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**CHARACTERISTIC FEATURES
OF THE MIDDLE TO UPPER PALEOLITHIC TRANSITION
IN EURASIA**

Proceedings of the International Symposium
“Characteristic Features of the Middle to Upper Paleolithic Transition
in Eurasia: Development of Culture and Evolution of *Homo* Genus”
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THE LATE MIDDLE PALEOLITHIC AND THE AURIGNACIAN OF THE SWABIAN JURA, SOUTHWESTERN GERMANY

Introduction

With several rich cave sites in the Ach and Lone Valleys, the Swabian Jura in southwestern Germany is one of the key regions for the study of the late Middle Paleolithic and the evolution of the early Upper Paleolithic or Aurignacian in central Europe. The long history of research and the abundance of deposits in many of the region’s caves provide great potential for conducting detailed studies of how Neanderthals and anatomically modern humans in the Swabian Jura organized their subsistence and daily life some 45–30 ka BP.

The sites

The most important Swabian sites are represented by the caves in the Ach Valley 15 km west of Ulm between Schelklingen and Blaubeuren and the Lone Valley 25 km north of Ulm. Many of these sites such as Hohle Fels, Geißenklösterle and Sirgenstein in the Ach Valley and Vogelherd, Hohlenstein-Stadel, Hohlenstein-Bärenhöhle, Bocksteinhöhle and Bockstein-Törle in the Lone Valley have yielded considerable stratigraphic sequences with both Middle and Upper Paleolithic deposits, while other caves are known for their Middle Paleolithic (Große Grotte and Kogelstein in the Ach Valley; Bocksteinschmiede and Haldenstein in the Lone Valley) or Upper Paleolithic (Brillenhöhle in the Ach Valley) assemblages respectively.

Chronostratigraphy

The Swabian cave sites play a crucial role in the discussion about the age and the cultural context of the late Middle Paleolithic and the early Upper Paleolithic or Aurignacian in central Europe. While for the Aurignacian a solid data framework is available, dates for the Middle Paleolithic are much more seldom and they still seem to be problematic. Both in Geißenklösterle and in Hohle Fels some dates for the Middle Paleolithic deposits are younger than those for the Aurignacian assemblages. Moreover, in the case of Geißenklösterle the dates do not show a clear pattern of increasing age with depth (Conard and Bolus, 2003, 2008). Of course, one has to keep in mind that the radiocarbon dates for

the Middle Paleolithic lie at the limit of the method and should be treated with caution. A lot of further systematic research will be necessary to make things clearer. At the present state an age of slightly greater than 40 thousand calendar years seems plausible for the late Swabian Middle Paleolithic.

The oldest dates for the Swabian Aurignacian fall into the same range. Again Geißenklösterle and Hohle Fels are the most important sites with more than 70 radiocarbon dates and a couple of TL dates for the Aurignacian deposits. In general, the uncalibrated radiocarbon dates for the Swabian Aurignacian range between 40 and 30 ka BP, with ages between 35 and 30 ka BP being more common than earlier dates. Seen in a European scale, this means that the Aurignacian appeared rather early in the Swabian Jura suggesting an early migration of anatomically modern humans into Swabia via the Danube Corridor (Conard and Bolus, 2003).

Although the dates for the Swabian late Middle Paleolithic and the Aurignacian overlap to a certain degree, it can be no doubt about the cultural stratigraphic relationship of both complexes. Robert Rudolf Schmidt (1912) following his excavations in Sirgenstein and Gustav Riek (1934) following his fieldwork in Vogelherd already pointed out that archaeologically sterile deposits separated the uppermost Middle Paleolithic from the lowermost Aurignacian. This was confirmed by Joachim Hahn in Geißenklösterle and, more recently, by Nicholas Conard in Hohle Fels (Hahn, 1988; Conard et al., 2006).

The Swabian Middle Paleolithic

Caves in both the Ach and the Lone Valleys have yielded deposits with Middle Paleolithic assemblages. Among these, assemblages of the *Blattspitzen* Group characterized by bifacial leaf points, although not sufficiently dated, seem to represent the latest expression of the Middle Paleolithic (Bolus, 2004a). Unfortunately, assemblages belonging to the *Blattspitzen* Group are rare in the Swabian Jura and in general only consist of few lithic artifacts. Other than colleagues in other parts of Europe, for instance eastern central Europe, the German research tradition does not view the *Blattspitzen* Group as an early Upper Paleolithic technocomplex but instead classifies it as belonging to the latest Middle Paleolithic. In this sense it might also be grouped among the so-called transitional technocomplexes, which have often been described in many parts of Europe but seem to be nearly lacking in Germany (Bolus, 2004b).

Other Middle Paleolithic assemblages, first of all those from Bocksteinschmiede (Wetzel and Bosinski, 1969), can be attributed to the *Keilmessergruppe* (Micoquian/Pradnikian). These assemblages include backed bifacial knives (*Keilmesser*), handaxes and a broad variety of side scrapers. Most Middle Paleolithic deposits, however, yielded non-standardized assemblages usually classified as Swabian Mousterian. In most cases these assemblages are not very rich and characterized by small irregular levallois cores and a limited set of formal tools, mostly side-scrapers.

Organic tools are very rare; they are only represented by bone points from Vogelherd and Große Grotte, a pointed rib from Vogelherd, and some bone re-

touchers from Vogelherd and Sirgenstein. Secure evidence of personal ornaments is completely lacking (Conard et al., 2006). The best evidence for anthropogenic features comes in the form of a fireplace at Sirgenstein and concentrations of burnt bone at sites including Große Grotte, Bockstein and perhaps Hohlenstein-Stadel. The use of bone as fuel suggests that wood and other plant fuels were not always available in sufficient quantities to supply the lighting, cooking and heating needs of the Neanderthal populations (Conard et al., in press). Horse and reindeer were the most frequently hunted animal species. Woolly rhino is much less frequent but reaches higher percentages than in the Swabian Aurignacian. Cave bear is abundant in all Middle Paleolithic sites but there is no clear indication that Neandertals hunted this animal. Human remains are very sparse and we know of only one Neanderthal femur from the Mousterian of Hohlenstein-Stadel. Nevertheless it seems plausible that Neandertals were responsible for all Middle Paleolithic assemblages in Swabia.

The low find density in most Middle Paleolithic sites of Swabia indicates that Neandertals visited most caves only sporadically and for short stays. The large number of cave bear bones shows that bears used the caves much more intensively than humans during the Middle Paleolithic.

The Swabian Aurignacian

The Swabian Jura is particularly well known for its Aurignacian deposits, especially those from Geißenklösterle and Hohlefels. Starting with the lowermost Aurignacian assemblages – Geißenklösterle, Archaeological Horizon (AH) III, and Hohlefels AH Vb – some 40 ka BP the material culture in Swabia changes dramatically. Abundant data from the Swabian sites show a wide spectrum of new artifact types, both lithic and organic, and a variety of personal ornaments as well as figurative art and musical instruments which are totally lacking in the local Middle Paleolithic assemblages (Conard and Bolus, 2006) (Fig. 1, 2). Evidence from the basal Aurignacian of AH Vb at Hohlefels demonstrates that the Swabian Aurignacian was fully developed from the beginning and contained the whole package of early Upper Paleolithic innovations including symbolic artifacts.

The lithic technology of the Swabian Aurignacian is based on a unidirectional blade and bladelet production; moreover there is also some evidence of systematic flake production. Blades, and to a much lower degree, bladelets were produced from platform cores while in most cases carinated blades served for the production of bladelets. This leads to the conclusion that the production of blades and bladelets followed frequently, but not exclusively, separate reduction sequences.

Retouched forms include a wide variety of tools such as carinated and nosed endscrapers (which might, as mentioned, also be seen as bladelet cores), simple endscrapers, burins of various types including busked and carinated burins, *Spitzklingen* (pointed blades), splintered pieces, truncated pieces and blades with lateral Aurignacian retouch. All of these forms are completely lacking in the preceding Middle Paleolithic of the region.

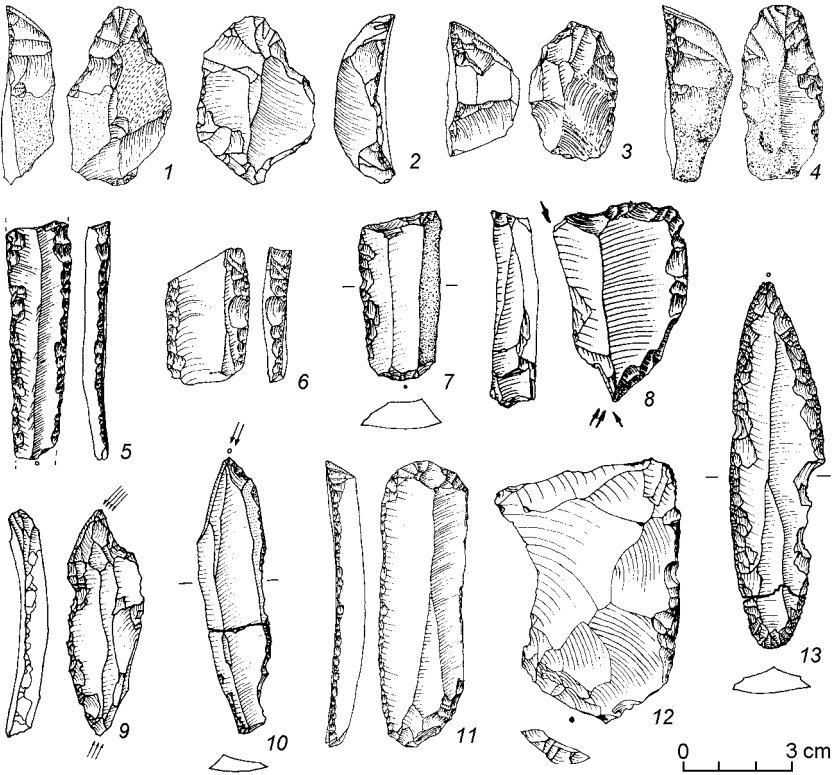


Fig. 1. Stone tools from the Swabian Aurignacian.

Organic tools are present with an important variety of types. First of all, projectile points have to be mentioned here. Pencil-shaped ivory points are known from the lowermost Aurignacian deposits of Geißenklösterle and Hohle Fels. Split-based bone points, type fossil of the early Aurignacian, are known from several sites including Bocksteinhöhle, Vogelherd and Geißenklösterle. At Hohle Fels split-based points are already present in the lowermost Aurignacian layer AH Vb with an age of down to 40 ka BP. Given the age of about 32 ka BP for one specimen from Brillenhöhle, split-based points appear nearly throughout the whole “lifespan” of the Swabian Aurignacian. Other types of organic tools include burnishers, awls, ivory rods and *bâtons percés* made of ivory.

Personal ornaments include a wide array of perforated and grooved teeth from carnivores and herbivores. Moreover, the Aurignacian sites have produced a variety of fully carved beads and pendants from mammoth ivory. Most characteristic are finely carved double perforated beads which have been found both in Ach and Lone Valley sites. They are not known from Aurignacian contexts elsewhere. All stages of production of the beads could be documented at Hohle Fels, Geißenklösterle and Vogelherd. Double perforated ivory beads appear through-

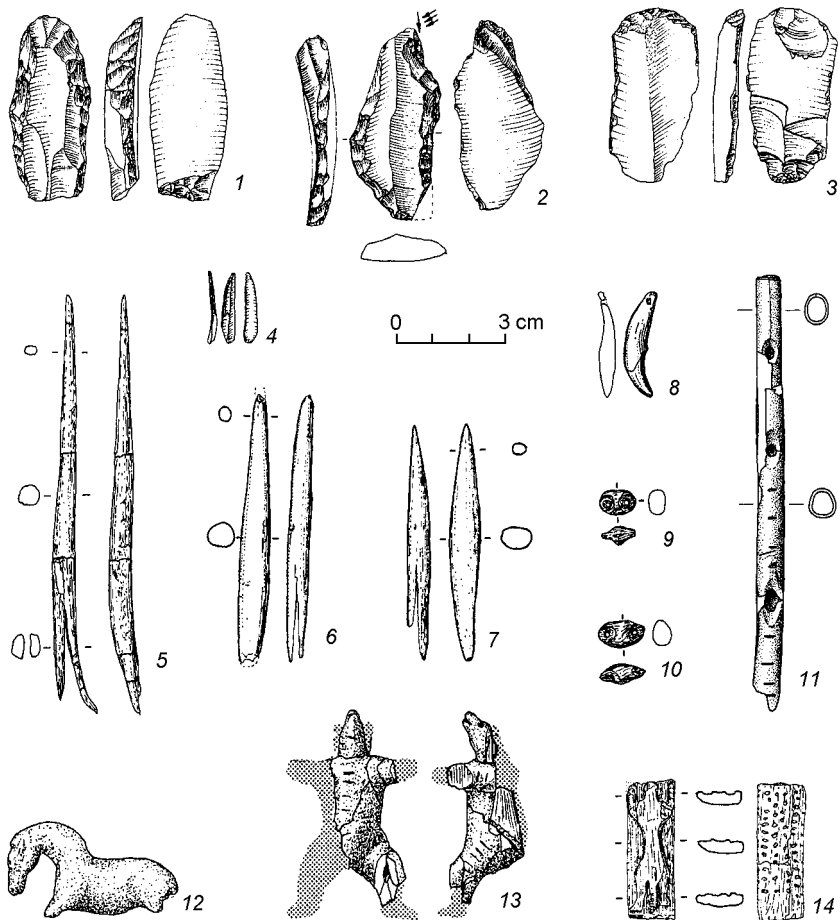


Fig. 2. Stone and organic tools, personal ornaments, art objects and a bone flute from the Swabian Aurignacian.

out the whole lifespan of the Swabian Aurignacian, the oldest specimens with an age of down to 40 thousand years coming from AH Vb of Hohle Fels and from AH III of Geißenklösterle, the youngest ones with an age of 30–29 thousand years coming from AH IIc of Hohle Fels and AH IV of Sirgenstein. Other forms include, among many others, basket shaped ivory pendants, small ivory discs and violin-shaped ivory beads.

In integral trait of the Swabian Aurignacian is the presence of figurative art represented first of all by small figurines carved from mammoth ivory. Until today, four caves – Hohle Fels, Geißenklösterle, Vogelherd and Hohlenstein-Stadel – have yielded about 50 art objects, often fragmentary, which represent the most impressive examples for symbolic artifacts within the Swabian Aurignacian and which date between 40 and 30 ka BP. In most cases animals are

depicted: mammoths, felines, horses, bison and other, less frequently depicted species including a bear, a waterbird and a fish. Regularly, the figurines bear symbolic signs the meaning of which is unknown to present-day people. A special group is represented by therianthrope figurines which combine human with animal features. Two of them, one from Hohlenstein-Stadel with a length of about 30 cm and one from Hohle Fels with a length of less than 3 cm, are referred to as *Löwenmenschen* (lion-men), since they show a combination of characteristics of lions and humans. A third object, a small ivory plate from Geißenklösterle, bears the half-relief of a figure with uplifted arms which might also represent a lion-man.

A singular piece of art is a Venus figurine carved from mammoth ivory which was discovered in the basal Aurignacian of AH Vb in Hohle Fels (Conard, 2009). The Venus is 6 cm high and lacks a head. Instead, an off-centre, but carefully carved ring is located above the broad shoulders of the figurine. Beneath the shoulders large breasts project forwards. The figurine has two short arms with carefully carved hands resting below the breasts. An oversized vulva is visible between the legs. A radiocarbon age of down to 40 thousand years makes this Venus the oldest of all figurines recovered from the Swabian caves and perhaps the earliest example of figurative art worldwide. With this discovery, the idea that three-dimensional female depictions of the Willendorf type developed not earlier than in the Gravettian some 10 thousand years later can be rejected.

Only 70 cm away from the Venus, the same find layer produced a flute made from a vulture bone (Conard et al., 2009). The fact that with this instrument already eight Aurignacian flutes are known from three Swabian caves – Geißenklösterle, Hohle Fels and Vogelherd – shows that a musical tradition existed in the Swabian Jura as early as 40 thousand years ago. Four of the flutes are made from bird bones, the other four are made from mammoth ivory. While it already affords some skills to make a flute out of a bird bone which is hollow by nature, it is a demonstration of technical mastery to carve a flute out of a massive piece of ivory. One of the most surprising observations is that it is possible with these Aurignacian flutes to play complex melodies just like with modern flutes of today.

The Aurignacian deposits in Hohle Fels yielded a number of features which are without doubt fire-related but represent dumping areas rather than real fireplaces. At least one fireplace was excavated in the lower Aurignacian (AH III) in Geißenklösterle.

Subsistence in the Swabian Aurignacian was based primarily on horse and reindeer just like in the Swabian Middle Paleolithic; moreover, there is a certain percentage of mammoth which was very sparsely exploited by Neandertals.

The Aurignacians of the Swabian Jura themselves are only known from three isolated teeth from Sirgenstein and one tooth from Hohlenstein-Stadel (Conard and Bolus, 2003). All belong to anatomically modern humans, and despite the scarcity of human remains, we consider anatomically modern humans responsible for the whole Swabian Aurignacian.

The find density in the Swabian Aurignacian is much higher than in the preceding Middle Paleolithic. This seems to indicate that the Aurignacians used the

caves much more intensive than the Neandertals. This is underlined by the fact that cave bear bones, though still numerous, are much less abundant than in the Middle Paleolithic when human presence in the caves had only been sporadic.

Discussion and conclusions

The archaeological record of southwestern Germany shows a clear break between the late Middle Paleolithic and the earliest Upper Paleolithic or Aurignacian. Although human fossils are sparse in Swabia, so far Neandertal remains have been found only in association with Middle Paleolithic artifacts and modern humans exclusively with Upper Paleolithic assemblages. Thus the fact that in most cases the late Middle Paleolithic and the Aurignacian are separated from each other by sterile or nearly sterile layers indicates that no Neandertals lived in the Swabian Jura when anatomically modern humans arrived there some 40 thousand years ago. The Swabian Aurignacian appears suddenly in a highly developed form containing numerous regionally unique signatures and differs strongly from the local Middle Paleolithic. Real transitional assemblages are lacking with the exception of few small assemblages belonging to the *Blattspitzen* Group.

An analysis of the find densities in Middle Paleolithic and Aurignacian deposits from Swabia demonstrates a shift in occupation intensity. Though the mere numbers of lithic artifacts, burnt bone, charcoal, anthropogenically modified faunal remains do not automatically reflect the time and intensity of occupation, most of these data reveal a factor of 10 or even 100 times more cultural debris per unit sediment volume during the Aurignacian versus the Middle Paleolithic (Conard, 2011; Conard et al., in press). Even if these figures are viewed as rough approximations, the intensity of occupation at carefully excavated and documented sites such as Hohle Fels and Geißenklösterle was far lower in the Middle Paleolithic than in the Aurignacian. This seems to reflect an increase in population densities in the Aurignacian relative to the Middle Paleolithic.

While most assemblages of the late Swabian Middle Paleolithic do not allow a classification other than “Swabian Mousterian”, the Swabian Aurignacian is characterized by a full package of Upper Paleolithic innovations such as new technologies and tool-types, both lithic and organic, a variety of personal ornaments, and, perhaps most impressive, figurative art and fully developed musical instruments, both belonging to the oldest examples known worldwide.

Given that many artifact forms, most notably certain personal ornaments, figurative mobile art and musical instruments, are exclusively limited to the Aurignacian of the Swabian Jura, this region can be viewed, within a polycentric framework, as one key center of cultural innovation during the early Upper Paleolithic (Conard, 2011). Other potential centers of innovation are located, for instance, in northern Italy and in southwestern France. The data from the Swabian Jura is consistent with the model of modern humans using the Danube Corridor as one main route of early Upper Paleolithic migration into central Europe (Conard and Bolus, 2003).

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TOWARDS A NEW “TRANSITION”: NEW DATA CONCERNING THE LITHIC INDUSTRIES FROM THE BEGINNING OF THE UPPER PALAEOLITHIC IN SOUTHWESTERN FRANCE

Introduction*

The significant number of palaeolithic sites in the south-west of France containing substantial stratigraphies presents the ideal framework for defining a regional archaeological sequence. As a result of this propitious situation, coupled with a well developed history of research, several models have been proposed to account for the diversity of archaeological facts. As they concerns the Upper Palaeolithic, the most commonly advanced model can be summarized as follows:

- The Chatelperronian is considered as a transitional techno-complex bearing a combination of Mousterian (scrapers, bifaces, Levallois) and Upper Palaeolithic traits (endscrapers, truncations, Chatelperronian points on blades). For sometime now this industry has been considered to have emerged from the local Mousterian of Acheulean Tradition (MTA) based on a single tool type; the backed knife, which is seen to have progressively evolved from the Audi point towards a lighter, more elongated type known as Chatelperronian point (Breuil, 1909; 1911). Seen at first as evidence for the acculturation of the final Neanderthals by anatomically modern humans (Demars and Hublin, 1989; Mellars, 1996), this industry is now more often perceived as representing an independent evolution of the Neanderthals towards the Upper Palaeolithic (d’Errico et al., 1998; Zilhão and d’Errico, 1999).

- The Early Aurignacian or Aurigancian “I”, according to Peyrony’s (1933) classification, whose type fossil is the split-based bone point, is the techno-comp

* Given the resolutely synthetic character of this article, we will not be able to cite the whole of the research which made it possible to produce. We endeavoured to have the references rich enough to make possible the constitution of a more complete bibliography.

lex that immediately follows the Chatelperronian. This industry presents traits which are markedly different from what is known before; the backed knife gives way to endscrapers, including carinated forms, retouched blades, splintered pieces, and, although rare, Dufour bladelets. Unlike the Chatelperronian, Early Aurignacian levels are not only rich in tools, but also contain pigments, structured hearths, ornaments, bone implements, and even parietal art. The Early Aurignacian is seen as the footprint of the arrival of a new population, anatomically modern humans (Mellars, 1996).

- The different phases or facies of the “Post-Early” Aurignacian remain relatively understudied. Generally, they show a reduction of the traits characteristic of the Early Aurignacian and a concomitant increase in burins, some of which serve as cores for the production of small twisted bladelets with alternate retouch (Dufour bladelets of the Roc-de-Combe sub-type). The variability of these industries is often neglected to such an extent that the Aurignacian itself has been considered as a block entity or largely confused the Early Aurignacian (Mellars, 2004).

Fortunately, other regional models exist which were constructed independently of those from the south-west France, however the latter continue to occupy an important place in the general debate concerning the Middle-to-Upper Palaeolithic transition. This contribution proposes a decoupling of biological evolution from that of cultural evolution based upon an understanding of lithic industries.

The systematic techno-economic (Inizan et al., 1995) and taphonomic analyses (Villa, 1982; Bordes; 2002) applied to these lithic industries, together with the integration of a geoarcheological approach (Texier, 2000) and the refinement of excavation techniques, represent several factors that have permitted a substantial re-evaluation of the body of evidence concerning the emergence of the Upper Palaeolithic in southwestern France. This data is too abundant to be resumed in this short contribution. Only the main, and now generally accepted, points that have led to this progressive abandonment of the replacement scenario and the advancement of new models will be discussed.

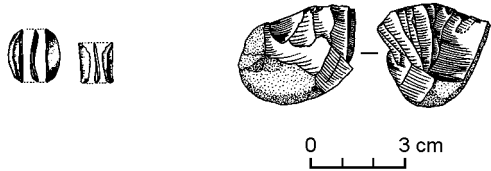
The Chatelperronian: an Upper Palaeolithic Industry

As it has sometimes been presented in the past (Rigaud, 1996), the Chatelperronian lacks “*souvenirs moustériens*” and in all cases where a rigorous taphonomic analysis has been applied, the pieces that do portray a Mousterian aspect have been shown to result from mixing with over-lying levels (Bordes, 2002; Bachellerie et al., 2007) or a problem with the original chrono-cultural attribution (Bachellerie and Normand, 2010). The origin of this industry is therefore an open question. There is nothing intrinsically ‘transitional’ about this industry that is defined by the production of relatively short, wide blades by “soft-stone” percussion (Bachellerie et al., 2007; Grigoletto et al., 2008). These blades are produced from the large face of small blocks or on the ventral surface of large flakes according to an opposed platform technique which serves to

maintain the rectilinearity of the blanks (Pelegri, 1995; Connet, 2002). These blanks are principally used to manufacture Chatelperronian points (whose use as projectile points does not seem systematic (Rios-Garaizar, 2008)), but also retouched blades and the occasional burin. The dimensions of these Chatelperronian points varies between 30 and 80 mm in length and 10 and 30 mm in width (Fig. 1). Endscrapers represent half of the retouched tools and are made on large, sometimes laminar flakes which are the secondary products of point production. These characteristics, together with the existence of a bone industry

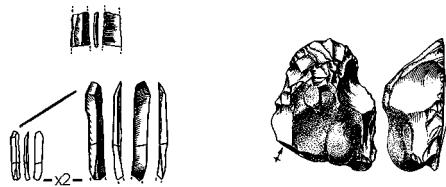
Middle Aurignacian

Abri Pataud couche 8



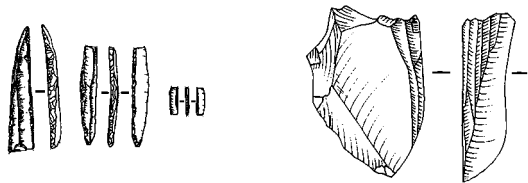
Early Aurignacian

Caminade Est couche F
Roc de Combe couche 7
Abri Pataud c. 11 à c. 13



Protoaurignacian

Le Plage couche K
Dufour



Châtelperronian

Roc de Combe c. 8
Canaule II
Les vieux Coutets

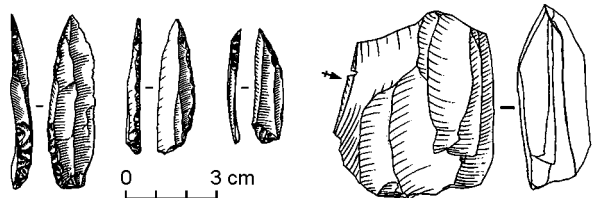


Fig. 1. The different phases of the Early Upper Palaeolithic identified in the south-west of France with characteristic tools and associated cores: Chatelperronian, Proto-Aurignacian, Early and Middle Aurignacian.

and personal ornaments (d'Errico et al., 1998), make for a genuine Upper Palaeolithic industry without any particular transitional traits (Bachelier et al., 2007; Soressi, 2010).

The Proto-Aurignacian: the missing-link rediscovered

In the 1960's Georges Laplace described an industry that he qualified as the *Protoaurignacian* and subsequently placed it between the Chatelperronian and Early Aurignacian according to a polymorphic model whereby this industry represented the undifferentiated Aurignacian-Perigordian synthetotype (Laplace 1966b). Laplace's, alternative theory was however not well received in the south-west of France and hence the Early Aurignacian remained the initial phase of the Aurignacian. Several attempts to isolate an Aurignacian "0" based on typological grounds (Delporte, 1984; Demars, 1992; Djindjian, 1993) were not unanimously accepted (Bordes, 2000). The typo-technological characterisation of this industry in Italy, followed by the south-east and then east-central France (Bazile and Sicard, 1999; Bon and Bodu, 2002), and finally Spain (Maillo-Fernández and Bernaldo de Quirós, 2010), ultimately led to the recognition of the Proto-Aurignacian in the Pyrenees and northern Aquitaine Basin where it stratigraphically underlies the Early Aurignacian (Bordes, 2002; Bordes et al., 2008).

This industry is most notably characterised by the intercalated production of blades and bladelets from the same block by soft-hammer percussion. Bladelets are also produced from the edges of flakes ("core burins"). Blades serve as blanks for the production of a variety of tools; endscrapers, numerous, often well-crafted, burins, and retouched blades. The scaled retouch characteristic of the Early Aurignacian is rare (Bon, 2002). The size of bladelets vary between 25 and 50 mm in length and are frequently curved (Fig. 1). While their typology varies (Bordes, 2002; Normand et al., 2008), the most frequent are Dufour bladelets and pieces pointed by a direct, marginal, and bilateral retouch, making them close to Krems Points. These pointed pieces should no longer be referred to as Font-Yves points as this tool type properly belongs to the Final Aurignacian (Pesesse, 2010). In the south-west of France this industry is now recognized at Isturitz (Normand et al., 2007), Gatzarria (Laplace, 1966b), Les Abeilles (Eizenberg, 2006), Brassempouy, La Ferrassie, Le Piage, Bos del Ser, Abri Dufour and Les Cottés (Soressi, 2010). The concept of standardised, axial, lithic armatures, shared by both the Proto-Aurignacian and Chatelperronian and absent in the final Mousterian of south western France (Jaubert et al., this volume), calls into question the rupture commonly seen between the Chatelperronian and Aurignacian (Bordes, 2002; 2006).

The Early Aurignacian: An industry "on the move"

All of the recent studies focusing on the Early Aurignacian have confirmed the typo-technological homogeneity suggested by earlier studies (Le Brun-Ricallens, 1993; Bon, 2002; Ortega et al., 2006; Bordes and Tixier, 2006; Teyssand-

ier, 2008). Debitage is focused on the production of large blades (between 10 and 20 cm long) from the front of a unipolar core by direct soft-hammer percussion. These blades, often transported over significant distances, are intensely retouched into various tools, above all, single and double endscrapers, and retouched blades (often with Aurignacian retouch) which are ultimately recovered as splintered pieces (*pièces esquillées*). Carinated scrapers are in fact cores for the production of small Dufour bladelets (between 20 and 40 mm in length) that occasionally bear inverse or alternate retouch (Dufour bladelets of the Brassempouy sub-type) (Le Brun-Ricalens et al., 2005; Pelegrin and O'Farrell, 2005; Bon, 2002). Raw material studies have noted the systematic displacement of objects over distances greater than 200 km, most notably between the north of the Aquitaine Bassin and the Pyrenees (Bordes et al., 2006). This succinctly defined industry appears well represented in western Europe and, to a lesser degree, in central Europe. No equivalent of the Early Aurignacian exists in the Near or Middle East, unlike the Proto-Aurignacian and Late Aurignacian of which we can find certain traces in the Levant and Zagros (Bordes and Shidrang, 2009; Le Brun-Ricalens et al., 2010).

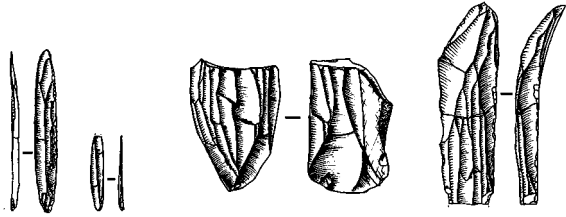
The Late Aurignacian: The end of a monolithic vision of the Aurignacian

The most recent study of several important sites from the south-west of France (Michel, 2010) has made it possible to distinguish at least six different phases of the "Post-Early" Aurignacian, certain of which were already identified by typological (Sonneville-Bordes, 1960; Delporte, 1984; Djindjian, 1993) or technological analyses (Chiotti, 1999; Lucas, 2000; Bordes, 2005). A techno-economic analysis has confirmed the coherence of this industries and demonstrated the impossibility of reducing the Aurignacian to a single monolithic entity (Le Brun-Ricalens and Bordes, 2007). The modalities and objectives of bladelet production have been studied in detail (Araujo Igreja, 2006; Le Brun-Ricalens et al., 2005; 2006) and can be summed up by the following main points (Fig. 1, 2):

- The Middle Aurignacian is characterised by the production of small bladelets (between 11 and 21 mm in length) that have a un-retouched convex left edge, while the opposite, rectilinear edge, is generally modified by a marginal inverse retouch which gives the blank a twisted profile. This asymmetry is connected to the shape of the associated cores (nosed endscrapers) whose front is itself asymmetric. This feature has allowed for a technological filiation to be established between the Early Aurignacian (curved bladelets) and the Late Aurignacian with twisted bladelets.
- The Late Aurignacian "I" is both well recognised and documented and, of all the Aurignacian industries, presents the most standardised retouched bladelets. These systematically twisted bladelets are produced by pressure and bear a lateralised and very marginal retouch; the right edge is systematically treated with a semi-abrupt retouch while the left edge, when modified, is done so by

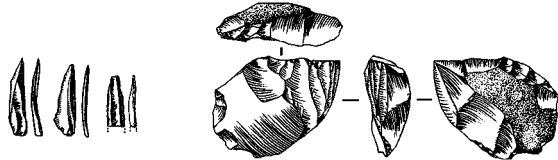
Final Aurignacian/
Initial Gravettian

Abri Pataud c. 6



Late
Aurignacian 3

Les Vachons, abri 2 c. 3
Le Flageolet c. VIII-1



Late
Aurignacian 2

Roc de Combe c. 5
Le Flageolet c. IX sup.



Late
Aurignacian 1

Caminade est, c. D2s
Roc de Combe c. 6
Le Flageolet c. IX inf.

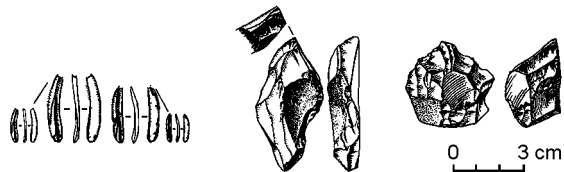


Fig. 2. The different phases of the Early Upper Palaeolithic identified in the south-west of France with characteristic tools and associated cores: Late Aurignacien and transition towards the Gravettian.

direct retouch. The dimensions of these bladelets is extremely normalised, between 12 and 19 mm in length, and are accompanied by very small burin spalls which are “pointed” by direct retouch on the left edge. They are associated with “busked burins” and “nosed endscrapers” which differ from those of the previous phase.

- The Late Aurignacian “2” approximates the previous system, but the rules that govern the objectives and production modalities are less strict, in particular,

the dimensions of the twisted bladelets are more variable (12 and 22 mm in length) and less regular, while the associated cores, called “destructured busked burins”, demonstrate less investment in the initial choice of core blanks.

- The Late Aurignacian “3” is above all recognised by its bladelet cores, called “Vachon burins”, which evince a sometimes thorough or complex preparation with a production pattern that extends to the lower face of the flake serving a core. Unfortunately, the majority of these industries were recovered during older excavations where sieving was not common practice and it is thus only recently that their bladelet component has been brought to light (Pesesse and Michel, 2002). These generally rectilinear and pointed bladelets, measuring between 20 and 60 mm in length, carry a direct, but marginal retouch on their right edge. This phase of the Aurignacian is often seen as closing the classic Aurignacian sequence as it witnesses the almost total disappearance of the main attributes which were up until now considered characteristic of this techno-complex.

- A final phase of the Aurignacian or Initial Gravettian has recently been brought into evidence (Pesesse, 2008; 2010) and is characterised the production of large, lightly twisted or rectilinear bladelets with lengths that vary between 32 and 70 mm. These bladelets bear a direct, semi-abrupt and bilateral retouch, but one that does not result in a point. These bladelets are produced, again in either an intercalated or continuous fashion, from the same blocks as blades. The term “Font-Yves bladelets”, characteristic of this phase (Ibid.), ought be reserved for these pieces alone and it is probably too simplistic to assign them either to the Aurignacian or Gravettian.

Thus, the “Post-Early” Aurignacian appears to be a complex entity which exhibits a certain logic in the gradual evolution of lithic armatures. The richness of the available data permits a chronological organisation of this phase according to its different technological facies. The origin of these variations appears to be stylistic, born from the evolutionary logic inherent in the traditions of these groups. Certain phases encompass a vast territory, while for others, our current information precludes the determination of their geographic extension, which could be limited.

Discussion

The outline presented here is by necessity simplistic. It would be ill-advised to assume that these preliminary results represent a definitive synthesis or a new work of reference. Even in such a small region as the south-west of France, there is still a considerable quantity of sites that remain to be studied before we can arrive at a meaningful synopsis of the Aurignacian as a whole. What can thus be said of reconstructions that try to envelope entire continents? It is indeed crucial that the present results are integrated with other techno-cultural and environmental spheres, unfortunately this is far from being the case.

However, while bearing in mind all its shortcomings, it still seems possible to assert that the available information does not support the classic model for

the emergence and development of the Upper Palaeolithic in the south-west of France; rather than a “revolution”, a gradual, multi-focal (Le Brun-Ricalens and Bordes, 2007; Le Brun-Ricalens et al., 2010) and arhythmic process (Teyssandier et al., 2010) determined, above all, by paleo-historic dynamics seems most appropriate (Valentin, 2006).

Taking into account the identified technological changes, we prefer an alternative paradigm to the two diametrically opposed and conventional models which propose either an “allochtone acculturation” or an “*in situ* evolution” to account for the observed developments. A hypothesis of *transculturation* (Le Brun-Ricalens and Bordes, 2010, Le Brun-Ricalens, in press), itself borrowed from Ethnology (Ortiz, 1940), represents a new model for the transition which posits technical or cultural transfer by *indirect lending*, that is to say, by the gradual and local assimilation and reinterpretation of external ideas according to the conventions and traditions proper to each cultural group. This *transculturation* model resonates more closely with cultural continuity than rupture and sees certain ideas and technical know-how circulated between connected individuals therefore rendering it unnecessary to envisage the migration of human groups over large distances.

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ODONTOMETRY OF *HOMO* DECIDUOUS TEETH FROM LATE PLEISTOCENE LAYERS OF ALTAI CAVES, SIBERIA

The processes responsible for the emergence of *Homo s. sapiens* in Eurasia have been the focus of much debate of archaeologists and anthropologists still now. Last century the so-called “Out of Africa” model has gradually become the dominant paradigm. The model primarily promotes a replacement of local Eurasian Upper Pleistocene populations by modern immigrants originating in Africa. However, the exact mechanism of the spread of modern populations is still debated.

The much more interesting results of new coming investigations are the mitochondrial and nuclear DNA sequence retrieved from a bone and a tooth excavated in Denisova Cave in the Altai Mountains in southern Siberia. The samples represent an unknown type of hominin that shares a common ancestor with anatomically modern humans and Neanderthals (Krause et al., 2010; Reich et al., 2010). The stratigraphy of the cave, where the bone and tooth were found, suggests that the Denisova hominins lived close in time and space with Neanderthals as well as with modern humans.

The genetic data of Denisova hominins display the appointed diversity of genotypes of *Homo*, and it is interesting how the variety of phenotypes of the Late Pleistocene Siberian hominin correlate with this tendency. Unfortunately, the anthropological remains from Siberian caves are fragmentary, and present mainly the odontological samples. So the morphological investigation has the strong limitation due to the poor preservation of the remains.

Anyway, nowadays studies provide additional criteria for comparing morphological and metric differences in the dentition of fossil hominins (Stefan, Trinkaus, 1998; Bailey, 2004; Bailey, Hublin, 2006; Quam et al., 2009; Crevecoeur et al., 2010). That is why the isolated dental remains became an imperative object of the investigation to be used for evaluating taxonomic affinities in individual specimens.

Material and methods

This study pertains to seven deciduous teeth of mandible found in different time during Altai-region excavations in the Okladnikov Cave (m_2 from the layer 7), Denisova Cave (m_2 from the layer 22.1, and i_1 from the layer 11.4),

Chagyrskaya Cave (*c* from the layer 6Б), and Strashnaya Cave (*c*, m_1 , m_2 from the layer 3.1A) (excavated by A.P. Okladnikov, A.P. Derevianko, V.T. Petrin, M.V. Shun'kov and A.N. Zenin).

It is necessary to notice that in the caves the different archaeological industries are fixed (Derevianko, 2009). The molar, recovered from Denisova cave (stratum 22.1), is the oldest sample from the Siberian anthropological findings. The 22 horizon has a data about 280 ka BP. The Middle Paleolithic industry, which started from this level, is developed during the eleven archaeological horizons (before the 12 stratum). The incisor from the 11 stratum of the Denisova cave belongs to the Upper Paleolithic industry, which covers the period of 50–35 ka BP. The molar from the Okladnikov cave has been recovered from a Mousterian horizons (so called Sibiryachikha culture), and the stratum presents the dates of $44\ 600 \pm 3300$ and $44\ 800 \pm 4000$ (Derevianko, Markin, 1992). The cultural materials from the Chagyrskaya cave is closed to Okladnikov cave Sibiryachikha culture, which in chronological scale is around 45–38 ka BP (Derevianko, 2009: 116). And the last, the Strashnaya cave odontological samples according to archaeological artifacts represent the Karakol tradition, which is the same as for Denisova cave Upper Paleolithic cultural materials.

Thus, the anthropological materials represent the three variants of cultural development in the Altai region: 1) the ancient stratum of Middle Paleolithic industry of Denisova cave, 2) the Mousterian Sibiryachikha culture from Okladnikov and Chagyrskaya caves, and 3) more or less synchronous to it Upper Paleolithic Karakol tradition from Denisova and Strashnaya caves.

Morphological features of the deciduous teeth are described qualitatively. Mesiodistal (MD) and buccolingual (BL) dimensions of deciduous teeth were made with a standard sliding caliper (Zubov, 2006). For the building of the tooth proportions there were calculated two indices. The index of crown ($VL \times 100 / MD$) was estimated for incisor, canines and molars; and, as an additional one the index of massiveness of crown ($MD \times VL$) was computed for the both types of molars.

All teeth were examined for pathological conditions, including carious lesions and enamel hypoplasia. Enamel hypoplasia was recorded as groove type (LEH), pit type, or plane type (Buikstra, Ubelaker, 1994; Goodman, Rose, 1991).

All teeth were microCT scanned using a SkyScan 1172 system at 100 kV, 100 mA, and with an aluminum-copper filter (the scan is from the Geological Faculty, Moscow State University). The software *SkyScan CTAn* was used to receive the information on the area of a surface and volume of three-dimensional objects.

Minimum number of individuals (MNI) and age at death

Denisova cave. Previously the deciduous molar from Denisova cave was studied by Ch. G. Terner (1990). He stressed that the tooth position is the lower first right molar. E. G. Shpakova (Shpakova, Derevianko, 2000) estimated it as a lower second left molar, and B. Viola (2009) confirmed the position of the

tooth. The preservation of the tooth is poor, because of the severe wear of the crown, postmortem broken away of pieces of enamel, and practically absent of the root. The root of the tooth is mostly resorbed due to antemortem age processes, and as a result a pulp cavity is exposed. The condition of the root resorption shows the possible age of the person around 10 years \pm 30 month (Bass, 1995). No pathological condition.

The deciduous incisor was found during excavation in the cave in 2010. The enamel of crown preserved good. The tooth height is limited due to the attrition of the crown, and the preserved height from lingual side is a little larger than from the labial one (Fig. 1). The root is flattened in a plane that is perpendicular to the axis of the crown. It is possible the lower incisor. The crown is not big,

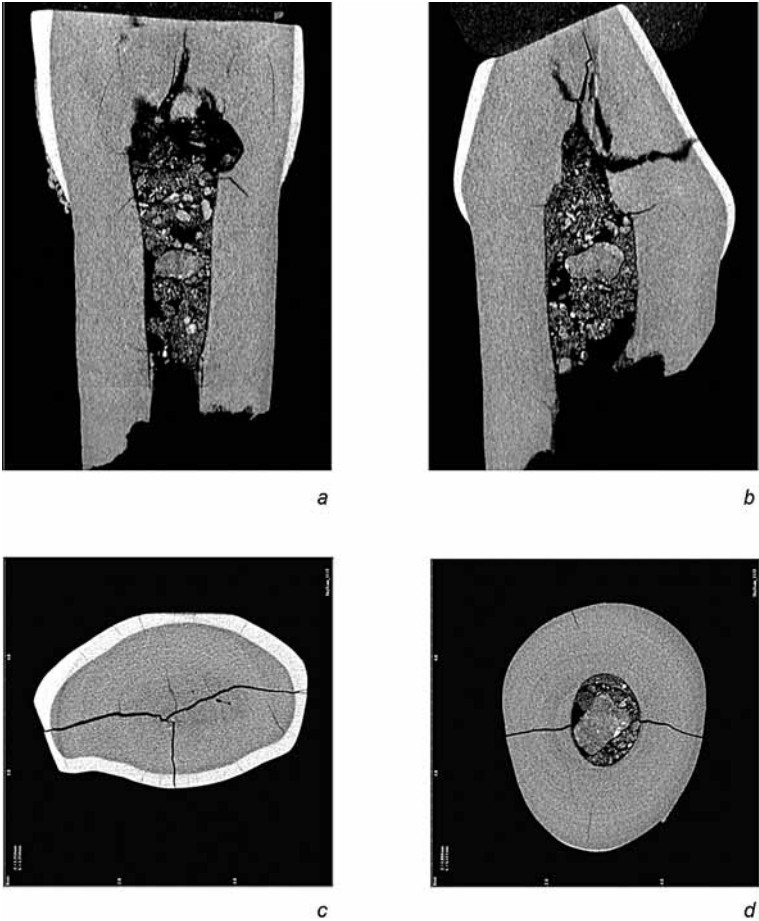


Fig. 1. The micro-CT images of the incisor from Denisova cave (layer 11.4).
a – labial view; *b* – lingual view; *c* – occlusal view; *d* – view from the root.

so it could be the lower central incisor. The incisor is not shoveled, and it has a less pronounced lingual swelling. The crown shows a minor attrition facet from the left side of lingual view (Fig. 1). So, it is possible the left incisor. The root is partly resorbed due to the age processes. The condition of the root resorption shows the possible age of the person around 5–6 years (Bass, 1995). No pathological condition.

Okladnikov cave. Previously the deciduous molar from Okladnikov cave was studied by Ch.G. Terner (1990). He stressed that the tooth position is the lower second right molar. E. G. Shpakova (Shpakova, Derevianko, 2000) and B. Viola (2009) confirmed the position of the tooth. The preservation of the tooth is enough good. It presents both complete crown and roots, but the ends of the mesial root are a little broken. The preserved parts of the roots do not show any resorption traces. It helps us to limit the interval of age at death of the person around 5 years \pm 24 month (Bass, 1995). No pathological condition.

Chagyrskaya Cave. The lower canine was found during excavation in the cave in 2008. Tooth is in a fitting condition. It is of a small size. The crown height has remained partially because of attrition. The root of the tooth practically not preserved due to the resorption processes. In vertical norm the crown form is asymmetric, with both distal and medial sides of enamel flows, and a crown is roundish in cervical position; so it is possible a canine (Zubov, 2006; Bass, 1995).

The tooth presents traces of considerable wear process of a crown as well as resorption of the root top, which testify the final stage of functioning of deciduous canine. According to the data, similar condition of canine corresponds to age about 10–12 years (Dobriak, 1960: 51).

Strashnaya Cave. Both the canine as two molars are assumed to come from the mandible of the same individual (Viola, 2009). The canine is mostly preserved. It is large tooth with asymmetric crown in occlusal view. It has a slight pronounced lingual swelling.

The first molar preserved mostly total, and it shows a complete crown with roots, but erosion postmortem processes destroyed the surface of it. It is a large tooth.

The second molar presents complete crown with roots; only the surface of them destroyed due to the postmortem processes.

The condition of preserved roots (with any resorption processes) of both frontal and molar deciduous teeth, and building-up the crowns of permanent canine and premolars stressed that age of the person could be around 6 years \pm 24 month (Bass, 1995). B. Viola (2009) stressed the possible age of the person as 7–9 years old. No pathological condition.

Thus, the seven deciduous mandible teeth from four Altai caves present at least 5 immature individuals (two persons from Denisova cave and every one person from others caves). The age of children falls from two biological categories: *Infantilis I* (3 individuals before the 6–7 years old) and *Infantilis II* (2 individuals before the 12–13 years old).

Comparative analysis

Frontal teeth

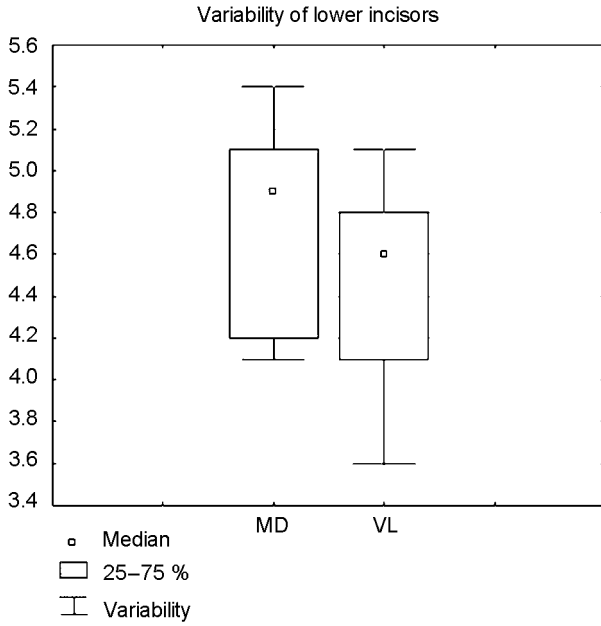
The incisor from Denisova cave (a layer 11.4) differs in the large sizes of a crown and especial at big VL dimension. For specification of taxonomy position of this sample has been collected comparative data of Eurasian Pleistocene deciduous first incisors from the Eurasian sites: Aubesier 8, Dederiyeh 1, Dolni Vestonice 36/5, Kebara 1, Kebara 16, La Madeleine 4, Lagar Velho 1, Qafzeh 10, Roc de Marsal, Shanidar 7, Skhul 10, Spy VI, Valdegoba 2, Arago 22, Chateaufort 2, Fond-qui-Pisse 1, Krapina_mdP, La Ferrassie 8, Le Figuier 1, Pech-de-l'Azé I (Billy, 1980; Crevecoeur et al., 2010; Hillson, Trinkaus, 2002; Quam et al., 2001; Sladek et al., 2000; Tillier et al., 2003; Trinkaus, 1983; Trinkaus et al., 2000; Trinkaus, pers. com.); and as scale points were used: average value on group of the European Neanderthal (1st group), average value on group of Middle Eastern Neanderthal (2nd group), average value on group of Middle Eastern Homo (3rd group), average value of modern American Caucasoid population (Black, 1978), average value of modern population of Europe (Quam et al., 2001) and average value of the Ancient Russian population (Buzhilova, unpublished) (accordingly 4th, 5th and 6th groups).

The variability of VL dimension for Eurasian Pleistocene Homo fluctuates in the variety from 3,6 mm to 5,1 mm with a median 4,6 mm (Fig. 2). The maximum values of the interval is fixed for Neanderthals from France (Arago 22 and Aubesier 8, Pech-de-l'Azé I). In contrast for them the samples of modern *Homo s. sapiens* and some Upper Palaeolithic examples from Europe (La Madeleine 4, Dolni Vestonice 36/5), and very close to them on morphology both Neanderthals Chateaufort 2 and Valdegoba 2 present the minimum values of VL dimension. In this range, the sample from Denisova cave comes for limits of 25–75 % of variability nearer to an interval of the maximum values.

