ARE NEANDERTHAL PORTRAITS WRONG?
NEANDERTHAL ADAPTATIONS TO COLD AND THEIR IMPACT ON PALAEOLITHIC POPULATIONS

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Abstract. On the basis of comparisons between the relative thickness of the walls of Neanderthal limb bones to those of the average modern human and the observation that bone mass increases as modern individuals add weight, this thought-piece proposes redefinitions of the appearance of cold-weather Neanderthals based on two biological adaptations to glacial climate. It suggests related biological and technological mechanisms for explaining the paucity of genetic or fossil evidence for extensive hybridisation between both early and recent Homo sapiens sapiens (‘Moderns’), on the one hand, and northern and western ‘classic’ Neanderthals, on the other. Its ‘insulation hypothesis’ includes an explanation of why a population resulting from an admixture of Neanderthals and anatomically modern humans may have been constrained to the Levant between at least c. 120–92 ka bp (H. sapiens sapiens at Skhul and Qafzeh) and c. 45 ka (H. sapiens sapiens at Geula). It goes on to propose reasons for the replacement of the classic Neanderthal suite of features after H. sapiens sapiens and at least some Neanderthals began showing modern behavioural adaptations and encountered one another as Moderns spread into or developed in western Eurasia during the initial Upper Palaeolithic.

Introduction

As readers of this journal know, a controversy has raged between two schools of thought over the transition between robust archaic Homo sapiens and ever more gracile ‘Moderns’. Did still robust early ‘Moderns’ completely supplant or at least genetically swamp even more robust archaic humans such as Neanderthals, as supporters of various forms of the Out-of-Africa hypothesis contend? Or do signs of increasing gracility in the fossil record show that Neanderthals evolved into modern Caucasians as the result of genetic drift in small populations and culturally influenced sexual selection? Robert Bednarik’s recent discussion of the implications of a footprint with apparent Neanderthaloid traits in the Chauvet Cave (Bednarik 2007) highlights the subject’s relevance to a rock art journal, since it relates to the authorship of the art of Chauvet. The possible adaptations to cold among Neanderthals in the northern and colder parts of their range, which I will lay out below, may fit with either school’s thinking concerning the transition. But the consequences of such adaptations in terms of sexual selection will take different routes based on which school is correct — or if the truth lies somewhere in between — and may ultimately influence our perception of the creators of the oldest cave art found to date in Europe.

* In his summation of evidence from Tabun, Skhul, Qafzeh and Geula, B. Arensburg noted that

[...] the Middle Palaeolithic human remains discovered in Israel disclose great morphological differences between European Neanderthals and the so-called Levantine Neanderthals. It has been, then, quite difficult to incorporate both groups into a single, homogeneous group. Conversely, the skeletal variance among all the Levantine Middle Palaeolithic fossils could hardly justify their segregation into two different populations (Arensburg 2002).

The morphological distinctions between western and northern Neanderthals, on the one hand, and the Middle Eastern population(s), on the other, was probably similar to the way skin colour changes with latitude in modern humans, but, instead of reflecting adaptations to different amounts of exposure to sunlight, they would have been due to temperature differences between glacially affected regions and the relatively more clement Middle East.

An un-answered riddle may be lurking in the limb bones of Neanderthals from the colder parts of their
range. As Robert Bednarik also noted, ‘[a]natomically, Neanderthals were very similar to modern humans, except that they were far more robust ... There were considerable differences among them, those of the later period in western Europe being typically more robust than others’ (Bednarik 2006). The bones are generally shorter than their equivalents from recent ‘Moderns’, but more robust both in overall thickness or diameter and in cross-section, where the thickness of the walls of the shafts is clearly greater than modern equivalents.

In *The Neandertals — of skeletons, scientists and scandal*, the authors mention how Trinkaus’s firsthand examination of the fossils, especially those from La Chapelle-aux-Saints and La Ferrassie in the Musée de l’Homme in Paris, had impressed upon him how massive and robust Neandertal legs and feet were. Nothing in the literature had prepared him for what he saw (Trinkaus and Shipman 1993: 367).

On the basis of a cross-sectional analysis of the Saint-Césaire 1 partial skeleton’s femoral diaphysis (shaft) at the subtrochanteric and midshaft levels, Trinkaus and his colleagues would later conclude that ‘the overall robustnesses of the femoral diaphyses of European Neandertals and early modern humans are similar once contrasts in body proportions are incorporated into the body size scaling’. But, then, they went on to say that

Saint-Césaire 1 matches these samples only if it is provided with Neandertal-like hyperarctic body proportions. And the rounded proximal femoral diaphysis of Saint-Césaire 1 is similar to those of earlier Neandertals, likely ... reflecting similar cold-adapted broad pelvic regions (my italics).

Interestingly, the observers also concluded that the Châtelperonian

Saint-Césaire 1 femoral midshaft exhibits the anteroposterior reinforcement characteristic of early modern humans. Consequently, Saint-Césaire 1 appears as a morphological Neandertal with hyperarctic body proportions who nonetheless had shifted locomotor patterns to more closely resemble those of other Upper Paleolithic humans (Trinkaus et al. 1998).

This change is fully in keeping with the technological and cultural shifts indicated by the accompanying Châtelperonian assemblage.

Other studies have concluded that Neanderthals were far more adapted to cold than Eskimos (Holliday and Ruff 1997; Holliday 1997a, 1997b), stating, for example, that ‘it appears that European Neandertals were “hyperpolar” in body shape, likely due to two factors: 1) the extremely cold temperatures of glacial Europe and 2) less effective cultural buffering against cold stress’ (Holliday 1997a).

Despite the recognition of these studies that any similarity drawn with early modern humans depended on fleshing out Neanderthals with ‘hyperarctic body proportions’, many theorists continued to assume that the relative thickness of such Neanderthal bone walls, as opposed to ours, was linked solely to Neanderthal brawn and the need to support the mechanical stress of their greater musculature relative to the average modern Homo sapiens sapiens. Based on this paradigm, it has also been assumed that muscular Neanderthals compensated for technological inadequacies by comparison to the Cro-Magnon ‘Moderns’ of the later Upper Palaeolithic by sheer endurance and brute force — bounding after their prey (Gibbons 1996; Lieberman 1997). Broken but healed Neanderthal bones have been seen as signs of frequent accidents due to such heightened activity.

