

Human Palaeontology and Prehistory (Palaeopopulations, Palaeogenetics, Migrations)

Ebb and flow or regional extinctions? On the character of Neandertal occupation of northern environments

Jean-Jacques Hublin^{a,*}, Wil Roebroeks^b

^a Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany

^b Leiden University, Faculty of Archaeology, P.O. Box 9515, 2300RA Leiden, The Netherlands

Received 26 October 2008; accepted after revision 7 April 2009

Presented by Yves Coppens

Abstract

In the course of the last 500,000 years, the Neandertal lineage was the first human group to extensively colonize the middle latitudes of western Eurasia up to 55° N. Although Neandertals were able to adapt to a variety of environments, their ability to cope with extreme glacial environments seems to have been very limited. Depending on the climatic cycles, their presence in the northern environments was essentially discontinuous. The periodical abandonment of some areas is generally interpreted as resulting in a movement of northern populations into southern refuges and a subsequent recolonisation of the northern regions. Here, we argue that the current palaeo-ecological, archaeological and palaeogenetic evidence supports a model of local extinctions rather than a habitat tracking model. **To cite this article:** J.-J. Hublin, W. Roebroeks, C. R. Palevol 8 (2009).

© 2009 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

Résumé

Flux et reflux ou extinctions régionales ? Sur la nature du peuplement néandertalien dans les environnements septentrionaux. Au cours des derniers 500 000 ans, la lignée néandertalienne représente le premier groupe humain à coloniser de façon significative les moyennes latitudes d'Eurasie occidentale jusqu'à 55° N. Bien que les néandertaliens se soient adaptés à des environnements variés, leur capacité à survivre dans des environnements glaciaires extrêmes semblent avoir été très limitée. Au gré des cycles climatiques, leur occupation des zones septentrionales fut essentiellement discontinue. Ces abandons périodiques de territoires sont généralement interprétés comme un mouvement de populations vers des zones refuges méridionales, suivi par une recolonisation des zones septentrionales. En réalité, les données paléo-écologiques, archéologiques et paléogénétiques plaident en faveur d'un modèle d'extinctions locales, plutôt qu'en faveur d'un modèle de suivi des déplacements du biotope. **Pour citer cet article :** J.-J. Hublin, W. Roebroeks, C. R. Palevol 8 (2009).

© 2009 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

Keywords: Neandertal; Climate; Demography; Mousterian; Glaciation; Interglacial; Refuge

Mots clés : Néandertal ; Climat ; Démographie ; Moustérien ; Glaciation ; Interglaciaire ; Refuge

1. Introduction

The Neandertal lineage represents a human clade that separated from the one leading to extant humans about

* Corresponding author.

E-mail address: hublin@eva.mpg.de (J.-J. Hublin).

half a million years ago [20]. To date, it is exclusively documented in Eurasia; the Mediterranean seems to have played a crucial role in the segregation of the two clades. Although humans are documented in Eurasia since at least 1.7 my BP [37], the colonisation of the middle and high latitudes resulted from a long process. The few well-demonstrated sites of European Early Pleistocene human occupation are thus far only found in the Mediterranean area. With the exception of earlier brief episodes related to warmer climatic conditions [29], the Neanderthal lineage was the first to colonise northern temperate latitudes, up to 55° N, in a wide range of environmental settings. The exact limits of their range are difficult to outline, due not only to differences in site preservation but also to research history and intensity. These differences apply especially to their eastern limits, which have recently moved 2000 kilometers eastward, as a result of new genetic analysis of morphologically unidentifiable fossil skeletal remains [24]. The majority of their fossils have been unearthed in the westernmost parts of their range, but current views of ‘core’ and ‘marginal’ areas in their distribution may change through future fieldwork in Asia. Distribution maps like those published by Krause et al. [24] are coarse-grained palimpsests, compounding many phases of range expansion and contraction on maps that give only a rough approximation of the former distribution of the species. Within these rough limits, Neanderthal presence must have varied, from continuous presence in some limited areas up to periodical excursions into many others, with total abandonment when environmental conditions deteriorated. This ‘ebb and flow’ of occupation has been well documented in the westernmost part of the Neanderthal world, where more than one and a half centuries of multidisciplinary studies of the fossil and archaeological record have created a rich database on Neanderthal presence and absence, especially detailed for the Late Pleistocene, i.e. from MIS 5e to MIS 3. The record from this time range is very rich in northern France, where large-scale excavations over the last three decades have uncovered more than 50 late Middle Palaeolithic sites between the valleys of the Somme and Meuse rivers.

