

The Earliest *Homo Sapiens* (*Sapiens*): Biological, Chronological and Taxonomic Perspectives

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Introduction

Since the introduction of the binomial nomenclature by Linnaeus in 1758, the present-day species of man (= modern Man) has been classified as *Homo sapiens*. Western Europe was initially privileged as being the region in which the species originated, as attested by the history of paleoanthropology. The first discoveries made at the end of the 19th century, at the Cro-magnon rock-shelter and at Chancelade in France and Grimaldi in Italy, were used to establish the existence of *Homo sapiens fossilis*. Alongside the Neanderthal line of descent, recognized from 1864 by King as a separate species (*Homo neanderthalensis*), a second descent lineage needed to be differentiated in Europe in order to account for the emergence of modern Man. The search for this European ancestor was to reach its apogee with the today abandoned theory of European Pre-sapiens peoples, of which the French anthropologist H. V. Vallois (1958) was one of the most fervent proponents.

It was those first discoveries made outside of Europe, more specifically from the Levant in the 1930s and the subsequent controversies that these engendered, that reopened the debate on the origins of modern humans. For some, the anthropological data brought to light by these discoveries, notably those relating to the Skhul and Qafzeh fossils in Israel, provided evidence of an interbreeding between Neanderthals and modern humans in that region (Thoma, 1965), though the origin of the latter group still remained to be determined. Others were coming to the view that an extra-European origin for modern Man was possible, on the basis of the evidence of the Skhul and Qafzeh fossils, which were being categorized as Proto-Cro-Magnons (Howell, 1958). At the same period, the position of the Neanderthals was being reassessed, with the movement towards a trinomial classification whereby two sub-species, *sapiens* and *neanderthalensis*, would be retained within the species *sapiens*.

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Over the last 20 years the debate over the origin of modern Man has broadened, with for a period the supporters of a theory of regional diversification of *Homo sapiens* (the multi-regionalist theory) being opposed by those holding to the single-source theory (the 'Out of Africa' model). At the same time, within the scientific community, the idea of *Homo neanderthalensis* as a separate species was being resurrected, supported by bone classification typology and drawing on arguments derived from paleogenetic analyses that buttressed the case for the existence of distinct species and for privileging an African origin for modern humans. The upshot of these debates is that scientific results may sometimes be interpreted in different ways according to the particular preoccupations of various researchers.

Definition of *Homo sapiens sapiens*, modern Man

Use of the qualifier 'modern' in paleoanthropology drew its origin, at the end of the 19th and the beginning of the 20th centuries, from a near-exclusive reference to European fossil remains from the Upper Paleolithic which were perceived as being ancestors of present-day populations. In the minds of many of those who have made use of this qualifier, it implies the acquisition of developed cognitive and cultural skills (Tillier, 1999: 18) though the definition of the biological and cultural 'modernity' of humans, which has difficulty being freed from an ideological overlay, could provide a source for vigorous debate at several research symposia. Today a more coherent approach has been taken in relation to the biological diversity of the first modern humans in Europe (Henry-Gambier, 2005a, b) and it is now clear that the more highly developed cultural practices required various millennia to become established, a perception which renders obsolete the theory that culture was a prime, defining factor.

However, one is obliged to observe that Europe, whether in relation to fossil modern humans or to Neanderthals, remains in the majority of phylogenetic studies an unavoidable point of reference for numerous researchers who remain very influenced by their immediate environment as far as present-day populations are concerned. M. H. Wolpoff was probably one of the first in 1986 to point out the bias represented by the choice of an exclusively European point of reference in any discussion of the modern affinities of particular fossil remains, an attitude which could lead, in extreme cases, to the complete exclusion of some present-day human groups.

