ANTHROPOLOGIE • XXXVII/1 • pp. 5 – 18 • 1999

ANDREJ A. VELICHKO

GLOBAL DISPERSAL OF HOMINIDS – A FEATURE OF THEIR COEVOLUTION WITH THE ENVIRONMENT

ABSTRACT: This chapter argues that the dynamic interplay of environmental factors and natural and sexual selection shaped the entire course of hominid evolution – specifically, that environmental transformations served as filtering mechanisms which selected for the best pre-adapted hominid populations. It suggests that the colonization of new habitats was a seminal component of hominid evolution but that this process was not continuous either in time or in space. Until some 2 Mya hominids remained only in tropical habitats after which they began spreading into temperate Eurasia through Northeast Africa, the Middle East, and the Caucasus. During the subsequent long period of some 500,000 years hominids occupied protected piedmont habitats. By the late Lower Paleolithic hominids undertook occasional forays into open landscapes north of the mountains. These initial colonization attempts were not synchronous in the different parts of Eurasia. Western Europe saw the earliest and the most continuous colonization of its northern plains. The increase in the continentality of the climate as one moved from the west to the east caused both the temporal and the spatial delay in hominid colonization. The open landscapes of Eastern Europe and Siberia, prior to being successfully colonized in the Upper Paleolithic, saw repeated advances and retreats of hominid populations.

KEY WORDS: African diaspora – Changing climates – Bio-cultural evolution – Colonization of Eurasia – Coevolution

INTRODUCTION

Throughout the course of evolution, hominids underwent a series of biological transformations. A better understanding of these transformations may permit us to predict the future of human evolution. This article uses geographical insights to examine how changes in the natural environment affected hominid evolution.

Explanation of a human ecosystem has always been a challenging endeavour. A major difficulty in understanding how this system operates stems from the unstable character of the interactions between its principal components: the individual, society, and the natural environment. What began as a single ecosystem which included the Pliocene environment and the earliest hominids, changed radically with the appearance of *Homo habilis*. The unified system fragmented into separate and autonomous components – the natural environment, the socio-biological component (hominids), and the social component – each replete with its own specific functional mechanisms.

THE COEVOLUTIONARY SCENARIO

Having researched the relationship between environmental transformations and human evolution for some time (Velichko 1971a,b, 1985, 1988, 1993, Gerasimov, Velichko 1974, Markov, Velichko 1967, Velichko, Gvozdover 1969, Velichko, Kurenkova 1990), I have repeatedly argued for the existence of parallel trends in evolution of each component of the human ecosystem.

The appearance of *Dryopithecus* coincided with a

progressive climatic cooling which, some 45–43 million years ago (Mya), followed the Eocene climatic optimum. This cooling initiated a glacial period with the development of the first mountain glaciers in Antarctica some 40–37 Mya. More advanced hominoids – *Kenyapithecus* and *Proconsul* – flourished during the first half of the Miocene. *Sivapithecus* and *Ramapithecus* spread widely during its second half, some 15–5 Mya. This period saw a global cooling during which the Drake Strait, the Circumantarctic Current, and the Antarctic continental ice sheets formed. Environmental changes in the Northern Hemisphere during this time included increased tectonic activity in the Alpides, the extinction of subtropical fauna, and the development of boreal biomes in the Northern Pacific (Golikov, Scarlato 1989). The divergence of the hominid lineage from that ancestral to the modern apes occurred some 10–8 Mya and coincided with a new cooling that witnessed the development of extensive Antarctic sea ice sheets (Velichko 1985). A period of significant landscape transformations, known as a Missinian Crisis, accompanied the appearance of the Australopithecines some 6–5 Mya. The earliest remains of Australopithecines (*sensu lato)* from Lothagam in Kenya date to around 5.5 Mya (Klein 1989). This period in hominid evolution was characterized by rapidly increasing aridity, migration of the evergreen forests towards the equator, the spread of the savannahs and semi-deserts into former forest habitats, and the expansion of the *Hipparion* fauna. The Mediterranean sea dried out almost completely, leaving a thick layer of evaporites on its bottom. The data from deep sea cores also suggest significant deterioration of climate and possible development of local glaciers in the high latitudes of the Northern Hemisphere at this time.

Another more significant climatic cooling event began around 2.5 Mya. During this period we see a progressive formation of the sea ice sheets in the Arctic and the spread of permafrost and tundra ecosystems in the Northeast Asia (Golikov, Scarlato 1989). Some scholars have argued that this period also saw the development of the earliest continental glaciation in Scandinavia as well as increasing aridity which, in the tropics, was accompanied by climatic deterioration (Frenzel 1967, Grichuk 1981). This period coincided with the appearance of *Homo habilis*. Their earliest remains come from Koobi Fora in East Turkana where they were found underneath a tuff dated to 2.6 Mya (Klein 1989). *Homo habilis*, however, did not totally replace the Australopithecines until the end of the Pliocene, with *Australopithecus robustus* surviving well into the Pleistocene.

The oldest lithic industries from the Hadar in Ethiopia also date to as early as 2.5–2.0 Mya (Klein 1989). Materials from Olduvai date to 1.75 Mya and the concentration of manuports at DK I there has been interpreted as the first evidence for habitation structures (see Klein 1989). These remains, as well as those of a presumed residential camp at Koobi Fora, correlate with the appearance of another hominid species – *Homo erectus*. The earliest remains of these hominids at Koobi Fora, in East Turkana, date between 1.8 and 1.6 Mya (Klein 1989).

By about 1.5–1.0 Mya, when a pattern of alternating colder and warmer periods with the interval of 200,000–300,000 years already established itself in the mid-latitudes, *Homo erectus* had spread to the northern limits of the subtropical zone and was present in both West and East Asia. Evidence for this comes from 'Ubeidiya, in the Jordan valley of Israel, which dates to around 1.4 Mya (Bar-Yosef, this issue), while evidence from Dmanisi, in the Caucasus, suggest an even older age (Dzhaparidze *et al.* 1989, Lordkipanidze, this issue).

This period witnessed significant changes in hominid adaptation to the natural environment. Having spread northward by some 1.0–0.8 Mya, *Homo erectus* abandoned tropical habitats – a niche common to all preceding hominid species – and entered the temperate zone. Hominid sites dating to the Brunhes/Matuyama paleomagnetic boundary (0.7–0.6 Mya) are found not just along the southern rim of the temperate zone (e.g., Azykh in the Caucasus) but also further north (e.g. Přezletice near Prague and Grass in northern France). Stone tools from Kärlich (Germany) have even been claimed to date to the Jaramillo paleomagnetic subchron some 0.9 Mya (Klein 1989).

The subsequent lower and middle Pleistocene periods witnessed further diversification of the genus *Homo* and an elaboration of hunting and gathering strategies. *Homo erectus* cranial remains from Vértesszöllös in Hungary, date to about 400,000 B.P., while the skull from Petralona in Greece dates to some 300,000 B.P. Lambert (1987) suggests that these hominids survived in Europe at least until the mid-Middle Pleistocene. The youngest remains of *Homo erectus* in Asia at Zhoukoudian in the People's Republic of China date to 460,000 B.P. and some other specimens can be as young as 230,000 B.P. (Rukang, Olsen 1985) (**editors' note:** recent chronometric dating of hominid remains from Java suggest that this taxon may have survived well into the Late Pleistocene – Swisher *et al.* 1996).

Other hominids, often referred to as pre-Neanderthals, co-existed with *Homo erectus* in Europe during this time. Their remains, exhibiting characteristics of archaic *H. sapiens*, are known from Tautavel in southwestern France and Steinheim in Germany.

During the Middle Pleistocene, a period that featured dramatic environmental fluctuations from interglacial zonality to periglacial hyperzonal landscapes (Velichko 1973), we see the appearance of Neanderthals. These specimens were found at Ehringsdorf and Pontnewydd and date to around 250,000–200,000 B.P. (Klein 1989).

The first half of the Würm (Visla/Valdai) glaciation saw the spread of the "specialized" (West European) Neanderthals represented, among others, by the specimens from La Chapelle and La Ferrassie. It had been argued that these Neanderthals evolved in geographic isolation under severe climatic conditions during the glaciation (see discussion in Klein 1989). We know, however, that another

form of Neanderthals, which exhibited more progressive traits co-existed with the Classic Neanderthals during the early Würm glaciation. I have previously argued that the climatic cooling during the first half of the Würm was not as dramatic as during its later part (Velichko 1988). Glacial periods during the middle to early late Pleistocene saw warmer paraperiglacial conditions compared to the late Pleistocene ones which were characterized by extremely cold and severe periglacial climates. These paleoenvironmental reconstructions suggest that both the specialized and generalized Neanderthals, who lacked physiological adaptation to glacial environments, survived in Eurasia due to these milder climatic conditions. A number of scholars have argued that the Neanderthals did participate in the transition from Middle to the Upper Paleolithic (see discussion in Anikovich, this volume). Typological similarities in lithic inventories from Middle Paleolithic and Upper Paleolithic layers at the sites in the Dnestr valley (Ukraine), for example, suggest a local Middle to Upper Paleolithic transition rather than a population replacement. The remains of early modern humans associated with Middle Paleolithic industries (e.g. at Qafzeh in Israel) and Neanderthals found at early Upper Paleolithic sites (e.g. Saint-Césaire in France) provide further support for a local transition from the Middle to the Upper Paleolithic.