Neanderthal sites are usually retrieved from sediments deposited in cool to cold environments. This should not come as a surprise, as 95% of the last 0.5 my witnessed colder conditions than the present day ones, with the exceptions of the interglacials MIS11 and MIS 5e. Partly because of this climatic environment and partly because of limited technological ways to respond to thermic stress, known postcranial Neanderthal remains are generally interpreted as demonstrating cold-adapted body proportions [19,44]. However, data from north-

western Europe show that Neanderthals were able to adapt to a wide range of environments, from full interglacial conditions such as at Caours (France) [2] and from the present excavations at Neumark-Nord (Germany) [14] to significantly colder contexts, as at Beauvais and Hénin-sur-Cojeul (France) [26]. Meanwhile, Neanderthals are absent in most of northwestern Europe at the peak of glacial events. The archaeological record shows important hiatuses in the presence of Middle Palaeolithic hominins, especially during the pleniglacial climatic conditions of MIS 4 (as well as for earlier colder periods, e.g. MIS 6), which cannot be explained by taphonomic processes, as these are the periods with the highest rate of loess formation, and hence the best preservation potential.

The standard explanation for this distribution pattern is that contraction of the habitable areas would have led to the displacement of Neanderthal populations into refuges, which are usually inferred to have been in the “South”. Middle Palaeolithic hominins would have tracked their preferred habitats, ‘overwintered’ the cold climatic conditions in southern areas, and recolonised the northern plains when environmental conditions ameliorated. This ‘ebb and flow’ of populations would explain the great richness of Neanderthal fossils in the south. For example, in France the majority of the 56 Late Pleistocene Neanderthal specimens were found in the southern half [28]. More importantly, archaeological data from southern France, and specifically from Aquitaine, suggest that there was always a hominin presence between approximately 350 and 35 ka, in glacial as well as interglacial settings [48]. And this pattern survived into the last glacial maximum, after anatomically modern humans replaced the Neanderthals in Europe [4].

For the colder phases of the glacial-interglacial cycles, we have indications that large parts of the Neanderthal range in northern Europe were deserted, with Neanderthals maintaining core populations in the south. However, one can question the evidence for the ‘ebb and flow’ pattern of Neanderthal peopling with northern Neanderthals moving southward to refuges, from which the north was colonised again. What are the arguments for such two-way hominin traffic, caused by expansion and contraction of available territory? If, for argument’s sake, we assume that the south harboured refuge areas, were the southern regions accessible for the northern populations? After all, there were already Neanderthals living in the south. Here we suggest that it is worthwhile to investigate an alternative hypothesis to the habitat tracking model: northern populations may simply have gone extinct.

2. Neandertal ecology and demographic pattern

Recent advances in the understanding of Neandertal ecology provide us with some arguments to test the two alternatives. Neandertals were large-bodied hominins with an average body mass surpassing that observed in most recent human populations. Even when compared to Palaeolithic modern Europeans, the estimated lean body mass of Neandertals is, on average, about 10 to 13 kg above the body mass of early and late Upper Palaeolithic humans [38]. Their bodies displayed pronounced musculature and varying levels of postcranial robusticity, especially high in the upper part of the body and in relation to manipulation activities [45]. This postcranial robusticity is related to a high level of activity generating intense biomechanical stress [8], but likely also partly related to Neandertals' adaptation to colder environments [31]. The Neandertals' large body mass and ecogeographical niche resulted in a costly body requiring a high basal metabolic rate (BMR). In addition, experimental studies and modeling show that their stockier proportions and shorter limbs implied a high energetic cost for mobility through the landscape, making food acquisition more costly [43,53]. Various computations have been produced to estimate their BMR and their daily energy expenditure (DEE) [1,7,41,42]. These estimates are always higher than those observed in recent hunter-gatherer populations. Churchill [7] estimates the Neandertal DEE between 3500 and 5000 kcal per day, widely above the DEE for extant recent hunter-gatherers from the circumpolar regions, which range between 3000 to 4000 kcal per day for males [42]. On top of the regular DEE, the energetic costs for growth and reproduction may have been significantly higher than the extant values. Because of the larger body size of the offspring, female Neandertals' energy requirements for reproduction (gestation and lactation) must have been relatively high compared to Upper Paleolithic and more recent humans. For the offspring itself, energy requirements for growth after weaning must have been higher due to larger body size and to likely faster growth [33,40]; these requirements must have been fulfilled by the group.

