

Commentary

Hominids and hybrids: The place of Neanderthals in human evolution

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As the first extinct human relatives to have become known to science, the Neanderthals have assumed an almost iconic significance in human evolutionary studies: a significance that has, of course, been greatly enhanced by the very substantial fossil and behavioral record that has accumulated since the original Feldhofer Cave skullcap and partial skeleton were accidentally uncovered, on a pre-Darwinian August day in 1856, by lime miners working in Germany's Neander Valley (1–3). Yet even now, 14 long decades later, paleoanthropological attitudes toward the Neanderthals remain profoundly equivocal. Thus, although many students of human evolution have lately begun to look favorably on the view that these distinctive hominids merit species recognition in their own right as *Homo neanderthalensis* (e.g., refs. 4 and 5), at least as many still regard them as no more than a strange variant of our own species, *Homo sapiens* (6, 7). This difference represents far more than a simple matter of taxonomic hair-splitting. For, as members of a distinct species, of a completely individuated historical entity, the Neanderthals demand that we analyze and understand them on their own terms. In contrast, if we see them as mere subspecific variants of ourselves, we are almost obliged to dismiss the Neanderthals as little more than an evolutionary epiphenomenon, a minor and ephemeral appendage to the history of *Homo sapiens*.

Any new information bearing on this matter is therefore extremely welcome, and there is no doubt that the claims advanced in this issue of the *Proceedings* by Duarte *et al.* (8) will be closely scrutinized by their colleagues. Briefly, Duarte *et al.* propose that the skeleton of a 4-year-old child, recently unearthed at the 24,500-year-old (24.5 kyr-old) site of Lagar Velho in Portugal, represents not merely a casual result of a Neanderthal/modern human mating, but rather is the product of several millennia of hybridization among members of the resident Neanderthal population and the invading *Homo sapiens*. Species (especially extinct ones) are often tricky to identify in practice, and speciation, the process (or more probably, assortment of processes) by which new species come about, is poorly understood. But by anyone's reckoning, long-term hybridization of this kind would indicate that the two populations belonged to the same species. So, if Duarte *et al.* are right, the case is closed: Neanderthals were indeed no more than an odd form of *Homo sapiens*. But is this claim reasonable on the basis of the evidence presented? To clarify this, some background follows.

"The Neanderthals" is the informal designation of a morphologically distinctive group of large-brained hominids who inhabited Europe and western Asia between ≈ 200 and less than 30 kyr ago (1, 2). They are sharply distinguished from modern humans by a wide range of cranial and postcranial characters (1–2, 4, 9–10), although they do share a number of derived bony features with other members of the endemic European/western Asian hominid clade that diversified in this part of the world after ≈ 500 kyr ago (10). Subsequent to ≈ 150 kyr ago, the Neanderthals appear to have been the sole surviving species of this clade. Given the strong degree of

Neanderthal apomorphy (anatomical uniqueness), it is unsurprising that the remarkable recent sequencing of a short stretch of mtDNA isolated from the Feldhofer individual revealed this specimen to be a distant outlier when compared with all modern human populations (11).

The Neanderthals were highly successful over a large region for a substantial period of time, but this situation changed dramatically with the arrival in Europe of the first modern humans, *Homo sapiens*. Indications are that these "Cro-Magnons" had begun to arrive both in eastern Europe (12) and in the far northeast of the Iberian Peninsula (13) by ≈ 40 kyr ago; and within little more than 10 kyr, the Neanderthals were gone. The mechanism of their eviction has long been debated, but there are four main possibilities (14). The first and second of these, that the Neanderthals were eliminated by the moderns in direct conflict or by indirect economic competition, both imply the separate species status of the former, as does any combination of the two. The alternatives, that the Neanderthals had simply evolved rapidly into moderns or that the genes of the invading moderns simply "swamped" those of the Neanderthals, both imply some form of species continuity.