Upper Paleolithic societies of anatomically modern humans flourished during the Last Glacial Maximum (LGM), the most abrupt and dramatic climatic cooling some 20,000–18,000 B. P. During this time, a wide permafrost zone spread along the southern limits of the continental ice sheets reaching as far south as the Bay of Biscay, the Caspian Sea, northern Kazakhstan, southern Siberia, Mongolia, and northern China (Velichko 1973). At the LGM winter temperatures dropped to –30°C even in the southern periphery of the periglacial zone (e.g. the middle Dnieper basin). Climate became extremely continental and arid, and tundra-steppes spread over the area formerly occupied by forests. This was the most dramatic period in hominid evolution, but technological innovations, advanced hunting and gathering economies, and complex social organizations permitted Upper Paleolithic groups allowed them to overcome this environmental threshold.

Finally, the transition from Pleistocene to Holocene some 10,000 B.P. saw yet another important threshold in hominid evolution – the transition from the Paleolithic to the Neolithic. This period was characterized by a reverse sequence of environmental transformations that saw progressive climatic warming, the degradation of permafrost over vast areas of Eurasia and North America, the regeneration of boreal forests, and decreasing aridity of the climate.

The above review of available paleoenvironmental, paleoanthropological, and archaeological data shows some broad temporal correlations in the evolution of all three components of the hominid ecosystem. It shows that changes in hominid evolution have always occurred in accord with the environmental transformations – the process I refer to here as the *coevolution* of the hominids and of the environment. More accurate temporal correlations between the events in this process, however, will become possible only with the refinement of the currently available chronometric methods.

THE ROLE OF THE ENVIRONMENT

Simple temporal correlations, however, do not explain how environmental transformations affected hominid evolution. Furthermore, numerous studies including my own (e.g. Velichko 1971a, 1985), have not documented the extent to which environmental changes determined the course of hominid evolution. As a result, many scholars, especially in the field of archaeology, express serious doubts about the deterministic effect of environmental factors (see e.g. Grigor'ev 1974).

We can begin delimiting the effects of environmental changes by outlining some options open to hominids when environments change. During major rapid transformations of the environment (e.g. glacial/interglacial cycles) hominids had the following three primary options:

1. *Local adjustment* to changing environments, which necessarily lead to changes in the types of adaptations (Alekseeva 1977);
2. *Range shift* (or migration), whereby the old adaptation is maintained by moving into an ecologically similar habitat;
3. *Extinction*, which may occur only under extraordinary circumstances such as geographic isolation of a population, earthquakes, *etc.* – an outcome which is very unlikely.

Data on hand show changes in these solutions undertaken by hominids through time and argue against a simplistic approach to environmental determinism. Although range shift are the least energetically costly solutions, the paleoanthropological record suggests that hominid adaptive responses during the earliest period of evolution took the form of local adjustments. During this time both natural and sexual selection played the most important role and were responsible for an increasingly high degree of polymorphism observed from the *Sivapithecus, Ramapithecus*, and *Gigantopithecus* to the Australopithecines. Each of these taxa seemed to have preferred specific habitats. With environmental changes (e.g. spread of savannahs, increasing aridity, *etc.*) some of them were better pre-adapted to the evolving landscapes than the others. Thus, environmental transformations had different effects on the evolution of the different hominid species – favouring some at the expense of others. Radical changes in the environment favoured the survival of those species which prepossessed more characteristics adaptive in the newly developing habitats (Velichko 1971, 1985, Klein 1989, Coppens 1994).

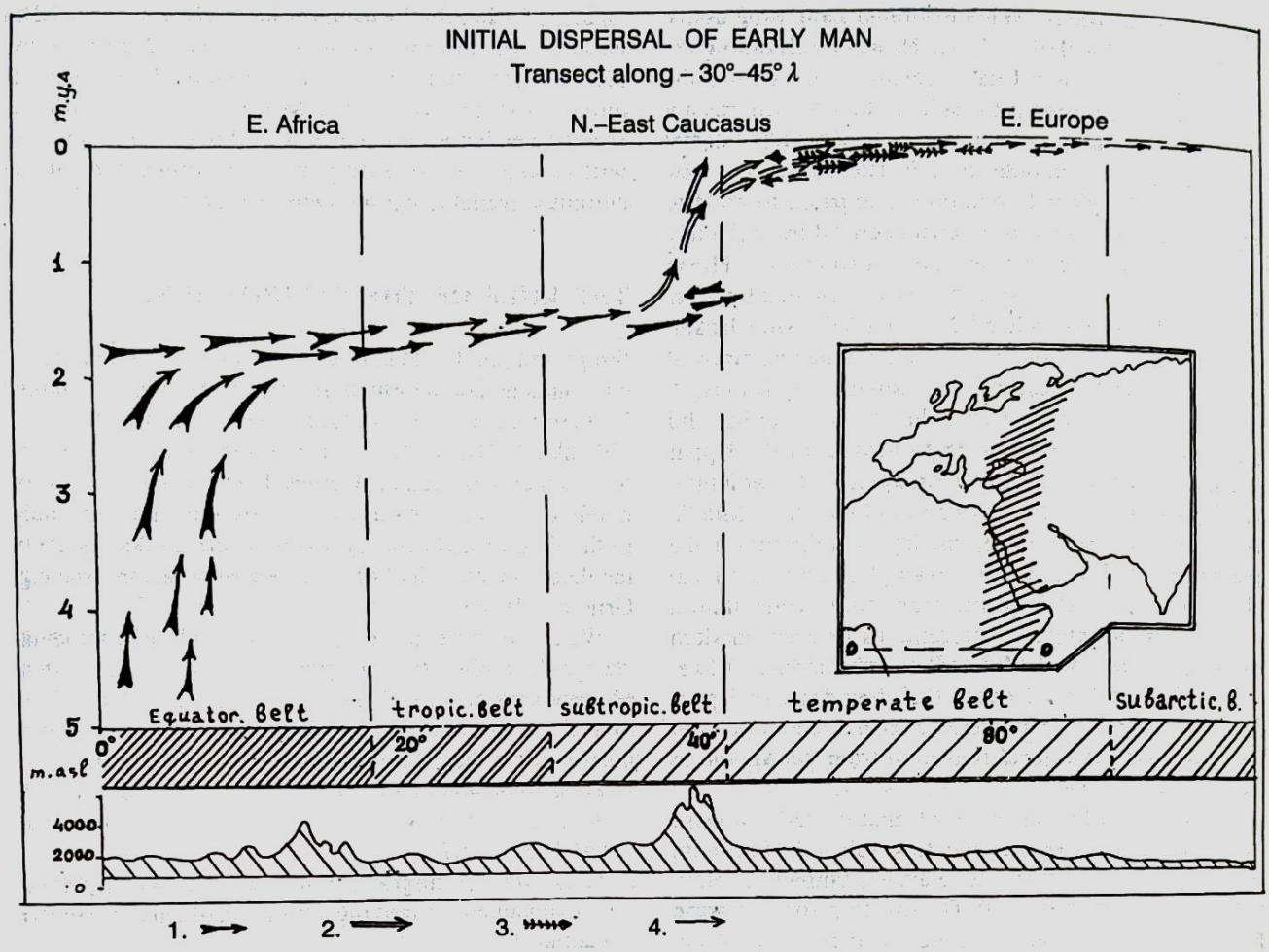


FIGURE 1. Initial dispersal of hominids from Africa to the Middle East and to Europe (a logitudinal transect between 30° and 45° N.). Legend: 1 – Early Lower Paleolithic, 2 – Late Lower Paleolithic, 3 – Middle Paleolithic, 4 – Upper Paleolithic

Environmental transformations favoured the evolution of later hominids as well. The high polymorphism seen among the Neanderthals outside the tropical zone was a direct result of mosaic environmental conditions in Eurasia (Velichko 1988). The degradation of climate, accompanied by the development of open periglacial landscapes, favoured the survival and spread of Neanderthal populations better adapted to the colder climate. Only the most sapient-like variants of the Neanderthals were able to adapt to extreme periglacial conditions. Similarly, further climatic deterioration during the Late Pleistocene glaciation led to the replacement of Neanderthals by anatomically modern humans.

In sum, environmental transformations served as filtering mechanisms that selected for the best pre-adapted populations. The dynamic interplay of environmental factors and natural and sexual selection shaped the entire course of hominid evolution.