These high energetic costs have a number of consequences regarding Neandertal ecology. Zooarchaeology provides us with the picture of efficient and flexible hunters mostly preying on large mammals with little exploitation of small game in most sites. Neandertals primarily relied on animal meat and on fat for their daily subsistence, and isotopic studies reinforce this picture [34]. In the middle latitudes, the proteins consumed by Neandertals were overwhelmingly of animal origin during cold periods as well as during the last interglacial [3].

Neandertals therefore appear to be highly carnivorous and at the top of the continental trophic chain.

Another possible consequence of their high DEE is their high residential mobility. Following Verpoorte [49], MacDonald et al. [27] have argued that because of the combination of a high DEE (at least 10% higher than that of Upper Palaeolithic modern humans), which included higher locomotion costs, Neandertals had a comparatively reduced effective foraging radius compared to Upper Palaeolithic modern humans. In a central-place foraging model, this radius is defined as the distance from a residential camp to the foraging patch at which the required amount of energy is equal to the net return of resources at that distance [49]. A shorter effective foraging radius implies a shorter occupation time per site and hence a higher residential mobility. According to MacDonald et al. [27], this may at least partly explain the low level of investment in on-site structures in the European Middle Palaeolithic.

All of these parameters also suggest that Neandertal population density must have been very low, including in the so-called refugial zones such as southwestern France, where a continuous occupation is observed. One expects Mousterian population densities in Europe to have been significantly lower than those of Upper Palaeolithic modern humans. In addition to purely biological and ecological factors previously exposed here, technological differences between the two periods have to be taken into account. Attempts have been made to estimate European population size by combining the archaeological evidence for the character of occupation and modern densities of hunter-gatherers in temperate to cold latitudes. Such estimates obviously depend on a large number of assumptions, but their heuristic value is unambiguous. For the Upper Palaeolithic, Bocquet-Appel et al. [5] estimate that from the Aurignacian to the Glacial Maximum, the European metapopulation remained in a positive quasi-stationary state, with about 4400–5900 inhabitants (95% confidence interval (CI95%): 1700–37,700 inhabitants). Estimates for the Mousterian are also predictably very low. With the size of the foraging area per group of 25 individuals around 80–100 km in diameter as suggested by the pattern of raw material transportation, Richter [36] computed the likely population size between 470 and 750 for the 'Mousterian of Acheulean tradition' distribution and between 1240 and 1940 for the MIS 3 Central European Micoquian.

Neandertals were costly organisms and top carnivores for which the carrying capacity of the environment was limited. It is therefore unlikely that refuge zones could have accommodated sizable intrusive groups during periods of climatic deterioration that caused

depopulation of northwestern Europe. Rather than resulting in an ‘ebb and flow’ movement of Neandertal populations tracking their preferred habitats, the periodic reduction of available areas could have instead led to an alternation of periods of extinction of northern populations and recolonisation of the northern areas by populations from the south. After each extinction in the north, a non-random sample of Neandertals survived in the south, and it was this population that produced the colonisers of the north once conditions improved. If this hypothesis [20,22] is correct, contraction of the available areas would have been accompanied by significant reduction of Neandertal population size. Repeated regional extinction of Neandertal populations would have led to repeated genetic bottlenecks. The two hypotheses, habitat tracking and regional extinction, allow a series of predictions that can be tested or discussed in the light of three sources of evidence: the archaeological record, Neandertal palaeogenetics and animal models.

3. The archaeological evidence for population movements

The archaeological record contains unambiguous data relating to the presence and absence of Neandertals in specific parts of their range, with an especially rich record in the west. As mentioned above, data gathered there show that Middle Palaeolithic Neandertals deserted the northern parts of their range during the colder parts of the last glacial cycle. The signal from more southern parts of Europe, such as the Aquitaine basin, suggests that Neandertals were there on a continuous basis, both in interglacial as well in glacial periods [48]. In fact, the largest number of sites there date to MIS 6 and MIS 4, but that could to some degree be a result of more favourable sedimentation processes in the colder periods of the glacial-interglacial cycles.

Raw material transport data as well as recent strontium isotope studies [35] have informed us about the distances covered by Neandertals. Occasionally stone artefacts were transported over very large distances, in both western and central Europe up to a few hundred kilometers [39], but these observations relate to very exceptional finds [12]. More importantly here, while both types of evidence relate to ‘movements’ of Neandertals, they do not allow us to discriminate between the two hypotheses.