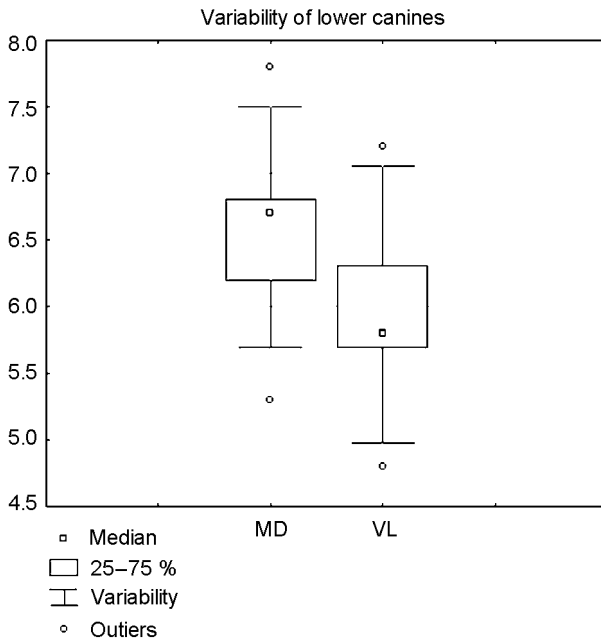
Thus, in result of previous step of comparison of the sample from Denisova cave shows obvious archaism condition of it; and the size of the tooth is close to the samples of Neanderthals (such as Middle Eastern Kebara 1 and Dederiyeh 1, and the most nearby to European Krapina mdP).

The variability of MD dimension for Eurasian Pleistocene Homo fluctuates in the variety from 4,1 mm to 5,4 mm with a median 4,9 mm (Fig. 2). In this range, the MD dimension of sample from Denisova cave comes for limits of 25–75 % of variability, and it is less than a median. The MD diameter of the Denisova sample is closed to the sizes of Middle Eastern samples of Shanidar 7 and Kebara 16, and to European one – Lagar Velho 1. These samples (including Denisova one) have not so big MD diameter as other Neanderthals, but they demonstrate the biggest MD dimension, as we fixed for the Upper Palaeolithic and modern sapiens.

The index of the crown present the position of the Denisova sample near the Middle Eastern Homo Qafzeh 10, and very closed to Shanidar 7 and Kebara 16. Thus, the deciduous incisor from Denisova cave has a separate position due to the big VL dimension and general massiveness of the crown,



a



b

Fig. 2a, b. Diagrams of the variability of Pleistocene *Homo* deciduous lower first incisors and canines.

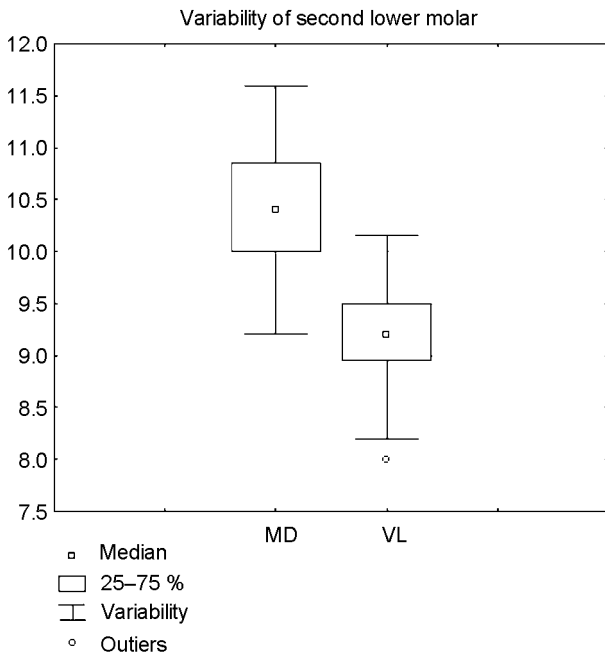
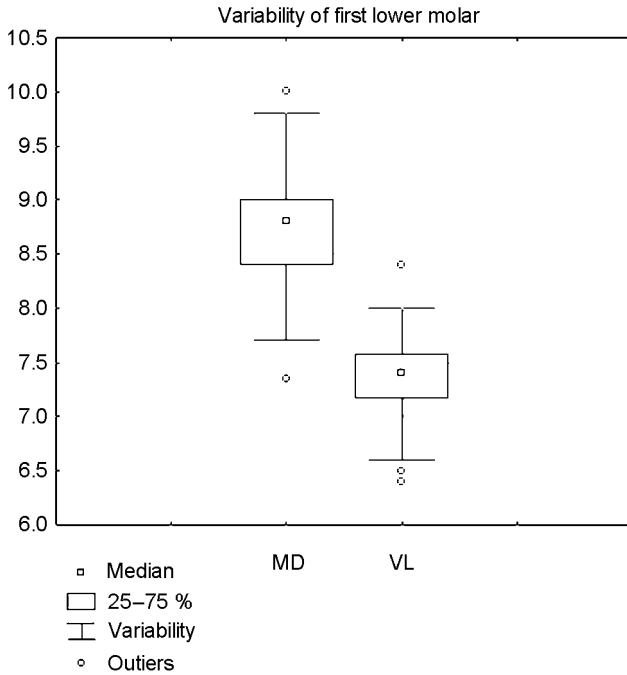


Fig. 2c, d. Diagrams of the variability of Pleistocene *Homo* first molars and second molars.

and its morphological traces are more closed to Middle Eastern Late Pleistocene Homo.

Canines from Chagyrskaya and Strashnaya caves. For specification of taxonomy position of the samples has been collected comparative data of Eurasian Pleistocene deciduous canines from the Eurasian sites: Archi, Chateauneuf 1, Chateauneuf 2, Combe-Grenal, Dederiyeh 1, Dederiyeh 2, Grotte du Renne 31, Kebara I, Kebara 4, La Ferrassie 8, La Madeleine 4, Le Figuier 1, Lagar Velho 1, Pech-de-l'Azé I, Qafzeh 4, Qafzeh 10, Qafzeh 12, Qafzeh 15, Qafzeh *sum*, Qafzeh / Skhul, Palomas 31, Palomas 95, Roc de Marsal, Skhul I, Spy VI, Zaskalnaya VI, Teshik-Tash (Bailey, Hublin, 2006; Crevecoeur, 2010; Hillson, Trinkaus, 2002; Tillier et al., 2003; Tillier, 1979; Trinkaus, pers. com., Gremyatchii, 1949; Kollosov et al., 1974); and as scale points were used: average value on group of the European Neanderthal (1st group), average value on group of Middle Eastern Neanderthal (2nd group), average value on group of Middle Eastern Homo (3rd group), average value on group of European Upper Paleolithic (4th group), average value of modern American Caucasoid population (Black, 1978), average value of modern population of Europe (Zubov, Khaldeeva, 1993) (accordingly 5th, and 6th groups).

The variability of VL dimension for Eurasian Pleistocene Homo fluctuates in the variety from 4,8 mm to 7,2 mm with a median 5,8 mm (Fig. 2). In this range, the sample from Chagyrskaya cave comes for limits of 25–75 % of variability, but the sample from Strashnaya cave comes out of it in the part of maximum values. The VL dimension of Chagyrskaya sample is more closed to sizes of Qafzeh 10 and European sample from Le Figuier 1. The dimension of Strashnaya sample is closed to Qafzeh 15 and Dederiyeh 2 patterns. Thus, according to VL dimension, the position of the both samples of Altai caves is nearly the Middle Eastern Neanderthals.

The variability of MD dimension for Eurasian Pleistocene Homo fluctuates in the variety from 5,3 mm to 7,8 mm with a median 6,7 mm (Fig. 2). In this range, the samples from Chagyrskaya and Strashnaya caves come out of limits of 25–75 % of variability into the side of maximum values. The MD dimension of Chagyrskaya sample is more closed to sizes of European Neanderthal Spy VI and Middle Eastern Neanderthal Dederiyeh 1, and the dimension of Strashnaya sample is closed to European Neanderthals from Roc de Marsal and Combe-Grenal. Thus, according to MD dimension, the position of both Siberian samples is nearly the European Neanderthals.

The index of the crown confirmed the position of the both Siberian samples to be closed to taxon of Neanderthal.

It is interesting to note the small contradictory tendency of the dimensions of the samples. The canine from the Chagyrskaya cave in comparison with a sample from Strashnaya is more gracile due to not so big VL diameter and the lesser MD length. According to the absolute dimensions the Chagyrskaya person is between the samples of European Neanderthals and closed to them gracile patterns of Middle Eastern Qafzeh and Dederiyeh. The more massive individual

from Strashnaya cave shows the same tendency to be between European Neanderthal (more massive forms) and Middle Eastern Homo (more massive samples from groups of Qafzeh and Dederiyeh). Similarity of the tendencies allows assuming the general biological origin of the persons from Chagyrskaya cave and Strashnaya cave. The opposite position of them could be the result of presentation of the more or less extreme variants of curve line of normal variability of the same biological population.

Molar teeth

The first molar from Strashnaya cave differs in the large sizes of a crown and especial at big MD dimension. For specification of taxonomy position of the sample has been collected comparative data of Eurasian Pleistocene deciduous first molars from the Eurasian sites: Barakai, Listvenka, Malta 1, Malta 2, Solovinaya Luka, Sungir 3, Teshhik-Tash, Bacho Kiro 1124, Brassempouy 112, Chateaufort 1, Chateaufort 2, Cisterna 3, Combe-Grenal, Cueva del Castillo 2, Dederiyeh 1, Dederiyeh 2, Garba IV, Gibraltar II, Grotte du Renne 18, Grotte du Renne 25, Grotte du Renne 33, Grub/Kranawetberg 1, Isturitz 2000, Kebara I, La Chaise 13, La Madeleine 4, La Quina 25, La Quina 761, Lagar Velho 1, Mießlingtal, Pech-de-l'Azé I, Qafzeh 4, Roc de Marsal, Shanidar 7, Skhul I, Valdegoba 2 (Bailey, Hublin, 2006; Condemi, 2004; Gambier et al., 2004; Garralda et al. 1992; Glen, Kaczanowski, 1982; Hillson, Trinkaus, 2002; Quam et al., 2001; Teschler-Nicola et al., 2003; Tillier, 1979; Gerasimov, 1935; Zubov, 1984; Shpakova, 2001; Kharitonov, 1985); and as scale points were used: average value on group of the European Neanderthal (1st group), average value on group of Middle Eastern Neanderthal (2nd group), average value on group of Middle Eastern Homo (3rd group), average value on group of European Upper Paleolithic (4th group), average value of modern American Caucasoid population (Black, 1978), average value of modern population of Europe (Quam et al., 2001), average value of modern population of Eurasia (Zubov, Khaldeeva, 1993) (accordingly 5th, 6th and 7th groups).

The variability of VL dimension for Eurasian Pleistocene Homo fluctuates in the variety from 6,4 mm to 8,4 mm with a median 7,4 mm (Fig. 2). In this range, the sample from Strashnaya cave comes out for limits of 25–75 % of variability in the side of the maximum values. The VL dimension of Strashnaya sample is closed to Caucasian sample from Barakai and Middle Eastern Dederiyeh 1. The index of the robustness confirmed the massive form of the sample, and it show the same tendency, because of it come out of the variability of the parameter.

The variability of MD dimension for Eurasian Pleistocene Homo fluctuates in the variety from 7,7 mm to 9,8 mm with a median 8,8 mm (Fig. 2). In this range, the sample from Strashnaya cave is out of the limits because of the biggest MD diameter (10,0 mm). The MD dimension of Strashnaya sample is closed to Middle Eastern Skhul I.

The index of the crown comes for limits of 25–75 % of variability, and the parameter is closed to the indices of European Neanderthals La Quina 761,

Combe-Grenal, and of the Middle Eastern Kebara I and summarized Qafzeh/Skhul. It is interesting that Upper Paleolithic Siberian sample from Listvenka (Krasnoyarsk region, 13 100 ± 410 (UBY-6965)) demonstrate the same tendency.

Thus, the comparative analyses of the first molar of the person from the Strashnaya cave confirmed its position very close to the taxon of Neanderthals. Anymore, the detail analysis gives the evidence to discuss the Middle Eastern origins of its antecessor.

Second molars from Denisova cave, Okladnikov cave and Strashnaya cave. For specification of taxonomy position of the samples has been collected comparative data of Eurasian Pleistocene deciduous second molars from the Eurasian sites: Listvenka, Solov'ynaya Luka, Malta 1, Malta 2, Barakai, Starosel'e, Sunghir 3, Teshik-Tash, Amud III, Bacho Kiro 559, Brassempouy 69, Caldeirão 11, Chateaufort 2, Combe-Grenal, Couvin, Cueva del Castillo 2, Dederiyeh 1, Dederiyeh 2, DV 36/6, Fontéchevade 2, Garba IV, Gibraltar II, Grotte du Renne 29, L'Hortus II, La Chaise 13, La Madeleine 4, La Quina 761, Lagar Velho 1, Les Rois A, Les Rois R50/33, Pavlov 7, Pavlov 8, Pavlov 9, Pech-de-l'Azé, Qafzeh 4, Qesem, Roc de Marsal, Shanidar 7, Skhul I, Skhul X (Bailey, Hublin, 2006; Condemi, 2004; Gambier et al., 2004; Garralda et al. 1992; Glen, Kaczanowski, 1982; Hershkovitz et al., 2011; Hillson, Trinkaus, 2002; Quam et al., 2001; Sladek et al., 2000; Tillier, 1979; Tillier et al., 2003; Toussaint et al., 2010; Trinkaus et al., 2001; Gerasimov, 1935; Zubov, 1984; Shpakova, 2001; Kharitonov, 1985); and as scale points were used: average value on group of the European Neanderthal (1st group), average value on group of Middle Eastern Neanderthal (2nd group), average value on group of Middle Eastern Homo (3rd group), average value on group of European Upper Paleolithic (4th group), average value of modern American Caucasoid population (Black, 1978), average value of modern population of Europe (Quam et al., 2001), average value of modern population of Eurasia (Zubov, Khaldeeva, 1993) (accordingly 5th, 6th and 7th groups).

The variability of VL dimension for Eurasian Pleistocene Homo fluctuates in the variety from 8,0 mm to 10,2 mm with a median 9,2 mm (Fig. 2). In this range, the oldest anthropological sample from Siberian Paleolithic from Denisova cave is much closed to the median level. The VL dimension of it is near the VL size of European Neanderthal Roc de Marsal and Middle Eastern Qafzeh 4. Into distinction of it the Okladnikov sample comes to the limits of the minimum level of the VL dimensions. The sample from Strashnaya cave is incredibly massive (like and the sample from Staroselie). Both of Okladnikov and Strashnaya samples find the analogies between European Neanderthals and Middle Eastern Homo (Chateaufort 2 and Skhul X for Okladnikov cave sample; Le Rois R50/33 and Qafzeh *sum.* for Strashnaya cave sample).

Thus, the Siberian samples (which mirror a long chronological period, but very local territory) come to the different positions of curve line of normal variability of biological population. And all of them demonstrate the same tendency

to be between the European Neanderthals and Middle Eastern Homo, and this allows assuming the general biological origin of them.

The variability of MD dimension for Eurasian Pleistocene Homo fluctuates in the variety from 9,2 mm to 11,6 mm with a median 10,4 mm (Fig. 2). In this range, the position of the sample from Denisova cave is near the median. The MD diameter of it is closed to Dederiyeh 2 and Amud III samples. Like in case of VL diameter analyses, the Okladnikov sample comes to the limits of the minimum level of the VL dimensions (near the Pavlov 8 and Siberian Malta 2), and the sample from Strashnay cave is incredibly massive (like and the sample from Le Rois R50/33). So, we fixed different tendencies. The oldest anthropological sample from Denisova cave presents clear relations with the Middle Eastern Neanderthals and Homo, and the massive variant of Strashnaya cave is closed to massive variants of European Neanderthals, and relative to them the gracile variant from Okladnikov cave is closed to Upper Palaeolithic finds from the Europe and Siberia.

The index of the crown confirmed this diversity of the samples. The Denisova cave person has not real analogies between the comparative samples, and it is more closed to Qafzeh *sum*, Teshik-Tash and Shanidar 7 samples. The Okladnikov sample has clear identity, and it is closed to European Neanderthal from Combe-Grenal. The person from Strashnay cave has much more similarity with European Neanderthal Le Rois R50/33.

The index of massiveness gives evidence to confirm the Middle Eastern origin of the antecessor of Denisova sample (closed to Amud III and Middle Eastern Homo), and it confirms the incredibly massiveness of Strashnaya, which has only one analogy as European Neanderthal Le Rois R50/33; the index of massiveness of sample from Okladnikov cave has analogies with Upper Palaeolithic samples (like Pavlov 7 and Pavlov 8).

Thus, the comparative analyses of the second molars from Denisova cave, Okladnikov cave and Strashnaya cave confirmed an important conclusion, that the oldest anthropological sample from Siberia – Denisova cave, possible has the Middle Eastern origin of the antecessor of it. The sample of Strashnaya cave demonstrates the massiveness of the crown, which could be “repeated” only on the example from European Neanderthal of Le Rois. And the sample from the Okladnikov cave is not so massive, and it is closed both to gracile forms of some European Neanderthals (Chateaufort 2 and Combe-Grenal), as massive forms of Upper Palaeolithic (Pavlov 7 and Pavlov 8).

Summary and conclusion

First of all, it is necessary to notice that deciduous teeth have not any selective effect due to the same milk food in different taxons of the *Homo*. What is more, due to the absent of the selection, the dimensions and the proportions of the deciduous teeth preserved “the memory” of the forms of the antecessor. That is why the appointed diversity of the deciduous teeth dimensions could reflect both the morphological as genetic specific differences of the fossil remains.

The previous studies of the deciduous teeth from the Altai caves emphasized the massiveness of them. As a result of comparative analysis of Siberian Paleolithic the massiveness was shown both for the Middle Paleolithic Altai samples, as for the Late Paleolithic Krasnoyarsk one, like Listvenka child (Shpakova, 2001). The second conclusion, which was done by the same author, highlighted the heterogeneity of the Paleolithic Altai samples. And, as E.G. Shpakova (2001) stressed the dissimilarity of them, possibly, could be explained by ancient background and immigration origin of them.

The comparative analysis, which was done in the scale of the Eurasian Late Pleistocene *Homo*, gave us an important conclusion, that the oldest anthropological sample from Siberia – Denisova cave, possible has the Middle Eastern origin of the antecessor of it. The child from Denisova cave (stratum 22) is much more closed to Amud III and more or less to any Middle Eastern Late Pleistocene *Homo*. The archaeological data, summarized by A.P. Derevianko (Derevianko, 2009), provide evidence that people came to the Altai region from the West and practiced the Levallois tradition. The early Middle Paleolithic traditions recorded in the Denisova cave is significantly different from the synchronous industries of the Eastern and Southeastern Asia, and they demonstrate considerable similarity to the cultural materials of the Middle East and Levant in particular.

All others samples of the Altai caves demonstrate more or less the tendency to be closed to different groups of Middle Eastern Neanderthals, European Neanderthals and Middle Eastern *Homo*, and this allows assuming the general biological Western origin of them. It is important to remind that they present two cultures like Mousterian Sibiryachikha one and Upper Paleolithic Karakol tradition.

What consolidate the Altai persons are samples from Chagyrskaya and Strashnaya caves (and they present two different cultures). Furthermore, both individuals of Denisova cave, as Okladnikov one are presented the different biological origins (and they present two different cultures). The detail analysis resulted that persons from Chagyrskaya and Strashnaya caves are more closed to taxon of the Neanderthal, and person from the Strashaya cave is more massive that child from the Chagyrskaya. As we stressed before, it could be the result of normal variability of the same biological population. Any way, according to archaeological data, there is a chance that the diversity of the samples from Chagyrskaya and Strashnaya caves could be as a result of a time separation of the population with the same biological origin.

The person from Denisova cave (stratum 11.4) has a separate position of the biological variability due to the proportions of the incisor crown, and its morphological traces are more closed to Qafzeh 10 and more or less to other Middle Eastern Late Pleistocene *Homo*. Because of the oldest sample of Denisova cave (stratum 22.1) has the same Middle Eastern origin, it is possible that oldest archaeological sample presents the antecedent generations of the Denisova population, and the younger archaeological sample of Denisova cave (stratum 11.4) is a descendant of it.

The person from Okladnikov cave has clear identity, and it is more or less closed to some forms of European Neanderthals, like as massive forms of Upper Paleolithic of Europe.

Thus, the comparative analyses of frontal and postcanine (molars) teeth confirmed the biological relations of the persons from Altay caves, because of the same Western Eurasian origins. Anymore, the detail analysis gives the evidence to discuss the different origin of the population from Denisova, Chagyrskaya-Strashnaya and Okladnikov caves. The children from Denisova cave reflect the long chronological period (about two hundred millenniums), and they demonstrate the same biological Middle Eastern origins of its antecessor. The person from Okladnikov cave shows the identity from the Pleistocene diversity with more or less relations to the European Neanderthals and some Upper Paleolithic forms. The children from the two caves of the same region – Chagyrskaya and Strashnaya, have clear biological variations of the same odontological type of general Neanderthals.

The one explanation could be built in this stage of the investigation. There were few waves of the migrants from the Western Eurasia to Altai region. The more ancient migration is from the Middle East (possible, Levant), and the few others noncontemporaneous migrations are from the same or more large (including a part of the Europe) area.

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SIBIRYACHIKHINSKY VERSION SITES OF THE ALTAI MIDDLE PALEOLITHIC INDUSTRIES

The Middle Paleolithic of Northern Asia is represented by sites with different states of preservation and concentrated mostly in the areas of Southern Siberia. The Altai region is recognized as one of such areas, where the density of site concentration is especially high and where cave and open sites have been found in the terrace deposits. The multi-layered cave sites of the northwestern Altai, Okladnikova and Chagyrskaya Caves, are standing out in the series of the Middle Paleolithic sites in Altai; the materials from these two caves are comparable with the Mousterian complexes from various regions of Eurasia and especially from the Southwestern Europe, Transcaucasia and the Middle East (Derevianko, Markin 1992; 1998; Derevianko, Markin, Zykina, Zykin 2009; Derevianko, Markin, Zykin 2009; Derevianko, Markin, 1995). Industries of these two caves are assumed to form a unique version of the regional Middle Paleolithic, for which the name “Sibiryachikhinskaya industrial development line” was put forward (Derevianko, 2009; 2010).

The two above-mentioned caves represent different karst formations. The south-facing Okladnikova Cave is situated in the belt of low-mountain Altai in the Anui River basin and consists of various interconnected and separate hollows – an overhang (situated 14 m above the level of the neighboring stream), a grotto, several galleries at different levels and also series of halls, located relatively far from the entrances. The north-facing Chagyrskaya Cave is located in the middle-altitude area of Altai and belongs to the section of the Charysh River valley, which drains the spurs of the northern slope of the Tigerekski ridge. The Chagyrskaya Cave has two neighboring halls, joined at an angle. The cave is located 25 m above the river level. The two caves are multi-layered (Okladnikova: layers 7, 6, 3, 2, 1; Chagyrskaya: layers 6a, 6b, 6c/1, 6c/2 (6a, 6б, 6в/1, 6в/2)), and can be characterized by the presence of homogenous industries with no signs of discontinuity.

In the Okladnikova Cave the majority of cave deposits (layers 2, 3, 6, 7) were formed under warm climatic conditions accompanied by development of forb-meadow-steppe vegetation. Certain variations can be observed only in the moisture of the climate conditions. The final stage of loose stratum (layer 1) formation was formed under somewhat different conditions, i.e. in the conditions

of open, not thickly forested, meadow-grassland spaces, with climate being damper and cooler, than it is nowadays. The paleontological materials, collected throughout the cross-section, serve as an indication of the “mixed” composition of the Late Pleistocene technocomplex, which highlights the uniqueness of the paleogeography of the mountain terrain. Avifauna also does not form an exception, consisting as it is, of various biotopes, which is also characteristic of the mountainous regions (Derevianko, Markin, 1992; 1998).

In the Chagyrskaya Cave (layers 6a–6c/2 (6a–6b/2)) the remains of large animal species, adapted to various landscape zones, i.e. steppe, forest-steppe and rocky environments were found (Vasil’ev, 2009). These include rhinoceros, small and big big (*cobaloid*) horse, bison – yak, caribou and red deer, Siberian ibex and wild ram. Isolated bones of mammoth, wolf and fox were also found. There are bones of cave hyena. Most of the remains (approximately 81 %) refer to ungulates and hemipterous, far less (approximately 19 %) refer to *Carnivora*. In respect to small mammals, V.S. Zazhigin points out to the remains of Siberian brown lemming (*Lemmus sibiricus*) found in the middle part of layer 6a and remains of yellow steppe lemming (*Eolagurus luteus*) found throughout the cross-section. Both species were widespread in Eurasia during certain intervals of Middle and Late Pleistocene and were typical elements of periglacial mammal fauna, corresponding to the periods of cooling and glacial maximums. A palinological analysis conducted at the Chagyrskaya Cave cross-section helps to reconstruct steppe conditions for the period of formation of layers 6a, 6b, 6c/1 (6a, 6b, 6c/1) and conditions of boreal evergreen and of deciduous coniferous forests during the accumulation of layer 6 c/2 (6b/1).

Structures of the sites have many common features, reflected primarily in the character of partitioning of flint remains. For the industries of the studied objects, no matter which layers the materials are obtained from, a scarce amount of evidences about the raw material flaking is observed. Small percentages of cores and edged and semi-edged bases in collections, even if not exclude completely, they significantly limit this cycle of stone treatment directly in the caves. At the same time, the amounts of tool forms seem to be quite significant, at times exceeding 20 %. Most likely, stone knapping was carried out somewhere away from the site, perhaps directly on the banks of rivers flowing nearby. The blanks were then delivered to the sites and turned into tools. As a result, one could find many debitage products, left after the retouching process and constituting 30–40 % of all the spalls. The data ratio between cores, potential blanks and tools indicates that every second – fourth blank went through secondary treatment. It is quite obvious that both sites can be characterized as hunting camps and this can possibly explain the homogenous typological selection of scrapers and scraper-knives. Economic activity of the primeval collectives of the Okladnikova Cave was associated with large game hunting, including hunting such animals as horse, argali, bison, rhinoceros and red deer. In the Chagyrskaya Cave the domination of bison remnants (over 54 %) can serve as a reflection of a hunter specialization of human collectives.

It was found out, that during the technocomplex formation of the Charyskaya Cave four types of local rocks were used: sedimentary (sandstone, siltstone-sandstone – 23 % of all artifacts), hornstones (16 %), effusive rocks (27 %) and jasperoids (around 33 %), among which the majority (29 %) are high-silicon jasperoids of Zasurinski suite (Kulik, Markin, 2009). It should be noted, that in the alluvium of the Charysh River, with the left side of which the cave is associated, all rock types used for the artifact production can be found, however, a different quantitative distribution of rock types can be observed. The effusive types constitute here over a half of all pebble material, while the presence of sedimentary rocks and particularly of hornstones is significantly lower, than their presence in the site's industry is. The amount of Zasurinski jasperoids is particularly low. Such evidences indicate the purposeful selection of raw materials. In the context of Okladnikova Cave the Zasurinski jasperoids (25,8 % of all the tools) are fairly important for the artifact production. On the other hand, a further petrographic comparison of the sites shows that overall they differ in terms of raw materials used. This way, in the Okladnikova Cave the use of hornstone makes up only 5%, majority of the tools (65 %) was made on sedimentary rocks and primarily on fine-grained sandstone (Kulik, Markin, 2003). Therefore, as to the use of the same raw materials, the single-type industries, represented in the caves, are still characterized by significant petrographical differences, the raw material factor not being the main one in the formation of such culture type in the Middle Paleolithic of the region.

A single-type inventory (Fig. 1–4), mainly based on the radial splitting of rocks, resulting in numerous spalls and a shift of the blank body from the axis of removal, is characteristic for the technocomplexes of these caves, no matter from which sediments they originated from. In the Okladnikova Cave apart from the radial cores, there are core samples represented, which reflect the technologies of the parallel and Levallois splitting. Scrapers and *déjeté*-type tools form a typological base of the tool selection. The majority of scrapers belong to single side- and transversal forms; there are fewer double parallel and convergent scrapers; there are single occurrences of scrapers with retouch along the perimeter, thinned backed scrapers, scrapers of the semi-*Quina* type, ventrally and alternatively retouched scrapers. It is important to note the presence of various scraper-knives with natural and retouched backs, which are either situated opposite the working retouched edges or adjoining the latter at an angle. Double and triple types of the *déjeté*-tools can be differentiated according to the number of working edges (diagonally truncated, diagonally-transversal et al.), their orientation, shape (double-concave, concave-convex, straight-concave et al.), secondary treatment techniques and angles between the working edges (acute-angled, right-angled et al.). The Levallois points and also isolated cases of tools of the Middle Paleolithic typology (scrapers, burins, chisel-like tools and borers) are found only in the technocomplexes of the Okladnikova Cave. The scarce groups of artifacts are represented by denticulate tools, tools with retouched encouches and points. Bifacies (backed forms with slanted thickened edges) (layer 7, 3, 2)

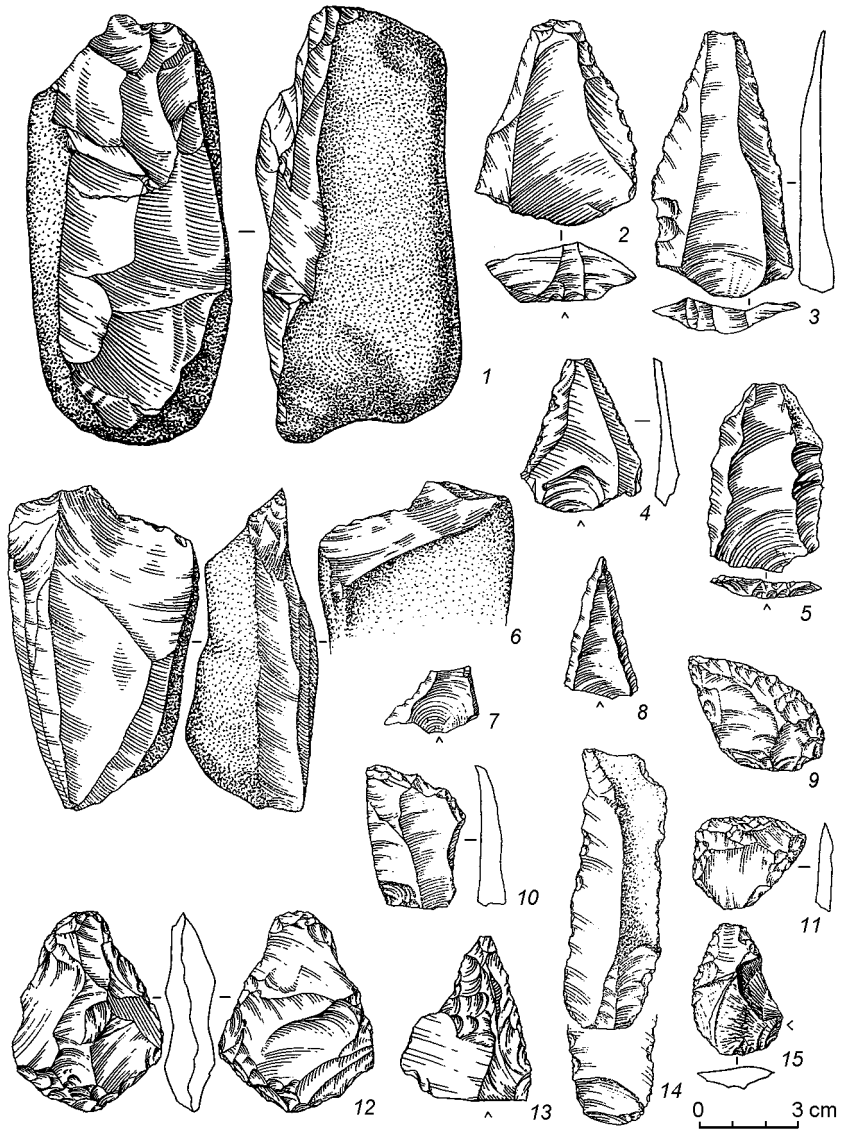


Fig. 1. Okladnikov Cave. Stone artifacts from layer 7.

1, 6 – cores; 2-5, 7, 8 – Levallois points; 9, 11 – déjeté-tools; 10, 13 – various types of scrapers; 12 – biface; 14, 15 – denticulate tools.

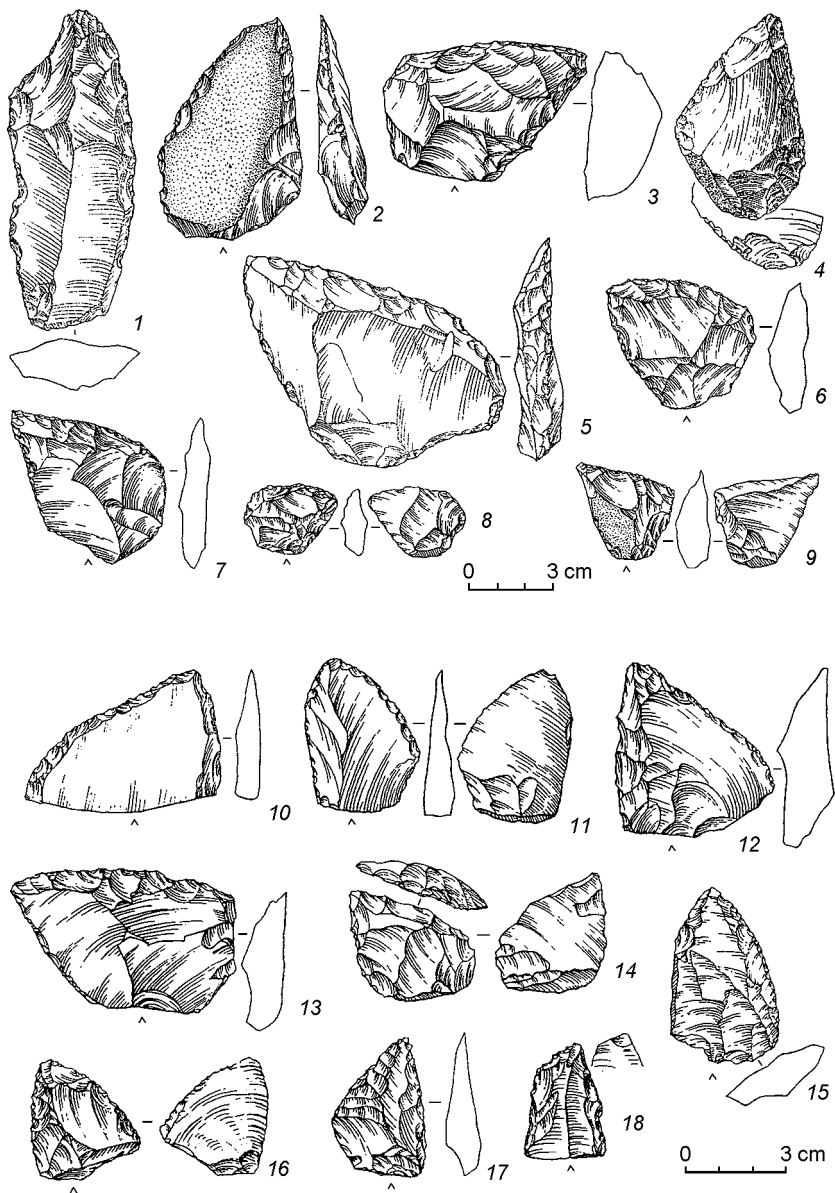


Fig. 2. Okladnikov Cave. Stone tools from layer 2.
 1 – side-scraper; 2–18 – déjeté of various types.

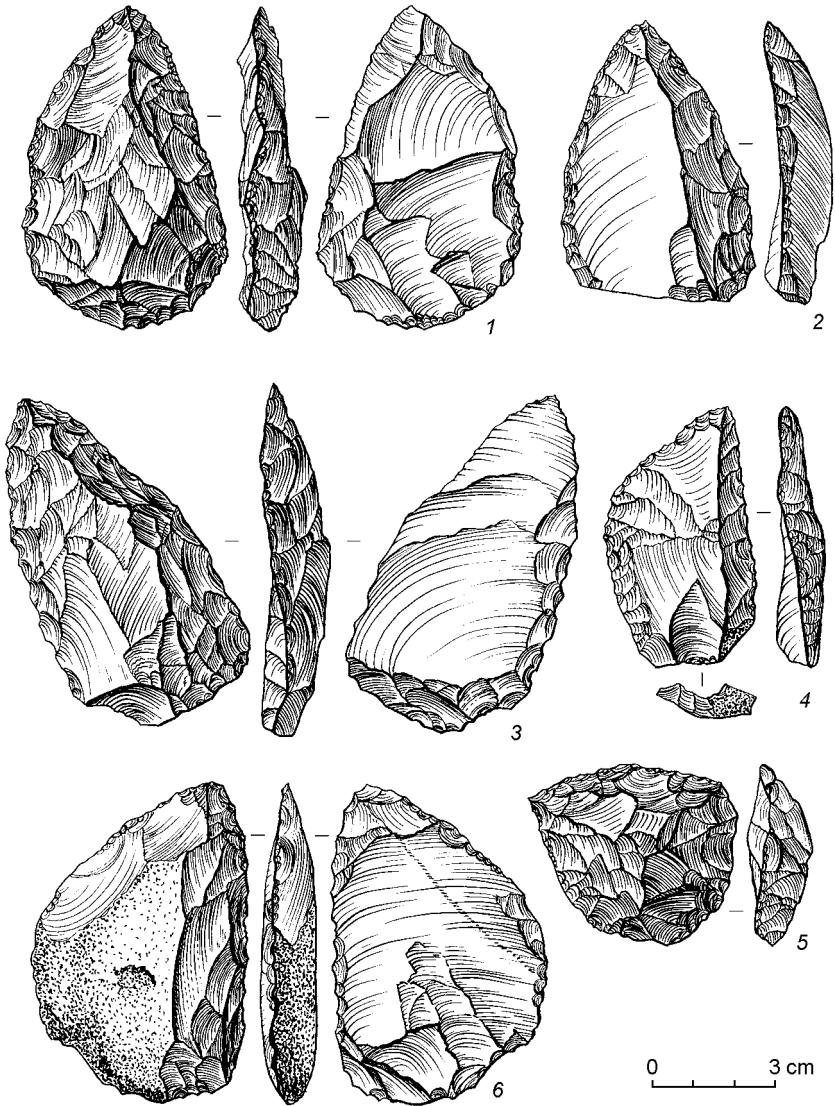


Fig. 3. Chagyrskaya Cave. Stone tools from layer 6c/1 (6B/1). Déjeté of various types.

were found in the Okladnikova Cave and oval flat-convex bifaces (base of layer 6b (66)) with thickened base and flattened active edge, formed by convergence of the longitudinal edges were excavated in the Chagyrskaya Cave. In layer 7 a biface was found, which is characterized by a flat-convex section, an elongated working part, side shoulders and blunted accommodation part. Tool treatment in the industries of the caves also seems identical, equally implemented in the

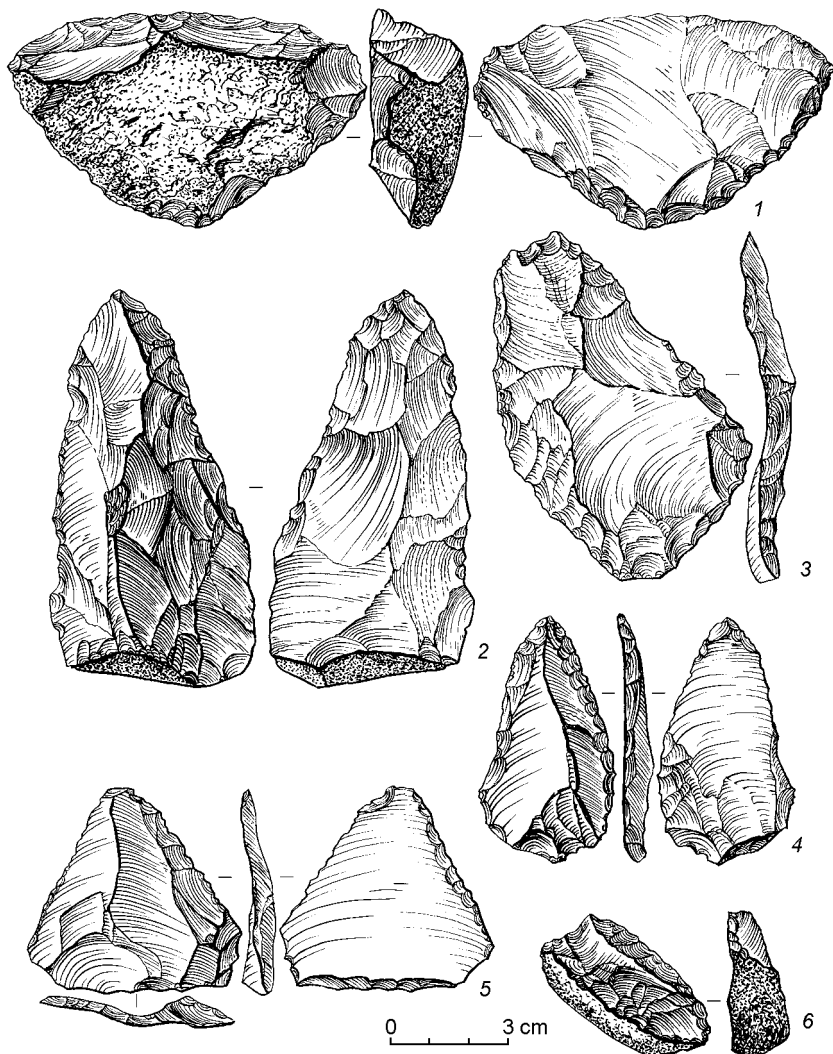


Fig. 4. Chagyrskaya Cave. Stone tools from layer 6b (66).

1, 2, 5 – scrapers of various types; 3, 4, 6 – déjeté of various types.

organization of working edges of the tools and of various tool parts. Secondary treatment was implemented mainly through various retouch techniques. The following retouch types dominate here: facial, semi-abrupt, average, semi-deep, invasive, double-row and stepped. Among the secondary treatment techniques, the most widely used retouch technique is the one, the application of which leads to the formation of backed and working elements (retouch, various types of encouches). Various types of blank thinning, including the one used for bulge

removal, basal thinning, thinning applied in fixing of the profile curvature, edge flattening and flattening of cross-sections of the angles between the working edges on the *déjeté*-type artifacts can be observed here (Derevianko, Markin, 1992; Derevianko, Markin, Zykina, Zykin, 2009; Derevianko, Markin, Zykin, 2009).

Overall, the structure of the technocomplexes in both caves is characteristic of the Middle Paleolithic, developing in the direction of Mousterian features, where the leading forms of artifacts are primarily represented by scrapers of various combinations.

In both caves anthropological materials were found, consisting of odontological remains and parts of postcranial skeleton. In the Okladnikova Cave (layers 7, 3, 2, 1) these are phalanxes, heel, femoral and shoulder bones, adult and child teeth and a patella, belonging to the Neanderthal anthropological type (Krause, Orlando, Serre et al., 2007). In the Chagyrskaya Cave second upper premolar of an adult (layer 6c/1 (6B/1), horizon 2), first cervical vertebra of an adult (layer 6b (66), horizon 4), lower incisor (right medial) of an adult (layer 6c/1 (6B/1), horizon 3), back surface of the distal condyle of the right tibia of an adult (layer 6c/1 (6B/1), horizon 3), deciduous tooth (left mandibular canine) of a child, aged 7–8 years were discovered.

The temporal indicators were so far determined for the technocomplexes from the Okladnikova Cave, the absolute age of which ranges from 44 800 to 33 500 years ago, which corresponds to the Karginian time. It is important to note that the initial stage of formation of the Middle Paleolithic industries in Altai, judging by the materials from the basal deposits of the Denisova Cave (layers 22, 21) and from the lower part of the section of the Ust-Karakol 1 site (layer 19) refers to the second half of middle Pleistocene in the interval between 282 and 133 ka BP. The materials from most of the cave and open sites (Denisova Cave, Ust-Karakol 1 site, Strashnaya Cave with layers, forming the middle part of the section, Okladnikova Cave, Ust-Kanskaya Cave, Tiumechin 1, 2 site, lower layers of the Kara Boms site) refer to the time between 100 and 44,8 ka BP (Derevianko, Shunkov, 2002; 2004; Zenin, Ulyanov, 2007; Paleoliticheskiye komplekсы..., 1998; Postnov, 2006; Prirodnaya sreda i chelovek..., 2003; Shunkov, 1990). Finally, the latest complexes (upper layer of the Okladnikova Cave) of the Middle Paleolithic, in accordance with the radiocarbon data belong to 33,5 ka BP (Derevianko, Markin, 1992). It is obvious that the regional Middle Paleolithic variant, represented by the unusual materials from the Okladnikova and Chagyrskaya Caves, should be viewed in these temporal limits.

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**ANTHROPOGENESIS AND COLONIZATION OF EURASIA
BY ARCHAIC POPULATIONS.
FORMATION OF ANATOMICALLY MODERN HUMAN**

Introduction

After publication of results of mtDNA genome sequencing (Krause et al., 2010) and nuclear DNA sequencing (Reich et al., 2010) of hominine from Denisova Cave, comments on the obtained research data followed (Martín-Torres, Dennell, Bermúdez de Castro, 2011; Gibbons 2011; etc.). They touch upon various important issues: hesitation about possible out of Denisovans from Africa around 1 Ma BP, consistency of the two models of origin of anatomically modern humans, issues of replacement and interbreeding and many others. Certainly, all these viewpoints appear to be of great interest and the results of DNA sequencing suggest fundamental estimation of acquired data and, which is more important, attempts to comply paleogenetic research results with anthropological and archaeological data.

Unfortunately, rich archaeological materials appear to be disregarded during these discussions. In publications devoted to the DNA sequencing results of the Denisova hominine results of field and laboratory archaeological investigations in the Altai during more than 30 years have been overlooked due to restricted size of articles. In the course of stationery investigation of more than 20 multilayer Paleolithic sites, which fall within the chronological interval of 300–10 ka BP, extensive materials have been obtained which allow approach differently to number of fundamental issues of material and spiritual culture of humans in the Altai. The important conclusion is that material and spiritual culture of humans in the Altai had been developing since 300 ka BP to the end of the Paleolithic without any significant influence from human populations with a different culture occupying adjacent territories. In the Altai, the Middle to Upper Paleolithic transition occurred during 50–45 ka BP. The early Upper Paleolithic is characterized by bone implements, artifacts suggesting signs of symbolic behavior and features of modern behavior. Archaeologists believed the mentioned material culture was produced by anatomically modern humans. However, the results of nuclear DNA sequencing appeared to be unexpected. Hominine from Denisova Cave was regarded as a sister group with Neanderthal population which

diverged from the lineage leading to anatomically modern humans even earlier than Neanderthals. Considering the fact, that descendants of the Denisova population occupied the territory of South Siberia and Mongolia till the Neolithic, we regard the Denisovans as anatomically modern humans and might be designated as a subspecies *H. sapiens altaiensis*.

Materials from Paleolithic sites in Africa and Europe suggest three scenarios (models) of convergent Middle to Upper Paleolithic transition, where independent formation of anatomically modern humans occurred.

Scenario 1 of the Middle to Upper Paleolithic transition covers the territory of East and Southeast Asia, where the formation of *Homo sapiens orientalis* subspecies took place (Derevianko, 2011a).

Scenario 2 refers to the rest part of Eurasia, where two subspecies of *Homo sapiens neanderthalensis* and *Homo sapiens altaiensis* were formed (Derevianko, 2010a, b).

Scenario 3 concerns East and South Africa where subspecies of *Homo sapiens africanensis* originates (Derevianko, 2011b). These four subspecies contributed to the emergence of the polytypic species *Homo sapiens sapiens* sensu lato.

Africa is a center of anthropogenesis

After publication of the first find of hominid fossils in eastern Kalahari, designated as an *Australopithecus*, by R. Dart in 1925, Africa has been regarded as the most probable geographic area of human origin (Dart, 1925). During 80 years hundreds of Australopithecine fossils of various degree of preservation have been found in South and East Africa. Taxonomic classification of Australopithecines was discussed in many hundreds of publications, where genera and species variations and phylogenetic relation were suggested. Australopithecine existed during the chronological period of 7 (6)–2.5 (1.5) Ma BP. They are classified into three major groups: early, gracile and robust Australopithecine.

Thus, around 6–7 Ma BP two lineages diverged from the common ancestor. First lineage comprises apes and the second lineage includes Australopithecine that eventually evolved into the *Homo* genus. So, the idea that humans originate from apes is irrelevant, we simply have common ancestor.

During last 20–30 years archaeologists, anthropologists, paleogeneticists and other researchers came to the ultimate conclusion that Africa was the cradle of mankind. The earliest sites with stone artifacts (choppers, choppings, spheroids, polyhedrons, and flakes with robust retouch) predominantly locate in Great Rift Valley in East Africa, extending in the meridional direction from the Dead Sea depression through the Red Sea and along the territories of Ethiopia, Kenya, Tanzania. In the Cada Gona River basin, more than 3 thousand of artifacts were found at 15 stratified sites and on the surface. Stone tools were located in the layer underlying the tuff level dated back to 2.6 Ma BP. Significantly, the simultaneity of artifacts and archaic hominids existence was recognized. The earliest *Homo* fossils discovered in the Omo River valley (2.4–2.0 Ma), Hadara (2.4–2.3 Ma) are simultaneous and reliably associated with lithic artifacts. Lithic industry from the earliest artifacts to the early Acheulian is regarded as the Oldowan.

It is characterized by pebbly and discoid cores, choppers, chopping tools and polyhedrons of different types, roughly retouched flakes.

Around 1.8–2 Ma BP *Homo ergaster-erectus* migrated from Africa and this was the first significant migration event which led to human dispersal across the globe (Derevianko, 2009a). Colonization of Eurasia by the earliest human populations was slow and hard. It was successful in the occupation of new territories, however affected by environmental conditions the populated universe considerably decreased. Presently, two major trajectories of the first migration wave can be identified. The first trajectory was associated with dispersal of earliest hominine groups across Near East and Iran to the Caucasus and possibly Anatolia and further to Europe. This is supported by occurrence of hominid fossils and pebble tools in Dmanisi (East Georgia) dated 1.7–1.6 Ma BP. In Europe, the earliest indisputable human occupations in Atapuerca, Spain, are chronologically attributed to 1.2–1.1 Ma BP.

The second migration trajectory of archaic hominids is associated with peopling of South, Southeast and East Asia. The Ubeidiya and Gesher Benot Ya'aqov sites in Israel date to 1.4–0.9 Ma BP. In South Arabia Al Guza and Sharhabil caves yielded pebble tools dated to 1.65–1.35 Ma BP. After that the earliest migrating populations moved in two directions: to the north into the areas of Central Asia (Tadzhikistan, Uzbekistan, Kazakhstan, Mongolia) and to the south from the Himalayas and Tibet to the territories of Pakistan, India, East and Southeast Asia.

Quartzite artifacts of 2 million-years-old were recovered in Pakistan. Researchers dispute about the age of Paleolithic sites in China including Dongtuo, Longupou, Xiaochangliang, Yanmou and others from 1.67–1.87 to 1.5 Ma BP and less. Dating approach to *Homo erectus* remains in Indonesia also arouses questions. During investigations of layer 4, where the juvenile cranium of *Pithecanthropus modjokertensis* had been discovered in, dates of 1.8 Ma BP were generated. Two other anthropological finds exposed in 1974 were dated to 1.66 ± 0.04 Ma BP. These data suggest that African *Homo erectus* have covered enormous distance for considerably short period of time and must have occupied South, Southeast and East Asia no later than 1.8–1.5 Ma BP.

