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THE NEANDERTHALS: A COLD-ADAPTED EUROPEAN MIDDLE PLEISTOCENE POPULATION?

ABSTRACT: The Neanderthals, a typical European population, are perhaps the best known fossil population with well-distinguished features. The attempt has often been made to explain the anatomical particularities of the Neanderthal fossils in terms of adaptation. Their traits would thus result from an adaptation to a cold natural environment. This hypothesis seemed all the more plausible, given that for a long time only European fossils belonging to stages 4 and 3 – recognized as cold stages – were considered to be Neanderthal. However, as we will see more closely in the second part of the present paper, we recognize today that the evolution of the Neanderthal lineage took place over the course of a long period of time and that certain Neanderthal features became differentiated before the stages 4–3. We recognize, therefore, that they cannot be interpreted solely as a consequence of adaptation to a rigorous climate. According to the present state of our knowledge, it appears that the particularity of the Neanderthal population should be principally interpreted as the result of geographic isolation. Of course, this isolation must be related to the unique geographic position of the European peninsula and to the particular climatic conditions that prevailed in Europe during the entire Pleistocene.

KEY WORDS: Neanderthals – Pre-Neanderthals – Proto-Neanderthals – Cold-adaptation – European Middle Pleistocene populations

The anthropological particularity of the European population in relation to the ancient fossil population of the ancient world may be attributed to the presence of a human population with well-distinguished characteristics: the Neanderthals. Since Coon's publication in 1962, the attempt has often been made to explain the anatomical particularities of the Neanderthal fossils in terms of adaptation (Brose, Wolpoff 1971, Trinkaus 1981, Ruff 1991, Schwartz, Tattersall 1996). These traits would thus result from an adaptation to a cold natural environment. This hypothesis seemed all the more plausible, given that for a long time only European fossils belonging to stages 4 and 3 – recognized as cold stages – were considered to be Neanderthal (*Figure 1*). However, as we will see more closely in the second part of the present paper, we recognize today that the evolution of the Neanderthal lineage took place over the course of a long period of time and that certain Neanderthal features became differentiated before the stages 4–3. We recognize, therefore, that they cannot be interpreted solely as a consequence of adaptation to a rigorous climate.

In this paper we will argue that the adaptational interpretation cannot alone account for the particular features exhibited by the Neanderthal population. According to the present state of our knowledge, it appears that the particularity of the Neanderthal population should

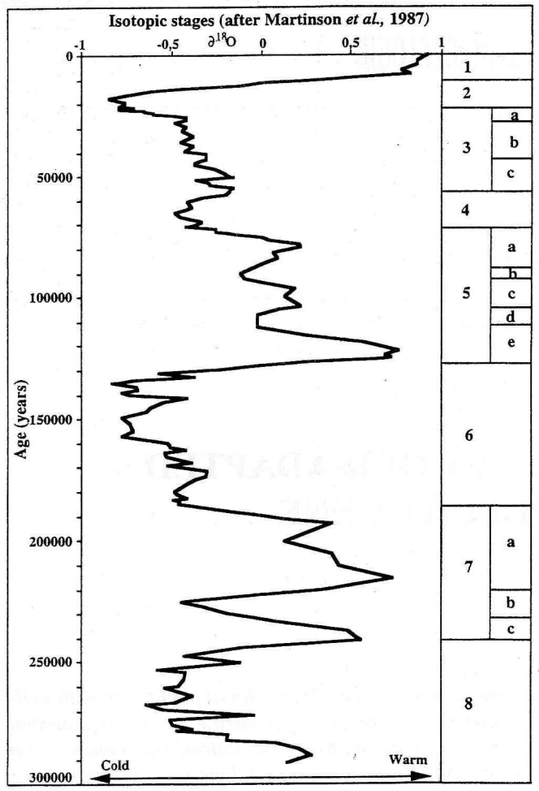

FIGURE 1. Diagram of isotopic stages (after Martison *et al.* 1987).