Another piece of evidence consists of an observation made by various workers [10,46] for the late Middle Palaeolithic record of northwestern Europe. There, in the beginning of the last glacial period, one observes

lithic assemblages different from the ‘usual’ Middle Palaeolithic in this area. They are characterized by a developed blade technology, with *lames à crêtes* and core tablets. The earliest traces of this technology are found at Seclin (northern France), where they have TL ages of approximately 80–100 ka [47]. Other sites with this kind of typical blade technology are Bettencourt and Fresnoy-en-Val, likewise dating to MIS 5 [25]. With the occupational hiatus of MIS4 this technology disappears completely in northern France, nor does one find evidence of it further south at the fringe or within the Aquitanian basin. It did not resurface with the recolonisation of these northern areas after MIS 4, thought to have been accomplished by bearers of other ‘cultural traditions’ [10]. The prominent presence of Levallois points in Early Weichselian (MIS 5) assemblages here likewise ends with the Lower Pleniglacial (MIS 4) occupational hiatus [15]. Although not conclusive, these observations do not support the habitat tracking model.

4. The paleogenetic evidence

The “regional extinction” model has implications for the Neandertal genetic pool. Considering the low level of population density in Europe until the end of the last glacial maximum [5], regional extinctions in the less favourable areas during climatic crisis would have resulted in genetic bottlenecks and, as proposed by one of us [20], in significant genetic drift episodes.

The study of Neandertal mitochondrial DNA (mtDNA) brings some support to the notion that Neandertal metapopulation suffered genetic bottlenecks. Effective population size and genetic variability are low in extant humans when compared to those observed in most living species of great apes, a puzzling finding given our much larger population size [13,23]. However, Neandertals show an even lower genetic diversity when compared to *Homo sapiens* as a whole. Estimates based on mean pair differences (MPD) within the mtDNA HVRI suggested that Neandertals (MPD=5.5) had an effective population size similar to that of modern Europeans (MPD=4.0) or Asians (MPD=6.3), but lower than that of modern Africans (MPD=8.1) [24]. The recent publication of the complete mtDNA sequence [16] provides more evidence that purifying selection in the Neandertal mtDNA was reduced compared to other primate lineages, and that they had an effective population size smaller than that of modern humans. Furthermore, when the easternmost Neandertal mtDNA sequences from Teshik Tash (Uzbekistan) and Okladnikov (southern Siberia) are compared to those of other Neandertals in the Caucasus and in western Europe, the Teshik Tash

mtDNA sequence seems to be more closely related to the mtDNA sequence from Scladina (Belgium) in western Europe than to the sequence from Okladnikov mtDNA [24]. More Neandertal mtDNA sequences will be necessary to shed light on this pattern. However, the lack of deep mtDNA divergence between central Asian Neandertals and western European ones suggests a short time of separation and a recent colonisation or recolonisation of the easternmost parts of the Neandertal range (*contra* [11]).

The likelihood of narrower genetic bottlenecks in Neandertals is also supported by phenetic analysis. Weaver et al. [54] used a series of statistical tests based on 37 standard cranial measurements from a sample of 2524 modern humans from 30 populations, and 20 Neandertal fossils. Results of modern human cranial measurements were compared to those in a genetic dataset consisting of 377 microsatellites typed for a sample of 1056 modern humans from 52 populations. The role of stabilizing selection in the two groups, and the importance of selection in the diversification of behavioural, physiological, or other morphological features (especially in relation with climatic adaptation) cannot be dismissed. However the results of these tests lead to the conclusion that, regarding cranial morphology, genetic drift is the most strongly supported explanation for the differences between Neandertal and modern human lineages that rapidly accumulated through time.

5. Animal models

The pattern of low genetic diversity seen in Neandertals is also found in other carnivores in Europe. Although recent intense hunting is sometimes considered a possible cause for regional low genetic diversity [17], a similar pattern is observed in all of northern Europe. Little or no mtDNA variability and low to moderate microsatellite variability are observed in otters, wolves, wolverines and lynxes in northern Europe [6,17,52]. This is most likely explained as the result of the expansion out of one southern refuge at the end of the last glacial maximum and of a subsequent bottleneck. The only northern species of carnivore that displays to some extent a higher level of genetic diversity is the brown bear [51]. This ‘bear case’ is interpreted as the result of two separate waves of recolonisation after the last glacial maximum. One started from a Spanish refuge and another from eastern Europe, the two meeting and forming a hybrid zone in Scandinavia [18].