Northern migration route of the earliest hominid populations followed to the north from the Himalayas and reached Central Asia. The earliest stratified localities are known in Tajikistan such as Kuldara (11th and 12th paleosols), Khonako II (8th paleosol) and Lakhuti (5th paleosol), which age is estimated as 800–600 thousand years old.

In the Altai, South Siberia, the Karama Paleolithic site was discovered, where four culture-bearing horizons falling within the chronological interval of 800–600 thousand years BP were identified (Derevianko, Shunkov, 2005).

All the Paleolithic localities associated with the first migration wave out of Africa are characterized by minimum core preparation or unprepared striking platform retaining cortex. Tool kits comprise micro- and macrochoppers, chopping tools, tools with nose-shaped working element, pebble scrapers, backed knives, etc. Typologically, this pebble industry refers to the Oldowan tradition.

Around 450–350 ka BP the second Out-of-Africa migration occurred. It expanded from the Near East and was associated with the dispersal of the late Acheulian industry associated with the Levallois flaking technique and occurrence of bifaces (Derevianko, 2009a). Spread of the Late Acheulian tradition to the eastern parts of Asia started from the Near East. On their migration route the new population encountered hominids of the first migration wave at many territories where the mixture of pebble and late Acheulian traditions was noted.

During the second migration wave out of Africa archaic populations reached Mongolia and India. They did not appear in East and Southeast Asia 400–300 ka BP. Since 1.8–1.5 Ma BP these territories demonstrate continuous development of lithic industries.

Bifacially worked tools and cleaver- and pick-shaped implements appear in China around 1 Ma ago at such Paleolithic localities as Yunxian and Pinliang. Around 30 Paleolithic sites with so called handaxes and cleavers attributed to the Lower, Middle and Upper Pleistocene. The most numerous collection of bifaces was discovered at the Baise basin, Guangxi Province, situated in the vicinity to the Chinese and Vietnamese border. Handaxes were found *in situ* within a lithological horizon dated to 800 ka BP on tektites. This horizon has yielded tools with bifacially worked cutting edge with chopping tools demonstrating various degree of secondary working among them. They remind the oldest handaxes from Africa. Emergence of bifacially worked tools reminiscent of the Acheulian technology in China should be regarded as the result of convergence, i.e. autochthonous development of local industry. Associated lithic materials from this region have nothing to do with the Acheulian industry. No similarly ancient handaxes have been recorded to the west from China. Thus, the Baise handaxes demonstrate a good example of convergence during the Lower Paleolithic. Bifacially worked tools demonstrating no morphological continuity with the Baise handaxes appear in different parts of China at different stages of the Paleolithic. Their emergence during later chronological periods is also the result of convergence caused by changes in adaptation strategies. For example, bifacially worked tools from Dingcun show different typological and technological features with the Baise handaxes and are chronologically 500–600 ka younger. Some researchers identify cleavers in toolkits from Paleolithic sites in Southeast Asia (Vietnam, Burma, Thailand). However, such cleavers and handaxes occur sporadically at sites attributed to different chronological periods and demonstrate typological differences with the Acheulian cleavers. Thus, we can state that the Acheulian industry did not spread over the territory of East and Southeast Asia. East, Southeast and South Asia seem to represent a vast territory where bifacial technique appears as a result of convergence. In India the Acheulian appears around 300–400 ka BP and it does not spread to the east. The Recent Out-of-Africa and Acheulian tradition are associated with the issue of *Homo sapiens sapiens* formation.

Two hypotheses on the origin of anatomically modern humans

Discoveries in archaeology, anthropology and paleogenetics during the recent 30 years turned the issue of anatomically and genetically modern humans'

formation and the Upper Paleolithic development one of the most debatable in social sciences.

The emergence of *H. sapiens sapiens* is chronologically estimated as 200–150 ka BP. The earliest fossils of anatomically and genetically modern humans were found in East Africa. However, these discoveries made the discussion of *H. sapiens sapiens* emergence and dispersal around the globe even more complicated. There are two major competing hypotheses about the origins of anatomically modern humans: the Recent African Origin (or Recent Out of Africa) hypothesis and the Multiregional hypothesis.

Presently the Recent Out of Africa model, advocating the idea that anatomically modern humans evolved in Africa 200–150 ka BP with their dispersal to Eurasia and Australia starting some 80–60 ka BP, has acquired greater support among geneticists, anthropologists and archaeologists. Initially *H. sapiens sapiens* occupied Eastern Eurasia and Australia, and later they spread across Central Asia and Europe. Proponents of Recent Out of Africa model treat the results of this colonization differently. Some scholars believe that the replacement of local aboriginal populations through conflicts and extrusion of those to regions with less favorable climatic conditions took place. That caused a growth of mortality, especially among infants, and a decrease in the birth rate. As a result, archaic people gradually disappeared. Other proponents of this scenario admit the possibility of continuous coexistence of *Homo sapiens sapiens* and *Homo neanderthalensis* (e.g., in Western Europe and Iberia). Contacts between migrant and autochthonous populations might have resulted in inter-cultural diffusion and sometimes even hybridization. Some researchers find the acculturation and cultural assimilation processes as the most probable, which caused a continuous merging of autochthonous populations with migrants.

However there is a compromise hypothesis stating that the migration of anatomically modern humans from Africa was followed by their hybridization and assimilation rather than by replacement of archaic humans (Smith et al., 2005; Kozintsev, 2004; 2009; and others). Hypothesis of anatomically modern humans' formation put a number of questions to the researchers.

Why did anatomically modern humans appear at least 150 ka BP while the Upper Paleolithic industry associated with *H. sapiens sapiens* emerged 50–40 ka BP?

If anatomically modern humans originated exclusively in Africa, then how and when did they colonize other continents?

If these humans introduced the Upper Paleolithic tradition to other continents, what characteristic features did this culture have, and why did technologically and typologically dissimilar Upper Paleolithic cultures appear in vastly remote regions of Eurasia nearly simultaneously between 50 and 40 thousand years ago?

Why were the regions with the Upper Paleolithic culture separated by vast areas where Middle Paleolithic cultures continued to exist?

If *H. sapiens sapiens* dispersed exclusively from Africa, how did they interact with autochthonous populations occupying those territories for many hundreds and even thousands of years?

What was the material and spiritual culture of anatomically modern humans migrating from Africa and how did it exceed the culture of preceding populations?

If anatomically modern humans had evolved 200–150 thousand years ago solely in East Africa, why did they start migrating out of Africa so late?

Based on the variability in modern DNA, the proponents of the Recent Single Origin hypothesis suggest that during 80–60 ka BP, a rapid population growth took place in Africa, and *Homo sapiens sapiens* “spilt out” to populate Eurasia. However it is incorrect to speak about the possible demographic “explosion” during the Paleolithic having no valid archaeological and anthropological grounds. Notably, during the Paleolithic with the average lifespan not exceeding 25 years, younger generations had to live without parents while still being immature. That caused a high infant and juvenile mortality rate. Thus, the inference about a demographic “explosion” seems to be ungrounded. But even if we subscribe to the idea that a rapid population growth took place in Africa 80–60 thousand years ago, stimulating a search for new resources and triggering the colonization of new territories, the question remains, why did people take such long eastward migration routes, which allegedly brought them as far east as Australia? According to archaeological data, anatomically modern humans colonized Australia 50–60 thousand years ago, while reaching South Africa only 40 thousand years ago, Central and West Africa, apparently less than 30 thousand years ago, and North Africa, about 50 thousand years ago. How can one explain that humans reached Australia first, and then settled the rest of Africa?

According to the proponents of Recent Out-of-Africa model, Australia was populated by migrants from Africa. However, how might it be that *Homo sapiens sapiens* for 5–10 thousand years managed to cover more than 10,000 km, having left no traces of their activity along their route? As for the autochthonous populations of South, East and Southeast Asia, if the autochthonous populations were replaced by *Homo sapiens sapiens* within 80–30 ka BP, a complete substitution of archaeological industry would have taken place; if acculturation took place, there should have been some significant changes in the material culture traced by archaeologists. Actually no substantial cultural changes are observed at Paleolithic sites situated in East Asia.

Lack of archaeological proofs is one of the reasons why advocates of the Recent African Origin theory have put forward a hypothesis of a southern migration route along the oceanic coast of Asia. Thus S. Oppenheimer (2004) states that the colonization of Australia took place approximately 70–65 thousand years ago and Flores and New Guinea Island were populated 75 thousand years ago. According to S. Oppenheimer, a lack of archaeological evidence for this migration route about 60–80 ka BP is caused by an inundation of the coastal zone of that period. A rise of sea level has concealed the early humans’ routes and they are impossible to find without surveying the seabed.

This explanation is unacceptable since at that time the sea level was not so low as to expose huge coastal territories from Western India to Malaysia, offering the alleged migrants a chance to cross the continental shelf without having

left any traces. Early human migration was a slow process, not a relay race. It is hard to conceive why the migrants should have moved directly to the east along the narrow coastal line rather than exploring the banks of the rivers which flow into the ocean and thus moving far to the north, where favorable ecological niches were available. If so, then again, material traces of this movement should have been left. Certain writers have hypothesized that anatomically modern human populations could have rapidly migrated from Africa to Australia by boats along the South Asian coast. However, not a single chopping tool or similar instrument necessary for the construction of boats was found in East or South Africa. There might be only one possible assumption explaining the point of view of proponents of the Recent African Origin hypothesis that the peopling of Australia occurred as a result of humans from Africa crossing a distance of more than 10 thousand kilometers over a short period (5–10 thousand years): the anatomically modern humans should have moved by regular or charter flights. The only thing left is to locate the airport of departure in Africa and airport of destination in Australia. This is the only way to explain the absence of archaeological evidence pointing to the global migration of anatomically modern humans from Africa to Australia.

However, along with the Recent African Origin hypothesis, there exists a different Multiregional hypothesis. It also has several possible modifications.

The essence of Multiregional hypothesis is that wherever *Homo erectus* sensu lato existed, they might eventually have evolved into anatomically modern humans. This hypothesis is predominantly supported by archaeologists and anthropologists who study the Paleolithic of East and Southeast Asia.

One of the authors and principal advocates of the Multiregional Hypothesis, M. Wolpoff, argues that multiregionalism does not imply that modern human populations originated in various regions of the world completely independently of one another and then evolved strictly in parallel. Rather, the theory allows for variously directed gene flow uniting all geographical populations into a single species (Wolpoff et al., 1984; Wolpoff, 1989; 1992; 1998; Wolpoff, Caspari, 1996; Wolpoff et al., 2000; and others).

The authors subscribe to the view, that wherever *Homo erectus* existed, evolution into *H. sapiens* and eventual formation anatomically modern humans of might have occurred as result of divergent development, gene flow, environmental influence and other factors. We bring forward archaeological facts supporting this idea.

Naturally, different environmental conditions, divergent evolution and other factors might have resulted not only in development of different adaptation strategies and variations in lithic industries but also formation of local anthropological features. Divergent evolution may account for variation both across Middle Paleolithic industries and across local physical types of archaic humans.

Excavations in Africa and Eurasia currently have yielded abundant archaeological material that allows us to put forward a hypothesis of three major geographic zones differing in patterns of Middle to Upper Paleolithic transition, which occurred between 100 and 30 thousand years ago. These major zones dem-

onstrate both convergent development of lithic industries and physical morphology of humans, which resulted in formation of anatomically modern humans.

Africa is one of the places of origin of anatomically modern humans

Starting in the 1990s, results of archaeological, anthropological, and genetic studies have unambiguously pointed to Africa as the place of the origin of humans. The earliest skeletal remains of anatomically modern men were found there at localities of the second half to final Middle Pleistocene: Florisbad (South Africa), Laetoli (Tanzania), Omo and Herto (Ethiopia), Jebel Irhoud (Morocco) and others of 200–150 ka BP. Anthropologists are unanimous in attributing these finds to the earliest representatives of modern humans.

In Africa, the Middle and the early Upper Pleistocene were characterized by lithic industries that substantially differed from the Middle Paleolithic industries of Eurasia. The beginning of the Middle Paleolithic or, as it is traditionally called by experts in African prehistory, the Middle Stone Age (MSA) is dated to 250–200 ka BP, to the period, when bifaces, cleavers and some other typical Acheulean implements disappeared. It should be noted, however, that the notion of the MSA is somewhat conventional since handaxes and cleavers were not equally common in various parts of Africa; nor did they disappear at the same time. So this criterion should not be regarded as universal and reliable for the entire African continent.

The Middle Stone Age in South Africa is subdivided into MSA I, MSA II, Howiesons Poort, MSA III, and MSA IV. No technical or typological continuity is traced among these stages and no reliable evidence of the uniformity of the Middle Stone Age industry is available. MSA I and Howiesons Poort are characterized by cores that are typologically and technologically similar to Upper Paleolithic blade cores. MSA II assemblages, if compared with MSA I, seem to be more archaic in terms of typology as well as in some traits of primary and secondary technology. The Howiesons Poort lithic industry dated within the range of 70–50 ka BP is especially noteworthy. At that period, blades were widely used as blanks for geometric microliths that, according to some researchers, served as inserts for composite tools. Howiesons Poort assemblages contain adornments made of sea mollusk shells, as well as evidence of the usage of ochre, and some other elements of symbolic behavior typical of the early Upper Paleolithic. The Howiesons Poort was replaced by more archaic primary and secondary technology. Distinct Upper Paleolithic industries appeared in that region after 30 ka BP.

Another evolutionary line is traceable in northeastern and East Africa. Industries such as the Aterian and Dabban, mostly characterized by the Levallois technique of primary reduction, formed there. Bifacial points are an artifact type common for the Aterian industry. Some of the points are tanged. Several other forms of tools also exhibit tangs (e.g., scrapers). Influence from the South and Central African industries can be traced at some East African sites. If the notion of the Upper Paleolithic is defined formally, in European terms, then in East Africa this period began rather late, from 30–25 ka BP. A principal point for

this discussion should be stressed: lithic industries in the northeastern, eastern, and southern regions of Africa differ markedly from Eurasian ones, including the Near East. Moreover, the formation of the Dabban culture in northeastern Africa finished by 40 ka BP under the influence of the Emiran industry formed in the Near East.

Anatomically modern humans – *Homo sapiens africanensis* – was the most genetically diverse and played the key role in the emergence of modern mankind.

The issue of *Homo sapiens neanderthalensis* and its contribution to formation of anatomically modern humans

Neanderthals *Homo sapiens neanderthalensis* were the first archaic people discovered by researchers. First Neanderthal fossils were found as early as in the mid-19th century in the Neander Valley in Germany. During the 150 years hundreds of different Neanderthal sites, settlements and burials have been investigated. Neanderthals were characterized by morphological features adapted to severe climate of boreal zone. They were short, stumpy very strong people. Their cranial capacity was 1400 cm³ and is generally similar to average cranial capacity of modern humans. Neanderthal Paleolithic localities were discovered in Near East, Southwest and Central Asia and in South Siberia.

However the fate of *Homo sapiens neanderthalensis* was tragic. Before the 1980s, many physical anthropologists believed Neanderthals were among the ancestors of modern humans. After the 1980s, when the first Neanderthal mtDNA was sequenced, Neanderthals began to be regarded as an extinct side branch, a separate species, which should be crossed out of human genealogy. At present, both the archaeological and the biological data suggest that the issue must be revised. One of most important is the relationships between the Neanderthals and the anatomically modern humans. Some believe that in Europe, Neanderthals were replaced by anatomically modern migrants from Africa. Others point to the possibility of hybridization. Erik Trinkaus, one of the leading physical paleoanthropologists, compared Neanderthals and modern humans with Early and Middle Pleistocene hominids with regard to 75 traits and concluded that about a quarter of these traits are shared by Neanderthals and modern humans, another quarter are Neanderthal autapomorphies, and about a half, those of modern humans (Trinkaus, 2006). This publication aroused the discussion in *Current Anthropology*. The opinions were divergent: some supported Trinkaus's conclusions, whereas others rejected them. Up to the present day, diametrically opposed views coexist.

Many archaeologists have pointed to the higher efficiency of the Neanderthal industries at the final stage of the Middle Paleolithic and to the fact that those humans developed many elements of basically modern behavior. Significant evidence of intentional burials among Neanderthals was identified. A.P. Okladnikov was the first to recognize the special burial ritual at Teshik-Tash Cave (Okladnikov, 1949). His hypothesis has subsequently been supported by other researchers. For example, Shanidar excavations produced reliable evidence of

Neanderthal burials (Solecki, 1971). A. Defleur (1993) and Y.A. Smirnov (1991) have reviewed abundant materials of Mousterian burial sites. However, certain researchers still doubt the existence of premeditative features of burials during the Middle Paleolithic (Gargett, 1999).

Certain researchers have pointed out many other features of modern human behavior in Neanderthals (Chase, Dibble, 1987; Lindly, Clark, 1990; d'Errico et al., 1998; Zilhão, 2001; d'Errico, 2003; Conard, 2005; Hovers, Belfer-Cohen, 2006; Conard, 2009; and others). In this respect, *Homo sapiens neanderthalensis* does not appear to be inferior to *Homo sapiens africanensis*.

The transitional industries like Châtelperronean, Uluzzo, Bacho Kiro, etc. may well have been associated with Neanderthals. These industries along with those from Castillo in Cantabria suggest that continuity existed between the Middle and the Upper Paleolithic in Western and Central Europe. Specifically, industries of horizons 18b and 18c at Castillo, dated within 42–37 ka BP (more than ten dates are available) combine Middle and Upper Paleolithic techniques and tool types (Cabrera et al., 2001). A mosaic nature of the industry, where Middle Paleolithic elements coexist with Aurignacean ones, as well as bone tools, and objects of art suggest that some Neanderthals used the proto-Aurignacean industries, which were in some respects transitional between the Middle and the Upper Paleolithic. Cabrera et al. (2001) claim that if the lower Perigordian or the Châtelperronean originated from the Mousterian of Acheulian tradition, then the Aurignacean may have originated from the Charante Mousterian of the Quina type, as F. Bordes had suggested. By far not all researchers subscribe to this view. Nevertheless, more and more facts come to light indicating continuity between the Middle and Upper Paleolithic industries in Europe and implying that Neanderthals played a certain, possibly even a major role, in this process.

The geneticists believe that Neanderthals are a sister group of modern humans (Green et al., 2010). Green et al. (the team includes geneticists, physical anthropologists, and archaeologists) note that the results of the Neanderthal DNA analysis are hardly compatible with the idea that all modern humans originated from a small group of African ancestors, who eventually dispersed in Eurasia and replaced their archaic predecessors without interbreeding (Green et al., 2010: 721). The total estimate of up to 4 % genetic introgression from Neanderthals to non-Africans (Green et al., 2010; Reich et al., 2010) implies that specific non-African groups such as Chinese, Papuans, and French do not differ in their affinity with the Neanderthals (Green et al., 2010: 721). It is beyond doubt at present that apart from cultural diffusion, hybridization and assimilation processes occurred in contact zones. In short, the genetic contribution of *Homo sapiens neanderthalensis* to modern mankind can hardly be denied at present.

East and Southeast Asia – one of the centers of anatomically modern humans' formation

East and Southeast Asia is characterized by a principally distinct scenario of the Paleolithic development as compared to other regions of Eurasia and Africa. In the Sino-Malayan zone and possibly in South Asia tools such as handaxes,

picks, cleavers and other similar tool types appeared as a result of convergent development ca 1 Ma BP. These tools are functionally close to the Acheulian implements, however are technologically and typologically distinct from those. Moreover, at the huge territory from the Near East and possibly the Caucasus to China, bifacial tools and the Levallois flaking technique appeared after 400 ka BP. In India the Acheulian was formed around the same time. Earlier bifaces from Bori, India, dating to ca 700 ka BP, and those found in China are a result of convergent evolution of the Lower Paleolithic industry.

Lithic technologies, practiced in East and Southeast Asia over nearly the entire Paleolithic, were based on manufacturing tools on flakes that were detached from cores. The Levallois system was unknown. No Middle Paleolithic in the European sense ever existed in the Sino-Malayan zone; rather, the industries evolved in a continuous manner throughout the Lower, Middle and early Upper Pleistocene, and no noticeable technological changes occurred over almost one million years. This does not imply a uniformity of industries. Dozens of cultures have been convincingly described by archaeologists in the Sino-Malaysian zone, but all of them appear to have been based on detaching flakes from discoid, orthogonal, and other types of cores, and these flakes were used as blanks for making tools. In the second half of the Upper Pleistocene, the knapping techniques became more sophisticated, better raw materials were introduced, new types of tools appeared, and there was some evidence of bone working. It is impossible, however, to draw a distinct boundary from which the Upper Paleolithic began in that territory. Within the chronological interval of 200–30 ka BP in the course of evolutionary development changes in stone knapping techniques, raw materials preferences and typology of tools are noticeable in this region. About 30 ka BP, the blade industry was introduced from Mongolia and Southern Siberia to North China (Derevianko, 2009b). In East and Southeast Asia, the use of blades for making tools was typical along with widely practiced autochthonous flake-based technology. The latter was best adapted to local environmental conditions, and adaptation strategies based on both flake and blade industries were equally effective. The role of blade industry was insignificant in South China and Southeast Asia.

Based on archaeological materials, it can be stated with certainty that over the entire Pleistocene, the evolving lithic industries of East and Southeast Asia differed from those of other parts of Asia. No innovations introduced from without can be traced in the Sino-Malayan zone in the 80–30 ka BP interval, which disagrees with the idea that Australia was populated by 60–40 ka BP by migrants from Africa. Were this so, the migration wave would have brought new lithic technologies and new tool types. Actually neither is observed. The hypothesis of a rapid movement of a migration wave along the part of the South Asian coastline which is currently submerged, and where traces of west to east migration such as Paleolithic sites should have been left, is quite implausible either. Under such a scenario, virtually unmodified African Paleolithic industries should have appeared in Sunda and Sahul. However, Paleolithic assemblages from both insular Southeast Asia and Australia dating to the 60–20 ka BP interval reveal the

same technological and typological features as do the Paleolithic assemblages of mainland Southeast Asia.

In general, in East and Southeast Asia the Middle to Upper Paleolithic transition differed considerably from that in Africa and Europe and followed a specific scenario. This area is characterized not only by autochthonous development of the Upper Paleolithic, but population of anatomically modern humans descended from *Homo erectus* locally.

The largest number of *Homo erectus* remains has so far been unearthed in China and Indonesia. Certain variations notwithstanding, they constitute a rather homogeneous group. Among the important finds are the Yunxian crania, dated to 936 ka (Le Site..., 2008). Their considerable endocranial volume (1152 and 1123 cm³) as well as the presence of bifaces and cleaver-like chopping tools point to both an advanced physical type and culture. A key role in reconstructing the evolutionary paths of *Homo erectus* is played by the Zhoukoudian Locality 1 fossils, which comprise craniodental remains and postcrania of 44 individuals. Their morphology has been reconstructed in considerable detail. These hominids, which resemble their Javanese counterparts, were included in the *Homo erectus* species at the subspecies level – *Homo erectus pekinensis*. Layers 1–12 of Zhoukoudian were dated to 690–230 ka by various methods. Later finds, dated to the late Middle Pleistocene and Upper Pleistocene, include those from Hexiang in the Anhui Province, Chanyang and Yunxian in the Hubei Province, Maba (Guangdong Province), Dingcun and Dali (Shanxi Province), Salawusu, Liujiang and Laibin (Gansu Province), Ziyang (Sichuan Province), Upper Grotto of Zhoukoudian. Some researchers believe that anthropological fossils of earlier and later hominids suggest evolutionary continuity. Upper Pleistocene fossils illustrate the prolonged evolution of cranial morphology in China, evidencing a unique ctanio-facial complex, which links the earliest East Asian humans with modern Chinese populations. Numerous fossils discovered in China over the recent 50 years provide the basis for tracing a continuous evolutionary development from *Homo erectus* and *Homo sapiens sapiens* during the Pleistocene. Wu Xinzhi (2004) notes that all or most Pleistocene crania found in China share numerous morphological peculiarities documenting evolutionary continuity. In addition, some exhibit a mosaic pattern of traits typical of *Homo sapiens erectus* and *Homo sapiens sapiens*, evidencing a gradual transition rather than abrupt replacement. In fact, *H. sapiens sapiens* and *H. sapiens erectus* may be viewed as two chronological subspecies within a single evolving species (Wolpoff et al., 1994). Human evolution in China appears to have included both continuous evolution and hybridization. The latter factor decreased the likelihood of speciation and preserved the unity of mankind as a species (Wu Xinzhi, 2004).

In China, a number of archaic human fossils was discovered, dating from the middle of the Middle Pleistocene to the early Upper Pleistocene: Xujiayao, Dingcun, Maba, Dali, and others. They variously demonstrate an evolutionary continuity between archaic and anatomically modern humans. The Jinniushan man, whose remains were found in the Liaoning Province of North China, is

one of the examples of this morphological intermediacy (Wu, 1988; Lu, 1995, 1996, 2003).

Fossils dating to approximately the same period were discovered in 1982–1983 in a karst cave in the Chaoxian District of the Anhui Province of Eastern China. The site is located 50 km away from Hexiang, where remains of *Homo erectus* were unearthed. The Chaoxian fossils include a maxilla and an occipital bone of a hominid (Bailey, Wu Liu, 2010). Their age is within 200–310 ka BP, and they also attest to an evolutionary continuity between archaic and anatomically modern humans.

Groves (1994) attributed the Dali and Jinniushan hominids to *Homo heidelbergensis* (Groves, 1994). Their evolutionary intermediacy is beyond doubt. While the endocranic capacity of Dali is 1120 cm³, a number of progressive traits of cranial morphology have prompted certain specialists to attribute it to *Homo sapiens* (Johanson, Blake, 1996).

The disputes around the place of fossils from China in the human evolutionary record are not incidental. These finds demonstrate numerous progressive traits, which, however, are interpreted differently, and the experts' views are highly divergent. Some believe that *H. heidelbergensis* originated in sub-Saharan Africa, from whence it dispersed over vast areas of Eurasia (Stringer, 1990; Rightmire, 2001). Others express an opposite idea: *H. heidelbergensis* allegedly originated in East Asia, and then migrated westward up to Africa (Etler, 2010). The archaeological data do not support either of these hypotheses since neither in China nor in territories intermediate between East Asia and Africa any cultural changes suggestive of either a westward or an eastward migration have been registered. Only one interpretation is possible: progressive biological traits are due to parallel evolution. Both in East Asia and in Africa, anatomically modern humans apparently originated from the same ancestral species – *Homo erectus sensu lato*.

In sum, progressive traits in East Asian fossils dating to 300–150 ka BP indicate progressive evolution *in situ*. The idea that *H. heidelbergensis* migrated to China from the west is disproved by the entire archaeological record. This is yet another example of physical anthropologists' reckoning without cultural facts.

The totality of evidence speaks in favor of a progressive *in situ* evolution of *Homo erectus* in East Asia over a span of more than one million years. This does not preclude the immigration of small populations from adjacent regions, small-scale gene flow, or admixture. Differences between the geographically separated late archaic populations were apparently caused by isolation. This is evidenced by finds from Ngandong, Java. Having preserved several distinctive features of *Homo erectus*, they reveal marked progressive traits as well while differing from the broadly contemporaneous fossils from China. Over a period of one million years, natural selection and other evolutionary forces may have eventually led to the transformation of *Homo erectus* populations of China into modern Mongoloid groups, and those of Java, into Australoid groups.

An important argument favoring the theory of the autochthonous evolution of human populations in China are new absolute dates relating to seven Paleolithic sites where *Homo sapiens sapiens* remains were found (Shen, Michel, 2007). These dates were derived from teeth and other remains. The dates are quite early and suggest that anatomically modern humans lived in China at least 100 ka (Ibid.: 162).

New information has been received regarding the Liujiang cave site in the Guanxi-Zhuang Autonomous Region of South China. In 1958, a well-preserved human cranium and several postcranial bones were found there. The fossil represents one of the earliest anatomically modern humans in East Asia. Other remains discovered in this horizon include those of *Pongo sp.*, *Ailuroda augustus*, *Sus sp.*, etc. Some of the animals are typical of Upper Pleistocene fauna. The most often cited date for the Liujiang cranium is ca 20 ka BP. Later stratigraphic studies demonstrated that the minimal age of the find may be 68 ka, the maximal age, over 153 ka, and the most likely chronological interval is 111–139 ka (Shen et al., 2002: 827).

The idea that East Asia may be yet another region where anatomically modern humans originated is supported by fossils from Zhiren Cave in the Guangxi-Zhuang Autonomous Region of South China (Liu Wu et al., 2010). The cave is a karst cavity in the Trias deposits, situated 34 m above the Hejiang River and 179 m asl. In the distant part of the cave, there is a gallery which, in the Lower Pleistocene, was filled with loose sediments. Most of these subsequently disappeared (seemingly washed away by water streams). Part of the sediments remained on the walls and on the ceiling of the cave. Later, the cave began to be refilled with loose material. The same geological pattern is observed in many caves of northern Vietnam. Sedimentation gaps are evidenced by several annular dripstone formations overlying the loose sediments. The age of two upper formations, estimated by the uranium method, corresponds to OIS 3 (average, 28–52 ka BP). The formation beneath them was dated to 87–74 ka BP. Underlying loose sediments, which contained two human molars and a mandibular fragment, were dated to 113–100 ka BP (average, 106.2±6.7 ka BP). Also associated with this layer were late Middle or early Upper Pleistocene faunal remains (*Elephas kiangnanensis*, *Elephas maximus*, etc.). A quarter of the recognized species are extinct. In the specialists' view, the uranium dates and the faunal remains suggest that human fossils from Zhiren correlate with the beginning of OIS 5 or possibly with OIS 6.

The Zhiren 3 mandible demonstrates a characteristically modern morphology of the external symphysis with a distinct mental protuberance, rather deep mental fossae, moderately developed lateral tubercles, and a vertical symphysis – a combination setting the Zhiren individual apart from all known late archaic humans. At the same time, the morphology of the lingual surface of the symphysis and a robust corpus link the individual with other archaic humans of the Pleistocene. The experts believe that the age and morphology of the Zhiren fossil demonstrate that anatomically modern humans may have migrated to East Asia and assimilated their archaic predecessors. Alternatively, they may have

originated in situ; in this case, however, admixture with archaic humans is also a possibility.

In 2003, 34 fragments of a human skeleton, whose age was estimated at 39–42,000 calendar years, were found at Taniuan Cave near Zhoukoudian (the site was designated Zhoukoudian Locality 27) (Shang et al., 2007; Trinkaus, Shang, 2008; Hu et al., 2009). The principal morphological characteristics including pedal ones, pointing to the use of footwear, are basically modern.

Nothing in the abundant archaeological record is suggestive of any migration to China from the west in the 120–100 ka BP time range. Given the similarity of Paleolithic industries in the Sino-Malayan zone and their distinction from those of the adjacent western regions, it can be stated that in the late Middle Pleistocene or in the early Upper Pleistocene, anatomically modern humans originated in East and Southeast Asia as well as in Africa.

Thus, the available archaeological and skeletal material is sufficient to claim that the migration wave of modern humans from Africa had not reached the Pacific coast. The evolution of Paleolithic industries in East and Southeast Asia in the 100–30 ka BP range proceeded quite differently from the way it developed in other regions of Asia or in Africa, making it possible to speak of a distinct Sino-Malayan scenario of the Middle to Upper Paleolithic transition and of the emergence, through in situ evolution, of a separate variety of anatomically modern humans in East and Southeast Asia – *Homo sapiens orientalis*.

The formation of anatomically modern humans in North and Central Asia

The Middle to Upper Paleolithic transition in the rest part from Eurasia followed a scenario different from the one observed in East and Southeast Asia. In the vast European territories, the Middle Paleolithic industries demonstrate significant divergence. However a number of techno-typological features makes it differernt from the Middle Paleolithic traced in Africa and Sino-Malayan zone, especially at the final stage.

The final Middle Paleolithic was characterized by blade techniques and standardization of toolkit across vast territories of Eurasia which laid the ground for the transition from the Middle to Upper Paleolithic.

The territory of the Altai, where new paleoanthropological materials have been found, might be a good example. Besides, recent genetic data have been obtained for anthropological materials from Denisova and Okladnikov Caves.

The earliest occupation of the Altai occurred no later than 800 ka BP as a result of the first migration wave of archaic humans from Africa and their dispersal around Eurasia. The oldest archaeological site of Karama has revealed four culture-bearing horizons with the upper chronological border about 600 ka BP. However, after 600 ka BP humans were forced to move out because of unfavorable environmental conditions. This area had remained unpopulated till 300 ka BP, when the second wave of archaic migrants with a different cultural tradition came there. New industry was characterized by the Levallois and

parallel flaking techniques. Thus, starting from 300 ka BP, a continuous development of cultural and behavioral traditions of archaic humans can be traced in the territory of the Altai.

During the last twenty-five years, in the course of extensive field investigations more than 70 culture-bearing horizons of the Lower, Middle and Upper Paleolithic have been exposed in 9 caves and more than 10 open-air sites in the Altai (Derevianko, Shunkov, Agadjanian et al., 2003; Derevianko, Shunkov, 2004). About 60 culture-bearing horizons with a various amount of archaeological and paleontological materials fall within a chronological range of 100–30 ka BP. Investigation of multilayered and well-stratified cave and open-air sites located in relative proximity to each other and in the same ecological environment provides with the maximum possible information allowing correlations between the sites and demonstrates a continuous techno-typological development of lithic industries over nearly 100 thousand years. In this respect, the Altai represents a unique area where extensive multidisciplinary research of paleoenvironment and material culture are carried out. Rich and well-documented materials from this area obtained in the course of field and laboratory investigations demonstrate a continuous development of the local Middle Paleolithic industry without any considerable impact of populations with a different culture.

At Denisova Cave, 13 culture-bearing strata were revealed. Some of them comprise several occupation horizons. The earliest finds, presumably of the late Acheulian period or early Middle Paleolithic, were recorded in stratum 22 (dated to 282 ka BP). Strata 20 to 12 represent the Middle Paleolithic, and strata 11 to 9 are attributed to the Upper Paleolithic.

The continuous evolution of the lithic industry is traceable throughout the Middle Paleolithic horizons. Finds from strata 19–12 attributable to the chronological period 90–50 ka BP are of a special importance. The assemblage contains Middle Paleolithic artifacts that are technically and typologically similar. Differences between the layers in various techniques of primary and secondary stone processing as well as those between the percentages of various tools are minor and indicate continuity caused by the change of adaptive strategies following environmental shifts.

The primary reduction is characterized by radial, Levallois and parallel flaking. The share of cores pointing to the parallel detachment of blades and blade blanks increases from the lower strata upwards. Upper Paleolithic implements become more numerous.

During the final stage of the Middle Paleolithic (60–50 ka BP), the Altai industry reveals two major developmental trends: Kara-Bom and Karakol. These two developmental trends might result from different adaptation strategies. The Kara-Bom site is located at an elevation of 1100 m asl., while Ust-Karakol 1 and Denisova Cave are situated at roughly 680 m asl. Obviously, both these traditions developed within an evolution of a single Middle Paleolithic culture. These two traditions gave rise to two variants of early Upper Paleolithic industries around 50–40 ka BP. The uniqueness of the Altai multi-layered Middle

Paleolithic sites, located within a comparatively small area, is that they provide rich information on the development of lithic industries from the Middle to Upper Paleolithic. The appearance of tools reminiscent of carinated scrapers and some other Aurignacian-like implements should be regarded not as the result of migrations but as having proceeded from the convergent development of the local industry.

Around 50 ka BP sub-prismatic cores, pressure techniques (signs of the employment of soft hammer technology have been recorded from earlier periods), carinated pieces, various modifications of end-scrapers, burins and other elements characteristic of the Upper Paleolithic culture appeared in the Altai technocomplexes. Their origin can be easily traced in the local final Middle Paleolithic. Some sites have yielded bone implements (needles, awls, bases for in-laid tools) and assemblages of non-utilitarian objects made of bone, stone and shells (beads, pendants, etc.) which provide evidence for the behavioral modernity of the Altai population as early as 50–40 ka BP. A stone bracelet with traces of polishing, burnishing and drilling appeared to be a pleasant encounter.

Around 45 ka BP the Sibiriyachikha culture of the Mousterian type associated with the Neanderthal population appeared in the Altai. Arrival of new occupants, employing dramatically different technological industry, makes them stand apart from the cultural and historical continuity of the Altai Paleolithic. This small population seems to have been extruded by anatomically modern humans from Central Asia (Teshik-Tash Cave in Uzbekistan). These hominids did not stay long in the Altai and who knows what happened to them. They might have been assimilated by the autochthonous population or became extinct.

Archaeological data accumulated during the past 30 years of studies at the stratified cave and open-air sites convincingly prove that the Upper Paleolithic industry, one of the most striking in Eurasia, formed in the Altai ca 50–45 ka BP. It had been forming during 20–30 thousand years: in the Middle Paleolithic horizons dated to 80–70 ka BP, Upper Paleolithic techniques of stone working and Upper Paleolithic tool types started to emerge. As a result of the evolutionary development of the Middle Paleolithic industry, the Upper Paleolithic formed in the Altai.

The human fossils from the Middle and Upper Paleolithic sites in the Altai are few, but they are important and have engendered a lively discussion. The issue concerns teeth and postcranial fragments from Okladnikov and Denisova caves. It has long been observed that the lithic industries of these sites are quite different. That of Okladnikov Cave is Mousterian and has been classified as a separate culture – Sibiriyachikha. That of Denisova, by contrast, reveals a progressive and gradual evolution of the Middle Paleolithic industry of the lower stratum 22, dated to 280 ka BP, through that of stratum 12 to a distinctly Upper Paleolithic industry of stratum 11, dated to 50–30 ka BP.

At Okladnikov Cave, five teeth of juveniles, aged 12–14, and children, aged 5–7, were found: a right lower second deciduous molar in the lower layer 7, a left lower first premolar, and a right first (second?) and left third per-

manent molars in layer 3. Also, fragments of postcranial bones were retrieved from layers 1–3 below the roof.

At Denisova, a left second lower deciduous molar of a 7–8-year old child was found in stratum 22.1, an upper left medial permanent incisor of an adult in stratum 12, and cranial fragments, teeth, and postcranial fragments in stratum 11.

Paleogenetic studies of the Altai fossils were conducted at the Max Planck Institute for Evolutionary Studies in Leipzig (Krause et al., 2007). Neanderthal mtDNA was extracted from three postcranial bones discovered at Okladnikov Cave layers 1–3. The fragment of an adult humerus, however, contained no Neanderthal mtDNA, so according to Krause et al., there are no indications that this was a Neanderthal (Ibid.: 902). Extraction of mtDNA from paleoanthropological materials is critical for understanding the taxonomic status of the Okladnikov Cave hominids.

Archaeological materials from Denisova cave including lithic and bone implements, non-utilitarian objects, traces of economic activity, presence of items brought from distant areas located hundreds of kilometers away, suggest modern behavior. The archaeologists had no doubts that people associated with this industry were anatomically modern. Therefore the results of the sequencing of DNA extracted from a digital phalanx of a human from Denisova Cave were quite unexpected (Reich et al., 2010). The nuclear genome of this individual diverges from the modern African reference genome by 11.7 % (CI: 11.4–12 %), whereas that of a Neanderthal from Vindija Cave, Croatia, by 12.2 % (CI: 11.9–12.5 %), i.e. the divergence is approximately the same. Based on these results, Denisovans and Neanderthals were sister groups, whose most recent common ancestor lived 640 ka BP. Their evolutionary trajectories were different, as seen from the fact that the Neanderthals were genetically more similar to modern Eurasians than to modern Africans; 1–4 % of genes of non-Africans were introgressed from the Neanderthals (Green et al., 2010). Whereas there was no gene flow from the Denisovans to modern Eurasians, there was a 4–6 % gene flow from the Denisovans to the ancestors of modern Melanesians, who are genetically opposed to other non-African populations.

The molar from Denisova Cave reveals neither Neanderthal nor modern synapomorphies, suggesting, in agreement with the results of the genetic analysis, that Denisovans were quite distinct from both Neanderthals and anatomically modern humans. The general conclusion is that the Denisovans were a sister group of the Neanderthals, but those groups had different evolutionary histories. At least two groups of hominids existed in Eurasia during the Late Pleistocene: western designated as Neanderthals, or *Homo sapiens neanderthalensis*, and eastern, including Denisovans.

Results of the decoding of nuclear DNA extracted from hominid remains from Denisova Cave point to an early migration of humans from Africa to the Near East and from there to the Altai. The phylogenetic split between Denisova humans and Neanderthals on the one hand, and the ancestors of modern Africans on the other, is estimated at 804 ka BP, and that between Denisova humans and Neanderthals, at 640 ka BP.

However, the analysis of mtDNA suggests that the ancestors of the Denisovans diverged from those of modern humans as early as 1 Ma, that is, twice as early as the Neanderthals.

The common ancestors of the Denisovans and Neanderthals have possibly migrated from Africa to the Near East before 800 ka BP. About 600 ka BP, some Near Eastern populations, which were rather ancestral to *Homo heidelbergensis*, migrated from the Near East to other regions of Eurasia.

Members of the paleogenetic team decided to refrain from deciding whether the Neanderthals and the Denisovans should be regarded as different species or as different subspecies. The name “Denisovans,” like the name “Neanderthals” merely points to the provenance of the respective fossils.

Based on the vast archaeological materials from the Paleolithic sites in the Altai, dated within 100–20 ka BP, it can be stated that the Upper Paleolithic culture with which the Denisovans were associated, emerged 50–45 ka BP, and that the behavior of those people was essentially modern. Because of the gene flow between the Neanderthals and the ancestors of modern Eurasians, and between the Denisovans and the ancestors of modern Melanesians, implying that both these Pleistocene populations were subspecies which contributed to the emergence of anatomically modern humans. In this sense, the Neanderthals should be designated as *Homo sapiens neanderthalensis*, while the Denisovans as *Homo sapiens altaiensis*.

Conclusion

Despite all the diversity of views regarding human evolution in the late Lower and Middle Pleistocene, it appears likely that the common ancestor of modern humans in both Africa and Eurasia was the polytypic species *Homo erectus* sensu lato. *Homo heidelbergensis*, *Homo rhodesiensis*, and possibly *Homo cepranensis* in Africa and Europe and *Homo erectus* in East and Southeast Asia were sister taxa, from which *Homo sapiens* sensu lato eventually originated in the Late Pleistocene. This, too, was a polytypic species, comprising four subspecies: *H. sapiens africanensis* (Africa), *H. sapiens orientalis* (East and Southeast Asia), *H. sapiens neanderthalensis* (Europe) and *H. sapiens altaiensis* (Southern Siberia and Central Asia).

Evidently, the contribution of these subspecies to modern human origins was unequal. The vast majority of researchers adhere to the hypothesis that *Homo sapiens sapiens* had originated in Africa and spread across Eurasia either simply replacing archaic humans or hybridizing with them. Both the nuclear and mitochondrial DNA indicate the highest genetic variation in Africans. Genetic studies are highly important, but it should be kept in mind that the results reported by the geneticists are sometimes very divergent. In fact, marked discrepancies exist even between studies published nearly simultaneously by members of the same research team. One such study reports that no evidence of hybridization between anatomically modern humans and Neanderthals is observed, whereas another study estimates the Neanderthal contribution to the modern non-African gene pool at 1–4 %. Also, the geneticists estimate the age of the most recent

common ancestor of modern groups differently. Not infrequently, specialists use skeletal finds separated by vast distances as a support to the idea of long-range migrations, although no archaeological facts favoring this idea can be brought forward. One example is the theory that *Homo heidelbergensis* migrated from Africa to the Near East, to Europe, and to China, and possibly back. Theoretically, the possibility of such migrations cannot be excluded; but they must be documented by archaeological evidence. However many physical anthropologists ignore the archaeological data altogether.

There is little doubt that my idea about four subspecies forming *Homo sapiens* sensu lato will prove totally unacceptable to most specialists. My purpose, however, is not to shock my colleagues but to prompt them to look at archaeological data. It is quite evident that humans who settled in East and Southeast Asia 150–30 ka BP developed their own industry which differed from the industries of adjacent regions. Virtually all archaeologists who have studied the Paleolithic of the Sino-Malayan area mention this fact. Notably, this industry was not “primitive” or “archaic” compared to its counterparts in other parts of Eurasia or in Africa; rather, it was adapted to the specific environmental conditions of that area. This by no means implies isolation. Pleistocene migrations of animals are traceable in both directions, west to east and east to west, suggesting that humans could have migrated likewise. The possibility of gene flow notwithstanding, however, no abrupt cultural changes in the Sino-Malayan zone can be traced. Therefore the range of migrations must have been rather limited, and immigrants were gradually assimilated by the natives.

In any event, no long-range migration from Africa is traceable in East or Southeast Asia in the 80–20 ka BP interval. There is no archaeological evidence of either replacement or even assimilation. Instead, the industry evolved gradually, and there is little doubt that the biological evolution was gradual as well, eventually resulting in the transformation of *Homo erectus* populations of the Sino-Malayan zone into the subspecies *Homo sapiens orientalis*.

A similar process of convergent development took place in North and Central Asia. Given that the Denisovans had made a 4–6 % genetic contribution to the gene pool of modern Melanesians, they cannot be regarded as an extinct branch in human evolution. Moreover, in North Asia and in most of Central Asia, Upper Paleolithic industries, which had emerged 50–45 ka BP, continued to evolve continuously up to the end of the Stone Age. There is no evidence of a migration of anatomically modern humans from Africa to that territory or to East or Southeast Asia. Apparently, both the taxon *Homo sapiens altaiensis* and the cultural tradition associated with it evolved in Southern Siberia in an uninterrupted manner.

The amount of information collected by specialists in human evolution, biological and cultural alike, is enormous, and the divergence of views is very considerable. Perhaps the time has come to try and integrate this information. The approach should be really integrative rather than parochial. The problem is truly multidisciplinary, and it cannot be resolved by either geneticists or physi-

cal anthropologists or archaeologists taken separately. One should respect the findings of the research done in neighboring areas. Hopefully, someday a truly integrative model (possibly based on a statistical approach) will be elaborated – one that would include all hypotheses put forward by the experts in various fields. This will provide a test for the entire range of conflicting theories, from the Recent African Origin theory to Multiregionalism in the broadest sense.

The authors would like to highlight the complex approach to solving the issue of the origin of *Homo sapiens sapiens* and point out the possibility of obtaining new and probably unexpected results of field investigations, as it happened with finds from Denisova and Okladnikov Caves in the Altai.

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HISTOMORPHOMETRIC STUDY OF JUVENILE HUMERUS AND FEMURS FROM OKLADNIKOV CAVE NEANDERTHALS

Introduction

Study of human ontogenesis is one of the most important areas of physical anthropology. And microanatomical investigation of evolutionary aspects of individual development has a great perspective.

Microstructural studies of fossil remains at all are rarely conducted, partly because of labor-consuming analysis, as well because it is intrusive.

In Russia histological methods were just applied to the Upper Palaeolithic humans. First E.N. Khrisanfova (1984) provided detailed histological description comparing Sunghir and Romankovo femora. Then M.V. Dobrovolskaya (Kozlovskaya) (2000) continued this analysis in context with a comprehensive palaeoecological study of Sunghir remains.

M. Schultz (1999) has demonstrated the resemblance between the Haverian systems of Australopithecines and apes. Histological description of an ulna from Neandertal and of a clavicle from Krapina suggests that Neanderthals resembled modern humans in this respect. At the same time, the histological analysis of Le Moustie 1 humerus has demonstrated that the rate of post-definitive bone remodeling was higher in Neanderthals, than in modern humans (Ramsay, Weaver, Seidler, 2005). This result probably contradicts with calculation of number of secondary osteons which have been used to provide estimates of the age at death of Shanidar Neanderthals (Thompson, Trinkaus, 1987). The comparison with modern humans suggests that none were much older than 35 years at death. The histomorphometric data were used to determine age at death of the Middle Pleistocene hominid from Boxgrove (Streeter et al, 2001). The authors noted more active rates of osteon creations then were expected for individual age. This pattern was explained by higher habitual strain level.

The goal of our study was to describe histological patterns of juvenile bones from Okladnikov Cave. The latter seemed to be necessary for biological age identification and further comparison of bone fragments separated in different layers of the cave. It was also important to estimate features of compact bone formation peculiar for Neanderthals in this group.

Skeletal samples

For histological analysis of Neanderthal remains from Okladnikov Cave we have prepared microscopical sections from juvenile right humerus, right and left femurs. According to macromorphological estimation, the bones belonged to individuals about 8 years at death (or even to one individual) (Mednikova, 2011; Mednikova et al., see current volume). Samples were taken from shifts at places of muscle attachments (deltoid muscle for humerus, m.quadriceps for femora) with joining medial and distal part of the shaft. Bone samples were put in special rubber and then polished using a Laborol-5 Struers polishing machine and Dia-Pro polishing suspensions with 1 μ diamond grains, and with an OP-U silicon suspension.

Methods

Light microscopy

On the first step of analysis sections were examined in reflected light using an Olympus BX-41 light microscope and were photographed with a colour view digital camera. The osteon size was measured with Olympus Cell software (image size 144 μ by 107 μ). Diameters of osteon and Haversian canal and area of resorbed cavities were measured. The histological patterns in place of muscle insertion were compared with areas far from attachment points.

Electronic microscopy

Further investigation was provided by the raster double-ray electronic microscope “Quanta 3D FEG” (FEI company production) with electron beam resolution 1.2 nm and 7 nm FIB (Ion beam resolution) at 30 kV at beam coincident point, with chamber vacuum 2600 Pa. Our investigation had pilot character and was for a first time applied to description of fossil remains.

Standard sputtering of gold by magnetron way for the right femur sample as well as standard thermal sputtering of carbon for the left femur sample was done.

Results

Light microscopy

Light microscopical examination of samples of humerus and right femur of Okladnikov Cave juveniles estimated features of some osteon parameters. Three parts of cortical layer were investigated. Maximal diameters of osteons were measured as well as osteon number and percent of non-remodeled subperiosteal area of circumferential lamellar bone tissue (Table 1).

Features of Haversian system were determined in limits of modern variations (Martin, Burr, 1998). Osteon numbers both for humerus and for femur seems to be larger than it was earlier described for adult Middle Pleistocene archaic forms like Boxgrove 1 and Shanidar 2 (Streeter et al., 2001).

The method of the age at death prediction was devised by G. Maat, M. Aarnts and Nagelkerke (2005) on the base of remodeling of circumferential la-

Table 1. Histomorphometric parameters obtained for circumferential zone (1), middle zone (2) and perimedullar zone (3) of juvenile right humerus and femur from Okladnikov Cave

Parameters	Humerus			Femur		
	1	2	3	1	2	3
Number of osteons	27	27	15	24	23	–
Maximal osteon diameter (μm)	350	420	310	250	230	–
Minimal osteon diameter (μm)	140	80	50	180	130	–
% non-remodeled area	0	–	–	18	–	–

mellar bone tissue in the anterior cortex of the femoral shaft. The process of the bone remodeling from 5 to 90 years for modern Homo was documented in details. Non-remodeled area can be considered as the reliable pattern of sub-adults (Maat et al., 2005). From this point, studied femur shows picture atypical for recent juveniles. The circumferential zone of lamellar bone is almost absent (18 % instead of 100 %). Moreover, it finds the closest analogy in microstructure of adult individuals between 50–60 years.

