

Whither the Neanderthals?

RICHARD G. KLEIN

The Neanderthals are the longest known and best understood of all fossil humans. In 1856, quarry workers cleaning out a limestone cave in the Neander Valley, Germany, found a partial skeleton for which the group is named. Today, several thousand Neanderthal bones are known from more than 70 individual sites. Yet, paleoanthropologists still debate just how much the Neanderthals differed from living humans and whether the differences help explain why the Neanderthals disappeared.

Most Neanderthal specimens are isolated skeletal elements, especially teeth and jaws, but nearly every part of the skeleton is represented in multiple copies. There are also more than 20 partial skeletons from individuals of both sexes and different ages.¹ More than 300 archaeological sites have yielded artifacts and broken-up animal bones that illuminate Neanderthal behavior and ecology.²

The Neanderthals evolved in Europe. Some of their distinctive anatomical features already mark European fossils that are more than 350,000 years old.³ Through a process of natural selection and random genetic drift, they emerged in full-blown form by 130,000 years ago. From then on, they were distributed more or less continuously from Spain to southern Russia; by 80,000 years ago, they had extended their range to western Asia (see the figure). They persisted in Europe and western Asia until at least 50,000 years ago and perhaps in some places until 30,000 years ago.

Everywhere they lived, the Neanderthals were the immediate predecessors of modern humans, and it has often been suggested that they were ancestral to living populations. However, at the same time that the Neanderthals occupied Europe and western Asia, other kinds of people lived in the Far East and Africa.⁴ The Africans were anatomically much more modern than the Neanderthals, and are therefore more plausible ancestors of living humans. Furthermore, surveys show that variants of mitochondrial DNA⁵ and the Y chromosome⁶ in living Eurasian humans derive exclusively from African variants that probably existed no more than 100,000 years ago.

Further support for this argument comes from mitochondrial DNA extracted from Neanderthal bones. The data indicate that the last shared ancestor of Neanderthals and living humans lived 500,000 to 600,000 years ago.⁷ Non-sex chromosomes of living humans may conceivably retain some Neanderthal genes,⁸ but the combined fossil and genetic evidence suggests that any

Neanderthal contribution to living populations was small. The Neanderthals may thus be regarded as a fascinating but extinct side branch of humanity.

Modern humans invaded the west Asian part of the Neanderthal range about 45,000 years ago. They subsequently swept northward and westward through Europe, swamping or replacing the Neanderthals within 10,000 to 15,000 years. The modern human triumph depended on technological, economic, and demographic advantages that were apparently grounded in an enhanced ability to innovate. This ability probably appeared first in Africa, but debate continues on how rapidly it evolved and whether it was rooted in biological change or in population growth and social reorganization. Fossils and artifacts are unlikely to resolve this issue, but genes underlying cognition might.

Neanderthal Physical Form

The Neanderthals were distinguished by large heads, massive trunks, and relatively short, powerful limbs.¹ Their average brain size equaled or exceeded that of modern humans, but their skulls also exhibit specializations that are unknown in any other people, fossil or living.⁹ These unique features underscore the likelihood that the Neanderthals represent a divergent evolutionary lineage.

The specializations include the extraordinary forward projection of the face along the midline, the tendency for the braincase to bulge outwards at the sides, a depressed elliptical area of roughened bone on the back of the skull, and an array of bumps and crannies in the vicinity of the mastoid process. In addition, high-resolution computed tomography has revealed a singular configuration of the bony labyrinth of the inner ear.¹⁰

These features apparently had a genetic basis, because they are already visible in young children. The labyrinth configuration was fixed even before birth. There is no indication that the specialized features attenuated through time: The latest Neanderthals, 60,000 to 30,000 years ago, express them just as strongly as their more remote ancestors. Modern humans completely lack them. The skull alone then is sufficient to preclude a major Neanderthal contribution to living human populations.

High activity levels and a strenuous life-style explain the power of Neanderthal limbs. The short limbs and massive trunk, which would conserve body heat, were probably an adaptive response to the mostly glacial climatic conditions under which

the Neanderthals evolved. Among living humans, such features particularly characterize Arctic peoples. The Neanderthals had even more massive trunks and shorter limbs, yet never faced true Arctic cold. The degree to which they adapted physically may reflect their limited ability to adapt culturally.

