

Out of Europe - The dispersal of a successful European hominin form

Out of Europe - Die Ausbreitung einer erfolgreichen europäischen Menschenform

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ABSTRACT - This paper presents the results and implications of a study of the geographical distribution of anthropological remains of Neandertals. Based on distribution maps of excavated Neandertal remains, the Neandertals are highlighted as an indigenous European hominin form which had its core-area in southern and southwestern Europe. The present study shows that Neandertals were adapted to moderate climate rather than to cold or even extremely cold climate. Under favorable climatic and environmental conditions, they repeatedly left their core-area to move into areas of temporary occurrence. During the last Glacial, Classical Neandertals enlarged their originally exclusive European settlement area, expanding into the Near East, parts of Central Asia and even as far as the Altai region. We call this dispersal the *Out of Europe*-Movement of the Neandertals. This movement started about the same time that Anatomically Modern Humans, who originated in Africa, started their movement Out of Africa. Possible encounters and interactions of both hominin forms are discussed.

ZUSAMMENFASSUNG - Die Schwerpunkte des Beitrages liegen auf der Verteilung der Knochenfunde von Neandertalern und den Schlussfolgerungen, die sich aus dieser Verteilung ziehen lassen. Auf der Grundlage von Kartierungen der bis heute ausgegrabenen Neandertalerreste werden die Neandertaler als eine genuin europäische Menschenform hervorgehoben, deren Kerngebiet in Süd- und Südwesteuropa lag. Eines der wichtigsten Ziele des Beitrages ist es, zu zeigen, dass die Neandertaler eher an gemäßigte als an kalte oder sogar extrem kalte Klimate angepasst waren. Unter günstigen klimatischen Bedingungen und Umweltverhältnissen verließen sie immer wieder ihr Kerngebiet, um in Gebiete vorzudringen, in denen sie sich nur zeitweilig, bis zur Verschlechterung der dortigen klimatischen Bedingungen bzw. Umweltverhältnisse, aufhielten. Offensichtlich im Verlaufe der letzten Eiszeit haben klassische Neandertaler ihr ursprünglich ausschließlich europäisches Siedlungsgebiet bis in den Nahen Osten, in Teile Zentralasiens und sogar bis in das Altai-Gebiet hinein erweitert. Wir nennen diese Ausbreitung die *Out of Europe*-Bewegung der Neandertaler. Sie setzte ungefähr zu der gleichen Zeit ein, als anatomisch moderne Menschen, die in Afrika entstanden waren, mit ihrer Bewegung *Out of Africa* begannen. Mögliche Begegnungen und Wechselbeziehungen beider Menschenformen werden diskutiert.

KEYWORDS - Neandertals, Neandertal evolution, Neandertal geography, Core-area, Anatomically Modern Humans, Out of Europe, Out of Africa, Middle and Upper Paleolithic
Neandertaler, Neandertaler-Evolution, Neandertaler-Geographie, Kerngebiet, anatomisch moderne Menschen, Out of Europe, Out of Africa, Mittelpaläolithikum, Jungpaläolithikum

Introduction

The Neandertals, which in 2006 celebrated the 150th anniversary of the discovery of the type fossil (see Schmitz 2006), are an indigenous European hominin form, the evolution of which started and developed on this continent, later moving into other regions outside Europe.

In this study we analyzed the dispersal of the Neandertals on the basis of the distribution of Pre-Neandertal, Early Neandertal and Classical

Neandertal fossils. In this context, the question of the core-area of the Neandertals is of crucial importance. It should be noted that our classification is not in complete agreement with all details of a phenomenon as complex as human evolution. In one case or another, the nomenclature used in this paper may be questioned by some anthropologists. Some slight simplifications are necessary to aid in sorting and analyzing objective data. Archaeological sites without human remains were deliberately not included in our study since, especially in regions where the presence of both Neandertals and Anatomically Modern Humans (AMH) overlapped in time, they can not be attributed with certainty to either of the hominin forms and are therefore not an appropriate proxy for

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the discussion of Neandertal distribution. Although in Europe no AMH have been found in association with Mousterian artifacts, justifying the attribution of all Middle Palaeolithic assemblages in Europe to Neandertals, the same can not be done for the Near East and for Central Asia. Here, Middle Palaeolithic lithic technology is by no means limited to Neandertals as, for instance, the assemblages associated with the AMH fossils from Skhul and Qafzeh demonstrate.

It is certain that the geographical range inhabited by Neandertals was even larger than the one indicated by their fossil remains. The geographical range presented here can only be viewed as a minimum range, albeit one that certainly was occupied by Neandertals. This does not, however, reduce the information provided by our data. For the sake of discussion and updating these data, we will be grateful for constructive criticism from our colleagues.

The present study concentrates on five main issues:

1) The basis of our considerations are maps which show the distributions of all known Early and Classical Neandertal fossil sites. In addition we mapped those fossils belonging to *Homo heidelbergensis* which show clear Neandertal features and thus represent direct predecessors of the Neandertals (Pre-Neandertals). In total we mapped 183 sites in 26 countries with fossils of Pre-Neandertals, Early Neandertals and Classical Neandertals. This comprehensiveness is of crucial importance since no comparable maps showing the distribution of all known Neandertal fossils were found in the literature, even including monographs dedicated exclusively to the topic of Neandertals. Either no map is given at all (e.g., Trinkaus & Shipman 1993; Finlayson 2004; Demarsin & Otte 2006) or, more frequently, maps are published which mirror regional research interests (and/or the knowledge) of the authors, or maps are presented that show a subjective selection of sites regarded by the authors to be 'important' (e.g., Stringer & Gamble 1993; Henke & Rothe 1994, 1999; Klein 1999, 2003; Tattersall 1999; Schmitz & Thissen 2000; van Andel & Davies 2003; Jöris 2005; Auffermann & Orschiedt 2006). In addition, other maps which had been rather complete at the time of publication several decades ago do not represent the present state-of-knowledge of Neandertal research (Trinkaus & Howells 1979). This last point should be stressed, since within the last decade important discoveries have been made, especially in the southern parts of Europe (see, for instance, Manzi 2004; Garralda 2005/2006). A recently published volume entitled 'Neanderthals Revisited' (Harvati & Harrison 2006) concentrates exclusively on anthropological aspects and does not revise the distribution maps of Neandertal fossils. It is surprising that so little attention is given to the overall distribution of Neandertal remains since maps showing all sites with Neandertal remains provide a good basis for a whole series of interpretations. For the foremost

archaeological question in this study, the quantity and type of Neandertal remains, along with the state of preservation of these fossils, is irrelevant. In the end one single Neandertal tooth is as good a witness for Neandertal presence at a site as a complete skeleton.