The osteobiography of modern Man depends essentially on anatomical characteristics of the skull bones, whereas those of the postcranial skeleton most often are presented as secondary in the majority of published descriptions. Modern humans have several characteristics in common with Neanderthals, such as an increase in brain volume, the flattening of the occipital angle and the lengthening of the inion-lambda arc on the posterior cranium and the reduction of facial prognathism and tooth size. The medial area of the facial skeleton is distinguished in modern Man by a configuration said to be in inflexion, with pronounced zygomatico-maxillary angulation and a canine fossa.

Among the characteristics of modern humans are the proportions of the cranial vault (high in relation to its length), a 'house-like' shape to the cranium in posterior

view resulting from high-positioned parietal eminences and parallel lateral walls, salient pyramidal mastoid processes, a vertical brow bearing frontal eminences, the absence of marked bony ridges, whether in the supra-orbital region or on the cranial posterior, and finally the presence of a bony chin.

The postcranial skeleton is described as being relatively slender, having numerous similarities with that of the Neanderthals, due to equivalent constraints imposed by posture and locomotion and bearing on several distinct anatomical regions (e.g. cervical lordosis, morphology of the vertebral column, long bones, hands and feet, etc.). Emphasis is placed in the literature on a limited number of specific characteristics which are always defined so as to justify a distinction with a morphology that is considered specific to the Neanderthals. However, the specificity of these features may come under re-examination with the discovery of new skeletons (which have begun to fill in some of the major gaps between the Australopithecines and *Homo sapiens*), or even more with the growing recognition of the extent of biological diversity.

To illustrate this issue, the example of the superior pubic ramus of the pelvis is revelatory. This is described as being short and broad in the vertical dimension in modern humans, whereas in Neanderthals it is distinguished by its elongation and its slenderness (e.g. McCown and Keith, 1939; Stewart, 1960; Trinkaus, 1976). Stringer et al. (1984: 54–5), in two comparative tables setting out syntheses of the anatomical characteristics of the skeletons of modern Man and Neanderthals, remained non-committal as to the phylogenetic significance that should be attributed to this set of features of the pelvis. Subsequent developments have justified their reticence, even if it is clear that their prudence has not always been followed; far from it in fact, given the number of authors who have chosen to confer a specific importance to the configuration of the superior pubic ramus (e.g. Rak, 1990). The understanding of the significance of this feature within the genus *Homo* has benefited from the discovery, among others, of the fossils of Sima de los Huesos in Spain and of Zhinnuishan in China. The expression of the configuration of this area of the pelvis cannot be stereotyped, as is indicated by the diversity of expression illustrated by the fossils included in the genus *Homo* and in the *sapiens* species, whether considering European, North Asian or Levantine examples (Arensburg and Belfer-Cohen, 1998; Rosenberg, 1998; Arsuaga et al., 1999; Tillier, 2005a).

Within the paleoanthropological community, the temptation remains strong to promote a typological classification (whose aim is primarily to make a clear distinction with the Neanderthals) rather than admit a mosaic-like evolution of modern features, a certain biological heterogeneity among early Old World modern humans in much the same way as among their contemporaries.

The very earliest modern humans (singly and doubly *sapiens*)

In the present state of knowledge, the earliest fossils attesting the presence of modern humans come from Southwest Asia and Africa. The paleontological evidence coming from China, Southeast Asia and the Australian continent is of more recent date (e.g. Mann, 1995; Wolpoff, 1999).

The Levant

The Near-East has yielded the chronologically best situated and most complete documentation, and the fossils directly concerned come from the Mousterian levels of two sites in the southern Mediterranean Levant. The phylogenetic affinities of the specimens from Skhul and from Qafzeh (Israel) with modern humans have been defined and discussed on the basis of the identification of resemblances between the peoples of the Upper Paleolithic and recent populations (McCown and Keith, 1939; Howell, 1958; Thoma, 1965; Vandermeersch, 1981; Mann, 1995; Tillier, 1999).