Claims for evidence of "transition" between Neanderthals and moderns, based on supposedly "intermediate" fossils dating from a short window of time around 40–30 kyr ago (15), have been refuted by the recognition that the fossils concerned are either typically Neanderthal or modern (10) and, in one significant case, had been misdated (16). Supporters of the continuity argument have thus tended lately to the view that the disappearance of Neanderthal morphology was due to extensive interbreeding between the Neanderthals and the incoming Cro-Magnons, who invaded in sufficient numbers to dominate the hybrid gene pool and thus the resulting phenotypes (7, 17). The problem has been, though, that nobody has had any idea what a Neanderthal/modern hybrid might look like in theory, and few have dared to suggest in practice that any particular known fossil represents such a hybrid. The Duarte *et al.* claim for the Lagar Velho skeleton is the closest anyone has recently come to such a contention, hence the intense interest that it seems sure to arouse.

The potential significance of the Lagar Velho claim is enhanced by the burial's Iberian location, because it seems that it was in this peninsular extension of Europe that the Neanderthals lingered longest. Outside Iberia, the latest Neanderthals, and survivals of their "Mousterian" culture, are significantly more than 30 kyr old. At the southern Spanish site of Zafarraya, however, the Mousterian may have lasted to ≈ 27 kyr ago (18) and is associated with typical Neanderthal remains at probably not much more than 30 kyr ago. Even more telling, isolated but reasonably diagnostic fossil teeth suggest that Neanderthals were living at the Portuguese cave sites of Salemas, Columbeira, and Figueira Brava at ≈ 29 –30 kyr ago (19, 20). For whatever reasons, the Neanderthals' last redoubt thus seems to have been in Iberia south and west of the Ebro. It is relevant here that while in certain other regions, Nean-

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FIG. 1. Mandible of recent 2–3 year old *Homo sapiens* (American Museum of Natural History, uncatalogued) illustrating the essential features of the symphyseal region. (*Upper*) Anterior view showing the central keel, which broadens at the mental tuberosity, fans out inferiorly, and terminates bilaterally in blunt “corners.” (*Lower*) Inferior view showing the marked thickness of the mandible in the symphyseal region compared to the corpus behind it and the contribution of the marginal attributes of the mental tuberosity to mandibular shape. Not to scale.

derthals of the 36–33 kyr period appear to have acquired some of the Cro-Magnons’ behavioral attributes by acculturation (21, 22), there is no evidence for this beyond the “Ebro line,” where—as in most other places—abrupt cultural replacement appears to have been the rule.

Nonetheless, if a claim is to be made that any 24.5-kyr-old fossil individual represents a Neanderthal/modern hybrid, the obvious place to try it is in Iberia, and especially in Portugal, where the time gap between this individual and the last plausible occurrence of Neanderthals may be as little as 2–3 millennia. In the larger scheme of things this is hardly an eon, but it is still probably around 200 generations—a long time in genetics. This is presumably why Duarte *et al.* refrain from identifying the Lagar Velho child as a 50:50 Neanderthal/modern hybrid; but by claiming that it is instead the product of a population that had been hybridizing for many centuries, they pose problems for themselves in analyzing it in terms of Neanderthal vs. Cro-Magnon traits. After so many generations, genetic introgression would necessarily have proceeded so far that dichotomous characterization of phenotypic traits



FIG. 2. Mandible of 3–4 year old Neanderthal from Roc de Marsal, France (Musé National de Préhistoire, Les Eyzies). (*Upper*) Oblique view of essentially featureless front of mandible, which is vertical yet also broad and somewhat arcuate from side to side. (*Lower*) Inferior view illustrating how uniformly thinner the symphyseal region is buccolingually compared to the bone farther back along the corpus. Not to scale.

would be implausible even in principle. The expected distribution of traits in hybrids that Duarte *et al.* discuss is that to be found in F₁ or F₂ hybrids, not 200 generations down the line.

