THE NEANDERTAL EXPERIMENT

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PROFESSOR WIL ROEBROEKS

FACULTY OF ARCHAEOLOGY
LEIDEN UNIVERSITY
THE NETHERLANDS

GERRIT HEINRICH KROON
(1868-1945)

INTRODUCTION

Our closest living relatives in the animal world are the chimpanzees, fellow primates with whom we shared a last common ancestor approximately six to seven million years ago (Glazko and Nei 2003, Stauffer et al. 2001). Geologically speaking that is only a short period of time. Not surprisingly, the genomes of humans and chimpanzees are very similar and differ in less than 1 percent of their DNA. But as a recent study (Hughes et al. 2010) shows, the Y-chromosomes differ in 30 percent of their DNA, meaning that these chromosomes are changing far faster in both species than the rest of the genome is. This is probably the result of the striking differences in mating patterns between the two species, which constitute only one of the many characteristics that separate "us" from "them".

Within the chimpanzee group, the split between the lineages leading to bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes verus*) happened about two to three million years ago. From then on these lineages also went different paths, geographically separated, with bonobos now living south of the River Congo (hence their nickname of *rive gauche* chimps) in an equatorial rainforest habitat, without any competition from other great apes. The two to three million years of separate ways made bonobos and chimpanzees differ in physical appearance as well as in important and well-publicized aspects of their behaviour - even though bonobos may not longer be seen as the peace loving, matriarchal and sexually liberated "hippies of the primate world" they have often been portrayed to be (De Waal 1995).

It is interesting to compare the physical appearances, the behaviour as well as the genetics of such closely related species as chimpanzees and bonobos; they diverged only recently and hence constitute clear examples of changes occurring over short periods of time, offering snapshots of evolution in action. Such comparative studies of primates have yielded important data regarding the development of the human niche and the evolution of human characteristics such as large brain size, high quality diets and our typical life histories (Aiello and Wheeler 1995, Kaplan et al. 2000, Milton 1993, Milton 1999).

The fossil record shows that in the course of the six million odd years since our divergence from the chimpanzee/bonobo lineage, a large number of hominin species emerged and went extinct again. In fact, until roughly 18,000 years ago, there was always more than one human species (or: sub-species) around (Wood 2009). Neandertals are our best known extinct relatives, and have fascinated us ever since their initial discovery in 1856, probably because they are so close to us, yet at the same time also different in many aspects of their anatomy and their behaviour. We, modern humans, shared our last common ancestor with the Neandertals at around 600-800 ka (ka =1000 years BP) (Green et al. 2008). Again, geologically speaking that is only very recently, which explains the many similarities between our lineage and theirs, that went extinct approximately 36,000 radiocarbon years ago (see below). As with bonobos and chimpanzees, the two lineages can be seen as an experiment of evolution - building on a comparable *Bauplan*, for a few hundreds of thousands of years adapting to very different environmental settings: our ancestors were mostly confined to Africa, where the earliest cranial remains of a modern human morphology date to about 200 ka (McDougall, Brown, and Fleagle 2005). As far as the evidence goes the Neandertal lineage was mostly confined to (western) Eurasia (see below).

In the last few decades Neandertal studies have added a tremendous set of data to the record that has built up since the first discoveries in the middle part of the nineteenth century. These data relate to their archaeology and the information on the environments in which their archaeology was produced, the chronology of their occupation of the various parts of their range and their skeletal record. Biochemical methods, gene sequencing studies and new computer techniques allow palaeoanthropologists to distill ever more information out of their skeletal remains, and add to our knowledge of lifestyles, life history and the ecology of early humans. Ancient DNA studies increasingly yield data on the divergence time for various species, on the geography of genetic diversity (phylogeographic structure), on where refuge areas may have been located for individual species in the past and by what colonization routes individuals dispersed from these refugia while recolonizing previously abandoned areas. Neandertal studies have profited from these exciting new developments more than the study of any other extinct hominin species has. The field now makes use of an excellent database regarding various aspects the Neandertal lineage. In this lecture, I want to provide an up to date overview of the "new" Neandertal record and its interpretation. In a sense the Neandertals will serve as a "pilot study" here, as an example of the exciting progress palaeoanthropology is making through the integration of a wide range of disciplines. As with chimpanzees and bonobos, we can address how different they were from us, where similarities do reside, despite of hundreds of thousands of years of separation of our lineages and what that possibly tells us about "Modern Human Behaviour" and its inferred uniqueness.

The Neandertal lineage can be seen as one of the many "experiments" of nature, as a lineage that survived, for some hundreds of thousands of year before disappearing, as many other lineages have done. I use the term "Neandertal experiment" in the sense of the ecologist Deevey. In his paper "Coaxing History to Conduct Experiments" (Deevey 1969) he stressed what he called "an essential point in ecological methodology": in ecology, as in astronomy, the experimental method is necessarily restricted to those experimental situations that history has already provided: "Where time is required to see a result, there is no substitute for history... especially evolutionary history ...provides some essential "experimental" conditions that need to be consciously sought and carefully attended to by the experimenter" (Deevey 1969: 40). When comparing the Neandertal record to that of modern humans, we look at the outcome of an experiment that ran approximately half a million years and is now being studied by a wide variety of scientific disciplines trying to understand how and why humans have evolved to work the way they do.

THE NEANDERTAL LINEAGE

Robustly built skeletons, large projecting faces and large human-sized braincases - with longer and lower skulls - are but a few of the features that distinguish Neandertals from modern humans (see below). The cranium of *Homo neanderthalensis* is especially distinctive with its thick, double-arched brow ridges, its laterally projecting and rounded parietal bones and the occipital 'bun' on its back. In fact, the very peculiar shape of Neandertal skulls makes it possible to diagnose even very fragmentary remains, such as the one recently uncovered from below the waters of the North Sea (Hublin et al. 2009). The list of typical Neandertal cranio-mandibular and postcranial traits is long. Not all Neandertals displayed these features, whereas some modern humans did display a few of them. The classic Neandertals of the last glacial period (115-40 ka), such as those from the type site in the Neanderthal in Germany and the ones from Spy (Belgium) (Semal et al. 2009), had most of these characteristics.

In fact, until the 1970s, Neandertals were seen as exclusively dating to the Late Pleistocene (c. 125-10 ka). Recent studies have expanded the "time depth" of the Neandertal phenomenon, by showing that characteristics used to determine the Late Pleistocene Neandertal phenotype can already be observed in Europe during the Middle Pleistocene (c. 800-125 ka). Speci-

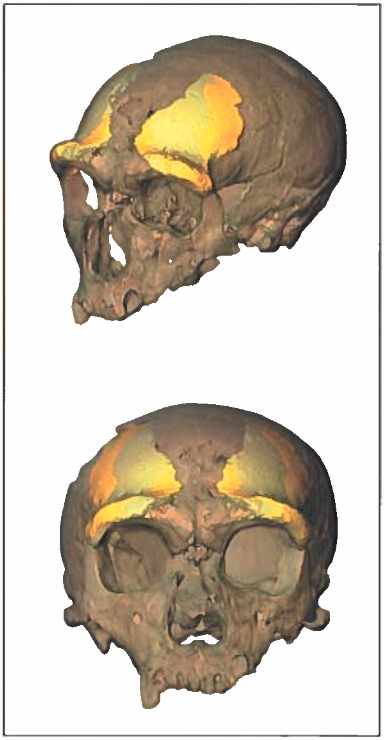

Figure 1: The Neandertal cranial fragment from the Zeeland Ridges, North Sea, mirror-imaged and superimposed on the La Chapelle-aux-Saints Neandertal skull with a maximum geometrical match (© MPI-EVA, Leipzig, cf. Hublin et al. *2009).*

mens assigned to Marine Isotope Stage (MIS) 7 (250-200 ka), such as Ehringsdorf (Germany) or Biache-Saint-Vaast (France) are clearly identifiable as Neandertals (Hublin 2009). The Swanscombe skull, thought to date to around 400 ka (MIS 11) already displays incipient Neandertal features (Stringer and Hublin 1999; Hublin 2009). The same applies to the very rich fossil hominin assemblage uncovered at the Sima de los Huesos (Pit of the Bones) site, near Burgos, Spain. This collection contains the remains of at least 28 individuals, many of them teenagers and young adults (Bermudez de Castro et al. 2004). The assemblage dates to the first half of the Middle Pleistocene and already contains many Neandertal apomorphies – evolutionary derived characters, unique to the lineage/species. Recent U-series dates of a speleothem inferred to postdate the fossils yielded an age of 600 + ∞ - 66 ka (Bischoff et al. 2007). Should this date proof to be correct, it would mean that the Neandertal lineage emerged much earlier than hitherto envisaged.