Neanderthal Behavior and Ecology

The modern successors to the Neanderthals are often known colloquially as the Cro-Magnons, after a French site where their bones were uncovered in 1868. In general, Neanderthal bones occur with artifact assemblages that archaeologists assign to the Middle Paleolithic cultural (or artifactual) complex, whereas Cro-Magnon bones occur with artifacts of the succeeding Upper Paleolithic complex. The use of separate names for the physical types and the artifact complexes allows for deviations from the usual rule of association.

Middle and Upper Paleolithic people shared many advanced behaviors, including a refined ability to flake stone, burial of the dead (at least on occasion), an interest in naturally occurring mineral pigments, full control over fire, and a heavy dependence on meat (probably obtained mainly through hunting). Both Neanderthal and Cro-Magnon skeletal remains sometimes reveal debilitating disabilities, indicating that both kinds of peoples cared for the old and the sick. There could be no more compelling indication of shared humanity.

Yet, archaeology also suggests many important behavioral differences. Unlike Upper Paleolithic Cro-Magnons, Middle Paleolithic Neanderthals left little compelling evidence for art or jewelry. Their graves contain nothing to suggest burial ritual or ceremony. They produced a much smaller range of readily distinguishable stone tool types; much more rarely crafted artifacts from plastic substances like bone, ivory, shell, or antler; and left no evidence for projectile (as opposed to thrusting) weapons. Their cave sites are generally poorer in cultural debris and richer in bones of bears and other cave dwellers (suggesting less dense human populations). They failed to build structures durable enough to leave an archaeological trace, and were confined to relatively mild, temperate latitudes. Finally, the Middle Paleolithic artifact assemblages that Neanderthals produced varied little through time and space. The Upper Paleolithic assemblages that Cro-Magnons made varied far more and are the oldest from which we can infer identity-conscious ethnic groups.

Hence, only the Upper Paleolithic anticipates the material record of historic hunter-gatherers, and only Upper Paleolithic people were fully modern in the sense that all historic people were.

Neanderthal/Cro-Magnon Contact

Consistent with an African origin for the Cro-Magnons, radiocarbon dating suggests that they displaced the Neanderthals about 45,000 years ago in western Asia and only 5000 to 15,000 years later in Europe. In Europe, the Neanderthals may have succumbed much earlier in the far east (Russia) than the far west (Iberia), but the supporting dates are sparse. There is also the ever-present

possibility of minute, undetectable contamination with recent carbon, which can make a sample that is 50,000 to 40,000 radiocarbon years old appear 20,000 to 10,000 years younger.

Such contamination may explain radiocarbon dates that suggest the survival of Neanderthals in southern Russia,¹¹ Croatia¹², and Spain¹³ for 7000 years or more after Cro-Magnons had appeared nearby. Only the alternation of Neanderthal and Cro-Magnon layers within a single site could provide unequivocal evidence for substantial chronological overlap. No known site provides such alternation. Wherever Middle Paleolithic and early Upper Paleolithic layers occur in the same site, the Upper Paleolithic layers directly overlie the Middle Paleolithic ones, with no indication for a significant gap in time. The implication is that in most places the Neanderthals disappeared abruptly.

Neanderthal/Cro-Magnon interbreeding has been suggested from occasional fossils, including a recently discovered Upper Paleolithic child's skeleton from Portugal.¹⁴ However, in each case, the anatomical indications are at best ambiguous, and few experts recognize any hybrids. Evidence for cultural contact is also sparse, except for one well-documented case from central France. Here, a site occupied by Neanderthals shortly before their disappearance has provided an undeniable mix of Middle and Upper Paleolithic artifact types, including well-made bone tools and jewelry.¹⁰ It also contains the only indisputable house ruin from a Neanderthal site.