Electronic microscopical study

According to light microscopical analysis humerus was deeply touched by diagenetic process. That is why in electronic microscopical investigation we focused on femoral samples for both sides. Specifically, we measured concentric lamellar breadth around Haversian canal with magnification 3000 (Fig. 1). Obtained parameters for both femurs vary from 4.5–6. These values are in borders of modern normal variation (3–7 μm) (Martin, Burr, 1998). Longitudinal size of the osteocyte lacuna generally ranges between about 10 to 20 μm . Our measures give the same results.

The absence of pilaster is one of the morphological patterns of Neanderthal morphology, and this feature was presented in Okladnikov group (Mednikova, 2011). Histological picture in the subperiosteal place of muscles attachment of the femoral midshaft demonstrates numerous lacunas directed straight inside (Fig. 2). Perhaps this picture reflects the stage of active bone remodeling beginning. This osteoclastic activity can be inspired, for example, by the local mechanical stress.

Discussion and conclusions

The specificity of the midshaft growth has been described on the base of the histological study. Studied bones show picture atypical for recent infants and juveniles and more common for aged modern adults.

The main distinguished pattern is reduction of the non-remodeled circumferential lamellar zone. From our point of view, this is the result of the original pathway of the growth. Distinctive feature consists in fast remodeling lamel-

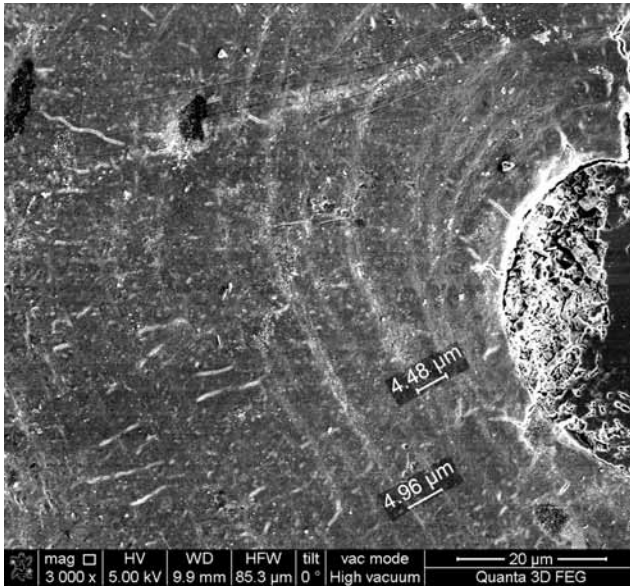


Fig. 1. Electronic microscopy of right femur from Okladnikov Cave. Measurements of distances between cement lines around Haversian canal in the middle zone of compact layer. Magnification 3000.

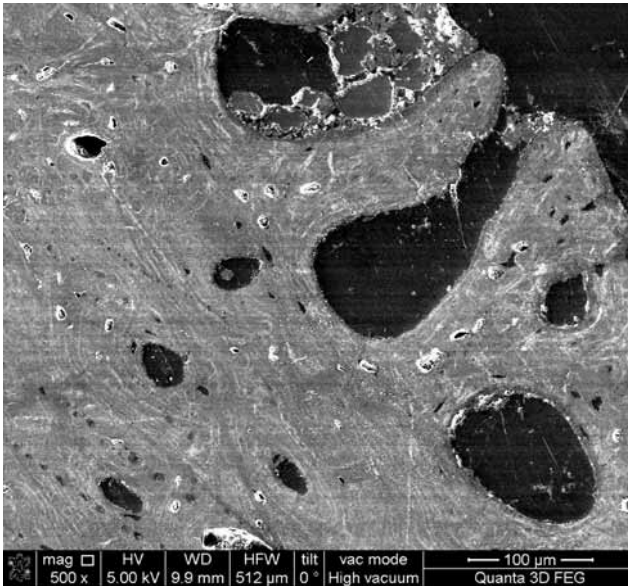


Fig. 2. Histological picture in the subperiosteal area of the same femur demonstrates numerous lacunas. Electronic microscopy. Magnification 500.

lar bone. Prompt osteon formation can be caused by the special hormonal profile as well as mechanical stress. This variant of bone remodeling can be result of parallel growth and aging processes. As well-known, this type of the ontogenesis is not typical for the *Homo sapiens s.* In any case there are histological indicators of the more fast aging for Neanderthal juveniles in Altai. Probably, significant inner robusticity of tubular bones is result of this type of the growth.

New histological data for South Siberian juvenile Neanderthals might confirm earlier proposition about European Neanderthals (Mednikova, 2007). It was pointed that late European Neanderthals (for example, adolescent Le Moustier 1 lived also about 40 ka) had “aged” before having reaching sexual maturity. And the term “aging” in this case only refers to the rapid remodeling of the bone tissue under enormous physical strain.

These first steps of the multilevel histological investigation discovered new evidence of specific rates of the ontogenesis of the archaic *Homo* forms (correctly of Neanderthals) which are expected to be different from those of modern humans.

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STABLE ISOTOPE (¹³C/¹²C AND ¹⁵N/¹⁴N) EVIDENCE FOR LATE PLEISTOCENE HOMININES' PALAEODIETS IN GORNY ALTAI

Introduction

Paleolithic cave sites of the Gorny Altai give new information to main stages of anthropogenesis and humankind peopling in Eurasia (Derevianko, 2009). Cultural continuity through Middle-Upper Paleolithic makes investigations in this region crucial for the understanding of human evolution. Recently published paleo-DNA study demonstrated ancient *Homo* forms migration and hybridization in the region (Reich et al., 2010). Initial peopling and further distribution of the humans in Eurasia have likely been connected with changes in the use of food sources and other adaptations to new environmental conditions.

Dietary ecology is one of the main ways to understand the lifestyle, adaptations and evolutionary development of hominins. The bases of hominin diet variability has been subject of long-term discussion in evolutionary anthropology. Paleodietary evidence can be gained from many sources (archaeology, archaeozoology, archaeobotany etc.), and recently isotope analysis emerged as a very productive tool for paleodietary studies. Stable isotopes analysis identifies dietary components based on the fundamental premise that certain categories of food sources have distinctive isotopic ratios. Thus the isotopic composition of human bone collagen shows the type of food sources used by an individual. The first isotopic investigations aimed to detect the use of maize, the degree of pastoralism, the use of marine resources by ancient human populations (Van der Merve, Vogel, 1978; Ambrose, 1986; Tauber, 1981). The isotopic composition of nitrogen (¹⁵N/¹⁴N) and carbon (¹³C/¹²C) are commonly used in this type of investigations (Van der Merwe, 1982; Schoeninger, 1989).

The pioneering stable isotope analysis applications to Pleistocene hominin diets based on bone collagen appeared in 1990s (Bocheres et al., 1991). This study demonstrated that the carbon and nitrogen isotopic composition of collagen can be used to place early humans into a broader context of fossil food webs.

The development of statistical mixing models further increased the quality of paleodiet reconstructions.

Isotopic investigations of the fossil human and animal skeletal materials from Late Pleistocene Europe contributed significantly to the general understanding of the Neanderthals' lifestyle. In one of the recent publications J.E. Hoffecker concluded that "the key to Neanderthal survival in such habitats may have been the hunting of mammoth and rhinoceros ..." (Hoffecker, 2009: 87). According to this opinion the Neanderthals hunted large mammal species of the upland steppe landscapes.

Our knowledge about Neanderthals from Asian parts of the area is exceptionally limited. First data on the isotopic composition of bone collagen were given in supplementary information to Nature's publication about Okladnikova Cave (Krause et al., 2007). During the radiocarbon dating of subadult and adult humerus fragments the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bone collagen were also obtained.

In this study, new human skeletal fragments from Okladnikov Cave and a new sample from Denisova Cave have been analyzed (Table 1) to get isotopic data for the paleoecological and paleodiet reconstructions of Asian late Pleistocene humans.

Table 1. Human bone samples from Gorny Altai caves

Sample	Site	Skeletal fragment
1	Okladnikov Cave (1984), level 3	Sub-adult, left femur
2	Okladnikov Cave, level 1	Right patella, adult
3	Okladnikov Cave, level 2	Right calcaneus, adult
4	Okladnikov Cave, level 2	Left calcaneus, adult
5	Okladnikov Cave, (1984), level 2	Right femur, sub-adult
6	Okladnikov Cave (1984), level 2	Humerus, sub-adult
7	Okladnikov Cave, level 2	Humerus, adult
8	Denisova Cave, level 11	Cranial vault

Materials and methods

The investigated bone fragments were obtained from collections of the Institute of Archaeology and Ethnology of the Siberian Branch of RAS. We sampled 7 fragments of postcranial skeletons from levels 1, 2 and 3 in Okladnikov Cave and one fragment of the cranial vault from level 11 of Denisova Cave (Table 2). In addition, one sample (ulnae fragment) was analyzed from Strashnaya Cave. The collagen was extracted from the bone fragments in the Laboratory for Biocenology and Historical Ecology of A.N. Severtsov Institute of Ecology and Evolution RAS (Moscow) using conventional method (Deniro, Epstein, 1981; Jørkov et al., 2007). Briefly, whole bone pieces (ca. 0.5 × 0.5 cm) were placed in 1M HCl at +3 °C till full demineralization. Then samples were washed with distilled water in centrifuge until neutral pH. The precipitate was dissolved during 24 hours in a HCl solution (pH 2.5) at 70 °C. Dissolved phase was lyophilized without filtration. All glassware used were sterile.

Stable isotope analysis was conducted using a Thermo-Finnigan Delta V Plus continuous-flow IRMS coupled with an elemental analyzer (Thermo Flash 1112) located at the Institute of Ecology and Evolution RAS. Samples were analyzed with reference gas calibrated against IAEA reference materials USGS 40 and USGS 41 (glutamic acid). The drift was corrected using internal laboratory standard (acetanilide). The isotopic composition of C and N was expressed in the δ -notation relative to international standards (VPDB and atmospheric nitrogen, respectively). All samples were analyzed in duplicate, the variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among replicated samples did not exceed 0.1 and 0.2 ‰, respectively.

Along with isotopic analyses, total nitrogen and carbon content (as %) was determined in all samples. %C and %N were close to the parameters of modern collagen samples and C:N atomic mass ratios were within the acceptable range of 2.9–3.6 confirming a good preservation of bone collagen.

Results and discussion

In the Okladnikova Cave samples the values of $\delta^{13}\text{C}$ varied little, from -20.1 ‰ to -19.1 ‰ (Table 2). The values of $\delta^{15}\text{N}$ were also very similar in all fragments analyzed (from 13.4 ‰ to 14.1 ‰). Obtained data are generally in agreement with previously published results (Krause et al., 2007; Table 3). Some differences (i.e. $\delta^{15}\text{N}$ from OxA laboratory) could be caused by different pretreatment methods.

One of the goals of our investigation was to determine the number of individuals and to separate bone fragments from different skeletons. However, the low variability in isotopic composition of different bone fragments makes this identification tentative only. The juvenile fragments were most similar, whereas the adult humerus ($\delta^{13}\text{C} = -20.1$) differed from all other adult postcranial fragments. Perhaps, all skeletal fragments belong to 3 individuals (1 child and 2 adults).

Table 2. Isotopic composition of bone collagen from Late Pleistocene Hominines of Gorny Altai. Stable isotope ratios of carbon ($\delta^{13}\text{C}$) are expressed in ‰ relative to VPDB and of nitrogen ($\delta^{15}\text{N}$) relative to AIR

Sample	$\delta^{13}\text{C}$, ‰	$\delta^{15}\text{N}$, ‰	atomic C : N
1. Okladnikova Cave, sub-adult, left femur, subadult	-19.3	13.4	3.4
2. Okladnikova Cave right patella, adult	-19.3	14.1	3.4
3. Okladnikova Cave right calcaneus, adult	-19.3	13.8	3.4
4. Okladnikova Cave left calcaneus, adult	-19.4	13.6	3.4
5. Okladnikova Cave right femur, sub-adult	-19.3	13.8	3.6
6. Okladnikova Cave humerus, sub-adult	-19.1	13.9	3.4
7. Okladnikova Cave humerus, adult	-20.1	13.7	3.4
8. Denisova Cave cranial vault, adult	-18.9	16.0	3.2

Table 3. Stable isotope composition of collagen of two bone fragments analyzed by different laboratories: Oxford Radiocarbon Accelerator, UK [OxA]; Leibniz Laboratory for Radiometric Dating and Isotopic Research, Germany [KIA]; Beta-Analytic, USA [Beta] and Institute of Ecology and Evolution, Russia [IEE]

Sample, laboratory	$\delta^{13}\text{C}$, ‰	$\delta^{15}\text{N}$, ‰
Adult humerus, KIA-27010*	-19.6	13.3
Adult humerus, our data (IEE-N237/9)	-20.1	13.7
Sub-adult humerus, KIA-27011*	-19.1	12.9
Sub-adult humerus, Beta-186881*	-18.9	13.5
Sub-adult humerus, OxA-154881*	-18.4	15.4
Sub-adult humerus, our data (IEE-N233/6)	-19.1	13.9

* Data from (Krause et al., 2007).

On the other hand, the low level of the variability in isotopic composition indicates low diversity of individual diets. This can be a result of relatively constant food supply and stable environmental condition.

The $\delta^{15}\text{N}$ values generally indicate high trophic level for the adults as well as for the juveniles. The carnivore Neanderthals' diet was shown before in numerous works (Bocherens et al., 1991; Bocherens, Drucker, 2003; Richards et al., 2000; Richards, Trinkaus, 2009), and this results were therefore expected. According to the new isotopic data the carnivore diet strategy was typical for the Asian Neanderthals as well as for European population.

Bone collagen is usually enriched in ^{13}C by about 5 ‰ relative to C_3 -based diet (Ambrose, Norr, 1993). The trophic enrichment for the ^{15}N is on average about 3 ‰ (Minagawa, Wada, 1984). But the degree of the ^{15}N enrichment ($\Delta^{15}\text{N}$) from prey to predator is species-specific and may vary in different ecosystems (Martinez del Rio et al., 2009; Caut et al., 2009). In particular, in the Middle–Upper Palaeolithic European terrestrial ecosystems this parameter significantly varied (Ambrose, 1991; Bocherens, Drucker, 2003); these authors recommend the use of the trophic enrichment factors of 0–2 ‰ for $\Delta^{13}\text{C}$ and 3–5 ‰ for $\Delta^{15}\text{N}$.

The $\delta^{15}\text{N}$ values of humans allows to estimate $\delta^{15}\text{N}$ of their main prey animals. Our results suggest that this could vary from about 8.5 to 10 ‰. Similar values were reported for large Pleistocene herbivores like mammoth and rhinoceros. For example, the $\delta^{15}\text{N}$ in mammoth bone collagen from Champ de Fouilles (France, Early Upper Paleolithic) varied from 7.6 to 9.7 ‰ (Jacobi et al., 2010). Collagen and keratinous mammoth and woolly rhinoceros tissues from Siberia also have $\delta^{15}\text{N}$ above 6.5 ‰ (Iacumin et al., 2000, 2005; Tiunov, Kirillova, 2010).

In contrast, the $\delta^{15}\text{N}$ in the Champ de Fouilles reindeer samples were within 2.6–3.6 ‰ (Jacobi et al., 2010). Deer bone collagen from Sunghir Upper Paleolithic site had $\delta^{15}\text{N}$ of about 5–6 ‰ (Dobrovolskaya et al., in press). For the samples from *Bos* bones of different European Middle-Upper Paleolithic sites $\delta^{15}\text{N}$ values reported are about 5–6 ‰ (Jacobi et al., 2010).

2001). Isotopic investigation of the Early Modern human from Tianyan confirms this point of view. Yaowu et al. (2009) suggested that carbon and nitrogen isotope ratios indicated a diet high in animal protein, and the high nitrogen isotope values suggest the consumption of freshwater fish. Tianyuan 1 had a $\delta^{13}\text{C}$ value $-17,6\text{‰}$ that was close to a carnivore (wild cat) and suggests also some use of C_4 -based foods. The $\delta^{15}\text{N}$ value (11.1‰) was significantly higher than that of the wild cat (8.7‰) and of the herbivores.

New isotopic data from an Upper Palaeolithic individual from north-east Siberian site Pokrovka 2 (27740 ± 150 BP) can also be used for comparison (Akimova et al., 2010). In contrast to the Tianyan case, bone collagen from Pokrovka 2 was characterized by moderate $\delta^{13}\text{C}$ (-18.4‰) and $\delta^{15}\text{N}$ (10.4‰) values. These values indicate terrestrial carnivorous diet. The analogous values were reported for the individual from Eastern European Upper Palaeolithic site Kostenky 8 (Middle Don, dwelling of Telmanovskaya camp): $\delta^{13}\text{C}$ of -18.3‰ and $\delta^{15}\text{N}$ of 10.9‰ . This similarity should indicate similar food sources and landscapes using (M. Dobrovolskaya, unpublished data).

Some Upper Paleolithic Eastern European individuals have the relatively high values of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, similar to those of Okladnikov Cave specimens. In particular, the bone collagen sample from Markina Gora (Kostenky 14) had $\delta^{13}\text{C}$ of -19.5‰ and $\delta^{15}\text{N}$ of 13.5‰ (M. Dobrovolskaya, unpublished data).

A previously studied human from Early Upper Paleolithic site Kostenki 1 had $\delta^{13}\text{C}$ -18.2‰ and $\delta^{15}\text{N}$ 15.3‰ (Richards et al., 2000). These unusually high values are strikingly similar to the isotopic signatures of human remains from Denisova Cave ($\delta^{13}\text{C}$ -18.9 and $\delta^{15}\text{N}$ 16.0 ; Fig. 1). The cranial vault studied goes from level 11 of Denisova Cave. The tooth from the same level was used for the paleo-DNA study (Reich et al., 2010). The unique taxonomic position of the Denisova Cave inhabitants implies that newly obtained isotopic data are of high importance. Similar isotopic signatures of the Denisova Cave individual and Early Upper Paleolithic humans from Eastern Europe can be a result of the similar behavioral patterns (food source using, landscape and climate preferences). Further investigation will verify this suggestion.

Unexpected results were obtained for the bone collagen sample from Strashnaya Cave. The individual had $\delta^{13}\text{C}$ of -19.1‰ , which is close to Okladnikova and Denisova caves specimens. However the $\delta^{15}\text{N}$ was 4.6‰ only. This extremely low value is untypical for Paleolithic humans. We therefore suggest that the bone fragment belongs to a bear skeleton. Isotopic investigation of Late Pleistocene European *Ursus spelaeus* have shown mainly herbivorous diet strategy with $\delta^{15}\text{N}$ values varying from 2 to 8‰ (Richards et al., 2008). Additional histomorphometric study is needed to verify the identification of this bone fragment.

Conclusions

This paper presents pioneering study of carbon and nitrogen stable isotope composition of human bone collagen from Gorny Altai Paleolithic caves. Obtained data suggest that animal protein of large herbivores formed a basic food

source for the Late Pleistocene inhabitants of Okladnikov Cave. Distinctive feature of Okladnikov Cave humans are high values of $\delta^{15}\text{N}$. This could be in part caused by arid environmental conditions. A human from Denisova Cave had more positive values of $\delta^{13}\text{C}$ (-18.9) and extremely high $\delta^{15}\text{N}$ values (16.0), comparable with some Eastern European Early Upper Paleolithic individuals (from Kostenki 1). Hypothetically this analogy comes from behavioral or local ecological similarity. The unusually low $\delta^{15}\text{N}$ values of the individual from Strashnaya Cave indicate a herbivorous animal (possible, bear). Further isotopic study of the animal bone samples from Gogny Altai caves will clarify the observed patterns.

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MODELS OF HYBRIDIZATION DURING RANGE EXPANSIONS AND THEIR APPLICATION TO RECENT HUMAN EVOLUTION

Introduction

Several lines of genetic, archeological and paleontological evidence suggest that anatomically modern humans (*Homo sapiens*) colonized the world in the last 60 thousand years by a series of migrations originating from Africa (Lahr and Foley, 1998; Prugnolle et al., 2005; Ramachandran et al., 2005; Liu et al., 2006; Mellars, 2006a, b; Handley et al., 2007; Klein 2008; Li et al., 2008; Deshpande et al., 2009). Until recently, an intense debate has been going on about the potential interactions that could have occurred during this range expansion (Krings et al., 1997; Wall, 2000; Currat and Excoffier, 2004; Eswaran et al., 2005; Plagnol and Wall, 2006; Fagundes et al., 2007; Hawks et al., 2008), but recent direct analyses of fossil nuclear DNA have revealed that 1–3 % of the genome of Eurasian has been likely introgressed by Neanderthal genes (Green et al., 2010; Reich et al., 2010), with Papua New Guineans showing even larger levels of admixture with another hominin specimen, Denisovans (Reich et al., 2010). It thus now becomes quite clear that the past history of our species has been more complex than previously anticipated, and that modern humans hybridized several times with local hominins during their expansion out of Africa, but the exact mode, time and location of these hybridizations remain to be precised. In this context, we review here a general model of admixture during range expansion, which lead to some predictions about expected patterns of introgression that are relevant to modern human evolution.

Simulation of spatial expansions with interbreeding

We have developed the SPLATCHE program (Ray et al., 2010) to simulate the genetic diversity of one or several samples in a spatially explicit landscape having been colonized from one or several introduction points. This framework allows one to study the pattern of neutral genetic diversity expected after a range

expansion into an empty or an occupied habitat, with or without interaction and competition between invading and local species. Neutral diversity can be easily modelled if the past demographic history of a species is known, thanks to recent progress in coalescent theory (see e.g. Wakeley, 2009, for a review), but this is rarely the case. However, one has often information on the geographic distribution of the species, as well as on current and past environmental data. This information can then be approximately translated into demographic information, such as local carrying capacities (i.e. population densities) or local migration rates, which should differ in various environments (Ray et al., 2008; Ray and Excoffier, 2009), and be used to simulate genetic diversity. The simulation of genetic diversity is done in two distinct steps in the SPLATCHE framework. A first step consists in forward simulations of the above mentioned demographic parameters, and a second step consists in backward coalescent (Kingman, 1982) simulations of genetic diversity conditional on demographic information recorded in the first step.

In Fig. 1a and 1b, we illustrate two time-points of the forward simulation of the expansion of a species in the territory of another one. At the beginning of such simulations, we assume that some areas are already occupied by a local species. A new invading species appears at an arbitrary position. We model the overlap of these species by making them evolve in two different layers (see Fig. 1c), where subpopulations (demes) of a given layer (species) can exchange migrants with neighboring demes of the same layer, but also interbreed with individuals of the other species that are present at the same location in the other layer, and which thus result in admixture events. The invading population can

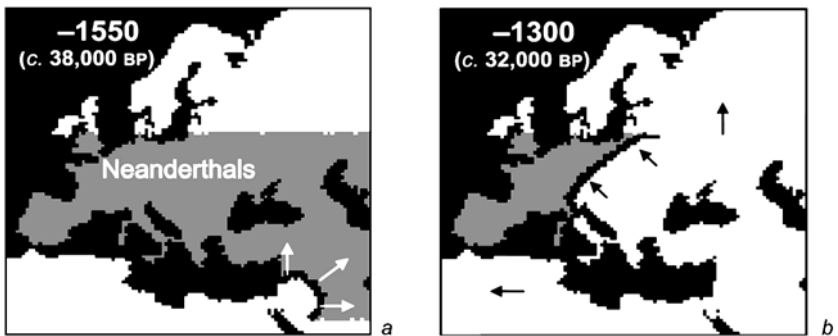


Fig. 1a, b. Representation and properties of a range expansion process with local interbreeding and competition with a local species.

Schematic representation of the range expansion of Paleolithic modern human populations into Europe and Middle-East, assumed to be already colonized by a Neanderthal subdivided population. Adapted from (Currat et al., 2008a). Expansion was assumed to have started 1600 generations ago (~40,000 years ago) from the Sinai peninsula, and expanded concentrically from this location in the Middle-east and into Europe. Grey area represents locations with Neanderthals only. Light grey area represents locations with modern humans only. Black area represents locations where Neanderthals and modern humans coexist and have the possibility to interbreed, which is at the edge of the modern human expansion wave.

send migrants to empty neighboring demes of its own layer, which are then logistically filled to their carrying capacity, and which can send further migrants to adjacent demes, thus progressively colonizing the whole world (see Fig. 1a, b).

As discussed elsewhere (Currat and Excoffier, 2004; Currat et al., 2008b), the rate of interbreeding is assumed to be density-dependent. At any location, the probability of a successful introgression event is thus defined as $A = \gamma(2N_i N_j)/(N_i + N_j)^2$, where N_i and N_j are the current deme densities of the two species. It results in the introgression of AN_i genes from species i to species j , and AN_j genes in the other direction for each generation. In this model, the parameter γ is a general measure of the strength of barriers to gene flow between species. We do not explicitly model the nature of these barriers, but they could be either prezygotic (and γ could for instance be considered as a measure of disassortative mating), postzygotic (and γ would be a measure of the fitness of the hybrid individuals), or any combination of factors preventing the successful mating of members of both species. In any case, a γ value of 0 corresponds to a total absence of interbreeding between the two species, a γ value of 1 corresponds to random mating between the two species, and any value in between implies that mating is locally non-random between the two species. Deme densities are then updated as $N'_i = N_i(1 - A) + AN_j$ to take interbreeding into account, and are then further updated to reflect logistic regulation, competition and migration (see Currat and Excoffier, 2004; Currat et al., 2008b, for more details).

Dynamics of the introgression

In Fig. 1d, we show the dynamics of the densities and interbreeding between the two species at a given arbitrary location on the invading wave front, where admixture can occur (shown as a black strip on Fig. 1a, b). In a few words, the local species that is initially at carrying capacities, suffers from competition with the invading species, and progressively declines until it goes extinct (Shigesada and Kawasaki, 1997), in line with recent models of Neanderthal decline (e.g. Banks et al., 2008). The invading species has a higher carrying capacity, which allows it to invade in our model. It grows logistically until it reaches its own carrying capacity. Introgression events will first be more frequent from the local to the invading species as the few invaders will initially have a higher chance to mate with locals than with other (rare) invaders. Introgression in the other direction will then become more frequent, and will reach a maximum when the two species have approximately equal densities, which is when the local species will have begun to decline sharply. This dynamics shows that i) the invading species will be introgressed when it has a very small density, ii) introgression can occur in both direction but the invading genes having introgressed the local population will disappear with this population iii) a gene introgressing the invading population will be found in multiple copies when the invading species has reached carrying capacity. It follows that with recurrent introgression events occurring at the wave front, the original gene pool of the invading population should become increasingly diluted (Chikhi et al., 2002), and we would expect

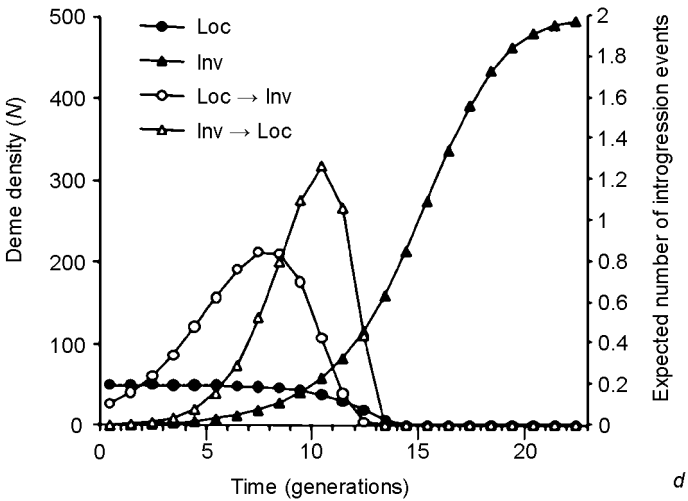
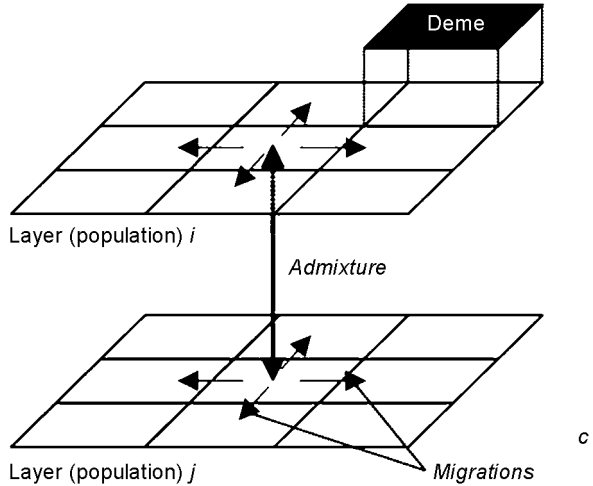


Fig. 1c, d. Representation and properties of a range expansion process with local interbreeding and competition with a local species.

c – schematic simulated interaction between Neanderthals and modern humans. Humans and Neanderthals are assumed to occupy two different population layers. Within layers, migrants can be exchanged between neighboring subpopulations (demes). Between layers, members of the two species can interbreed if they occupy the same location;

d – illustration of the local demographic and introgression dynamics. We plot the evolution of population densities and introgression events over time at a given location of the lattice using demographic parameters from scenario C1 described in Table 1, $\gamma = 4\%$, and assuming no migration from neighboring demes for simplicity. At generation zero, the local species is at carrying capacity, and an invading species with a higher carrying capacity appears. Note that introgression first occurs from the local to the invasive species. Loc \rightarrow Inv: Introgression events from the local to the invading species. Inv \rightarrow Loc: Introgression events from the invading to the local species.

to see a massive introgression of local genes in the territories newly colonized by the invading species unless the hybrids are heavily counter-selected (Currat et al., 2008b; Excoffier et al., 2009).

Introgression levels as a function of interbreeding success

For quite a wide range of demographic scenarios (such as those listed in Table 1), we find that the genome of an invading species should be massively introgressed by the genes of the local (and potentially extinct) species, if more than 10 % of effective interbreeding events are successful, as measured by the parameter γ (Fig. 2). Note that in several scenarios, much less than 10 % effective hybrid fitness is sufficient to have >95 % introgression (scenario C1, C3, C6 and C7). Note that even when the density of the invading species is 100 times larger than the local one, complete introgression of the invading species occurs when effective hybrid fitness exceeds 10 % (cases C2 and C5). When the invading species is only two time more abundant than the local species, high levels of introgression also occur for moderate levels of interbreeding (cases C6 and C7). Overall, the final level of introgression is positively correlated with the size of the local population (compare cases C2 and C3), and negatively correlated with the size of the invading population (compare cases C1 and C2 or C4 and C5). Introgression is also favored when gene flow between adjacent demes is restricted (compare cases C1 and C4, C1 and C6, as well as C2 and C5). This makes sense, because genes introgressed from the local population at the wave front will compete with migrant genes from the invading populations if gene flow is high, and will be thus less amplified by the demographic growth. Therefore, intraspecific gene flow protects against interspecific introgression, a phenomenon that has been confirmed when comparing levels of introgression in species with sex-biased dispersal, where genetic markers preferentially transmitted by with

Table 1. Parameters of the simulated invasion scenarios studied in a simple square world of 100 x 100 demes, initially entirely settled by a local species. The source of the invasion is arbitrarily located in deme at position <5; 5>

Scenario	Local species		Invasive species	
	K	Km	K	Km
C1	50	1	500	10
C2	50	1	5000	100
C3	500	10	5000	100
C4	50	10	500	100
C5	50	10	5000	1000
C6	50	1	100	10
C7	500	10	1000	100

Note. K – Carrying capacity; Km – Number of emigrants sent each generation to neighboring demes of the same species at carrying capacity. Each generation, a given gene has thus probability m to migrate to neighboring demes. In all scenarios, the intrinsic rate of growth (r) was set to 0.5.

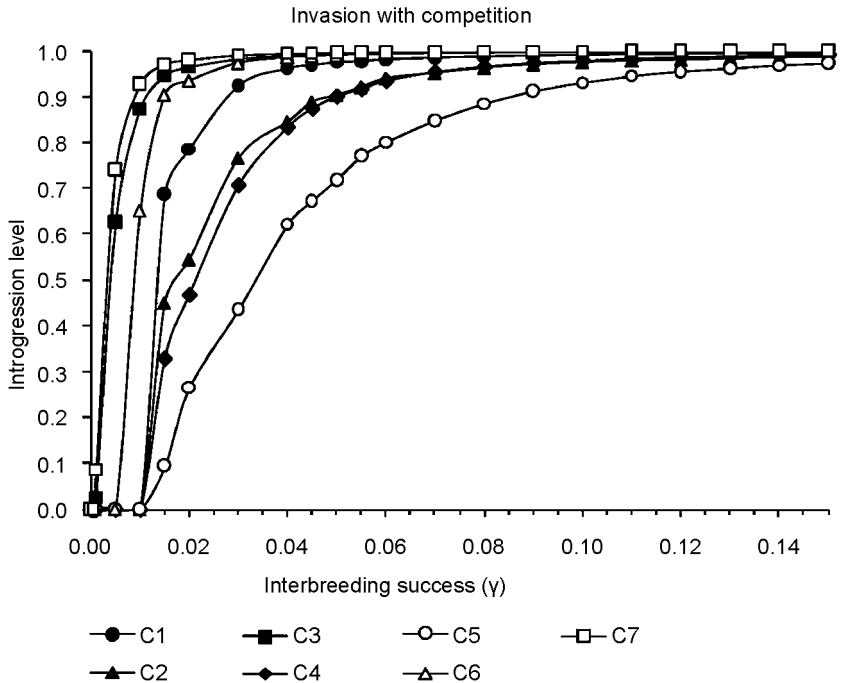


Fig. 2. Proportion of genes introgressed into a given species as a function of the level of successful interbreeding (γ □), assuming that the two species compete for local resources. Reported introgression levels were obtained as averages over 10,000 simulations. Case simulation parameters C1–C7 are described in Table 1. Interbreeding success can be considered as the fitness of genes transferred into a new background by interbreeding. Adapted from (Currat et al., 2008b).

the dispersing sex very generally show lower levels of introgression than other markers (Petit and Excoffier, 2009).

Implications for the human-Neanderthal hybridization process

The results presented here strongly suggest that if Neanderthal and modern humans had freely interbred, one would expect to see massive amounts of Neanderthal introgression into our genome. The fact it is not the case suggests that interbreeding occurred at a much lower rate than under random mating. While the results presented above were not obtained with simulations specifically adapted to the past demography of these two species, our result suggest that the effective fitness of their hybrids was certainly much less than 10 %, or that less than 10 % of all potential hybridization events have actually occurred due to strong assortative mating promoted by social, behavioral or ecological barriers to reproduction.

It has been proposed that human-Neanderthal admixture only occurred in the Middle-East, before Europeans and Asians diverged, since all Eurasians show

approximately the same amount of introgression (Green et al., 2010; Reich et al., 2010). However, in our model of hybridization during a range expansion where interbreeding can occur over the whole range of the local species, populations from very different geographical locations can also show very similar levels of introgression, despite having hybridized with different local sub-populations (see Fig. 1a in Currat and Excoffier, 2004; or Fig. 5 in Currat et al., 2008b). Postulating a continuous hybridization over the whole Neanderthal range seems more parsimonious than proposing that hybridization only occurred in a small portion of the Middle-East and not afterwards because i) it authorizes admixture in Europe where human-Neanderthal interaction is documented (Hublin et al., 1996; e.g. Mellars et al., 2007; but see Higham et al., 2010), and ii) the fact that the ancestors of Papua New Guineans have hybridized later with Denisovans precisely shows that hybridizations with hominins occurred several times and in different places.

It seems therefore that envisioning that admixture of modern humans with other hominins occurred in a range expansion context is a more natural framework for explaining observed patterns of introgression. It also naturally explains why this introgression was apparently asymmetric (Green et al., 2010), without need to invoke selective processes like Haldane's rule. Compared to a model of instantaneous admixture, models of admixture during expansions require much lower levels of interbreeding to account for the same final level of introgression (Nordborg, 1998; Currat and Excoffier, 2004). It implies the existence of strong reproductive barriers between modern humans and other hominins, the nature of which (cultural, ecological, genetic) remains to be assessed.

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**THE AFRICAN MIDDLE STONE AGE: EARLY EVIDENCE
FOR THE ORIGINS OF SYMBOLIC MATERIAL CULTURE
AND ITS SPREAD INTO EURASIA**

For decades the origins of behaviour termed “modern” and associated with *H. sapiens* was thought to lie in Europe. By extension and on the assumption that fully syntactical language is associated only with modern humans it was thought the origins of language lay also in Europe. This suggests a *terminus post quem* of c. 35–40 ka for modern language. One method of testing this hypothesis is by critical examination of material artefacts recovered from archaeological sites that date to older time periods in Africa.

Two stages of the Middle Stone Age (MSA) are of particular importance in southern Africa in challenging the stereotypic model, namely the Still Bay dated at c 75 ka and the Howiesons Poort at c. 65 ka. Recent excavations or reanalysis of materials excavated from Klasies River, Diepkloof, Sibudu, Peers Cave and Blombos Cave has produced crucial evidence that refutes a European origins model. At the latter site the recovery of marine shell beads, engraved ochre, and evidence for the regular manufacture and use of bone tools and finely made bifacial points at this and other sites suggests a level of cognitive behaviour not previously associated with Middle Stone Age people. This seems also to be the case in the later Howiesons Poort with the presence of lithics and social behaviours that appear precocious for this time period. The capacity for these behaviours, including the acquisition of language skills, is likely to have evolved over a long period of time.

Evidence for behavioural modernity is manifest in our ability now to “read” the artefacts – a point of much contention and debate but most archaeologists agree that personal ornaments and “art” are distinct and absolute markers of symbolically mediated behaviour. They also provide the first direct evidence of human ability to store information outside the brain. Modern language, defined by Wynn as involving the interweaving of grammar and the ability for semiotics and pragmatics, arguably goes hand in hand with human behaviour that is symbolically organised. While earlier language may or may not have lacked syntax I argue that by 75 ka or even 100 ka syntactical language was essential to share and transmit the symbolic meaning of beadworks, abstract engravings, ochre

decoration and possibly tool form and function. Once in place the transmission of symbolic meaning, in effect style, social rules and theory could not, as Ingold points out, have been accomplished by demonstration alone but would have required symbolic language.

A key question is why the material and social innovations that are thought to represent symbolically driven behaviour and modern language are apparent at some MSA sites in southern Africa and yet seem absent at others. One answer is that culture complexity and innovation is a heuristic strategy. The evolution of complex traditions does not necessarily drive the evolution of still more sophisticated imitations or traditions. The fitness of the material innovations at some MSA sites may not have been selected for during all periods of the MSA or in all regions of Africa. However once symbolically mediated behaviour and the building blocks of modern language were in place, an event that dates to at least 75 ka, the social and technical skills of humans in at least parts of Africa rapidly advance to the point of their successful expansion out of Africa by c. 60 ka.

Future and ongoing excavations at MSA sites in southern and eastern African will further provide vital information for understanding the development of fully modern human behaviour and language during the Late Pleistocene in Africa, and possibly how this behavioural package later spread to the rest of the Old World.

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A NEW LOOK AT THE END OF THE MIDDLE PALAEOLITHIC SEQUENCE IN SOUTHWESTERN FRANCE

In particular regions of Eurasia, where Mousterian assemblages have produced dates contemporaneous with the arrival of the first anatomically modern humans, different hypotheses have been advanced to account for the persistence of certain final Neanderthals populations, including their possible isolation (The Last Neanderthals..., 1996; The Mediterranean..., 2008) in such areas as the south of the Iberian peninsula and Gibraltar (Finlayson et al., 2010), the Crimea (Pettitt, 1998; Chabai, 2003; Monigal, 2006), or even the Caucasus (Golovanova and Doronichev, 2003). For the rest of western and central Europe, the question of the end of the Middle Palaeolithic is sometimes overlooked given the presence of certain techno-complexes commonly referred to as “transitional”. These industries immediately succeed the local Mousterian and are therefore often attributed to the final Neanderthals: for example, the Chatelperronian (Pelegrin, 1995), Ulluzian (Peresani, 2008) or Lincombian-Ranisian-Jerzmanovician (LRJ) (Flas, 2006). It is due to the persistent interest of researchers in this single “transition” and its associated industries that the very end of the Middle Palaeolithic remains insufficiently studied. In this contribution we would like to return to the final Neanderthal occupation *sensu stricto* of Western Europe, more particularly, as it pertains to the south west of France.

The main elements and historical background of the “classic” hypothesis concerning the end of the Middle Palaeolithic and the emergence of the Upper Palaeolithic in the south west of France can generally be resumed by the following:

- According to early researchers, the Mousterian of Acheulean Tradition (MTA) industries, such as those originally defined by D. Peyrony (1930) and then F. Bordes (1953), occupy the summit of stratified sequences.

- The MTA was subsequently subdivided by F. Bordes into two variants (Bordes, 1981); the Mousterian of Acheulean Tradition A (with numerous bifaces together with scrapers and backed knives) followed by an MTA-B (reduction in the quality and number of bifaces in favour of backed knives and Upper Pal-

aeolithic tools types). Transitional (A-B) levels can exist such as those described at Pech de l'Azé I (Bordes, 1954; 1955).

- The MTA-B, given its place at the top of several Mousterian sequences and below the Chatelperronian (the “Lower Perigordian” following Peyrony’s original terminology (1933) or the “Castelperronian” for others (Context..., 1993; Rigaud, 2000)), is still considered to be a natural candidate for the emergence of this transitional industry (Pelegrin, 1990) which is itself ultimately succeeded by the Aurignacian.

- Several authors (Peyrony, 1948; Bordes, 1968; Pelegrin, 1995) have considered the MTA-B variant, for reasons both stratigraphic and typo-technological, as the origin of the “Perigordian”, a no-longer recognized techno-complex, but one whose former “Perigordian I” has become what we know today as the Chatelperronian or Castelperronien (Lévêque and Vandermeerch, 1980; Rigaud, 1996).

- While still linked to the Mousterian of Acheulean Tradition, the Chatelperronian is, on the other hand, markedly different from the initial phases of the Aurignacian. Known as the Aurignacian I or Early Aurignacian with split-based bone points, this techno-complex, described as being monolithic over a substantial geographic extension, is considered to be intrusive in western Europe (Peyrony, 1933; Bordes, 1972). According to this view, known as the “replacement model”, the Aurignacian in general is often conflated with the Aurignacian I in particular and has come to be seen as the material proxy for the anatomically modern human colonisation of Europe, most famously represented by the remains of Cro-Magnon man (Stringer and Andrews, 1988; Mellars and Stringer, 1989).

- Despite still being sparse during the second half of the 20th century, the human remains that were associated with the MTA as well as the Chatelperronian or “Lower Perigordian” were generally attributed to (Combe-Capelle) or assumed to be (Pech de l'Azé I) modern human and not Neanderthal. The coexistence of these two human lineages, as well as the variability of regional sequences across Europe, has led researchers to propose a polycentric model for the emergence of the Upper Palaeolithic. In terms of lithic industries, this model relies heavily on the presence of Upper Palaeolithic tool types in late Middle Palaeolithic assemblages such as endscrapers and burins, but above all, backed knives in the MTA-B (Bordes, 1972). The hypothesis of a gradual *in situ* evolution of the Upper Palaeolithic was relegated to a minority position in the eighties (Cabrera-Valdes et al., 2001; Maillo et al., 2004; Bernaldo de Quiros et al., 2010).

- The 1979 discovery of a Neanderthal skeleton from a Chatelperronian context at Saint-Césaire (Lévêque and Vandermeersch, 1980) lent further credibility to the stratigraphic position of the Chatelperronian human remains from Arcy-sur-Cure already attributed to the “Paleanthropians” (Neanderthals) by Leroi-Gourhan (1958). Despite the fact that F. Bordes (1981) considered the

Saint-Césaire discovery to be somewhat “awkward”, a new paradigm was born whereby the Chatelperronian assemblages became the handiwork of the Neanderthals and were thus seen as representing a genuine “transition” whose configuration could result from either acculturation (Demars and Hublin, 1989) or, given that the Chatelperronian was now seen as a Neanderthal epiphenomenon, a local evolution from a Mousterian substrate. Furthermore, the emergence of symbolic expression was no longer inherently connected to the appearance of modern humans (D’Errico et al., 1998).

- The few human remains recovered from MTA contexts have now been attributed to the Neanderthals such as at Pech de l’Azé I (Maureille and Soressi, 2000) or Jonzac (Jaubert et al., 2008; Richards et al., 2008).

- The reanalysis of the several MTA assemblages dated to within MIS 3 has clarified lithic production sequences (Soressi, 2004; Soressi et al., 2007; 2008; Guibert et al., 2008) and has reaffirmed the existence of a laminar component within the MTA geared towards the production of backed knives and Upper Palaeolithic tool types. This has led some to suggest that this industry could be the origin of the Chatelperronian (Pelegrin and Soressi, 2007).

- This body of work as a whole has functioned to reinforce the replacement model which sees a population of anatomically modern humans, bearing the Aurignacian, who colonised Neanderthal Europe, be it still “Mousterian” or “transitional” (Mellars, 2004; 2006).

The debate concerning the “transition”, which has progressively emerged from the above outline, illustrates the fact that the other final Middle Palaeolithic cultural manifestations besides the MTA are rarely considered. However, we have recently shown that the MTA is not the final expression of the Mousterian in south-western France (Jaubert, 2010a; 2010b). Despite recent positions to the contrary (Pelegrin and Soressi, 2007), this demonstration significantly weakens, if not annuls, the theory of a direct and gradual succession of the type MTA A → MTA-B → Archaic “Castelperronian” (Contexte..., 1993) → Chatelperronian.

At least one lithic techno-complex (LTC), if not two, follow the MTA in several well dated sequences: a Denticulate Mousterian with Discoidal debitage (Thiébaud, 2005; Thiébaud, 2007) and potentially a Levallois LTC with large scrapers (Asselin, 2006; Jaubert, *op. cit.*). This is also true in regions on the margin of, or outside the MTA phenomenon, such as in Bourgogne with the Arcy-sur-Cure sequences (Girard, 1978; 1980; 1982; Lhomme et al., 2005) or, as is the case on the other side of the Rhone valley, with the Neronian as originally proposed by Combier (1990) and more precisely characterised by L. Slimak (2004, 2008).

Furthermore, a recent reconsideration of the relevant faunal data has also permitted the construction of a new bio-stratigraphic framework for the end of the Middle Palaeolithic and the beginning of the Upper Palaeolithic (Discamps et al., *in press*). Taking into account the stratigraphic data and available absolute

dates, it has been possible to correlate significant changes in the character of faunal assemblages with the regional bioclimatic record (Sánchez Goñi et al., 2008). At least three different techno-complexes from the end of the Mousterian can be placed between the Quina Mousterian (correlated with Heinrich event 6, ~60 ka BP) and the debut of the Upper Palaeolithic (correlated with Heinrich event 4, ~40 ka BP) (Fig. 1, 2).

We would like to discuss the two LTC that mark the end of the Middle Palaeolithic of south-western France as well as the relevant archaeological sequences.

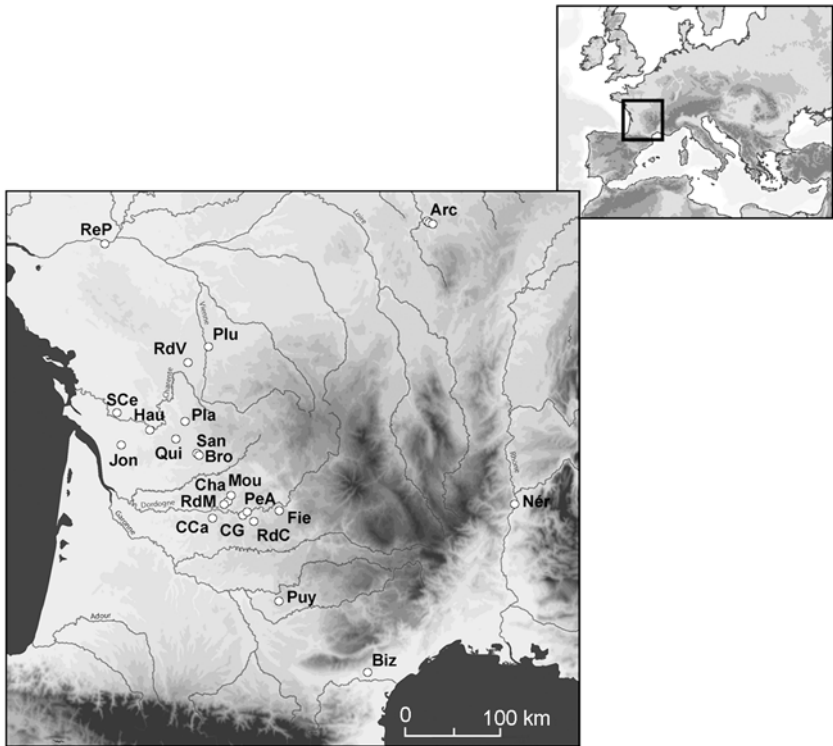


Fig. 1. Geographical framework of the Final Middle Paleolithic. Location of the main sequences discussed in the text.

Arc – Arcy-sur-Cure (grottes de l’Hyène, du Renne); Biz – Tournal de Bize; Bro – Brouillaud; CCa – Combe-Capelle; CG – Combe-Grenal; Cha – Chadourne; Fie – Les Fieux; Jon – Jonzac (Chez Pinaud); Hau – Hauteroche; Mou – Le Moustier; Nér – Grotte Néron; PeA – Pech de l’Azé I; Pla – Le Placard; Plu – Les Plumettes; Qui – La Quina; Puy – Puycelci (La Rouquette); RdC – Roc de Combe; RdM – Roc de Marsal; RdV – Rochers-de-Villeneuve; ReP – Roc en Pail; San – Sandougne; SCe – Saint-Césaire (La Roche à Pierrot).

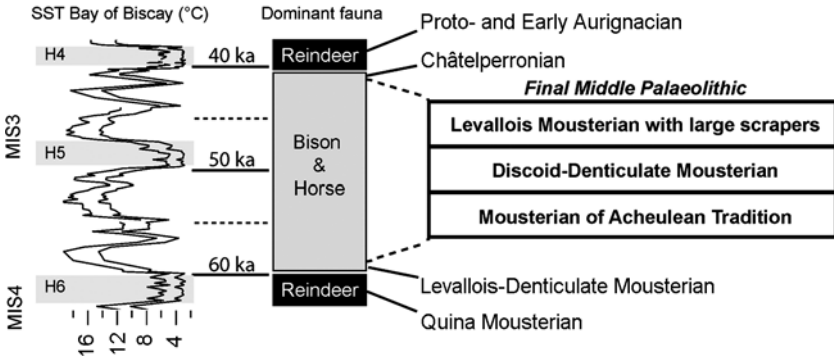


Fig. 2. Chronological framework of the Final Middle Paleolithic. Synthesis of proposed correlations between paleoclimatic records (Bay of Biscay sea surface temperatures, after Sánchez-Goñi et al., 2008), hunted fauna, and lithic techno-complexes (after Discamps et al., in press). The three principle techno-complexes from the end of the Middle Paleolithic are highlighted.