TABLE 1. The derived features of the Neanderthals.

	CRANIUM and FACE	
Superior view	1)	Position of maximum width of the cranium in th back, on the parietals after the *meatus acusticu externus*.
Lateral view	2)	The zygomatic process is on the same level as th *meatus acusticus externus*.
	3)	On the temporal bone, the presence of a *tuberculun mastoideus anterior*.
Occipital view	4)	The so-called "bomb shape" of the cranium i occipital view.
	5)	The occipito-mastoid region with the *juxmastoi eminentia* more developed than the mastoi process.
	6)	The presence on the occipital bone of the bi-arched transverse occipital torus and the suprainiac fossa.
Facial view	7)	The complete fused form of the supra-orbital torus
	8)	The shape in extension of the face with th modification in shape of the zygomatic bones; th frontal apophysis and the body of the maxillary bone with the absence of *fossa canina*.
	JAW	
Ramus	1)	Lateral development of the condyle.
Body	2)	The displacement of the mental foramina belov the first molar.
Dentition	4)	Large anterior dentition in comparison to th posterior.

be principally interpreted as the result of geographic isolation. Of course, this isolation must be related to the unique geographic position of the European peninsula and to the particular climatic conditions that prevailed in Europe during the entire Pleistocene. These two factors led to genetic isolation of the European population beginning with the archaic population of Europe (*Homo erectus sensu lato*, or *Homo heidelbergensis* or *Homo antecessor*) (Andrews, Franzen 1984, Bonifay, Vandermeersch 1991, Franzen 1994, Roebroeks, van Kolfschoten 1995, Ascenzi *et al.* 1996, Bermúdez de Castro *et al.* 1997).

In examining the relation of the evolution of Neanderthal features to cold adaptation, the present paper will be divided into three parts: In the first part we will resume the anatomical particularities of the Neanderthals; in the second, we will retrace the chronological order of emergence of these characteristic Neanderthal traits; in the third, we will attempt to relate this data to the various adaptational interpretations elaborated by different authors. These interpretations will be critically examined in light of our knowledge of the climatic conditions that prevailed in Europe during the Pleistocene.

THE NEANDERTHALS

For a long time the scientific community considered every feature not present in modern man to be a Neanderthal feature. The absence of fossils for comparison outside of Europe only led to an exaggeration of the role of European fossils in human evolutionary history. Today we know that the Neanderthals are a population which inhabited only a small part of the ancient world *(Figure 2)*. There thus never was an evolutionary phase in which Neanderthals might be considered to be the ancestors of mankind as a whole.

Numerous discoveries of ancient fossils throughout the world make it possible to attempt a differentiation between archaic (plesiomorphic) features and derived (apomorphic) specialized features. Indeed, an archaic feature may well have persisted over time among different human forms and thus be found among different fossil groups. For this reason, such features cannot by themselves be diagnostic traits, as can be, however, features which are unique to a single lineage. During the past ten years, a large number of studies have been undertaken comparing single fossils presumed to be Neanderthal with *Homo erectus* and with

