Man and his ancestors – the legacy and fate of Neanderthal Man

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First discovered in lime quarries in the Neander Valley near Dusselorf, Germany, in 1856, Neanderthal Man (*Homo neanderthalensis*) was the first modern hominid species to be named[1]. Since the discovery of the original fossil (subsequently named as Neander 1), numerous Neanderthal fossils, varying from sets of teeth to virtually complete skeletons, have been discovered at numerous European and Central Asian sites, including La Chapelle-aux-Saints and Moustier (France) and Shanidar (Kurdistan)[1–4]. Neanderthals have been variously classified as *Homo neanderthalensis* (a separate species from humans in the genus *Homo*) or *Homo sapiens neanderthalensis* (a different subspecies under the same species as humans, which indicates a far closer relationship). Anatomically, Neanderthals appear to represent the 'typical' caveman and were more robustly built than modern humans with distinctive morphological features, including prominent brow ridges, a large barrel-shaped chest, short and powerful limbs, large teeth, and a broad nose and nasal passages[1,4]. The robust Neanderthal body proportions can be probably explained as thermoregulatory adaptations for coping with cold temperatures. They made rather sophisticated tools (the Mousterian implements), were probably efficient hunters, used fire, wore clothing, buried their dead and occasionally even made ornamental objects[1,4]. Neanderthals appear to have disappeared from the fossil record about 30,000 years ago after inhabiting parts of Europe and Western Asia from Siberia to the Middle East. During the latter part of their history, Neanderthals probably came into contact with modern humans. This arrival seemed to coincide with their decline, a process which is still not completely understood[1,4–6].

When studying the evolution of mankind, one question which frequently arises is: what was the fate of the Neanderthals? Did they evolve into modern man or are they a sister line of evolution which simply went extinct? What is their genetic contribution to the modern human lineage?

Detailed statistical studies performed on Neanderthal and early human skeletons showed little anatomical evidence that Neanderthals were the direct ancestors of early humans[7–12]. Analysis of Neanderthal craniofacial shapes by Harvati *et al.*[8] demonstrated an unusually high level of morphological difference from modern human populations even if Upper Paleolithic European human specimens are considered, indicating that humans and Neanderthals belonged to separate species. Neanderthals appeared to possess a dental pattern quite distinct from modern humans[9]. Also, study of limb bones, particularly ratio of the length of the upper arm to the forearm and the length of the thigh to the shin bones indicated that while Neanderthals inhabited and were well adapted to cold climates, early *Homo sapiens* (and the Cro-Magnon man who was far more anatomically similar) had longer forearms and shin bones, and probably arose in more tropical climes[1,12]. Longer forearms and shin bones allow more heat to be radiated and indicate a hotter climate of origin. Thus, Neanderthals and early *Homo sapiens* appeared to be separate species which co-existed in different regions of the world and maybe even sympatrically for a considerable period of time, indicating that Neanderthals were probably not ancestral to extant human populations.

The possibility that Neanderthals could interbreed with modern humans and provide inputs to the modern human gene pool is another important aspect which needs to be considered. However, most initial genetic studies provided little evidence of the same. Mitochondria – organelles involved in respiration and energy production in cells – contain small amounts of DNA. Mitochondrial DNA (mtDNA), unlike nuclear DNA, is maternally inherited without recombination and occurs in many copies per cell[1,12,13]. By comparing these mutations, scientists can estimate how species evolve. Krings *et al.*[14] extracted a short segment of mtDNA, hypervariable sequence 1, from the Neander 1 fossil, amplified the DNA by polymerase chain reaction (PCR) and compared its sequence with DNA obtained from modern humans. The mean number of differences between modern human and Neanderthal DNA in the sequence of the segment of DNA analysed was found to be 25.6 bases. In comparison, the difference within modern humans is very small; the entire global population differs by only eight bases in the corresponding segment of DNA. Also, while Neanderthals inhabited the same geographic region as contemporary Europeans, the observed differences between Neanderthal and European DNA sequences was no less than those between Neanderthal DNA and that obtained from Asians, Africans or Australians[14]. Sequence comparisons and phylogenetic analyses indicated that Neanderthal mtDNAs fall outside the range of variation found among humans, suggesting that Neanderthals did not contribute significant amounts of mtDNA to the human lineage[13–16]. Currat and Excoffier[5] estimated the maximum interbreeding rates between the two populations to be smaller than 0.1%, despite a likely cohabitation time of more than 12,000 years.

