and archaeological observations. Of these three, the archaeological record is the most sensitive indicator of regional-scale changes on a millennial timescale. Within the broad scope of the Mousterian in Europe and Central Asia, archaeologists have recognized regional variants that cover hundreds of thousands of square kilometers of geographic area. But archaeological evidence is highly specific and particular to a given region. As we examine a detailed case study within a region, it may be difficult or impossible to find morphological and genetic correlates of changes in archaeological industries and traditions. Archaeology does provide insight into the ways the Neandertals maintained their population in the face of regional movements, suggesting logistical strategies that may have involved temporary summer occupations at some distance from their core territories.

The genetic data force us to adopt a new stance on the nature of Neandertal populations. A long, slow evolution of Neandertal populations cannot account for the evidence of long-distance interactions and movement on relatively short time scales. The redefinition of Neandertal population groupings should begin immediately. We may soon have genetic data from many more Neandertal specimens. Given the unexpected finding of diversity from the Denisova specimen (Reich *et al.*, 2010) it is possible that some other Asian “Neandertal” populations will turn out to represent equally divergent human populations. As we consider the “Southwestern Asian” Neandertals in Howell’s (1957) review, we can already see how that collection of specimens may have included a heterogeneous collection representing several distinct populations. Anthropologists today disagree about whether Shanidar, Amud and Kebara should be counted among the Neandertals.

We should not too readily assume that gene sequences from such specimens would fall within the known pattern of Neandertal genetic

variability. It is conceivable that these samples represent Denisovans or an equally divergent ancient population. The counterargument to such a hypothesis is that Neandertals must have mixed with modern humans somewhere, and the likely geographic location for such exchange, before modern humans spread throughout Eurasia, was the Levant. Nevertheless, the Altai Mountains were a point of population interaction across potentially tens of thousands of years, within a smaller land area than West Asia. The Levant, Arabian peninsula, Mesopotamia, Anatolia and the Caucasus constitute a large area in which diverse populations of Neandertals and other archaic humans may have coexisted.

Several important questions have not been addressed in this paper. Late Neandertals, in the period after 40,000 years, remain to be genetically sampled. They may represent a further stage of population turnover within the Neandertals, or may bear the influence of modern human ancestry. The morphology of Central Asian Neandertals remains poorly known, as does the pattern of connection between Central Asia and Southwest Asia. What we now know is that the traditional category of “classic” Neandertals is insufficient to describe the genetic variability and dynamics of Late Pleistocene Europeans. That finding alone should cause us to revisit the connection between skeletal and archaeological evidence of Neandertals.

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