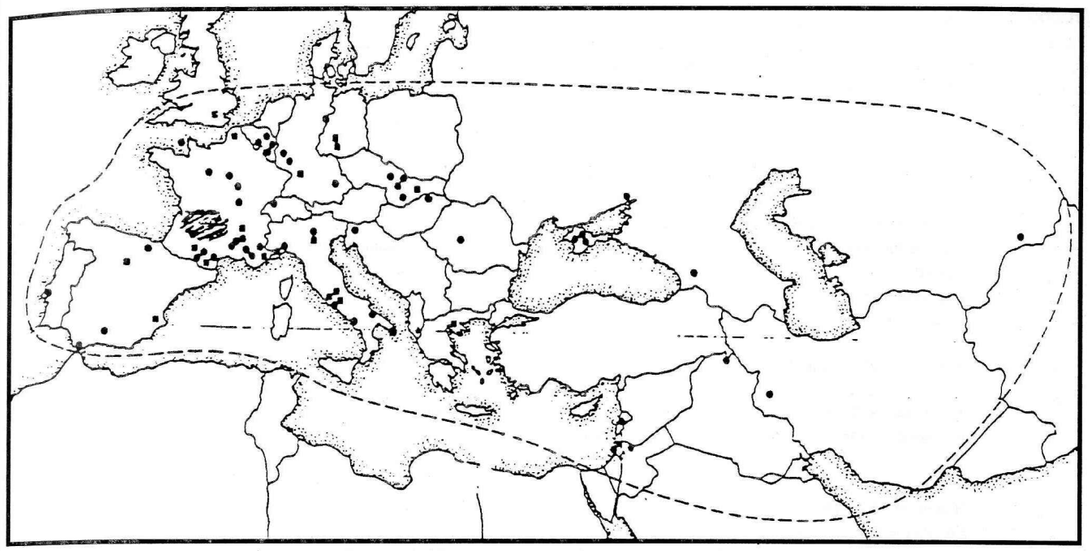

FIGURE 2. Geographical location of the Neanderthals and pre-Neanderthals.

modern humans (Stringer *et al.* 1984, Trinkaus 1988, Franciscus, Trinkaus 1988, Rak 1990, Churchill, Trinkaus 1990, Condemi 1991, 1992, Couture 1992, Hambucken 1993, Stringer, Gamble 1993, Villemeur 1994, Maureille 1994, Nara 1994, Elyaqtine 1995, Schwartz, Tattersall 1996). All of these studies have the merit of refining morphometric analysis, giving an increasingly precise idea of Neanderthal bone morphology while taking into account a certain variability among Neanderthals.

The Neanderthals from an anatomical point of view

The morphology of the Neanderthals, especially on the cranium and the mandible, is now well known. The Neanderthals can be defined by three kinds of features.

First, by the presence of archaic traits (plesiomorphic), inherited from ancestral European forms (Franzen, 1994, Bonifay, Vandermeersch 1991, Roebroeks, van Kolfschoten 1995, Ascenzi *et al.* 1996, Bermúdez de Castro *et al.* 1997). Worth mentioning are, for example, the great overall robustness, the low cranial vault, the absence of frontal protuberances, the absence of a chin.

The second kind of features are derived traits which the Neanderthals share with modern humans. Among these are the strong cranial capacity (1518 ± 169 on the average among Neanderthals), the marked curvature of the occipital and the reduction of the size of the third molar.

The derived features which are truly diagnostic for Neanderthals are those indicated in *Table 1*.

When did the differentiation of the Neanderthal lineage start?

The recognition of unique (derived) Neanderthal features on the ancient human fossils makes it possible to trace the emergence of the Neanderthal lineage. In the present state of our knowledge, it can be affirmed that Europe was the cradle of the Neanderthals, the place of differentiation and evolution of this population.

Western Europe shows a chronological sequence that permits to reconstruct an evolutionary pattern which occurred over a long period of time, in other words, during at least 450,000 years (Trinkaus 1988, Couture 1992, Condemi 1992, Maureille 1994, Nara 1994, Elyaqtine 1995). When they are sufficiently complete to permit analysis, ancient fossils discovered in Europe clearly show the evolution and diversification leading to the Neanderthals which, far from brutal or sudden, was progressive. Over the course of time, the fossils increasingly exhibit Neanderthal traits. In Europe (western and central Europe), all of these pre-Würmian fossils, beginning from about 450,000 years ago, must be considered in our opinion to be pre-Neanderthals, in other words fossils which preceded, both chronologically and phylogenetically, the Würmian Neanderthals *(Table 2)*. The presence of Neanderthal traits among these fossils shows that the differentiation of this typical European population was already underway.

ORDER OF SUCCESSION OF THE NEANDERTHAL TRAITS ON THE WESTERN AND CENTRAL EUROPEAN FOSSILS

The evolution of the Neanderthals which occurred over a long period of time, spanning at least 450,000 years, may be traced thanks to the identification of apomorphic features. Among the pre-Würmian European fossils, a

TABLE 2. The evolution of European populations.