But the greater robustness of Neanderthal skeletons relative to ours may not be entirely due to the need to withstand the stress and carry the weight of more muscle than the average ‘Modern’ — it could also
partially have been a hyperarctic adaptation to support the extra weight of a layer of insulating fat. Skeletons of corpulent people today show how bone-mass increases as a person becomes fatter to support the stress of extra weight. Although thicker bone walls and greater bone density would probably have been largely inherited by Neanderthals — rather than just being the kind of mechanical reaction seen to modern obesity — such traits may have provided the reinforcement required both by the extra weight of a fatty layer and strong musculature. If so, Neanderthal insulation was almost certainly an adaptation to glacial periods.

When Charles Darwin and Captain Robert Fitz Roy sailed through the Beagle Strait in Tierra del Fuego, Darwin was shocked to see that the Fuegians were naked in falling snow. Lightly clad or naked mothers were seen nursing equally naked babies amid icebergs:

... a woman, who was suckling a recently-born child, came one day alongside the vessel, and remained there ... whilst the sleet fell and thawed on her naked bosom, and on the skin of her naked baby!

... the women either dive to collect sea-eggs, or sit patiently in their canoes ... with a baited hair-line' (Darwin 1839).

Female Fuegians, who were the only members of the population who actually swam in the frigid waters according to E. Lucas Bridges, were also unusually plump by Native American standards. ‘The Yahgan women’, he wrote, ‘were short and fat’ and ‘were always good swimmers, but it was a very rare thing to find a male Yahgan who could swim’. Girls ‘learned to swim in infancy, and were taken out by their mothers in order to get used to it. In winter, when the kelp leaves were coated with a film of frost, a baby girl out with her mother would sometimes make pick-a-back swimming difficult by climbing onto her parent’s head to escape the cold water and frozen kelp’ (Bridges 1948: 62–64). Despite this evidence of habituation, a woman’s ability to spend a lifetime naked in frigid water and weather was probably based largely on biological adaptations. The layer of subcutaneous insulating fat which made Yahgan women plump was both thicker and more evenly distributed than the equivalent layer in indigenous women to the north and than it probably had been in their ancestors when they passed through those warm latitudes on their way to Tierra del Fuego where the ‘earliest human colonization occurred ... c. 11 ka bp, in tundra-like environmental conditions’ (Rabassa et al. 2000).

The fact that pre-Columbian Americans with the darkest skins lived exclusively in the equatorial regions provides another example of how quickly skin chemistry and structures become adapted to local conditions, since Amazonian Indians shared the same Palaeolithic ancestry as the lighter-skinned Native Americans living to the north and south. Their common ancestors, who had crossed northern areas to reach the Americas, would almost certainly have been relatively light-skinned. Yet the exigencies of living under tropical sunlight were able to reverse previous adaptations to the reduced light of northern latitudes in just a few millennia.

Whether (and if) the last common ancestor of classic cold-weather Neanderthals and Moderns existed around:

• 465 000 to 600 000 years ago, as Disotell proposed on the basis of phylogenetic analysis of Neanderthal mitochondrial DNA (Disotell 1999), or
• between 365 000 and 853 000 years ago (Ovchinnikov et al. 2000), or
• around 465 000 bp with confidence limits of 317 000 and 741 000 (Krings et al. 1999), or,
• in the most recent and exhaustive studies of nuclear genes, between ‘1015 and 465 kiloyears (k yr)’ with confidence levels of 95% (Foley and Mirazón Lahr 2007), with averages of 516 kyr (Green et al. 2006) and 706 kyr (Noonan et al. 2006) being calculated for this event,

then the Neanderthal line underwent as many as four ice ages — the Günz, Mindel, Riss and Würm. The
And, indeed, Neanderthals seem to have left such evidence at Arcy-sur-Cure (d’Errico et al. 2000, 2001), where the Châtelperronian assemblage includes a plethora of awls. But before that, the evidence for manufacture of weather-tight apparel grows desperately thin. Heavy wear on Neanderthal front teeth certainly suggests that Neanderthals were processing hides by using their teeth as a grip to hold them taut while scraping them clean, but, without being pieced and sewn together, skins alone can only be loosely bound around the body if one is to remain manoeuvrable.

If one accepts that the differentiation of human head and body lice around 107 000 years ago indicates that clothing, which would have provided an independent habitat for body lice, was first used consistently only shortly before that time (Kittler et al. 2003, 2004), then one must assume that Neanderthals may have relied on some other means of insulation until then — if not largely afterwards as well. Ian Tattersall was doubtful of the premise linking the split between lice species to the origins of clothing because it seemed to him that Neanderthals could not have survived cold climates for over 100 000 years before the split without apparel (Travis 2003). But if cold-weather Neanderthals had developed biological insulators, they would not have needed weather-tight garments to survive in their normal range. As a corollary, they may not have had as many incentives to adopt or perfect clothing, even when they had the technology and functionally hairless ‘Moderns’ began competing with them in colder areas.

If their adaptations were as much biological as cultural, both male and female Neanderthals probably developed far thicker or more effective layers of subcutaneous insulation over successive ice ages than the female Moderns of Tierra del Fuego. Unlike Homo sapiens sapiens San women, who often have the capacity to store fat locally in their buttocks as a buffer against starvation while maintaining their overall sleekness for the rapid ventilation of excess heat in a desert environment, Neanderthals would have acquired more generalised fat both as a (seasonal) covering insulator and storage organ.

* But that probably was not their most surprising adaptation. During the heyday of freak shows, people with entirely furry faces and bodies due to a congenital hormonal condition called hypertrichosis were often exhibited. Pedro Gonsalvo was one of the first individuals with hypertrichosis to enter the historical record. In 1557, just a year after he was born in the Canary Islands, he was presented at the court of Henri II of France. Pedro later fathered three hairy children of his own who were also exhibited in European courts and examined by such savants as Aldrovandi. One of these children, Tonetta Gonsalvo, was even painted around 1583 by Lavinia Fontana. Other individuals...
who have exhibited this trait, which is rare but falls within the genetic range of fully functional humans, have been Julia Pastrana in the 1800s and Fedor Jef- tichew, who was known variously as Jo-Jo, The Dog-Faced Boy, and the Russian Wolf Man.