2) As a direct result of mapping all fossil sites, the importance of the southern latitudes of Europe for the evolution and distribution of the Neandertals is stressed. Southern and southwestern Europe are highlighted as core-areas of the Neandertals.

3) The dispersal of Neandertals out of Europe and into the Near East and parts of Central Asia during the last Ice Age is discussed. The direction of dispersal seems clear, since there is no indisputable evidence for direct ancestors of Neandertals from either eastern Europe or western and central Asia.

4) Southern Europe is addressed as an area that served as a refuge for not only different temperate-mammalian species, but also for Neandertals as well.

5) In conclusion we argue that the Neandertals were not a typical cold-adapted hominin form. Although they were able to cope with cold climates and live within different environments, they were adapted to more moderate climates and environments, such as existed in the Mediterranean region, even during ice ages.

Neandertal evolution

According to the present fossil evidence, the origins of the Neandertals can be detected exclusively in Europe; no direct ancestors with Neandertal traits have been found outside Europe. Most likely, the Neandertals evolved out of later forms of *Homo heidelbergensis* (see Harvati 2007), whose European lineage can be traced as far back as about 800 000 BP. Sound fossil evidence comes from the famous *Homo antecessor* fossils from Gran Dolina at Atapuerca near Burgos in Spain (TD6 fossils) (Bermúdez de Castro et al. 1997; Aguirre & Carbonell 2001) and perhaps the cranium from Ceprano in Italy (Manzi et al. 2001). Until recently, these fossils represented the earliest Europeans. In a press release from the end of June, 2007 (Arsuaga et al. 2007), a human premolar from Sima del Elefante at Atapuerca was introduced to the public which, according to biostratigraphic and palaeomagnetic dating, has an age of at least 1.2 million years, making it the oldest anthropological proof of human presence in Europe.

Pre-Neandertals

A key site for the process which could be called 'neanderthalization' is Sima de los Huesos at Atapuerca (Bermúdez de Castro et al. 1999). Until recently, the oldest fossils from this site had been dated to ca. 300 000 BP. New high resolution U-series dates suggest that some fossils may be up to 600 000 years old (Bischoff et al. 2007). The fossils, representing

about 30 individuals, yield some of the first diagnostic Neandertal features, suggesting that the fossils represent a species that was on the threshold of what may be referred to as Neandertals. These fossils (*Homo heidelbergensis*), showing distinct Neandertal features, are called here Pre-Neandertals (Appendix, Tab. 1). Sites containing Pre-Neandertal remains include Arago (Tautavel) in France, Petralona and perhaps Apidima in Greece, Vertesszöllös in Hungary, Swanscombe in Great-Britain, and Reilingen, Steinheim, and perhaps Bilzingsleben in Germany (see Hublin 1988).

Early Neandertals

After ca. 200 000 BP European hominins can clearly be distinguished from *Homo heidelbergensis*. In this study we use the term Early Neandertals for all pre-Weichselian/Würmian Neandertal fossils (Appendix, Tab. 1). Among the earliest are the fossils from Grotte du Lazaret near Nice and from Bau de l'Aubesier, both in France, and from Pontnewydd in Wales. Similarly, the fossils from the Eemian interglacial such as the Saccopastore skulls and the skeleton from Grotta di Lamalunga, all from Italy, and most of the human remains from Krapina in Croatia are regarded as Early Neandertals.

Classical Neandertals

Classical Neandertal fossils appear in the largest number starting with the last glacial ca. 115 000 years ago (Appendix, Tab. 1). Among the best known is the type specimen discovered in the Neander Valley (Neandertal) in 1856. Others include Scladina (Sclayn) in Belgium and Artenac in southwestern France which can be classified as early Classical Neandertals. Some of the most famous Neandertal sites such as La Ferrassie, Le Moustier, La Quina, and La Chapelle-aux-Saints, all in southwestern France, are included as well. A small Neandertal province outside Europe is situated in the Near East with sites like Amud, Kebara, and Tabun in Israel, Dederiyeh in Syria, and, further to the East, Shanidar in Iraq. More recently, two other Neandertal provinces were recognized: one in the western part of central Asia (with the well-known site of Teshik-Tash, for a long time thought to be the easternmost site with Neandertal remains) and the other one even further away from Europe in the Altai region. All sites available from the published literature are listed in Appendix, Tab. 1.

Neandertal geography

According to the so-called 'accretion model' the Neandertals evolved in Europe out of already 'europeanized' humans of the *Homo heidelbergensis* type (see Harvati 2007). In the course of their evolution from Pre-Neandertals to Classical Neander-

tals, European hominins were more or less isolated from contacts with other hominin forms (Hublin 1998; Dean et al. 1998). Thus, the Neandertals were "children of Europe," being well adapted to European conditions. Despite strong criticisms of the accretion model by some colleagues (see, for instance, Hawks & Wolpoff 2001) and despite a lack of evidence for the geographical isolation of Europe for long periods of time, we use this model in our study. Because of their adaptive abilities, the Neandertals proved to be a successful hominin form for nearly 200 000 years. It should be stressed that with their good adaptation to Europe, the Neandertals, unlike their successor, did not cause the extinction of a major animal species in Europe. This may, to a certain extent, be due to the low population densities that Neandertal populations probably had – population structure is, in fact, also part of an adaptation.

By plotting the distribution of Neandertal sites on two maps, it is possible to analyze the location of the Neandertal core-area. In this study the core-area is defined as representing an area in which Neandertals, from their first appearance onwards, lived continuously. This excludes northern or central Europe, since this region was nearly depopulated during the cold maxima of the Saalian/Rissian and Weichselian/Würmian glaciations (see also Finlayson 2004, 110-113).