INITIAL COLONIZATION

Environmental factors also affected hominid dispersals and colonizations of new areas. With progressive cooling the hominids kept spreading further north into progressively less favourable habitats. On face value we can argue that this was due to new technological sophistication, more elaborate social organization, and the availability and abundance of animal food resources in the periglacial regions. Faunal resources, however, were similarly abundant in the southern steppes and savannahs. This suggests that the colonization of unknown periglacial environments was energetically more costly than local adaptive adjustments to familiar steppe and savannah habitats (Alekseev 1984).

Given that this hominid dispersal into the temperate zone did not occur simply out of sheer curiosity, I suspect that it must have been triggered by progressive population growth and the ensuing increased need for food resources. By the time hominids reached the temperate zone, they already

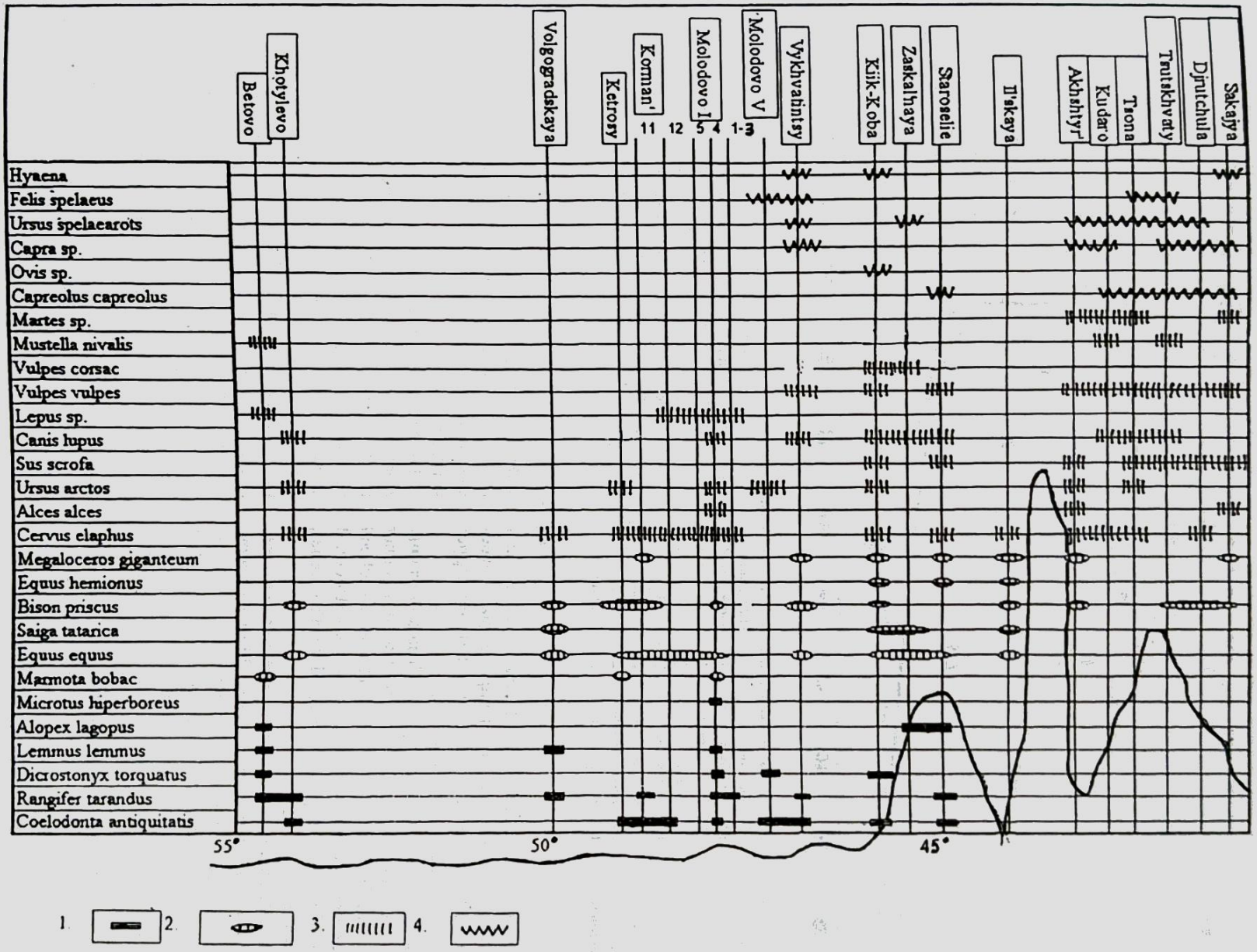


FIGURE. 2. Faunal composition at archaeological sites north and south of the Major Caucasus Range. Legend: 1 – arctic and periglacial species, 2 – steppe species, 3 – forest species, 4 – mountain species.

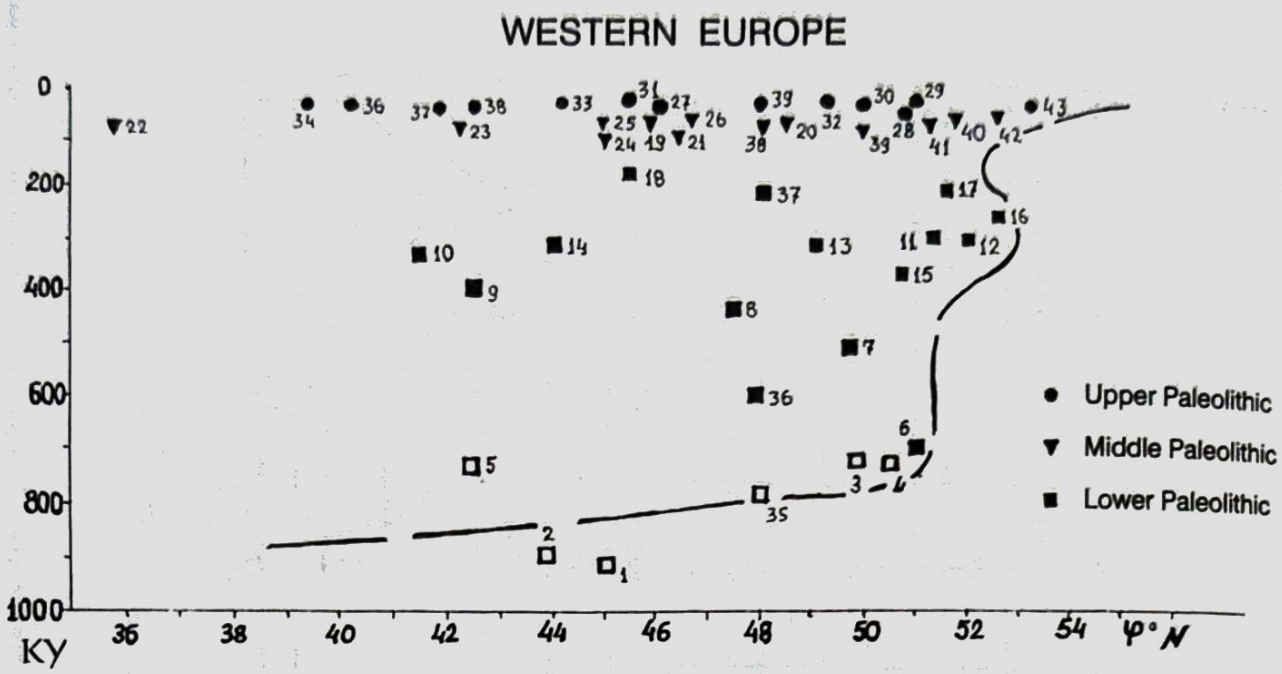


FIGURE 3. Schematic model for the initial hominid colonization of Western Europe:

1 – Soleihac	9 – Tautavel	17 – Ehringsdorf	25 – Le Moustier	33 – Grimaldi
2 – Le Vallonnet	10 – Petralona	18 – Fontéchevade, La Chaise	26 – La Quina	34 – Romito
3 – Přezletice	11 – Swanscombe	19 – Saint-Césaire	27 – Abri Pataud	35 – Korolevo
4 – Kärlich	12 – Hoxne	20 – Arcy-sur-Cure	28 – Spy	36 – Los Cazares
5 – Isernia	13 – Steinheim	21 – La Chapelle	29 – Ranis	37 – Altamira
6 – Boxgrove	14 – Terra Amata	22 – Gibraltar	30 – Spadzista	38 – Hortus
7 – Mauer	15 – Bilzingsleben	23 – Circeo	31 – La Madeleine	39 – Korolevo
8 – Vértesszöllös	16 – Pontnewydd	24 – La Ferrassie	32 – Dolní Věstonice	

possessed adaptive features – both biological and cultural – which allowed them to survive in paraperiglacial climates of the Middle Paleolithic and even harsher Upper Paleolithic periglacial conditions.

The hominid dispersal into temperate habitats certainly did not have a continuous and uniform pattern in either time or space. It occurred in several stages which echoed global changes in the development of such structural elements of the landscape as latitudinal zonality, relief, etc. (*Figure 1*).