Whether the common ancestor of Neanderthals and modern humans was Homo antecessor or another closely related hominin, that ancestor probably had functionally naked skin as an adaptation to loping after prey in warm climates, where a cooling mechanism was required to offset heat generated by the chase — a role fulfilled in modern humans and probably most ancient hominins descended from Homo ergaster by evaporated sweat. But the ancestor probably had at least as much of a latent potential in its genome for a hairy body and face as modern humans. Over the hundreds of thousands of years after the apparent split that led to Neanderthals and Homo sapiens sapiens, descendants in the Neanderthal lineage who had more body or facial hair during a succession of Eurasian ice ages would have had a greater chance to survive to reproductive age. Although fat makes a good insulator — especially for large warm-blooded mammals in water — many mammals who must survive cold air as well as cold water — such as the fur seal — adapt by acquiring both thicker subcutaneous fat and fur.

Cold-weather Neanderthals probably did the same — within limits, since too much subcutaneous fat would have made them inefficient at hunting and avoiding dangerous animals. For example, Neanderthals would never have required the same degree of fat as seals, whose blubber sags out of water, making them highly vulnerable to terrestrial predators. Instead, Neanderthals probably would have evolved the most efficient mix of insulators for their climatic conditions, with fur complementing a subcutaneous layer that was just thick enough to give protection in their locale without becoming an encumbrance. Analysis of the Neanderthal genome may soon prove the combination.

* But the evidence of how different mixtures of musculature and fat affect modern bone anatomy may also suggest how the details of Neanderthal fossils were affected by changes in mechanical loading (body weight) as well as inherited traits in various climates. Although both increased weight and greater muscle strength are ‘independently associated with higher bone mass’ (Bauer et al. 1993), musculature and adiposity leave different signatures on modern skeletons (Slemenda et al. 1990, 1994). Unfortunately, these markers are both complex and subject to variables. Not surprisingly, one of the key variables is gender (Reid et al. 1992), making it imperative to sex fossils when trying to translate insights gathered from modern individuals. Among the numerous complexities is the ironic fact that repetitive sports such as ballet and gymnastics actually lower bone density due to increased bone resorption (Muñoz et al. 1996).

Despite the complexities, several analyses either give comfort to an insulation hypothesis or suggest ways to test it. A study on how bones change, with particular focus on the femur in premenopausal women, noted that ‘[i]nitial fat mass was the only measure of body composition that was a significant predictor of the slope of Ward’s triangle’ in the femur, while ‘only fat mass and changes in fat mass were positively associated with total body bone mineral density change. Increases in fat mass were associated with a (small) increase in total body bone mineral density. For each kg of fat added or lost, bone mineral density changed 1 mg/cm²’ (Houtkooper 1995). Another study noted that ‘Femoral bone mineral density increased significantly but not linearly as the fat compartment progressed from the lowest to the highest tertile’ and that femoral bone density increased when ‘higher fat [was] associated with substantial muscle’ (Sowers et al. 1992). Finally, a third study found both that ‘[d]aily activity had no effect on BMD’ (bone mineral density) and that ‘[b]ody weight was a better predictor of BMD than ... any other factor’ (Mazess and Barden 1991). These observations that the body’s fat burden influences its skeleton — with special focus on the femur, Ward’s triangle and total body bone mineral density in Neanderthals — offer several hopes of testing for subcutaneous insulation.

Another study, whose results were not skewed by obese individuals, concluded that ‘[l]arge (skeletal)
frames at the shoulders, arms, and knees are related to carrying large amounts of muscle. Conversely, wide hips and knees are associated with increased amounts of adipose tissue throughout the whole body' (Chumlea et al. 2002). This is particularly telling given robust Neanderthal legs and pelvies and the fact that the cold-weather specimens studied by Markku Niskanen and Juho-Antti Junno were not broad-shouldered (Niskanen and Junno 2004).

Another avenue for future testing may lie in a re-examination of the pronounced muscle attachment sites, which are often cited as proof of the extreme strength of Neanderthals. But a proviso is in order, since ‘the attachment site morphological parameters measured in’ a study carried out by Ann Zumwalt (six limb muscle and one mastication site) ‘do not reflect muscle size or activity. In spite of decades of assumption otherwise, there appears to be no direct causal relationship between muscle size or activity and attachment site morphology, and reconstructions of behaviour based on these features should be viewed with caution’ (Zumwalt 2006). It is also noteworthy that the Skhul/Qafzeh and EUP specimens which Niskanen and Junno otherwise contrasted with cold-weather Neanderthals seemed just as muscular based on their muscle insertions (Niskanen and Junno 2004), so Neanderthals may not have been unusually brawny for the period. Returning to Zumwalt, ‘[a]n individual’s sex, age, hormone levels and genetics may all influence entheseal response to muscle activity ... but the extents of these influences are currently entirely unknown’ (Zumwalt 2006). In other words, one must proceed with caution. All the same, it would be worth determining whether the muscle attachments of muscle-bound athletes differ from those of Rubeneshque ones, in which case resemblances to Neanderthal equivalents might support one hypothesis over another.

Finally, changes in mechanical loading in adults due to either fat or muscle does not affect limb bone anatomy generally but specifically, affecting the diaphyseal (shaft) cross-sectional size, for instance, rather than articular size (Ruff et al. 2005a). As one study puts it, ‘fat and lean mass have independent influences on bone mass, but ... their relative influence may vary by bone site depending on the trabecular content, physical mobility, and muscularity of the site’ (Hla et al. 1996). Equally importantly, bone mineral mass and bone density are greater for the same body mass index (BMI) in some ethnic groups such as Pacific Islanders than others such as Europeans or Asians, showing that a BMI may reflect utterly different skeletal constitutions in lineages which have evolved separately for even a few dozen millennia, let alone hundreds (Rush et al. 2004).

It would therefore be foolhardy to get into the maze of technical considerations covering point-by-point comparisons between modern skeletons of various types of athletic and adipose individuals and the limited set of partial Neanderthal fossils in this initial paper, although osteological analyses (including morphometric mapping of the diaphyses of long bones [Zollikofer and Ponce de Leon 2001] and the avenues I have mentioned above) may offer ways to test its suggestions. Until that study is carried out, though, the evidence of Neanderthals’ thick diaphyseal cross-sections, including Ward’s triangle, and the contrast between their heavily built lower body and low shoulder dimensions both argue for the insulation hypothesis over the prevailing brawny paradigm.