The first map (Fig. 1; see also Appendix, Tab. 1) presents the distribution of sites with Pre-Neandertal and Early Neandertal fossils. While ten sites with Pre-Neandertals, four of them with uncertain attribution, are too few to allow relevant comparisons between northern and southern latitudes, most of the 27 sites with Early Neandertal fossils, even with five of them being of uncertain attribution, are found in southern latitudes.

Southwestern France is often regarded as the core-area of the Neandertals and it is in fact the region with by far the densest distribution of sites with Neandertal fossils, especially when Classical Neandertals, presented in the second map (Fig. 2; see also Appendix, Tab. 1), are considered. Regarding southwestern France as the exclusive core-area, however, underestimates the importance of the Mediterranean region, including Spain and Italy, where Neandertals also seem to have lived more or less continuously. Thus, according to our definition, at least Spain and Italy must also be included in the core-area of the Neandertals.

It is unclear if Neandertals lived continuously in the Balkans and Croatia. The fossil evidence is not strong enough to make definitive statements, though in Croatia, with the Krapina and the Vindija sites, there is evidence for the presence of both Early Neandertals and very late Neandertals (Radović et al. 1988; Smith et al. 1999; Higham et al. 2006; Janković et al. 2006). Greece has not been in the focus of Palaeolithic research and the fossil evidence is very sparse. It is



Fig. 1. Distribution of sites with Pre-Neandertal (triangles) and Early Neandertal (squares) fossils (for the names of the sites see Appendix, Tab. 1).

Abb. 1. Verbreitung der Fundstellen mit Fossilien des Prä-Neandertalers (Dreiecke) und frühen Neandertalers (Quadrate) (Fundstellen siehe Appendix, Tab. 1).

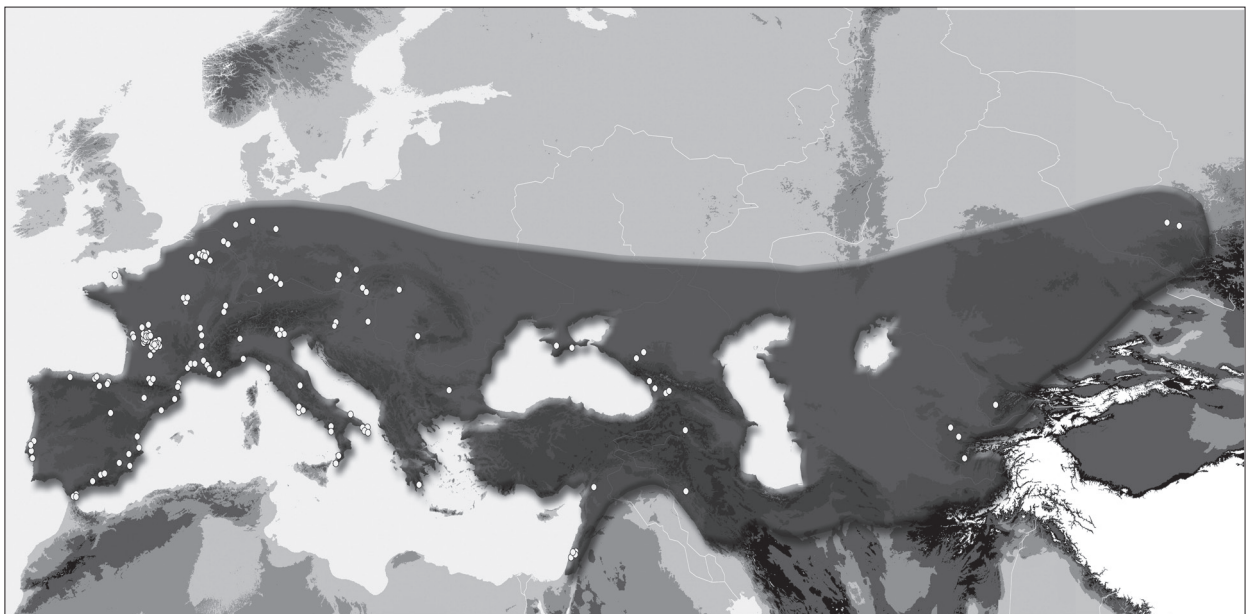


Fig. 2. Distribution of sites with Classical Neandertal fossils (for the names of the sites see Appendix, Tab. 1).

Abb. 2. Verbreitung der Fundstellen mit Fossilien des klassischen Neandertalers (Fundstellen siehe Appendix, Tab. 1).

interesting though, that with the Petralona and possibly the Apidima fossils two out of ten sites with Pre-Neandertals are to be found in Greece. The situation in Turkey is similar in that here, too, Palaeolithic research has not been in the focus of interest. While Palaeolithic hominin fossils in general are also sparse (Kappelman et al. 2008), the attribution of several human remains from Karain cave north of Antalya (Otte et al. 1998) to Neandertals has still to be confirmed.

If or how Israel and the eastern Mediterranean region might be regarded as belonging to the

Neandertal core-area remains open to discussion. The first question concerns the phylogenetic position of the skull fragment from Zuttiyeh (Galilee) (see Klein 1999, 432 with further references). Zuttiyeh represents a *Homo heidelbergensis*-like form, and since this fossil, with an estimated age between 200 000 and 280 000 years, does not show clear Neandertal affinities at a time when European Neandertal-derived features are already observed (Hublin 1998), it does not contradict an exclusive European origin of the Neandertals.

Another question concerns the attribution and age of the major Tabun fossils. While it is not certain that the Tabun 1 skeleton of a female Neandertal really belongs to the C complex (it may also belong to the overlying B complex), there is no doubt that the Tabun C2 mandible belongs to the C complex. This mandible, however, has both archaic and modern-like features (see Quam & Smith 1998) and can neither be attributed to AMH nor to Neandertals with certainty. For this study the younger chronology of the Tabun C complex is used since the majority of dates places this complex between ca. 80-90 000 BP (see references below). More recent ESR and U-series analyses that suggest an older age for both Tabun B and C (Grün & Stringer 2000) and TL dates yielding tentative age estimates as old as ca. 170 000 BP for the C complex (Mercier et al. 1995) still have to be confirmed. It should be stressed here that even if Israel were included into the core-area of the Neandertals, it would be in full accordance with the view given below since this area also lies within the southern latitudes with moderate climate.