Current views on the emergence of the Neandertal lineage (see Hublin 2009) are not only based on palaeontological evidence, but increasingly on palaeogenetic data. Green et al.'s (2008) study of Neandertal mtDNA suggested a date of 660 ± 140 ka for the most recent common ancestor of the two lineages, i.e. for genetic coalescence. This estimate is based on a separation date of six to seven million years ago for humans and chimpanzees. Estimates based on the autosomal sequence give a coalescence time of 700 ka, and a separation time for the populations of about 370 ka (Noonan et al. 2006). Different populations are expected to become visible in Eurasia and Africa from around 400 ka, which fits well with the European evidence, unless the Sima de los Huesos assemblage is really as old as the U-series date suggests: this date is close to the coalescence date and older than most of the estimates for the separation of African and western Eurasian populations (Hublin 2009).

Abundant evidence now exists which shows that hominins were present in the southern parts of Europe from approximately one million years ago onward (Carbonell et al. 2008), with range expansions into the north also considerably earlier than previously envisaged (Parfitt et al. 2005, Roebroeks 2005, Roebroeks 2006); possibly even earlier than the 700,000 years old artefacts recently uncovered at Pakefield (United Kingdom) (Parfitt et al. in prep). A more substantial occupation of the middle latitudes (up to 55 degrees North) is indicated from the second half of the Middle Pleistocene onward, from around MIS 13 (Roebroeks 2006). The Boxgrove site, West Sussex (United Kingom), with its

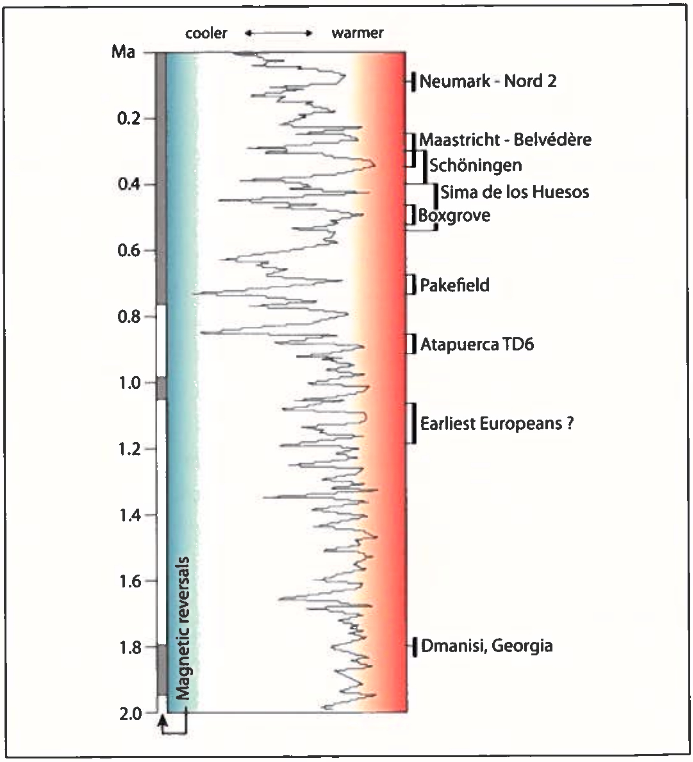

Figure 2: Cooler and warmer intervals during the last two million years, as judged by oxygen-isotope studies, which provide benchmarks for dating, as do the magnetic reversals indicated in the figure. The approximate chronological position of some archaeological key sites is indicated.

pristine Acheulean record, dates to this period. The site yielded a hominin tibia which once belonged to a heavy and muscular (possibly over 90 kilograms in weight) probably male person, a rough contemporary of the individual whose lower jaw was recovered in sediments of the Neckar river near Heidelberg, Germany.

Whether these individuals belonged to the stock from which the Neandertal lineage developed is unclear yet. It is a distinct possibility though, given that there were always hominins present somewhere in western Eurasia from that time period onward (Roebroeks 2006) and that the African and the Eurasian lineages separated at around 400 ka. Furthermore, Bermudez de Castro et al. have described the *heidelbergensis* type specimen from the Neckar deposits as already Neandertal-like (Bermúdez de Castro et al. 2004). It is therefore not unlikely that the process of Neandertalisation did begin with the first substantial occupation of the northern temperate latitudes (Roebroeks 2001). In this paper I concur with Hublin's accretion model, that includes within the Neandertal hypodigm fossil evidence that is older and less derived (e.g. the Atapuerca fossils) than the fossils of "classic" Neandertals from the Late Pleistocene. The latter are still seen by some as the exclusive members of the Neandertal club (see Hublin 2009 for a discussion).

Genetic studies performed at the Max Planck Institute for Evolutionary Anthropology in Leipzig (Germany) are producing very important data on the character of this "club" and its much discussed relationship to our species. In the genetic realm, for instance, the FOXP2 gene is thought to be important for the evolution of language, by helping to establish neuromuscular control of the organs of speech. There now is evidence (Krause et al. 2007a) that Neandertals had the modern human mutations at FOXP2, which suggests that these mutations must have occurred some time before the above mentioned split between Neandertals and modern humans (Krause et al. 2007a; Green et al. 2008). This points to important similarities between the two groups, but other data shows differences: for instance, MtDNA studies of 15 Neandertal individuals, sampling a large part of their range and almost 60,000 years of their existence, show that they all had one haplogroup in common that is now so rare that it has not been recorded in modern humans yet. The completion of the nuclear genome, expected to be published in the course of 2010, will allow researchers to compare three billion base pairs between Neandertals and *Homo sapiens* and to detect even very low levels of genetic exchange between the two groups. As far as the currently available evidence goes, if exchange did occur, it must have been biologically unimportant.

A WESTERN EURASIAN SPECIES?

Neandertals are usually seen as a western Eurasian species, but we know in fact little about the limits to their range, both in terms of their actual former distribution and regarding the factors which set limits to where they could successfully survive (Adam Jagich, in prep.). The limits to the Neandertal geographical range are usually constructed by drawing lines around the maximum distribution of their fossil remains. Differences in site preservation as well as in research intensity and research history make such estimates very rough and preliminary (Dennell and Roebroeks 2005). This is well illustrated by the recent 2000 km extension of the eastern edge of their range, the result of genetic analysis of skeletal remains that could not be assigned to species on morphological grounds (Krause et al. 2007b). This shift highlights how little we know about the former distribution of Neandertals. We should not be surprised if future fieldwork – or genetic studies - would yield Neandertal fossils – or Neandertal-like DNA sequences - even further east, in Mongolia or China. The longest occurrence of the Neandertals is documented in western Europe, but other areas remain poorly explored, including areas within Europes such as northern Russia (Pavlov, Roebroeks, and Svendsen 2004). We simply do not know the location of Neandertal core area(s), that is, the areas where environmental conditions suited them best and where they were most abundant.

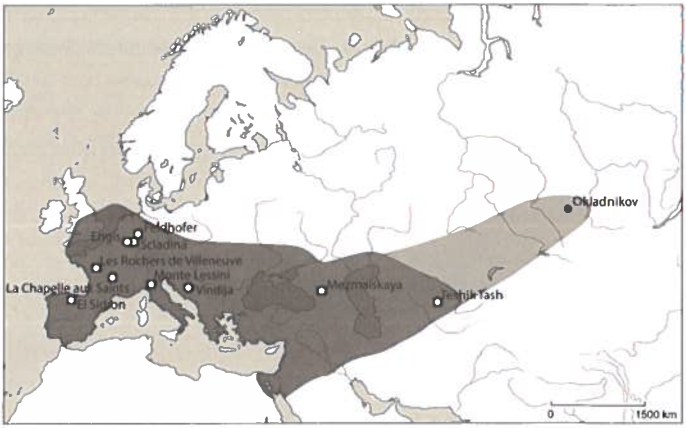

Figure 3: The Neandertal range as reconstructed on the basis of the morphology of fossils is indicated in dark grey. The recent mtDNA based eastward extension of the range is in light grey. Open circles indicate sites that yielded Neandertal fossils from which mtDNA sequences were obtained. The Okladnikov site produced undiagnostic skeletal remains, with a Neandertal mtDNA signal (redrawn after Krause et al. *2007).*

Judging from the *current* distribution of their fossils (including the recent mtDNA eastward extension into southern Siberia), the size of the Neandertal range was roughly ten million km^2, i.e. significantly larger than Australia (7,7 million km^2). Within that area, their presence must have varied, fluctuating with the rhythms of climatic oscillations and the resulting variations in resource availability. Some areas may have seen a more or less continuous presence of groups of Neandertals, whereas in others, such as in the northern margins of their range, discontinuity may have characterized their occupation in the long term (Hublin and Roebroeks 2009). For instance, on the basis of the English record, Ashton and Lewis (2002) have suggested that this northwestern part of their range was deserted between MIS 6 and MIS 3, i.e.

from the next-to-last glacial (Saalian) to the middle part of the Last Glacial (Weichselian): an occupational hiatus of more than 100 000 years and a striking difference to the signal from the other side of the Channel. There occupational hiatuses also do occur, but are considerably shorter (Goval 2008). In fact, the Early Weichselian Middle Palaeolithic record, while non-existent in England, testifies to a very abundant presence of Neandertals in Northern France.