Returning to the question of fat and fur as insulators, while the lineage that led to Neanderthals was adapting to cold conditions, our ancestors were living in Africa’s heat and, if anything, underwent selective pressures to lose further hair except in areas of chafing, sexual signalling and cranial protection from radiation (not to mention the utility, noted by Darwin, of a swimming parent’s mane).

The fact that some of the European skeletons of the last Neanderthals seem to be just as ‘classic’ as ones from 60,000 years before, when Neanderthals first encountered our species, compounded by a perceived shortage of evidence for hybridisation between the two populations, led James Shreeve to theorise in The Neanderthal Peace (Discover Magazine, Sept. 1995) that the Neanderthal lineage evolved such different sexual signals from our own while isolated in western Eurasia by seas, deserts and glaciers that the two populations no longer recognised each other as potential mates when Early Moderns left Africa and encountered Neanderthals in the Middle East around 110,000 years ago. Revising the basis for his hypothesis slightly, I would go further: cold-weather Neanderthals and Moderns apparently did not produce many hybridised offspring despite the fact that the populations probably had two quite different opportunities.

The first would have occurred after so-called anatomically modern humans, represented by fossils from Qafzeh and Skhul, made the incursion into the Middle East 110,000 years ago. Despite Arensburg’s inability to find absolute criteria that would differentiate Levantine Neanderthals from local Middle Paleolithic Moderns (Arensburg 2002), Erik Trinkaus cites ‘[m]ultiple lines of evidence (which) indicate that the Qafzeh and Skhul sample represents a temporary northward expansion of these earliest modern humans into that region, after which they were replaced by Neandertal populations dispersing southward’ (Trinkaus 2007). Whether or not this is true, the first opportunity for producing hybridised offspring seems to have left little imprint, except perhaps in the Middle East.

The second opportunity for extensive hybridisation probably took place after the M168T mutation (which is exhibited on Y-chromosomes by all non-African males but only a few Africans) occurred between 35,000 and 89,000 years ago (Ke et al. 2001; Underhill...
et al. 2000) — long after anatomically modern humans first appeared and then perhaps disappeared from the Levant. A second dispersal of African Moderns — carrying the mutation — would have led to an entirely new opportunity for hybridisation between early Moderns and Neanderthals.

Shreeve accurately noted that ‘[t]he human mate-recognition system is overwhelmingly visual’, but then concluded that Neanderthals and Moderns failed to ‘hybridise’ because they used different facial expressions to show sexual readiness. ‘Faces are exquisitely expressive instruments’, he wrote.

By one estimate, the 22 expressive muscles on each side of the face can be called on to produce 10 000 different facial actions or expressions ... Among this armoury of social signals are stereotyped, formal invitations to potential mates. The mating display we call flirtation plays the same on the face of a New Guinean tribeswoman and a lycéenne in a Parisian café ... But the underlying message is communicated by the anatomy of the face itself.

Shreeve’s (1995) suggestion is provocative. As we will see, visual cues may indeed explain the failure of cold-weather Neanderthals and Moderns to mix significantly during the periods when they overlapped. But not in the way Shreeve suggests. The impersonality of some human sexuality, which includes such cruelties as rape and expressions about having sex with a woman ‘with a bag over her head’, contradicts the notion that the two populations ignored each other because they were indifferent to each other’s facial means for inviting intercourse. The same occasional impersonality contradicts the idea that mere differences in chins and brows and other facial structures would have kept Neanderthals and Moderns apart.

But if European Neanderthals were furry from head to toe whereas Homo sapiens sapiens were functionally naked of fur, then the differences in visual cues over the entire body would have been overwhelming and could indeed account for the failure to mix significantly. After all, clinical studies and widespread therapy for modern women who have either ‘excess’ body or facial hair suggests that even moderate hairiness is a huge handicap for women of our lineage seeking mates.

So imagine the reaction of early Moderns coming out of Africa around 110 000 years ago with nearly bald bodies and faces when they met plump furry bipeds: Neanderthals. Despite the fact that both lineages shared the same Mousterian technology and well-developed hyoid bones which suggests that they both had some ability to speak, the early Moderns might have classified the Neanderthals they met in the Middle East as utterly different from themselves.

Or not. Arensburg’s opinion that distinctions between Middle Palaeolithic Levantine fossils do not warrant their segregation into separate populations begs the question of whether those fossils reflect a transitional population. The appearance of Neanderthals most adapted to cold and the quite different appearance of Moderns issuing from the south may have reduced the frequency of mating between the two populations. But Levantine Neanderthals probably did not exhibit cold weather adaptations to the same degree as their brethren to the north and west, so the impediments to mating between them and Early Modern immigrants from Africa would not have been nearly as strong.

But, then, why did not any resulting hybridisation of the Levantine population with its trademark gracileisation spread quickly across Europe until the end of the Middle Palaeolithic, some 60 000 years later? Probably because the means for making weather-tight clothing were not available until the Mousterian gave way to more laminar, microlithic and bone-based technologies — at which point a person with functionally naked skin might have enjoyed advantages over a naturally insulated individual even in frigid conditions. Just being able to add, subtract, loosen or tighten layers would have given a person relying on technology for warmth considerably more flexibility and efficiency than one who could not shed insulation, putting individuals exhibiting classic Neanderthal traits suddenly at a disadvantage.

So whether there were one or two distinct Levantine populations, gracile individuals would have been limited to warmer climates until they could make up for the lack of natural insulation by making artificial insulators that were just as protective. But once Mousterian technologies did give way to ones which exploited bone, antler and ivory more commonly and effectively, while also extending the amount of cutting edge which could be extracted from a given stone, the dispersal of gracile traits would have shot up for a second reason. Not only could gracile individuals now make more protective clothing and compete with biologically insulated humans in cold climates, but they could travel much farther from stone sources, thereby increasing the potential for mating over larger ranges.

Since neither advanced clothing manufacture nor higher mobility away from lithic sources were in place for the replacement of cold-weather Neanderthal traits while early Moderns and Levantine Neanderthals shared Mousterian technology in the Middle East (or represented extremes of a localised transitional population), the question shifts to the end of the Neanderthal era. As both western Asian Moderns and Neanderthals developed or acquired Upper Palaeolithic technologies, individuals with increasingly gracile ‘Modern’ traits start to appear in the colder northern and western parts of Neanderthal territory, suggesting their expansion.