Altogether, our distribution maps emphasize the significance of the western Mediterranean region and southwestern France, while western and northern France, as well as Germany and other parts of central Europe, are situated merely on the periphery of the distribution. If one considers the bioclimatic zones of Rivas-Martínez (1996) as shown by Finlayson (2004, Fig. 5.3a), it becomes obvious that the core area with permanent Neandertal presence covers the Mediterranean and sub-Mediterranean zones. Most parts of the temperate continental and boreal zones appear to have seen no Neandertal occupation.

The distribution of the Classical Neandertals (Fig. 2) demonstrates that the Iberian peninsula (21 sites with relatively certain Classical Neandertals and five sites with possible Classical Neandertals in Spain, Portugal, and Gibraltar), and Italy (20 sites with relatively certain Classical Neandertals and one site with possible Classical Neandertals) together have yielded as many sites with Classical Neandertals as France (47 sites with relatively certain Classical Neandertals and one site with possible Classical Neandertals). The distribution maps also demonstrate that Classical Neandertal populations may have been as dense in Italy and Spain as in southwestern France. This is in contrast with the whole of central Europe where (in Germany, Belgium, Switzerland, the Czech Republic, Slovakia, Croatia, and Hungary) only 24 sites with relatively certain Classical Neandertals and four sites with possible Classical Neandertals are known. In addition, Italy shows a large number of sites with unambiguous Neandertals; a fact that even in recently published maps has not been appreciated, especially when only 'important' sites are mapped (see above). It must be admitted that the distribution of Neandertal fossils shown in the distribution maps presented in this study may be influenced by different states of

research in certain European and non-European regions and also by different geographic conditions. By far the most Neandertal fossils have been found in caves, making it easy to imagine that regions without or with few caves are probably underrepresented.

This study shows that Neandertals were indigenous Europeans who without doubt extended their distribution into relatively high northern latitudes, who occupied high mountain ranges and who, under favorable climatic and environmental conditions, left their core-area regularly. Fossils in the Near East and Central Asia show that at least the Classical Neandertals moved "Out of Europe". As of now no unambiguous Pre-Neandertals and Early Neandertals have been found outside Europe. The fossil from Azykh in Azerbaijan, sometimes discussed as an Early Neandertal, is mentioned in most publications as being of uncertain attribution (e.g. Henke & Rothe 1994, 435), or is of an archaic *Homo sapiens* or *Homo heidelbergensis* attribution (Klein 1999, 338).

In addition to the general distribution of sites with Neandertal fossils, several facts speak in favor of the Neandertals being regarded as a hominin form adapted to moderate climate (see also Aiello & Wheeler 2003; van Andel et al. 2003; Finlayson 2004) and of regarding southern and southwestern Europe with their Mediterranean and sub-Mediterranean environments as the core-area of the Neandertals.

- First of all, it should be emphasized that the morphological features of the postcranial skeleton, often claimed to be the result of cold-adaptations of the Neandertals, may rather be due to a need for high mobility and close contact hunting (see Finlayson 2004, 87). In addition some of the cranial features may even reflect adaptations to life in the "peripheries of hot, humid regions" and/or "subtropical to moderate biotopes" (Czarnetzki 1995, 105).

- Neandertals were able to work harder organic materials (bone, antler, etc.) as is documented, among others, by bone tools found in the cave sites of Große Grotte and Vogelherd, both in southwestern Germany (Conard et al. 2006), and in the open-air site of Salzgitter-Lebenstedt in Lower Saxony (Gaudzinski 1999). The fact that they worked harder organic materials much more rarely than AMH might be explainable by their adaptation to more moderate climates and environmental conditions. The presence of different kinds of wood in sufficient quantities in the Mediterranean and sub-Mediterranean landscapes inhabited by Neandertals would not have supported the development of a substantial and elaborate bone and antler technology. Only when they had moved into regions lacking or nearly lacking trees would they have needed such a technology at all (for instance in Salzgitter-Lebenstedt). Instead, the Neandertals would have used the wood easily available to them, since it is much easier to work than bone or antler. Due to preservation, however, we know of only very few wooden artifacts from

Neandertal contexts, such as those from Abric Romani in Spain (Carbonell & Castro-Curel 1992).

- An adaptation by Neandertals to mild climates and favorable environmental conditions may also be suggested by the lack of archaeologically detectable traces of durable dwelling structures (see Kolen 1999).

- Recent studies by Erik Trinkaus (2005) also fit into this scenario. He states that the frequent use of solid footwear is provable not earlier than in the Gravettian (isolated earlier evidence from China has recently been described: Trinkaus & Shang in press). During the Gravettian, AMH started to conquer permafrost regions, which is only possible with both effective overall clothing and solid footwear. While there can be no doubt that the Neandertals, too, had effective clothing, they seem to have walked predominantly wearing light footwear (if not sometimes barefoot), which, according to Trinkaus' study, is also true for the Middle Palaeolithic AMH of the Near East. Light footwear is reasonably effective and sufficient when living in regions with relatively temperate climate. This does not, of course, exclude the occasional use of more solid footwear by Neandertals.

- In this context the Pre-Neandertals and the Early Neandertals can be regarded as predators within a "core area of the interglacial fauna" in the sense of Wighart von Koenigswald (2003). Like other predators, Pre- and Early Neandertals could have temporarily entered colder regions of central Europe as areas of temporary occurrence. Only with the Classical Neandertals, however, is there solid evidence for a spread towards more eastern and north-eastern regions outside the Mediterranean and sub-Mediterranean core-area. The fact that Neandertals sporadically occupied the North European Plain only during warm intervals is very convincingly illustrated by Clive Finlayson (2004, Fig. 5.3b).