Alopex lagopus, the arctic fox, provides us with the reverse example, as it is a species currently limited to Scandinavia and northern Siberia, but with a consid-

erable southern range of expansion during the colder conditions of MIS 2. In this case, palaeogenetics allow us to observe the result of a dramatic contraction of their habitat, possibly somewhat analogous to the Neandertals case discussed above, though in an opposite direction. The question is whether the populations outside of the extant Holocene refuges – including final Pleistocene specimens from Magdalenian sites in the German Rhineland – contributed to the genetic composition of the current population. The results of an ancient mitochondrial DNA study by Dalén et al. [9] demonstrate that the arctic fox became extinct in mid-latitude Europe at the end of the Pleistocene and did not track its habitat when it shifted to the north. The populations that survived in Scandinavia and Siberia represent a distinct genetic lineage.

6. Discussion and conclusion

The straightforward view of two-way traffic of ancient hominin populations does not fit with what we have come to know about the ecology of Neandertals, with the palaeogenetic and comparative evidence nor, to a lesser degree, with their archaeological record. The Neandertal lineage has a deep ancestry, as indicated by genetic studies as well as by the study of their fossil record. With the first substantial occupation of temperate Pleistocene Eurasia from the Middle Pleistocene onward, the pattern of regional extinction and recolonisation sketched here may have become an important demographic factor in the history of humankind, possibly for the first time at such a large scale. Further refining and testing the hypotheses sketched here will only be possible by integrating the data produced by the various disciplines that study the development of the human niche. For the time being, the hypothesis of regional extinction is difficult to fully demonstrate. In effect, the importance of both processes, habitat tracking and regional extinctions, may have varied between regions of the Eurasian continent, or have co-occurred in combinations dictated by a wide variety of factors. However, in light of the available evidence, regional extinction of populations exposed to environmental degradation was likely the main mechanism at work in Eurasia during the Pleistocene climatic cycles and the subsequent fluctuations of Neandertal metapopulation size. Primarily because Neandertals were top carnivores requiring a large territory per unit, their presence seems to have been characterized by a very low density and a chronologically discontinuous occupation, except in some limited areas. Indeed the pattern of their low genetic variability is reminiscent of those observed in other species of large

carnivores in the same latitudinal range. Although Neandertals could adapt to varied environments, it is not until the expansion of modern humans to the high latitudes that ominins were able to colonize arctic environments [30,32]. The presence of modern humans in northern environments must also be characterized as highly ‘discontinuous’, with major parts of their northern ranges being deserted around the Last Glacial Maximum [50]. However, their biological and cultural adaptations may have set less severe constraints on their range limits than was the case with Neandertals.

The ‘regional extinctions’ hypothesis discussed here has strong implications in terms of Neandertal evolutionary mechanisms. It explains their low genetic diversity and the importance of drift in the course of their evolution. Rather than the usually envisaged ‘ebb and flow’ of Neandertal occupation, repeated phases of regional extinction and subsequent colonisation may have been an important demographic factor in the emergence and subsequent development of the Neandertal lineage, including its final demise [21].

Acknowledgments

We are grateful to P. Depaepe and J.-L. Locht, the organisers of the *Journées SPF* at Amiens (F), March 28–29, 2008, devoted to the interpretation of the Palaeolithic record of northwestern Europe, as this venue led to a series of inspiring discussions which formed the core for this paper.