Notable among the modern-derived features are the height of the cranial vault, the so-called 'house-like' shape of the cranium in posterior view, a vertical forehead with a supraorbital region only moderately salient (consisting of two arches, one supraorbital, the other supraciliary), a posterior cranium distinguished by a rounded occipital profile with a distinct external protuberance, a mid-facial region revealing a canine fossa and a mental protuberance (Fig. 1). Within the fossil sample set, the expression of a certain cranial variability may be observed among the adult subjects and the interpretation of this, notably as suggesting a sexual dimorphism, is not obvious, the most often for want of convincing skeletal diagnostic components (i.e.



Fig. 1. Adult from Qafzeh 6 (upper left and right); Qafzeh 9 estimated in the range 15–19 years (bottom left); and the adolescent from Qafzeh 11 (bottom right). These three specimens show the development of modern features within a single site. (Photos Dubure and A. Pinchasov)

the pelvis). While female sex has been definitely established for Qafzeh 9, an individual whose pelvic bones were all present, the masculinity attributed to Qafzeh 6 (Fig. 1) rests only on cranial characteristics that denote a certain robustness (Vandermeersch, 1981).

At Qafzeh as at Skhul, several individuals (both adults and juveniles) have retained some archaic characteristics (for example the size of the tegmen tympani on the temporal bone, the presence of a genioglossal fossa on the inside surface of the symphyseal region of the mandible), which can be absent in later humans from the Upper Paleolithic (Vandermeersch, 1981; Tillier, 1999). The persistence of these features and the way individual variability should be interpreted remains a theme for debate which leads some authors to moderate somewhat the 'modernity' of certain individuals, and even to signal the possibility of masked dissimilarities, affecting for example the internal brain structure, independently of a marked brain size (e.g. Klein, 1989, 1999; Stringer, 1994; Wolpoff, 1999).

The Skhul and Qafzeh fossils are associated with a Mousterian tool industry referred to as type Tabun C (Garrod and Bate, 1937; Bar-Yosef, 1989, 2000; Boutié, 1989; Hovers, 1997). The antiquity of these human occupation sites, originally proposed, in the case of Qafzeh, on the basis of biostratigraphical data (Tchernov, 1981), took some time to establish definitively (Tillier and Tassy, 1987; Arensburg and Tillier, 1989). This was not achieved until confirmation was obtained through radiometric dating methods, applied successively at the Qafzeh and Skhul sites (Schwarz et al., 1988; Valladas et al., 1988; Stringer et al., 1989; Mercier et al., 1993; Yokohama et al., 1997).

The earliest modern humans of the Levant date back to more than 90,000 years BP (Before the Present) (Table 1), and several tens of thousands of years separate them from their successors in the area, whose presence is attested for the Upper Paleolithic at Qafzeh and Hayonim in Israel and at Ksar 'Aqil in Lebanon (Bergman and Stringer, 1989; Arensburg et al., 1990; Tillier and Tixier, 1990). What could be established about their origins and their predecessors?

Africa

Data emerging from molecular biology, combining analyses of mitochondrial DNA, autosomal nuclear DNA and, to a lesser degree, those bearing on the polymorphism of the Y chromosome, are cited to uphold the hypothesis of a single origin for modern humans and to situate this origin in Africa. However, according to specialists, the scenario is not as simple as that. In the opinion of Cavalli-Sforza et al. (1994: 93): 'The split between Africans and non-Africans was the earliest in human evolutionary history, a suggestion subject to the validation of the hypothesis that rates of evolution are constant. The genetic tree does not necessarily tell us whether the first humans were in Africa and expanded to Asia, or vice versa.' The mitochondrial DNA analyses recently carried out on one of the Lake Mungo fossils in Australia, which bears witness to an arrival of modern humans on that continent, seems to tend in the same direction (Adcock et al., 2001). As Barriol (2001) observed, if Eve is African, could Adam be Asian?