The main feature of this initial dispersal into new areas was its temporal and spatial discontinuity. Most of hominid evolution took place in the tropical areas which saw the least pronounced climatic fluctuations. Available data suggest that hominids, most likely, initially dispersed from Africa into the temperate regions through the Middle East (Amirkhanov, Bar-Yosef, Wolpoff, this issue). It is also possible that hominids colonized temperate Europe from Northwest Africa (see Klein 1989). The subtropical deserts which dominate Africa today have a recent origin and resulted from an increase in the atmospheric pressure in subtropical latitudes. In the late Pliocene and the early Pleistocene these latitudes saw wetter climates which may have permitted hominids to spread to subtropical habitats and from there further north. The patchiness of the pertinent data on hand today from north-western Africa and south-western Europe make the later scenario a hypothetical one at present.

Following their first appearance in the middle latitudes, *Homo erectus* populations did not spread further north into the temperate zone. Rather, they remained in the mountainous regions for some 500,000 years. This period witnessed an increase in tectonic activity which resulted in the formation of the Alpides, the youngest mountain belt stretching from the Alps in the west to the mountain chains of Central Asia in the east. Rapid growth of the mountains, however, did not occur until much later – some parts of the Himalayas, for example, rose as much as 1 km during the late Pleistocene. At the onset of the Pleistocene, Eurasian mountains were much lower than today and featured milder climatic regimes. During the early part of the Lower Paleolithic hominids already inhabited different parts of the Alpides, being present primarily at lower elevations (e.g. Dmanisi, Azykh, Karatau, Orce).

Although extensive colonization of these regions was complicated by active geomorphic processes (e.g. frequent earthquakes, land slides, mud flows, and rapid mountain streams), hominids could have spread northward along the

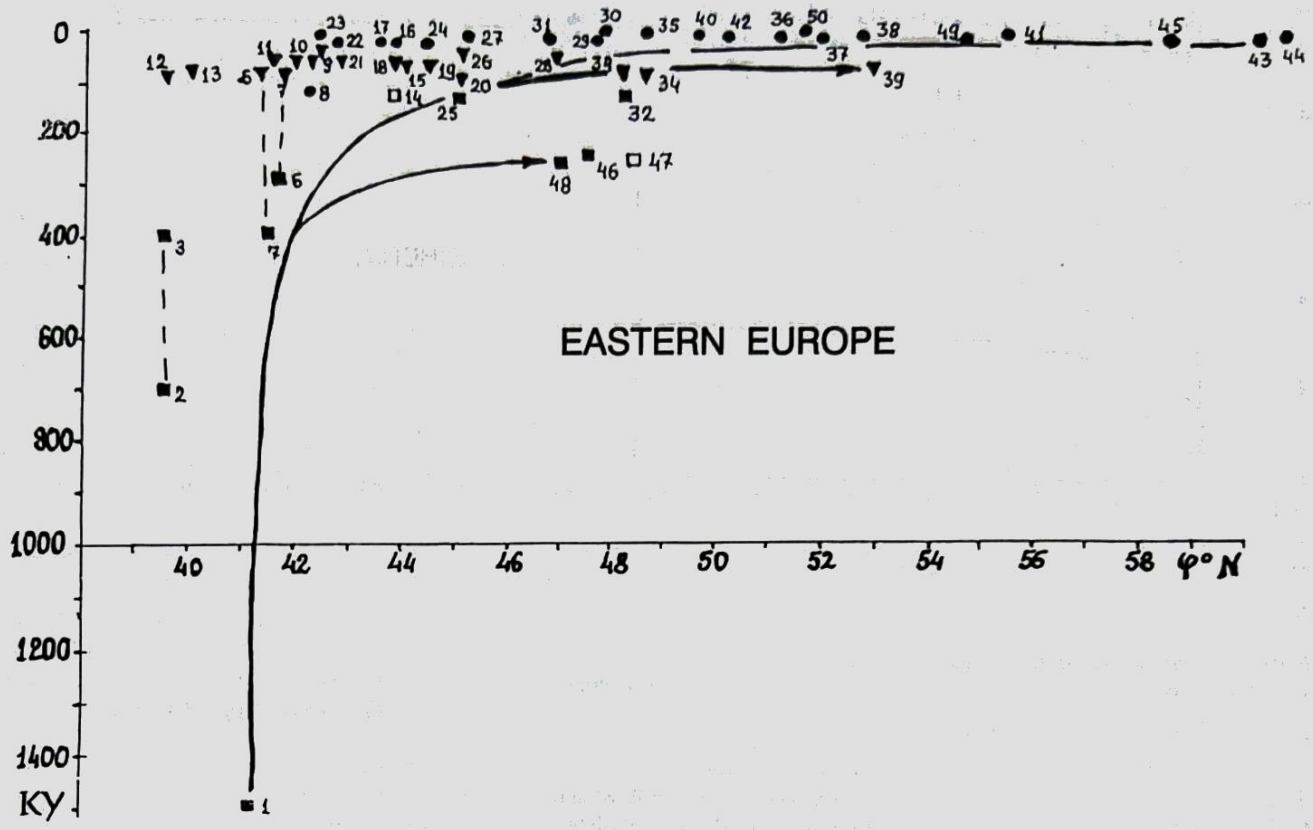


FIGURE 4. Schematic model for the initial hominid colonization of Eastern Europe:

1 – Dmanisi
2 – Azykh (Lower Paleolithic)
3 – Azykh (Middle Paleolithic)
4 – Kudaro (Lower Paleolithic)
5 – Kudaro (Middle Paleolithic)
6 – Tsona (Lower Paleolithic)
7 – Tsona (Middle Paleolithic)
8 – Tsutskhvaty (Lower Paleolithic)
9 – Tsutskhvaty (Middle Paleolithic)
10 – Djurchula
11 – Ortvala-klde (Middle Paleolithic)
12 – Taglar
13 – Erevanskaia
14 – Akhstyr (Lower Paleolithic)
15 – Akhstyr (Middle Paleolithic)
16 – Akhstyr (Upper Paleolithic)
17 – Navalishenskaia (Upper Paleolithic)
18 – Navalishenskaia (Middle Paleolithic)
19 – Malaia Vorontsovskaia
20 – Barakaevskaia
21 – Sakajia (Middle Paleolithic)
22 – Sakajia (Upper Paleolithic)
23 – Apiancha
24 – Gubski Naves
25 – Kiik-Koba
26 – Zaskalnaia
27 – Suren'
28 – Rozhok
29 – Amvrosievka
30 – Kamennaia Balka
31 – Anetovka
32 – Vykhvatinski Naves
33 – Sukhaia Mechetka
34 – Ketrosy
35 – Molodovo I & V
36 – Kostenki
37 – Pushkari
38 – Eliseevichi
39 – Khotylevo
40 – Mezhirich
41 – Sungir'
42 – Kirillovskaia
43 – Medvezhia
44 – Byzovaia
45 – Talitskogo
46 – Khriaschi
47 – Luka Vrublevetskaia
48 – Gerasimovka
49 – Zaraisk
50 – Kostenki

mountain valleys. It appears that they did not do so but remained in the Alpides for a long period. During their stay in the Alpides, regions to the north were already undergoing the development of glacial climates. The mountains served as a natural barrier protecting the hominids from cold northerly air masses. Well-protected areas at lower elevations also supported abundant plant and animal resources providing favourable habitats for the hominids. The distribution of the animal species at the Lower Paleolithic and the Middle Paleolithic sites on the East European (Russian) Plain and in the Caucasus provide strong evidence for the protective role of the Alpides biome.

Figure 2 shows that the cold-tolerant fauna is found only at the sites located north of the Major Caucasus range.

This long period of hominid occupation of the Alpides signals the *initial successful colonization* of temperate environments. Although the archaeological record shows occasional hominid presence in more open areas north of the mountains, the Alpides remained their primary habitat for the entire period. I deliberately use the word *presence* here instead of *colonization*, because this term implies opportunistic forays rather than the permanent occupation of these area. These forays into new areas, at least during the initial appearance of hominids in the Alpides, occurred