References

- [1] L.C. Aiello, P. Wheeler, Neandertal thermoregulation and the glacial climate, in: T.H. van Andel, W. Davies (Eds.), *Neandertals and modern humans in the European landscape during the last glaciation*, McDonald Institute for Archaeological Research, Cambridge, 2003, pp. 147–166.
- [2] P. Antoine, N. Limondin-Lozouet, P. Auguste, J.-L. Locht, B. Galheb, J.-L. Reyss, É. Escudé, P. Carbonel, N. Mercier, J.-J. Bahin, C. Falguères, P. Voinchet, Le Tuf de Caours (Somme, France): Mise en évidence d’une séquence Eemienne et d’un site paléolithique associé, *Quaternaire* 17 (2006) 281–320.
- [3] H. Bocherens, D. Billiou, A. Mariotti, M. Toussaint, M. Patou-Mathis, D. Bonjean, M. Otte, New isotopic evidence for dietary habits of Neandertals from Belgium, *J. Hum. Evol.* 40 (2001) 497–505.
- [4] J.-P. Bocquet-Appel, P.Y. Demars, Populational kinetics in the Upper Palaeolithic in Western Europe, *J. Archaeol. Sci.* 27 (2000) 551–570.
- [5] J.-P. Bocquet-Appel, P.-Y. Demars, L. Noiret, D. Dobrowsky, Estimates of Upper Palaeolithic meta-population size in Europe from archaeological data, *J. Archaeol. Sci.* 32 (2005) 1656–1668.
- [6] I. Cassens, R. Tiedemann, F. Suchentrunk, G.B. Hartl, Brief communication: Mitochondrial DNA variation in the European otter (*Lutra lutra*) and the use of spatial autocorrelation analysis in conservation, *J. Hered.* 91 (2000) 31–41.
- [7] S.E. Churchill, Bioenergetic perspectives on Neandertal thermoregulatory and activity budgets, in: K. Harvati, T. Harrison (Eds.), *Neandertals revisited: New approaches and perspectives*, Springer, Dordrecht, 2006, pp. 113–134.
- [8] S.E. Churchill, J.A. Rhodes, How strong were the Neandertals? Leverage and muscularity at the shoulder and elbow in Mousterian foragers, *Period. Biol.* 108 (2006) 457–470.
- [9] L. Dalén, V. Nyström, C. Valdiosera, M. Germonpre, M. Sablin, E. Turner, A. Angerbjörn, J.L. Arsuaga, A. Götherström, Ancient DNA reveals lack of postglacial habitat tracking in the arctic fox, *Proc. Natl. Acad. Sci. USA* 104 (2007) 6726–6729.
- [10] P. Depaepe, Le Paléolithique moyen de la vallée de la Vanne (Yonne, France): matières premières, industries lithiques et occupations humaines, Éditions SPF (2007) 299 p.
- [11] V. Fabre, S. Condemi, A. Degioanni, Genetic evidence of geographical groups among Neandertals, *PLoS ONE* 4 (2009) e5151.
- [12] J. Féblot-Augustins, Raw material transport patterns and settlement systems in the European Lower and Middle Palaeolithic: continuity, change and variability, in: W. Roebroeks, C. Gamble (Eds.), *The Middle Palaeolithic occupation of Europe*, University of Leiden, Leiden, 1999, pp. 193–213.
- [13] P. Gagneux, C. Wills, U. Gerloff, D. Tautz, P.A. Morin, C. Boesch, B. Fruth, G. Hohmann, O.A. Ryder, D.S. Woodruff, Mitochondrial sequences show diverse evolutionary histories of African hominoids, *Proc. Natl. Acad. Sci. USA* 96 (1999) 5077–5082.
- [14] S. Gaudzinski, W. Roebroeks, On Neandertal subsistence in last interglacial forested environments in northern Europe, in: N. Conard, J. Richter (Eds.), *150 years of Neandertals*, Springer, in press.
- [15] E. Goual, Définitions, analyses et caractérisations des territoires des Néandertaliens au Weichselien ancien en France septentrionale (Approches technologiques et spatiales des industries lithiques, élargissement au Nord-Ouest de l’Europe). Lille, Thèse, Université des Sciences et Technologies de Lille, 2008.
- [16] R.E. Green, A.-S. Malaspina, J. Krause, A.W. Briggs, P.L.F. Johnson, C. Uhler, M. Meyer, J.M. Good, T. Maricic, U. Stenzel, K. Prüfer, M. Siebauer, H.A. Burbano, M. Ronan, J.M. Rothberg, M. Egholm, P. Rudan, D. Brankovic, Z. Kucan, I. Gusic, M. Wikstrom, L. Laakkonen, J. Kelso, M. Slatkin, S. Paabo, A complete Neandertal mitochondrial genome sequence determined by high-throughput sequencing, *Cell* 134 (2008) 416–426.
- [17] L. Hellborg, C.W. Walker, E.K. Rueness, J.E. Stacy, I. Kojola, H. Valdmann, C. Vila, B. Zimmermann, K.S. Jakobsen, H. Ellegren, Differentiation and levels of genetic variation in northern European lynx (*Lynx lynx*) populations revealed by microsatellites and mitochondrial DNA analysis, *Conserv. Genet.* 3 (2002) 97–111.
- [18] G.M. Hewitt, The genetic legacy of the Quaternary ice ages, *Nature* 405 (2000) 907–913.
- [19] T.W. Holliday, Postcranial evidence of cold adaptation in European Neandertals, *Am. J. Phys. Anthropol.* 104 (1997) 245–258.
- [20] J.-J. Hublin, Climatic Changes, Paleogeography, and the evolution of the Neandertals, in: Takeru Akazawa, Kenichi Aoki, Ofer Bar-Yosef (Eds.), *Neandertals and modern humans in western Asia*, Plenum Press, New York, 1998, pp. 295–310.
- [21] J.-J. Hublin, What can Neandertals tell us about modern origins? in: P. Mellars, K. Boyle, O. Bar-Yosef, C. Stringer (Eds.), *Rethinking the human revolution*, McDonald Institute for Archaeological Research, Cambridge, UK, 2007, pp. 235–248.