REGIONAL EXTINCTIONS AND GENETIC HOMOGENEITY

The factors causing occupational hiatuses have been at stake in the debate regarding the environmental tolerance of early hominins, and especially of Neandertals. Part of that debate focused on the question whether Neandertals were able to survive in full interglacial forested environments (Gamble 1986, Gamble 1987, Roebroeks, Conard, and van Kolfschoten 1992, Roebroeks and Speleers 2002). These forests were seen as challenging places in which to make a living as a hunter-gatherer, with the dispersed nature of animals and small size of plants contributing to high exploitation costs. Much of the discussion focused on their presence or absence in Last Interglacial (Eemian) settings. With the recent discoveries of high resolution Last Interglacial (Eemian) sites at Caours in the Somme valley (France) (Antoine et al. 2006) and by our own fieldwork at Neumark-Nord 2, near Halle (Germany), it has become abundantly clear that Neandertals were indeed successfully making a hunting-gathering living in the very interglacial periods. And even hundreds of thousands of years earlier hominins were present in by all means full interglacial conditions, e.g. at Beeches Pit, United Kingdom (Preece et al. 2007, Roebroeks 2007).

Figure 4: Excavations at Neumark-Nord 2, final days, August 2008. Left of the centre of the picture is an elephant tusk, recovered in the middle of the Last Interglacial (Eemian) archaeological find level.

Our recent large scale excavations of the Middle Palaeolithic site Neumark-Nord 2 yielded a rich archaeological assemblage, containing c. 20,000 Middle Palaeolithic flint artefacts and approximately 120,000 faunal remains. The warm-temperate fauna includes straight-tusked elephant, rhinoceros, bovids, equids, deer, bear, small carnivores and the pond tortoise *Emys orbicularis.* Many of the faunal remains are covered in traces of butchering and opening of their bones for marrow extraction. Excavations took place in an open cast lignite quarry, south of Halle (Germany), where the archaeology was contained within the infill of a small and shallow sedimentary basin, resulting from movements in the underlying Tertiary lignite deposits. The former waterhole probably functioned as a magnet location for animals in a predominantly forested environment, which may explain the abundance of archaeological finds there (Sier et al, submitted).

While interglacial environments may not have constituted the barrier they once were thought to be, the record clearly suggests that there was regional discontinuity in Neandertal presence.

The rich record from northern France showes a lack of traces of occupation during the first glacial maximum of the Weichselian (MIS 4). But what was the character of these discontinuities? Did Neandertals "give up" northern France whenever climate deteriorated, moving south to areas with better resource availability and moving north again when conditions ameliorated? In other words, did populations move, tracking their preferred habitat? Or did regional populations occasionally simply die out? Is it possible to discriminate between the two alternatives on the basis of the fossil record?

Jean-Jacques Hublin and I (2009) have recently made an attempt to use archaeological, palaeogenetic and comparative data to address this very issue (see also Roebroeks et al. 2010, in press), starting from the clear pattern in the French record. Our review of the evidence strongly suggests that the straightforward image of a "two-way-traffic" between north and south, with Neandertals tracking their habitat in the rhythm of Pleistocene environmental changes, does not fit well with data on the ecology of Neandertals, their archaeological record, their palaeogenetics and with what we know about other animals. Instead, we suggest that from the very first substantial colonisation of temperate Pleistocene Eurasia, i.e. from the Middle Pleistocene onward, a pattern of repeated regional extinctions and subsequent recolonisation may have become a very important factor in the demographic history of these hominins. The distribution of Neandertals was occasionally reduced severely as northern parts of their range were abandoned, with regional extinctions leading to substantial reduction of Neandertal overall population size.

Palaeogenetic data are very informative in this domain. Studies of Neandertal mitochondrial (mt) DNA suggest a very low genetic diversity for Neandertals. Their effective population size - which describes how large a population has to be to carry its level of genetic diversity – was similar to that of modern Europeans or

Asians, but lower than Africans. Briggs et al. Recently estimated that the effective population may have included less than 3,500 females (Briggs et al. 2009). Krause et al. (2007b) compared mtDNA sequences obtained from the easternmost Neandertal fossils from Teshik Tash (Uzbekistan) and Okladnikov (Siberia) to those from the Caucasus and western Europe. Surprisingly, the Teshik Tash sequence turned out to be more similar to Scladina (Belgium) than to its nearest neighbours at Okladnikov or in the Caucasus. This suggests a lack of deep divergence and a short separation time only. Neandertals from Vindija (Croatia) and the Feldhofer Grotte in Germany, the type site specimen, separated by 850 km, yielded identical mtDNA sequences, again underlining small effective population size (Briggs et al. 2009). The Briggs et al. study presented five complete mtDNA genomes from a wide area, from Spain in the west to the Caucasus in the east. The authors estimate that the most recent mtDNA ancestor of these five Neandertals lived around 110,000 years ago, much more recent than the beginning of the Neandertal lineage. These findings suggest that the large area sampled by this study was recolonized relatively recently, from an area where the environment was most suitable and Neandertals were most successful, but whose location is unknown thus far.

The genetic effective population size estimates set limits on the lower range of the size of Neandertal census population, but is it possible to get more specific estimates for total population size? Extant hunter-gatherers primarily depending on terrestrial animals – as we know Neandertals did (see below) - occur in low densities, usually below 1,57 person/ 100 km^2 (Binford 2001). Using these and other data on forager population Roebroeks et al. estimate that Neandertal census population size over their entire range of 10,000,000 km^2 – from Spain into Siberia - would have been between 38,600 and 157,000 individuals; i.e. maximally one factor larger than the effective population size of about 14,000 individuals suggested by the genetic data briefly reviewed above (Roebroeks, Hublin, and MacDonald in press 2010). Neandertal body size and shape indicates that they had relatively high energetic requirements, as discussed in more detail below. Based on this and the likelihood that parts of this large range would have been uninhabited, actual population size would have been smaller still. Significant reductions in population size or population bottlenecks occurred especially during the coldest phases of glaciations as a result of regional extinctions as discussed above.

Low effective population size and the occurrence of severe genetic bottlenecks must have had major implications for the evolution of the Neandertal lineage. With such small populations, the fixation by chance of genetic traits, also known as drift, would have become a crucial factor in shaping the Neandertal lineage, alongside natural selection. The view that genetic drift is important in explaining the divergence between Neandertal and modern humans finds independent support in a study of cranial features of Neandertals and modern humans (Weaver, Roseman, and Stringer 2007). Hublin's (1998) accretion-model, which sees Neandertal morphology as the result of a more than 300,000 years long process of accretion of features, likewise supports the role of genetic drift (cf. Hublin 2009; but see also Hawks and Wolpoff 2001). Natural selection obviously also played a role in Neandertal morphology, especially in the development of their body proportions (Holliday 1997): a wide body shape with relatively reduced distal segments of the limbs (see below).

SOME NEANDERTAL CHARACTERISTICS

Neandertals were large-bodied hominins with an average body mass larger than that observed in most recent human populations, including Upper Palaeolithic modern Europeans. It is not clear what may have selected for their large body size. Climatic conditions, size-dependent mortality factors and/or aspects of their foraging niche, such as close encounter-hunting (see below) have been suggested as possible explanations. Their large body size is also consistent with their (presumed) low population densities (Walker and Hamilton 2008). Whatever the cause(s), their bodies displayed pronounced musculature and varying levels of postcranial robusticity, which has been related to a strenuous lifestyle, but is also interpreted as partly related to Neandertals' adaptation to colder environments, to thermoregulation (Pearson 2000). Neandertals had a high basal metabolic rate (BMR). Their stockier proportions and shorter limbs implied high energetic costs for mobility, which made food acquisition more costly (Weaver and Steudel-Numbers 2005). Various calculations have been produced to estimate their BMR and their daily energy expenditure (DEE) (Churchill 2006, MacDonald, Roebroeks, and Verpoorte 2009, Sorensen and Leonard 2001, Steegmann, Cerny, and Holliday 2002), always yielding estimates higher than those observed in recent hunter-gatherer populations. Churchill (2006) estimates the Neandertal DEE between 3500 and 5000 kcal per day, above the DEE for extant hunter-gatherers from the circumpolar regions (3000 to 4000 kcal per day for males). Snodgrass and Leonard recently suggested that Neandertal energy expenditure may have been even higher than all these previous studies suggest. They reached their higher estimates by including the energy costs associated with seasonal metabolic elevation in response to acute cold stress and the consumption of a diet extremely high in protein (Snodgrass and Leonard 2009).