The mix may mean that Neanderthals could imitate Upper Paleolithic/Cro-Magnon neighbors. But if Upper Paleolithic technology allowed more effective use of natural resources and larger human populations, it is puzzling that Neanderthals failed to adopt it more widely. If they had done so, then their unique skeletal traits and genes would be more obvious in succeeding populations.

Cognition and Neanderthal Extinction

Except for the French site just cited, there is little to suggest that Neanderthals could behave in a modern, Upper Paleolithic way. This inability may explain why they disappeared so quickly and completely. However, Neanderthal brains were no smaller than those of modern humans. If there was a difference in brain function, it resided in soft tissue that cannot be inferred from empty skulls. Hence, neither archaeology nor fossils can reveal Neanderthal cognitive capacity.

This issue is important not only for illuminating Neanderthal disappearance. Fossils show that between 130,000 and 50,000 years ago, the African contemporaries of the Neanderthals were more modern in anatomy, but archaeology suggests that they closely resembled the Neanderthals in behavior.⁴ A change in brain function about 50,000 years ago could explain why modern Africans subsequently expanded to Eurasia.

The discovery that FOXP2, a gene involved in speech and language, achieved its modern sequence less than 200,000 years ago¹⁵ provides tentative support for such a change in brain function. A truly persuasive case may depend on the isolation of genes that are expressed differently in the brains of apes and people.¹⁶ Many human gene variants will turn out to be very ancient, but if there was a brain change around 50,000 years ago, one or

more variants should coalesce to about this time. Fossil bones could provide a further test, now that some have been shown to retain organic compounds that bear on brain function.¹⁷

The longest continuous debate in paleoanthropology is nearing resolution. Modern humans replaced the Neanderthals with little or no gene exchange. Almost certainly, the Neanderthals succumbed because they wielded culture less effectively. The main question that remains open is whether Neanderthal genes explain their failure to compete culturally.

References

1. E. Trinkaus, P. Shipman, *The Neandertals: Changing the Image of Mankind* (Knopf, New York, 1993).
2. P. A. Mellars, *The Neanderthal Legacy: An Archaeological Perspective from Western Europe* (Princeton Univ. Press, Princeton, NJ, 1996).
3. J. L. Bischoff et al., *J. Archaeol. Sci.* **30**, 275 (2003).
4. R. G. Klein, *The Human Career: Human Biological and Cultural Origins* (Univ. of Chicago Press, Chicago, ed. 2, 1999).
5. M. Ingman, H. Kaessmann, S. Pääbo, U. Gyllensten, *Nature* **408**, 708 (2000).

Article 35. Whither the Neanderthals?

6. P. A. Underhill et al., *Nature Genet.* **26**, 358 (2000).
7. M. Hofreiter, D. Serre, H. N. Poinar, M. Kuch, S. Pääbo, *Nature Rev. Genet.* **2**, 353 (2001).
8. A. R. Templeton, *Nature* **416**, 45 (2002).
9. A. P. Santa Luca, *J. Hum. Evol.* **7**, 619 (1978).
10. J.-J. Hublin, F. Spoor, M. Braun, F. Zonneveld, *Nature* **381**, 224 (1996).
11. I. V. Ovchinnikov et al., *Nature* **404**, 490 (2000).
12. F. H. Smith, E. Trinkaus, P. B. Pettitt, I. Karanovic, M. Paunovic, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 12281 (1999).
13. J.-J. Hublin et al., *C. R. Acad. Sci. Paris Ser. IIA* **321**, 931 (1995).
14. C. Duarte et al., *Proc. Natl. Acad. Sci. U.S.A.* **96**, 7604 (1999).
15. W. Enard et al., *Nature* **418**, 869 (2002).
16. W. Enard et al., *Science* **296**, 340 (2002).
17. H.-H. Chou et al., *Proc. Natl. Acad. Sci. U.S.A.* **99**, 11736 (2002).

RICHARD G. KLEIN is with the Program in Human Biology, Stanford University, Stanford, CA 94305, USA. E-mail: rklein@stanford.edu

From *Science*, March 7, 2003, pp. 1525–1527. Copyright © 2003 by American Association for the Advancement of Science. Reproduced with permission from AAAS.
www.sciencemag.org