The Discoid-Denticulate Mousterian

This industry is defined in techno-typologically terms by a Discoid debitage (*sensu* Boëda, 1993; *Discoid Lithic Technology...*, 2003) principally associated with a notch and denticulate tool-group; Clactonian notches, diverse types of denticulates, Tayac points, etc. (Thiébaud, 2005; 2007). The scraper component is generally very poorly, if not sporadically, represented. Even if the majority of assemblages employed by F. Bordes to formulate “his” definition of Denticulate Mousterian (Bordes, 1963) can be confused, this new definition is more precise than the original definition, which should no longer be employed. In fact, several forms of a “Denticulate Mousterian” exist that, apart from their typologically “denticulate” component, differ radically; for example, Combe-Grenal level 20, though attributed to a Quina Mousterian laden with denticulates, it is still not a Denticulate Mousterian *sensu stricto* (Faivre, 2008), this is similar to other industries attributable to a Levallois Mousterian with denticulates such as at Roc-de-Marsal (level III, Thiébaud, 2003), La Quina (level 7, Park, 2007) or Jonzac (level 9, Thiébaud *in* Jaubert, 2008).

In addition to the different sequences at Arcy-sur-Cure, this LTC is known from numerous sites in south-western France (Thiébaud, 2005) and always in a stratigraphically coherent position: Combe-Grenal (levels 11 to 16) Brouilaud (level D) Hauteroche (level 1, 3), Sandougne (levels A-B), Chadourne (c. A, A-B), La Quina Amont (levels 4a, 4b, 5, 6a, 6b, 6c), Les Rochers de Villeneuve (level N), Saint-Césaire (Egpf-Egp-Egf or c. 10-11-12 after Thiébaud et al. 2009), le Placard (level 6), Les Fieux (levels J-K), Roc-de-Combe (level B), Puyelsi (level A), Roc-en-Pail (level 5) among others.

From an archeo-stratigraphic point of view the following can be established:

- When this LTC is present in the same sequence as the Chatelperronian, it never follows or is interstratified with the latter and therefore systematically underlies it as can be seen at Roc-de-Combe and Saint-Césaire. This is also the case outside of the South West such as with the Grotte du Renne and Grotte du Bison at Arcy.

- At least three sites present sequences where the Discoid-Denticulate Mousterian overlies the MTA; Saint-Césaire, La Quina, and Brouillaud.

- When this LTC is found in the same sequence as the Quina Mousterian, it systematically overlies it as at Placard, Hauteroche, Combe-Grenal, La Quina, Chadourne, Puycelsi, and Roc-en-Pail (Mellars, 1969; 1996).

- Several cases of recurrences or unexpected interstratifications (Les Fieux, Combe-Grenal (top of the sequence), Le Moustier) require verification or further discussion as to whether or not the initial attribution of this LTC was indeed correct as well as the LTC that complete the sequence.

The Discoid-Denticulate Mousterian has produced direct dates from the following sequences:

- La Quina ($43 \pm 3,6$ ka BP);

- Saint-Césaire, level 10: $40,9 \pm 2,9$ ka BP (mean of 9 TL dates); level 11: $38,2 \pm 3,3$ ka BP (mean of 2 TL dates) and level 12: $42.4 \pm 4,3$ ka BP (TL) (Contexte..., 1993);

- Roc-de-Combe, $44.700 \pm 2,900$ and 50.000 ± 2.400 in radiocarbon years (Bordes, 2002).

It has also been indirectly dated at Rochers de Villeneuve by a *terminus ante quem* provided by the overlying level dated to between 40.7 ± 9 and 45.2 ± 1.1 ka BP (*infra*). If we exclude the significantly older date from Roc-de-Combe, the time period concerned is therefore between 38.2 and 44.7 ka BP. To our knowledge, no human remains are clearly associated with this assemblage type.

While the fauna associated with this LTC is dominated by horse and bison (Discamps et al., in press), complex subsistence practices (specialized, communal, and seasonal hunting strategies associated with surplus food storage, anticipation of prey movements and needs scheduling) concerning Bison have been identified at Mauran, La Quina, and Puycelsi (Rendu et al., in press).

Based primarily on the construction of archeo-stratigraphies from the South-West of France and surrounding regions (the Bourgogne and Centre-Ouest) our hypothesis maintains that this LTC follows the MTA, which was up until now considered to be the last Mousterian facies in France. This is no longer the case. Given that the “hyper-mousterian” techno-typological profile of this LTC diverges considerably from that of the MTA (no laminar products nor Upper Palaeolithic tool types) it cannot therefore be considered as a legitimate candidate for the origin of the Chatelperronian. Furthermore, when the Chatelperronian is present in the same sequence it directly follows this lithic techno-complex, which once again accentuates the rupture between the Middle and Upper Palaeolithic and leaves no space for any concept of a “transition”.

The Levallois Mousterian with large scrapers

In the same manner, although very different from the previous example, another LTC is also stratigraphically posterior to the MTA: a Levallois Mousterian with large scrapers. Typologically, it could be confused with certain Ferrassie Mousterian assemblages due to the presence of Levallois debitage (recurrent centripetal) and a tool component dominated by scrapers, particularly, double scrapers and well-crafted, sometimes sizeable, double-convergent scrapers. Our present knowledge can be summarized by the following:

- This LTC is known from the sequence of Rochers de Villeneuve (c. Jr) in the Vienne where it overlies a Discoid-Denticulate Mousterian (Asselin, 2006) and is dated to between 40.7 ± 9 and 45.2 ± 1.1 BP. MtDNA analysis of a human femur fragment recovered from this level has confirmed its attribution as being Neanderthal (Beauval et al., 2005; 2006).

- Levels E, F1, and F2 from the Grotte du Bison at Arcy (Yonne) present a comparable succession whereby a Levallois Mousterian overlies a Discoid-Denticulate LTC (Lhomme et al., 2005).

- Level J (J1-J2-J3-J4-5) of Le Moustier (Lower Shelter) is also relevant given the fact that it is stratigraphically posterior to both an MTA level (H) and a poorly defined Denticulate level (I) dated to 40.9 ± 5 ka. Level J, which contained the Neanderthal burials (Maureille, 2002) was dated by to $40.3 \pm 2,6$ ka BP and undoubtedly merits further attention. Unfortunately, the material recovered by Peyrony demonstrates an over-representation of larger pieces and retouched tools suggestive of a recovery bias. However, very preliminary observations of the material indicate the co-occurrence of both discoid and Levallois debitage. This layer is overlain by a still poorly published Chatelperronian level dated to 42.6 ± 3.7 ka BP (Valladas et al., op. cit.).

- It is very probable that level E₂ sup of Saint-Césaire (Charente-Maritime), attributed to the Chatelperronian during excavations (Contexte..., 1993), contains to some extent a Levallois component that can be linked to this techno-complex with large scrapers (Bordes et al., 2010).

- While the fauna is once again dominated by Bison and Horse, assemblages securely attributable to human agents appear much more rare than was the case with the Discoid-Denticulate Mousterian. This techno-complex is for the moment essentially represented by paleontological sites demonstrating only an ephemeral human presence with lithic remains often associated with hyena dens, a carnivore particularly abundant during this period (Discamps, 2010). This is the case at Rochers de Villeneuve and perhaps at Les Plumettes in the Vienne (Airvaux, 1987; Primault; 2003).

Discussion

Before the Early Aurignacian, Proto-Aurignacian, and the Chatelperronian (Bordes et al., this volume) the South-West of France witnessed an ultimate phase of Neanderthal occupation that cannot be confused with either the debut of the Upper Paleolithic, the arrival of the first modern humans, or even the

“transitional” industries. This occupation is clearly more recent than the Mousterian of Acheulean Tradition industries of MIS 3. At least one, if not two, lithic techno-complexes (LTC) have recently been dated and documented:

- a Discoid-Denticulate Mousterian (Thiébaud, 2005; 2007) followed chronologically by
- a Levallois Mousterian with large scrapers which still requires further documentation.

These LTC, estimated to date between 45 and 39 ka BP, have been studied from a techno-typological standpoint based on the identification of one or several main products and groups of associated tools, only once their stratigraphic integrity had been verified by a taphonomic analysis (geoarchaeological, systematic inter-level refitting, etc.)

The veritable Mousterian character of these lithic techno-complexes does not detract from their modernity and in no way supports the idea that the disappearance of the Neanderthals was due to their following a “dead end” cultural trajectory. It only serves to highlight that for long periods of time during the Pleistocene, human groups were not only substantially tied to their surrounding ecosystems, but were considerably limited by paleo-historic mechanisms.

Interdisciplinary approaches (litho-stratigraphy – geoarchaeology – dating programs – paleoanthropology – paleogenetics – palaeontology – biochronology – archaeozoology – lithic techno-typology – use-wear analysis – pigments) must be employed in the coming years to refine this framework. In addition to confirming, and where necessary, clarifying this new archeo-sequence, one of our principle objectives was to contribute new and updated information to the debate surrounding why the Neanderthals disappeared in western Europe.

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**ARCHAIC HOMININS IN EAST AND SOUTHEAST ASIA:
A REVIEW ABOUT THEIR DIVERSITY AND DISTRIBUTION
BEFORE THE EMERGENCE OF MODERN HUMANS**

Anatomically modern humans (*Homo sapiens*) appeared in Eurasia sometime during the late Pleistocene, and spread over a wide area of the continent by the end of MIS 3. The development of this scenario sparked an interest in relationships between dispersing modern and local archaic human populations during the last glacial period in Eurasia. Such an issue is most intensively studied in western Eurasia under the themes of possible contact or behavioral differences between Neanderthals and early modern humans (e.g., Mellars et al., 2007; Trinkaus, 2007; Green et al., 2010; Higham et al., 2010; Zilhão et al., 2010). When we turn our eyes to eastern Eurasia, a contrasting picture emerges. In this vast terrain holding various climatic and geographic zones ranging from tropical to arctic, humid to dry, mountainous to flat, and continental to insular areas, several distinctly different groups of archaic *Homo* were present in the late Pleistocene (Bae, 2010).

The known archaic *Homo* groups that persisted until the late Pleistocene in this region include *H. erectus* from west Indonesia (Ngandong, Java), *H. floresiensis* from east Indonesia (Liang Bua, Flores), and post-*erectus* grade archaic *Homo* from China (Maba, Xujiayao, etc.). A recent surprising but welcomed addition to this array of east Eurasian archaic *Homo* is the “Denisovans” (Krause et al., 2010; Reich et al., 2010), whose affinities with these known Asian fossil groups are yet to be established. In this paper, we briefly review fossil and some archaeological evidence of these extinct hominins from the middle to late Pleistocene of East and Southeast Asia. Particular attention is paid to those localities where the authors have intensive research experiences, namely, the Indonesian and Japanese Archipelago.

One reasonable approach in a study of geographic variation in *Homo* is to consider information from other mammalian biogeography. Mainly based on this perspective, Bae (2010), in his review of the later middle Pleistocene hominin fossils from eastern Asia, divided the entire area into the northern and southern regions with the Qinling mountain range of China being set as the boundary between the two. Thus, he included southern China into his “SE Asia”, whereas

his “Northeast Asia” referred to the area north to the Qinling mountain range. However, because we currently do not know if hominin populations also followed this pattern of geographic variation, our geographic terminology at the present stage of the research follows that of general one in which Southeast Asia is restricted to the area south to China.

Continental Southeast Asia. In spite of its obvious importance in hominin evolutionary and dispersal histories in eastern Asia, unfortunately so far only a few, fragmentary fossil specimens of archaic hominins are known from this region. The reported hominin remains from the middle/late Pleistocene contexts include isolated teeth from Tham Kuyen, Ma U’Oi, and other karstic cave sites in northern Vietnam (Schwartz et al., 1995; Demeter et al., 2005), and the Thum Wiman Nakin cave, Thailand (Tougaard et al., 1998). The teeth from Thum Wiman Nakin and Ma U’Oi have been compared with various fossil and extant *Homo* taxa. Both archaic and derived/modern features are noted by the reporters, but the morphological information from these fragmentary specimens was not enough to infer hominin evolutionary systematics in the region (Tougaard et al., 1998; Demeter et al., 2005).

Sundaland (west Indonesia). Relatively abundant fossil cranial specimens of *Homo erectus* are known from the Indonesian island of Java. During the glacial period when the sea level lowered, this island was a part of the continental land mass called Sundaland. Terrestrial fauna in this area are similar to but impoverished compared to those in the continental Asia, suggesting some degree of filter effect or access restriction between the two regions (Van den Bergh et al., 2001).

Javanese *Homo erectus* fossils from the late Pleistocene contexts are known from the terrace deposits at Ngandong. The Ngandong *Homo erectus* assemblage includes a number of well-preserved crania which is informative to understand their affinities and evolutionary relationships with their contemporaries from the other regions. The Ngandong *Homo erectus* crania can be easily distinguished from those of the early Middle Pleistocene Zhoukoudian *Homo erectus* from northern China, and are also distinct from later middle/late Pleistocene archaic *Homo* from the Asian mainland (Dali, Jinnuishan, Maba, etc.). They share some commonalities with the early Pleistocene Javanese *Homo erectus* from Sangiran and Trinil. The recently discovered Sambungmacan 4 calvaria highlighted the presence of an intermediate form connecting the two chronological assemblages from Java (Baba et al., 2003), and our recent intensive craniometric study supports the generally held view of continuous, gradual morphological changes of Javanese *Homo erectus* from the early to late Pleistocene in a geographically isolated environment (Kaifu et al., 2008).

However, presently we have little information regarding the archaic *Homo* populations on the continental Southeast Asia, Malay Peninsula, and other Indonesian islands except for Flores (see below). Thus we do not know the exact distribution of Javanese *Homo erectus*-like population during the Pleistocene. There is a claim that Ngandong *Homo erectus* (and a part of the Sambungmacan

Homo erectus as well) persisted for some time after the arrival of *Homo sapiens* in this area, but the reported their young ages (50–30 ka: Swisher et al., 1997) are not unanimously accepted.

Wallacea (East Indonesia). Fossil bones of *Homo floresiensis* reported in 2004 from the Liang Bua cave on Flores, located to the east of the Wallace Line (the southeasternmost boundary of the continental Asian ecozone), were astonishing discoveries that opened our eyes to recognize that archaic hominins had successfully crossed the sea to reach an isolated island (Brown et al., 2004; Morwood et al., 2005; Fig. 1). Currently, the origin of this new, short-statured and small-brained species is unclear, with Javanese *Homo erectus* and East African *Homo habilis* often nominated as potential ancestral groups (Morwood and Jungers, 2009). Future discovery of new hominin fossils from the Soa Basin, western central Flores, is expected to shed new light on this issue. Archaeological evidence from the Soa Basin suggests that an archaic hominin popula-



National Museum of Nature and Science, Tokyo

Fig. 1. Life-sized reconstruction of LB1, the type specimens of *Homo floresiensis*, made at the National Museum of Nature and Science, Tokyo, in 2009.

tion was present on the island at least by one million years ago. Forty-seven stone artifacts recovered from the deposits immediately below the ignimbrite layer that yielded an $^{40}\text{Ar}/^{39}\text{Ar}$ ages of 1.02 ± 0.02 Ma (Brumm et al., 2010a). A total of 556 stone artifacts are reported from the site of Mata Menge dated to 0.80–0.88 Ma. These artifacts closely resemble those from Liang Bua in terms of stone reduction sequences, although some minor differences are noted between the two assemblages (Brumm et al., 2010b).

A group of *Homo floresiensis* had used the cavern of Liang Bua as late as ~17 ka, in an environment where highly endemic species of Komodo dragon, dwarf Stegodon, giant marabou stork, and giant rat represent larger-bodied fauna. Because their highly unique physical characteristics are considered to have been the results of insular dwarfism at least partially, and because the island Java had been occupied by *Homo erectus* during much of the Pleistocene, the distribution of *floresiensis*-like populations may have been restricted to Flores or its neighboring Wallacean islands, if any. Since modern humans had already settled in Australia by ~45 ka, *Homo floresiensis* and early modern humans coexisted in Wallacea for substantial period of time. It is tempting to speculate contact between them, but unfortunately such record has so far not been found in the deposits of the Liang Bua cave.

In this relation, the reported technological similarities between stone artifacts manufactured by *Homo floresiensis* and early Holocene *Homo sapiens* at the Liang Bua cave are interesting (Moore et al., 2009). To date, all the human skeletal remains recovered from the Pleistocene deposits of Liang Bua predating ~17 ka are exclusively those of *Homo floresiensis*, whereas the Holocene stratigraphic unit postdating 11 ka yields only *Homo sapiens* skeletal remains. Thus the artifacts from the upper and lower levels can be allocated to those of *Homo sapiens* and *Homo floresiensis*, respectively. Curiously, the early Holocene stone technology by *Homo sapiens* was largely similar to that of *Homo floresiensis*, with drastic changes observed only in the mid-Holocene associated with Neolithic and Palaeo-Metallic burials. Thus, the stone reduction sequence of Pleistocene *Homo floresiensis* persisted through the Holocene occupation by modern *Homo sapiens* at Liang Bua (Moore et al., 2009). Such overall stasis in lithic technology across the Pleistocene/Holocene boundary is observed in a wide area of Southeast Asia and Sahul. The background of these technological continuities may be an interesting question to infer inter-relationships between local archaic hominins and *Homo sapiens* at the time of their possible contact.

Continental Northeast Asia (China, Korea, Mongolia). China is the only East Asian country which has yielded substantial fossil specimens of Pleistocene archaic *Homo*. Among these, a partial cranium from Maba (southern China) and skull fragments from Xujiayao (northern China) may be dated to earliest late Pleistocene or latest middle Pleistocene (Wu and Poirier, 1995; Brown, 2001). The informative cranial collection further expands if we include later middle Pleistocene specimens from Dali, Jinniushan, etc. Researchers agree that all these

fossils are derived from and should not be included in *Homo erectus* represented by the remains from Zhoukoudian Lower Cave and a series of Indonesian sites. Such comparatively advanced forms appeared in the Chinese fossil record by later middle Pleistocene. However, morphological affinities and taxonomy of these post-*erectus* grade, archaic Chinese *Homo* are highly controversial as reviewed by Bae (2010).

Recently a partial skeleton and fragmentary mandible with modern morphology were excavated from the late Pleistocene sites of Tianyuan (northern China) and Zhiren (southern China) Caves, respectively. It is suggested that these specimens exhibit morphological sign of admixture with or gene flow from archaic forms of *Homo* (Shang and Trinkaus, 2010; Liu et al., 2010).

A few existing hominin fossils from karstic cave sites in North Korea are suggested to be those of archaic *Homo* (Bae, 2010). Such specimens include the cranial fragments belonging to a juvenile individual from Yokpo Daehyundong but presently little published information is available to evaluate their morphological affinities. The presence of premodern hominins is evident from the lithic assemblages including handaxes/Large cutting tools excavated from Chongokni and other sites along the Imjin/Hantan River, northern South Korea. Currently, the dates of these assemblages are controversial (middle or late Pleistocene) and the absence of hominin fossils makes it difficult to infer their makers.

A cranial fragment recovered from Salkhit, eastern Mongolia in 2006 (Tseveendorj, 2006), was reported to show primitive morphology which recalls that of Neanderthals (Coppens et al., 2008; Bae, 2010). However, some researchers see more modern morphology in it and question the above assessment (Braga, in Crooson, 2010). The specimen actually resembles the Zhoukoudian Upper Cave 101 cranium in a posteriorly receding forehead with a weak midline keel, a wide anterior frontal squama, and the development of the superciliary arches (Kaifu and Fujita, in press).

Insular East Asia (Japan). Mammalian fauna in the middle and late Pleistocene of Japan exhibits some commonalities with those on the Asian mainland (Iwase et al., in press). Thus, it is theoretically possible that archaic hominins, such as those represented by Zhoukoudian Lower Cave or Jinniushan in northern China, were also distributed in the archipelago. However, in spite of exceptionally dense archaeological survey that has so far recorded approximately 10,000 Upper Palaeolithic sites dated between ~40–15 ka, no unequivocal Lower or Middle Palaeolithic sites are known from this area. Although some researchers believe that there are a few archaeological sites predating 40 ka that may be ascribed to premodern humans (e.g., Sato, 2005; Matsufuji, 2010), this view is not widely accepted. One of the current questions attracting attention of archaeologists is if the oldest lithic assemblages dated ~40 ka, which includes some non-standardized components of lithic type, is the product of premodern humans, or the dramatic increases in the number of archaeological sites on the archipelago collectively signals, irrespective of their lithic types, the arrival of modern humans (Sato, 2006; Tsutsumi, in press).

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**MIDDLE/UPPER PALEOLITHIC INTERFACE
AT VINDIJA CAVE (CROATIA)
IN THE CONTEXT OF CENTRAL EUROPE AND THE ADRIATIC**

The Paleolithic sites of Croatia are generally situated in two main geographic regions, continental and Adriatic. The most famous sites (Krapina, Vindija, Velika Pećina) are situated in continental area of northwestern Croatia (Hrvatsko Zagorje), which differs geographically and ecologically from the Mediterranean sites situated farther south on the Adriatic coast and its hinterland (Fig. 1). Krapina yielded Neandertal remains associated with a Mousterian industry. Unlike Krapina, Vindija and Velika Pećina also contain Upper Paleolithic stratigraphic units and these sites have an important role in the debate on the patterns of Neandertal/early modern human interactions and the Middle/Upper Paleolithic transition in central Europe. Evidence from Vindija were recently discussed in several papers from archaeological, paleoanthropological, geological and genetic perspectives. Different interpretations have been given for determination of lithic industry in level G1, associated with Neandertal remains. In this paper alternative interpretations of the Middle/Upper Paleolithic transition in Vindija Cave will be presented in the context of central Europe and eastern Adriatic region.

The Vindija Cave is situated 2 km west of the village of Donja Voća, and 20 km west of Varaždin. The cave is more than 50 m deep, up to 28 m wide and more than 10 m high (Fig. 2).

S. Vuković (1950), who first visited the site in 1928, excavated the cave for more than thirty years with some interruptions. M. Malez started systematic excavations at Vindija in 1974, and fieldwork continued every season until 1986. During this period most of the lithic and faunal material as well as all of the fossil human remains known from the site were recovered. The stratigraphic profile, which is about 9 m high, comprises about twenty strata which, according to Malez and Rukavina, (1979), covered the period from the onset of the

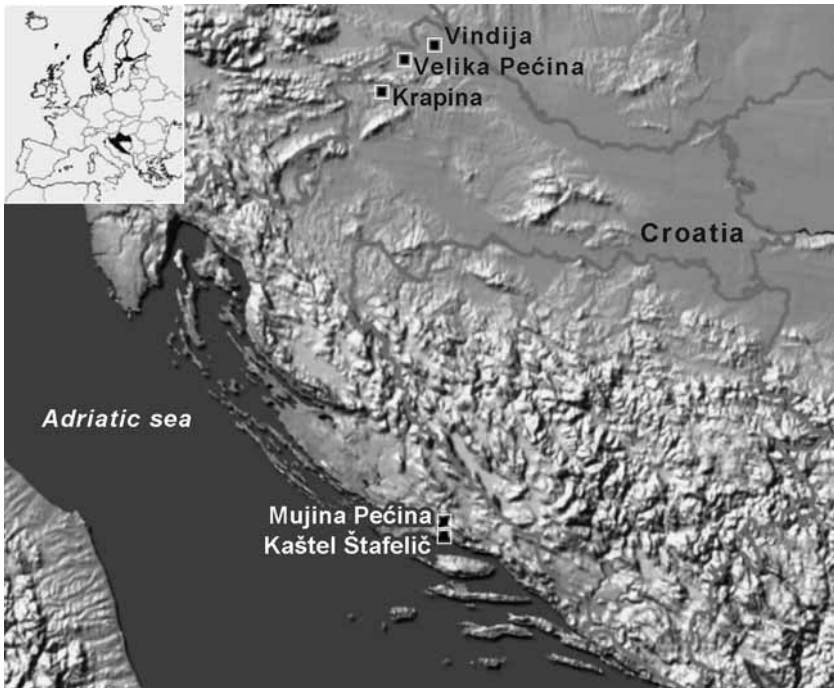


Fig. 1. Location of important Mousterian sites of Croatia.



Fig. 2. View from Vindija cave. (Photo: I. Karavanić).

Riss glaciation (oxygen isotope stage 6 or earlier) through the Holocene. The G complex, comprising five stratigraphic levels, numbered G1 (top) through G5, produced the Neanderthal skeletal remains from the site. Level G3 contained approximately 100 fragmentary Neanderthal skeletal remains associated with a late Mousterian industry. These remains were dated to over 42 ka BP by radiocarbon AMS (Krings et al., 2000) and four years later to about 38 ka BP by the same method (Serre et al., 2004). There is also another AMS radiocarbon date on Neanderthal bone from unit G (level unknown) that yielded results of about 44 ka BP (Green et al., 2010).

A series of human skeletal remains derive from level G1, and diagnostic morphology from these specimens identifies the remains as Neanderthals (Smith and Ahern, 1994; Smith et al., 1999). Several different radiocarbon dates on bone samples from this level have been obtained (see Ahern et al., 2004, Table 1). The most important are direct dates from Neanderthal skeletal remains. These bones were first dated to 28 and 29 ka BP, respectively (Smith et al., 1999). The same samples were redated, using a more accurate technique, to about 33 ka BP (Higham et al., 2006), which corresponds well with one of the previous dates obtained on animal bone (Karavanić, 1995).

Neanderthal skeletal remains from level G3 show distinct changes in facial morphology compared to earlier Neanderthals; and these differences characterize the entire G3 Vindija sample, not just selected specimens (see Smith, 1984; Wolpoff, 1999; Ahern et al., 2004; Cartmill and Smith, 2009). These changes include: shape of the supraorbital torus, reduced size of maxillary alveolar height and nasal breadth, more vertical mandibular symphysis, etc. In all of these, the Vindija G3 specimens are intermediate between the geologically earlier Krapina Neanderthals and early modern Europeans, although still closer overall to the former sample (Smith, 1994; Karavanić and Smith, 1998; Cartmill and Smith, 2009). The small sample of Neanderthals from level G1 show the same basic morphological characteristics as those from comparable elements in the G3 sample (Smith and Ahern, 1994). The Vindija morphological pattern played an important role in the development of the Assimilation Model of modern human origins (Smith et al., 1989). This model argued for small, but not insignificant, contributions of Neanderthals to the immigrant early modern human populations of Central Europe. Most recently, the Vindija morphological pattern has been seen as reflecting small amounts of modern human biological influence in a late Neanderthal population (Smith et al., 2005; Cartmill and Smith, 2009; Janković et al., 2011a). The Assimilation Model is the equivalent of the Mostly Out of Africa genetically based model, as well as the recently dubbed “Leaky Replacement” Model (see Gibbons, 2011).

Most recently, the biological focus on Vindija has shifted from morphology to paleogenetics, as the approximately 3 billion base pair Neanderthal genome sequenced in 2010 is derived from three small, non-diagnostic fragments of long bones from the site (Green et al., 2010). Comparative analysis of this genome with those of recent humans demonstrated a slightly closer relationship between

Neanderthals and modern Eurasians than between Neanderthals and Africans. Green and colleagues determined that the most parsimonious explanation for this was a Neanderthal contribution of 1–4 % to modern populations after their emergence from Africa. This, along with the recent interpretation of the Denisova genome (Reich et al., 2010; Gibbons, 2011), supports the interpretation that archaic Eurasian populations consistently contributed small amounts to expanding modern populations, which had their ultimate origins in Africa. Geneticists may refer to this as the “Leaky Replacement Model” (Gibbons, 2011), but it is fundamentally the Assimilation Model.

An additional observation from this study bears mention. While there was evidence of Neanderthal genetic contribution to early modern population, there was no genetic indication of early modern contribution to late Neanderthals. Green and colleagues note that gene flow typically is reflected in the gene pool of colonizing populations (early modern humans) rather than in resident populations, in this case the Neanderthal. However, they indicate that other forms of gene flow, for example from early moderns to Neanderthals, are not excluded by their study (Green et al., 2010: 721). The fact that the Vindija Neanderthals consistently exhibit morphology that approaches early modern humans more than other Neanderthal samples do may well be an indication of early modern influence in a late Neanderthal population.

Lately, it has been claimed by Zilhão (2009) that the most recently published dates of 33–32 ky BP (Higham et al., 2006) for the Vindija G1 layer Neanderthals are likely minimum dates and the actual age of these remains must be older in order for the assimilation model to apply. That is simply not the case, particularly if Vindija is seen as an indication of gene flow into Neanderthal populations. In any event, if the Vindija dates are minimum ages the same also applies for the earliest anatomically modern humans in Europe.

Much of the debate concerning the possibility of Neanderthal-early modern interaction is based on the archaeological industry found at Vindija. It is likely that some of the lithic material (e.g. Vi 1061, Vi 3383) indeed represents pseudo-tools, as argued recently by Zilhão (2009). However, the argument that the industry is Szeletian is certainly not a novel idea. M. Malez (1979) argued this more than 30 years ago, although it is unclear whether he was referring to the G1 unit specifically, or to some other G unit layer. Likewise, J. Svoboda (1999) noted some similarities between the G1 layer of Vindija and Szeletian industry. In contrast, J. Kozłowski (1996; personal communication) recognizes more similarities with the Levallois Mousterian complexes of the Central European and the Balkans. Both assessments are not without problems. The G1 layer does not contain any evidence of Levallois technology although the assemblage can be defined as late Mousterian. This is also the case for the G3 assemblage. The evidence for presence of the Szeletian industry in G1 is based solely on one tool, a nicely shaped bifacial point. There is no evidence of *in situ* production of this tool; and it was made on non-local raw material, red radiolarite, that was probable imported from Hungary (Montet-White, 1996; Biró and Markó, 2007).

Therefore, this uncharacteristic piece for the Vindija assemblage (bifacial pieces from the G3 layer are typologically different and made on local raw material) is not suitable for a cultural determination, especially in case of Szeletian, a culture that has yet not been proven to exist at a single Croatian site.

The presence of pseudo-tools and results of refitting (Bruner, 2009; Zilhão, 2009) confirms that there was mixing present in different layers, and that the presence of certain Upper Paleolithic lithic tool types made on high quality silex from the G1 and G3 layers might be explained as a result of this mixing. Analysis by K. Bruner (2009) suggests vertical mixing as a result of depositional processes included a total of 2,4 % of identified lithic tools. About 8 % of the artifacts from G1 layer could be refitted. However, some of the material from layers below and above G1 could be refitted into a single artifact, which suggested to Bruner (2009: 77) that G1 is one of the most disturbed layers at the site. It needs to be noted, however, that we have long recognized that both bioturbation and cryoturbation occurred at Vindija and likely resulted in mixing of elements from different layers in some parts of the cave (Smith, 1984; Karavanić and Smith, 1998). However they are not seen uniformly throughout the site, and the area where many of the relevant finds are derived do not show evidence of disturbance. In light of the documented disturbance of layers, the Olchevian hypothesis as the transitional industry of the G1 layer (Karavanić, 2000b; 2007) is not likely. It is more probable that Middle and Upper Paleolithic typological characteristics of the G1 stone tool assemblage resulted from mixing of the material between levels than from a specific transitional industry. However, the problem of the association of Neanderthal remains and the Upper Paleolithic bone points is still open. Results of taphonomic analysis show that the preservation of bone tools from G1 is similar to that of the bone remains of large mammals and humans from this same level, suggesting they all derive from the same context (Karavanić and Patou-Mathis, 2009). These bone points and Neanderthal remains do not show trampling traces (except base fragment of so called Mladeč point – Vi 2510). It should be noted that distinctive reddish sediment typical of the G1 layer was imbedded in the so called Mladeč type bone point Vi 3439 and in Neanderthal skeletal remains from the same level.

Further, considering the percentage of the lithic material for which refitting was possible that proved the mixing of the layers was relatively low, we believe that the change in the raw material seen from G3 to G1 (much more silex and much less quartz in G1 than in G3) is much more significant as a reflection of behavioral change. As shown by Ahern and colleagues (2004, Table 9), Level G1 has an intermediate pattern of raw material use between Mousterian level G3 and Upper Paleolithic levels.

In contrast to Zilhão (2009: Table 2) who sees the G1 layer material as mix of Szeletian, Aurignacian I and II, and material from Fd/d layer as Aurignacian II or III/IV, we offer two possible explanations. The first possibility is that the lithic industry of G1 represents Mousterian. The bifacial stone point is seen as an import, a result of the contact of various Neanderthal groups from northwest-

ern Croatia and Hungary. The Upper Paleolithic elements, especially the bone points, and possibly some lithic types, are the result of contact (exchange or acculturation) between Neanderthals and early anatomically modern groups.

The second possibility is that although the lithic industry is Mousterian and the aforementioned stone bifacial point is imported, the presence of the bone points and Upper Paleolithic lithic tools in the G1 layer is a result of mixing with the upper layers of the site. If this is the case, then the industry present in stratigraphic layers Fd/d and Fd is Aurignacian (as suggested by Karavanić in 1995 and Kozłowski in 1996). However, due to the variability of the Aurignacian industry (see Churchill and Smith, 2000; Kozłowski and Otte, 2000; Teyssandier et al., 2009), the low percentage of typical Aurignacian stone tools in Vindija, and the fact that lithic industry is typologically different from the Aurignacian known at French sites, we are not comfortable using terms Aurignacian I, II, III/IV for the Vindija assemblage (see Miracle, 1998).

However, at the sites in Croatia and Slovenia, early Upper Paleolithic bone points are often found with very little lithic material, with the exception of the Potočka Zijalka site. Therefore, another possibility is that the lack of more typical Aurignacian stone tools at Vindija and other sites is the result of some type of functional specialization connected to specific hunting activity (cf. Hahn, 1977).

Although direct dating of the bone points from Vindija and Velika Pećina failed (Smith et al., 1999), an age of 34 ky BP was determined for the “i” layer of Velika Pećina (Malez and Vogel, 1970). Thus the same age can be assumed for the bone points (most likely with split bases) from the same layer of the same site (Ibid.). A bone point (most likely with a split base) from Divje Babe I (Slovenia) comes from a layer that has been dated to about 35 ky BP (Nelson, 1997), while the Mladeč type points from Potočka Zijalka are dated to between 31 and 29 ky BP (Hofreiter and Pacher, 2004). Likewise, the Mladeč type points from the Mamutova cave in Poland near Krakow date to between 33 and 32 ky BP (Wojtal, 2007), early Upper Paleolithic points from German sites have been dated to between 32 and ca. 27 ky BP (Conard and Bolus, 2003, 2008; Bolus and Conard, 2006), and the (proto) Aurignacian split-base points from Trou de la Mère Clochette in northeastern France have been dated to between 33 and 35 ky BP (Szmídt et al., 2010). Although some of these sites are geographically quite distant from Vindija, it should also be noted that some of their dates are older than the Vindija Neanderthals, while other are younger. Although we do not have direct dates on the points, dates from comparable archaeological layers suggest that the bone points from Velika Pećina and Divje Babe I are older than, or contemporaneous with the Vindija Neanderthals. If we adhere to the generally accepted view that such points are associated with modern humans, this also raises the question of possible interactions between these groups.

From the eastern Adriatic, only a single bone point has been found. This is from layer H at the site of Šandalja II in Istria. It is relatively small compared to the points from Central Europe and has a split-base and rounded cross section.

It is similar to points from the Franco-Cantabrian Magdalenian (L.G. Straus, personal communication); and based on the recent dates for the layer F at Šandalja II, it should be older than 32 ka BP (M. Richards, personal communication). Except for the Šandalja II site, only one other Aurignacian and one Mousterian site are known from the Istrian region of Croatia. The Dalmatian area has several known Mousterian sites, of which only the site of Mujina Pećina near Kaštela City has been systematically excavated. The sites dated to the early Upper Paleolithic are rare in this area, as well as in the whole eastern Adriatic (Karavanić, 2009; Mihailović, 2009). Further, no industry from a single site of the eastern Adriatic region shows progressive transitional nature, and there is no evidence of *in situ* transition at any site in this region. For example, there is no single Ulluzian site, although this industry is present at the sites in Italy and Greece (Koumouzelis et al., 2001; Peresani, 2008).

It is not clear why no site in the eastern Adriatic region thus far documents the Middle/Upper Paleolithic transition, and why early Upper Paleolithic sites are very rare. Possible reasons for this are that: not many sites have been explored, flooding or abrasion as a result of the uplift in the sea level, low population density of the area during the Middle/Upper Paleolithic transition and during the early Upper Paleolithic.

It is of crucial importance to continue research that will include mapping and test excavations of both cave and open-air sites in both regions of Croatia. It is also likely that vast areas occupied by Paleolithic hunter and gatherers have been erased from the map by the uplifts of sea level at the end of Pleistocene. Despite such destruction, some, such as the site of Kaštel Štafilić, are still preserved under water. Efforts invested in the investigation of underwater sites would add to our knowledge on the mobility patterns of Mousterian people and may help in solving the riddle of the transitional period in the eastern Adriatic region. Regional differences between the northwestern and Adriatic parts of Croatia must be understood both in terms of geographic factors, as well as in the complexity of human processes during the Middle-to-Upper Paleolithic transition.

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THE MIDDLE-UPPER PALAEOLITHIC TRANSITION IN THE CANTABRIAN REGION (a Mosaic Model)

Introduction

It has become almost a cliché to begin any work on Middle to Upper Palaeolithic Transition in Europe with a reference to the fact that it has been one of the main topics of prehistoric studies. This interest arises because it concerns one of the key points in human evolution: the appearance of Anatomically Modern Humans (AMH).

A few decades ago it was assumed with little discussion that the Middle Palaeolithic was the work of the Neanderthals, and the Upper Palaeolithic that of the AMH. It was also assumed that the AMH possessed better cognitive capacities than did the Neanderthals (Mellars, 2006).

However, Transitional complexes, like the Châtelperronian, which was classified as Upper Palaeolithic, are clearly associated with Neanderthals at Saint Césaire (Leveque and Vandermeersch, 1980). A blade technology was in use in Europe from 150 kya (Delagnes et al., 2007) and bladelets appear from the end of the Mousterian (Bernaldo de Quirós et al., 2010). Other aspects, like any absence of structuring of the habitat or of symbolic behaviour among Neanderthals, can also be refuted (Jaubert and Delagnes, 2007).

Moreover, the nature of the Aurignacian itself has been brought into question. Its origins are not clearly known, since the Near Eastern Aurignacian is intrusive in that region and more recent than the European one (Belfer-Cohen and Goring-Morris, 2007). The “qualities” identified as “novel” in it, such as the stone industry, bladelets or ornamental and symbolic pieces, while probably due

to AMHs, have been identified in much older contexts in the Middle Stone Age (MSA) in Africa (McBrearty, 2007).

In Europe, the arrival of the AMH is currently associated with the Aurignacian and the replacement of the Neanderthal populations because of higher levels of technological development and better exploitation of territory. Neanderthal groups, in a last effort, were considered to be able to mimic certain cultural features of the Aurignacian, giving rise to “transitional technocomplexes” (Mellars, 2006). However, this hypothesis, too, should be reviewed. Some researchers, while still accepting a break, believe that AMH arrived in several waves (Davis, 2007) and in some cases did not even make Aurignacian items (Svoboda, 2007). Other researchers consider that the Upper Palaeolithic, not the Aurignacian, has some of its roots in the native populations of Europe prior to the arrival of the Aurignacian, as would be demonstrated by the Châtelperronian or the Transitional Aurignacian (Cabrera and Bernaldo de Quirós, 1990; d’Errico et al., 1998; Cabrera et al., 2006).

In this new situation of re-adjustment, if not of complete change, in the scientific paradigm relating to the Middle to Upper Palaeolithic Transition, research efforts are being directed to know when and why Modern Behaviour appeared. This expression defines the moment when human groups begin to make a “special”, “symbolic” material culture different from those of previous populations. Hence, only the name of the problem has changed. The equation AMH and Aurignacian has been replaced by that of AMH and Modern Behaviour.

There is difficulty to find an epistemological definition for “Modern Behaviour”. Basically, the term refers to the greater development of cognitive abilities in AMH in comparison to that of other human groups, especially Neanderthals (Soressi, 2005). Thus, the debate is limited to whether such Modern Behaviour is innate to AMH or develops at some moment in evolution (Henshilwood and Marean, 2003; Klein, 2003).

However, with regard to Neanderthal populations, some previous questions must be considered. Firstly, it may seem inappropriate to compare the cognitive abilities of two populations when one of them is extinct (Langley et al., 2008). Another problem of relevance is how to measure such “Modern Behaviour”. For this purpose, a series of “trait lists” have been drawn up (Mellars, 2006). Nevertheless, many of these traits would prevent certain contemporary groups of hunter-gatherers from being considered as having Modern Behaviour (McBrearty, 2007). Even if these trait lists are taken as indicative of Modern Behaviour, Neanderthals would have to be seen as developing it not only from the transitional technocomplexes, but also from the Mousterian (Langley et al., 2008; d’Errico et al., 1998; Cabrera et al., 2006).

The Cantabrian region is one of the parts of Europe where a complex transition between the Middle and Upper Palaeolithic is found, and so fits neatly into this debate. Hence, the objectives of this paper are to record the archaeological and anthropological complexity of this region and put forward an explanation for this process.

The Cantabrian Region between 50 kya and 30 kya

Mousterian

The end of the Mousterian in the Cantabrian Region presents no characteristic that splits it off from previous stages. It is normal to take as belonging to the end of the Mousterian those levels dating of ≤ 50 kya, while in this region it ends at dates rather under 40 kya, as evidenced at Esquilieu (34.3–39.0 kya) or El Sidrón (40.8–38.2 kya, Baena et al., 2006; Lalueza et al., 2005). Mousterian deposits are relatively abundant in the region. Sites like Arrillor, Lezetxiki, Axlor, El Castillo, Cueva Morín, Covalejos or Esquilieu were studied from a technical and typological perspective (Fig. 1).

In general, there is wide variation in the *chaîne opératoire* used (Fig. 2): Quina, Levallois and Discoid methods at Esquilieu; flakes and points Levallois and Quina methods at Axlor, Discoidal methods at El Castillo, Cueva Morín and La Flecha. Cleavers are common at El Castillo and Cueva Morín (Baena et al., 2005; González et al., 2006; Bernaldo de Quirós et al., 2010).

Among the *chaînes opératoires* identified, one of the most interesting involves the bladelets production in El Castillo, Cueva Morín, Covalejos, Esquilieu and Lezetxiki (Cabrera et al., 2004, Bernaldo de Quirós et al., 2010; Martín et al., 2006). These bladelets are obtained by using various methods such as Levallois, prismatic or opportunistic cores and some of them show a semi-abrupt retouch.

As for “symbolic” behaviour during the Late Mousterian, mention must be made of the Lezetxiki, in which two sea shells appeared in Level III and a further two in Level IVc, both Neanderthal occupation layers. These shells may have been used as pendants (Arrizabalaga, 2006). Furthermore, in Level 21 at the El Castillo a fragment of core with a line formed by four chipped dots and a fifth opposite was found.

Transitional Aurignacian

This technocomplex has been identified exclusively in Levels 18b and 18c of the El Castillo and dates back between 40 kya and 38.5 kya (Bernaldo de Quirós and Maíllo-Fernández, 2010).

Technologically, lithic production is dominated by Discoid methods (Fig. 3). In a more limited way, a bladelet *chaîne opératoire* has also been identified, very similar to the one already described for the Late Mousterian. However, other schemes of the carinated endscraper type and carinated burin are present.

Both levels have very similar typological composition. The set is dominated by substrate blanks, although pieces of Upper Palaeolithic type (sidescrapers and burins).

The blanks of the Transitional Aurignacian are predominantly of a technology that may be termed “Mousterian”, as has already been commented. What is really significant about this stone industry is that, while blanks of Mousterian type are used, the tools made from them are of Upper Palaeolithic tradition.

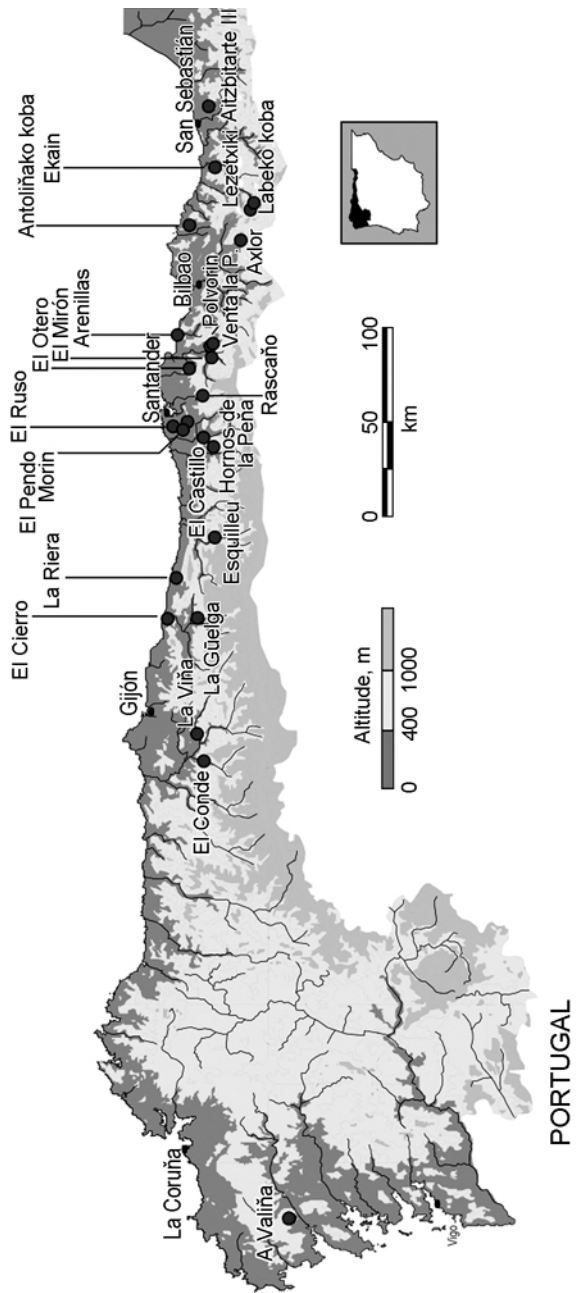


Fig. 1. Map of Cantabrian Region with sites cited in the text.

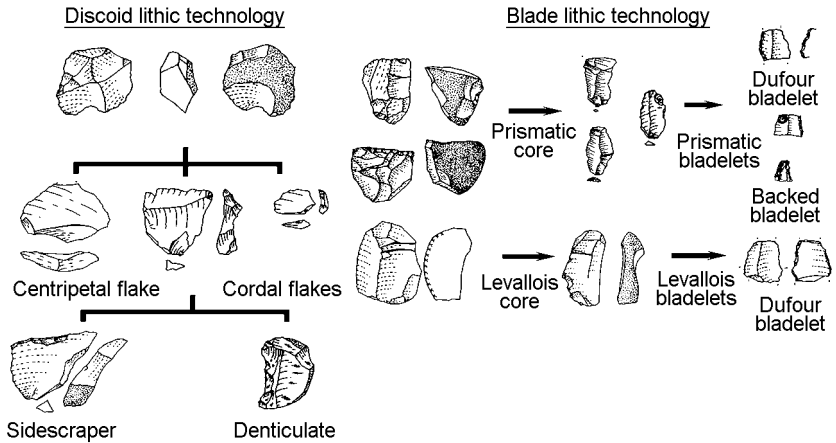


Fig. 2. Middle-Upper Palaeolithic lithic technology. Mousterian.

Bone industry is very sparse, but significant. In Level 18c the findings comprised two distal point fragments, a fish-hook, and a handle. There were also pieces with incisions and engravings (Fig. 3).

In both levels also appeared elements of a symbolic nature. In Level 18c a fragment of a chisel with groups of incisions, an ungulate diaphysis with incisions and a fragment of a flat bone with an engraving of the head of a herbivore were found. In addition, in Level 18c a fragment of a deer's hyoid bone on which was engraved the rear of a herbivore, as well as a flat piece of sandstone with a series of lines appeared (Fig. 3; Cabrera-Valdés et al., 2006).

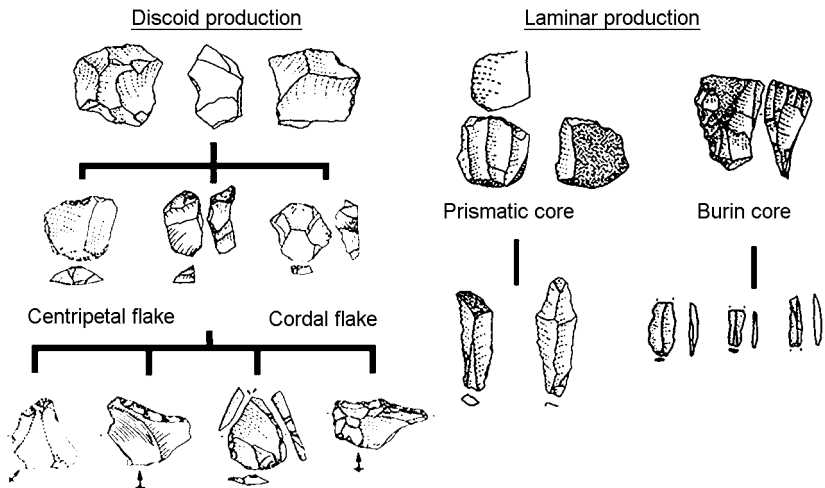


Fig. 3. Middle-Upper Palaeolithic lithic technology. Transitional Aurignacian.

Châtelperronian

This technocomplex is sparsely present in the Cantabrian Region. It has been identified in some few sites: Cueva Morín, Labeko Koba, Ekain and La Güelga (Maillo-Fernández, 2007). Moreover, except for Cueva Morín, archaeological remains are very scarce (see Fig. 1). This technocomplex has some dates between 38.6/34 to 30 kya.

Technologically, lithic production is dominated by discoid methods and unipolar and bipolar prismatic ones. The bipolar blades are used to make Chatelperronian points (Fig. 4). No specific production of bladelets has been noted in the Cantabrian Châtelperronian.

Typologically, Châtelperronian points and backed pieces are found in very small proportions, and some authors have classified the Cantabrian Châtelperronian as atypical (Carrión, 2002). We disagree of such interpretation considering it a regional characteristic of this technological complex.

Bone industry is very sparse, only Level IX at Labeko Koba offers a range of pieces. This involves a distal fragment from a spear with a slightly flattened or oval section and a few tools falling into the category termed slightly bone industry (Mujika, 2000).

Archaic Aurignacian

This is the best known technocomplex of the Middle to Upper Palaeolithic Transition in Cantabrian region (see Fig. 1). Technologically, it can be based on the studies performed at El Castillo, Cueva Morín, Covalejos, Labeko Koba and La Viña (Cabrera et al., 2004). Its time-span runs from 36.5 kya to 30 kya.