Likewise, the energetic costs for growth and reproduction of their large bodies and brains must have been significantly higher, with major implications for the social life of these hominins: Neandertal anatomy placed heavy demands on pregnant females and females with children, as they had to fuel growth of body and brain, both during pregnancy and after birth (Aiello 2007, Aiello and Key 2002). Some kind of re-distribution of food within the group must have afforded the necessary resources for females to invest heavily in offspring in these phases of their life. There is some debate over the maturation speed of Neandertal individuals as compared to modern humans. Humans have large brains, grow slow, mature late and live long compared to other mammals and primates. Given the large - even somewhat larger than extant humans - brain size of Neandertals, one could infer that, like modern humans, they invested in a long life span, with a long learning phase in early life when the skills and knowledge necessary for a successful hunting and gathering career were acquired (Kaplan et al. 2007). While some evidence suggests that Neandertals may have maturated somewhat faster than modern humans (Ramirez Rozzi and Bermúdez de Castro 2004), other researchers have stated that the modern human variability in maturation rates is large and that Neandertal growth patterns fall within the modern human range (Guatelli-Steinberg et al. 2005). Neandertal infants probably required years of care, as modern children do, and some form of cooperation between individuals in order to care for infants and to provision mothers is likely.

NEANDERTAL SUBSISTENCE

How did Neandertals afford this high energy expenditure, how did they pay the costs for their expensive bodies? A large number of rock shelters and an increasing number of open air sites have produced faunal remains studied (and published) in sufficient detail to build solid inferences on subsistence. The 1980s and 1990s saw a fierce debate over the question whether pre-modern humans, including Neandertals, were capable of hunting medium- to large-sized animals. Lewis Binford was the most outspoken advocate of a pre-modern scavenging subsistence mode (Binford 1981, Binford 1985, Binford 1989, Stiner 1994, Stiner and Kuhn 1992). Our understanding of early hominin subsistence improved enormously through the methods and techniques that were developed by the various participants in this debate. And one thing has become abundantly clear: Neandertals were full-fledged hunters of medium-sized and large mammals, a position now also defended by once fierce proponents of the scavenging hypothesis. While the history of the debate is well-known, it needs to be pointed out that this history does bear a striking light on some of our disciplinary practices. In the 1980s, Neandertals were seen as only capable of hunting down the occasional "small animals and rodents, particularly rabbits" (Binford 1985:319). Now, with Neandertals back on the stage as hunters of larger mammals, new hypotheses regarding differences in adaptation between Neandertals and modern humans focus on the (inferred) *absence* of exploitation of small mammals, birds and fish by pre-modern humans – an archaeologically incorrect assumption, as we will see later. In this revisionist view, modern humans exploited these game species to a much greater extent and it was this "Broad Spectrum Revolution" (Stiner 2001, Stiner, Munro, and Surovell 2000) that allowed modern humans to maintain large population sizes, it is claimed now. We seem to have come full circle, with the

Fig 5: A fragment of a horse sacrum from Schöningen, Germany, still bears deeply incised cut marks caused by a flint implement during butchering approximately 350,000 years ago (from: Voormolen 2008).

same attributes once considered to be "archaic" now being seen by their very proponents as an integral part of what constitutes "modern human behaviour". It makes one wonder which other now cherished ideas we will have to discard in the next decades.

As far as the archaeological record goes, the hominins who created the Boxgrove archaeological record were probably already experienced hunters (Roberts and Parfitt 1999; Villa and Lenoir 2009; see also Rabinovich et al. 2008 for still earlier claims). This was certainly the case with the hominins who made the wooden spears of Schöningen (Germany), some 100,000 years later, as demonstrated in detail in a recent study of the faunal assemblage (Voormolen 2008). This site, located at the shore of a small lake, yielded an exceptional assemblage, including wooden spears, stone tools and the remains of about twenty horses. Voormolen's (2008) study of the horse remains shows that they were expertly exploited for their meat, their marrow and probably also for their hides. Schöningen is an exceptionally well-preserved site, dated to 300-400 ka. From Schöningen onward, we can follow (early) Neandertal hunting and butchering activities all over the Old World, based on a large number of well-documented and extensively studied assemblages (Roebroeks 2001), up to the specialized reindeer exploitation activities at the Last Glacial (Weichselian) site of Salzgitter-Lebenstedt (Germany) (Gaudzinski and Roebroeks 2000). Study of the reindeer excavated there (minimum nuber of individuals: 86) shows that after the hunt, animals were butchered and in subsequent systematic marrow processing of the bones, adults were clearly preferred. From their bones, again, lower quality marrow bones were neglected. A strong focus on primeness of resources is also documented in other domains of Neandertal life (Gamble and Roebroeks 1999). We obviously do not know how many episodes of hunting and butchering were involved in the formation of the Salzgitter reindeer assemblage, but there is evidence that hunting activities there occurred in autumn. The resulting palimpsest with its clear pattern of hominid selection against young and sub-adult animals shows strong similarities to the much later Late Glacial reindeer assemblages from the famous Ahrensburg tunnel valley sites near Hamburg (Gaudzinski and Roebroeks 2000, Gaudzinski and Roebroeks 2003).

*Figure 6: Dietrich Mania in 1994, displaying a skull of a large male bovid (*Bos primigenius*), butchered on the shore of the Last Interglacial lake of Neumark-Nord 1.*

Hunting of prime state medium-sized and large mammals fuelled the Neandertal body, from the very beginning of their lineage in the first half of the Middle Pleistocene onward (Roebroeks 2001). In the Levant, Neandertals even appear to have *over*-hunted some mammal species around Kebara Cave (Israel) (Speth 2004, Speth and Clark 2006). Neandertals were apparently highly carnivorous, occupying a very high trophic position focused on the consumption of medium- and large-bodied terrestrial herbivores. Smaller game stood at least occasionally on their menu too, including tortoises, rabbits and birds, as documented from some sites on the southern edge of their range, in detail at for instance

Figure 7: Excavations at Neumark-Nord 2, final days, August 2008. An excavation square with fragmented bones of large mammals, broken up to extract the marrow content

Bolomor Cave in Spain (Blasco 2008, Blasco and Fernández Peris 2009). There is also some thus far rare evidence from northern sites, e.g. from Salzgitter-Lebenstedt in Germany.

A comparable signal comes from stable isotope (carbon and nitrogen) studies of Neandertal skeletal remains. Isotopic methods indicate the source of dietary protein over many years of life. Applied to Neandertal remains (Richards 2007, Richards and Trinkaus 2009) they show that the Neandertal individuals studied thus far (n=13) had a similar diet through time (roughly 120-40 ka) and in different regions of Europe. The isotopic evidence indicates that in all cases Neandertals were top-level carnivores who obtained most of their dietary protein from large herbivores. This also applies to the Neandertal skull fragment from the North Sea (Hublin et al. 2009). In the middle latitudes, the protein consumed by Neandertals were overwhelmingly of animal origin during cold periods as well as during the Last Interglacial (Bocherens et al. 1999). At Jonzac, in southwestern France, a Neandertal juvenile had a diet similar to that documented in adult Neandertals elsewhere (Richards 2008). Early modern humans (n=14) (40-27 ka) exhibited a wider range of isotopic values, and a number of individuals has evidence for the consumption of aquatic (marine and freshwater) resources. This includes the individual from Pestera cu Oase (Romania), the oldest directly dated modern human in Europe (36,000 radiocarbon years BP), with the highest nitrogen isotope value of all the early modern humans studied thus far (Richards and Trinkaus 2009).

However, these stable isotope signals are derived from protein intake only. In recent years, increasing awareness of the limitations (and risks) of a high protein-intake have placed more emphasis on other food sources than just lean meat (Speth 1991, Speth and Spielmann 1983). With modern humans lean meat can compose no more than 35% of dietary energy before a protein ceiling is reached. Neandertals could have obtained alterna-

Figure 8: Reindeer ulna/radius from Salzgitter-Lebenstedt (Germany) with enlargements of the proximal locations with cutmarks (from: Gaudzinski and Roebroeks 2000).

tive food sources, such as fat, from their prey animals, especially from the marrow and the brain (Speth 1991, Speth and Spielmann 1983), whereas plant resources must have been important too, if only to moderate the high nitrogen levels of lean meat. Thus far they hardly show up in the record though (Jones 2009).