- This scenario perfectly fits with evidence from southwestern Germany. In this region, at every site where reliable data are available, there is an occupational hiatus separating the Middle Palaeolithic layers, attributed to Neandertals, and the overlying Aurignacian layers, which in this region are attributed to AMH (Conard & Bolus 2006; Conard et al. 2006). Moreover, in this region there is only very sparse evidence for typical transitional industries that were most likely produced by late Neandertals (Bolus 2004). The possibility of a distinct occupational hiatus during the transition from the Middle to the Upper Palaeolithic is supported by the fact that there have been other occupational hiatuses in southern Germany and in central Europe in general. One hiatus is linked with the first Glacial Maximum of the last Ice Age as seen, for instance, in Sesselfsgrotte in Bavaria (Richter 1997, 22-23; Freund 1998, 189-200, 279-281) or in Poland (Kozłowski 2000); another one, affecting larger parts of central Europe, occurs during the Late Glacial Maximum (Terberger 2001). This results in the

scenario of a settlement of central Europe by Neandertals in the Middle Palaeolithic, interrupted during the first Glacial Maximum, a re-colonization by Neandertals with the start of the Interpleniglacial, again followed by another occupational hiatus (caused by climatic conditions?) about 40 000 years ago. After this hiatus, it was AMH and not the Neandertals who entered central Europe and who, after the Last Glacial Maximum, were responsible for the final re-colonization of central Europe.

- There are no such hiatuses south of the Alps as is exemplarily demonstrated by the stratigraphic sequence of Fumane Cave in the Italian Pre-Alps (Cremaschi et al. 2005). Even during the Last Glacial Maximum there was no hiatus in Italy as is shown by the stratigraphic sequences at several well-dated sites (Mussi & Peresani 2004) as well as by the cultural continuity from Gravettian to Epigravettian.

Finally, it should be mentioned that all models, especially those based on radiometric dates, regard southern Europe (including the southern part of central Europe) as the region where Neandertals survived the longest. It is also the region where important transitional technocomplexes such as the Châtelperronian and the Uluzzian evolved (see, e.g., Finlayson 2004, Fig. 7.2 and Fig. 7.3). Even with the new and revised chronology (Higham et al. 2006), Vindija cave in Croatia (Karavanić & Smith 1998, 2000; Smith et al. 1999; Janković et al. 2006) is the site where fossil remains of Neandertals are dated more recent than elsewhere in Europe (ca. 32-33 000 BP). It should not be overlooked that the refuge area of the Neandertals in southern and southwestern Europe is more or less congruent with their core-area as suggested in this paper.

Out of Europe and Out of Africa: Did they meet?

When discussing the dispersal of Neandertals, some aspects of the dispersal of AMH should be addressed. For the origin and spread of AMH we accept the Out of Africa II-model (e.g. Brüner et al. 2004; Brüner 2006). During the late Middle Pleistocene and larger parts of the Upper Pleistocene, Africa and Europe were inhabited by different hominin forms that for a long period of time did not have any contact with one another. On one continent there are the Neandertals as "children of Europe," perfectly adapted to European climate. On the other continent there are AMH as "children of Africa," genetically and biologically evolved under warmer climatic conditions. At the beginning of the last Glacial, both Neandertals and AMH were on the verge of leaving their home continents. It is interesting that obviously both species – Neandertals on their way Out of Europe and AMH on their way Out of Africa – all moved first into the Near East.

While until recently a longer period of coexistence of both hominin forms in the Near East was suggested,

new and more reliable radiometric dates suggest that in Qafzeh and in Skhul AMH lived some 90-120 000 years ago, while about 80-90 000 years ago Neandertals lived in the cave of Tabun (Schwarcz et al. 1988; Valladas et al. 1988; Stringer et al. 1989; Grün et al. 1991; Quam & Smith 1998; Coppa et al. 2005; Grün et al. 2005). About 60 000 years ago, Neandertals occupied Kebara in the southern Carmel Mountains (Valladas et al. 1987; Schwarcz et al. 1989) as well as Amud north of the Sea of Galilee some 50 000 years ago (Valladas et al. 1999). In the light of these new dates, it seems unlikely that Neandertals and AMH lived over longer periods of time in neighboring caves. The dates suggest that modern humans and Neandertals alternately occupied the caves, although interactions between the two hominins cannot be excluded (see, for instance, Kaufman 2001).

This scenario is supported by the diet inferred from stable isotope data gained from animal teeth from the find layers with Neandertal fossils in Amud and from the find layers with AMH fossils in Qafzeh (Hallin et al. 2001, 2002, 2003; Gibbons 2003). Unfortunately, none of these studies has been formally published yet, and the cited references are all abstracts. According to the data presented in these abstracts, AMH hunted animals – mainly goats and less frequently gazelles – which imply a relatively warm and dry climate with winter rains, similar to the modern climate in Israel. The Neandertals, on the other hand, hunted more gazelles than goats suggesting a cooler climate with more regular precipitation, including summer rains, throughout the year. Although preferential hunting patterns cannot be ruled out until the data is formally published, taken at face value this data suggests that AMH came to the Near East during warm and dry periods, returning to more southern regions during colder and more humid periods. Neandertals, however, entered the Near East during cooler and more humid periods, at the same time leaving the northern regions of Eurasia when climate there had turned unfavorable – a hypothesis that Ofer Bar-Yosef and others have already published (Bar-Yosef 1988, 1989; Tchernov 1998; see also Holliday 2000). One must take into consideration that 'cool' in the context of Neandertal presence in Israel must be seen in relation to the especially warm and dry periods during AMH presence; to speak of "cold-adapted Neandertals" (Gibbons 2003) in a region where even during cold maxima antelopes were frequent, is surely not justified.

It is remarkable that there is no unambiguous evidence that Neandertals ever moved to Africa, the home continent of AMH (although some colleagues think there are Neandertal influences, however slight, in North Africa: Smith et al. 1995), while AMH did move to Europe, the home continent of the Neandertals, where they arrived as 'strangers'. In the course of their dispersal within Europe, AMH might have met Neandertals, who still lived in parts of this continent. Considering that they advanced as far as into the Altai

region about 40-50 000 years ago (Okladnikov Cave and probably Denisova Cave: Goebel 1999; Krause et al. 2007), Classical Neandertals were still in the course of expanding their settlement range when they may have encountered AMH.