Is the evidence provided by paleontology capable of erasing these uncertainties in relation to Africa? The anthropological documentation that allows consideration of the presence there of modern humans older than those of Skhul and Qafzeh is far from being concordant with this. The problems are linked to difficulties inherent in the establishment of a rigorous chronology, to the fragmentary state of human remains in some cases and, in some instances, to the circumstances of their discovery. Three regions south of the Sahara are involved to various degrees: South Africa (with the Klasies River Mouth and Border Cave sites), Ethiopia (with the formations of Omo Kibish in the south and Herto-Bouri in the north) and Sudan with the Singa skull.¹ To the north of the Sahara, two sites, one in Morocco and the other in Libya, should also be taken into consideration.

The data emerging from East Africa are without doubt the least problematic. The fossils of the Herto-Bouri formation, unearthed in 1997, seem to be the best circumscribed in their context of origin, and several sources of information agree on their dating, at around 150,000 years (White et al., 2003). They consist of two adult individuals and one child who demonstrate a mosaic of both modern and archaic features: this latter characteristic has led their discoverers to postulate that they could belong to a population 'that is on the verge of anatomical modernity but not yet fully modern' (White et al., 2003: 745). Among the archaic aspects to be considered are the persistence of a supraorbital torus and a set of morphometric features affecting the lower part of the face and reflecting a certain robustness.

Until this discovery, the two specimens found in the Omo river valley around 40 years ago were generally put forward as the most ancient representatives of modern humans in Africa (Day, 1972; Brauer, 1991), although the reliability of the dating carried out on shells which situated them as more than 130,000 years old has been questioned (Smith, 1993). For this material, more recent geochronological evidence, which is not easy to correlate with the original data, favours an early age (McDougall et al., 2005). The two skulls show a significant individual variation: the more incomplete one, Omo Kibish 2, has retained archaic features such as the low height of the cranial vault, a withdrawn frontal profile, a developed supraorbital relief, a sagittal contour of the posterior cranium that is unflattened and a broadened nuchal plane (Day, 1972; Day and Stringer, 1982); Omo Kibish 1 attests to modernity in relation to these above-mentioned features, to which can be added the presence of a bony chin and postcranial bones that come within the range of known variations for present-day populations.

As regards the South African fossils, controversy is far from over, whether in relation to the Border Cave specimens or those of the Klasies River Mouth, but for different reasons. In the case of the first, one of the most complete pieces, the Border Cave 1 skull, possesses general characteristics that are anatomically modern, but questions remain over the circumstances of its discovery and hence over the relationship of the fossil to the archaeological context.

On the other hand, there is no doubt about the archaeological context at the Klasies River Mouth and the dates are firmly identified as between 80,000 and 150,000 BP according to level (Deacon, 1993; Vogel, 2001; Feathers, 2002). However, there are differences of view over the phylogenetic affinities of the human remains, several of which, because of their fragmentary state (teeth in the case of the oldest

Table 1. Chronological distribution of the earliest human fossils associated with the species *Homo sapiens* for which affinities with modern Man are questioned on various levels

Fossils	Dating	Radiometric techniques/ Other data	Sources
Skhul (Israel)	119,000 ± 18,000 BP ≥ 101,000 BP	TL ESR	Grun and Stringer (1991) Mercier et al. (1993)
Qafzeh (Israel)	92,000 ± 5000 BP ≥ 100,000 BP ≥ 100,000 BP	TL ESR γ Spectrometry	Valladas et al. (1988) Schwarcz et al. (1988) Yokoyama et al. (1997)
Border Cave (Sth Africa)	≥ 90,000 BP ?		Brauer (1991: 200)
Omo Kibish (Ethiopia)	≥ 130,000 BP ?	⁴⁰ Ar/ ³⁹ Ar Stratigraphy	Day (1972) Mcdougall et al. (2005)
Klasies River Mouth (Sth Africa)	110,000/60,000 BP	ESR Biostratigraphy Biostratigraphy	Deacon (1993) Vogel (2001) Feathers (2002)
Haua Fteah (Libya)	? ?	Mousterian	McBurney (1975)
Jebel Irhoud (Morocco)	130,000/160,000 BP	ESR Biostratigraphy	Hublin (1991)
Singa (Sudan)	≥ 140,000 BP	ESR	McDermott et al. (1996)
Herto Bouri (Ethiopia)	≥ 150,000 BP	⁴⁰ Ar/ ³⁹ Ar	White et al. (2003)
Zuttiyeh (Israel)	≥ 150,000 BP	Ur/Th Biostratigraphy	Gisis and Bar-Yosef (1974) Vandermeersch (1995)