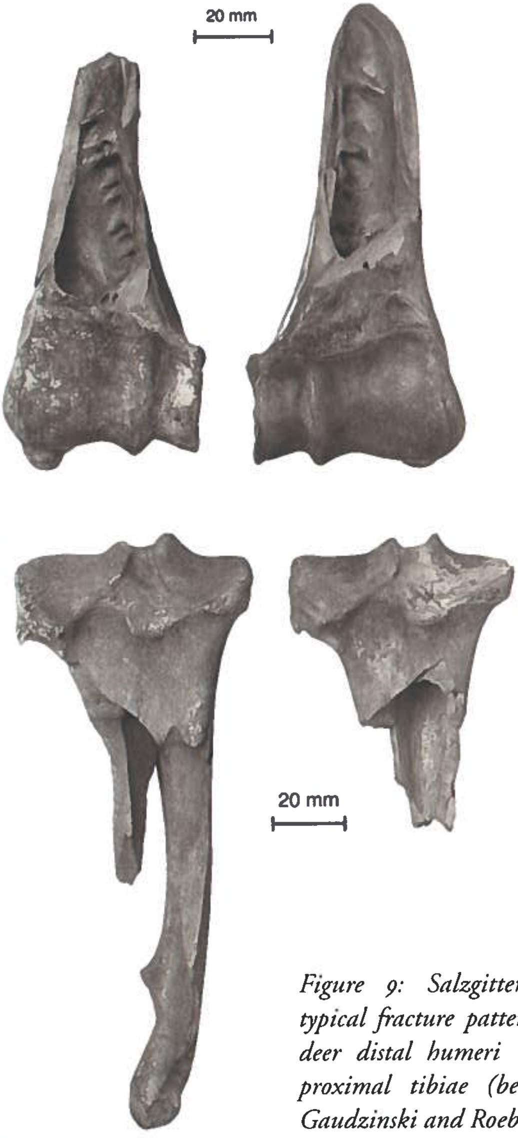

Figure 9: Salzgitter-Lebenstedt: typical fracture patterns for reindeer distal humeri (above) and proximal tibiae (below) (from: Gaudzinski and Roebroeks 2000).

During our recent excavations at Neumark-Nord 2, Wim Kuijper (Leiden) was able to retrieve charred plant remains from the main archaeological layer: fragments of hazelnut (*Corylus avellana*), of kernels of blackthorn (*Prunus spinosa)* (Fig. 10) and of acorns (*Quercus* sp.). Contemporaneous (Last Interglacial) find levels at the neighbouring site of Rabutz, studied before and during World War 1, yielded 11 burnt hazelnuts (Weber 1920; Toepfer 1957). While associated with archaeological finds, these findings do not constitute direct solid evidence for the dietary use of these plants by Neandertals.

Figure 10: Charred fragments of Prunus spinosa *(blackthorn) kernels from the Last Interglacial archaeological level at Neumark-Nord 2 (photo W. Kuijper) (largest fragment c. 0,5 cm).*

In an attempt to move beyond the bare observation that Neandertals hunted, Gerrit Dusseldorp (Leiden) studied the Neandertal archaeozoological record from an Optimal Foraging Theory (OFT) perspective. OFT states that organisms forage in such a way as to maximize their energy intake per unit time. In other words, they behave in such a way as to find, capture and consume food containing the most calories while expending the least amount of time possible in doing so. Applications of OFT models to hunter-gatherers have been helpful in quantifying predator-prey relationships and to understand the prey choices made by groups in different types of environments and how these structure hunter-gatherer diversity (Kelly 1995). Applying OFT is already a difficult enterprise in real time, but applying it to the Neandertal record entails a considerable amount of problems to be dealt with (Dusseldorp 2009). Nevertheless, given what we know about Neandertal biology and behaviour and given the data on their natural environment, it is possible to predict which prey species they will exploit in which order in a given environment. By comparing that ranking to the archaeological record, one is in fact "coaxing history to conduct experiments" (Deevey 1969). Dusseldorp's exploratory PhD-study focused on two large faunal Middle Palaeolithic assemblages from cool-temperate to warm-temperate periods: Biache-Saint-Vaast in northern France (MIS 7-6, 250-180 ka approximately) and Taubach in Germany (Last Interglacial, MIS 5^{e}, 125-115 ka). At both sites, Neandertals focused on the large mammals available, save for the largest ones, the elephants, which they seem to have avoided. Neandertal prey animals included the (dangerous) brown bear, which was exploited both at Biache-Saint-Vaast and at the full interglacial site Taubach - judging from the distribution of cutmarks at both sites also for their skin. The differences between the fully forested (Last Interglacial) environment at Taubach and the more open (but wooded) Biache-Saint-Vaast environment is neatly reflected in the exclusive focus on solitary animals at Taubach, a good illustration of Neandertal capacities to adapt to the poorer interglacial biotopes, as discussed above. In more open environments they may have shifted their attention to more gregarious animals, culminating in the successful hunting of herd animals such as reindeer in the Last Glacial. Apparently, Neandertals were efficient and flexible hunters, experts at using knowledge of landscapes and animal behaviour to ambush and kill large and dangerous prey species in a wide range of environments.

NEANDERTAL TECHNOLOGY

Judging from their archaeological record, they accomplished these hunting activities with a very simple technology, dominated by simple cutting tools, with little change over time and place and by wooden thrusting and/or throwing spears, the best examples of which come from the Schöningen site discussed above. Hartmut Thieme has uncovered eight spears thus far, 1,8 to 2,5 m long and 29-50mm in diameter. While five were made out of individual spruce, one was made out of pine (Thieme 1997). Given the fact that their maximum thickness and weight is situated at a third of the way from the tip, these spears have been interpreted as javelins (Rieder 2000), though others have opted for a close quarter thrusting weapon interpretation (Shea 2006). The yew spear uncovered amongst the remains of an elephant at Lehringen dates to the last interglacial, and is at least 200,000 years younger than the Schöningen assemblage (Adam 1951, Thieme and Veil 1985). Stone-tipped spears may also have been a part of Neandertal hunting weaponry, at least already from MIS 6 onward (Villa and Lenoir 2009), but good evidence for projectile – long-range - weapons has not been recovered from a Neandertal context. Their spears may indeed have been thrown and successfully used up to a distance of 15 m (Villa and Lenoir 2009), but compared to Upper Palaeolithic modern humans, the Neandertal way of hunting looks more geared towards close encounter hunting, in which their heavy and muscular bodies were part of the hunting equipment. Some researchers have indeed suggested that their limb structure might signal short bursts of great power. This "close quarter hunting" interpretation agreed nicely with the unusual pattern of injuries in Neandertal skeletal remains, which is thought to be somewhat similar to extant rodeo rider traumas (Berger and Trinkaus 1995). New research (Hutton Estabrook 2009) challenges this interpretation of the Neandertal record though. In a test of the Berger and Trinkaus interpretation, Hutton Estabrook found no evidence that Neandertals experienced trauma more frequently or differently through their body beyond present day hunter-gatherers, nomads and semi-nomads and medieval farmers: "Therefore, the assertion that trauma played a more influential role in the lifeways of Neandertals than any of these other groups is not supported by the data. These results imply Neandertals possessed a higher degree of cultural and/or physical adaptation to mitigate their environmental stresses than previously suggested by some of the research into their trauma" (2009: 436).

As discussed by Villa and Lenoir (2009), ethnographic and historic data suggest that in historic times thrusting and throwing spears were mainly used for hunting medium-sized and large mammals. In that sense, Neandertal hunting weapons and their archaeozoological record make a perfect match. Many of the faunal assemblages indicative of hunting activities come from sedimentary settings that hominins may have used to disadvantage prey animals before killing them at close range with their spears. For instance, the Schöningen finds were recovered from the borders of a former lake, which may have been used to disadvantage prey animals (L.R. Binford, pers. comm. 2000, Voormolen 2008). Given their technology and the large size of their (sometimes dangerous) prey animals, close cooperation between individual hunters may have characterized Neandertal subsistence strategies.