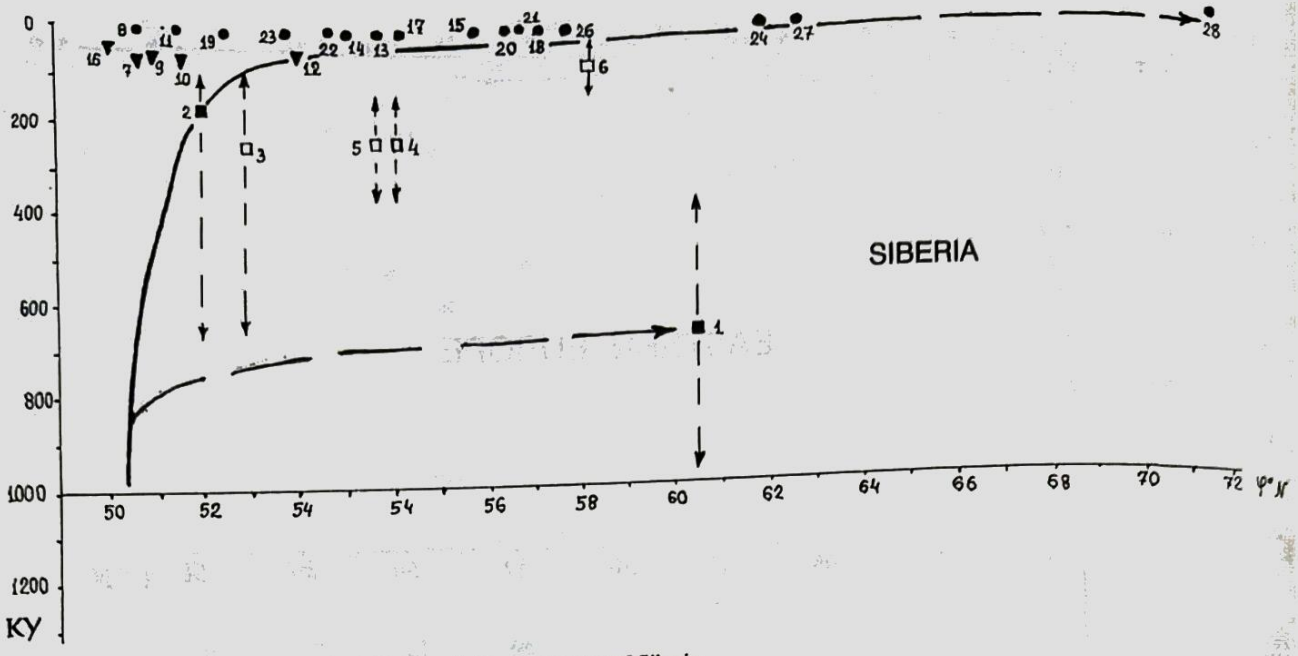


FIGURE 5. Schematic model for the initial hominid colonization of Siberia:

1 – Diring Uriakh
2 – Ulalinka
3 – Kumary
4 – Bratsk
5 – Igetey I
6 – Ust-Olekma
7 – Ust-Kanskaia (Middle Paleolithic)
8 – Ust-Kanskaia (Upper Paleolithic)
9 – Strashnaia (Middle Paleolithic)
10 – Denisova (Middle Paleolithic)
11 – Denisova (Upper Paleolithic)
12 – Dvuglazka
13 – Shikaevka II
14 – Volchia Griva
15 – Mogotchino (Upper Paleolithic)
16 – Kara-Bom (Middle Paleolithic)
17 – Afontova Gora
18 – Ust-Kova (Upper Paleolithic)
19 – Malta
20 – Druzhinikha
21 – Kurung I
22 – Malaia Syia (Upper Paleolithic)
23 – Kokorevo I
24 – Duktay
25 – Ezhantsy
26 – Ust-Mil
27 – Jkhine I
28 – Berelekh

in a cyclical pattern of initial colonization and abandonements in favour of their previous habitats.

There were significant regional differences in the hominid colonization of the northern plains of Eurasia. Three basic regions can be distinguished which include: (1) western Europe, (2) eastern Europe, and (3) Siberia.

Western Europe

In western Europe (*Figure 3*), the time lag between initial hominid occupation of the mountains and their spread into northern plains was much shorter than in the eastern part of the continent. The earliest Lower Paleolithic finds in the Somme valley in northern France and at Kärlich in central Germany contain characteristic scatters of lithic concentrations within poorly structured cultural layers and date to around the Brunhes/Matuyama paleomagnetic boundary (*ca* 700,000 B.P.) (Klein 1989). By the second half of the middle Pleistocene hominids reached southern Britain (Hoxne, Swanscombe). Open landscapes in Central Europe (Mauer, Vértesszöllös) and lowlands of northern Germany (Bilzingsleben) were intensively colonized between 500,000 and 400,000 B.P.

The data on hand suggest an oscillating colonization of western Europe by the Lower Paleolithic hominids throughout most of the Pleistocene. Available chronometric dates and geographic locations of these sites show that northern areas were occupied during the interglacials while hominids returned to the south during the glacials.

Eastern Europe

In eastern Europe, Paleolithic colonization of new areas followed a distinct step-like pattern (*Figure 4*). Here, hominids remained in the mountain regions throughout almost the entire Lower Paleolithic (e.g. Dmanisi, Kudaro and Azykh in the Caucasus). Very few middle Pleistocene sites or localities are found on the plains north of the mountains, and contain only sparse lithic remains (e.g. Khutor Mikhajlovskij and Vykhvatintski). These archaeological data suggest that Lower Paleolithic hominids in this region, being poorly adapted to boreal climate, made only initial attemptive forays into the plains, and repeatedly returned back to their well-protected mountain habitats.

Significant changes in hominid adaptation occurred during the Middle Paleolithic. Climatic amelioration during the last interglacial and mild paraperiglacial conditions at the beginning of the last glaciation allowed Middle Paleolithic groups to colonize southern portion of the Russian Plain. Archaeological record from such sites as Molodovo and Korman' in the Dniester valley and Rozhok

in the Sea of Azov region clearly shows successful adaptation to harsh glacial environments (Chernysh *et al.* 1977, 1982, Praslov 1969, Velichko 1988). Even at the beginning of the last glaciation Middle Paleolithic groups attempted forays into both southern (Sukhaia Mechetka in the Volga valley) and northern portions of the Russian Plain (Khotylevo I in the Desna Valley, and possibly Gonichata I and II in the Upper Kama Valley (Guslitser, Pavlov 1993 – but see also Gribchenko, Kurenkova, this issue).

Intensive colonization of vast East European periglacial landscapes began at the end of the Late Pleistocene after 40,000 B.P. Upper Paleolithic sites on the Russian Plain such as Kostenki (in the Don valley), Mezhirich and Dobranichevka (in the middle Dnieper basin), Khotylevo II, Eliseevichi, and Yudinovo (in the Desna basin) all post-date 40,000 B.P. (Soffer 1985, Gribchenko, Kurenkova, this issue). During the Upper Paleolithic, human groups undertook occasional forays into more northerly regions. For example, during the Briansk interstadial, some 30,000–24,000 B.P., they moved as far as 56° N (Sungir' in the Kliaz'ma valley) and may have reached the Arctic Circle (Byzovaia in the Pechora valley) (see Gribchenko, Kurenkova, this issue).

Siberia

The Paleolithic occupation of Siberia followed a somewhat different pattern (*Figure 5*). Archaeological data suggest that hominids first appeared in the mountains of southern Siberia during the Lower Paleolithic (Abramova 1989, Derevianko *et al.* 1997, Drozdov *et al.* 1990, Medvedev *et al.* 1990, Mochanov 1977, Tsejtlin 1979). Geochronological data from the earliest sites, however, are often problematic. Some of them, like Ulalinka in the Altai region, have been found in the deposits dated from the end of the Pliocene to the Middle Pleistocene. Other sites such as those from Igetejskiy Log in the Angara basin, lack reliable stratigraphic correlations with regional sequences. The northernmost site of During-Iuriakh, in the middle Lena valley, has been assigned a broad range of dates from the Lower to the Middle Pleistocene (Alekseev *et al.* 1990, Derevianko *et al.* 1997).

In spite of these chronological problems, it is clear that the Siberian region was not progressively colonized during this earliest period. As in other regions, it probably saw a back-and-forth pattern of hominid occupation. During one of the warmer intervals during the lower Pleistocene, hominids had advanced far north (During-Iuriakh) where they eventually were not able to adapt to progressive climatic deterioration.

Unlike in European record, the Siberian one shows no significant attempt to reach the northern areas during the Middle Paleolithic. Such cave sites as Strashnaia, Denisova, Dvuglazka, and Ust'-Kanskaia present evidence for the continuous Middle Paleolithic occupations of only the mountains of southern Siberia (Derevianko *et al.* 1997, Laukhin 1993).

Most of the Upper Paleolithic sites from Central and Western Siberia are also found in the southern piedmont and mountainous regions. Others however, in western Siberia, show evidence for human occupation of the plains during that time period (Volch'ia Griva in the Irtysh valley). The spread of Upper Paleolithic groups into northern Siberia is well documented by a number of sites in the middle Lena basin. Mochanov (1992) suggested that human groups first appeared here during the Early Upper Paleolithic some 30,000 B.P. Others, emphasizing problematic dates for such sites as Ust'-Mil' and Ikhine, argue that Upper Paleolithic groups inhabited the middle Lena basin no earlier than 20,000–15,000 B.P. (Abramova 1989). The archaeological data thus suggest that a threshold in the hominid colonization of Siberia occurred at the Middle to the Upper Paleolithic transition when human populations reached northern Siberia. Prior to this, hominids continuously occupied only the mountainous regions of southern Siberia.