Several important genetic events apparently affected our lineage, back in Africa, during the interval. First is the fact that the root of all human Y-chromosomes has been clocked to approximately 59 000 years ago (within a possible range of 40 ka – 140 ka \( \text{yr} \)) (Thomson et al. 2000). Second was the
previously cited mutation on the Y-chromosome (M168T) shared by all non-African populations and a few Africans. ‘To test the hypotheses of modern human origin in east Asia,’ Ke et al. ‘sampled 12127 male individuals from 163 populations and typed for three Y-chromosome biallelic markers (YAP, M89 and M130). All the individuals carried a mutation at one of the three sites. These three mutations (YAP+, M89T, and M130T) coalesce to another mutation (M168T), which originated in Africa about 35000 to 89000 years ago. Therefore’, the team concluded, ‘the data do not support even a minimal in situ hominid contribution in the origin of anatomically modern humans in East Asia’ (Ke et al. 2001). The fact that 89000 yr is also much more recent than the first presence of anatomically modern humans in the Levant is a further reason to suspect that the first Levantine Moderns were not the source of the expansion of Moderns throughout the Eastern Hemisphere around 55000 years ago.

When this article was first submitted, two unique mutations of the FoxP2 gene (caused by nucleotide substitutions at positions 911 and 977 of exon 7) that permit rapid and precise movements of the tongue and lower face and affect the Broca and Wernicke speech areas of the brain were thought to have swept the human population within the last 200 millennia (Enard et al. 2002). If the common ancestor of Moderns and Neanderthals had lived earlier, then Neanderthals might not have been able to speak as well as Moderns, unless they had benefited from independent adaptations. But a recent study of DNA from two Spanish Neanderthals indicates that they had precisely the same mutations as Moderns (Krause et al. 2007). So replacement theories based on communication or mental advantages of one type of human over the other are still baseless or unproven.

Whether or not one type had such advantages, just as humans classify bonobos or chimps as ‘animals’ largely because of their fur, despite their considerable physical and behavioural resemblance to ourselves, once Moderns had the tool kit to survive extreme cold and expanded into the range of the cold-weather Neanderthals, as opposed to just the Levant, they would probably have dismissed such Neanderthals as animals not unlike bears, regardless of their ability to use the same tools and, probably, speak. Sexually, neither of the two lineages would have been attracted to the other because the visual cues for attractiveness were wrong from top to bottom.

That being said, late Middle Palaeolithic and early Upper Palaeolithic human fossils from across Europe often exhibit a mixture of archaic and modern traits, including residual robustness in early ‘Moderns’ (Bednarik 2007) that reminds one of the mixed evidence from earlier in the Middle East. But do these fossils from the period embracing encounters between Moderns and cold-weather Neanderthals demonstrate (a) complete population replacement; (b) a natural if rapid progression from a Neanderthaloid set of features to a modern array of traits under the sudden influence of new clothing technology, the advent of culture as a force in determining and amplifying the criteria of sexual selection, and the relentless pruning of genetic drift; or (c) population replacement of cold-weather Neanderthals by Moderns with a slight admixture of Neanderthal features?

On the one hand, some specimens ascribed to Neanderthals show some modern features (La Quina 9) (Stefan and Trinkaus 1998), while the few fossils of ‘Moderns’ which are still temporally secured through direct dating and/or meticulous excavation to the Aurignacian such as specimens from Mladěč (Wolpoff et al. 2000, 2006; Wild et al. 2005; Frayer et al. 2006; Minugh-Purvis et al. 2006; Trinkaus et al. 2006), Les Rois (Vallois 1958a, 1958b; Trinkaus et al. 2003), Oase from Peštera cu Oase (Trinkaus et al. 2003; Rougier 2007), Peštera Muierii, Romania (Soficaru et al. 2006), Cioclovina (Soficaru et al. 2007), Brassempouy (Henry-Gambier et al. 2004), and La Quina Aval (Martin 1936 and, for all the above, Trinkaus 2007) often exhibit archaic features including heavy tori in males, occipital buns, and signs of residual robustness. Although many of these features can be interpreted as deriving from African later archaic and early modern humans, they have also been seen as falling between those exhibited by northern Middle Palaeolithic Neanderthals and Gravettian Cro-Magnons.

In a communication with the author echoing his on-line article, ‘Beads and the origins of symbolism’, Robert Bednarik pointed out that ‘[t]here are in fact literally dozens of specimens that are intermediate between Robusts (such as Neanderthals) and Graciles, e.g. Lagar Velho, Crete, Drigge, Starosel’e, Rozhok, Akhshtyr’, Romankovo, Samara, Sungir’, Podkumok, Khyalynsk, Skhodnya, as well as Chinese remains such as those from Jinniushan. Stringer et al.’s complete separation is fundamentally false, and the Portuguese specimen’, found at Abrigo do Lagar Velho (Zilhão 2000, 2001), ‘is not even particularly convincing’. Perhaps the human remains from level Gc at Vindija (Wolpoff et al. 1981, Karavanic and Smith 1997) should be added to this list, since they ‘exhibit a Neandertal morphological pattern, albeit with certain features that approach modern human morphology to a greater extent than most other Neandertals’ (Smith et al.1999). Also, despite the dispute concerning the relevance of the Portuguese fossil to this discussion (Dobson and Geelhoed 2001), it should be pointed out that the southern-most European Neanderthals, such as those of the Iberian peninsula, might not have exhibited the proposed cold-weather adaptations to the same degree as their relatives in such places as Arctic Russia — and, for the reasons examined above,
may have had the fewest obstacles for hybridisation with intruding Moderns.

That being said, it is far from certain that all the indicators of gracilisation of some late Neanderthals blend into the robustness and archaism of the first European Moderns. Although biologically insulated Neanderthals would not have been as motivated to produce weather-tight apparel as people who were functionally hairless, clothing could still have caught on as a means of reducing the mortality of children and those with a relative lack of natural insulators. As with jewellery, the adoption of clothing is also likely to have led to its variation and use for signalling status, adding impetus to its use. If cold-weather Neanderthals had even rudimentary clothing and their techniques for making it were improving, as the intensive use of awls in the Châtelperronian assemblage from Arcy-sur-Cure suggests (d’Errico et al. 2001), individuals with less natural insulation may have survived longer, resulting in gracilisation even as western Eurasian Moderns were undergoing independent gracilisation, without either the former population evolving into the latter, or the populations hybridising extensively, if they were separate entities.