PRINCIPAL SITES	Stage δO^2	AGE	HUMANS
Cro-Magnon (F)		28,000	Modern Humans
St. Césaire (F)		35,000	
La Ferrassie (F)		40,000	
La Chapelle-aux-Saints (F)	3–4		
Neanderthal (D)			"Classical" Neanderthals
Spy (B)		45,000	
Regourdou (F)			
Guattari (I)			
Salzgitter-Lebenstedt (D)			
Saccopastore (I)		110,000	
La Chaise: B.D. (F)	5	–	Proto-Neanderthals
Ehringsdorf (D)		130,000	
La Chaise: S. (F)			
Biache-St-Vaast (F)			
Steinheim (D)			
Reilingen (D)	7–11	180,000	"Late" Pre-Neanderthals
Swanscombe (GB)			
Bilzingsleben (D)			
Atapuerca: S.H. (S)			
Petralona (G)		<350,000	
Arago (F)	11–13	450,000	
			"Early" Pre-Neanderthals
Mauer (D)			
Boxgrove (GB)	13–15	475–620,000	
Visogliano (I)			
			"archaic" European Humans
Atapuerca: G.D. (S)	18–20	700,000	*Homo erectus* / (*Homo antecessor*) //
Ceprano (I)	22	800,000	*Homo heidelbergensis* / "archaic" *Homo sapiens*?
Dmanisi (Georgia)		<1,800,000	*Homo ergaster*? / *Homo erectus*?

progressive increase, from the oldest to the most recent, in the number of Neanderthal features (Couture 1992, Condemi 1992, 1996, Maureille 1994, Nara 1994, Elyaqtine 1995) may be noticed. The fossils preceding "classical" Neanderthals may be termed "pre-Neanderthal" or "proto-Neanderthal" both in a chronological and phylogenetic sense. The different stages of this evolution leading to the Neanderthals may be summarized on the basis of three great fossil groups (cf. *Table 2*):

1. Early pre-Neanderthals;
2. Late pre-Neanderthals;
3. Proto-Neanderthals.

The traits present in each of the groups are as follows:

The early pre-Neanderthals
They correspond to archaic fossils (before stage isotopic oxygen 11) which present only a few Neanderthal traits. Which Neanderthal traits emerged among this group o fossils?

The first Neanderthal features can be observed on th face. This morphological change of the face is visible o Arago XXI, whose age is estimated to be 450,000 year old (de Lumley, de Lumley 1982). The zygomatic bone i rather flattened out with a swelling of the frontal apophysi of the maxillary bone.

Beside this, a lateral development of the mandibula condyle may be observed on the mandible of Arago 2 an 13. On this same jaw from Arago we observe a backwar displacement of the mental foramen which shifts bac under the first molar. These features (backwar displacement of the mental foramen and latera development of the condyle) are related to a morphologica change of the face. Thus, it seems that the first change and signs of diversification among Neanderthals occurre on the face and on the mandible.

The Neanderthal features present on Arago are also found on other European fossils: on the mandible and on the face of Atapuerca SH (Arsuaga *et al.* 1993, 1997). The face of Petralona anticipates that of the Neanderthals (Trinkaus 1988, Condemi 1992, Couture 1992, Stringer, Gamble 1993, Maureille 1994, Nara 1994, Elyaqtine 1995).

By contrast, the occipital region is still very archaic, as may be seen from the occipital bone of Petralona which is entirely comparable to that of Vertesszöllös. Concerning the other regions of the cranium, all of these fossils are very archaic, notably in the morphology of the parietal bone.