Radiometric methods: TL = Thermoluminescence; ESR = Electron Spin Resonance; Ur/Th = Uranium Thorium dating

specimens, fragments of mandibles, frontal and zygomatic bones for the more recent) have given rise to contested interpretations. For some, Klasies River Mouth supplies the proof of the early presence of modern humans in South Africa with the arguments attested in support of this view being a diminished supraorbital relief, the apparent slenderness of the mandibular morphology or the size of the teeth (Brauer, 1991); for others, the specimens reflect archaic forms as shown by the absence of a bony chin and the robustness of the zygomatic bone, while the reduction in teeth size is not held to be a relevant criterion (Deacon, 1993; Smith, 1993; Mann, 1995). Nevertheless, it is worth recalling that it is these South African fossils that remain the most frequently cited in the specialist literature, beside those more recently discovered at Blombos (Grine and Henshilwood, 2002), for their chronological support of the hypothesis of an early African origin for modern humans.

The regions situated north of the Sahara are often excluded from this discussion, doubtless because of their geographical remoteness with respect to the supposed cradle zone. The Jebel Irhoud fossils in Morocco represent for the present the only anthropological evidence of Mousterian occupation to the north of the Sahara, along

with those of Haua Fteah in Libya. The two mandibular rami found at Haua Fteah in a Mousterian context (McBurney, 1975) do not permit a very extensive diagnosis (Tillier, 1992), but the situation is different for the Moroccan specimens. These latter comprise two adult crania and three sets of children's bones (Hublin and Tillier, 1988; Hublin, 1991; Tixier et al., 2001). Several anatomically based arguments allow the envisaging of a continuity of population between these peoples and the first modern humans and justify the designation *Homo sapiens*, of which they might conceivably represent an earlier stage of development than the Levantine examples. Their positioning in relation to these latter raises the question of their possible status as archaic *Homo sapiens*. An attribution of these fossils to isotope stage 6, that is, to beyond 130,000 years BP, should not indeed be ruled out (Hublin, 1991).

All the fossils discovered in Africa are either more recent than those of the Levant or are associated under the appellation of archaic *Homo sapiens*. The understanding of this evolutionary stage (grade) is far from being unanimous in relation to where the boundaries lie, but it nevertheless allows the conclusion that not all members of *Homo sapiens* are necessarily modern humans, as shown by the appendage, for some groups of them, of a subspecific name.

The concept of archaic *Homo sapiens* and its extension

Not all authors apprehend in identical fashion the concept of an archaic *Homo sapiens*, which leads to contrasting interpretations. For G. Brauer (1991), the evidence from Africa would allow the distinction of a sequential archaic *Homo sapiens* lineage whose categorization appeared to him somewhat artificial in that it would group together the fossils of all *sapiens* hominids prior to the first modern humans on that continent. These fossils would present, alongside features inherited from *Homo erectus*, more evolved characteristics relating to an increase in brain volume, hence justifying such a distinction.