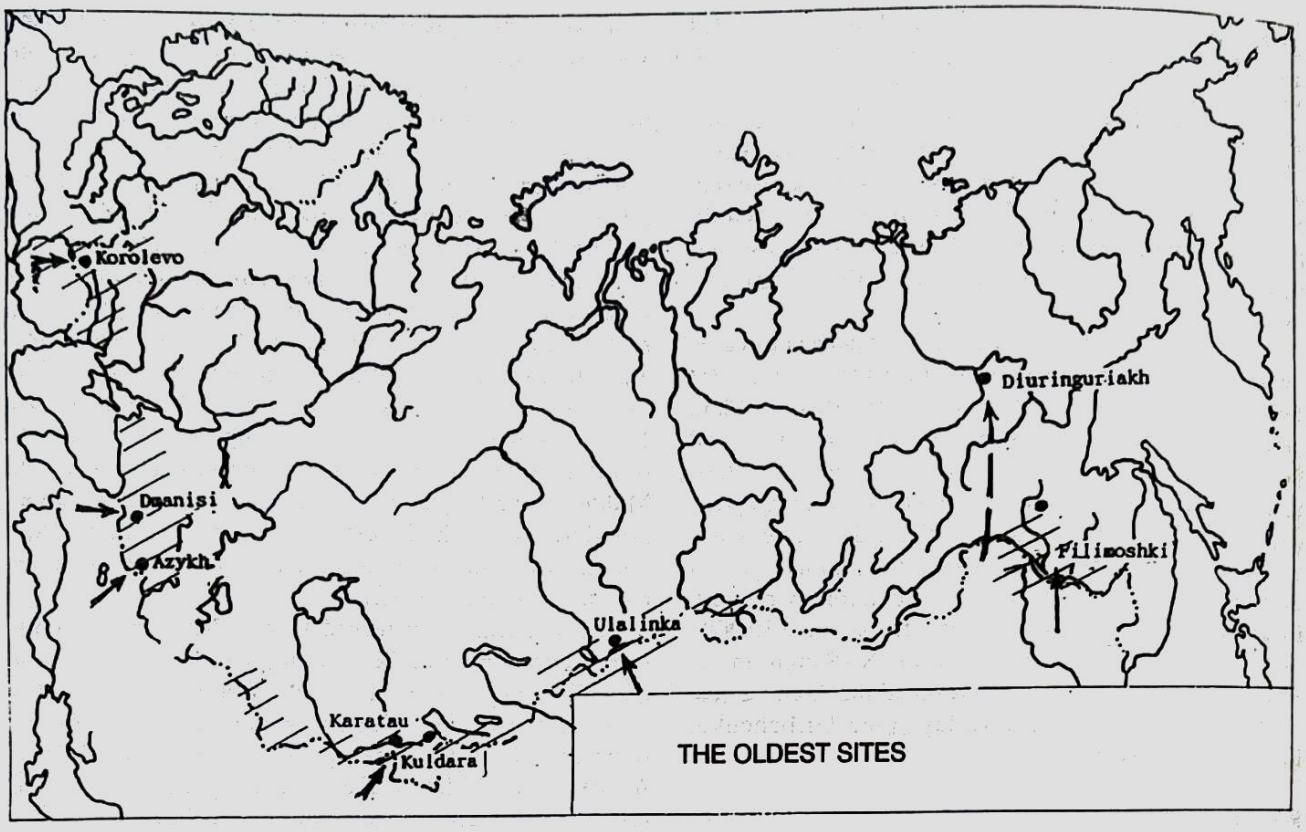
The archaeological record shows that human groups spread into northern Siberia along the valley of the Lena river. The upper Lena basin is located in the Baikal continental rift zone. Such a human spread northward somehow mirrors the linear spread of early hominids from Africa into the Middle East. Such a parallelism in the routing of the spread may reflect the linearity of the colonization process, but the possibility that the pattern is just a result of either insufficient research or of taphonomic factors leave the issue moot.

The Regional Records Compared

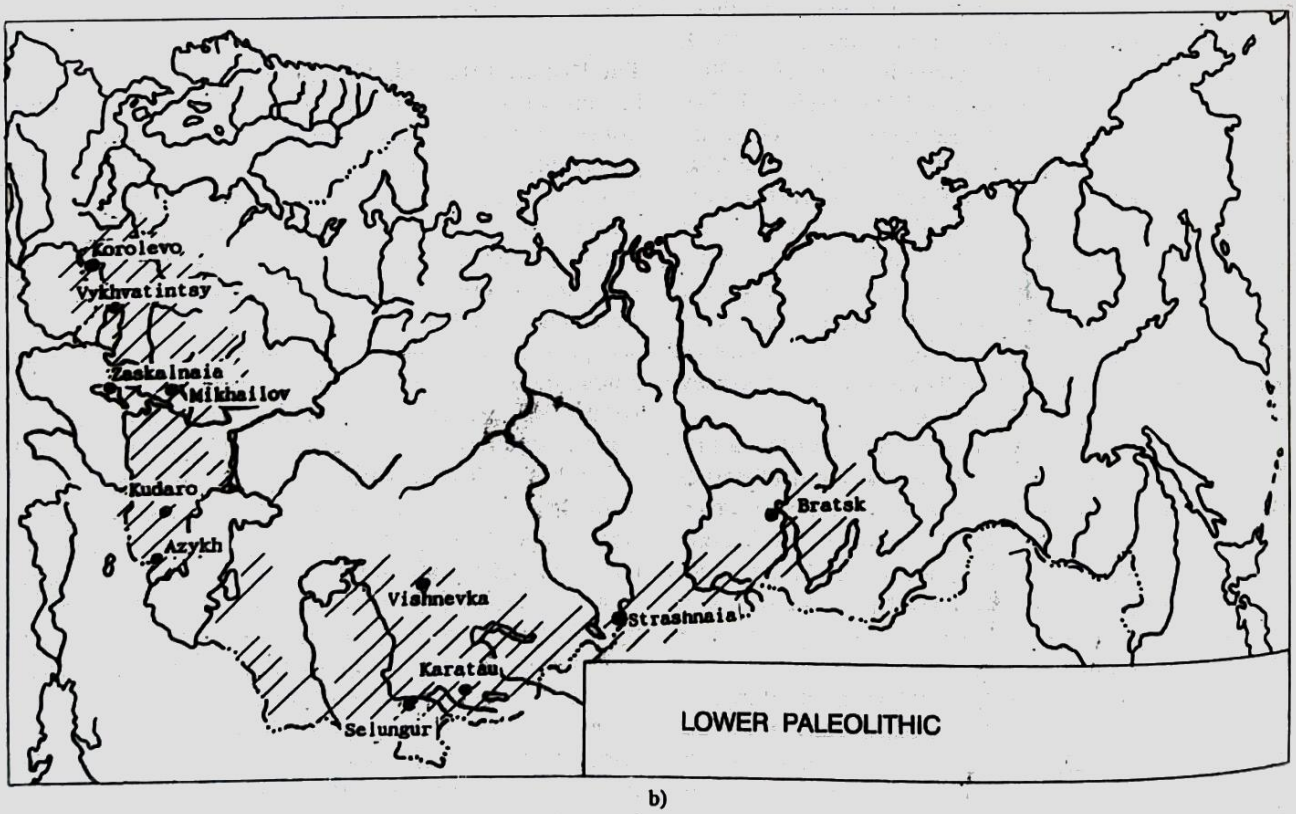
In sum, we see three distinct types of hominid dispersal from the tropical zone into high latitudes. The Central Asian pattern differs from these three, but limits of space preclude its inclusion in this discussion. In none of these regions did the hominid colonization follow a gradual progressive pattern. All three regions saw periods of long continuous occupation of only those landscapes to which the hominids were better adapted. In all three regions such continuous occupation during the Lower Paleolithic occurred in the mountains along the southern periphery of the temperate zone. This residential stability lasted longer at the beginning of the initial colonization than towards its end.

Despite these similarities, there are quite pronounced differences in the colonization of the three regions. In western and central Europe colonization proceeded much more gradually and smoothly than in other regions. In Eastern Europe it followed a step-like pattern characterized by alternating periods of occupational stability and dispersal into new areas throughout the entire Paleolithic (*Figure 6, A–D*). Finally, in Siberia, the period of stable hominid occupation lasted throughout the Lower Paleolithic and the Middle Paleolithic, while the spread into northern areas occurred only during the Upper Paleolithic.