The late pre-Neanderthals
All of the fossils stemming from the isotopic stages between 11 and 6 may be included in this group of late pre-Neanderthals (cf. *Table 2*). It includes fossils which display a systematic presence of Neanderthal features in corresponding bone regions (among all of the adult and child specimens), notably in the occipital region, in the mastoido-occipital region and in the frontal region. Thus, the occipital bone already exhibits all the Neanderthal features and they are practically indistinguishable from those of classical Neanderthals.

In the same manner, the mastoid regions among western European fossils are similar to those of the classical Neanderthals. On the occipital bone the Neanderthal morphology is already present (Swanscombe, Steinheim, Bilzingsleben A3, Biache – St-Vaast 1, Reilingen, La Chaise – abri Suard). Where the parietal bones are preserved, they show a modification in form and, above all, in the position of the parietal protuberances which are found in intermediary position between the high position characteristic of modern man and the lower position of the archaic fossils considered to be *Homo erectus sensu lato*.

Another anatomic region differentiates itself among this second group of fossils: the region of the supra-orbital torus (Trinkaus 1988, Stringer, Gamble 1993, Condemi 1992, Nara 1994). This can be noticed on the recent fossil discoveries in France in the Suard cave and at Biache (Vandermeersch 1978, Piveteau 1970). The fossils of that period display the presence of the continuous supra-orbital torus of the Neanderthals – in other words, the complete fusion of the ciliar and supraorbital arc. These features are also exhibited on the frontal B4 of Bilzingsleben (Mania, Vlček 1987, 1993).

Along with the presence of all of these derived Neanderthal features, a group of archaic traits persist, such as the weak cranial capacity (clearly observable on Biache 1, or La Chaise – abri Suard) and the pronounced thickness of the bone (Bilzingsleben, Biache – St-Vaast 2, La Chaise – abri Suard).

The proto-Neanderthals – in other words, the last predecessors of the Neanderthals.

These fossils exhibit a larger number of Neanderthal features (notably in the facial region), and the loss of a certain number of archaic traits (above all the reduction of the bone thickness) no longer observed in the Neanderthals. All of the fossils from the isotopic stage 5 are included in this group: Saccopastore 1 and 2; La Chaise-abri Bourgeois-Delaunay, Ehringsdorf and Reilingen (Trinkaus 1988, Condemi 1992, 1996, Stringer, Gamble 1993).

Due to the presence of a large number of Neanderthal features, these fossils can be considered to be Neanderthal. However, they are also distinguished from classical Neanderthals by the presence of a large number of archaic features, as well as of a quantity of incompletely developed Neanderthal traits. These latter traits concern the facial morphology (zygomatic bone, nasal bone, and maxillary bone) and the temporal morphology (mandibular fossa, mastoid process, position of the zygomatic process).

ARE THE PARTICULAR FEATURES OF THE NEANDERTHALS RELATED TO ADAPTATION TO SEVERE CLIMATIC CONDITIONS?

As we have noted in the first part of this article, the particular anatomy of the Neanderthals has often been accounted for in terms of adaptation.

According to this interpretation, the Neanderthal population would have adapted to a cold natural environment. The anatomical features which are most often quoted to support this interpretation concern the morphology of the Neanderthal limb bones and the particular morphology of the face.

Let us briefly analyze these two points.

The adaptation of the limb bones
For over a century attempts have been made to define certain rules of adaptation capable of accounting for the general trend of human variability. These rules, known as Bergmann's and Allen's rules (Bergmann 1847, Allen 1877) may be summarized in the following way:

Bergmann's rule postulates that, in cold conditions, body mass tends to be larger, while Allen's rule suggests that body extremities will be shorter. Both can be explained by the need of organisms to minimize the body surface area relative to their volume and weight in order to conserve heat in cold conditions. In this way, they can more closely approximate the ideal shape of a sphere, which has the minimum surface area for its volume. This rule seems to operate in a general way among modern human populations. Thus, equatorial populations tend to be linear and have relatively long extremities when compared to polar populations, which tend to be stocky and have relatively short extremities. Since the Neanderthals lived in relatively cold climates, we would thus expect them to be heavy and to have short limbs.