- [22] J.-J. Hublin, Origine et évolution des Néandertaliens, in: B. Vandermeersch, B. Maureille (Eds.), *Les Néandertaliens. Biologie et Cultures*, Éditions du CTHS, Paris, 2007, pp. 95–107.
- [23] H. Kaessmann, V. Weibe, G. Weiss, S. Paabo, Brief communication: Great ape DNA sequences reveal a reduced diversity and an expansion in humans *Nature* 27 (2001) 155–156.
- [24] J. Krause, L. Orlando, D. Serre, B. Viola, K. Prüfer, M.P. Richards, J.-J. Hublin, C. Haenni, A.P. Derevianko, S. Paabo, Neanderthals in central Asia and Siberia, *Nature* 449 (2007) 902–904.
- [25] J.-L. Lochet (Ed.), Bettencourt-Saint-Ouen (Somme), Cinq occupations paléolithiques au début de la dernière glaciation, Éditions de la Maison des sciences de l'Homme, Paris, 2002, 169 p.
- [26] J.-L. Lochet, C. Swinnen, P. Antoine, P. Auguste, M. Patou-Mathis, P. Depaep, C. Falgueres, M. Laurent, J.-J. Bahain, Le gisement Paléolithique Moyen de Beauvais (Oise), *Bull. Soc. Prehist. Fr.* 92 (1995) 213–226.
- [27] K. MacDonald, W. Roebroeks, A. Verpoorte, An energetics perspective on the Neanderthal record, in: M. P. Richards, J.-J. Hublin (Eds.), *The evolution of hominid diets: Integrating approaches to the study of Palaeolithic subsistence*, Springer, Dordrecht, 2009, pp. 211–220.
- [28] A. Mann, B. Maureille, Les Néandertaliens européens, in: B. Vandermeersch, B. Maureille (Eds.), *Les Néandertaliens. Biologie et Cultures*, Éditions du CTHS, Paris, 2007, pp. 69–85.
- [29] S.A. Parfitt, R.W. Barendregt, M. Breda, I. Candy, M.J. Collins, G.R. Coope, P. Durbidge, M.H. Field, J.R. Lee, A.M. Lister, R. Mutch, K.E.H. Penkman, R.C. Preece, J. Rose, C.B. Stringer, R. Symmons, J.E. Whittaker, J.J. Wymer, A.J. Stuart, The earliest record of human activity in northern Europe, *Nature* 438 (2005) 1008–1012.
- [30] P. Pavlov, J.I. Svendsen, S. Indrelid, Human presence in the European Arctic nearly 40,000 years ago, *Nature* 413 (2001) 64–67.
- [31] O.M. Pearson, Activity, climate, and postcranial robusticity, *Curr. Anthropol.* 41 (2000) 569–607.
- [32] V.V. Pitulko, P.A. Nikolsky, E.Y. Giry, A.E. Basilyan, V.E. Tumskoy, S.A. Koulakov, S.N. Astakhov, E.Y. Pavlova, M.A. Anisimov, The Yana RHS site: Humans in the Arctic before the last glacial maximum, *Science* 303 (2004) 52–56.
- [33] F.V. Ramirez Rozzi, J.M. Bermudez de Castro, Surprisingly rapid growth in Neanderthals, *Nature* 428 (2004) 936–939.
- [34] M.P. Richards, Diet shift at the Middle/Upper Palaeolithic transition in Europe? The stable isotope evidence, in: W. Roebroeks (Ed.), *Guts and brains: An integrative approach to the hominin record*, Leiden University Press, Leiden, 2007, pp. 223–234.
- [35] M.P. Richards, K. Harvati, V. Grimes, C. Smith, T. Smith, J.J. Hublin, P. Karkanas, E. Panagopoulou, Isotope evidence of Neanderthal mobility, *J. Archaeol. Sci.* 35 (2008) 1251–1256.
- [36] J. Richter, Neanderthals in their landscape, in: B. Demarsin, M. Otte (Eds.), *Neanderthals in Europe. Proceedings of the International Conference, held in the Gallo-Roman Museum in Tongeren, ATVATVCA, Gallo-Roman Museum, Luik-Tongeren, 2008*, pp. 17–32.
- [37] G.P. Rightmire, D. Lordkipanidze, A. Vekua, Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia, *J. Hum. Evol.* 50 (2006) 115–141.