For other authors, the category of archaic *Homo sapiens* should include early fossils that establish an evolutionary stage which prefigures a totally modern morphology. The 'archaic' appellation is thus justified ipso facto only for fossils originating outside of Europe. This would therefore apply, in Africa, to the Moroccan specimens from Jebel Irhoud mentioned above, or else to other fossils contemporary with or older than these, such as those of the Herto–Bouri formation in the Afar depression referred to earlier, for which the authors have proposed a new subspecies *Homo sapiens idaltu* (White et al., 2003). The common aspect of all African fossils so associated would be the predominance of primitive features over derived features, which would justify maintaining these specimens on a 'lower' level of development. It may be claimed that corroboration for this gradualist perception is to be found in the geochronological data. B. Vandermeesch (2005: 16) thus calls attention to a perceived consensus among researchers – one which would reserve the appellation of archaic *Homo sapiens* to 'non-European fossils with ages of more than 150,000 years'. In the same way, this author had considered how in the Levant the Zuttiyeh fossil from Israel could constitute one of the final developmental stages in this region of the lineage that led to the first modern humans (Vandermeersch, 1995).

However, the Middle East region generally has yielded a significant number of fossils (in Israel, Syria and Iraq) which remain under debate because the recognition of their taxonomic status has generated no unanimity. The biological and cultural relationships between the various regional groups of fossils raise more questions than answers. A consensus is nevertheless emerging to acknowledge that those fossils derived from the Tabun, Amud, Kebara, Hayonim, Dederiyeh and Shanidar sites are *Homo sapiens*², and are anatomically different from the first modern humans of Skhul and Qafzeh (e.g. Vandermeersch, 1981; Trinkaus, 1991, 1995; Mann, 1995; Arensburg and Belfer-Cohen, 1998; Tillier et al., 2003; Tillier, 2005a, b). For those which have undergone radiometric dating they are either older – Tabun and Hayonim (Grun and Stringer, 2000; Mercier et al., 2000 and undated; Mercier and Valladas, 2003) – or more recent – Kebara and Amud (Valladas et al., 1987; Valladas et al., 1999; Rink et al., 2001) – in the region than the Skhul and Qafzeh fossils.

For most of these Levantine fossils, the significance of the archaic features that they display (relating to the height of the cranial vault, the sagittal contour of the forehead, the development of the supraorbital area, the anterior region of the mandible, etc.) has been and remains a subject of debate, including, for some authors, in terms of affinities with the Neanderthals of Europe (e.g. Vandermeersch, 1981; Trinkaus, 1995; Hublin, 2000; Condemi, 2003). The anatomical characteristics which distinguish them both from the European Neanderthals and from the Skhul/Qafzeh peoples are giving rise to conflicting interpretations, and the debate is not new, having begun with the earliest publications (e.g. McCown and Keith, 1939; Howell, 1958; Thoma, 1965; Suzuki and Takai, 1970). The same fossils can variously be categorized as archaic *Homo sapiens*, as Neanderthals or as a migrant population of *Homo sapiens* that had evolved locally. The desire to recognize the existence, outside of the first modern humans of the Levant, of a single biologically homogeneous human group most often takes precedence over the acceptance of the phenotypal diversity and secondarily of the non-contemporaneity of the fossils. The history of the way in which the region was populated can only be reconstructed by taking into account its particular character as a crossroads where various influences intersected (Arensburg and Belfer-Cohen, 1998; Tillier, 2005a, b).

Europe, a meeting-ground between *Homo sapiens (sapiens)* and *Homo (sapiens) neanderthalensis*?

Presently available anthropological data support a late arrival of modern humans in Europe, following a gradient from east to west, and the fossils for which modern status presents absolutely no ambiguity are of a date later than 40,000 years ago. From that time on they are accompanied by an archaeological context which denotes a marked cultural innovation.

The oldest evidence would appear to be from southeastern Europe, from the site of Pesterța cu Oase in Romania, with a jawbone for which a direct age situated between 34,000 and 36,000 years BP has been obtained by Carbon-14 (¹⁴C) dating using the AMS³ technique (Trinkaus et al., 2003). The site of Mladec in Moravia (Czech Republic) yielded, during very early excavations, numerous specimens

whose strict contemporaneity and association with the Aurignacian cultural context have sometimes been questioned. However, direct dating has recently been carried out on four of the specimens and has proved to be consistent (Wild et al., 2005), situating the fossils at around 31,000 years BP⁴. The Romanian and Czech fossils attest the persistence, alongside the derivation of modern features, of certain archaic characteristics, associated essentially with the facial skeleton (e.g. interorbital and nasals widths, dimensions of the dental arcade, robustness of the jawbone). The selection of features reflecting a Neanderthal influence, such as the 'horizontal-oval' configuration of the opening of the mandibular canal on the mandibular ramus of Pesteră cu Oase 1 (Trinkaus et al., 2003) cannot in our view be validated.