Direct high-throughput sequencing of over one million base pairs of nuclear DNA extracted from a 38,000-year-old Neanderthal fossil essentially free of contamination from modern human DNA and detailed comparisons with human and chimpanzee genomes by Green *et al.*[17] reveal that modern human and Neanderthal DNA sequences diverged probably about 500,000 years ago. Such findings appear to provide evidence for the 'out of Africa hypothesis' that modern humans evolved from a probably African ancestor. This would make the direct evolution of humans from Neanderthals improbable as virtually no Neanderthal fossils have been discovered in Africa. Humans then migrated all over the world 50,000–100,000 years ago and replaced other hominid populations, including Neanderthals with relatively little interbreeding[1,12,18–20]. Although the 'out of Africa hypothesis' (alternatively called the Noah's Ark hypothesis) is generally accepted, some scientists also cite a 'multiple origin hypothesis' (regional hominid populations slowly evolving into modern humans) and propose that humans arose from Neanderthal populations or at least interbred with them[1,12].

The understanding of the relationships between humans and Neanderthals became more complex after Green *et al.*[21] analysed nuclear DNA sequences obtained from Neanderthal bones found in Vindija, Croatia and inferred that between 1% and 4% of the genomes of people in Eurasia could be derived from Neanderthals. Thus, there might have been some limited interbreeding between Neanderthals and *Homo sapiens* in Europe and Asia; however, such interbreeding did not appear to have occurred with African *Homo sapiens*. Neanderthals and modern human populations probably separated from each other between 270,000 and 440,000 years ago, and Neanderthals probably contributed to the genetic ancestry of present-day humans outside Africa. However, this contribution appeared to be relatively minor. Their findings continued to support the hypothesis that the majority of genetic variants originated from Africa and spread with the migration of anatomically modern humans while providing a challenge to the simplest version of the 'out of Africa' model[21]. Some subsequent genetic studies and analysis of the HLA antigens have also indicated interbreeding between humans and Neanderthals, although estimates of Neanderthal contribution to non-African human genomes remain between 1% and 3% (refs 22–24). Interbreeding of humans with Neanderthals may have provided them with 'hybrid vigour' strengthening their immune systems and providing them with increased capabilities to combat diseases. However, many HLA genes might have arisen prior to humans diverging from Neanderthals[24].

So what was the ultimate fate of the Neanderthals? This remains to be clearly elucidated, although much of the modern genetic evidence indicates that a limited amount of interbreeding between humans and Neanderthals could possibly have occurred. Although certain fossil skeletons discovered at Lagar Velho in Portugal and Peştera Muierii in Romania have been claimed to represent human–Neanderthal hybrids[25–27], paleontological support for interbreeding still remains comparatively rare[1,22].

Why the Neanderthals became extinct is also still not clearly known, although several theories have been proposed to explain their demise. Fossil records indicate that the Neanderthals began to decline towards extinction around 30,000–40,000 years ago, although some radiocarbon dating studies have suggested that Neanderthals might have survived in Asia till about 24,000 years ago[1,26,27]. Interestingly, their decline also appeared to coincide with the arrival of anatomically modern humans[1,4–6,26,27].

Briggs *et al.*[28] assembled complete mtDNA genomes using Neanderthal fossils taken from Spain, Germany, Croatia and Russia. Although the Neanderthal specimens spanned around 30,000 years and 4,200 km, analysis revealed that mtDNA genetic diversity in Neanderthal populations who lived 38,000–70,000 years ago was only one-third of the diversity present in contemporary humans indicating a small effective population size of Neanderthals, much smaller than that of modern humans and extant great apes[28]. Prolonged inbreeding, as is likely to occur in small populations, could have led to reduced fitness in Neanderthals. It has been estimated that when Neanderthals first encountered anatomically modern humans who migrated into Eurasia, their prolonged inbreeding led to their being at least 40% less fit[27]. Reduced fitness could lead to low levels of immunity, making them more susceptible to parasites and pathogens. Also ancient *Homo sapiens* may have carried diseases against which the Neanderthals had little immunity. A small population would be more susceptible to catastrophic events and genetic drift, and might be less suited to cope with adverse conditions which a larger population might be able to tide over.