- [38] C.B. Ruff, E. Trinkaus, T.W. Holliday, Body mass and encephalization in Pleistocene *Homo*, *Nature* 387 (1997) 173–176.
- [39] L. Slimak, Y. Giraud, Circulations sur plusieurs centaines de kilomètres durant le Paléolithique moyen. Contribution à la connaissance des sociétés néandertaliennes, *C. R. Palevol.* 6 (2007) 359–368.
- [40] T.M. Smith, M. Toussaint, D.J. Reid, A.J. Olejniczak, J.-J. Hublin, Rapid dental development in a Middle Paleolithic Belgian Neanderthal, *Proc. Natl. Acad. Sci. USA* 104 (2007) 20220–20225.
- [41] M.V. Sorensen, W.R. Leonard, Neanderthal energetics and foraging efficiency, *J. Hum. Evol.* 40 (2001) 483–495.
- [42] A.T. Steegmann, F.J. Cerny, T.W. Holliday, Neanderthal cold adaptation: physiological and energetic factors, *Am. J. Hum. Biol.* 14 (2002) 566–583.
- [43] K.L. Steudel-Numbers, M.J. Tilkens, The effect of lower limb length on the energetic cost of locomotion: implications for fossil hominins, *J. Hum. Evol.* 47 (2004) 95–109.
- [44] E. Trinkaus, Neanderthal limb proportions and cold adaptation, in: C.B. Stringer (Ed.), *Aspects of human evolution*, Taylor & Francis LTD, London, 1981, pp. 187–224.
- [45] E. Trinkaus, The 'robusticity transition' revisited, in: C.B. Stringer, R.N. Barton, J.C. Finlayson (Eds.), *Neanderthals on the edge: papers from a conference marking the 150th anniversary of the Forbes' Quarry discovery, Gibraltar*, Oxbow Books, Oxford, 2000, pp. 227–236.
- [46] A. Tuffreau, Contextes et modalités des occupations humaines au Paléolithique moyen dans le Nord de la France, in: N.J. Conard (Ed.), *Settlements dynamics of the Middle Paleolithic and Middle Stone Age*, Kerns Verlag, Tübingen II, 2001, pp. 293–314.
- [47] A. Tuffreau, S. Révillion, J. Sommé, B.V. Vliet-Lanoë, Le gisement paléolithique moyen de Seclin (Nord), *Bull. Soc. Prehist. Fr.* 91 (1994) 23–46.
- [48] A. Turq, Reflections on the Middle Palaeolithic of the Aquitaine Basin, in: W. Roebroeks, C. Gamble (Eds.), *The Middle Palaeolithic occupation of Europe*, University of Leiden, Leiden, 1999, pp. 107–119.
- [49] A. Verpoorte, Neanderthals energetics and spatial behaviour, *Before Farming* 3 (2006) 1–6.
- [50] A. Verpoorte, Limiting factors on early modern human dispersals: The human biogeography of late Pleniglacial Europe. *Quat. Int.* (2008) 1–9.
- [51] L. Waits, P. Taberlet, J.E. Swenson, F. Sandegren, R. Franzen, Nuclear DNA microsatellite analysis of genetic diversity and gene flow in the Scandinavian brown bear (*Ursus arctos*), *Mol. Ecol.* 9 (2000) 421–431.
- [52] C.W. Walker, C. Vila, A. Landa, M. Linden, H. Ellegren, Genetic variation and population structure in Scandinavian wolverine (*Gulo gulo*) populations, *Mol. Ecol.* 10 (2001) 53–63.
- [53] T.D. Weaver, K. Steudel-Numbers, Does climate or mobility explain the differences in body proportions between Neanderthals and their Upper Paleolithic successors? *Evol. Anthropol.* 14 (2005) 218–223.
- [54] T.D. Weaver, C.C. Roseman, C.B. Stringer, Were Neanderthal and modern human cranial differences produced by natural selection or genetic drift? *J. Hum. Evol.* 53 (2007) 135–145.