All other fossils whose association with modern Man has been established with certainty are less than 30,000 years old, and among them are the occupants of the Cro-Magnon rock shelter in France (Henry-Gambier, 2002). This latter people, long used as the holotype of the *Homo sapiens sapiens* dating from the Aurignacian period, have an age not exceeding 28,000 years.

Did the Neanderthals contribute to the genetic pool of modern humans? Can one detect among the last Neanderthals the influence of a genetic exchange between the two populations? An infant's skeleton discovered in the Mezmaiskaya Cave in the northern Caucasus has been directly dated at 29,195 ± 965 years BP (Golovanova et al., 1999). A chronological linkage to the Mousterian and implicitly a Neanderthal affiliation have been proposed (Golovanova et al., 1999), even though the age derived is more recent than those accepted up until then for this cave, both for the Mousterian levels and for those of the Early Upper Paleolithic, and though no samples of fauna or stone tool industry have been associated with the deposit. For this very young child (whose age at death is estimated at between seven months *in utero* and two months post-natal), two of the arguments put forward in the preliminary study, the weak development of the mastoid process on the temporal bone and the lengthening of the *foramen magnum*, are juvenile features common to all children of the species *Homo sapiens* (Tillier, 1998; Coqueugnot and Le Minor, 2002), and only the first of these persists in the adult Neanderthal (Barriel and Tillier, 2002). The final argument bears upon the proportions of the long bone segments, but the discriminating value of the crural index (length of the tibial diaphysis × 100/length of the femoral diaphysis) is not as pronounced in Paleolithic children (Barriel and Tillier, 2002: Table 1).

Remains of Neanderthal bones have been dated by the ¹⁴C method at Vindija in Croatia and the results obtained for two of these (Churchill and Smith, 2002) give a recent date, being respectively 28,740–27,300 years BP for one and 29,880–28,280 BP for the other. Such a late presence of Neanderthals in Croatia as well as to the east of the Black Sea would tend to stand against established hypotheses privileging the southwest of Europe and notably the Iberian peninsula in the genetic isolation of the group (e.g. Vega Toscano, 1990; Zilhão, 1993; Hublin et al., 1995; Zilhão and Trinkaus, 2002).

The possibility of a gene exchange between modern humans and Neanderthals has been postulated on various occasions by authors to account for either the presence of characteristics situated at the outer limits of the observed variational range (the *tolerated* variation would be the more appropriate term for certain very

typologically oriented analyses), or for that of 'mixed-type' features. New investigations are possible with the development of three-dimensional imaging, as illustrated by the comparative study of the labyrinth and the semicircular canals of the inner ear. Spoor et al. (2003) suggest that marked differences exist in the configuration of the labyrinth between modern humans and Neanderthals, and that these differences may be used for purposes of phylogenetic analysis. When studying the labyrinth of Neanderthal adolescent Le Moustier 1 from the Dordogne region, Spoor et al. (2003) observed that the fossil presents a more modern morphology than the other Neanderthals tested, and somewhat reluctantly admits that: 'Conclusive attribution will be impossible when dealing with labyrinths similar to that of Le Moustier 1, which entirely fall in the morphological overlap zone of Neanderthals and modern humans.' This atypical configuration of the labyrinth is offset against the possibility of a late dating, giving possible credence to the influence of a gene exchange between Neanderthals and the earliest modern humans (Spoor et al., 2003: 162). Such a hypothesis still remains to be confirmed in relation to several parameters, including those of the dating of the fossil and of the identification of older modern humans.