In their reconstruction of the body size and shape of Palaeolithic period Europeans, Markku Niskanen and Juho-Antti Junno concluded that ‘[a] shift in body proportions from the Neandertals and the EUP specimens was probably due to a complete or nearly complete population replacement. However, more effective cultural buffering from cold temperature’ — which would have included the ability to make clothing increasingly weatherproof — ‘could have also played a role by relaxing selection pressure to maintain hyperarctic body design’ (Niskanen and Junno 2004, 29–30) demonstrates how such gracilisation of cold-weather Neanderthals and robust but distinct early ‘Moderns’ could easily have occurred simultaneously but separately, creating a mirage of convergence. Differences in dental patterns between fossil individuals hint that this may be largely true. A study by Shara E. Bailey demonstrated that both the specific ‘dental traits (e.g. taurodontism)’ and ‘the overall dental pattern of Neandertals’ are ‘distinctive’. Based on phenetic distance measures, outgroup analysis, and genetic affinity analysis’, she ‘rejected the hypothesis of continuity between Neandertals and modern humans’. Bailey went on to use ‘analyses of Mean Measure of Divergence (MMD) to assess the affinities of 11 populations representing early Anatomically Modern Humans, Upper Paleolithic Europeans, recent modern humans and Neandertals. The 17-trait MMD analysis demonstrated that, dentally, Neandertals are quite divergent from all modern humans. The results suggest two major clusters: Neandertals and modern humans’ as well as two sub-clusters within the modern human cluster. One linked Upper Paleolithic Europeans with recent North Africans and Europeans. The other linked early Anatomically Modern Humans with Late Pleistocene Africans and recent Sub-Saharan Africans. These results did not support either biological continuity or significant admixture between Neandertals and Upper Paleolithic Europeans. However, they did not disprove that some degree of admixture may have occurred (Bailey 2000, 2003).

A mirage of convergence may also be inferred from the fact that when David Serre and his colleagues compared mtDNA from ‘samples considered as anatomically ‘transitional’ between modern humans and Neandertals, such as Vindija and Mladeč’, with the mtDNA ‘from four Neandertal fossils from Germany, Russia, and Croatia’, the samples ‘fail[ed] to show any evidence of mtDNA admixture between the two groups’ (Serre et al. 2004). Equally important, the study showed that all [four] Neandertal remains analyzed yielded mtDNA sequences that are not found in the human mtDNA gene pool today but are similar to those found in four previously published Neandertals (Krigs et al. 1997, Krigs et al. 2000; Ovchinnikov et al. 2000; Schmitz et al.). (Serre et al. 2004)

Earlier, William Goodwin and Igor V. Ovchinnikov had found that Neandertal DNA is different from modern human mtDNA, forming a distinct group. Based on this evidence it is not possible to say whether Neandertals and modern humans did interbreed, however based on the Neanderthal and modern humans analysed to date it is possible to conclude that Neandertals did not pass any of their mtDNA on into the modern European mtDNA pool (Ovchinnikov and Goodwin 2001).

Yet another study, this time of mtDNA drawn from Neanderthals and two human fossils dated at between 23000 and 25000 years old, found that the latter appeared to have genetic sequences fully compatible with the variation observed both in contemporary and in ancient samples of anatomically modern humans, and certainly... do not show any special relationships with the almost contemporary Neandertals (Caramelli et al. 2003).

Even an anatomical study which had found similarities between the features of the Mladeč specimens and ones exhibited by Neanderthals (Wolpoff et al. 2001) and helped spark the search for genetic links between the populations was called into question when a metric study of facial shape in the Mladeč specimens revealed no evidence of Neanderthal affinities... For example, the nasofrontal angles of the Mladeč1, 2, and 5 specimens were found to diverge strongly from the smaller values for the Neanderthals and to fall instead among the values for other Upper Palaeolithic European crania and for the Skhul and Qafzeh specimens (Bräuer et al. 2004).
Also, the earliest modern fossils from such east and north-east African sites as Aduma, Bouri, Haau Fteah, Herto and Omo-Kibish, which date to between 75 to circa 160 ka, exhibit a blend of modern features with archaic and robust ones that foreshadow many (but not all) of the details of the troubling European Aurignacian fossils — even though the oldest specimens can hardly be derived from Neanderthals. Although anatomically transitional specimens from Europe might indeed have resulted from a slight admixture of Neanderthals into an intruding population of Moderns, one does not have to resort to theories of local gracilisation of Neanderthals into modern Europeans or of extensive hybridisation between Neanderthals and Moderns to explain all the archaic features of transitional fossils like the ones from Mládeč since such individuals could just as easily have inherited many of their ‘archaic’ features from even earlier African Moderns.

If I may be permitted to re-arrange a few sentences by Robert Bednarik, he wrote:

The type fossils of the Neanderthals, the late ‘classical Neanderthals’, are far from being typical specimens. The most probable explanation for their archaic features is that at certain times, determined by the periodic times of cold climate, European populations became rather isolated from the main body of Old World hominids. They probably represent regressive marginal populations, and to use their very fragmentary DNA data, as has been attempted recently, to explore the evolutionary history of the human mainstream population of Africa and Asia is futile (Bednarik 2000).

While Bednarik has long argued that ‘the European Robusts lumped together as “Neanderthals” left an imprint on modern Europeans’ (pers. comm. Nov 2007), he also noted that the late ‘classical Neanderthals’ of western Europe had developed specialised adaptations to cold in isolation. (To go back to Bednarik’s point about the ‘human mainstream population of Africa and Asia’ for a moment, before arriving in Europe, intruding Moderns from Asia might well have picked up a slight admixture of Neanderthal traits in warm climates where Neanderthals did not exhibit cold-weather adaptations to a significant degree, just as earlier anatomically modern humans may have done during the Middle Paleolithcic in the Levant.)