Concerning the tendency to be "stocky and heavy-built", the Neanderthals, as we have seen in part I, exhibit

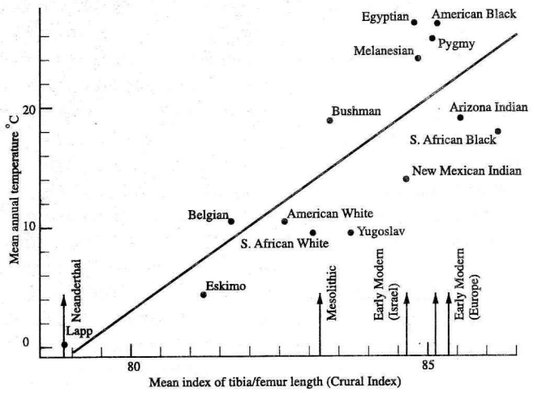

FIGURE 3. Proportions of the limb bones (after Stringer, Gamble 1993).

great robustness, even if this feature is not limited to this fossil population. The Neanderthal robustness is found throughout the body: large and wide rib cage; long clavicle; wide scapula with large muscle attachments along the rear edge; large shoulder and elbow joints; wide hips; large hip joint (rotated outwards); hand with strong grip and wide fingertips; rounded, curved and thick-walled femur shaft; large and thick patella; thick-walled tibia; large ankle joint; wide and strong toe bones. The Neanderthals are robust, above all in the anatomical regions connected to muscles, whose mass must have been quite large, as is shown by the great curvature torsion of certain bones (notably those of the forearm).

Regarding the shortening of limb extremities, as Trinkaus has noted as early as in 1981, the European Neanderthals show a shortening of the distal extremities, resulting in shorter forearms and lower legs. Two indexes illustrate this shortening: the relative proportions of the leg in relation to the thigh (crural index) and of the forearm in relation to the arm (brachial index). This small index among the Neanderthals is similar to that of contemporary populations living in the arctic regions (Eskimos and Lapps, for example) and illustrates an adaptation to this environment *(Figure 3)*. Bergmann's and Allen's rules, attempting to explain variations of shape and size among living populations, thus apply to the Neanderthals.

Is it possible to situate the origin of this adaptation in the Neanderthal lineage? Did this adaptation first take place during stages 4–3, at the time of the classical Neanderthals? It is difficult to answer these questions, given the paucity of post-cranial bones corresponding to the periods prior to the classical Neanderthals. However, the fragment of the tibia found at Boxgrove in England and dated at the isotopic stage 13 (Roberts *et al.* 1994) is large in size (maximum length 375 mm) and greater than among Neanderthals (Wolpoff 1996).

The great size of the tibial diaphysis of Boxgrove does not provide any information concerning the relative proportions of the lower limbs of this fossil, of its crural index, but it seems to be generally agreed that this individual was not small in size. According to Wolpoff (1996) it is "the tibia of one of the largest humans known, the dimensions of the sizeable shaft fragment suggesting a height of close to 1.8 m, larger than any of the much later European Neanderthals. ... Its larger diameter and thick shaft walls combine to suggest that this was a very powerful and active person" (p. 511). We recall that this fossil is a contemporary of Mauer, discovered in Germany, represented by a jaw. The Mauer jaw is characterized by its large dimensions, larger than those of the Neanderthals.

These data allow to advance the hypothesis that the European population present during the isotopic stage 13, which includes the tibial diaphysis of Boxgrove, prior to the great cooling down of stage 12, does not seem to present any adaptation to the cold. It would be interesting in this regard to study the relevant data on the Tautavel fossils, where several long bones have been found, as well as on the fossil remains of Atapuerca Sima de los Huesos, in order to be able to determine whether this adaptation originates during stage 12 or if it is to be sought at a later period (during stages 10, 8, 6).