In view of such observations, what conclusions should be retained? The existence of a diachronic evolution within the Neanderthal lineage, the recognition of individual variation affecting the fossil population as for any human population, the limitations of a typological classification starting out from a phenotype (which has long been conceded in the case of present-day populations) or all three at once? A range of questions which seem further from the orientations of the proponents of a rapid replacement of populations (Hublin, 2000; Stringer, 2002; Couture and Hublin, 2005) than from those of the advocates of a process of assimilation between the first modern humans and the last Neanderthals (Duarte et al., 1999; Zilhão and Trinkaus, 2002).

The interpretation of the scientific results varies according to the particular leanings of one group or the other. Could therefore a more solid structure for argument be found in the results of genetic analysis? Might paleogenetics contribute to raising the veil which masks the taxonomic uncertainties that persist for this critical period of the Paleolithic, and can it help provide some definite conclusion regarding whether to classify representatives of the two populations as subspecies (*Homo sapiens*, subspecies *neanderthalensis* or *sapiens*) or as separate species (*Homo neanderthalensis*, *Homo sapiens*)? The fragments of Neanderthal mitochondrial DNA sequences published to date from fossils from Germany, Croatia, France and the Caucasus (in the latter case the individual tested was the child whose attribution remains to be established) reveal a significant divergence from equivalent sequences in present-day humans (Krings et al., 1997; Krings et al., 1999; Krings, Capelli et al., 2000; Ovchinnikov et al., 2000; Schmitz et al., 2002; Beauval et al., 2005).

Nevertheless, this divergence between present-day man and Neanderthal is significantly less than that which exists between two species of chimpanzees, and it reflects rather more the variation between two subspecies of *Pan troglodytes* (Barriel and Tillier, 2002). Furthermore, it should be mentioned that other sequences obtained from Neanderthal bones have not reached the stage of publication, as they have not been authenticated for various reasons (presumed contamination, absence of reproducibility between laboratories, etc.). Finally, the known genetic variability

from within the Neanderthal population is established only on sequences of mitochondrial DNA and the involvement of the nuclear genes remains unknown, for want of analyses.

Another question mark relates to the identification of a divergence with the equivalent sequences in fossil modern humans. An initial analysis has been published based on the fossils from the Paglicci Cave in Italy, dated at 24,000 years BP (Caramelli et al., 2003), and the results show that the sequences can be situated within the present-day human range of variation. However, as Barriel (2005) points out, the acceptance of their authentication has provoked a number of reactions and the possibility of a contamination between ancient and modern specimens has been raised in relation to these (Abbott, 2003). This author lucidly observes that, for certain experts in ancient DNA analysis, 'if, in a laboratory applying all the requisite precautions an ancient Neanderthal sequence is obtained and presents resemblances with sequences of present-day humans (or falls within their range of variation), this will never be taken as the sign of a participation of Neanderthals in the genetic heritage of modern humans but as definitive evidence of contamination' (p. 386).

In summary, the prospects offered by paleogenetic research to make up for the limitations of paleoanthropology, to find answers for the questions concerning the relationship between modern humans and Neanderthals and to reach a more coherent grasp of the issue concerning the origins of present-day populations (*Homo doubly sapiens*) throw up numerous questions and all the obstacles have not yet been removed.

Paleoanthropology, from its viewpoint, casts major doubt on the thesis according to which man has always evolved in the same direction.

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Translated from the French by Colin Anderson

Notes

1. The incomplete Singa skull, as described by Spoor et al. (1998), is pathological, which poses certain problems of interpretation.
2. Y. Rak, for his part, supports a placement in the species *Homo neanderthalensis* (1990).
3. Accelerator Mass Spectrometry.
4. A closely similar age may well be determined for the early-discovered human bones at Kent Carven in Great Britain (Henry-Gambier, 2005b).