Returning to the paucity of evidence for either hybridisation or the evolution of classic Neanderthals into Moderns, in a recent consideration of the morphological aspects of European Moderns older than 33 000 yr as well as Gravettian fossils, Erik Trinkaus concluded that they show an ‘anatomical pattern congruent with the autapomorphic (derived) morphology of the earliest (Middle Paleolithic) African modern humans’. But he went on to note that ‘they exhibit a variable suite of features that are either distinctive Neandertal traits and/or plesiomorphic (ancestral) aspects that had been lost among the African Middle Paleolithic modern humans. The ubiquitous and variable presence of these morphological features’ — including ‘aspects of neurocranial shape, basicranial external morphology, mandibular ramal and symphysyal form, dental morphology and size, and anteroposterior dental proportions, as well as aspects of the clavicles, scapulae, metacarpals, and appendicular proportions’ — ‘in the European earlier modern human samples can only be parsimoniously explained as a product of modest levels of assimilation of Neanderthals into early modern human populations as the latter dispersed across Europe’ (Trinkaus 2007).

So, despite several millennia of contact, one or more mechanisms apparently reduced breeding between the two populations to ‘modest’ levels. My hunch is that classic cold-weather Neanderthals were victims of a paradoxical tragedy, due in part to their own innovations, which made their biological insulators increasingly irrelevant and burdensome, while those same innovations in the hands of Moderns — acquired independently or in part from Neanderthals — gave them a decided advantage. Add the rapid expansion of people exhibiting gracile traits compatible with adjustable artificial insulation (as opposed to biologically fixed insulation) to a tendency of both populations to disdain one another as potential mates, and the more robust Neanderthal paradigm would have been doomed.

Even if cold-weather Neanderthals and invading Moderns bred on occasion, which seems likely, the mechanisms I have described could still have severely limited the number of such encounters and the reproductive success of the resulting offspring, who might have been shunned more often than not — perhaps even by both populations. Add the tendency of genetic drift to prune branches with few or no descendants to the pressure of sexual selection and genetic swamping by fresh intrusions by Asiatic Moderns throughout later pre-History and one can see how many traits acquired by European Moderns from Neanderthals could have been progressively eliminated.

Further implications

This radically different version of what cold-weather Neanderthals looked like and why Neanderthals in general may not have hybridised to any extent with grotesquely bald hominids — except perhaps in the Middle East — whose ancestors had only left the tropics a few millennia before, may have further implications.

First, as mentioned earlier, the proposed Neanderthal adaptations to cold weather should be testable both genetically and by further osteological analysis. Secondly, the need to build up fatty insulation would have been seasonal, which suggests that there may have been dietary implications — which may be trackable both as chemical signatures in fossils and by focusing on paleozooology data.

Thirdly, if Neanderthals were not quite as muscular...
as has been theorised, but muscular and plump, then they may not have depended so much on brawn and hunting as their brains (which were larger on average than those of Moderns) and more varied and sophisticated methods of hunting, foraging and even fishing than have generally been ascribed to them. For example, in a remarkable study, Maja Paunovic and Fred H. Smith reported that the ‘majority of the identified remains’ from Vindija Cave belonged to ... prized taxa such as trout, pike perch or edible frog(s), and was found in sediments together with Neandertal bones as well as in association with Mousterian and Aurignacian artefacts dated to OIS 3. Thus, in contrast to previous theories of long-distance following of herbivores, a territorial model of exploitation of all animal sources is more plausible for ... Neandertals, from Vindija cave (Paunovic and Smith 2002).

The highly specialised tool assemblage and predation on reindeer at Salzgitter-Lebenstedt in northern Germany provides another example of the extent of Neandertal cultural adaptation to specific dietary opportunities.

Although Neandertals are often described as having been conservative to a fault, and, by an illogical extension, incapable of change, the final millennia of their existence were marked by a cultural florescence that included the Châtelperronian (Bailey and Hublin 2006), Uluzzian, Szeletian (Allsworth-Jones 1986, 1990), Bohunician, which combines aspects of the Levalloid Mousterian and the Aurignacian (Svoboda 1993), Olschewian (Bayer 1929), and eastern European Strelets and Spitsyn cultures, not to mention the blade industry described in Level CA at Riencourt-Lès-Bapaume (Ameloot-Van Der Heijden 1993; Tuffreau 1993a, 1993b) (which is related to similar blade assemblages at Seclin as well as at Molinons and Lailly in the Yonne (Depaepe 1997; Deloze et al. 1994). These cultures variously used polished bone tools, burinated blades, backed knives, leaf points and jewellery (d’Errico et al. 1998, 2003; Bednarik 1992, 2000). The fact that the lowest Proto-Aurignacian strata at the Castillo Cave appear to be incoherent with the presence of Moderns in western Europe (Cabrera Valdes and de Quiros 2004), since there is no evidence for them east of the Balkans that early, suggests that even elements of the Aurignacian tool-kit may ultimately be re-assigned from Moderns to Neanderthals. In that case, who borrowed from whom?

To quote my notes from a presentation entitled ‘Le symbolisme au Castillo depuis 50 000 ans, et son contexte européen’ by Victoria Cabrera Valdes and Federico Bernaldo De Quiros at a conference at the Musée de l’Homme, Paris, on 16 January 2004, the Aurignacian ages (Oxford and Tucson) for the following layers in Castillo are: 18B – 37 100, 37 700, 38 500 and 40 700 yr; 18C – 39 500, 39 800, 40 000 and 40 000 yr (Cabrera Valdes et al. 2001). Similar AMS dates for the lowest Aurignacian bed at El Castillo were published in 1989 (37.7 (± 1.8) ka yr, 38.5 (± 1.8) ka yr, 40.0 (± 2.1) ka yr as well as for the Aurignacian at l’Arbreda cave in Catalonia (average 38.5 ± 1.0 ka yr) (Cabrera Valdes and Bischof 1989). Cabrera Valdes and De Quiros assert that the oldest known presence of Moderns in the area dates to c. 33 000 yr. I presume they are referring to Brassempouy (Henry-Gambier et al. 2004), Les Rois 1 (Vallois 1958a) and La Quina Aval (Martin 1936). Just as strange as the early Aurignacian dates, Cabrera Valdes and De Quiros report that classic Mousterian radial cores co-exist with Aurignacian Dufour bladelets and muzzle scrapers. Also, a bone found at Castillo with pure graphite lines suggestive of an animal head and another with the probable lower rear quarters of an animal drawn with sharpened manganese are 7000 to 8000 years older than the oldest Aurignacian art known from Germany. Can one be certain these objects were not made by Neanderthals? (Cabrera Valdes and de Quiros 2004).