It is beyond the scope of this paper to enter into the vivid discussion about the presumed advantages of AMH over Neandertals (see, for instance, Stewart 2004). However, it should be recalled that Neandertals and AMH were equal in their chance of survival. In Israel it was the archaic hominin form, the Neandertals, which, after a preceding short period of inhabitation by AMH, stayed there until about 50 000 BP. In this sense, Neandertals appear to have 'replaced' AMH there and not vice versa. Once AMH had arrived in Europe, it took several thousands of years until the last Neandertal had disappeared.

Recently, the period of coexistence between Neandertals and AMH in Europe, which had been supposed to have lasted up to 10 000 years, has been seriously questioned and may have been much shorter than expected (in general: Conard & Bolus 2003; Mellars 2006; revision of Mezmaiskaya: Skinner et al. 2005; new dates for Vindija G₁: Higham et al. 2006). New AMS dates (ca. 28 000 BP) for the Mousterian levels of Gorham's Cave in Gibraltar, however, suggest a possibly longer period of temporary overlap (Finlayson et al. 2006). Even a temporary coexistence of two hominin forms does not necessarily imply that there were interactions. Topographic features, for instance, may have prevented two groups from meeting, although from the point of view of mere distance they were neighbors. This could be true for Spain, where high-altitude mountains separate the coastal regions from inland regions (as in Cantabria) or the major river systems from each other.

As of now there is no unambiguous proof either from the Near East or from Europe that Neandertals and AMH met and interacted (see Conard 2006). The evidence from the Near East has been discussed above. As for Europe, especially the Châtelperronian and the Uluzzian have been regarded as results of acculturation processes (e.g. Mellars 1999), implying that Neandertals and AMH must have met and interacted more often than only occasionally. This point of view has been questioned (see Zilhão & d'Errico 1999; d'Errico et al. 2003) and the issue is far from resolved. Even with the probable period of coexistence being shorter than earlier expected, and even with the sites from the Swabian Jura that contain some of the best high resolution stratigraphies in central Europe yielding negative evidence (Conard et al. 2006), we see the possibility that Neandertals and AMH met and interacted in Europe.

Conclusions

The Neandertals originated in Europe and large parts of their evolution took place exclusively on this

continent, making them well adapted to European conditions. Often Neandertals are regarded as a cold-adapted hominin form; it is one of the main purposes of this paper to present a revision of that opinion. There is no doubt that Neandertals had the capability to live in harsher climates, and they successfully did so, as sites in northern latitudes indicate. But as a hominin form adapted to milder climates they had to 'learn' to do so (by cultural adaptation?). Without doubt Neandertals lived within different environments and under different climatic conditions, from forested environments of the Mediterranean to tundra regions. They have been found in association with hippopotamus (e.g., Grotta Guattari: Mussi 2001), but also with reindeer (e.g., Salzgitter-Lebenstedt: Gaudzinski & Roebroeks 2000). Nevertheless, the latter is no proof of a cold-adaptation from the start. That the morphological features of the Neandertals need not be the result of cold-adaptations has been stated above. Although the body proportions of the Neandertals have often been compared with those of Arctic Inuit, Neandertals entirely dressed in hide clothes and living under harsh ice-age conditions in the area of the northern and western Mediterranean are hard to imagine since even in times of glacial maxima the temperatures of the Mediterranean (Thiede 1978) were not lower than those in the southern North Sea and Baltic Sea today. The pollen record from the Mousterian levels of several caves in Mediterranean Spain gives proof of olive trees (Carrión et al. 1999), while contemporaneous levels in central Europe are characterized by permafrost and very harsh climatic conditions.

An important consideration for approaching these issues is a concrete understanding of the location of the Neandertal core area. For such an assessment, it is of utmost importance that maps showing all sites with Neandertal remains instead of maps showing just subjective selections are produced. In this study the core-area was defined as the area in which Neandertals from their first appearances onwards have more or less continuously lived. According to this definition, not only southwestern and southern France can be regarded as the core-area, but at least Spain and Italy must also be included. Early Neandertals repeatedly left their core-area to move into areas of temporary occurrence, but there is no unambiguous evidence that they left Europe (Fig. 1).

The Classical Neandertals not only largely enhanced their habitation area by entering new areas of temporary occurrence, they also started a movement, or – much more likely –, several movements 'Out of Europe' which led them not only to the Near East, but also into parts of central Asia and – at the end of the Middle Palaeolithic – even as far as the Altai region (Fig. 2). Doing so, they repeatedly entered cold regions and adapted to harsher climatic conditions. Nevertheless it seems that the Neandertals did not live under extremely cold conditions (see also

Finlayson 2004). Their dispersal into regions as far away from Europe as the Altai region may have been possible due to the existence of woodlands or at least semi-wooded environments, as is indicated by a map published by Clive Finlayson and José Carrión (2007). The response of Neandertals to a dramatic climatic deterioration in an area of temporary occurrence should be addressed more deeply by future research. Perhaps they tried to return to their core-area which they may have left generations before. This, however, may have been prevented by the Neandertal populations still living there. By analogy with the modes of exchange in the Pleistocene mammalian fauna of central Europe (von Koenigswald 2003), it is likely that these populations outside the core-area went extinct. In times of climatic amelioration, new groups of Neandertals may have left the core-area and the whole process started again.

Viewed from this perspective, AMH, coming from the East some 40 000 years ago, entered a largely depopulated area when they arrived in central Europe: a region which belongs neither to the core-area nor to the refuge area of Neandertals. This scenario is supported by the occupational hiatus between the Middle and Upper Palaeolithic horizons in southwestern Germany and by only sporadic appearances of typical transitional industries in the western part of central Europe. When AMH, moving southward from the North, entered into the core-area of the Neandertals in southern and southwestern Europe, it was the AMH who came 'out of the cold' and it was AMH who were better adapted to the cold, at least better than the Neandertals living contemporaneously in Spain or Italy. Once AMH had occupied the northern parts of the Neandertal core-area, even in times of climatic improvement, it was no longer possible for the Neandertals to leave their core-area (or refuge area respectively) and expand to the North as they had done prior to the arrival of AMH. Instead, their former core-area was continuously reduced and contracted until the last Neandertals only survived in certain refuge areas within their former core-area, such as southern Spain and Croatia (and perhaps the Crimea and the Caucasus region: Marks & Chabai 1998; Ovchinnikov et al. 2000; Adler & Tushabramishvili 2004). This contraction of the habitation area certainly played an important role in the extinction of the Neandertals as an autonomous hominin form (see also Stewart et al. 2003). Without doubt, these processes were much more complex. It is hoped that this study provides the framework for future research that can address the complexities of the replacement with much more detail.