Technologically, lithic production is dominated by unipolar prismatic method (Fig. 5). One of its essential characteristics is that there is a continuum from blade to bladelet production. It can be stated that an output of bladelets is the principal aim of this laminar *débitage*, which is different to Chatelperronian one.

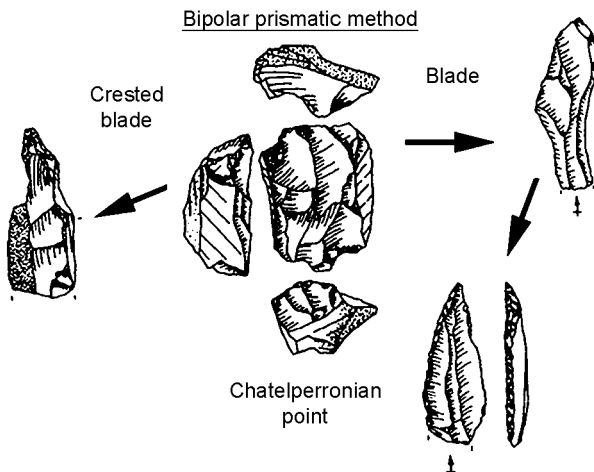
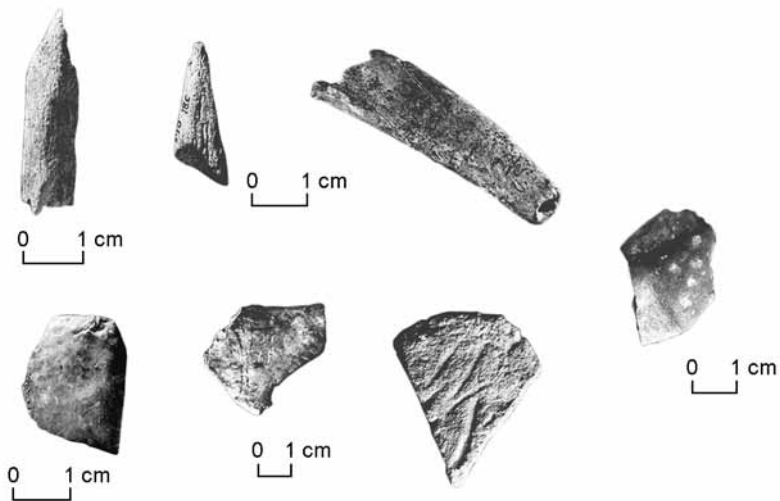


Fig. 4. Middle-Upper Palaeolithic lithic technology. Chatelperronian.



Blade/bladelet production

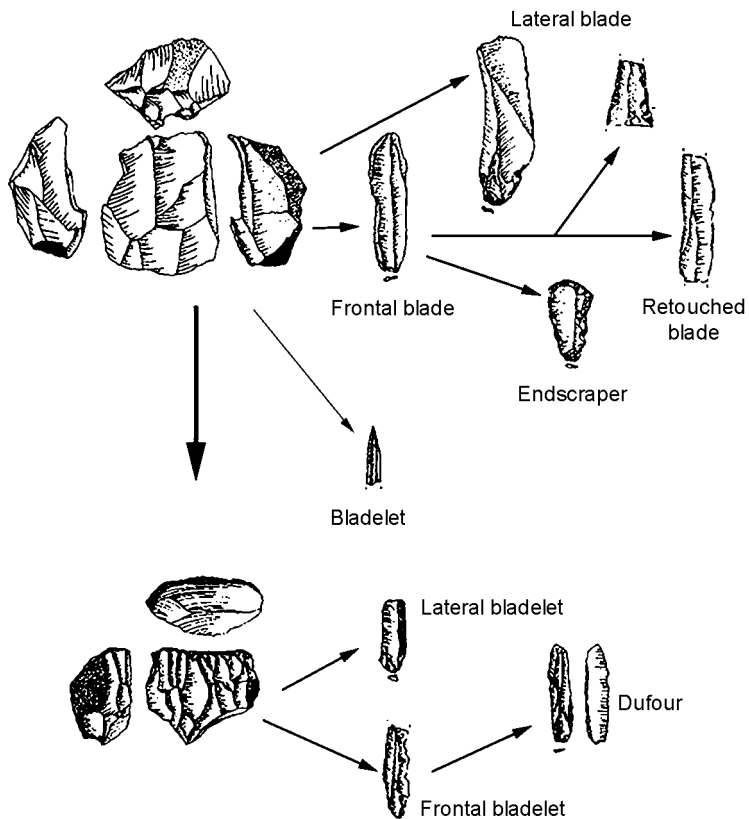


Fig. 5. Middle-Upper Palaeolithic lithic technology. Archaic Aurignacian.

The flakes *débitage*, using Discoidal methods continues to have a prominent place (41.6 % of the retouched blanks from Morín 8 are flakes).

Among retouched tools, the most characteristic is the Dufour bladelet, Dufour subtype. Endscrapers are more numerous than burins. Aurignacian blades are present in a small way. Finally, mention must be made of the strong presence of substrate pieces.

Bone industry is very sparse. There were some spear fragments in Cueva Morín, El Castillo and Labeko Koba (González Echegaray, 1971; Tejero et al., 2006; Mujika, 2000).

Early Aurignacian

This is not very well documented technocomplex in the Cantabrian region (see Fig. 1). The most significant deposits are La Viña, Polvorín, Covalejos, Cueva Morín and Labeko Koba. There are few datings for this technocomplex, falling into the bracket 30 kya to 28 kya (Cabrera et al., 2004).

The first point to be raised, in relation to the previous technocomplex, is the dissociation between the blade and bladelets productions (Fig. 6). The blades are obtained from unipolar prismatic cores and the bladelets from carinated cores.

In the Cantabrian Region the two *facies* detected in France (Castanet and Ferrassie) are not found. Hence, in this region the label to be given must be generic Early Aurignacian. The Early Aurignacian is characterized by an increase in thick carinated endscrapers and a low percentage of Dufour bladelets. Aurignacian blades become more numerous than the Archaic Aurignacian and the presence of burins is slight.

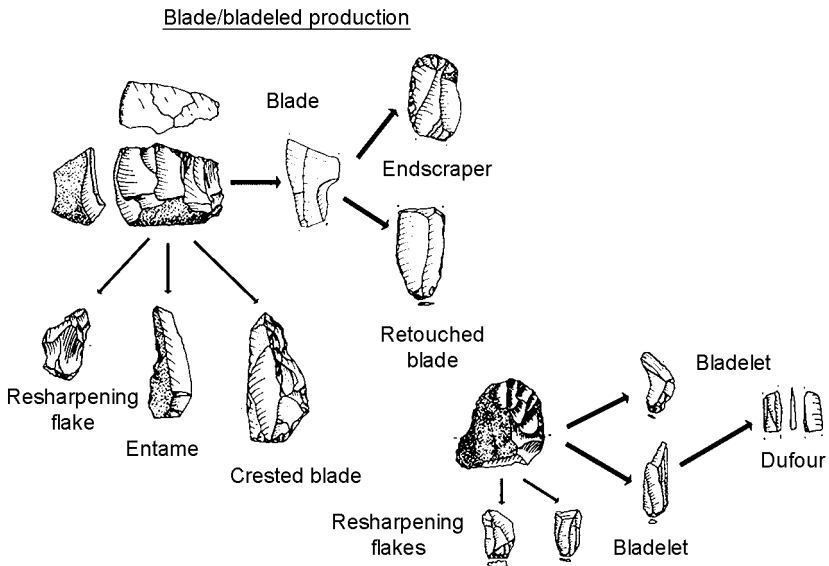


Fig. 6. Middle-Upper Palaeolithic lithic technology. Early Aurignacian.

Many of the collections from the Early Aurignacian in the Cantabrian Region lack any bone industry: some splint base points in Polvorín I, Covalejos and some spears fragments at Labeko Koba (Cabrera et al., 2004).

Materials classified as ornaments are sparse. There are just a few pendants made of atrophied canine teeth of *Cervus elaphus* at Cueva Morín, steatite pendants and fragments of unworked amber at Cueva Morín and El Pendo (Ibid.).

Definition of the Model of Transition from Middle to Upper Palaeolithic

In the Cantabrian Region there is archaeological evidence that fits very poorly into the model termed *Human Revolution*. Some of the elements characteristic of the Aurignacian can already be found in the Mousterian. Similarly, elements typical of the Mousterian survive on into the earlier phases of the Upper Palaeolithic (including the Aurignacian). Hence, a mosaic model based on innovations and survivals in the Cantabrian Region has to be suggested (Table 1).

Innovations

During the Mousterian it is possible to see in the Cantabrian Region a series of pieces of archaeological evidence that would be characteristic of the Upper Palaeolithic. The first of these is the production of bladelets. It is true that this is not a standardized output, as happens in the Archaic Aurignacian or Early Aurignacian. Nevertheless, this bladelet production is based on varied methods (pseudo-prismatic, Levallois, opportunistic) in various deposits like El Castillo, Cueva Morín, Lezetxiki, Covalejos or El Esquilieu (Bernaldo de Quirós et al., 2010; Arrizabalaga, 2006; Martín et al., 2006; Baena et al., 2005). Moreover, some of these bladelets present semi-abrupt lateral retouching like the Dufour bladelets typical of the Archaic Aurignacian.

Furthermore, there is evidence of the Neanderthals complex or symbolic behaviour during the later part of the Mousterian. Thus, for instance, the shells found

Table 1. Archaeological record in M-U Palaeolithic Transition in Cantabrian Region

	Late Mousterian	Transitional Aurignacian	Chatelperronian	Archaic Aurignacian	Early Aurignacian
Discoid débitage	+	+	+	+	+
Bone industry		+	+	+	+
Ornaments/ Symbolic	+	+			+
Bladelets	+	+	+	+	+
Blades		+	+	+	+
Carinated cores		+		+	+
Burins		+	+	+	+
Backed pieces		+	+	+	

at Lezetxiki had been specially gathered and may in some cases have been used as pendants (Arrizabalaga, 2006). The pebble with chipped dots from El Castillo (Cabrera-Valdés et al., 2006) would also fall within this classification.

Within the techno-complexes of the Early Upper Paleolithic, the Transitional Aurignacian offers a noteworthy set of movable artistic items and bone industry with a dating between 40 kya and 38.5 kya. The set, as noted above, comprises engraved pieces, pendants, and points and punches made of antler and bone (Cabrera-Valdés et al., 2006).

It must be also noted that the isolated deciduous teeth found on level 18b are closer, both morphologically and metrically to those of Neanderthals than to AMH (Garralda, 2005a, b).

Survivals

The opposite way, it may be observed It should also be point out that there are elements characteristic of the Mousterian within the technocomplexes of the Early Upper Palaeolithic (Transitional Aurignacian, Châtelperronian and Archaic Aurignacian). Firstly is the lithic technology typical of the Cantabrian Mousterian, of Discoidal type, which is very common in technocomplexes of that region. In relation to this, substrate pieces (sidescrapers, denticulates and notched) are numerous not merely in the sets covered here, but in the whole of the Early Upper Palaeolithic in the region (Straus, 1992).

Moreover, studies performed on the dental remains from ungulates in deposits from El Castillo, Cueva Morin and El Pendo during the Middle to Upper Palaeolithic Transition reveal there was continuity in the strategies for catching prey, as regards the animals' sexes, ages and hunt seasons (Pike-Tay et al., 1999).

Discussion

The "Human Revolution" hypothesis and the appearance of the Upper Palaeolithic must at the very least be nuanced in the light of new finds from the Cantabrian region and other regions in Europe. The independence of certain transitional technocomplexes, like the Châtelperronian or the Uluzzian, with respect to the Aurignacian (D'Errico et al., 1998; Bietti and Negrero, 2007) and the appearance in the Late Mousterian of elements considered characteristic of "Modern Behaviour" bear this out (Cabrera et al., 2004; Langley et al., 2008). In fact, the formation of Modern Behaviour itself would appear to be a gradual process (McBrearty, 2007; James and Petraglia, 2005; Brumm and Moore, 2005).

Moreover, an assessment must be made of certain initial matters. The first is that it is still not wellknown what human type made the majority of the transitional complexes and the earliest Aurignacian. The oldest AMH remains hitherto found in Western Europe with the Aurignacian are no older than or date from about 30 kya (Brassempouy or Les Rois, for example; Garralda, 2006). Similar dates seem to apply to Cioclovina and Muierii (both in Rumania, but lacking a context), or Mladeč (Czech Republic, with an associated Aurignacian). Perhaps the Oase 1 mandible (Rumania) could be a little older (Trinkaus et al., 2003), but, like the skull from Oase 2, it lacks any archaeological context.

The second matter is that neither the origin, nor the rate of formation of the Aurignacian, are known. In fact, some researchers hold that AMH came into Europe before the Aurignacian, with the Bohunician (Svoboda, 2007).

Finally, there is no knowledge of the social networks there may have been among the various groups who inhabited Europe in the period 50 kya to 35 kya. Thus, there are numerous possible scenarios for contacts. We hold that there was a mosaic-like transition, in which archaeological evidence for Modern Behaviour arises in a gradual and heterogeneous way, with forward and backward movements, until the first technocomplexes of the Early Upper Palaeolithic (including transitional complexes) were formed, and with them the Archaic and Early Aurignacian. The hypothesis that Modern Behaviour burst abruptly into Europe thanks to AMHs and the Aurignacian must be subject to nuances. A view that the Aurignacian arrived from the Near East cannot nowadays be sustained (Belfer-Cohen and Nigél-Morris, 2007). Similarly, the hypothesis put forward by some researchers that AMH and the Aurignacian arrived in two waves (Davis, 2007) cannot be maintained, especially when technocomplexes like the Bachokirian seem to have more relation to the Middle Palaeolithic than to the Upper one (Tsanova, 2006).

In turn, there is ever more frequent archaeological evidence dating from the Middle Palaeolithic and Transitional complexes that confirms there was “Modern Behaviour” on the part of Neanderthals (D’Errico, 2003; Zilhão, 2007; Langley et al., 2008). Furthermore, this new Modern Behaviour was undertaken before the earliest fossils indicating the presence of AMH in Europe occur and also the first archaeological evidence associated with them (probably the Aurignacian).

Thus, a number of hypothetical scenarios arise: a) Neanderthals began their Behaviour Revolution before the arrival of AMH in Europe; b) AMH occupied Europe before the first traces of the Aurignacian (it should be remembered that the MSA was the creation of AMH) and Neanderthals started to modify the items forming their archaeological record before AMH. In the light of current archaeological evidence, the Aurignacian does not appear in Europe as a monolithic, or even homogeneous, technocomplex (Teyssandier, 2006). Hence, it could correspond to a migratory entry of AMH into Europe, or to heterogeneous formation by populations of AMH already resident in Europe.

It therefore seems clear that explanatory models on a continental scale must be abandoned. We should like to put forward as a working hypothesis the possibility of a mosaic-like transition in which different scenarios for change are possible. In the Cantabrian Region, evidence for Modern Behaviour begins before there is any evidence for the arrival of AMHs in the region. However, this sort of transition may well be completely different in other regions.

Concluding remarks

Taking into account the analyses of the archaeological evidence in the Cantabrian Region, we can present the following conclusions:

a) The Cantabrian region constitutes an archaeological context in which items typical of the Upper Palaeolithic appear during the final stages of the Mousterian. These include the blade technology, personal ornaments and objects of a symbolic nature. On the other hand, archaeological items characteristic of the Mousterian survive on into the Early Upper Palaeolithic.

b) The archaeological evidence from the Cantabrian Region and other zones in Europe forces the rejection of, or at least the imposition of nuances upon, the hypothesis of a Human Revolution.

c) Hence, a new scenario arises in Europe in which great explanatory models on a continental scale must be abandoned and an attempt must be made to get to know in a detailed and in-depth fashion the varying contexts at a regional level. Only then will it become possible to put forward continent-wide explanatory models that will reflect the different forms of transition.

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**POSTCRANIAL HUMAN FOSSILS FROM ALTAI MOUNTAINS:
DENISOVA AND OKLADNIKOV CAVES PEOPLE
AND THEIR TAXONOMICAL POSITION**

Introduction

Postcranial morphology is an important item in the study of fossil hominids. A huge number of features were described which can differentiate between anatomically modern humans and representatives of so called “archaic” anatomy of genus *Homo* (including *H. habilis*, *H. erectus sensu lato*, *H. neanderthalensis*).

Speaking generally, early moderns tend to have higher stature, high pilastic and platymeric femoral indices, very platynemic tibial bones, strong muscle markings in attachment points throughout the skeleton, high brachial and crural indices etc. Neanderthal traits combine massive with some exceptions limb bone shifts, as well large articular surfaces. Postcranial features of erectoid fossils in spite of remarkable variability of values can be well recognizable too. Among them there are medullar stenosis of tubular bones and lateral elongation of some shifts.

The nature of many such traits remains to be unclear. Even the most generalized “archaic” pattern – the robusticity or the massiveness of tubular bones – has controversial explanations. From one point, changes in robusticity were interpreted as shifts in activity patterns, because mechanical loading can increase the thickness of long bone diaphyses (e.g. Martin, Burr, 1989; Ruff et al., 1993).

The second hypothesis was that many of differences in robusticity between Neanderthals and early modern humans appear to be related to climatic adaptations (e.g. Pearson, 2000).

The third concept can be that many of postcranial patterns have genetic background. Certainly, the morphological similarity doesn't always reflect kinship, but usually it does.

Careful description of morphological manifestations is the only way to understand the areas of distribution of bearers of archaic features. Southern Siberia is a unique place for study of fossil man. Archaeologically, the local Pleistocene sites are the best of the studied in Northern Asia (for example, Derevianko, Shunkov et al., 2003; Derevianko, 2009, 2010). Amazing results of palaeogenetic investigations discovered fact of Neanderthal presence in

Okladnikov Cave about 40 ka as well simultaneous existence of earlier unknown hominin in Denisova Cave (Krause et al., 2007, 2010; Reich et al., 2010).

But the extreme poor preservation and fragmentation of palaeoanthropological material from all Altai caves should be mention. Consequently, it remains unknown what the Denisovan looked like or how he behaved, and perhaps never will without a more complete fossil finds and its morphological consideration. The origin and anatomical peculiarities of Siberian Neanderthals also wanted to be clarified.

Current publication is devoted to summarizing some results of description of human postcranial elements, which were found during excavations of Denisova and Okladnikov caves (Mednikova, 2011a, b). Those bones belonged to several individuals, both adults and juveniles. Goals of the study were identification of Altai human fossils, as well as discovery of their morphological peculiarity and search of the closest analogies in circle of fossil hominid forms.

Denisova Cave

After palaeogenetic studies it can be assumed that in Denisova Cave lived somebody who was not modern human and not Neanderthal either. Genetically Denisovans and Neanderthals seem to be closer relatives, than modern humans. The morphological study should test this proposition.

Postcranial human remains from Denisova Cave are presented by only proximal pedal phalanx, possibly of the 4th or 5th digit of the left foot (Mednikova, 2011a). The bone belonged to adult individual (Fig. 1). It was relatively elongated, with very robust and massive diaphysis (Ibid., see Table 1). The shaft of basic phalanx of hominin from Denisova Cave was more developed in breadth

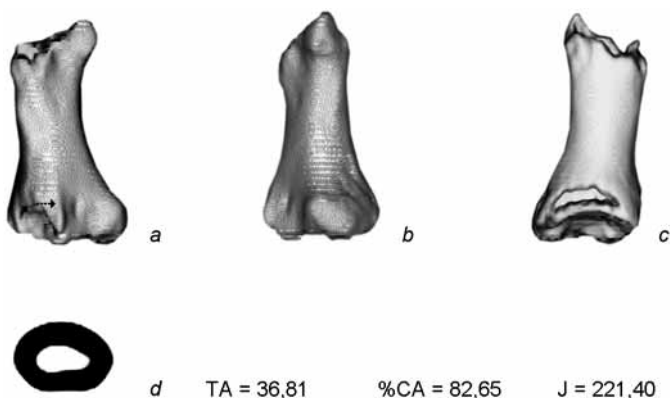


Fig. 1. Patterns of Denisovan pedal phalanx better seen on CT scan images.

a – form of plantar tubers indicates the bone of left foot (medial tuber is pointed, 3D reconstruction); *b* – lateral plantar tuber has typical dome-form (3D reconstruction); *c* – dorsal-proximal orientation of basal facet gives evidence for reconstruction of typical locomotion (3D reconstruction); *d* – form of cross-section and inner robusticity at the level of the midshaft as features of “archaic” morphology (TA – total area, % CA – index of corticalisation, J – polar moment of inertia).

than in height. Such a pattern differs the bone from modern Homo and brings it together with Pleistocene representatives (both Neanderthals and early anatomically modern humans). Moreover, the Denisovan phalanx was wider in comparison with mean data of Pleistocene archaic Homo and, from this point it was more archaic than in Neanderthals.

Remarkable lateral crest indicates strong development of plantar ligaments and muscles, being connected with physical loads.

Dorsal-proximal orientation of the base can be associated with specific “heel-off” movements (heel-and-toe walk). Such kind of locomotion is essentially faster than usual walking. It can be proposed the Denisovan owner of phalanx was a great stayer, and that the last trait could be useful for Palaeolithic hunter in mountain landscape. Additionally, modern sportsmen trained in sport walking move on straight legs, in opposite to ordinary people who bend their legs in knee joints and damp foots. Heel-off locomotion could create additional influence for pelvic girdle and for vertebral column of Denisovan human, as well for his lower extremity itself. Such habit gives something new to the lifestyle of hominins from Denisova Cave.

In various aspects the phalanx shows closest similarity with Shanidar 4 Neanderthal and Tianyuan anatomically modern pedal elements (Mednikova, 2011a, Tables 2 and 3).

Speaking generally, Denisovan pedal phalanx is equally far (less differentiated) from Neanderthals or early anatomically modern humans. Moreover, by extreme massiveness of diaphysis it seems to be more archaic than Neanderthal phalanx and is the most far from modern anatomical variants. Large articular surface of the base adds impression about clear non-modern structure of this pedal phalanx.

Gracilisation of middle proximal phalanges has been considered as a feature of shoes wearing (Trinkaus, 2005). The external and inner robusticity of Altai find supports proposition that Denisovan heel-and-toe speedster didn't use foot protecting shoes.

Okladnikov Cave. “Common drawing” of Altai Neanderthals

Postcranial remains from Okladnikov Cave consist from juvenile right humerus, right and left femurs, navicular bone, adult humerus, patella, right and left calcaneus, metatarsal bone, talus and two manual phalanges (4th or 3rd row and 2nd row).

In spite of their belonging to people of various age the bones allowed to summarize an image of skeletal constitution in that population (Mednikova, 2011b). Features of juvenile members of the group could be also used for the purpose of study of dynamics of development of some taxonomic important traits.

Imagine some generalized skeleton combined from all elements which had been excavated in layers 1, 2 and 3 of Okladnikov Cave. Of course, it should be noted that many fragments belonged to females (or even to one female).

The degree of sexual dimorphism among the “nearest” by distance to Altai Shanidar Neanderthals was relatively high. We could consequently use some statistical correction, taking into account possible increase of body size for males of this group. But for European Neanderthals the level of body size differences between males and females might be less, and this should also be considered.

Total body size

Based on the size of the middle manual phalanx the male stature could vary between 160–163 cm. The female stature couldn’t exceed values known for Neanderthal women in Near East – about 158 cm.

The upper extremities girdle

The body of juvenile humerus is even, straight, without torsional twist. Diaphyseal midshaft section has triangular form; medullar cross-section is oval and enlarged in anterior plane. High robusticity of cortical layer and small development of medullar cavity are noticeable (Fig. 2a).

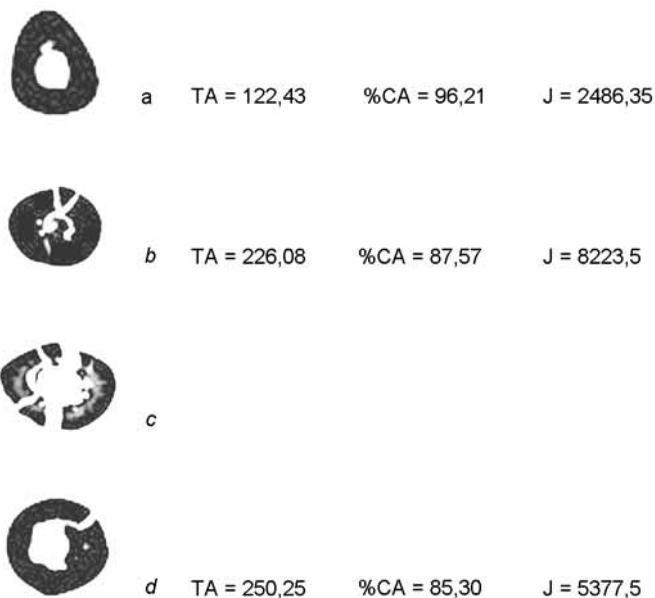


Fig. 2. Tubular juvenile bones from Okladnikov Cave belong to the most massive for Neanderthal children (closest analogy – Teshik-Tash juvenile of the same developmental age from Uzbekistan). Features as in fig. 1.

a – cross-sectional geometry of right humerus at the middle part of diaphysis (midshaft itself is destroyed); *b* – cross-sectional geometry of right femur at the middle part of diaphysis; *c* – cross-section of right femur in subtrochanteric area shows “erectoid” elongation of diaphysis; *d* – cross-sectional geometry of left femur at the middle part of diaphysis.

According to size of the adult lower humeral epiphysis this form belongs to the most gracile one for the Middle and Upper Palaeolithic.

If the middle manual phalanx belongs to the 3rd row, it falls to Neanderthal group where situates between Crimean and Near Eastern forms. It has relatively robust and thick body of the phalanx, relatively large proximal height, flattening of head. If it is of the 4th row, the phalanx is long enough for Neanderthals, especially those in Near East. By the ratio of the length, the midshaft breadth and the base it has intermediate position between Skhul 4 and Kiik-Koba, remaining behind the majority of smaller Neanderthals both European and Near Eastern origin.

Middle phalanx of the 2nd digit has very high, but relatively narrow for Neanderthals body in the midshaft; a relatively narrow and strongly flattened head.

The lower extremities girdle

Medial-lateral elongation of diaphysis of right juvenile femur is observed in the middle and in the subtrochanteric area (Fig. 2*b, c*). Presumably external pilaster in adults is absent. Wide gluteal tuberosity is present. Low neck-shaft angle is comparable to values of early Homo. In addition, there seems to be an extreme robusticity and shortening of the neck, inner robusticity of diaphysis, especially the widening of lateral walls (Fig. 2*b-d*).

5th metatarsal bone is small with hypertrophied articular breadth in the base. Talus is short with small length of neck and head. Calcaneus is short, gracile. Nevertheless, transversal sizes of articular surfaces are strongly enlarged. Heights of metatarsal bones are increased.

Summing up, human fragmentary remains from Okladnikov Cave show something in common in spite of belonging to different individuals of various sex, age, including children: a specific composition of archaic and unique traits. Morphology of those postcranial skeletons is similar to Neanderthals, but there are some archaic features joined them with *H. erectus*. There seem to be very little similarities to early anatomically modern humans from Near East (with exception of some form indices of talus). And finally there exists a row of peculiar traits, probably typical for this Altai group, and it has gotten under effect of founder, by the isolation, genetic drift or biological adaptation to life of condition of low or middle elevation zone of Altai highland. The common gracility postcranial bones of this group make generalized morphological trend, reflected in peculiar widening of articular surfaces, transversal hypertrophy of patella etc.

Criteria of similarity and distinction of postcranial remains from Okladnikov Cave with another fossil forms of hominids

Similarity with Neanderthals: small body sizes, configuration of humeral diaphysis, relative large condylae, inner robusticity of tubular bones, lack of femoral pilaster, wide gluteal tuberosity, robust, thick patella, relative

short talar neck and head, long trochlea of talus, increase of articular trochlear surface and posterior facet of calcaneus, morphology of middle manual phalanges.

Differences from Neanderthals (and similarity with H. erectus): too low femoral neck angle, hypertrophy of lateral walls of femoral diaphysis, anterior-posterior flattening of femur.

Differences from early anatomically modern humans of Skhul group: very small body sizes, low neck-angle of femur, inner robusticity of tubular bones, lack of femoral pilaster.

Unique features: extreme level of shortening and robusticity of femoral neck, very strong shortening of talus and calcaneus, remarkable widening of articular surfaces of the 5th metatarsal base and talar trochlea, wide relative breadth of patella, relative high talus.

Neanderthals and anatomically modern humans in Central and Eastern Asia

In China and Japan in the same period is considered the appearance of people with traits of modern anatomy. Their comparison with Altai Neanderthals seems to be very important.

The infant skeleton Yamashita-cho from Okinawa is older than 32 ka BP (Trinkaus, Ruff, 1996). The femoral fragments from Okladnikov Cave demonstrate archaic traits in opposite to Japanese find. Yamashita-cho has an external pilaster, and Altai child hasn't, even being biologically older. The strong difference reflects in position of femoral neck – very low in Altai femur and modern high in Japanese one. The femoral cortical development was very different for two forms, and Altai one had very thick walls of tubular bones.

So it should be concluded the various taxonomic position of these representatives of genus *Homo*, settled continental and island parts of Asia in relatively limited chronological period.

The recent investigated Tianyuan 1 adult skeleton from China has been determined as the “best seen as modern without being entirely modern” (Shang, Trinkaus, 2010, p. 193).

By many points he looks different from Altai hominids. He had larger articular breadth of the humerus, another form of trochlea, wider *fossa coronoidea*. But the middle manual phalanx from Okladnikov Cave was remarkably longer than for Tianyuan. Opposite to Altai Neanderthals, Chinese human had clear femoral pilaster, large talus with long neck, wide calcaneus, wider in the midshaft 5th metatarsal bone. But the *sustentaculum* of Altai hominids had been robust. The common feature for both forms could be the low neck-angle of the femur, which trend might be interpreted as a result of high and intensive physical activity in subadult age. To sum up, Altai hominids were clear representatives of archaic postcranial morphology as well some of their contemporaries from China were anatomically modern.

Search of morphological analogy for Altai Neanderthals

We have got a picture of mosaic observations. Presented by the fragments of infant and adult skeletons, at first look those remains inform very little of the topic of grounders of this Altai group. But little by little a composition of morphological analogies is getting more and more apparent.

Firstly, the infant humerus from Okladnikov Cave is alike Tabun C1 (McCown, Keith, 1939) by the cross-sectional index in the midshaft.

Secondly, right infant femur demonstrates medial-lateral elongation of diaphysis, pointed as a peculiar feature of erectoid morphology. In Neanderthals it was noted for Tabun. Pilastric index of the right femoral bone from Okladnikov Cave (87,18) seems to be close to the index of strongly flattened femur Tabun C 1.

Thirdly, the left infant femur analogically shows slight prolongation in the lateral direction.

Fourthly, the adult humerus is similar to the most gracile forms, and closest among them are the Middle Palaeolithic Shanidar 6 (Trinkaus, 1983) and Tabun C1.

About the bone one reported the absence of Neanderthal DNA and its late dating (Krause et al., 2007). But the analysis unproven presence of the Neanderthals genes couldn't be negative for the 100 percent. In such situation reliable could be positive result. Probably, the preservation problems influenced the data of that molecular study. Based on the morphological pattern of this remain more argued seems to be a proposition of archaeologists (Derevianko, 2009a) that all individuals from the Okladnikov Cave belonged to the one Middle Palaeolithic population. Noticably, this adult humerus is alike the most gracile forms of the Middle and the Upper Palaeolithic, such as Near Eastern Shanidar 6, Tabun C1 (and later Ein Gev) and European Oberkassel 2, Predmosti 9, Pataud 230.

Fifthly, the patella matched by the length (height) with Tabun C 1 one. All another Neanderthals had larger patellar bones.

Sixthly, right calcaneus from Okladnikov Cave is alike Tabun C 1 by body breadth and height.

Seventhly, adult talus from Okladnikov Cave joins with Tabun C 1 by the total length, neck and head length, by small for Neanderthals size of articular facet of lateral malleolus.

Eighthly, the middle manual phalanx of the 3rd or 4th row is in the field of variability of Shanidar males by the articular length and breadth in the midshaft. According to index of robusticity it falls to the middle phalanx of the 3rd row Tabun C1.

Ninthly, the destroyed middle phalanx of the 2nd row is like Tabun C1 by the height (flattening degree) and, lesser, by the breadth of the head.

The dating of Tabun C1 skeleton remained for a long time controversial, and one of the last version was more than 122 ± 16 ka BP (Grun, Stringer, 2000).

It could be considered a relatively short attempt of colonization of Southern Siberia by Neanderthals about 45–40 ka (Derevianko, 2009). Then Israel archaic forms could be for Altai humans ancestral one. Mosaic features of similar-

ity join Tabun and Okladnikov people possibly reflecting genetic relationships between two palaeopopulations. Taking into account geographical (and possible chronological) distance, Exodus of Neanderthals with such morphotype cannot also be excluded from some third, intermediate centre.

***Archaic hominids in Siberia
and the problem of contact of various fossil forms***

Like Tabun E1 and later Tabun C1 Near Eastern fossils Neanderthal remains from Altai demonstrate some patterns of more archaic, erectoid morphology.

Generally speaking, *Homo erectus sensu lato* were ancestral forms both for Neanderthals and for anatomically modern humans. And appearance of some their features in Neanderthals or modern descendants was possible. Moreover, sometimes it creates illusions of the closest kinship. But that is not the only explanation of certain erectoid patterns in archaic humans from Okladnikov Cave.

Biological species can be determined as a genetic closed system of populations only in relation to another species, metaphorically as a brother to a brother (or sister) (Mayr, 1974). Traditional schedule draws two sister species, evolving from initial one.

A.S. Severtsov (2008) has proposed a new metaphor *species-father and species-son*, describing the situation when the parental species remains and the next species is evolving from him outside the fundamental ecological niche.

There is a lot of evidence for late distribution of *H. erectus* in Asia. From this point discovery of Denisovans is especially important. Notably can be the cross-section of Altai archaic forms in time and space, because the distance between caves Okladnikov and Denisova is about 100 km.

About 50 ka years ago in Southern Siberia appeared intriguing situation of possible contact between various taxonomic branches. One of them (Denisovan), the long time settled this territory, was closer ancestral *species-father*. Hypothetically, the back-cross-hybridization became possible. Correctly speaking, back cross is unwell term for supposed events, because it is hybridization of the first generation hybrid with one of parental forms or analogous by the genotype form. Interestingly, that “authentic” back-cross overcomes sterility of far hybrids of the first generation.

Conclusion

Basing on data of human postcranial remains Altai mountains became place of refuge for various representatives of genus *Homo* with archaic morphology. Due to structural patterns of preserved pedal phalanx the hominin from Denisova Cave is expected to be bearer of more “archaic” traits than Neanderthals or especially as early anatomically moderns of the Skhul group. But noticeable can be mosaic similarity of Denisovan phalanx with eastern fossils of various taxonomic states (Shanidar 4 Neanderthal in Iraq and Tianyuan modern in China). That means possible common ancestry or hybridization of various representatives of

archaic and modern anatomy in Asia. The hypothesis of back-cross hybridization with parental form (erectoid or standing closer to common ancestor like Denisovan) could explain overcoming of reproductive barrier in far derived forms.

The more “numerous” but also fragmentary Neanderthal remains from Okladnikov Cave demonstrate “archaic” patterns typical for representatives of their taxonomic group. They are especially close to Tabun C1 in Israel, and this fact indicates the possible source and direction of migration to Altai. Remarkably, that, according to archaeological data, 250 ka years earlier the same migratory way used ancestors of previous Altai taxon – Denisovans.

The group of South Siberian Neanderthals was peculiar not only because of their extremely small body size even for Neanderthals, but also by a touch of “erectoid” features. At the same time some proportions both in talus and calcaneus join Altai Neandertals with the anatomically modern humans of the Skhul group. Such sophisticated and contradictory package of morphological patterns could indirectly reflect complicated history of human moving into eastern Eurasia. Asia was area of migratory movements of so called archantrops, palaeoanthrops and neanthrops. And the aftereffects of their close settling might become clear very soon.

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MULTI-LEVEL APPROACH TO IDENTIFICATION OF TUBULAR JUVENILE BONES OF NEANDERTHAL HUMANS FROM OKLADNIKOV CAVE

Introduction

Our study combines results of separated investigations of fragmentary non-adult remains from excavations in Okladnikov Cave in 1984.* The bones have been found in various stratigraphic layers, No. 2 and 3. And the question arises: could those fragmentary remains belong to one individual or they couldn't. To prove alternative hypothesis the various methods of bone description was used. The multi-level approach was based on macro-morphological evaluations, including data of inner robusticity, on the comparative data of microstructure of bone tissue, on the estimations of mineral content by non-destructive method and on isotopic analysis, reconstructed the palaeodiet.

Methods

The common morphological description gave evidence for biological age estimations as well geometrical study of bone properties could be used from the point of belonging to one individual. The measurements of postcranial remains were provided in standard manner. The features of inner robusticity were estimated on breaks of bony fragments and, alternatively, after computer tomography measured on transversal slices in Dicom Viwer programme. The cross-sectional geometrical traits were estimated according to formulae for ellipse and circle.

Histological study has been done on the base of light reflected and electronic microscopy. We used Olympus BX-41 microscope fixing pictures by color view digital camera and raster double-ray electronic microscope "Quanta 3D FEG".

* Participation of authors: M.M. provided morphological analysis, histological analysis, took part in CT-scanning; M.D. – isotopic study and histological analysis; V.S., E.M., E.V. – CT scan investigation; A.T. – isotopic study.

Advances in computer tomographic scanning technologies last years have generated a great deal of interest in dual energy CT. A single energy CT image doesn't fully characterize objects under the study. X-ray attenuation to materials with different atomic numbers has different energy depends, so the multi-energy CT allows to investigate structures more fully, including general chemical estimations. Using of two X-ray spectra just has been applied to diagnostics of coronal diseases, to detection of primary stages of acute gout. The dual energy CT scanner technology makes possible to differentiate between organic materials of various composition, e.g. calcium oxalates and increments of uric acid. That means the method can be used for non-destructive study of bone structures for purposes of indirect evaluation of mineral content of skeleton.

The dual energy CT scanning was to the first time applied to palaeoanthropological material in case of Okladnikov human remains. Scanning was done by tomograph "Discovery HD 750" of "GE Healthcare" production (USA). The primary width of cut was 0,625 mm (64 cuts for 1 turn of the tube), tube parameters – 80 and 140 kVp. Dual energy data were analyzed using "Windows Advantage 4.5" work station and "GSI Viewer" programme. Starting the investigation, we presumed that there are individual (as well sex, age-related) variations of mineral content of bone tissue. So, mineral presence in skeleton of one individual even inside one population can be unique. Comparing values of concentration of calcium salts and uric acid in isolated fragments, we accepted presumption that similar level could indicate their belonging to one human.

Stable isotopes (^{13}C and ^{15}N) signatures were obtained. Isotopes values were determined at the Stable Isotope Laboratory Severtsov Institute of Ecology and Evolution RAS (Moscow) by mass-spectrometer Thermo Finnigan DELTA V plus.

Results

Morphological study

Owner of the humerus belonged to the age group *infantilis II*. Morphologically and parametrically the individual is close to Teshik-Tash Neanderthal from Uzbekistan whose biological age had been detailed argued: 7–9 years by post-cranial skeleton и 9–10 years – by teeth eruption. We used this skeleton as basic reference point for age estimations of Okladnikov juvenile bones. Even taking into account remarkable individual variability, 8–10 years is the most possible age of the owner of the humerus from Okladnikov Cave.

The diaphyseal parameters of right femur are a little smaller in comparison to Teshik-Tash. Individual could be at the same age or a little younger – 7–8 years.

Parametrically, left femur could belong to the previous individual. 7–8 years.

The reconstructed lengths of humerus and both femurs from Okladnikov Cave as well their diaphyseal parameters were compared with standards of recent *H. sapiens* development. The same work was done for Teshik-Tash child. Because earlier his biological age (about 9 years) was relatively accurate detected on the base of different criteria, we could estimate reliability of Holocene standards use for Neanderthals.

The degree of differences in estimations of humerus and femurs for one child (Teshik-Tash) is the same as for the isolated fragments of humerus and femurs from Okladnikov Cave. That means, Altai bones could belong to one juvenile.

The study of cross-sectional properties could clear up how the fragments correspond. Having the upper part of right femoral diaphysis and the lower one from the left side we could compare the approximately parameters in the middle of diaphyses only. But the midshaft in both cases is estimated approximately. Comparative data show that Altai femurs have enormous robust walls, humerus is still more robust. Consequently, their belonging to one child cannot be excluded.

Results of histological analysis

Using light and electronic microscopes we have got a row of pictures with various magnifications (see Dobrovolskaya, Mednikova, current volume). The juvenile humerus shows strong diagenetic change to be considered from this point. Right and left femurs demonstrate identical microanatomical patterns. In spite of the peculiarity of histological picture, atypical for modern Homo, the belonging of juvenile bones to one Neanderthal child seems to be very possible.

Results of the dual-energy scanning

Compact layers of tubular juvenile bones

In first investigation we estimated mineral compound in compact layers of tubular bones. The parts of diaphyses, far from breaks and external damages, were chosen.

All tubular bones show close values of mineral compound. But the larger dispersion of calcium degree for humerus might reflect its worst preservation.

Parts of spongy tissue of juvenile remains

(tubular bones, navicular bone)

To compare patterns of mineralization of tubular juvenile bones we have to test the spongy tissue in spite of its specific structure. As a comparative sample an animal bone as well navicular (juvenile) human bone from the same cave was used. Unexpectedly, both spongy bones have larger mineralization than tubular bones. Taking into account diagenetic problem, on the base of this data the belonging of navicular bone to the same child cannot be argued.

Results of isotopic study

One of the goals of isotopic investigation (see Dobrovolskaya, Tiunov, current volume) was to determine number of Neanderthal individuals in Okladnikov Cave and to combine bone fragments from adult and juvenile skeletons. Certainly, the similarity of the isotopic signals for this group in whole made our results hypothetically. But the maximal likeness was expressed in juvenile fragments. That means, perhaps, all skeletal fragments from Okladnikov Cave originated from remains of 3 individuals (1 child and 2 adults). Although the low

level of the isotopic parameters variability can be result of stable food source and environmental condition and possibilities of the individual isotopic patterns are strongly limited and poorly informative.

Conclusion

Morphologically, all tubular bones could belong to one child about 8–9 years at death. Even if there were different children they were very close by the level of biological development. The owners (owner) of bones died during the so called juvenile stage of ontogenesis.

Histological study discovered identical picture for right and left femurs. Functional difference of humerus and its diagenetic change after death can explain some patterns of that fragment, but its belonging to the same subadult cannot be excluded.

The dual energy CT is a perspective approach to nondestructive study of palaeontological materials of great value. The method allows test degree of after-death degradation of mineral component of bone tissue. When the mineral compound is well preserved, partly estimation of intravital concentration of inorganic substances is possible. The dual energy investigation showed that all tubular juvenile bones seem to be one Neanderthal child.

Isotopic investigation also gives evidence for probable number of individuals. Common similarity of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the group could make individual identification problematic. The low level of the isotopic parameters variability reduces our conclusion reliability. Nevertheless according to this analysis juvenile fragments are the closest.

Multi-level approach argues belonging of studied juvenile remains (humerus and two femurs) to one individual. Taking into account fragmentary and isolated character typical for Neanderthal remains the result might be important for further study of correlations of various features in this taxon of *Homo* representatives.

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LEVANTINE PERSPECTIVES ON THE MIDDLE PALEOLITHIC/ UPPER PALEOLITHIC TRANSITION

Due to its position at the crossroads of Africa and Eurasia, the Levant plays an important role in the lively debates on the emergence of the Upper Paleolithic in Eurasia and on the relationships between Neanderthals and Modern Humans. The presence in Kebara Cave of a fully-fledged Upper Paleolithic blade industry (early Ahmarian), dated ca. 43–42 ka. uncal BP (Bar-Yosef et al., 1996, Rebollo et al., in press) suggests that the Upper Paleolithic emerged earlier in this area than elsewhere (Bar-Yosef, Pilbeam, 2000). Thus the Levant provides a good opportunity to define the technical repertoire of the human population just prior to the onset of the Upper Paleolithic, and to discuss the processes involved in its emergence in this region.

The Late Middle Paleolithic

Our researches on the Kebara sequence as well as on the main Levantine Late Middle Paleolithic lithic assemblages (Amud cave, Tor Faraj, Bezez cave, Umm el Tlel, Keoue cave, Tabun) (Bar-Yosef and Meignen, 1992; Meignen and Bar-Yosef, 1991; 1992; in prep.) allowed us to characterize the Late Middle Paleolithic by the following criteria:

- prevalence of Levallois recurrent unidirectional method of flaking, often convergent;
- great emphasis upon the production of subtriangular (convergent/pointed) Levallois blanks, of elongated proportion;
- core reduction following the widest face of the block (“débitage facial”), with the use of hard hammer technique and an “internal” percussion gesture.

The tool-kits are mainly composed of unretouched Levallois blanks (often convergent); retouched pieces are of the Mousterian type (side scrapers, retouched points); UP tool types are scarce.

All these assemblages are part of a large technical entity (the Levallois techno-complex) whose traditions are in this Late Middle Paleolithic characterized by an efficient débitage system (simple core preparation, but with careful faceting of striking platform), unipolar core exploited in a continuous process integrating the cortical elongated éclats débordants in the flaking sequence (recurrent mode and several exploitation surfaces) and the production of relatively elongated

convergent blanks (or even blades in some contexts). This technical entity is widespread at the end of the Middle Paleolithic, between 70 and 45 ky, across all the ecological zones of the Levant (Mediterranean zone and its arid margins). It seems that a fixed technical system existed over a large geographic range, with this unidirectional Levallois flaking becoming the technological paradigm in the Levant during this time; many (but not all) Late Middle Paleolithic industries conform to this unifying conceptual framework (Hovers, 1998). This system was nonetheless flexible, as is shown by the variability of the details of core reduction tactics.

This technical repertoire, thus constitutes the base from which the subsequent Upper Paleolithic develops, regardless of the phenomena responsible for its formation (evolution in place, in continuity with these foundations? diffusion of ideas superposed onto this initial technical background? total replacement?).

It is worth noting that the exclusivity of the Levallois flaking system during the Late Middle Paleolithic in the Levant stands in striking contrast to the high diversity of technical systems in Western Europe during the same period (especially during isotopic stage 3 (Delagnes and Meignen, 2006)). The large predominance of this unidirectional Levallois production system might have facilitated the emergence of systematic blade productions. Moreover the Levantine Middle Paleolithic also differs substantially from its Western European counterparts in terms of its greater emphasis on the production of elongated convergent Levallois blanks.

And this predominant production of pointed products in the late Middle Paleolithic must be highlighted as it immediately precedes the prevalent productions of convergent points and blades during what is now generally called the “Initial Upper Paleolithic” (IUP) following Kuhn definition (Kuhn, 2004).

The Initial Upper Paleolithic: previously called “transitional industries”, a term globally abandoned now. We avoid also the term “Emirean” often used in this area, as the early excavations in Emireh cave do not provide sufficient stratigraphic resolution and taphonomic information to consider these assemblages as a good reference.

The existence in the Levant of an “intermediate” phase, comprised of both Middle and Upper Paleolithic characteristics, and thus straddling the two, has long been accepted (Belfer-Cohen and Goring-Morris, 2007 and references therein), even if its limits are still largely debated. At Kebara, this so-called “transitional” period is not represented; there is a short stratigraphic gap between the Late Middle Paleolithic (units XII–V) and units IV–III, in which full-fledged Upper Paleolithic assemblages have been identified (Early Ahmari occupations dated to ca. 43/42 ka. BP (Bar-Yosef et al., 1996; Rebollo et al., in press)). Therefore, in order to test the two hypotheses – either this shift in lithic technology emerged locally, elsewhere in the region, or it resulted from diffusion through cultural contacts or even migration – it is necessary to analyze assemblages from other sites. The Ksar-Akil rock shelter, which contains a long archeological sequence including both Late Middle Paleolithic

and very early Upper Paleolithic assemblages is currently the best candidate for this endeavor.

In previous papers (Meignen and Bar-Yosef, 2002; 2004), we showed that in the so-called “transitional assemblages” (Initial Upper Paleolithic) of Ksar-Akil (layers XXV through XXI), immediately underlying layers XXII–XIX (which are considered now as Ahmarian (Belfer-Cohen, Goring-Morris, 2003)), the subtriangular blades and elongated points that are morphologically similar to Levallois products were in fact obtained using partly a Levallois flaking system (mainly via a unidirectional convergent scheme), as well as, more often, through a developing volumetric concept of core exploitation, seen in the semi-prismatic, prismatic, unidirectional convergent or, more rarely, bidirectional cores. Many of the convergent end-products still have faceted striking platforms and were knapped with a hard hammer with an “internal” percussion gesture. Through the Initial Upper Paleolithic layers (layers XXV through XXI), Ohnuma and Bergman (1990) observe the inception of the soft hammer technique, shown by linear and punctiform striking platforms, as well as the removal of platform lips by abrasion. Though it should be noted that this progressive trend is not observed at Uçagizli, an other Initial Upper Paleolithic site in Turkey, where soft hammer use is considered to appear abruptly in layer E at the beginning of the Ahmarian (Kuhn, 2004). In the Initial Upper Paleolithic layers in Ksar-Akil, the retouched tools are mostly Upper Paleolithic types (including endscrapers and burins) and specific tools called chamfered pieces, a “cultural marker” found only in the Northern Levant.

Several Levantine sites preserving Initial Upper Paleolithic layers have been published during the last decade (Uçagizli I-F (Ibid.), Tor Sadaf (Fox, 2003), Umm el Tlel “Paléolithique intermédiaire” (Boëda et Bonilauri, 2006; Bourguignon, 1998)). Detailed observations of the technical steps for elongated productions (blades and points) observed in these Initial Upper Paleolithic assemblages show the same general trend in which a Levallois approach is replaced by blade productions in series, most often with an emphasis on Upper Paleolithic tool types, even if in some assemblages, sidescrapers and denticulate may be still relatively common. Two specific shaped tools are associated with Initial Upper Paleolithic assemblages, but they are not ubiquitous and never abundant: the Emireh point found throughout the Levant (Mediterranean zone and the Negev) and the chamfered pieces mostly known from caves in the Northern Levant.

Assemblages from Boker Tachtit (Marks and Kaufman, 1983) must be considered as a specific case. Contrary to Marks’s opinion (who considered Boker Tachtit level 1 as a Terminal Middle Paleolithic with Levallois core reduction), our technological study (Meignen, 1996) has highlighted an Upper Paleolithic volumetric concept of flaking (core reduction from the narrow face of the core; core maintenance by crested blades), but still with a systematic platform faceting and use of the hard hammer percussion technique (in few cases probably with a marginal gesture). In term of tool-kits, Upper Paleolithic

tool types are well represented, Emireh points are characteristic. Thus, despite its early dating (46/47 ky BP; Marks, 1983), Boker Tachtit 1 is clearly an Initial Upper Paleolithic assemblage in which the Levallois *sensu stricto* component has already disappeared and in which the volumetric core reduction is mostly bidirectional. Together with the presence of the Emireh points, all these criteria set apart the southern Initial Upper Paleolithic of Boker Tachtit from the Northern Initial Upper Paleolithic as identified in Uçagizli and Ksar-Akil.