I argue that the observed interregional differences in the patterns of hominid colonization are related to the

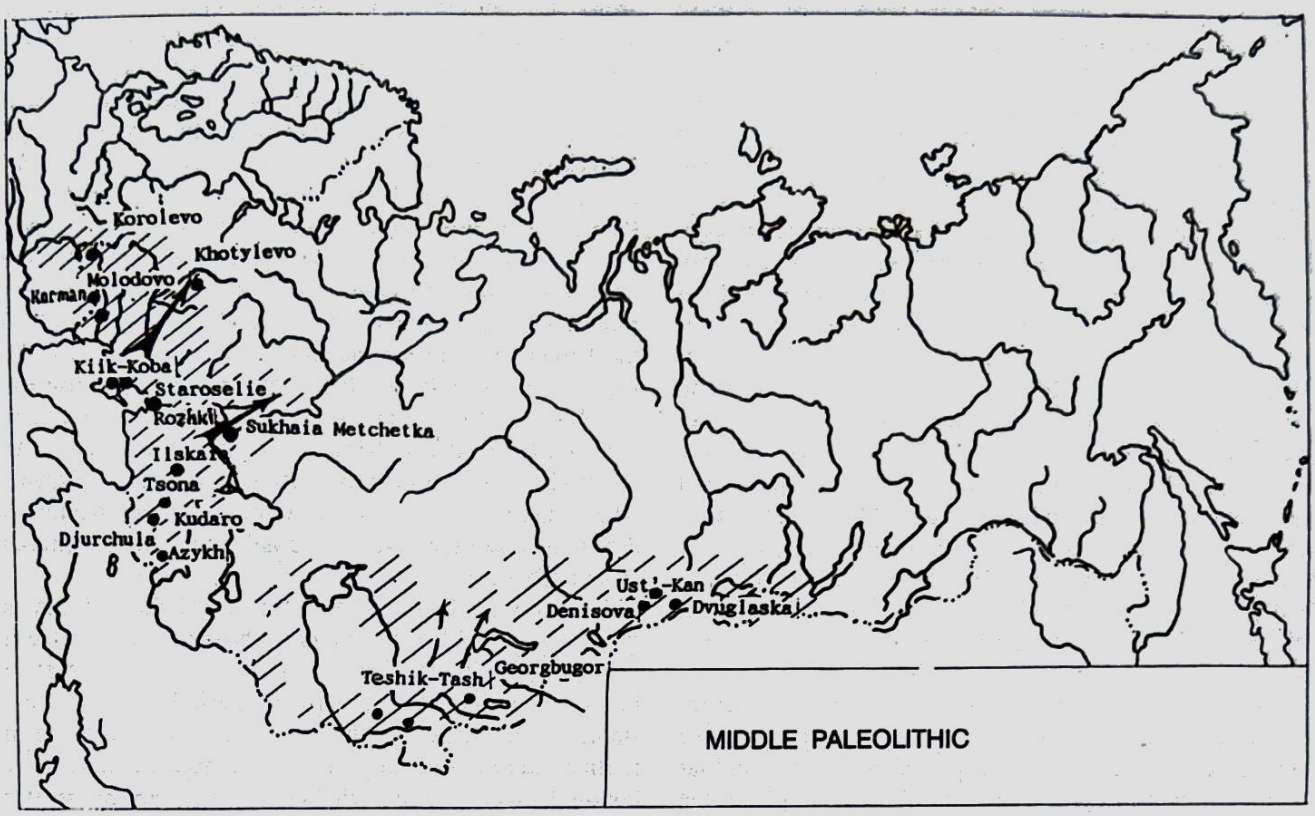


a)

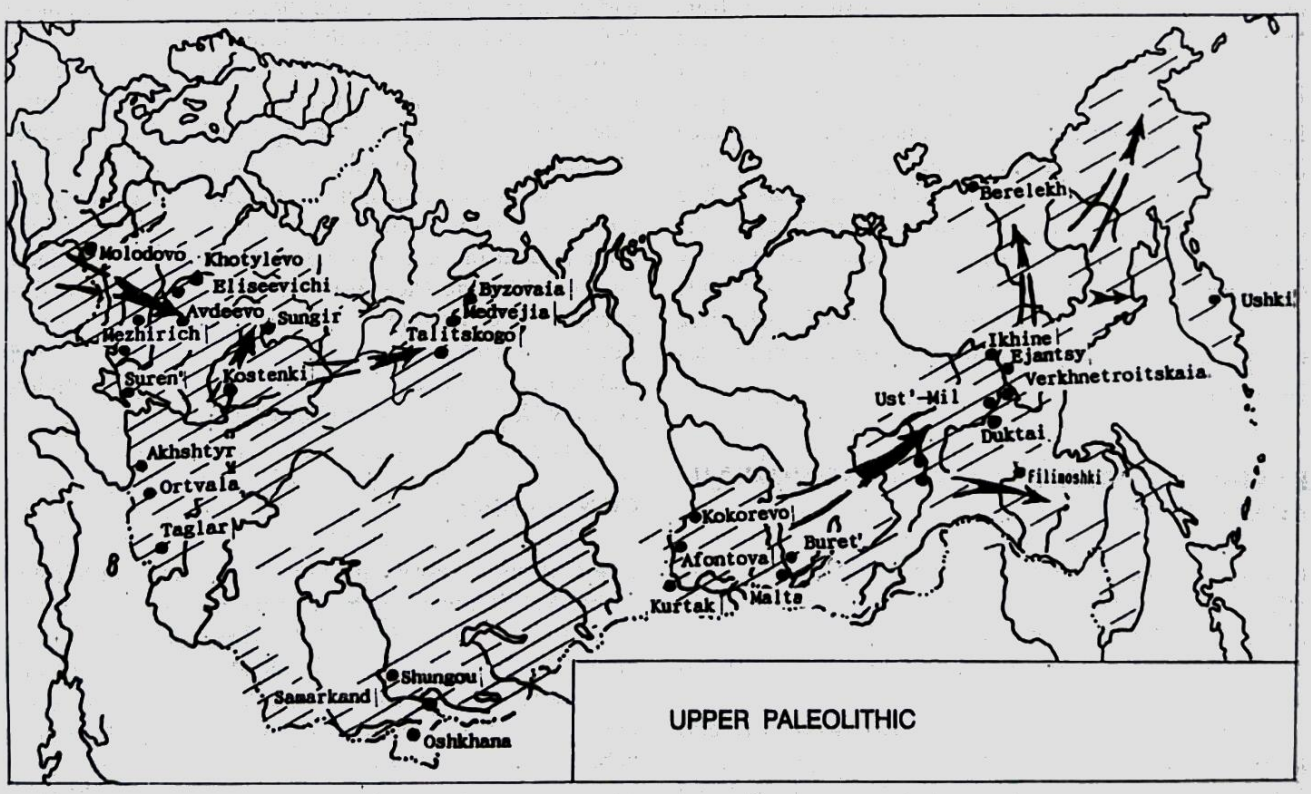


b)

FIGURE 6. Stages of Paleolithic hominid colonization of Eurasia (colonized areas are shaded; arrows indicate main directions of colonization): a) earliest sites, b) Lower Paleolithic, c) Middle Paleolithic, d) Upper Paleolithic.


Korolevo
Khotylevo
Molodovo
Karmana
Kiik-Koba
Staroselie
Rozhki
Sukhaia Metchetka
Ilskaia
Tsona
Kudaro
Djurchula
Azykh
Ust'-Kan
Denisova
Dvuglaska
Teshik-Tash
Georgbugor
MIDDLE PALEOLITHIC

c)


Berelekh
Molodovo
Khotylevo
Eliseevichi
Byzovaia
Kostenki
Avdeevo
Sungir
Talitskogo
Ushki
Ikhine
Ejantsy
Verkhnetroitskaia
Ust'-Mil
Duktai
Filinoshki
Akhshtyr
Ortvala
Taglar
Kokorevo
Buret'
Afontova
Malta
Kurtak
Shungou
Samarkand
Oshkhana
UPPER PALEOLITHIC

d)

climatic gradient, particularly to the west-to-east increase in continentality. Due to the ameliorating effect of the Atlantic Ocean, climate in western Europe remained relatively mild even during glacial and stadial periods. The least pronounced climatic changes in this region permitted hominids to adapt gradually and to progressively colonize new landscapes. The more continental climate in Eastern Europe required a longer period for hominid adaptation. Finally, hominids were able to adapt to extremely continental and severe climate of northern Siberia only in the Upper Paleolithic. This suggests that, although cultural transitions from the Lower to the Middle to the Upper Paleolithic occurred in different regions roughly at the same time, there was an increase in temporal and spatial delay from west to east in hominid colonization of new landscapes. In western Eurasia, hominids occupied vast open areas as early as the Lower and the Middle Paleolithic. Occasional forays into the East European Plain are first recorded only during the Middle Paleolithic, while in Siberia they did not take place until the Upper Paleolithic. All this indicates a latitudinal spatial asymmetry in the initial colonization of northern Eurasia.

The archaeological record also shows some similarities between the regions. The early, if not the earliest, sites of any subsequent archaeological period are often found far north (sometimes up to a thousand kilometers) from the sites of the preceding period. This is particularly characteristic of the Middle to Upper Paleolithic transition in eastern Europe. Along with the local succession from Middle to Upper Paleolithic layers in the southern portion of the Russian Plain (Molodovo and Korman' in the Dnestr Valley), we also see the appearance of Early Upper Paleolithic sites more than 900 km north-east of this area (Kostenki-Streletskaia culture along the Middle Don (**editors' note** – but see Anikovich, this volume). While one may interpret such a spatial discontinuity in the distribution of archaeological sites as indicative of a very rapid spread of the later groups into northern areas, I argue that occasional distant forays by the groups of a preceding culture offer the most parsimonious explanation for this phenomenon.