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Appendix, Tab. 1. Sites with Pre-Neandertal (P), Early Neandertal (E), and Classical Neandertal (C) fossils. A question mark (?) indicates an uncertain attribution. Question marks not included in the maps (Figs. 1 and 2).

Appendix, Tab. 1. Fundstellen mit Fossilien des Prä-Neandertalers (P), Frühen Neandertalers (E) und Klassischen Neandertalers (C). Unsichere Zuordnung ist mit einem Fragezeichen (?) gekennzeichnet. Fragezeichen in den Karten (Figs. 1 & 2) nicht dargestellt.

Country	Site	Attribution	Reference
Armenia	Erevan (also Yerevan)	C	Bader et al. 1976
Belgium	Couvin	C	Semal et al. 2005
	Engis	C	Semal et al. 2005
	Fonds-de-Forêt	C	Semal et al. 2005
	Goyet	C	Semal et al. 2005
	La Naulette	C	Semal et al. 2005
	Scladina (also Sclayn)	C	Semal et al. 2005
	Spy	C	Semal et al. 2005
	Trou Walou (also Grotte Walou)	C	Draily et al. 1999
	Bulgaria	Bacho Kiro	C?
Channel Islands	Saint Brelade (also La Cotte-de-S.-B.)	E	Stringer & Currant 1986
Croatia	Krapina	E (+C?)	Radović et al. 1988
	Vindija	C	Higham et al. 2006
Czech Republic	Kůlna	C	Jelínek 1988
	Šipka	C	Vlček 1969
	Švédův stůl (with Ochoz)	C	Vlček 1969
France	Angles-sur-l'Anglin	C	de Lumley 1976c
	Arago (Tautavel)	P	de Lumley 1976a
	Arcy-sur-Cure/Grotte de l'Hyène	C	de Lumley 1976c
	Arcy-sur-Cure/Grotte du Loup	C	de Lumley 1976c
	Arcy-sur-Cure/Grotte du Renne	C	Hublin et al. 1996
	Artenac	C	Mann et al. 2002
	Aven de Vergranne	E	de Lumley 1976a
	La Balauzière	C	Trinkaus 1995
	Bau de l'Aubesier (also Aubesier)	E	Lebel et al. 2001
	Biache-Saint-Vaast	E	Rougier 2003
	Castaigne (also Caminero)	C	Vandermeersch 1976
	Castel-Merle (also Abri des Merveilles)	C	Trinkaus 1976
	La Cave/Vilhonneur	C?	Vandermeersch 1976
	La Chaise/Bourgeois-Delaunay	E	Piveteau 1976
	La Chaise/Suard	E	Piveteau 1976
	La Chapelle-aux-Saints (also Bouffia Bonneval)	C	Heim 1976

France (continued)	Châteauneuf-sur-Charente (Melon and Hauteroche)	C	Vandermeersch 1976
	Combe-Grenal	C	Heim 1976
	La Crouzade	C	de Lumley 1974
	La Ferrassie	C	Heim 1976
	Font-de-Gaume	C	Garralda 2007
	Fontéchevade	C	Chase et al. 2007
	Font-qui-Pisse	C	Trinkaus et al. 2000
	Genay	C	de Lumley 1976c
	Hortus	C	de Lumley 1974
	Jaurens	C	Bouvier 1982
	Jonzac	C	McPherron et al. 2006
	Lazaret	E	de Lumley 1974
	Macassargues (also La Verrerie)	C	de Lumley 1974
	Malarnaud	C	de Lumley 1976b
	Marillac (also Les Pradelles)	C	Vandermeersch 1976
	Mas Vieil	C	Heim 1976
	La Masque	C	de Lumley 1974
	Monsempron	C	Heim 1976
	Montgaudier	C	Mann & Vandermeersch 1997
	Montmaurin/La Niche	E	Billy 1985
	Moula-Guercy	C	Defleur et al. 1999
	Le Moustier	C	Heim 1976
	Orgnac 3	E	de Lumley 1976a
	Pech-de-l'Azé	C	Soressi et al. 2007
	Petit-Puymoyen	C	Vandermeersch 1976
	Peyrards (also Baume des Peyrards)	C	de Lumley 1974
	Le Placard	C	Vandermeersch 1976
	Le Portel	C	de Lumley 1976b
	Pradayrol	E?	Séronie-Vivien & Tillier 2002
	Putride	C	Trinkaus 1995
La Quina	C	Vandermeersch 1976	
Ramandils	C	Boutié 2000	
Régourdou	C	Heim 1976	
René Simard	C	Trinkaus 1995	
Rigabe	C	de Lumley 1974	
Roc-de-Marsal	C	Heim 1976	
Rochelot	C	Tournepiche et al. 1996	