Climatic changes, gradual or sudden, may have played a role in the extinction of Neanderthals[29]. While Neanderthal body proportions indicate that they were well suited to survive in a cold climate, they might have failed to adapt to rising global temperatures[27]. Conversely, if conditions became extremely cold, arid and adverse, and food sources very scarce (as might have occurred in the wake of the Campanian Ignimbrite eruption, which occurred around 40,000 years ago[30]), Neanderthals could have suffered more since with their larger and more robust build, they would need more calories to survive than *Homo sapiens*. If the animals they usually hunted declined in numbers or became extinct due to changes in climatic conditions, Neanderthals would be more vulnerable to starvation. Additionally, early *Homo sapiens*, unlike the more exclusively carnivorous Neanderthals, appeared to have at least rudimentary ideas about agricultural practices[1], and could thus probably produce and utilize sources of food which the latter could not.

Neanderthals could also have been replaced by early humans either through conflict or competition. As *Homo sapiens* and Neanderthals were similar species with possibly similar patterns of resource utilization, they might have competed for the same ecological niches. As postulated by Gause (1934), if two closely related species compete for a common niche, the stronger competitor would thrive while the weaker competitor would suffer competitive exclusion[31,32]. Early humans may have proved to be simply better competitors.

Around 40,000 years ago, hominids appeared to undergo a sort of 'cultural revolution'. Tools became far more sophisticated with distinct blades (the Aurignacian implements) and works of art including sculptures, beaded ornaments and complex cave paintings at Chauvet, Lascaux, Aldène, Fumane and Arcy-sur-Cure appeared[1,33,34]. Anatomically modern humans and not Neanderthals have been associated with the Aurignacian and early Upper Paleolithic industries[1,9,33], indicating a possible sudden increase in intellectual capacity with which the Neanderthals were unable to keep pace. Being more technologically advanced and armed with more sophisticated hunting implements, early humans might have proven to be more efficient hunters. Agricultural practices would also allow a given area to support more individuals, enabling an increase in early *Homo sapiens* populations.

A 'cultural revolution' may also have played a role in strengthening social bonds within or between tribes. Far-reaching and extended social networks could have made important contributions to promoting human survival[1,35]. When conditions became adverse, early humans, being better at networking, would be able to receive and pass on more information about foraging grounds where prey could be hunted, or where fruits and tubers could be gathered. They could exchange tools and enlist the support of their neighbours in times of need. This would improve their chances of survival under unfavourable conditions or when they came into conflict with their Neanderthal competitors. Although individually stronger, the more individualistic

Neanderthals were apparently unable to cope with such teamwork, and this could have led to their eventual demise.

Based on current evidence, the fate of the Neanderthals might be difficult to determine with absolute certainty. However, it seems reasonable to assume that they were outcompeted by early *Homo sapiens* who were more technically and socially advanced, and slowly but surely pushed towards extinction. In addition to competition with early humans, a variety of other factors, including reduced fitness due to inbreeding and inability to adapt to changing environments and climate could have contributed to the ultimate demise of Neanderthals.