Still, the claim of mixed ancestry for the Lagar Velho child ultimately rests on the morphology of the specimen. How does this hold up? Duarte *et al.* begin with the skull, represented by a temporal fragment and a partial lower jaw. In describing the temporal bone, they remark that the mastoid and juxtamastoid eminences project basally to an approximately equal extent—a characteristic they claim to be intermediate between Neanderthals and moderns. However, this is a variable feature among Neanderthals (10), and, more importantly, the individual was 4 years old and thus was developmentally only at the point at which the mastoid process begins to expand significantly downward among modern humans (23). Almost certainly, as an adult this individual would have shown the typical modern conformation of the region, with a projecting mastoid process. There appears to have been no horizontal suture running beyond the parietal notch, as is found even in young Neanderthals. And, regrettably, no information is provided on the internal aspect of the petrosal, which would be highly informative.

Although damaged, the mandible conforms anteriorly precisely to the highly characteristic “inverted-T” conformation we have recently described for *Homo sapiens* (24), and the relative thickness of the mandible across the symphysis in inferior view is also typical for our species (24, 25), as are the mental fossae (compare Figs. 1 and 2). The angulation of the subincisal region is variable among both Neanderthals and moderns and does not argue here for Neanderthal influence. As described, the mandible lacks any sign of the internal

pterygoid tubercle invariably present even in very young Neanderthals (26) or of the lingula on the mandibular foramen typical of this species. In contrast, the anteriorly positioned mental foramen and the symmetrical sigmoid notch are typical of modern humans (27).

Duarte *et al.* restrict their comments on the teeth of the Lagar Velho child to their size, which reveals nothing remarkable. However, there are consistent differences in morphology that distinguish Neanderthal from modern molars, deciduous included. In the Lagar Velho individual, illustrations seen show an apomorphically *Homo sapiens* morphology of the M₁ and dm₁. Both of these teeth lack the distinct talonid basins and the closed trigonids, ringed by compressed and internally placed cusps, that are so typical of the Neanderthals. Furthermore, they are typically modern in showing root divergence close to the crown. All in all, there is nothing about the craniodental elements thus far known and described that would be unusual for a *Homo sapiens* at this young developmental stage.

Much of Duarte *et al.*'s argument for mixed descent of the Lagar Velho child depends on inferred limb proportions in the immature postcranial skeleton. However, as Holliday (28) has recently demonstrated, limb indices are unreliable population discriminators in the late Pleistocene. And while Duarte *et al.* have demonstrated that the Lagar Velho child was quite heavily built, it is likely that most paleoanthropologists will require evidence of specific morphologies that point in this direction before accepting that the specimen displays evidence of Neanderthal admixture. And the morphological evidence presented is very thin. Thus, the length of the pubic ramus, a classic archaic/modern discriminator, falls within the modern range (8), and the symphysis itself is not plate-like as it is in Neanderthals. The morphology of the radius is that of a modern human with a fairly anteromedially oriented tuberosity. This bone does not show the shaft curvature, the large tuberosity, and the long, thin neck characteristic of Neanderthal radii. And the tibia, like the femur, is hard to evaluate in the absence of the epiphyses; it does not appear significantly different from what one might expect to find in a robust modern human of this age.

In summary, the analysis by Duarte *et al.* of the Lagar Velho child's skeleton is a brave and imaginative interpretation, of which it is unlikely that a majority of paleoanthropologists will consider proven. The archaeological context of Lagar Velho is that of a typical Gravettian burial, with no sign of Mousterian cultural influence, and the specimen itself lacks not only derived Neanderthal characters but any suggestion of Neanderthal morphology. The probability must thus remain that this is simply a chunky Gravettian child, a descendant of the modern invaders who had evicted the Neanderthals from Iberia several millennia earlier. However, in this contentious and poorly documented field, any new data are eagerly sought, and Duarte *et al.*'s courageous speculations will doubtless spur much-needed new research.

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