Neandertals were very regular users of fire, as testified by the abundant presence of heated flints, charred bones and charcoal at many of their sites from at least 300 ka onward (Roebroeks 2007). In fact, they used fire as a tool in a way which is (erroneously) seen by some as unique to modern humans. For instance, a recent study (Brown et al. 2009) suggests that early modern humans at the site of Pinnacle Point in Southern Africa regularly employed heat treatment to increase the quality and efficiency of their stone tool manufacture process, 72,000 years ago. The authors further infer that the technology required a novel association between fire, its heat and a structural change in stone with consequent flaking benefits that demanded "…an elevated cognitive ability". They also suggest that as these early modern humans moved into Eurasia, their ability to alter and improve available raw material and increase the quality and efficiency of stone tool manufacture may have been a behavioral advantage in their encounters with the local Neandertals.

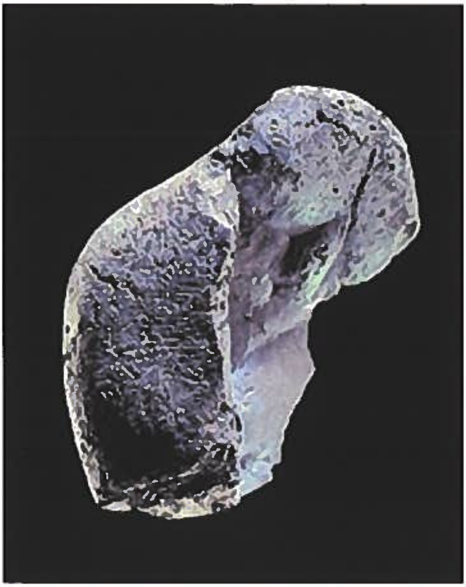

Figure 11: A small piece of birch bark pitch from Königsaue A, Germany. Used as a haft for a flint flake, the negative scars of the flint flake it once enveloped are still visible on its inside (max. dimension c. 3 cm - © Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt, Juraj Lipták).

With this interpretation Roberts et al. ignore the published evidence regarding Eurasian Middle Palaeolithic pyrotechnology. Two well-documented cases of fire-related production of adhesives suggest that Neandertals had a degree of mastering of fire that transcended the comparatively simple process of heating of stone for improvement of flaking quality. The usage of various types of synthesized adhesives to fix implements to their hafts was common in Neandertal technology, as shown by a series of recent studies of biomolecular traces of such hafting as well as polish on stone tools resulting from contact with hafting adhesives. Boëda and colleagues presented Mousterian tools with traces of bitumen on their surfaces, excavated at the site Umm El Tlel (Syria), on the southern edge of the Neandertal world (Boëda et al. 2008, Boëda et al. 1996, Boëda, Geneste, and Griggo 1999). These artefacts come from two sets of find layers, one dated to around 42 ka, one to around 70 ka. Two-third of a large sample of Levallois flakes (n=300) proved to have micro-traces of a black substance that gas-chromatography-mass spectrometry studies showed to be natural asphalt, the source of which was at 40 km east of the site. After collecting, the raw bitumen had been subjected to high temperatures.

A site on the northern side of the Neandertal range shows evidence suggestive of Neandertal "High-Tech"-procedures in the production of adhesives (Koller, Baumer, and Mania 2001).The site is Königsaue and the levels from which the finds derived are thought to be from the early part of the last glacial period, over 80,000 years old (see Koller et al. 2001 for discussion). Mania's fieldwork at Königsaue produced two pieces of pitch, one (Fig. 11) showing a fingerprint as well as the imprint of a stone tool and the structure of wood cells (Grünberg 2002). Chemical analysis demonstrates that the material is birch bark tar. Koller et al. stress that chemically comparable pitches can easily be produced with modern technical methods, e.g. by using air-tight laboratory flasks and temperature control facilities, within a small temperature interval, from between a minimum of 340°C to a maximum of 400°C, and in the absence of oxygen. At lower temperatures, no tar is produced, while higher temperatures will destroy any tar that may have formed. How this was actually achieved by Neandertals (and later prehistoric modern humans) is not known (Pollard and Heron 1996). Comparable finds reported from the Italian site of Campitello Quarry (Mazza et al. 2006), show that the deliberate selection and production of birch bark tar is a practice that can be followed back into the Middle Pleistocene, to MIS 7 at least. The birch bark tar finds briefly mentioned here do testify to the pyrotechnological knowledge of Neandertals from at least MIS 7 onward, i.e. roughly coinciding with the significant "boom" in the occurrence of burnt flint artefacts in the Neandertal archaeological record (Roebroeks 2007). By the current state of affairs, Neandertals used fire as an engineering tool to synthesize birch bark tar tens of thousands of years before some modern humans at Pinnacle Point decided to put their stone raw material in it.

The record clearly shows that Neandertals hafted some of their tools. Many archaeologists consider the development of hafting to mark a major watershed for both technology and "the human mind", as it brings together three separate elements into a single tool: the shaft, the stone tool (a point or a scraper/knife) and the haft itself (Wynn 2009). While at least some Neandertals did have a (thus far often neglected) hafted technology, not all modern humans did (see below).

NEANDERTALS IN SPACE

While Neandertal usage of fire is uncontested, their fires burnt in very shallow pits or usually on the surface of their camp sites only, as they invested very little in structuring their hearth places or their camp sites in general. In fact, from the whole of the Middle

Palaeolithic we only know three cases of simple stone-lined fire places, all from the late Middle Palaeolithic, two in southern France (Les Canalettes and La Combette) and one (Vilas Ruivas) in Portugal. The ephemeral nature of their hearths fits in a general pattern of limited investment in space: if Neandertals constructed dwellings, judging from their record these too must have been very ephemeral ones (Kolen 1999). Nevertheless, even ephemeral structures such as simple windbreaks could have been highly effective aids to help them stay warm and may have conferred significant thermoregulatory benefits (Chu 2009).

The abundant data on the transport of raw materials in the Neandertal world display a pattern of limited investment in the transport of raw material. In some cases Neandertals did transport stone artefacts over large distances, up to several hundreds of kilometres, but these are very exceptional observations (Slimak and Giraud 2007). The recently reported 60 km transport of a pigment stained *Pecten* shell from Cueva Antón, Spain (Zilhao et al. 2010), fits the known transport pattern. The displacements of such rare pieces may have been embedded in regular subsistence related moves, as suggested by the striking transport differences between western and eastern parts of Europe (Féblot-Augustins 1999, Roebroeks, Kolen, and Rensink 1988) and by the consistent recurrence of exotic materials from specific sources over very long periods of time (Roebroeks and Tuffreau 1999). However, almost all the raw materials used at Lower and Middle Palaeolithic sites come from nearby sources, at less than five kilometres (Féblot-Augustins 2008, Geneste 1985, Roebroeks, Kolen, and Rensink 1988).

As for other "investments" in space, some Neandertals did bury their dead, which explains to some degree the rich skeletal record we have for this lineage. The first finds in the Neanderthal itself probably concerned a burial (Schmitz 2006), as seems to have been the case at Spy, in Belgium (Semal et al. 2009). Despite (or: because) of some healthy scepticism (Gargett 1989, Gargett 1999), it is now well established that burying dead individuals was a part of the behavioral repertoire of some Neandertals, though the intentions with which these disposal activities were performed are unknown: intentions do not fossilize, only actions do. The same applies to the indications for cannibalistic practices by Neandertals: we do know that they butchered conspecifics in ways in which they exploited other animals (Defleur et al. 1999), but the motives behind these activities are elusive. Two sites dating to different periods from the rich Atapuerca locality in Spain provide examples of the difficulties in interpreting evidence for cannibalistic practices and possible burial. At Atapuerca, cannibalistic activities are documented at TD6, dating to the end of the Early Pleistocene. Here it concerns the dismemberment of minimally eleven (*Homo antecessor*) individuals, most of them younger than ten years (Fernández-Jalvo et al. 1999). Members of the Atapuerca team have suggested that the (later) Sima de los Huesos assemblage, discussed above, owes its existence to a Middle Pleistocene burial ritual (Carbonell et al. 2003).

We do not know why Neandertals buried their dead, or why individuals were butchered, even though such practices have often been interpreted in "symbolic" terms. It is notoriously difficult to infer "symbolic behaviour" from prehistoric archaeological finds (Botha 2008) and beyond burials the Neandertal record has yielded very little material evidence to interpret in such speculative terms. Their usage of pigments is well attested (Soressi and D'Errico 2007). At Maastricht-Belvédère (The Netherlands) 14 small pieces of haematite (Fig. 12) were recovered from sediments that date to at least 250 ka (Roebroeks 1988). Many mundane "non-symbolic" explanations are possible and plausible for the presence of such pigments at hunter-gatherer sites, for instance their usage in the preparation of hides (Keeley 1980), for medicinal purposes (Velo 1984) or as a loading agent for adhesives (Wadley 2005).