In light of these findings, the footprint with Neanderthaloid features from Chauvet becomes even more suggestive (Bednarik 2007). In addition to the Aurignacian toolkit, when it comes to art, one might ask, who borrowed from whom? Or, instead of one lineage ‘borrowing’ from another, does the Palaeolithic art of Europe have its roots in parallel evolution of symbol-manipulation by two separate lineages and some cross-fertilisation once they met?

A reservation is in order, though, concerning the relevance of at least one Chauvet image to my hypotheses. The section in question encompasses the ‘Chauvet Venus’, which shares a leg with an anthropomorphous figure whose arm is laid on the inside of one thigh and whose bison head is positioned above the vulva, on (or in) the ‘Venus’s’ belly. While the vulva and bison head are both blackened with manganese, suggesting hair, the legs are unpigmented, suggesting exposed skin. This seems to indicate that the creators fit the modern paradigm of humans with skin that is almost naked except around the genitalia and scalp — exactly what one would expect if they were intruding Moderns.

If the footprint is indeed Neanderthaloid instead of a Modern’s foot splayed by hard use, several options should be considered: one, that one of my hypotheses, concerning body hair, is wrong and that cold-weather classic Neanderthals fit the modern naked-skin paradigm. Two, that a Neanderthal who had nothing to do with the art visited the cave. Three, that the footprint was left by a person with a mixture of traits, including an archaic foot and a modern body hair pattern, indicating rapid loss of biological insulators either as the result of improved clothing technology or some hybridisation with Moderns, or both. Fourth, and most outlandishly, that a still-furry cold-weather Neanderthal was indeed the author of both the footprint and some of the art, but illustrated a very different kind of female — a woman from the intrusive population with her startlingly marked pubic zone. I doubt it, but the jury is still out on the nature and relevance of the foot to the cave imagery.

All the same, the range of Neanderthal accom-
plishments probably remains severely under-estimated. For example, a close examination of the edges of triangular Mousterian ‘hand-axes’ suggests that the genre should be divided into at least two distinct categories — those with a more roughly knapped base which were probably hafted into a grip along that edge, creating a pointed knife, and others with ‘unfinished’, roughly knapped ‘tips’ — which were probably set into handles to make spatulate utensils like ulus.

Just as the observation of edgework may enrich the Neanderthal toolkit, the presence of drilled teeth in Châtelperronian assemblages confirms the existence of another innovation that I have discussed above in the context of weather-tight clothing and lacing — the existence of thongs or string in this late Neanderthal culture. Although the teeth are somewhat controversial because of the possibility of stratigraphic mixture, in their thorough study White and Taborin ultimately decided that ‘...quantitative tendencies (e.g., species choice for animal teeth, preference for suspension by means of basal incisions around the circumference of the tooth root) of the Arcy Châtelperronian ornaments stand in some contrast to early Aurignacian ornamental assemblages’ (White and Taborin 2000; paraphrased in White 2002). The cords associated with such drilled teeth could also have been used to make numerous tools, which, being organic, would not have survived, as well as the first weather-tight clothing for Neanderthals who needed it.

When the possibility that Neanderthals or transitional individuals marked by residual Neanderthaloid features produced some of the earliest art is added to the rest of Neanderthal accomplishments during the early Upper Palaeolithic, one is forced to abandon the idea that our Modern lineage represented the only ‘behaviourally modern humans’ when it left Africa around 55,000 years ago. To quote Steven Churchill and Fred Smith's conclusion:

... a number of observations are suggested by the current data: 1) the Middle Palaeolithic of Europe appears to have been made exclusively by Neandertals; 2) Initial Upper Palaeolithic industries (with the exception of the Bachokirian) appear to have their roots in the late Middle Palaeolithic industries of their respective regions; 3) all of the human fossils yet recovered from Initial Upper Palaeolithic (except the Bachokirian) contexts for which any diagnostic morphology is present have their greatest morphological affinities with Neandertals and not early modern humans (Churchill and Smith 2000).

In light of Neanderthal accomplishments that seem just as remarkable as any by contemporaneous *Homo sapiens sapiens*, the appellation, ‘behaviourally modern humans’, is simply a misnomer that perverts objectivity — one might almost say a form of racism disguised and buffered by an intervening 30,000 years.

In summation, whether Neanderthals invented their later technologies independently or, perhaps even more amazingly, were able to create their own versions of objects introduced by migrants bearing adjustable insulation even as Neanderthals were being decimated by disease carried by arrivals from microbially rich environments to the south, cold-weather, Middle Palaeolithic Neanderthals will probably turn out to be more capable, far furrier and more roly-poly than any reconstruction of them to date.

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Schulz, H.-P., B. Eriksson, H. Hirvas, P. Huhta, H. Jungner,


RAR 25-865

Editorial note: Comments are invited from readers to test the controversial aspects of this paper, but should preferably emphasise the relevance of its hypotheses to palaeoart research.

There is little a mere review can do to capture the intensity of Bednarik's tale: it relates to conventional scientific writing as pure ethanol relates to an evening glass of cool white wine. In his pages, compressed, stripped down to basics, is the entire political, environmental and ideological history of the coastal Pilbara ... Bednarik's volume includes a series of remarkable photographs capturing the range of carvings and their spectacular siting ... Bednarik has penned an art historical 'J'accuse, an unfamiliar form of public argument in this nation of whispered co-options, stakeholder coalitions and backroom deals.'

Nicolas Rothwell, The Australian

'The word journey is often used today as a metaphor for a range of human and personal experiences, but in Australian Apocalypse this word has found a near-cosmic significance. The book is about Australia, a continent that is defined most of all by distance and remoteness. The antipodal terminus of the migration of one of the earliest human groups to have left Africa, Australia became the lure for modern European explorers and also a dreadful prospect for their ostracised fellow men ... Bednarik's determination in the pursuits of scientific goals gave rise to the activism of a believer, and he began organising local groups and environmentalists, arranging scientific seminars, orchestrating media campaigns, and seeking the help of national and international institutions in preventing the destruction of rock art in Australia, Portugal and elsewhere. The narrative of the intrigues and personal motives in these confrontations is captivating, and the substantial successes and promised hopes are encouraging.

What is most remarkable about the book are the exuberant energies of its author, his extraordinary intellect and his commitment to science. Bednarik single-handedly undertook a Leibnitzean task of creating a 'calculus' for the scientific study of rock art, and fought valiantly to save this discipline from opportunistic theories such as those of shamanism.'

Dr Ahmed Achrati, Rock Art Research

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ROBERT G. BEDNARIK

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