It should be noted that the features attributed to the adaptation to cold cited above are found on the Neanderthals of the Near East, for example on Kebara. However, the Levantine climate being quite different than that of Europe, it presents two possibilities: either the Neanderthals of the Near East, as often emphasized (Condemi 1985, 1988, 1992, Bar Yosef 1988, Bar Yosef, Vandermeersch 1993), derive from cold-adapted European Neanderthals, and were not in the Levant for a period long enough to get adapted to a more favourable climate, or else it has to be admitted that the traits described above cannot be accounted for solely on the basis of the adaptation to the cold.

The facial morphology

The other anatomical region cited in relation to the adaptation of the Neanderthals to the cold concerns the particular morphology of the face, and above all of the extension of nasal cavities.

Among the Neanderthals, both the internal and external size of the nasal cavities is very large. The nose must have been remarkably prominent. In fact, in some cases as, for example, with La Chapelle-aux-Saints, the nasal bones jutted out almost horizontally below the brows. Since we know that one of the principal functions of the nose is to warm and moisten air that is breathed in, Coon (1962) supposed that the prominent nose of the Neanderthals was positioned far forward in order to lengthen their noses and thus the nasal cavity used to warm and humidify the cold and dry air of their Ice Age environment as a means of protecting brain tissues.

This explanation is however problematic since, in comparison to modern skulls, the Neanderthal combination of great nose length and breadth is unusual.

Modern cold-adapted people, such the Arctic Inuits, tend to have long but narrow nasal openings. On the other hand, broad noses are found mostly among people adapted to warm conditions. This could suggest that the Neanderthal nasal form might have retained an archaic shape, which is corroborated by the fact that the morphology of Neanderthals is also found among pre-Würmian European fossils (Schwartz, Tattersall 1996, Arsuaga *et al.* 1993, Wolpoff 1996).

In spite of the paucity of post-cranial pre-Würmian fossils, a number of fossil faces and nasal cavities are available from this period, ranging from isotopic stages 12 to 5 (Arago XXI, Petralona, Steinheim and Atapuerca SH, Saccopastore 1 et 2). The available data show that the Neanderthal morphology appears prior to the period of classical Neanderthals. Indeed, this morphology exists on the fossils of Atapuerca SH, as the authors who have studied these fossils (Arsuaga *et al.* 1997) have noted: "The Neanderthal morphology clearly derives from that seen in Atapuerca SH Cranium 5" (p. 268).

Certain authors, such as Wolpoff (1996), following Coon (1962), emphasized another adaptation evidenced in the blood supply to the face. Here, the foramina that bring blood vessels to the facial tissues are very numerous and very large among the European Neanderthals. This feature, associated with a highly developed maxillary sinus, would support the hypothesis of an adaptation to the cold by the Neanderthals.

CONCLUSION

On the basis of what has been explained above we can conclude that:

1) The features believed to be in relation to cold adaptation are present in the Neanderthals. They essentially involve the face and the proportions of limb bones.
2) The adaptive features, above all of the face, are present well before the stage 4–3, which is the period of the classical Neanderthals.

It is difficult to determine exactly when these adaptive features of the face appeared. It may be supposed that they emerged during stage 12. If this is the case, an explanation must still be given for the fact that these cold-adaptive features persisted over a long period of time and were even maintained during the successive interglaciary stages (interglacial 11, 9, 7 and 5), thus under the mildest climatic conditions.

The explanation for the persistence of these features might be sought, as has been emphasized (Hublin 1990, Roebroeks *et al.* 1992), in terms of the indirect repercussions that climate may have on populations. Hence, climate may have consequences for the territorial extension of populations, concerning what might be termed the occupability of territories. The extension of forests during the interglaciary stages may have impeded the mobility of populations and thus their possibilities for genetic exchange. This may also involve reduction or fragmentation of the population.

As it is recognized, these two factors had an effect on the persistence or loss of certain genetic features. In conclusion, it is probable that the particular climate during the entire middle Pleistocene had an effect on the European population, above all in leading to an isolation of populations limiting their genetic variability and introducing genetic drift.

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