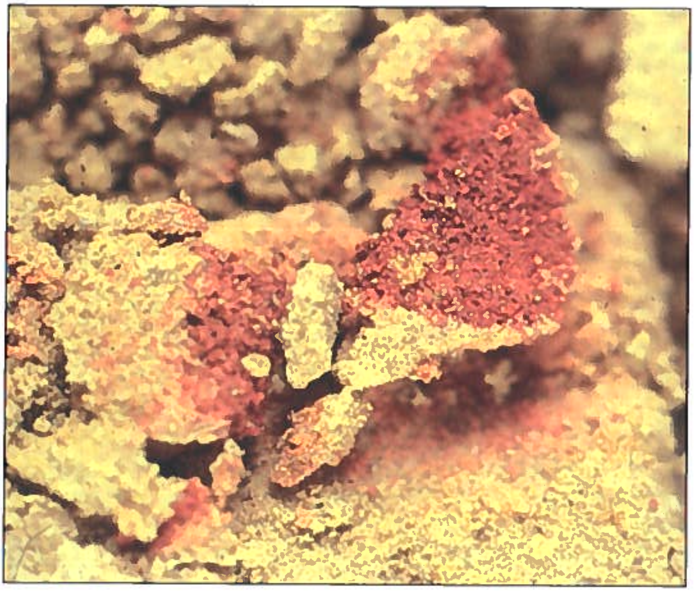

Figure 12: A concentrate of reddish material in the silty sand matrix of Site C (Maastricht-Belvédère). X-ray powder diffraction analyses by C. Arps showed that this "red ochre" stain was caused by haematite (size of fragment c. 1 cm, photo J. Pauptit)

There do exist a number of claims for personal ornaments being associated with the "transitional" industries of the latest Neandertals, such as the Châtelperronian (d'Errico et al. 1998). Álvarez Fernández and Jöris (2008) point out that these "Châtelperronian" ornaments come from a few find levels only, whereas more than 120 Châtelperronian sites are known from France and Spain. In their view all such finds derive from find layers which contain a mix of Aurignacian and preceding industries. Their study concludes that the earliest evidence for personal ornaments in the European record is related to the arrival of modern humans (Alvarez Fernandez and Jöris 2008). For the whole of the preceding odd million years *not one* unambiguous intentionally perforated or decorated object is known. From the start of the European Upper Palaeolithic, such items were made from a wide range of materials. Some of them, such as marine shells, testify to the existence of far flung social networks of exchange, distributed over hundreds of kilometers. In terms of personal ornaments and of "art", the Neandertal record is refreshingly sterile.

NEANDERTALS AND MODERN HUMANS

Table 1 gives a brief comparison of the record of Neandertals and modern human (Upper Palaeolithic) hunter-gatherers in Europe. It is well established that modern humans emerged in Africa, at approximately 200,000 years ago (McDougall, Brown, and Fleagle 2005). From there they dispersed over the Old World, and arrived in Europe at around 35,000 C14-years BP (see below). The broad picture is clear: Upper Paleolithic modern humans taken as a whole had a broader diet, invested more in various technological domains, including projectile technology and on-site structures, expanded their geographic range, and produced various forms of art, none of which has ever been recorded from a Neandertal context. The differences between these two records are usually interpreted in cognitive terms, with Neandertals being on the cognitively challenged, "non-linguistic", "non-symbolic"' side of the equation. While that is still a mainstream view, other explanations have stressed the importance of ecological differences between the two lineages for explaining the differences in their archaeological records (and/or the demise of the Neandertals). Verpoorte (2006) for instance focused on one of the most fundamental characteristics of any animal: its energetic requirements, and succeeded in explaining some of the peculiarities of the Neandertal record in this way. As mentioned above, Neandertal energetic requirements were considerably higher than those of Upper Paleolithic modern humans. These differences were caused by a range of factors, including Neandertals' larger body mass, high locomotion costs and their high activity levels. As a result, their strategies regarding mobility, investment in space, inhabiting northern environments (Verpoorte 2009), and innovation of technologies were selected under energetic constraints that were different from those of modern humans (Roebroeks and Verpoorte 2009, Verpoorte 2006). For instance, Verpoorte concluded that the trade-offs that the Neandertals faced implied that they had to move camp more frequently (as suggested by the archaeological record too) than with modern humans. Moving more frequently implies that the use-life of a camp site is shorter and camps are more ephemeral. With shorter anticipated use-life, one should expect less investment in site features, such as dwellings and other structures. Why invest energy in a structured hearth or dwelling if it is likely to be abandoned in a few days? Given the short periods of time Neandertals were present at "camp sites," their lack of investment in "site furniture" we so clearly see in the record becomes understandable. The absence of dwellings and other structures in the Middle Paleolithic record does not so much reflect a lack of organizational skills, planning depth, or "fully modern language" as some have stated, but rather an optimal solution to mobility under the high energetic constraints that Neandertals had to cope with.

European Late Middle Palaeolithic (125-40 ka)	**European Upper Palaeolithic (40-10 ka)**
Neandertals	Modern humans
Robust, energetically costly bodies [1,2]	Gracile, energetically less costly bodies [1,3]
Efficient hunters, relatively narrow focus on larger mammals [3,4,5]	Efficient hunters, with somewhat broader prey choice, including smaller game and fish [3,4,5]
Stable isotopes: top carnivores with heavy emphasis on larger mammals [6]	Stable isotopes: comparable to Neandertal signal, with some individuals consuming significant amounts of fish [6]
Distribution south of 55 degrees North [7]	Northward range expansion [7]
Lithic technology, including laminar reduction, discoidal and Levallois [7,8,9]	Variety of lithic reduction strategies, including bladelet production [7,9]
Thrusting spears, little investment in projectile technology [9]	Well-developed projectile technology in bone, antler, ivory, and stone [9, 10]
Very limited investment in on-site structures [9]	Structured hearths common[9]
Burials, without grave goods [8]	Elaborate burials [7]
Use of pigments [11,12]	Figurative portable and parietal art, personal ornaments[10]

Table 1: Biological, behavioral, and cultural comparisons between the late Middle Palaeolithic and the Upper Palaeolithic in Europe (Roebroeks 2008). References: 1 - Churchill, 2006; 2 - Sorensen and Leonard, 2001; 3- MacDonald et al. 2009 ; 4 - Hockett and Haws, 2005; 5 - Kuhn and Stiner, 2006; 6 – Richards and Trinkaus 2009; 7 - Roebroeks and Verpoorte 2009; 8 - Gamble and Roebroeks, 1999; 9 - Verpoorte, 2006; 10 - Mellars, 2004; 11 - Soressi and d'Errico, 2007; 12- Zilhao et al. 2010

EXIT NEANDERTALS

After a presence of a few hundreds of thousands of years in (western) Eurasia, Neandertals seem to have left the scene around 36,000 radiocarbon years ago, i.e. approximately around 41 ka (based on IntCal09: Reimer et al. 2009). That is just around the time when anatomically modern humans enter Europe (Jöris and Street 2008) as well as China (Shang et al. 2007). These recent years have seen some debate on the chronology of their disappearance, with claims for southern refuge areas in the Mediterranean younger than 30,000 calendar years BP and a supposed interstratification of Châtelperronian (Neandertal) and Aurignacian (modern human cultural) find levels at some sites pointing towards a significant period of *cohabitation* of the two species in Europe (Finlayson et al. 2006, Mellars 2004). All of these claims have proven to be weakly grounded though, and the latest direct and unproblematic dates for Neandertal skeletal remains yield radiocarbon ages of around 36,000, with the earliest modern human in Europe, from Pestera cu Oase (Romania), being slightly younger, from around 35,000 radiocarbon years (Jöris and Street 2008) – the Oase remains are contemporaneous with the remains of the first modern humans in China, from Tianyuam near Zhoukoudian (Shang et al. 2007).