France (continued)	Rochers-de-Ville-neuve	C	Beauval et al. 2005
	Saint-Césaire	C	Vandermeersch 1984
	Soulabé-las-Maretas	C	de Lumley 1976b
	Vaufrey	C	Garralda et al. 2004
	Vergisson	C	de Lumley 1976c
Georgia	Cuckvati (also Bronze Cave)	C	Adler & Tushabramishvili 2004
	Djruchula (also Dzhurchula)	C	Adler & Tushabramishvili 2004
	Ortvale Klde	C	Adler & Tushabramishvili 2004
	Sakazia (also Sakhazia)	C	Ullrich 1992
Germany	Balver Höhle	C?	Jöris 2005
	Bilzingsleben	P?	Vlček 2002
	Hohlenstein-Stadel	C	Kunter & Wahl 1992
	Hunas	C	Alt et al. 2006
	Klausennische	C	Abel 1936
	Neandertal	C	Schmitz 2006
	Ochtendung (Wannen)	E	Condemi 1997
	Reilingen	P	Dean et al. 1998
	Salzgitter-Lebenstedt	C	Hublin 1984
	Sarstedt	C	Czarnetzki et al. 2001
	Sesselfelsgrötte	C	Rathgeber 2006
	Steinheim	P	Hublin 1988
	Taubach	E	Adloff 1920
	Warendorf-Neuwarendorf	C	Czarnetzki & Trellisó Carreño 1999
	Weimar-Ehringsdorf	E	Vlček 1993
Gibraltar	Genista	C?	Garralda 2005/2006
	Devil's Tower	C	Garralda 2005/2006
	Forbes' Quarry	C	Garralda 2005/2006
Great Britain	Pontnewydd	E	Day 1986
	Swanscombe	P	Stringer & Hublin 1999
Greece	Apidima	P?	Harvati & Delson 1999
	Lakonis	C	Harvati et al. 2003
	Petalona	P	Stringer 1983
Hungary	Remete Felső	C?	Churchill & Smith 2000
	Subalyuk	C	Trinkaus 1995
	Vertesszöllös	P?	Day 1986
Iraq	Shanidar	C	Trinkaus 1983
Israel	Amud	C	Suzuki & Takai 1970
	Kebara	C	Bar-Yosef & Vandermeersch 1991
	Shovakh (also Me'arat Shovakh)	C	Trinkaus 1987

Israel (continued)	Tabun	C	McKown & Keith 1939
Italy	Altamura (Grotta di Lamalunga)	E	Manzi 2004
	Archi	C	Manzi 2004
	Grotta del Bambino (also G. delle tre porte)	C	Manzi 2004
	Buca del Tasso	C	Manzi 2004
	Calascio	C	Manzi 2004
	Casal de' Pazzi (also Rebibbia-C. de' P.)	E	Manzi 2004
	Grotta del Cavallo	C?	Manzi 2004
	Circeo/Grotta Breuil	C	Manzi 2004
	Circeo/Grotta del Fossellone	C	Manzi 2004
	Circeo/Grotta Guattari	C	Manzi 2004
	Fate	C	Manzi 2004
	Fenera (also Monte Fenera)	C	Manzi 2004
	Fumane	C	Manzi 2004
	Grimaldi/Grotta del Principe	E?	de Lumley 1974
	Janni di San Calogero di Nicotera	C	Manzi 2004
	Madonna dell'Arma	C	Cauche 2007
	Maglie	C	Manzi 2004
	Melpignano	C	Manzi 2004
	Mezzena	C	Caramelli et al. 2005
	Molare (also Il Molare a Scario)	C	Manzi 2004
	Grotta del Poggio	E	Manzi 2004
	Saccopastore	E	Manzi 2004
	San Bernardino	C	Manzi 2004
	Santa Croce di Bisceglie	C	Manzi 2004
	Sedia del Diavolo	E?	Manzi 2004
	Taddeo	C	Manzi 2004
	Tagliente	C	Manzi 2004
Portugal	Columbeira/Gruta Nova	C?	Garralda 2005/2006
	Figueira Brava	C	Garralda 2005/2006
	Oliveira	C	Garralda 2005/2006
	Pesada (Gruta da Aroeira)	E?	Trinkaus et al. 2003
Salemas	C?	Garralda 2005/2006	
Romania	Ohaba Ponor (also Bordul Mare)	C	Cârciumaru 1999
Russia	Barakai (also Barakae-vskaja)	C	Faerman et al. 1994
	Denisova Cave	C	Goebel 1999
	Mezmaiskaja	C	Ovchinnikov et al. 2000
	Okladnikov Cave	C	Krause et al. 2007

Slovakia	Dzeravá skála (also Pálffy)	C?	Churchill & Smith 2000
	Gánovce	E	Vlček 1969
	Šala	C	Vlček 1969
Spain	Arrillor	C	Garralda 2005/2006
	Atapuerca/Galería	P?	Carbonell Roura et al. 1999
	Atapuerca/Sima de los Huesos	P	Bermúdez de Castro et al. 1999
	Axlor	C	Garralda 2005/2006
	Bañolas (also Banyoles)	C	Garralda 2005/2006
	Bolomor	E	Garralda 2005/2006
	Carigüela (also Carihuela)	C	Garralda 2005/2006
	Los Casares	C?	Garralda 2005/2006
	El Castillo	C	Garralda 2005/2006
	Cova Forada	C	Garralda 2005/2006
	Cova Negra	E	Garralda 2005/2006
	Cueva Negra del Estrecho del Quípar	C	Garralda 2005/2006
	La Flecha	C?	González Echegaray & Freeman 1998
	Gabasa (also Los Moros de Gabasa)	C	Garralda 2005/2006
	Cova del Gegant	C	Daura et al. 2005
	Horá	C	González Echegaray & Freeman 1998
	Lezetxiki	E	Garralda 2005/2006
	Mollet I	E	Maroto et al. 1987
	Pinilla del Valle	C	Diario de Atapuerca 2006
	El Salt	C	Garralda 2005/2006
El Sidrón	C	Garralda 2005/2006	
Sima des las Palomas del Cabezo Gordo	C	Garralda 2005/2006	
Tossal de la Font	C	Garralda 2005/2006	
Valdegoba	C	Quam et al. 2001	
Zafarraya	C	Barroso Ruiz & de Lumley 2005	
Switzerland	Cotencher	C	Bay 1984
	Saint-Brais II	C	Le Tensorer 1998
Syria	Dederiyeh	C	Akazawa & Muhsen 2003
Tajikistan	Khudji	C?	Trinkaus et al. 2000
Ukraine	Kiik-Koba	C	Vlček 1973
	Zaskal'naya (also Ak-Kaya)	C	Ullrich 1992
Uzbekistan	Anghilak	C?	Glantz et al. 2004
	Obi-Rakhmat	C	Glantz et al. 2004
	Teshik-Tash	C	Trinkaus 1995

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