To sum up, the label “Initial Upper Paleolithic” refers to assemblages characterized by essentially Upper Paleolithic inventories of retouched tools (burins, endscrapers and retouched blades) sometimes with still a significant number of Middle Paleolithic types (sidescrapers and broad points). They demonstrate a dominant blade production from core reduction strategies combining both Levallois and Laminar (volumetric) concepts. Most of the blades (frequently with convergent edges) are wide, not very regular, with faceted platforms, and indicate still the use of hard hammer technique in large proportion. Such assemblages are largely spread in the Levant (for instance Boker Tachtit lev. 1–4, Ksar-Akil XXIV–XXI, Tor Sadaf A–B, Uçagizli I–F, Intermediate Paleolithic in Umm-el-Tlel, to cite the more secure).

What are the relationships between all these Initial Upper Paleolithic assemblages? should we lump them together in a unique entity or still view them separately?

At a large scale, this “techno-complex” demonstrates an internal variability that could be evaluated on several criteria: more or less developed persistence of Middle Paleolithic tool types, of Levallois core reduction strategies, variable frequencies of the hard hammer versus “soft (organic or soft-stone) hammer/marginal gesture” technique, relative presence/absence of retouched points, presence/absence of intentional bladelet production. These internal variations have been identified at local scale, for instance in the El Kown basin (Boëda, Bonilauri, 2006). They have also been recognized in different stratigraphical contexts. Whether these variations represent a diachronical trend is not easy to decipher, taking into account the ambiguities of dating during this time gap. Few dates are presently available for these assemblages: Boker Tachtit level 1: 46/47 ky (published quite a long time ago, and then at the limits of the C14 resolution); Uçagizli I–F: between 36 to 41 ky (but considered partially problematic and probably underestimated (Kuhn, 2004)); around 36 ky for Umm el Tlel intermédiaire. The estimated age for Ksar-Akil “transitional layers” (Mellars and Tixier, 1989) should be abandoned in the discussion as it results from indirect dating based on an uncontrolled rate of sedimentation.

In some cases, some technological changes (such as the development of soft hammer/marginal percussion gesture) are observed in stratigraphical sequences thus demonstrating their likely diachronical meaning, at least locally (Ksar-Akil (Bergman, Ohnuma, 1987), Uçagizli (Kuhn, 2004), Tor Sadaf (Fox, 2003)).

But taking into account the few well documented sites, it is probably not yet the time to build a general evolutive sequence for this Initial Upper Paleolithic

entity; in fact it is even possible that the observed situation results from a non linear appearance of each Upper Paleolithic characteristics. Indeed data presently available show that the change in the core reduction strategies does not appear to be an abrupt phenomenon. It does not occur everywhere at the same time (non synchronous changes at different locations in the region) and more over, it seems that no global linear chronological evolution can be recognized; in these various assemblages, different production systems (Levallois for the elongated products and true laminar productions with a hard hammer) coexist in different proportions over relatively long periods, with no synchronic changes observed over the entire region. For instance, the assemblage of Boker Tachtit layer 1, the oldest Levantine Initial Upper Paleolithic if we accept the ^{14}C dates of 46–47 thousand BP (Marks, 1983), already no longer contains a Levallois *sensu stricto* production (Meignen, 1996), while layers III2a' and II base' at Umm el Tlel (Paléolithique intermédiaire), dated to $36,000 \pm 2,500$ and $34,530 \pm 890$ (Boëda et al., 1996), still have a strong Levallois component oriented toward the production of elongated triangular products.

Thus these changes in technology, even if we can consider them as globally progressive, did not occur at the same rhythm in the different places, but more in a “mosaic” pattern (Kozłowski, 1990). The pattern is different for the retouched tools: the Upper Paleolithic-type tools, and in particular, end-scrapers and burins made on elongated blanks, dominate nearly all the assemblages of the Initial Upper Paleolithic from the beginning of its existence, while they are very few in the Late Middle Paleolithic assemblages. There is thus a discrepancy between the technical changes in term of core reduction strategies (an intentional production of elongated convergent blanks, but using varied flaking methods that were still evolving) and the functional and formal changes in the retouched tools, which probably appeared abruptly at the beginning of the Initial Upper Paleolithic.

While the intentional production of convergent laminar blanks seems to be an extension of a tendency already present in the Late Middle Paleolithic, the systematization of Upper Paleolithic-type tools on elongated blanks has not been clearly identified in this former period, indicating a break in the domain of retouched tools. But the persistence of convergent tools from the Late Middle Paleolithic to the Initial Upper Paleolithic constitutes the common background of the tool-kits.

In terms of blank production and core maintenance methods, it is thus relatively easy to establish a link between the Late Middle Paleolithic, with its particularities, and the Initial Upper Paleolithic of this region.

Late Middle Paleolithic: exclusivity of the Levallois core reduction strategies, oriented towards the production of convergent pieces (even points); unidirectional core exploitation in a continuous process, without specific core shaping at each step of the reduction. Core exploitation follows the widest surface of the core; use of hard hammer/internal percussion gesture.

Initial Upper Paleolithic: the aim of the production is also convergent products, often elongated, obtained still through a Levallois core reduction

strategy but coexisting with an increasing volumetric exploitation for blade production (in which the core is reduced in a continuous process). According to the assemblages, core reduction follows the widest face of the core (“débitage facial”) or the narrow face (“débitage frontal”). In all of these toolkits, meanwhile, extensive platform faceting, the use of a hard hammer and internal percussion, remain the rule for a long time.

Nevertheless, the relative homogeneity, as broadly defined above, of the Initial Upper Paleolithic allows to separate this technological “entity”, from the “Early Upper Paleolithic”, a label that we suggested to keep for the earliest appearance of fully-fledged Upper Paleolithic assemblages (Meignen, 2006).

The Early Upper Paleolithic: is characterized by quasi-exclusive Upper Paleolithic tool inventories (including pointed blades/bladelets), thin blade/bladelet production following Laminar concept (prismatic cores) and emphasis on the soft (organic or soft stone) hammer technique together with abrasion/marginal percussion gesture. As a consequence, in these Early Upper Paleolithic assemblages, faceting tends to disappear and platforms are mostly punctiform or linear. Whether this technological shift from hard hammer percussion to soft (or soft stone) hammer/marginal gesture percussion was an abrupt or a progressive phenomenon is not yet clear (see Ohnuma, Bergman, 1990, and more recently Marks, 2003: 260; Kuhn, 2004 for the discussion). But it is in any case a major technical event, together with careful shaping of the cores, as part of a process of better control on the regularity of the end-products – blade/bladelet – production in the development of the Upper Paleolithic (Meignen, Bar-Yosef, 2004). In the Levant, this full-fledged Early Upper Paleolithic begins with the early Ahmarian identified in Kebara Units IV–III (Bar-Yosef et al., 1996), Ksar-Akil XX–XIV (Belfer-Cohen et Goring-Morris, 2003), Boker A (Monigal, 2003), Tor Sadaf (Fox, 2003), Uçagizli layers A–D (Kuhn, 2004).

Moreover, in few sites with good preservation conditions, ornaments and simple bone artifacts are present (Ksar-Akil, Uçagizli; Kuhn et al., 2001).

This full-fledged Upper Paleolithic seems to be the result of a general trend previously described in the Initial Upper Paleolithic internal variability. Such a long-term continuity with the appearance of a new percussion technique together with the disappearance of the Levallois-like technology has been identified for instance in the stratigraphic sequences of Uçagizli in Turkey (Kuhn, 2004), in the multilayered site of Ksar-Akil in Lebanon (Ohnuma, Bergman, 1990), and at Tor Sadaf in Jordan (Fox, 2003).

The duration of the transition to the Upper Paleolithic in the Levant is considered by some researchers to have been relatively brief (a few thousand years), which led them to suggest a phenomenon of rapid acculturation (Tostevin, 2000; Bar-Yosef, 2000). But this idea of short duration seems to be mostly a consequence of the scale of observation. In a symposium dealing with “rhythms of change and innovation in the prehistoric record”, Kuhn recently demonstrates that within the sequence of Uçagizli cave from Initial Upper Paleolithic to the Ahmarian, major changes in the large and small game diet, in the different

elements of lithic technology and the appearance of ornaments, occurred. But few of them seem to be closely coordinated, and none correlate strictly with the cultural shift (beginning of the Ahmarian) (Kuhn, oral communication 2011). The data presently available at different well stratified sites tend to show that the period of technical changes, which clearly were not simultaneous everywhere in the Levant, always extend through time within each site and thus seem to indicate a “long lasting technological pattern, one that exhibits an internal evolutionary dynamic of its own” (Kuhn, 2003: 66). In the same way, Boëda and Bonilauri (2006) develop the idea of an Intermediate Paleolithic during which several contemporaneous assemblages in the process of transformation would have resulted in different lithic compositions, coexisting in the limited area of the el Kown Basin.

Nonetheless, considering what we have just described, it appears that the technical knowledge acquired during the Late Middle Paleolithic could have constituted the base for the development of local Upper Paleolithic laminar productions (Initial Upper Paleolithic and later Ahmarian) since they were already quite similar to them. Recently, Marks (2003) included all these laminar assemblages in what he called “leptolithic lineage” putting aside the Levantine Aurignacian “which has nothing whatsoever to do with the local Middle Paleolithic/Upper Paleolithic transition” (Belfer-Cohen and Goring-Morris, 2009).

The processes underlying the development of the exclusively laminar toolkits of the Upper Paleolithic of this region would thus correspond to one of two scenarios: either the generalization of new technical traits that would have emerged within certain local groups in the Levant, as is indicated by the Ksar-Akil sequence; or a phenomenon of diffusion (the arrival of new tool design -in the form of endscrapers and burins at the ends of elongated blanks) superposed onto a background of technical knowledge that was receptive due to its similar tendencies and “ways of doing”, in association with these new objectives.

It is highly probable that the emergence of the Upper Paleolithic (represented in the lithic domain by the development of more or less exclusive productions of blades and bladelets, the regularity of products tending toward standardization and by the panoplies of Upper Paleolithic tools on blades) did not occur following a single process in all regions, and even in the same region. If we take into account the few available radiometric dating, the onset of the full-fledged Upper Paleolithic in Kebara cave would happen around 43/42 ky as an in situ evolution, while the Ahmarian, more recent in Umm el Tlel, probably results from a local diffusion phenomenon into the inland area.

It is possible that exterior influences (population movements or diffusion of ideas) served as stimulants for the emergence, in some areas, of these new organizations. Meanwhile, the repertoire of the Middle Paleolithic/Initial Upper Paleolithic technical knowledge is such that the hypothesis of its development in place is just as likely. In our current state of knowledge, strong exterior influences do not appear necessary to explain the transformations observed in the lithic productions of the Levant.

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EVIDENCE FOR AT LEAST FOUR HUMAN DISPERSALS BETWEEN AFRICA AND EURASIA

An outdated view is that only two major human migrations between Africa and Eurasia are needed to explain existing data: the migration of the ancestors of *Homo erectus* from Africa to Eurasia explaining the fossils in Dmanisi (Georgia) around 1.8 million years ago (Mya), and the migration of modern humans bearing Upper Paleolithic technologies from Africa to Eurasia 45–65 thousand years ago. However, ancient DNA sequences as well as new archaeological evidence compel a more complex view. To explain the genetic, archaeological and fossil data, at least four major migrations between Africa and Eurasia must have occurred, with the directionality of some migrations as yet undetermined. Further analysis of genetic, fossil and archaeological data, may be able to resolve some of the open questions.

This essay begins with a caveat: the author has no expertise in archaeology or paleoanthropology. Nevertheless, the author believes that genetic evidence from ancient DNA (the area in which he is an expert) has implications for the interpretation of the history of human migrations between Africa and Eurasia in the last two million years. It seems important to put the genetic evidence together with the archaeological and fossil records as this may make it possible to learn more than would otherwise be possible. Thus, this essay is written with the realization that some of the discussion of the archaeological and fossil evidence will be naïve, but in the hope that attempting to present it along with the genetic data will stimulate discussion. I begin by reviewing the evidence for at least four major human migrations between Africa and Eurasia.

From Africa to Eurasia (>1.8 Mya)

Australopithecines, whose fossil record is restricted to Africa and dates to 2–4 Mya, are acknowledged to be the ancestors of modern humans. To explain the fact that *Homo erectus* fossils are found in Dmanisi Georgia by 1.8 Mya and elsewhere in Asia after that time, there must have been a hominin migration from Africa to Eurasia before 1.8 Mya.

Direction unknown (>600 kya)

Homo heidelbergensis fossils are present in both Africa (for example Bodo and Broken Hill) and Eurasia (for example, Mauer and Atapuerca) after 600 kya (Lieberman, 2011). Under the assumption that *Homo heidelbergensis* did not evolve independently in Africa and Eurasia which seems biologically implausible, there must have been at least one additional migration from Africa to Eurasia, or from Eurasia to Africa, to explain the presence of *H. heidelbergensis* fossils in both places <600 kya.

Direction unknown (<440 kya)

The analysis of the Neandertal genome has shown that Neandertals and modern humans descend from a common ancestor 270–440 thousand years ago (Green et al., 2010). More recently, analysis of the Denisova genome showed that Denisovans and Neandertals descend from common ancestors more recently than either shares ancestors with modern humans (Reiche et al., 2010). Thus, the common ancestral population of modern humans, Neandertals and Denisovans must have lived in either Africa or Eurasia between 270–440 thousand years ago, and migrated from one to the other to explain the subsequent distribution of their descendents in both places.

From Africa to Eurasia (>45 kya)

The Out-of-Africa expansion of modern humans, which displaced most of the previous inhabitants of Eurasia, occurred at least 45,000 years ago.

While the evidence above makes it fairly clear that there were at least four major migrations, many questions remain unanswered, and two are discussed below.

Discussion

Where did the Homo erectus ancestors of present-day humans live?

Many paleoanthropologists believe that the *Homo erectus* lineage leading to modern humans likely spent all of its in Africa, with the non-African *Homo erectus* like Dmanisi and subsequent Eurasian *Homo erectus* being a “dead end” that went extinct due to subsequent waves of migration out of Africa.

Why do researchers believe that the main trunk of the tree leading to modern humans – in the time when our ancestors were *Homo erectus* – live in Africa? One line of argument as far as I can tell is parsimony: the fact that so many other parts of the human fossil record both ancient (e.g. *Australopithecines* and older) and more recent (e.g. modern human origins) are in Africa, and so it seems parsimonious to hypothesize that the lineage leading to modern humans in the interim period might also have been in Africa as well. However, a history in which the main trunk of the modern human lineage was always in Africa is no longer more parsimonious than the alternative of a Eurasian location in the context of the minimum of four waves of migration between Africa and Eurasia.

Another line of argument for an African location of our *Homo erectus* ancestors is climate. Africa is warm, and so would have provided a congenial habit for *Homo erectus*, in comparison to northern parts of Eurasia during the many ice ages. However, there are also many southern refugia in Eurasia, and so a climate-based argument does not provide compelling evidence for an African location for our *Homo erectus* ancestors.

In fact, the fossils provide marginally more evidence for a Eurasian than for an African location for *Homo erectus* from 1.0–1.8 Mya. The first *Homo erectus* fossils are found in Dmanisi in Eurasia, and do not appear definitively in Africa until ~800,000 years later. The absence of a *Homo erectus* fossil record in Africa over this period could reflect a scant fossil record, or that the lineage was in Eurasia during this time.

Where did the ancestors of Neandertals, Denisovans and modern humans live?

Here I discuss the evidence for where the common ancestors of Denisovans, Neandertals and modern humans lived 270–440 thousand years ago before they separated.

Evidence that the ancestral population may have lived in Eurasia

The evidence in favor of a Eurasian location for the common ancestors of Neandertals, Denisovans and modern humans is primarily fossil-based. The key observation is that some of the *Homo heidelbergensis* fossils from Europe (including from the Sima de los Huesos in Atapuerca dating to 500–600 kya), have derived traits that are shared with Neandertals. This includes an occipital bun, a suprainiac fossa, an inflated mid-face around the nasal aperture, a long occipital squama above the inion, a high position of the glabella, and a variety of dental traits (Arsuaga et al., 1993; Hublin et al., 1995; Hublin, 2001; Lieberman, 2011; Martínón-Torres et al., 2007). If they are not homoplasies, these traits suggest some degree of genetic continuity between the *Homo heidelbergensis* who lived in Europe >500 kya the Neandertals who lived there <200 kya.

Evidence that the ancestral population may have lived in Africa

Evidence for the view that the ancestral population lived in Africa comes from an interpretation of the archaeological record. McBrearty and Brooks (McBrearty, Brooks, 2000) argue that Africa has the earliest archaeological evidence for the Middle Stone Age/Middle Paleolithic, which is the stone tool industry shared by Neandertals and modern humans. If so, then the Middle Paleolithic was “invented” 270–400 kya by *H. heidelbergensis* in Africa, and it is reasonable to hypothesize that the people who invented these technologies then migrated out of Africa leading to the ancestors of Neandertals (and Denisovans). This date is encouragingly very similar to the estimated date of Neandertal-modern human separation, at 270–440 kya (Green et al., 2010).

The major problem with the African-origin hypothesis for the common ancestral population of Denisovans, Neandertal and modern humans is that it cannot explain the fossil evidence of sharing of traits between Neandertals and 500–600 kya *Homo heidelbergensis* in Europe. If an African origin is true, these shared traits either would need to be explained by (i) homoplasy or (ii) alternatively reflect gene flow from the *Homo heidelbergensis* natives of Europe into migrants from Africa who might have subsequently replaced them. There is no evidence for gene flow in the data, although this does not prove that it did not occur. Gene flow would predict that present-day Africans are closer to Denisovans than to Neandertals, but we detect no evidence of an archaic element in Neandertals not seen in the Denisovans, and indeed, a hint of the opposite (Reich et al., 2010).

Denisovans – a new challenge for understanding archaic human migrations

The recent sequencing of the genome of a hominin from Denisova Cave in southern Siberia showed that the Denisovans were a population of archaic hominins that was a sister group to Neandertals but that was also distinct in regard to its genetics and its dental morphology. We know almost nothing about the Denisovans from non-genetic information or material outside of Denisova cave. For the Neandertals, there is a rich fossil record including many archaeological sites and a clear understanding of their stone tool tradition and geographic distribution. In contrast, we are not able to tie the Denisovans to particular fossils or tool use traditions outside of Denisova Cave.

We now know, however, that Denisovans were spread across an extraordinarily broad geographic range, and were not an isolated population in central Siberia. The reason for this is that the Denisova genome sequencing paper showed that the relatives of the Denisovans contributed genetic material to the ancestors of present-day New Guineans 9,000 kilometers away (Ibid.). It seems unlikely that the gene flow with New Guinean ancestors reflects a history in which the migration of modern humans from Africa to New Guinea more than 45,000 years ago took a path through southern Siberia. Recent work with Mark Stoneking (in submission) has analyzed the signal of Denisova gene flow in many island southeast Asian populations, and provided circumstantial evidence that the gene flow may have occurred in southeast Asia itself, since Aboriginal Australians, New Guineans and Philippine Negritos sharing the signal, while Andamanese Negritos and Malaysian Negritos who are also ancient populations from southeast Asia do not.

Given that the Denisovans seem to have been distributed across a very large geographic region, why is there not an archaeologically well defined entity with which we can identify them? It is tempting to hypothesize that the enigmatic Mapa and Dali fossils from China might be related to the Denisovans (Ibid.), and we could learn more about this if we had better morphological information on the people from Denisova Cave. Given that the Denisovans are a sister group

to Neandertals and only slightly more distantly related to modern humans, it is also tempting to hypothesize that they might be similar to the putative *Homo heidelbergensis* ancestors of all three groups. However, there is no *Homo heidelbergensis* fossil record in Asia, which is difficult to reconcile with a population that was geographically spread from southern Siberia to southeast Asia.

Conclusion

In this essay, the author has described the evidence as he understands it for at least four major human dispersals between Africa and Eurasia in the last two million years. It seems important to understand how the human populations who were living as recently as 50,000 years ago throughout Africa and Eurasia – including modern humans, Neandertals, Denisovans and *Homo floresiensis* – are related to these original migrations.

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**THE MIDDLE TO UPPER PALAEOLITHIC TRANSITION
IN EURASIA AND NEANDERTHAL “EXTINCTION”:
ANALOGIES FROM THE CIS-BAIKAL NEOLITHIC OF SIBERIA
AND CANADIAN ARCTIC CULTURE HISTORY**

Introduction

The Middle to Upper Palaeolithic transition in Eurasia remains intensely debated. Scenarios argue for a single, monocentric, monophyletic origin from Southwest Asia, spreading west and east, or multicentric, multilineal, homotaxial developments (Derevianko, 2009; 2010; *The Emergence...*, 1990; Vishnyatsky, 2008).

No consensus exists about what caused the fate of the Neanderthal evolutionary group. Most, relying entirely on negative evidence, invoke extinction due to inability to cope with the MIS 3 Interpleniglacial sharp bioclimatic oscillations, limited cognitive and innovative capabilities (Mellars, 1996), shrinking demography. They are falsified by evidence of long-term versatile land use strategies, coping with varied Mid- and early Late Pleistocene habitats and bioclimatic fluctuations, technological innovations and cognitive repertoires.

Both issues are discussed by analogical sources inference. Some archaeologists reject analogical arguments as unreliable, though scientific theory rests mainly on analogy (Harré, 1972: 171–175). The comparative sources considered for the subject issues are the Cis-Baikal Siberian Neolithic Mid-Holocene horizons series, and the Canadian Arctic Palaeoeskimo to Neoeskimo Late Holocene culture history.

The Cis-Baikalian Neolithic and Canadian Arctic sequences each show linear continuity through change and biocultural replacements similar to the Upper Palaeolithic emergence. Bioclimatic stress or innate behavioural limitations fail to explicate Neanderthal “extinction”. The Cis-Baikal Neolithic and Canadian Arctic sources offer guidelines for a holistic investigation of Upper Palaeolithic emergence and Neanderthal extinction dynamics. Culture historical processes and Homo intraspecific polytypic variability remain plausible interpretations.

The Subjects

The Neanderthal Evolutionary Group

It emerged in Europe from the *H. heidelbergensis* morphospecies, spreading to the Near East, Central Asia, Western Siberia. Neanderthal remains generated studies and debates about total morphological pattern and phylogeny. Microevolution, intra-specific variability, restricted but significant gene flow (Yotova et al., 2011) favour a subspecies taxonomic diagnosis (Wolfpoff, 2009).

Archaeological repertoires of subsistence, land use strategies, technological innovation, cognition repertoires, apposite with a subspecies verdict, refute implicitly (Rolland, 1999; Zilhão, 2010) psychogenetic limitations causing the Neanderthal demise:

A broad-spectrum omnivorous diet complemented specialized medium and megaherbivores exploitation: Abri des Pêcheurs Freshwater fishes; Les Canalettes Freshwater fishes; Grotte XVI Salmon; Gibraltar Caves Marine shellfish; Los Aviones Marine shellfish; Las Perneras Marine shellfish; Moscerini Cave Marine shellfish; Amud Cave Edible cereal seeds phytoliths; Abri Agut Edible wild pulses; Lehringen Burnt hazelnuts; Rabutz Burnt hazelnuts; Weimar-Ehringsdorf Burnt nuts, hazelnuts, apples, mushrooms;

Neanderthals settling Mediterranean, temperate Atlantic, periglacial, boreal, continental habitats and occupying alpine high latitudes indicate ecological polymorphism;

Lithic, bone and teeth, shell technologies showed innovative time-binding trends: Achenheim Intensifying exploitation of finer-grained lithic materials; Champ-Grand Long distance >400 km transport of exotic flints; Late Pleistocene Northwest Europe True blade-core flaking emergence; Umm el Tlel, Kuneitra, Königsau, Inden-Altdorf Hafting with bitumen, glue; Canalette Coal burning fuel; Inden-Altdorf, Abric Romani, Raj Cave, Molodova Dwelling, artificial protective structures;

Materially expressed cognitive behaviour evidence: Intentional burials at Middle Palaeolithic sites of West Eurasia (Defleur, 1993); Combe-Grenal, other sites: defleshing indications, probable secondary burials; Moula-Guercy: defleshing, ritual cannibalism. Collective representations, some foreseeing figurations (Leroi-Gourhan, 1964: 69): Swanscombe Middle Gravels Handaxe with embedded Cretaceous echinoid bivalve; Cueva Antón Perforated pecten shell painted outside with goethite and hematite; Los Aviones Shells as red ochre palettes; Bruniquel Artificial stalactites arrangement around a stalagmite circle; Le Maras-3 1 m red ochre circular floor between blocks with reindeer bones, tools, large quartz hammerstone with ochre percussion stigmas; Grotte Néron Trimmed bottom pebble pot with red ochre traces; Roche-Cotard Peripherally worked trapezium flint flake and vertical natural tubular perforation with purposefully inserted bone splinter across; Arcy sur Cure, Hyène Deposit with introduced 2 iron pyrite blocs, 1 spheroid fossil polyp, 1 fossil gastropode; Riparo Fumane Raptors bones cut marks near feather insertion areas; Oldisleben Wedge-shaped 16.6 cm long, 3.8 wide bone fragment with a set of 13 sub-parallel perpendicular

artificial clear incision grooves upper right, and 8 diagonally arranged grooves, lower left. A bone with schematic human outline; Tata Rounded mammoth tooth with red ochre traces.

The Middle to Upper Palaeolithic Transition

Table 1 outlines the Late Pleistocene Middle to Transitional and Classic Upper Palaeolithic succession in Western Eurasia and Siberia. Multilinear series indicate change through continuity from Middle to Transitional Upper Palaeolithic, followed by a stratified classic Upper Palaeolithic threshold with a broader range of material culture expression and population replacement. The series suggest Western Eurasia and Siberia constituting an accelerating cultural differentiation and intensification ferment (Vishnyatksy, 2008), as function of cultural antecedents magnitudes (Rolland, 1999: 329, Table 3). Scant evidence linking Transitional and early Upper Palaeolithic horizons and fossil humans during MIS 3 due to differential bone preservation conditions (Bouvier, 1971). Neanderthals remains a likely agency for the linear Middle to Upper Palaeolithic Transition in Europe.

The Sources

Analogical Inferences in Archaeology. Reactions against analogical inferences (Gould and Watson, 1982) claim that searching for similarity or identity relations remains fundamentally faulty. Misleading if misused, analogy remains indispensable (Ascher, 1961) for opening new research lines. Analogical argument logic transposes selectively information sources to subject for *similarities* or *dissimilarities*, comparing variable sources and subjects showing similarities but evaluated against dissimilarities (Wylie, 1985: 93–107).

Table 1. Late Pleistocene Middle to Transitional to Classic Upper Palaeolithic Succession in Western Eurasia and Siberia

Europe	Near East	Siberia
<i>Classic Upper Palaeolithic Technocomplexes</i>		
<hr/>		
<i>Transitional Upper Palaeolithic</i>		
Chatelperronian, Néronian, Uluzzian, Fumanian, Szeletian, Bohunician, Bacho Kirian, Streletskian	Ahmarian, Baradostian	Altai Complex, Mal'ta Transitional, Makarovo Stratum
<i>Later Middle Palaeolithic technocomplexes</i>		

Table 2. Cis-Baikalia Late Mesolithic to Neolithic/Early Bronze Age of Siberia and Canadian Arctic Palaeoeskimo to Neoeskimo Successions

Cis-Baikalia*	Canadian Arctic
Early Bronze Age: Glazkovo 5200–3400	Inuit 1500 + AD
Late Neolithic: Isakovo, Serovo 6000–5000	Thule 1000–1500
Middle Neolithic 7000–5800	Early, Middle, Late Dorset 500 BC – 1000 AD
Early Neolithic: Kitoi, Other 8000–6800	Pre-Dorset/Independence 1500–500 BC
Late Mesolithic 8800–8000	Northeast Asia Late Neolithic

* Calibrated BP.

The Cis-Baikal Neolithic/Bronze Age of Eastern Siberia. The Siberian foraging Neolithic periodization (Table 1), known from mortuary sites, developed from local Mesolithic roots (Kuzmin, 2007; Prehistoric Foragers..., 2003; Weber and Bettinger, 2010; Weber et al., 2002; Prehistoric Hunter-Gatherers..., 2010). This taiga-dominated continental region comprised a biogeographic mosaic of habitat resources influencing Mid-Holocene subsistence and land use strategies. Time series show technological innovation thresholds and cyclical, rapid changes.

Late Mesolithic: No mortuary site; hunting, fishing, sealing (?); dispersed mobile groups; little social differentiation.

Early Neolithic: Kitoi cemeteries; pottery; deer hunting, fishing, sealing, narrow food spectrum, supplies erratic; low mobility, large local group and family sizes, social differentiation. Population cranial phenotype varied, robust, archaic-like (Gerasimova, 1992; Mamonova, 1983).

Middle Neolithic: No mortuary sites; no population or cultural hiatus (Kuzmin, 2007); Late Mesolithic similarities.

Late Neolithic/Early Bronze Age: New Europoid-like Serovo, Glazkovo populations; new technology (composite bow, tanged arrowheads, fish lures); broad spectrum, abundant subsistence, more deer, sealing, less fish; higher intergroup mobility, smaller local groups, larger regional population; little social differentiation.

The Canadian Arctic Palaeoeskimo to Neoeskimo Succession

Settling this vast marginal unoccupied far north triangle of tundras and frozen coastlines with extreme harsh climate, precarious, dispersed, seasonally constrained food resources, scarce raw materials, became feasible by specialized technologies, versatile scheduling, flexible extensive social networks repertoires (Eastern Arctic Prehistory..., 1976; McGhee, 1982; 2001; Rudenko,

1961; Wright, 2001). Although Palaeo- and Neoeskimo peopling waves were separate, human biology, ethnic, linguistics point to common ancestral origins.

Pre-Dorset-Independence: Obscure origin, probably Northeast Asia and Bering basin; two tradition streams; a first rapid expansion through Canadian Arctic, West Greenland (“Inuk” hair DNA, affinities with Siberian Nganasans, Koryas, Chukchis); high mobility, cultural homogeneity, flexible social units; focus on land mammals (muskox, caribou), plus sealing, fishing; finely made small flint tools; winter tent camps, snow shelters (?).

Dorset Series: Dorset culture developed directly from Pre-Dorset, adapting to colder climate change in Central, Eastern, High Arctic, Labrador Strait; bow and arrow loss; small flint, jade, quartz tools, jadeite slate, simple harpoons; small bone, ivory animal, human figures; large, semi-subterranean rectangular winter houses; muskox, caribou hunting, walrus, seal hunting.

Thule/Inuit: New population, probably emerging from the Bering Basin cultural ferment, spread rapidly throughout the Arctic. Progressively displacing Dorset peoples. More advanced technology: toolmaking shift to bone, ivory, antler, native copper, Greenland’s Cap York meteoritic iron; dogsleds, snow houses, toggle harpoons; new focus on large sea mammals (whale, walrus, narwhal, seals) accessed by “umiak” and “kayak”. Historic Inuit direct ancestors.

Discussion and conclusion

“Specific comparative analogical” sources offer guidelines with refined chronology and a broader biological, demographic, ecological, cultural range; ethnological, linguistic historical linkage.

Dissimilarities. Culture historical changes in the circumscribed Cis-Baikalia region, influenced by habitat diversity and resources fluctuations, were not determined by the dominant continental climate. Kitoi and Transitional Upper Palaeolithic show comparable cultural diversity, though the latter without population physical stress, or an interim phase like Middle Neolithic; Canadian Arctic culture historical changes, conditioned by episodic fluctuations in a perennially forbidding environment, necessitated relocating and animal food staple shifts. Each cultural Period shows widespread cultural homogeneity cohesion, conservatism over vast territories fostered by mobility, flexible subsistence and social organization. Although Canadian Arctic and the Neanderthal Middle/Transitional Upper Palaeolithic realms were large-scale, the rapid peopling of vacant spaces happened during the Mid-Holocene, whereas Europe was occupied continuously since Early or Mid Pleistocene times, amalgamating different ecosystems and intensifying a land-based subsistence, instead of shifting to specialized coastal exploitation.

Similarities. Sources and subjects, though separated in time and without historical connections, show an analogous (not identical) culture development typology highlighting continuity through change, followed by sharp discontinuity thresholds involving population replacements, technological innovation, nu-

merous, specific, more articulated culture elements (Kroeber, 1963: 222–223). These accelerating punctuated time series indicate a determinant role of cultural antecedents. Population replacements in all three sources and subjects accommodate Homo polytypic intraspecific variability ranges (demes, subspecies), ruling out environment change stresses (Banks et al., 2008; Sørensen, 2011) or psychogenetic limitations. Pre-Dorset to Dorset linear transition is analogous with Middle to Upper Palaeolithic Transition, though the former involved subsistence and settlement shifts conditioned by climatic change. Kitoi shows a cultural heterogeneity comparable with Transitional Upper Palaeolithic, while the Serovo, Thule and Aurignacian horizons present an analogous geographic ubiquity with increased cultural homogeneity.

Guidelines. This trial formulation remains a descriptive pattern typology of culture developments, which entails identifying efficacious variables as the next step. Technological change stands out for both sources and subjects, though pointing to other evidence. Technology, as open behavioural system interacting with the environment, social organization and cognitive repertoires, may reflect intensification and differentiation changes in social and cognitive systems (Moyer, 2003: Chapters VI, VII), a dimension overlooked by Palaeolithic research. The puzzling protracted multi-generational Neanderthal disappearance resulted from complicated interactive contacts (avoidance, confrontation, competitive displacements, restricted gene flow) with expanding *H. sapiens sapiens*, whose efficient technology fostered demographic growth. Comparing the Kitoi and Serovo social organization, and exploring the Late Dorset/incoming Thule inter-populations contact dynamics could improve understanding the eventual Neanderthal demise.

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**THE BOHUNICIAN ON THE MIDDLE DANUBE:
DATING, RAW MATERIAL PROCUREMENT, TECHNOLOGY,
TYPOLOGY AND ITS RELATIONSHIP
TO LOCAL CONTEMPORARY CULTURAL UNITS**

The very beginning of the Upper Paleolithic on the Middle Danube is characterized by a behavioral shift. People avoided protected sites in caves and rock-shelters located in highlands, which were settled during the Middle Paleolithic (MP), and occupied the open landscape instead. Most Early Upper Paleolithic (EUP) sites are strategically located at elevated locations flanking big river valleys and basins.

During the MP/UP transitional period, i.e. 50–40 kya, two main cultural units were documented in Moravia: the Bohunician and the Szeletian. While the fully UP culture – the Aurignacian – is known from nearby Austria (Willendorf), in Moravia it was documented only in its middle phase dated to between 34–40 kya. In recent years, all three cultural units were the subject of new investigations, both artifact analyses and field research. New field surveys and excavations increased the number of stratified and absolutely dated collections and yielded new data used in debates about the MP/UP transitional period on the Middle Danube. The results relevant to the Bohunician are the subject of this paper.

The main Bohunician site-cluster is represented by a significant concentration of sites around the Stránská skála cliff (the outcrop of Stránská skála-type chert) in Brno basin. Other important site-clusters are located at Ondratice/Želeč, Bobrava river valley and the Mohelno area. Isolated implements which show the use of evolved Levallois technology are known from many other sites; however, their relationship to the Bohunician is not clear. Only Bohunice (several units), Stránská skála (several units), Tvarožná and Líšeň have been excavated. The remainder of the sites are surface collections lacking a stratified context.

The Bohunician has been dated by ¹⁴C, TL IRSL and OSL methods (Richter et al. 2009 with ref., Nejman et al. in press). While the (calibrated) radiocarbon dates have a relatively wide spread (between 40–48 kya), a TL weighted mean result of eleven artifacts from Bohunice 2002 excavation yielded a result of 48.2 ± 1.9 kya. Based on the radiocarbon record and comparing the Bohunician radiocarbon dates with Szeletian dates (Vedrovice V, Želešice) and Early

Aurignacian (Willendorf) sites, the Bohunician may have been contemporaneous with both of the latter mentioned cultural units.

The Bohunician lithic economy is characterized by utilization of local cherts supplemented by infrequent imports (up to max. 10 %). The Stránská skála-type chert was utilized in the Brno basin, local quartzite and chert were utilized in Ondratice/Želeč and in Krumlovský les area the local Krumlovský les-type chert dominated. Radiolarite was imported from the White Carpathians and erratic flint from northern Moravia.

The Bohunician technology was originally defined as a mixture of Levallois technology and Upper Paleolithic blade core reduction. Later, based on the analysis of refitted cores from Stránská skála where both techniques were used on the same core, the definition was refined as a contextual fusion of Levallois and Upper Paleolithic technologies (Škrdla, 2003). All reconstructed cores show the tendency towards production of Levallois points (or a series of points) as the target artifact. In this concept blades were removed in order to shape the frontal surface of the core and represent (technologically) a secondary product. However, the blade blanks were frequently used for tool production. Bifacial reduction plays a specific role in producing leaf-shaped points documented only at the Brno-Bohunice type site.

The Bohunician typological spectrum represents a mixture of MP tool types including points (Levallois, bifacially flat-retouched and leaf-shaped, Mousterian, etc.) and sidescrapers, with UP tool types represented mainly by endscrapers and infrequent burins. The UP tool types were made on Levallois points.

In recent years (2002-present) a new EUP project was established in cooperation between Institute of Archaeology in Brno and University of Minnesota in Minneapolis (with more participating universities, institutes and individuals). The main aim of the EUP project is a search for new EUP sites and undertaking excavations in order to refine the stratigraphic and chronological contexts of the Bohunician and to study the homogeneity of Bohunician collections.

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TESTING FOR POPULATION ADMIXTURE USING GENOMIC DATA

We have entered the era in which the sequencing of whole genomes, including genomes recovered from fossils, is relatively easy. Genomic data can answer previously unanswerable questions about the history of human and other populations. In this paper, we will present a method for analyzing genomic data when one genome is sequenced from each population of interest. This method was used in both the Neanderthal and Denisova genome papers (Green et al., 2010; Reich et al., 2010). David Reich, in another paper, will describe the applications to the Denisova genome in some detail. Here, we will describe the method in general terms and emphasize its utility for testing for admixture between populations including testing for admixture between Neanderthals and the ancestors of present-day non-African populations.

Nucleotide configurations

The starting point is a set of 4 aligned DNA sequences, one from each of four populations. In this context, a population is a group that is considered separately and without regard to taxonomic status. We assume one of the populations is known to be an outgroup with a history quite distinct from the others for a long time. The other three populations are ones whose past relationship is in question. In the analysis of the Neanderthal genome, chimpanzees were the outgroup and the interest was in the relationship between Neanderthals and various pairs of present-day human populations from which genomic sequences were obtained (San, Yoruba, French, Han Chinese, and Papuan).

At each nucleotide position in the aligned sequences, we denote the nucleotide on the outgroup chromosome by an A (for ancestral), regardless of whether it is an A, C, G or T. If a different nucleotide is found at the same position in the sequence from any other group, it is denoted by a B and called the derived nucleotide. We do not care what the derived nucleotide is, only that it differs from the ancestral nucleotide. We will ignore the possibility that a third nucleotide is found. Sites at which three or four nucleotides are found are eliminated from further analysis because they indicate either a high mutation rate or, more likely, error in at least one of the sequences.

With the requirement that the outgroup always has an A, there are 8 possible configurations of A's and B's: AAAA, BAAA, ABAA, AABA, BBAA, BABA, ABBA, BBBA, where the populations are written in order with outgroup always last. AAAA indicates that all four sequences have the same nucleotide at a site, BAAA indicates that only population 1 has a different nucleotide, etc. We focus our attention on the three configurations which have two B's and two A's. There are two reasons for doing so. First, observing the derived nucleotide in two of the four sequences reduces the possibility that sequencing error created the pattern. In contrast, if only one sequence differs from the others at the site (BAAA, ABAA, and AABA), the single derived nucleotide could either be the result of a real mutation or of sequencing error. Second, the configuration tells us something important about the history of the nucleotide position. The mutation rate for nuclear genes is so low that the two derived nucleotides had to be descended from the same mutation at some time in the past and then inherited by both descendant chromosomes, as illustrated in Fig. 1*a*. As shown, the configuration BBAA implies that the sequence from populations 1 and 2 at that site had a common ancestor (i. e. they coalesced) more recently than did either 1 and 3 or 2 and 3.

The genetic history of each nucleotide position is called the “gene genealogy.” If there has been recombination, different positions have different gene genealogies. Therefore, different sites may have different configurations of derived and ancestral alleles. However, by comparing a large number of nucleotide positions, which is possible with genomic data, any feature of the history of the three populations of interest that tends to cause one type of gene genealogy to occur more often than another will be reflected in the frequencies of the three configurations that have two ancestral and derived nucleotides each.

We start by assuming a simple model of population history, one in which populations 1 and 2 separated from each other, and before that their ancestral population separated from population 3, as shown in Fig. 1*b*. There are no genes exchanged among any of these populations after they are separated. In that case, the populations are behaving as good species, whether or not they are recognized as having specific status. Now consider the gene genealogy of a single nucleotide position. The three possible gene genealogies are shown in Fig. 1*c*. The question is which of the gene genealogies is more likely, given the population history we have specified. The answer is obtained using what is called coalescent theory in population genetics. The coalescent theory necessary to predict the probabilities of the three gene genealogies under several models of population history is well developed (Durand et al., 2011). Here we will summarize that theory in non-mathematical terms, trying to summarize the qualitative predictions under different assumptions about population history.

The basic idea of coalescent theory is that each nucleotide position has a gene genealogy that represents the sequence of meiotic events from ancestor to descendant going back in time. When two lineages in a gene genealogy are separate, it means that the homologous positions in two different sequences have

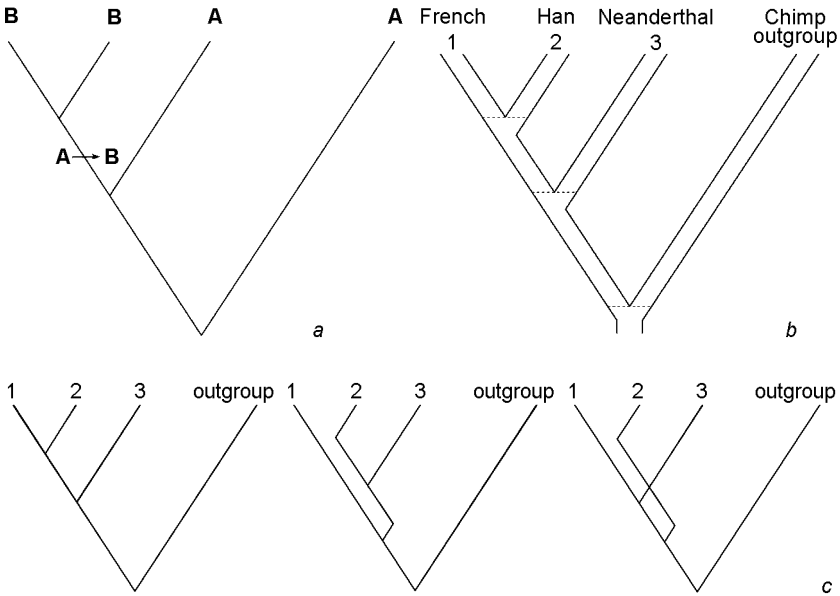


Fig. 1. a – illustration of gene genealogy that results in the configuration BBAA after one mutation from the ancestral allele (A) to the derived allele (B); *b* – illustration of a history of the French, Han Chinese, Neanderthal and Chimpanzee populations which assumes no gene flow after population separation; *c* – illustration of the population history of the three gene genealogies that can create a pattern with two derived alleles (BBAA, ABBA, and BABA) with a single mutation.

distinct ancestries. When two lineages join, then the two lineages are descended from a single ancestral chromosome. Considering the process going backwards in time, we say that the two lineages coalesce. Going forward in time, a coalescent event indicates that an individual has two offspring who are siblings. Each sibling carries a lineage that is ancestral to one of the two descendants whose sequence is being considered.

Coalescent theory was developed in the 1980s by Griffiths, Hudson, Kingman, Tavaré and others, and is summarized in the recent textbook by Wakeley (2009). There are four basic ideas from coalescent theory that are relevant for the discussion here. First, any two lineages in a randomly-mating population have a probability $1/(2N)$ per generation of coalescing, where N is the effective size of the population. The implication of this is that if there are three lineages in a randomly-mating population, each pair of lineages has the same chance of coalescing. Second, two lineages in different populations have no chance of coalescing while the populations are distinct from each other. Third, lineages from separate populations will be able to coalesce in the populations ancestral to those populations. For example, in Fig. 1*b*, lineages initially in populations 1 and 2 will have the opportunity to coalesce in the population ancestral to the

those populations. However, it is not certain that they will coalesce in that population. Whether they do so or not depends on the length of time that population remained distinct (i. e., the length in generations of the internal branch of the population tree). If the branch length is much less than $2N$, it is quite possible that the two lineages will not coalesce, but if the branch length is much longer than $2N$ is it quite likely that they will. Fourth, gene flow from one population to another moves a lineage of the gene genealogy from one population to the other with a probability that depends on the rate of gene flow. For example, assume there was gene flow from Neanderthals (population 3) to the ancestors of the present-day French population (population 2). The effect of that gene flow is to move the lineage from the French population into the Neanderthal population, as shown in Fig. 1c. As a consequence, gene flow allows two lineages to coalesce more recently than if there had been no gene flow.

With chromosomes sampled from each of four populations, each site has its own gene genealogy. If there is no recombination in a genomic region, as is the case for mitochondrial DNA and the non-recombining portion of the Y-chromosome, then all sites have the same gene genealogy. For nuclear DNA, recombination ensures that different sites have different gene genealogies, although sites that are closely linked are likely to have the same or nearly the same genealogies. The coalescent theory outlined above allows us to predict the probabilities of each of the three gene genealogies that can produce one of the nucleotide configurations (BBAA, ABBA, BABA). We consider only three gene genealogies because we assume that the nucleotide configuration was created by a single mutation from the ancestral to the derived nucleotide.

First, for the population history represented by Fig. 1b, we can see that genealogy I is more likely to be found than either II or III. The reason is that, because populations 1 and 2 are descended from a common ancestral population, there was extra time for the lineages from populations 1 and 2 to coalesce in that ancestral population and result in genealogy I. In order for either genealogy II or genealogy III to be produced, lineages 1 and 2 would have to have not coalesced in that ancestral population and then either lineages 1 and 3 or 2 and 3 would have to have coalesced first in the population ancestral to all three population. Therefore, with the population history shown in Fig. 1b, the configuration BBAA is more likely to be found than either BABA (which is associated with genealogy II) or ABBA (which is associated with genealogy III).

We can also conclude that genealogies II and III are equally likely because they can both be produced only if the ancestral lineages from each of the three populations are present in the population ancestral to all three. In that population, each pair of lineages has the same chance of coalescing, so lineages 1 and 3 have the same chance of coalescing first as do lineages 2 and 3. Therefore the configurations BABA and ABBA should be equally frequent if the population history in Fig. 1b is correct. Therefore, the qualitative predictions of coalescent theory tell us that $n_{BBAA} > n_{BABA} = n_{ABBA}$ for this population history, where n_{BBAA} etc. indicates the number of nucleotide positions with each of the configurations.

We illustrate the previous discussion with results from Supplement 15 of the Neandertal genome paper (Green et al., 2010). For the three populations (French, Han, Neanderthal), the counts are $n_{BBAA} = 364,200$, $n_{ABBA} = 74,477$, and $n_{BABA} = 73,089$. A blockjackknife statistical test which takes account of the fact that sites close to one another are not independent shows that the last two numbers are not significantly different.

These data are consistent with the population history in Fig. 1b with the French and Han populations being populations 1 and 2 and the Neanderthal being population 3. That is not the only population history these data are consistent with, however. We would expect the same qualitative results if there were ongoing or past gene flow between the French and Han populations. Gene flow between these two populations in either or both directions would only increase the probability that the Han and French lineages would coalesce and hence would increase the number of BBAA configurations while not disturbing the equality of the ABBA and BABA counts. Also, gene flow between the Neanderthal and the population ancestral to the French and Han populations would preserve the equality of the ABBA and BABA counts. Such gene flow would be equally likely to move the Han or the French lineage into the Neanderthal population, if they had not already coalesced.

When the ABBA and BABA counts are unequal, some feature of the population history created the asymmetry. It is convenient to quantify the extent to which these counts are unequal using the normalized difference called the D -statistic,

$$D = \frac{n_{ABBA} - n_{BABA}}{n_{ABBA} + n_{BABA}}, \quad (1)$$

which was suggested by David Reich and Nick Patterson when analyzing the Neanderthal genome. $D = 0$ means the counts are equal; $D > 0$ implies that population 2 is more similar to population 3 than is population 1 and $D < 0$ implies that population 1 is more similar to population 3 than is population 2.

We consider the situation in which $n_{BBAA} > n_{ABBA}$, n_{BABA} but for which D is significantly less than 0. This is what was found in the Neanderthal study when population 1 was one of the three non-African populations (French, Han and Papuan) and population 2 was one of the two African populations (San or Yoruba). For example, D (French, San, Neanderthal) = -0.042 ± 0.005 ($n_{ABBA} = 95,347$, $n_{BABA} = 103,612$). This and similar results tell us that something in the history of these populations has destroyed the symmetry expected from the simple history represented by Fig. 1b. There are at least three possibilities which we will discuss in turn.

(i) *Gene flow between Neanderthals and the ancestors of French*: Gene flow between Neanderthals and the ancestors of the French population after the ancestors of the French and San populations split would create extra similarity of the French to the Neanderthal and account for the negative D -statistic. The reason is that gene flow would create additional chances for the French and Neanderthal

genetic lineages to coalesce, as illustrated in Fig. 2*a*. The San and Neanderthal lineages would not be able to coalesce until they were both present in the population ancestral to present-day humans and Neanderthals.