The disappearance of the Neandertals is often seen as the result of "a straightforward case of direct competition for space and resources between the two populations, in which the demonstrably more complex technology and apparently more complex organization of the anatomically modern populations would have given them a strong competitive advantage over the Neanderthals" (Mellars 2004). How and why Neandertals disappeared from the Eurasian scene is not clear though, and not everybody would agree with Mellars' straightforward view of their disappearance. For instance, Relethford suggests that genetic data used to address the evolutionary relationship between archaic (including

Neandertals) and modern humans may be telling us more about the demographic rather than the phylogenetic history of our lineages (Relethford 2001, Relethford 2008). Given the larger human population size in Africa, over time Neandertals may have become extinct through genetic "swamping" of larger populations of modern humans moving into Europe. Under this model, the Neandertal gene pool could have been assimilated rather than replaced, even in the absence of the often envisaged major behavioral, cultural, and/or biological differences between the two hominin taxa. With the current dating evidence, it is even possible that modern humans moved into Europe and western Eurasia because Neandertals had disappeared there. After all, modern humans had been at the limits of the Neandertal range at the beginning of the Late Pleistocene already, at around 100 ka, in the Levant, which became (again) part of the Neandertal range later. In fact, from this perspective it took modern humans at least 50,000 years to move into the Neandertal core areas further north. And also striking is the fact that modern humans seem to have entered Australia a few thousand years before we see them appear in Europe. In this scenario, the disappearance of the Neandertals was nothing very special: just the final extinction in a longer series of regional extinctions that led to repeated significant reductions in population size and characterized their presence in the northern temperate latitudes.

Nevertheless, given what we know about the Neandertal record, and given the chronology of the transition including the fossil record discussed above (Jöris and Street 2008), the main factor instigating the disappearance of Neandertals seems to have been the arrival of a modern human competitor in the Neandertal stronghold of Western Eurasia (and maybe much further east), around 38,000–35,000 14C BP. These competitors required less energy and preyed upon the same animal species as Neandertals while at the same time broadening their diet to include species not commonly exploited by Neandertals. Some of them had a more diverse subsistence base as far as the archaeological record and some isotope studies suggest (Richards and Trinkaus 2009). This may have afforded them with selective advantages over the Neandertals with their dietary focus on large terrestrial mammals. In addition, Snodgrass and Leonard (2009) argue that high energy requirements and a diet associated with elevated metabolic costs and seasonal energy shortages would have had a strong impact on energy available for reproduction for Neandertals. Nutritional studies have shown that more diverse diets are linked to lower infant mortality rates and longer life expectancies (Hockett and Haws 2003, Hockett and Haws 2005). From this nutritional ecology perspective, Neandertal subsistence strategies would have been inferior to competition from other human populations consuming a diverse range of food types. ”In head-to-head competition, Neandertal populations consuming a lower diversity of essential nutrients would not have been able to maintain their genetic uniqueness in the face of healthier and longer-living AMHs populations - in short, the Neandertals would have been demographically swamped by the more reproductively-successful AMH populations” (Hockett and Haws, 2005: 30). A small demographic advantage in the order of a two percent difference in mortality could have resulted in the rapid extinction of the Neandertals, in approximately 30 generations (Zubrow 1989) – a dramatic illustration of the short (archaeologically undetectable) timescale over which small differences (in this case: biological parameters) can have major implications.

DISCUSSION

Neandertals were efficient and flexible foragers, who were present in (western) Eurasia for hundreds of thousands of years, surviving the large-scale changes brought upon this area by the alternation of glacial and interglacial periods. The Neandertal record reviewed here shows that they were experts at using knowledge of landscapes and animal behaviour to ambush and kill large and dangerous prey in a wide range of environments. That kind of flexibility is seen by various workers as a significant characteristic of modern human foragers, who in every environment consume the largest, highest quality and most difficult- to-acquire foods, using techniques that often take years to learn (Kaplan et al. 2007, MacDonald 2007). As with modern humans, the Neandertal adaptation was both flexible – as explained above – and also narrow and specialized in that it was based on extremely high investments in brain tissue and probably in learning. Given their simple technology, the motto "the more you know the less you need" might apply to Neandertals too. Though flexible, their dietary focus was rather narrow compared to modern humans, but becomes understandable if we take both their energetic requirements and their environmental contexts into consideration. We have also seen that they may have undergone many phases of regional extinctions, and that population numbers were probably sometimes very low, possibly even close to extinction, before they finally went extinct approximately 40,000 years ago.

The Neandertals as well as the modern humans of Table 1 are generalizations, homogenized standard hominins, reduced to some of the (inferred) archaeological characteristics of their species. Such comparisons can be heuristically valuable, but by focussing too much on the differences between the two meta-groups we do run the risk of overlooking the variation within the record of the two lineages. For instance, seen from a wider geographical perspective, the European Upper Palaeolithic record with its rich mobile and parietal art, is an outlier in the Palaeolithic world of modern humans, once described by Clive Gamble as the product of "arctic hysteria" (Gamble 1993). There is simply variability in the archaeological record of Pleistocene hunter-gatherers, as is the case with present-day foragers (Kelly 1995). Though less conspicuous, the record of the Neandertals also displays variability over the very large time and space of their existence. As an example, data from southern and northern populations indicate that they may have differed in their skeletal form, with somewhat more gracile individuals on the southern edge of their range (Aiello and Wheeler 2003), whereas differences in their diets have been suggested on the basis of faunal data (Barton 2000, Stiner et al. 1999). Dental microwear studies likewise suggest variation in Neandertal dietary habits, with some Neandertals resembling recent hunter-gatherers dependant on meat, others - southern European ones from more forested environments - indicating a more mixed diet (El Zaatari 2007). Given the large range size of Neandertals, such diversity is to be expected: conditions in the northern parts of their range could have led to the high-risk foraging strategies described above, while southern conspecifics may have exploited less risky resources, including more smaller mammals and plants.

Even more importantly, some modern human populations created archaeological records that display striking similarities to the Neandertal one (cf Roebroeks and Verpoorte 2009). A very interesting example of such a record comes from Pleistocene Tasmania, which was connected to the Australian mainland until the rise of sea levels at the end of the Pleistocene (Holdaway and Cosgrove 1997). The Tasmanian archaeological record shows that there was a Late Pleistocene population of modern humans who used a Middle Palaeolithic lithic technology, a non-hafted organic technology and hunted systematically and seasonally prey animals significantly smaller than Neandertals did. Like Neandertals, these modern humans did not construct stone-lined hearths or archaeologically visible dwelling structures, and they produced very little art, a few hand stencils only. Holdoway and Cosgrove (1997) pointed to the confounding nature of the Tasmanian Late Pleistocene and the Neandertal archaeological records for the debate on "Modern Human Behaviour". Tasmanians were modern humans, who as far as their archaeological record goes, were behaving very much like Neandertals did in Europe. On top of that, the Tasmanian record might be reflective of the whole Australian continent at 45 ka (O'Connell and Allen 2007). What separates the Tasmanians and the Neandertals are the clear differences in environmental structures and probably half a million years of evolutionary divergence. Nevertheless, the records are strikingly similar and these similarities in their technology, hunting behaviour, butchery and prey selection give us cause to re-evaluate the whole concept of "Modern Human Behaviour" (Cosgrove and Roebroeks in prep.). It has become too much of an abstraction, an untested projection into the past, of a homogenized view of what is in fact very diverse behaviour by modern (as well as earlier) humans, as shown by the Neandertal-Tasmanian "experiment". This experiment might be read as indicating that the Neandertal record as reviewed here falls within the variability of the modern human record, despite of several hundreds of thousands of years of separation.

Earlier I referred to Deevey's (1969) attempt to coax history to conduct experiments. Palaeoanthropologists can work with a huge database of millions of years of human evolution in their quest to understand how and why humans and human systems have evolved to work they way they do *now*. If we ask the right questions, we can use that database and let history run the experiments for us. Verpoorte's (2006) exploration of the role of energetics can be seen as such an experiment, like Dusseldorp's (2009) OFT studies of the Neandertal archaeozoological record, or the comparison of the Neandertal and Tasmanian record discussed above. In that latter case, we have an experiment with a time depth of about half a million years. Another such "experiment" will soon finish its first stage with the completion of the Neandertal nuclear genome, probably in 2010. Its detailed comparison to the human one will shed exciting light on the changes which occurred in our lineage in the last half million years. Thus far, geneticists could "only" observe the changes which accumulated in the six to seven million years since our split from the chimpanzee lineage – the Neandertal sequence will yield a reference point much closer in time and many data relevant to our recent evolution.

Much of the progress discussed in this paper is based on the more direct cooperation and exchange between a wide range of disciplines studying the history of the human niche: palaeolithic archaeology, primatology, biomolecular studies, nutritional studies and genetics, to mention but a few. All of these fields have become too large for an individual even to master only one of them – the amount of papers that become available on line in these fields almost every day is staggering. New disciplines will probably emerge as a result of this exponential generation of knowledge, just as in Darwin's days new fields came into existence from the vast ocean of new knowledge - Palaeolithic archaeology, for example (Gamble and Kruszynski 2009). As in Darwin's days, we can only make progress through cooperating, through integrating these endless landscapes of new knowledge, turning them into testable models of the past, thus coaxing history to conduct ever more exciting experiments on the evolution of the human niche.

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