1. Mckie, R., *Ape-Man the Story of Human Evolution*, BBC Worldwide Ltd, London, 2000, pp. 144–187.
2. King, W., *Q. J. Sci.*, 1864, **1**, 96.
3. Trinkaus, E., *Am. J. Phys. Anthropol.*, 1985, **67**, 19–41.
4. Roebroeksa, W. and Soressia, M., *Proc. Natl. Acad. Sci. USA*, 2016, **113**, 6372–6379.
5. Currat, M. and Excoffier, L., *PLoS Biol.*, 2004, **2**, e421.
6. Stringer, C. and Davies, W., *Nature*, 2001, **413**, 791–792.
7. Bräuer, G., Broeg, H. and Stringer, C. B., In *Neanderthals Revisited: New Approaches and Perspectives. Vertebrate Paleobiology and Paleoanthropology* (eds Hublin, J. J., Harvati, K. and Harrison, T.), Springer, Dordrecht, The Netherlands, 2006, pp. 269–279.
8. Harvati, K., Frost, S. R. and McNulty, K. P., *Proc. Natl. Acad. Sci. USA*, 2004, **101**, 1147–1152.
9. Bailey, S. E., Weaver, T. D. and Hublin, J. J., *J. Hum. Evol.*, 2009, **57**, 11–26.
10. Stringer, C. B., In *Origins of Anatomically Modern Humans. Interdisciplinary Contributions to Archaeology* (eds Nitecki, M. H. and Nitecki, D. V.), Springer, Boston, MA, USA, 1994, pp. 149–172.
11. Hublin, J. J., Spoor, F., Braun, M., Zonneveld, F. and Condemi, S., *Nature*, 1996, **381**, 224–226.
12. Strickberger, M. W., *Evolution*, Jones & Bartlett Publishers, Massachusetts, USA, 1995, pp. 437–480.
13. Green, R. E. *et al.*, *EMBO J.*, 2009, **28**, 2494–2502.
14. Krings, M., Stone, A., Schmitz, R. W., Krainitzki, H., Stoneking, M. and Pääbo, S., *Cell*, 1997, **90**, 19–30.
15. Orlando, L., Darlu, P., Toussaint, M., Bonjean, D., Otte, M. and Hänni, C., *Curr. Biol.*, 2006, **16**, R400–2.
16. Schillaci, M. A. and Froehlich, J. W., *Am. J. Phys. Anthropol.*, 2001, **115**, 157–166.
17. Green, R. E. *et al.*, *Nature*, 2006, **444**, 330–336.
18. Cann, R. L., Stoneking, M. and Wilson, A. C., *Nature*, 1987, **325**, 31–36.
19. Stringer, C., *Nature*, 2003, **423**, 692-3, 695.
20. Pagani, L. *et al.*, *Am. J. Hum. Genet.*, 2015, **96**, 986–991.
21. Green, R. E. *et al.*, *Science*, 2010, **328**, 710–722.
22. Vernot, B. and Akey, J. M., *Science*, 2014, **343**, 1017–1021.
23. Abi-Rached, L. *et al.*, *Science*, 2011, **334**, 89–94.
24. Callaway, E., *Nature*, 2011, **476**, 136–137.
25. Soficaru, A., Dobos, A. and Trinkaus, E., *Proc. Natl. Acad. Sci. USA*, 2006, **103**, 17196–17201.
26. Higham, T. *et al.*, *Nature*, 2014, **512**, 306–309.
27. Harris, K. and Nielsen, R., *BMC Biol.*, 2017, **15**, 73.
28. Briggs, A. W. *et al.*, *Science*, 2009, **325**, 318–321.
29. Finlayson, C. and Carrión, J. S., *Trends Ecol. Evol.*, 2007, 213–222.
30. Fitzsimmons, K. E., Hambach, U., Veres, D. and Iovita, R., *PLoS ONE*, 2013, **8**, e65839.
31. Chapman, J. L. and Reiss, M. J., *Ecology Principles and Applications*, Cambridge University Press, 2000, pp. 106–119.
32. Gause, G. F., *The Struggle for Existence*, Williams & Wilkins, Baltimore, USA, 1934.
33. Verna, C., Dujardin, V. and Trinkaus, E., *J. Hum. Evol.*, 2012, **62**, 605–617.
34. González-Sainz, C., Ruiz-Redondo, A., Garate-Maidagan, D. and Iriarte-Avilés, E., *J. Hum. Evol.*, 2013, **65**, 457–464.
35. Adler, D. S., Bar-Oz, G., Belfer-Cohen, A. and Bar-Yosef, O., *Curr. Anthropol.*, 2006, **47**, 89–118.

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