(ii) *Gene flow between San and a “ghost population”*: It is also possible that there was a population for which we do not have genetic data that exchanged genes with the San population (Fig. 2*b*) and caused them to be slightly less similar to the Neanderthal than the French population is. Following Beerli (Beerli, 2004), we call this other population a ghost population because it affects patterns in the genetic data even though it cannot be seen itself. For gene flow from a ghost population to result in a negative *D*-statistic, however, requires the strong assumption that the ghost population had a separate population history until some time before the ancestors of Neanderthals and humans were descended from an ancestral population, as shown in Fig. 2*b*. It is not enough for there to have been gene flow with other present-day African populations from which we do not have DNA sequences. Such gene flow almost certainly occurred but it would not cause the San sequence to differ from the Neanderthal more than the

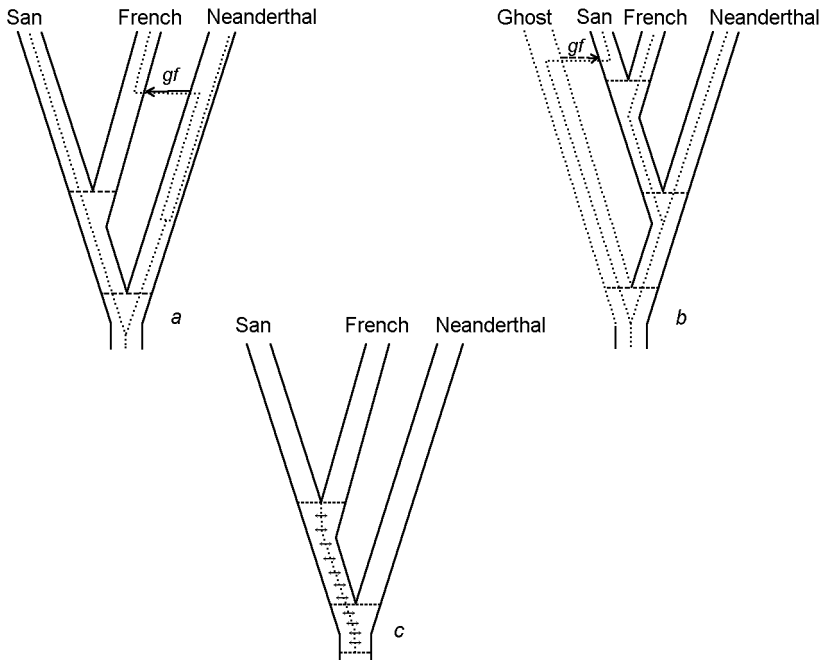


Fig. 2. Illustration of three possible population histories that could account for a negative *D*-statistic which indicates that French are slightly more similar to Neanderthals than are the San.

a – recent gene flow between the ancestors of Neanderthals and the ancestors of French; *b* – recent gene flow from a highly diverged “ghost” population into San; *c* – persistent subdivision in the population ancestral to the French and San populations.

French sequence does because all the African lineages would have the chance to coalesce before the ancestral human population joined the ancestors of the Neanderthal population. In comparing Neanderthals with present-day humans, it is not logically impossible that there was such a distant and completely unknown population in Africa that could have exchanged genes with the ancestors of the San, but there is no evidence that such a population existed. It does not seem to be either parsimonious or likely to assume that gene flow from such a ghost population accounts for the non-zero D -statistic found.

(iii) *Ancient population subdivision*: The third possibility is that there was geographic subdivision of the population ancestral to the modern French and San populations and that this subdivision persisted for long enough in the past that it led to greater similarity of the French and Neanderthals than of the San and Neanderthals (Fig. 2c). The idea behind this model is that before the ancestors of present-day San and French became isolated from one another because of geographic separation, their ancestors might have been partially isolated because of, say, a geographic barrier to dispersal. Such a barrier would not have completely prevented interbreeding between the two subpopulations but it might have restricted gene flow between them sufficiently that coalescence of lineages in the two subpopulations would have been considerably delayed. Population subdivision of this type greatly increases the effective population size. If the subdivision existed before the time that the ancestors of the Neanderthal population could freely interbreed with the ancestors of the French population, then genealogy II would be somewhat more frequent than genealogy III, thus accounting for the negative D -statistic observed. Our calculations for this model show that gene flow does not need to be greatly restricted in order to be consistent with $D \approx -0.04$ – 0.05 (Durand et al., 2011).

This hypothesis about population history is also logically possible, but like the hypothesis of gene flow from a ghost population, it does not seem to be a very likely explanation for the patterns in the human-Neanderthal data set. It requires not only that there was some subdivision, which is quite probable, but that the subdivision persisted for the several hundred thousand years in the population ancestral to present-day human populations. Although such long-lasting subdivision might well occur in populations of animals that have narrow ecological tolerances and restricted dispersal abilities, it does not seem plausible that such a barrier could severely restrict gene flow for hundreds of thousands of years in the ancestors of present-day humans, who were almost certainly highly mobile and adaptable.

We conclude, then, that the non-zero D -statistics found when a non-African population (French, Han or Papuan) was compared with an African population (San or Yoruban) is caused by gene flow between Neanderthals and the ancestors of present-day non-African populations. What we know about humans and their ancestors makes the other two explanations appear much less likely. In the analysis of other populations, however, prior knowledge might point to a different conclusion. Non-zero values of D -statistics might indicate gene flow from

a ghost population or ancient population subdivision, rather than gene flow among the populations for which sequence data are available.

In summary, we have emphasized the utility of configuration counts and the D -statistics derived from those counts for understanding the history of populations from which DNA sequence data are available. The analysis of one sequence per population may seem quite restrictive, but it has some distinct advantages. When two or more sequences are available from the same population, the gene genealogies and corresponding configuration counts depend not only on the history of population separation and gene flow but also on the effective size in each population. That adds a level of complexity and uncertainty that may make it difficult to determine whether there was past gene flow between populations. In contrast, the configuration counts and D -statistics are acutely sensitive to asymmetries in population history and do not depend so strongly on assumptions about past population sizes, which are necessarily poorly known.

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MORPHOLOGY AND TAXONOMY OF THE FOSSIL HOMINID IN WESTERN ASIA*

The position of the so-called “disputable finds” in the modern taxonomy of fossil hominids is incredibly complicated and confusing. Among mentioned findings the Palestinian hominids are most hotly discussed. The remains from Skhul and Tabun caves were well described by Ya.Ya. Roginsky in 1977, nevertheless these specimens have not yet found their place in the taxonomy of the paleolithic forms. The mosaic structure of the skull and the skeleton of these hominids forced the scientists to accept the different points of view regarding their status. One believed that Palestinian hominids were half-breeds, the others supposed that they were transitive forms, third scholars considered them as predecessors of *Homo sapiens*.

To make clear the taxonomy positions of mentioned and other fossils from Western Asia the brief description of findings under the question is given below.

1. Qesem cave is situated on the lower western slopes of the Judean Hills, about 12 kilometers east of Tel Aviv and the Mediterranean coast. This is karst cave filled with sedimental rocks. All archaeological findings from Qesem were attributed to Acheulo-Yabrudian cultural complex (AYCC). Thus archaeological cultural layers are dated to Acheulean, that precedes straight Mousterian.

Fauna from the site is quite rich. The remains of deer dominates in the collections. Other species of animals include bison (*Bos*), horse (*Equus*), wild pigs (*Sus*), turtles (*Testudo*), and red deer (*Cervus*). Not all the body parts of the animal were present at the site, that means they were firstly treated far from cave, then cutted and brought in. There were cut marks of stone tools and traces of burnt on the several bones. Many dates testify the cave was inhabited approximately between 420 and 200 ka.

Human teeth were found in the upper and lower cave layers and at least at three different archaeological contexts. Three of those (C1, P3, P4) were found in the lower layers of Amudian context and was dated to about 300 ka. One of the rest teeth (C1) was defined in Yabrudian context and the other four (I2, M3, di2, dm2) were correlated with Amudian context in which the blades dominated.

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The teeth i2 и M3 was found in close proximity one of another. One of the teeth (dm2) dated to 300Ka at the same time the other ones dated to earlier Paleolithic epoch (400–200 ka). The cultural complex (AYCC) where teeth were found is unique to the Levant. It is the local phenomenon spread from Central Siria to Central Israel without any evidence of African or/and European cultural connections. Given dates let us say that hominin specimens from Qesem are the most ancient to date in Southwest Asia.

2. Amud Cave (where the skeleton of young man about 25 years old was found) is situated at the shore of the lake of Gennesaret in Israel. This individual has quite huge cranial capacity (1740–1800 cm³) and was very tall (more than 180 cm). The dating with electron spin resonance method – 50–40 ka.

3. The child skeleton, skeleton and mandible of the adult individual were found at Kebara cave (Israel). The adult mandible has slightly formed mental eminence. Some bones have sapiens traits nevertheless some scientists attribute these findings to the circle of the neanderthal forms. The findings are dated to 61–48 ka.

4. The remains of the 21 individuals with the tools of Moustierian type were found in Jebel Qafzeh cave near Nasareth, Israel. The skeleton Qafzeh 9 of an adult, thought to be a young woman, was the most complete. The male skull Qafzeh 6 is the most well preserved. The most of the anthropologists regards these fossils as the most ancient representatives of *Homo sapiens* out of Africa. They were estimated to be 115–92 ka using modern dating methods.

5. The remains of 10 people of different ages were found in the Mousterian cultural layer of the rock shed Mugaret-es-Skhul of the Mount Carmel, Israel. The series consists of 8 male and 2 female skeletons. The dating of the finds – 100–70 ka. We studied in detail only two specimens. This is individual Skhul V (the skeleton belonged to the tall adult man 30–40 years old) and Skhul IV (the remains belonged to the adult individual of 40–50 years).

6. The woman skeleton was found in Mugaret-et-Tabun cave of the Mount Carmel, Israel. The skull has some neanderthal-type characteristics, but according to occipital region morphology it has similarity with sapiens-type forms. The find is dated to 41 ka (old), 120 ka (new one).

7. Five skulls with postcranial bones described from Shanidar (Iraq). The skeleton of the elderly male (Shanidar 1) is well preserved. It is dated to 46 ka.

We carried out the analysis of the taxonomic status of the number of the disputable Paleolithic fossils according to supraorbital and zygomaxillaris areas, trigonometrical angles of neurocranium and facial cranium, and as well as parameters of the mandible.

It is interesting to estimate the position of the disputable, in our opinion, finds regarding the species taxa of *Homo* recognized to date (Tables 1, 2).

The tables 1, 2 shows that remains Skhul V, Skhul IV and Amud have about 50–60 % of sapiens traits of facial skeleton. Brouken Hill has more neanderthal-type traits, though to some extent displays sapiens-type traits of facial skeleton. Tabun looks more like neanderthal-type.

Table 1. The position of the “disputable finds” according to different traits characterized the skull

Specimen	Brouken Hill	Skhul V	Amud	Tabun
1	n	n,s	n	n
2	n	s	e, n	n
3	n	s	e, n	n
4	n	s	s	–
5	n, s	s	s	–
6	s	s	n,s	–
7	e	n, s	e	e, n
8	n, s	n, s	e, s	–

Notes: 1 – descriptive (non-metric) traits of the supraorbital area; 2 – metric traits of the supraorbital area; 3 – indices of the supraorbital area; 4 – descriptive (non-metric) traits of the zygomaxillar area; 5 – metric traits of the zygomaxillar area; 6 – indices of zygomaxillar area; 7 – trigonometry of neurocranium (braincase); 8 – trigonometry of splanchnocranium. e – *Erectus*; n – *Neanderthal*; s – *Sapiens*.

Table 2. The position of the “disputable finds” according to different traits characterized the mandible

Specimen	Amud	Arago II	Skhul IV	Banyolas	Tabun
1	s	n	s	n	n, s
2	s	e, n	s	e, n	n, s
3	s	–	e	–	–
4	n	e, n	s	e, n	n, e

Notes: 1 – descriptive (non-metric) traits of mandible; 2 – metric traits of mandible; 3 – mandible indices; 4 – mandible trigonometry.

We analyze the results in detail.

Based on the descriptive characteristics the supraorbital region of Amud (Fig. 1) has neanderthal-type traits. These include such expressive traits of the Neanderthals as slightly lowered region and almost absent supraorbital groove in the ofrion area. From the number of metric parameters Amud is similar to Shanidar I, Skhul IV, Arago XXI, Tabun I. In the zygomatic region Amud has untypical for Neanderthals zygomatic notch and also no swelling at the base of the frontal proces of maxilla, that inherent Neanderthals. From the metric parameters and the indices of the zigomaxillar region the finding is close to Oberkassel I, Sunghir I, Fish Hook, and Skhul V. The angular parameters of the neurocranium show the similarity with those of Ngandong XI and Steinheim. The trigonometry of the facial skeleton is similar to that of Skhul V, Florisbad, Sunghir I, Gibraltar I. The lower jaw displays sapiens traits in the number of parameters (even the marks of mental eminence). However, the analysis of the mandible trigonometry showed the closeness of this finding to La Ferrassi and Tabun. This group is characterized by the relatively broad alveolar arch at the

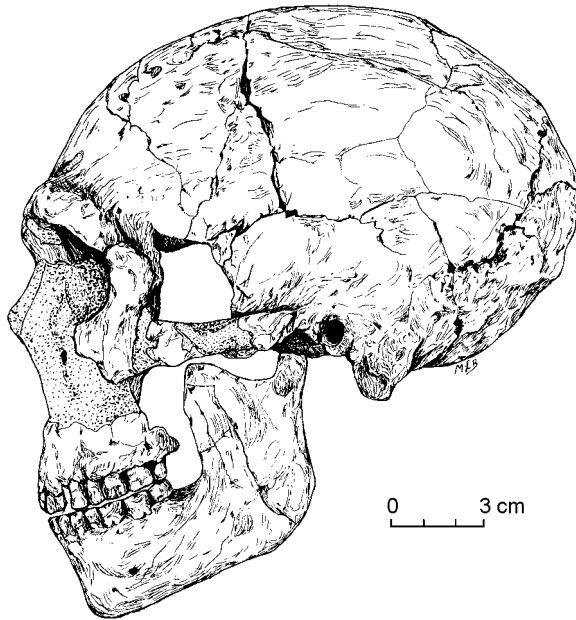
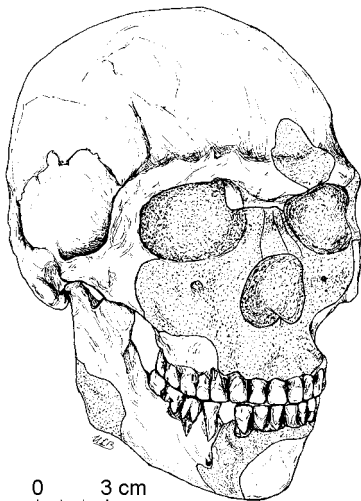


Fig. 1. Amud I.

level of the second molars, low-lying mental foramen and the small size of the angular width.

According to the number of descriptive and metric traits the supraorbital area of Skhul V (Fig. 2) is similar to those of Mladech V and Brno I, therefore, we can say that it has neanderthal-sapiens morphology. The zygomatic area also has sapiens values of the number of parameters. The angle between the frontal and temporal processes of the zygomatic bone is equal to 115° being a marker of the modern man. In addition, the zygomatic area of Skhul V has a fairly high curvature index of the zygomatic bone and of the form of the frontal process.



The mentioned features brings it together with Oberkassel I and Broken Hill. According to the comparative analysis of the form-building angles of the neurocranium Skhul V is close to Amud, Broken Hill and Ngandong XI. Based on the craniotrigonometry parameters

Fig. 2. Skhul V.

they are close to the Upper Paleolithic sapiens and differ from the classic Neanderthal by the relatively higher ear height, the more flattened occiput and more narrow forehead. During statistical analysis of the forming angles of the facial skeleton it has been found that the Skhul V is characterized by the relatively large parameters of the average width of the facial skeleton and the narrow base of the frontal process of the maxilla, the wide nose part of the maxilla and the short temporal process of the zygomatic bone. These features actually bring it together to the Amud, Gibraltar I, Fish Hook, and Florisbad, Sungshir I.

Studying the standard cranial characteristics the scientists have confirmed long ago the presence at Skhul V sapiens-type parameters (large cranial capacity (1518 cm³), high cranial vault, low orbits with sufficiently high and broad face) and neanderthal-type traits (strongly developed brow ridges, a considerable bones thickness, a relatively sloping forehead).

We studied in detail the mandible of Skhul IV. From several traits (such as, for example, the length of the alveolar arch, the length of the three molars) the finding is close to Amud and Banolas. The large transverse diameter of the condyle and the relatively small intercanine width brings the finding to Skhul IV, Amud and La Ferrassi. The comparative analysis of the mandible indices revealed the closeness of Skhul I to Brno III, Oberkassel I and II, Atlanthropus III. The trigonometry of the mandible displays some similarity in mandible-forming angles among the number of the specimens – Skhul IV, Amud, Banyolas, Le Moustier I and II.

The descriptive and metric traits of the supraorbital area of Tabun brings it together with La Chapelle aux Saints and La Ferrassi. The neanderthal promi-

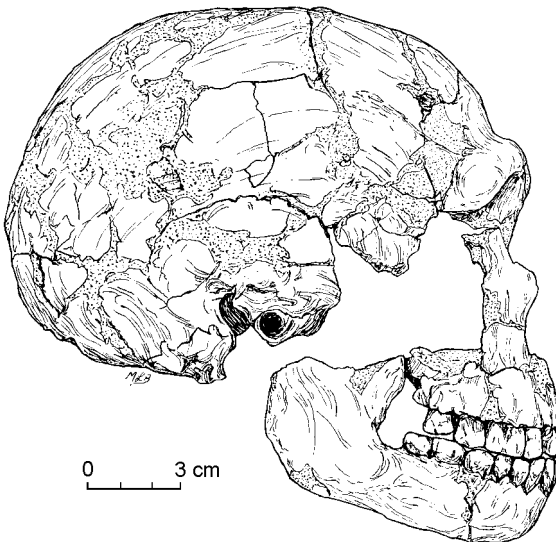


Fig. 3. Tabun I.

nence on the basis of the frontal process is likely present. According to the neurocranium trigonometry data Tabun occupies the intermediate position between the two groups. One group consists of La Chapelle aux Saints, La Ferrassi, Monte Circeo and the other one includes Skhul V, Amud, Brocken Hill and Ngandong XI. The lower jaw in a number of metric, descriptive and trigonometric parameters is similar to those of the Amud and La Ferrassi.

This study confirms one more time the uneven pace of the evolution of the different parts of the skull (Bunak, 1980; Khrisanfova, 1985) and the dependence of the taxonomic significance of the some traits on the imbalance in their phyletic development. Our data statistically confirm the earlier stated hypothesis about the greater rate of the facial skeleton features formation in anthropogenesis, than neurocranium ones. The metric traits change in phylogeny more intensive than structural (descriptive) ones.

The traits characterised the different taxa are also present in the description of Qafzeh, Shanidar (Fig. 4) and Kebara that we did not study intentionally. For example, Qafzeh 6 and 9 along with sapiens features (a high cranial vault, a modern structure of the zygomatic region, the presence of canine fossa, mental eminence) have the archaic features (advanced supraorbital relief, massive mastoid process, prominent occiput).

The researchers suggest three scenarios based in any case on the morphological details of Qesem teeth. Under the first scenario, the Qesem is the local population of archaic *Homo*, settled in south-western Asia during the Middle Pleistocene. This assumption is, to a considerable degree, based on the study of the stone Qesem industry. Its cultural complex tools indicate local origin, with-

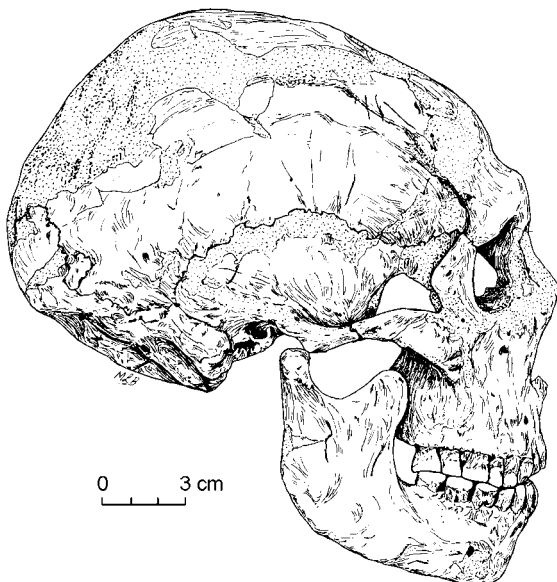


Fig. 4. Shanidar I.

out any connections with African and European cultural complexes of that time. Although we can say that the similarity between the individuals from Qesem and the groups of the individuals from Skhul-Qafzeh localities can be seen at the number of teeth morphological parameters.

The second scenario is one of the large-scale. According to this Neanderthal man was also formed in Southwest Asia. The presence of shovel-shaped and lingual cusped upper incisors can indicate the emergence of the neanderthal morphology complex in Southwest Asia in the Middle Pleistocene. The similar situation was described in Western Europe, where the evolutionary origin of the classic Neanderthals was preceded by “morphological roots”, stretching deep into the Middle Pleistocene. Under this scenario, Southwest Asia would be a region where a subspecies of Neanderthal man – the Southwest Neanderthal would have appeared along with the classic Neanderthals of Western Europe. To the opinion of some researchers Tabun, Amud and Shanidar can be attributed to those Southwest Neanderthal. Nevertheless, the great similarity of the studied teeth samples from Skhul-Qafzeh calls into question the priority of the second scenario, as long as most of the modern scholars considers the mentioned findings belong to the circle of the sapiens-type forms.

Under the third scenario there were more than one Pleistocene human taxon in Qesem. The mandibles teeth stratigraphically overlaid deeper (older). They are identified as belonging to the earlier archaic taxon. The differences between these chronologically disparate patterns can reflect the evolution of the population at the level of the formation of the new species, and may explain the local population replacement.

The advance of these alternative scenarios in Southwest Asia should not affect the emergence of the other points of view. To our opinion, all three scenarios are not enough contradictory. The closeness of the specimen from Qesem to the Neanderthals on the one hand, and to the sapiens-type group of Skhul-Qafzeh on the other, as well as the chronological and morphological intergroup heterogeneity of Qesem endings can testify that this or these specimens from Israel are likely belonged to taxon *Homo heidelbergensis*.

Discussion and interpretation

Western (Southwest) Asia territory was always on the way of migrations from Africa to the East and from the West to Europe. The multiple vectors of the migrations most probably did not allow sympatric forming of the new *Homo* species in this region. Therefore initially *Homo ergaster* and later, probably, *Homo heidelbergensis* (having some sapiens and/or neanderthal morphology traits) formed different metis variants in Western Asia. These variants were maximum stabilized as the subspecies. Exactly these considerations make us to describe the Palestinian hominids as forms of neanderthal-sapientoid (Skhul), erectus-neanderthal (Tabun, Shanidar, Amud) or erectus- sapientoid (Qafzeh 6) origin and define their taxonomy rank according to their predecessor species. It seems that *Homo heidelbergensis* was the predecessor of west asian polymorphous populations in almost all cases. This species with *Homo erectus* and *Homo ergaster*

represents. Currently the most of anthropologists considers this species to be the predecessor of *Homo sapiens* and *Homo neanderthalensis*. And they really have good reasons. If it is true, then *Homo heidelbergensis* as predecessor had to possess separate morphology traits of sapiens and neanderthals. Having later formed complexes of the new species these traits became apomorphies.

While defining the taxonomy rank of the “disputable” findings it is also necessary to take into account dating.

1. The interval from 200 to 100–70 ka.

This period is characterized as the forming of Neanderthals as the species specialized for cold climate. The probability of the coming of neanderthaloid forms (the forms with some neanderthal traits, but not with the whole neanderthal complex) from the East is proved by findings of the mentioned forms in Western Asia (Tabun, Skhul). Few in number and isolated species of *Homo neanderthalensis* was probably formed in Western Europe around 100 ka as the result of the metisation between european and asian erectoid forms. The odontology of the classic Neanderthals suggests the possibility of such metisation. They have asian incisor shoveling and African epicrysta (Zubov, 1995). Probably, the majority of the metis forms became transition to the new species. There is no difference between transition and metis forms in this case. Approximately in that time anatomically modern humans appeared in Africa in the conditions of the marked polymorphism (Item, 2004). It seems the speciation was sympatric and the main destabilizing factors might be the social ones. There are more complicated cultures of the stone tools, the transmission of the information from generation to generation through the sign, speech, probably generalized one signals and supposed variety of the structures of the primitive society among them (Vasilyev, 1999).

The Palestinian forms of the following epoch are most likely metises of erectoid-neanderthaloid forms from East and erectoid – sapiens forms from Africa. Especially there are clear erectoid – sapiens forms Qafzeh 6 and erectoid-neanderthaloid Tabun on this territory (Thoma, 1957).

This period can be described as the formation time of the new Neanderthal species cranial complexes in Europe and the sapiens complexes in Africa. The traits of mentioned complexes are found in migration zones like Western Asia in this period and might be found earlier.

2. The interval from 100–70 to 30 ka.

This is the period of existence and disappearance of the classic Neanderthals in Western Europe. Modern human are wide spread. Nevertheless west Asian hominids of this time (Amud, Shanidar, Kebara) demonstrate the absence of the species cranial complex, they keep showing mosaicism in their cranial characteristics.

The existence of the stable adaptive zones for Upper Paleolithic sapiens and classic Neanderthals at the same time on the same territory can be probably explained not only by their geographic but also by population conditionality.

The complexes of the apomorphic traits in *Homo neanderthalensis* and *Homo sapiens* are typical for this period – the time of coexistence of the mentioned species.

In our opinion all the forms in transitive unstable adaptive zones, possessing any part of erectoid traits must be referred to *Homo erectus*, *Homo ergaster*, *Homo heidelbergensis*. And their temporary unrevealed position in taxon can be described by the term “the circle of forms”. The same can be said about so-called west asian forms of Skhul group, progressive neanderthals of Ortu group and the metis neanderthaloid-sapiens individuals of Upper Paleolithic in Europe, referring them to the circle of the neanderthal-type forms.

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LATE PLEISTOCENE HOMININS FROM THE ALTAI MOUNTAINS, RUSSIA

Since the early 1980s, intensive research in the Altai mountains by researchers of the Institute of Archaeology and Ethnography, Siberian Branch, Russian Academy of Sciences, Novosibirsk significantly improved our understanding of the Middle and Upper Palaeolithic of this area. In the course of the investigation of numerous cave and open air sites, hominin dental and postcranial remains were recovered from both Middle and Upper Palaeolithic contexts.

Recent ancient DNA studies of some of these remains indicate that two or possibly even three different groups of hominins were present in the region during OIS 3. Here we will give a short overview of the Altai hominins, and discuss whether the morphological evidence is compatible with the results of the genetic analyses.

Neanderthals *Okladnikov*

The main interest of the Okladnikov hominids lies in the mtDNA sequences and direct ¹⁴C dates available for the postcranial remains (Krause et al., 2007). In addition, remains of several individuals representing different body parts are available.

The Okladnikov dental remains are much better preserved than the material from Denisova, Chagyrskaya and Strashnaya caves, but are still very hard to interpret. They preserve some archaic traits, such as the strongly crenulated and complex occlusal surface, but in general lack the derived traits seen in Neanderthals. The Okladnikov 2 M₁ shows a marked anterior fovea, a trait frequently

seen in Neanderthals, but it does not possess a midtrigonid crest, a trait seen in 96 % of Neanderthal M_1 s (Bailey, 2002). Similarly, the M_3 s show a complex occlusal surface with a large anterior fovea. They also have a mid-trigonid crest that is interrupted by the median sulcus (Grade 1 midtrigonid crest according to the scale of Bailey, 2002), with the crest being higher than the mesial marginal ridge. This is reminiscent of Neanderthal mid-trigonid crests, but these are generally uninterrupted.

It is interesting to note that all three of these teeth have a marked and continuous midtrigonid crest on the EDJ. Korenhof (1960, 1961) proposed that the EDJ topography is more conservative than the enamel surface, thus in some way conserving the ancestral morphology. Olejniczak and colleagues (2004, 2007), studying a diverse primate sample could also lend support to Korenhof's hypothesis. Accepting this hypothesis, it could be argued that the marked midtrigonid crest on the Okladnikov teeth is a retention of ancestral morphology, and thus the lack of a continuous midtrigonid crest is secondary. One could hypothesize that the ancestors of this population, being Neanderthals, showed a continuous midtrigonid crest on the enamel surface, but lost it later, possibly by genetic drift due to geographic isolation. The main problem with this hypothesis is the limited knowledge of the prevalence of a Neanderthal-like midtrigonid crest on the EDJ in modern humans. If this trait is as frequent as indicated by Korenhof's (1979) data, then the presence of this trait in the Okladnikov specimens could be simply accidental.

Okladnikov 1, a dm_2 is rather modern human-like, exhibiting a square crown with peripherally placed cusps, and no midtrigonid crest. Similarly, the Okladnikov 3 P_3 is not very diagnostic, but still unlike Neanderthals in the lack of an essential crest connecting the protoconid and metaconid and the presence of a rather symmetrical outline and several lingual accessory cusps.

The postcranial remains are not easy to assign to any taxon. Okladnikov 6, a middle phalanx of the hand is rather archaic, very robust and showing a wide and flattened distal end. As this morphology is present in Neanderthals (Musgrave, 1973), but also the Atapuerca Gran Dolina and Sima de los Huesos remains (Lorenzo et al., 1999), and even the WT-15000 *Homo erectus* juvenile (Walker and Leakey, 1993), as well as possibly in Early AMHs, it can not be used to assign Okladnikov 6 to any taxon.

Similarly, the morphology of the Okladnikov 7 child humerus is inconclusive. The mediolateral flattening of the distal half of the shaft is frequent in Neanderthals, but is also seen at Atapuerca Sima de los Huesos (Carretero et al., 1997) and in *Homo erectus* (Walker and Leakey, 1993, Weidenreich, 1941). It also seems to be present in some Early AMH, such as Jebel Irhoud 4 (Hublin et al., 1987), Taramsa Hill (Vermeersch et al., 1998) and Qafzeh 10, 12 and 15 (Tillier, 1999). The presence of a relatively thin medial pillar and a large olecranon fossa, typical for Neanderthals, can not be ascertained due to the breakage of the distal end, but the preserved part of the medial pillar looks rather thin relative to the size of the whole bone.

Okladnikov 8, a child femur probably belonging to the same individual as Okladnikov 7 is very badly preserved, and does not give any information as to the biological affinities of this individual.

The Okladnikov 9 adult distal humeral fragment is also rather undiagnostic. It does not preserve the pillars medially and laterally of the olecranon fossa, but the fossa itself seems absolutely very small, and is outside the range of variation of Neanderthals. This is in part linked to the very small size of the specimen, as relative to both articular and biepicondylar breadth, it is not extremely small, and is inside the Neanderthal range of variation. The medial epicondyle is rather small, and is thus more similar to modern humans. Taken together, the morphology of this specimen is more modern than Neanderthal-like.

Chagyrskaya cave

Chagyrskaya cave, excavated since 2007 by S.V. Markin, yielded a Mousterian industry very similar to Okladnikov cave. Besides the lithics and a rich fauna, several very fragmentary human remains were also found. Based on the lithic industry, and first preliminary mtDNA analyses we assign these remains tentatively to Neanderthals.

Chagyrskaya 1 is a very small, worn upper deciduous canine with marked labial convexity and marginal ridges. Chagyrskaya 2 is an atlas fragment of an about 2–3 year old child, both of these remains derive from layer 6b.

Chagyrskaya 3, an upper P⁴ fragment and Chagyrskaya 4, a lower incisor worn to the cervix come from the underlying horizon 6v. Both seem rather small, and have very short roots outside the range of variation reported for Neanderthals (Bailey, 2005; Walker et al., 2008). Chagyrskaya 4, the lower incisor has an extreme case of hypercementosis.

Denisovans

Denisova cave

Denisova cave is the reference site for the Middle and Upper Palaeolithic of the Altai, due to its long stratigraphic sequence and rich faunal and cultural remains. Several layers from the sequence also yielded human remains.

Some of the remains from Denisova cave yielded mtDNA and nuclear DNA sequences that are distinct from both Neanderthals and modern humans (Krause et al., 2010; Reich et al., 2010). Based on these differences, and the separate population history of this group, Reich et al. (2010) proposed the name “Denisovans” for them. Sadly, the material is very fragmentary, and only gives limited morphological insight.

Denisova 1 was described as an upper I¹, ascribed by Turner (1990) to a Neanderthal, while Shpakova (2001) and Shpakova and Derevianko (2000) interpreted it as a modern human, with possibly some elements of admixture from East Asian *Homo erectus*. Comparative studies show that this specimen is actually a very worn incisor fragment of a large bovid (bison?).

Denisova 3 is a small fragment of a distal manual phalanx of a child from Layer 11.2, morphologically completely undiagnostic, but with very good preservation of both mtDNA and nDNA. The mtDNA of this specimen is unlike Neanderthals and modern humans, and indicates a split of this mt lineage about 1 Mya. Interestingly, the evidence from the nDNA is very different, showing that this hominin belonged to a population more closely related to Neanderthals than to modern humans, splitting from the Neanderthal lineage about 350–250 ky ago. The Denisova 4 upper M^{2/3} derives from Layer 11.1, and based on its mtDNA belongs to the same population as the phalanx. It is extremely large, with robust, splayed roots and inflated, bulging cusps. Its size and morphology is compatible with the interpretation that it derives from a group distinct from both modern humans and Neanderthals.

Upper Palaeolithic modern Humans

Strashnaya cave

Strashnaya cave, in the northwestern part of the Altai, was originally excavated in 1969–1970 under the direction of A. Okladnikov, with a second campaign undertaken in 1989 by Derevianko and colleagues. Since 2005, the site has been excavated again by the late A. Zenin.

The stratigraphy of the site is rather complex, with stratigraphic levels 1 and 2 probably dating to the Holocene. Level 3 – from which the gros of the artefacts, and the hominid derive from – was subdivided into three substrata, 3₁, 3₂ and 3₃ (The Palaeolithic of Siberia..., 1998).

The lower part of Layer 3 includes a blade-based, Levallois Mousterian of the Kara-Bom type, while the upper part (3₁) contains an Upper Palaeolithic assemblage. A ¹⁴C date of 19150 ± 80 is available for 3₁ from an ornamented reindeer bone fragment.

The hominid remains derive from an area near the cave wall, where horizon 3₁ is slightly mixed with older deposits, and thus their attribution to the Upper Palaeolithic is not completely secure. They consist of 8 teeth probably belonging to the same individual, about 7–9 years old, and a fragment of the distal humerus of an adult.

Metrically, most teeth of Strashnaya 1 are well beyond the range of variation of both recent and Upper Palaeolithic modern humans, and are even at the upper limit of the Neanderthal distribution. The only exception is the I², the only tooth that differentiates well metrically between these groups; here Strashnaya 1 is significantly smaller than all Neanderthals. Morphologically, the dentition preserves several plesiomorphic features, such as the marked anterior fovea on the M₂, and the complex lingual relief of the C_{inP}, but typical derived characters of Neanderthals, such as a midtrigonid crest are missing. The I² shows shoveling both lingually and labially, without a marked lingual tubercle. This is very much unlike the shoveling seen in Neanderthals or in Asian *Homo erectus*, and more reminiscent of the double shoveling seen in recent North Asians and Native Americans. Strashnaya 3, from the same horizon, is a very robust, adult right

distal humerus fragment including the superior margin of the olecranon fossa and about 115 mm of the shaft.

Solovynaya Luka

In 1996, Kiryushkin and colleagues discovered a mandible fragment of a child in the cave of Solovynaya Luka. The remains are associated with a late Upper Palaeolithic, but there are no absolute dates available for the layer. The mandible preserves the left dc_{inf} - dm_2 and M_1 . Shpakova (2001) interpreted the teeth as indicative of Western Eurasian affinities, and saw similarities to Upper Palaeolithic mandibular remains from Samarkandskaya, Sunghir and Cro-Magnon 3.

Remains of indeterminate affinity

The Denisova 2 dm_2 represents the earliest human fossil from Central Asia. It derives from Layer 22.1 of Denisova cave, dating to at least OIS 5e, and thus it is of great importance for the understanding of the colonization of this region. Sadly, this completely worn and exfoliated deciduous molar gives us very little information beyond clear evidence for the presence of hominids.

A midshaft fragment of an ulna derives from the Middle Palaeolithic layer 6 of Strashnaya cave. This specimen has very thick cortical bone, but is otherwise undiagnostic.

A lower P fragment was described from Logovo Gieny cave by Chikisheva et al. (2007), without any archaeological context. The tooth is extremely badly preserved, and its hominin identification is extremely doubtful, as the relief of the crown consists of a single crest running mesiobuccally (if oriented like a hominin premolar), separating two large, flat wear facets. The extremely thin enamel is also unlike hominin premolars.

Conclusions

The Okladnikov cave remains, identified as Neanderthals based on their mtDNA, are morphologically in many traits unlike European or Near Eastern Neanderthals. They lack Neanderthal autapomorphies like the midtrigonid crest on lower molars, and present in general a rather generalized archaic morphology. Similarly, the remains from Chagyrskaya are morphologically not clearly identifiable as Neanderthals. Taken together with the evidence for specimens that show a mosaic of Neanderthal, archaic and modern traits in Central Asia (Glantz et al., 2008), this might indicate considerable geographic variation in Neanderthals.

The morphology of the remains assigned to the Denisovans is also unclear. The Denisova 3 phalanx fragment is too small for any conclusions. The Denisova 4 $M^{2/3}$ is remarkably large, and is differentiated from Neanderthals by its robust, strongly splayed roots, marked crown flare and large talon basin. More detailed comparisons await the discovery of more complete remains.

We still know little about the Upper Palaeolithic inhabitants of the region. The teeth from Strashnaya cave are especially interesting, as they show some similarities to the Sinodont morphological pattern, seen in present-day North Asians and Native Americans.

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INITIAL EARLY UPPER PALEOLITHIC ASSEMBLAGES IN THE JAPANESE ISLANDS

Introduction

As the study of modern human dispersals throughout the world progresses, recently the emergence of modern human behavior has been discussed in various regions (McBrearty and Brooks, 2000; Conard, 2008; Habgood and Franklin, 2008; Barker et al., 2007). The Japanese Islands are no exception. Japanese Paleolithic researchers studying archaeological and paleontological records on the Islands are also interested in this research topic (Dispersal..., 2009). A current working hypothesis is that locally observed modern human behavior emerged as technological adaptations to the changing environmental conditions of the Japanese Islands (Izuho, 2009). Studies focusing on initial Early Upper Paleolithic assemblages in the Japanese Islands are important to clarify technological adaptations to the specific environmental settings by the first modern humans who settled there in this time period. Furthermore, it is important to examine human behavior from lithic analysis because of the lack of human fossils in the Japanese Islands during the initial Early Upper Paleolithic period and earlier time periods.

In this paper, I outline characteristics of initial Early Upper Paleolithic assemblages on the Japanese Islands.

General background

The Upper Paleolithic in the Japanese islands is divided into the Early Upper Paleolithic and the Late Upper Paleolithic with the Aira-Tn marker tephra (AT; ca. 25,000–24,000 RCYBP) as a boundary (¹⁴C Ages..., 2000: 42–43). This key tephra has a wide geographic distribution that covers almost all of the Japanese islands. The AT erupted at the end of the MIS 3 between 28,000–29,000 cal BP based on AMS radiocarbon dates, the marine core data of the Japan Sea and Oxygen Isotope data from GISP2 (Aoki and Arai, 2000; Machida, 2005). Using key marker tephras, the South Kanto Plain deposit containing initial Early Upper Paleolithic assemblages is estimated to be accumulated after around 40,000 cal BP (Machida, 2005). Therefore, the dates of Early Upper Paleolithic assemblages fall roughly between 40,000 cal BP and 28,000 cal BP.

More than 200 Early Upper Paleolithic sites have been excavated in the Japanese Islands. Cultural chronologies are constructed on the basis of both stratigraphy and technological analyses of stone tools. The chronology of the Early Upper Paleolithic in the Musashino Upland in the South Kanto Plain around Tokyo provides a standard for the entire Japanese islands since the 1970s. Here, there are relatively thick Pleistocene deposits containing Paleolithic artifacts coupled with many Paleolithic site excavations since the first stage of research history. Qualitative technological analyses of Early Upper Paleolithic stone tool assemblages were dominant in Japan by the beginning of the 1990s. Studies based on the analysis of the process of technological changes in lithic assemblages during the Early Upper Paleolithic in Japanese Islands (Sekki Bunka Kenkyu 3., 1991; Sato, 1992) provide the basis of current research. Previous studies indicated that initial Early Upper Paleolithic (ca. 40,000–35,000 cal BP) assemblages in the Japanese Islands belong to an industry including adzes (with a ground-edge) and trapezoids, unique features compared with those in the surrounding areas in East Asia (Fig. 1, 2).

Initial Early Upper Paleolithic assemblages in the Japanese Islands

In previous studies, I presented quantitative data in terms of lithic raw materials selection, core reduction, and formal tool production of Early Upper Paleolithic assemblages from the Musashino Upland to discuss their transitional

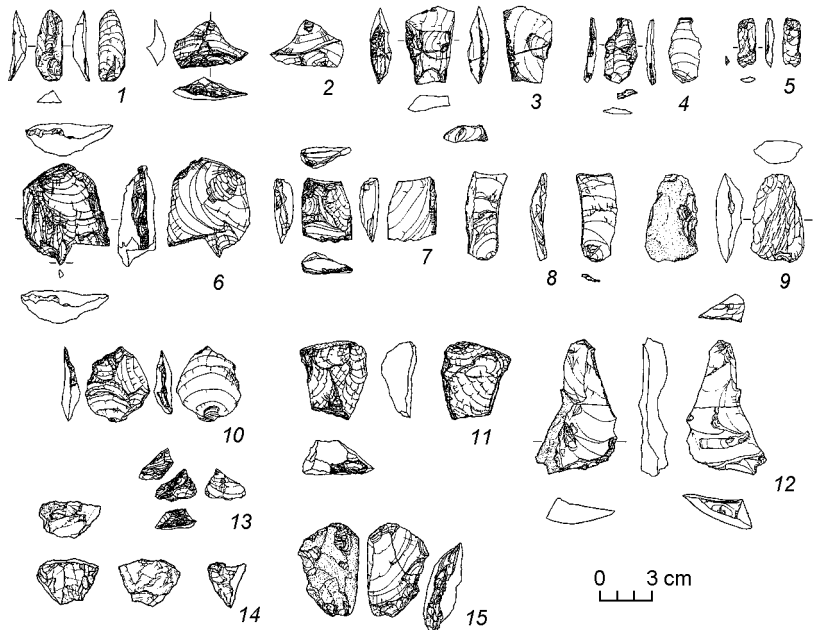


Fig. 1. Formal tools (Formal flaked tools) from Musashidai site Loc. A AH Xa and AH Xb on the Musashino Upland, initial Early Upper Paleolithic (Musashidai Iseki I, 1984).

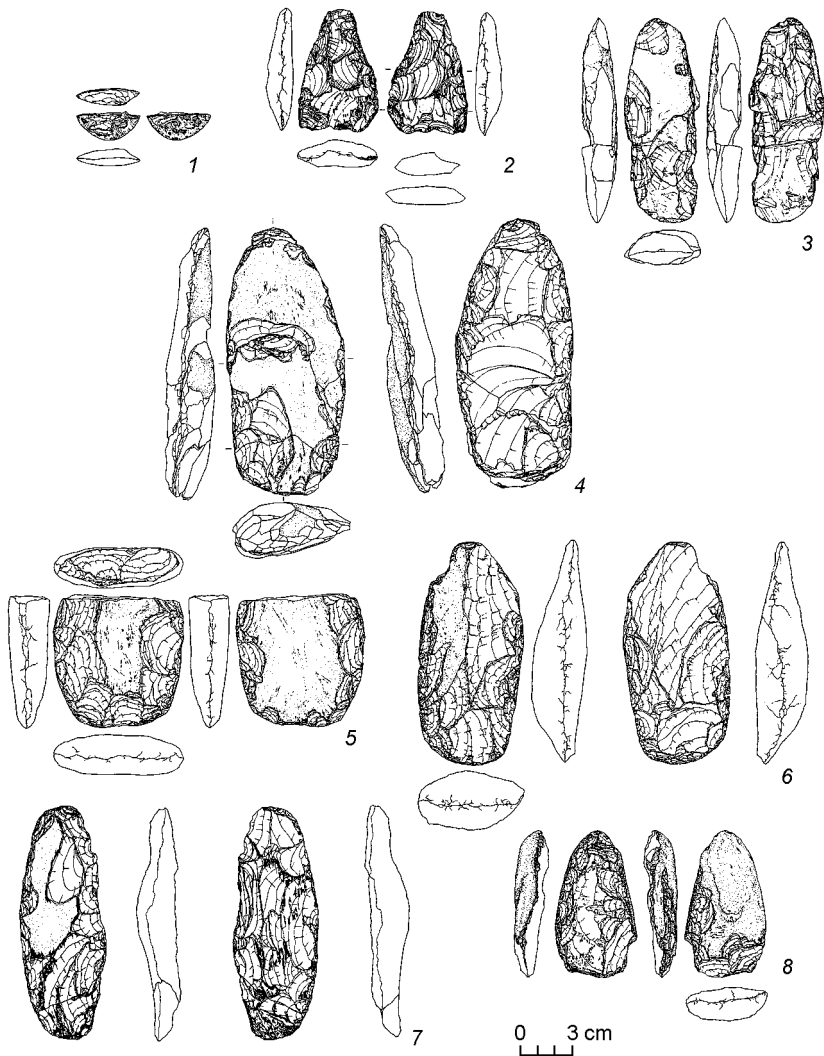


Fig. 2. Formal tools (Adzes) from Musashidai site Loc. A AH Xa and AH Xb on the Musashino Upland, initial Early Upper Paleolithic (Musashidai Iseki I, 1984).

processes and the characteristics of initial Early Upper Paleolithic assemblages (Yamaoka, 2004; 2006; 2009). In this series of studies, I suggested that quantities of blades, formal flaked tools, and high-quality exotic lithic raw materials (e.g., obsidian) were extremely low in initial Early Upper Paleolithic assemblages. However, blades and formal flaked tools such as trapezoids were often made of high-quality exotic raw materials. On the other hand, amorphous flake tools made of locally available low-quality chert and core tools like adzes (with a ground-edge) were abundant in these assemblages. The mean weights of lithic

artifacts in the assemblages are heavier than those of later periods. These patterns suggest the possibility that unmodified flakes and core tools containing adzes were the dominant lithic tools in this period. Groups of hunter-gatherers on the Musashino Upland during the initial Early Upper Paleolithic preferentially employed generalized core reductions, coupled with frequent use of locally available materials.

These characteristics of lithic raw material utilization are considerably distinct from those of later Upper Paleolithic lithic assemblages in the Japanese Islands and contemporaneous lithic assemblages in other geographical regions. In these later Upper Paleolithic assemblages in the Japanese Islands, the blade technology and formal flaked tools as well as high-quality (exotic) lithic raw materials are dominant. Therefore, initial Early Upper Paleolithic assemblages on the Japanese Islands are thought to represent one variation of lithic raw material utilization and stone tool technology during the Upper Paleolithic.

I explained these changes in lithic raw material utilization from the initial to later periods of the Early Upper Paleolithic in terms of technological adaptations in the Japanese Islands. These adaptations include transformations in the scale of foraging territories and residential mobility as well as some changes in the utilization of technologies associated with organic raw material.

Many studies suggested that human foraging territory expanded during the final Early Upper Paleolithic, based on the presence of considerable amounts of obsidian from Shinshu, a few hundred kilometers away from the Musashino Upland (Kanayama, 1990; Tamura, 1992; Ito, 1998; Suwama, 1998; Ishimura, 2002, Maji, 2003; Yoshikawa, 2003). In Japanese Paleolithic research, there were two hypotheses concerning lithic raw material procurement strategies in the beginning of the discussion, one based on direct procurement (Ono, 1975) and the other based on exchanges (Harunari, 1976). Recently, most researchers seem to discuss raw material procurement from the assumption of “embedded strategy” (Binford, 1979). However, there is no data to discuss specific foraging routes between obsidian provenance areas and sites on the Musashino Upland, and, there is no direct evidence to solve how lithic raw materials were procured. Therefore, I indicated only a possibility of relative differences in the scale of foraging territories with smaller areas during the initial Early Upper Paleolithic than later periods of the Early Upper Paleolithic (Yamaoka, 2004).

Moreover, the increasing reliance on obsidian for formal flaked tools from the initial to the final Early Upper Paleolithic was clearly demonstrated in my previous studies (Yamaoka, 2004; 2006; 2009). Given the frequent use of blade technology and lighter formal flaked tools in the assemblages of the final Early Upper Paleolithic, it is possible that the residential mobility of foraging groups increased during this time (Andrefsky, 1998). On the other hand, the residential mobility of foraging groups during the initial Early Upper Paleolithic is thought to have been relatively low because of infrequent use of blade technology and lighter formal flaked tools coupled with heavier mean weights of lithic artifacts.

In addition to changes in foraging territorial scale and residential mobility, modification in lithic raw material utilization could have been related to some alterations in the utilization of technologies associated with organic raw material (while not archaeologically visible but presumably existing), possibly in response to changes in the environmental setting (Yamaoka, 2004; 2009). As opposed to abundant occurrences of formal flaked tools and blade technology during the final Early Upper Paleolithic, which are ubiquitously found among Japanese Late Upper Paleolithic assemblages, unmodified flakes and core tools containing adzes are dominant in initial Early Upper Paleolithic assemblages. As noted before, these earliest Upper Paleolithic assemblages are regarded as unusual in comparison to lithic assemblages of the same period elsewhere in the world. However, the tool assemblages of the initial Early Upper Paleolithic appear somewhat similar to Pleistocene lithic assemblages of Southeast Asia, where it is thought that informal lithic tools were frequently utilized for producing perishable tools (Hutterer, 1976). Use-wear analysis of adzes shows that they functioned to perform multiple tasks, including hide scraping and wood-cutting (Tsutsumi, 2006). In addition, evidence of breakage patterns suggests that large adzes could have been used for heavy-duty tasks (Sato 2006). Thus, the most probable use of the larger adzes was for clearing the forest and wood working (Tsutsumi, 2006).

Paleoenvironmental data seems to support the possibility of some significant changes in the organic raw materials available during the Early Upper Paleolithic in this region. In the Kanto Region where the Musashino Upland is located, analysis of pollen spectrum and evidence of plant fossils show the occurrence of a vegetational change from broad-leaved deciduous forest to coniferous forest towards the onset of the Last Glacial Maximum (Tsuji and Kosugi, 1991; Ito, 1992). This shift of forest types roughly corresponds with the transition from the initial Early Upper Paleolithic to the final Early Upper Paleolithic. In addition, opal phytolith analysis shows the expansion of grassland vegetation from the initial to the later time periods of the Early Upper Paleolithic (Sase et al., 2008). This transformation roughly correlate with decreasing quantities of adzes within assemblages. Therefore, groups of hunter-gatherers during the initial Early Upper Paleolithic are thought to have been heavily depended on floral resources in their whole organizational technology.

Conclusion

This paper outlined characteristic of initial Early Upper Paleolithic assemblages on the Japanese Islands. Those characteristics could be explained based on the scale of foraging territory and residential mobility as well as technological organization in that time period. They suggest the study of initial Early Upper Paleolithic assemblages in the Japanese Islands is an important contribution to the study of the diversity of technological adaptations and potential abilities of modern humans in their initial dispersal to East Asia.

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ABBREVIATIONS

- IAE SO RAN – Institute of Archaeology and Ethnography, Siberian Branch
of the Russian Academy of Sciences (Novosibirsk)
- MGU – Moscow State University
- MOIP – Moscow Society of Naturalists
- RAAS – Russian Academy of Agricultural Sciences
- SB AS USSR – Siberian Branch of the USSR Academy of Sciences
- SB RAS – Siberian Branch of the Russian Academy of Sciences
- URAO – University of Russian Academy of Education

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