ENVIRONMENTAL DYNAMICS AND HOMINID ADAPTATIONS

Having considered how evolution of the environment affected colonization of new habitats by hominids, I now turn to consider the relationships between the dynamics of the natural environment and hominid cultural adaptations, particularly their material components.

I have shown above that climatic fluctuations were of greater frequency and magnitude in the temperate zones than in the tropics. This suggests that the less pronounced climatic and environmental changes in the tropics may have permitted a greater stability in long-term hominid adaptations there. I have previously suggested that this would result in a slower rate of culture change in the tropics as compared to that in higher latitudes (Velichko 1971, Gerasimov, Velichko 1972). Archaeological data on hand at that time appeared to support the hypothesis that when the higher latitudes underwent dramatic environmental transformations in the form of Pleistocene glacial/interglacial cycles, hominids there developed Upper Paleolithic cultures while groups who occupied the lower latitudes still maintained Middle Paleolithic technological traditions (Alekseev 1978, Grigor'ev 1977). Subsequent research, however, negated this hypothesis. The Middle to the Upper Paleolithic transition occurred roughly at the same time, about 40,000 B.P., both in Africa and Eurasia (Goebel *et al.* 1993). Early anatomically humans have been reported from Africa (Klasies, Border Cave I) dating to about 125,000, significantly preceding those from Europe, where the earliest remains of anatomically modern humans date to no older than the second half of the last glaciation (Klein 1989).

What my reading on the extant record shows today is that the more stable environments, those found in southern latitudes, permitted hominids to remain more conservative in their material culture for longer periods of time. Less stable environments, on the other hand, such as those in northern latitudes of Eurasia, offered more challenges for hominid survival. These challenges were met by greater changes both in morphology and in behaviour. While these changes were more on the level of morphology during the earlier stages of human evolution, during the later phases they were increasingly more tied to behavioural changes.

Regional and latitudinal environmental differences clearly affected the cultural adaptations of Upper Paleolithic people. Survival in open periglacial landscapes required adaptations to highly seasonal environments. They could not have been possible without winter clothing and tools for making them, the construction of substantial shelters, and the use of storage facilities to store food. Upper Paleolithic sites from the Russian Plain found in periglacial environments (e.g. Mezhirich, Avdeevo, Eliseevichi, Yudinovo, Timonovka) clearly show this high elaboration of material culture (Soffer 1985, Velichko *et al.* 1977, Velichko, Kurenkova 1990).

CONCLUSION

Colonization of new habitats was a seminal component of hominid evolution, from the emergence of the genus *Homo* up to some 25,000–20,000 B.P. when Upper Paleolithic groups occupied the Arctic. Evidence on hand show that this process was not continuous either in time or in space. Until some 2 Mya hominids remained only in tropical habitats. Current evidence suggests a linear patterns of hominid spread into temperate Eurasia through northeastern Africa, the Middle East, and the Caucasus. During the subsequent hundreds of thousands of years, the hominids occupied piedmont habitats that were

protected from the northerly winds. By the late Lower Paleolithic we see hominids undertaking occasional forays into open landscapes north of the mountains. These initial attempts to colonize new areas were not synchronous in the different parts of Eurasia. Western Europe likely saw the earliest and the most continuous colonization of its northern plains. The increase in the continentality of the climate as one moved from the west to the east in Eurasia caused both the temporal and the spatial delay in hominid colonization. The open landscapes of eastern Europe and Siberia, prior to being successfully colonized by Upper Paleolithic populations, saw repeated advances and retreats of hominid populations.

REFERENCES

ABRAMOVA Z. A., 1989: Paleolit severnoy Azii. In: P. I. Boriskovskij (Ed.): *Paleolit Kavkaza i severnoy Azii.* Pp. 145–243. Nauka, Moscow.

ALEKSEEV M. N., KAMALETDINOV V. A., ZIGERT H., GRINENKO O. V., GNIBIDENKO Z. N., GRAVIS G. F., SHAMSHINA E. A., 1990: *Problemy geologii paleoliticheskogo pamiatnika Diuring-Yuriakh.* Yakutsk.

ALEKSEEV V. P., 1978: *Paleoantropologya zemnogo shara i formirovanye chelovecheskikh ras.* Paleolit. Nauka, Moscow.

ALEKSEEV V. P., 1984: *Stanovlenye chelovechestva.* Politizdat, Moscow.

ALEKSEEVA T. I., 1977: *Geograficheskaya sreda i biologiia cheloveka.* Mysl', Moscow.

CHERNYSH A. P., IVANOVA I. K., GORETSKIY G. I. (Eds.), 1977: *Mnogosloynaya paleoliticheskaya stoianka Korman' IV.* Nauka, Moscow.

CHERNYSH A. P., IVANOVA I. K., GORETSKIY G. I. (Eds.), 1982: *Molodova I: unikal'noe must'erskoe poselenie na srednem Dnestre.* Nauka, Moscow.

COPPENS Y., 1994: East side story: the origin of humankind. *Scient. Amer.* 270: 88–95.

DEREVIANKO A. P., POWERS R., SHIMKIN D.(Eds.), 1997: *The Paleolithic of Siberia.* The University of Illinois Press, Champaign-Urbana, Illinois.

DROZDOV N. I., CHEKHA V. P., LAUKHIN S. A., 1990: *Khronostratigrafia paleoliticheskikh pamiatnikov sredney Sibiri.* Nauka, Novosibirsk.

DZAPARIDZE V., BOSINSKI G., BUGIANISVILI T., GABUNIA L., YUSTUS A., KLOPOTOVSKAYA N., KVAVADZE E., LORDKIPANIDZE D., MAJSURADZE G., MGELADZE N., NIORADZE M., PAVLENISVILI E., SCHMINKE H. U., SOLOGASVILI D., TUSABRAMISVILI D., TVALCRELIDZE M., VEKUA A., 1989: Der Altpaläolitische Fundplatz Dmanisi in Georgien (Kaukasus). *Jahrbuch der Römisch-Germanischen Zentralmuseums Mainz* 36: 67–116.

FRENZEL B., 1967: *Die Klimaschwankungen des Eiszeitalters.* Braunschweig.

GAMBLE C., SOFFER O., 1990: Pleistocene polyphony: the diversity of human adaptations at the last glacial maximum. In: C. Gamble, O. Soffer (Eds.): *The World 18,000 B.P.* Vol. 1. Pp. 1–23. Plenum Press, New York.

GERASIMOV I. P., VELICHKO A. A., 1974: Problema roli prirodnogo faktora v razvitii pervobytnogo obschestva. In: A. A. Velichko (Ed.): *Pervobytnyi chelovek i prirodnaia sreda.* Pp. 7–16. Institut Geografii, Moscow.

GOEBEL T., DEREVIANKO A., PETRIN V., 1993: Dating the Middle-to-Upper Paleolithic transition at Kara Bom. *Curr. Anthrop.* 34,4: 452–456.

GOLIKOV A. N., SCARLATO O. A., 1989: Evolution of Arctic ecosystems during the Neogene period. In: Y. Herman (Ed.): *The Arctic Seas.* Pp. 257–280. Van Nostrand Reinhold, New York.

GRICHUK V. P., 1981: Drevneysheye materikovoe oledenenye v Evrope, yego priznaki i stratigraficheskoe polozhenie. In: A. A. Velichko (Ed.): *Voprosy paleogeografyi pleystotsena lednikovykh i perigliatsial'nykh oblastey.* Pp. 7–35. Nauka, Moscow.

GRIGOR'EV G. P., 1974: Metodicheskye osnovaniia dlia razreshenyia voprosa sootnoshenyia prirodnogo okruzhenyia i kul'tury cheloveka. In: A. A. Velichko (Ed.): *Pervobytnyi chelovek i prirodnaya sreda.* Pp. 65–71. Institut Geografii, Moscow.

GRIGOR'EV G. P., 1977: *Paleolit Afriki – vozniknovenye chelovecheskogo obschtsestva.* Nauka, Leningrad.

GUSLITSER B. I., PAVLOV P. V., 1993: Man and nature in northeastern Europe in the Middle and Late Pleistocene. In: O. Soffer, N. D. Praslov (Eds.): *From Kostenki to Clovis: Upper Paleolithic – Paleo-Indian adaptations.* Pp. 175–188. Plenum Press, New York.

IVANOVA I. K., 1965: *Geologicheskyi vozrast iskopaemogo cheloveka.* Nauka, Moscow.

KLEIN R.G., 1989: *The Human career: Human biological and cultural origin.* University of Chicago Press, Chicago.

LAMBERT D., 1987: *The Cambridge Guide to Prehistoric Man.* Cambridge University Press, Cambridge.

LAUKHIN S. A., 1993: Kontseptsyia poetapnogo zaselenyia severnoy Azii paleoliticheskim chelovekom. *Doklady AN* 332,3: 352–355.

MARKOV K. K., VELICHKO A. A., 1967: *Chetvertichnyi period.* Vol. III. Nedra, Moscow.

MEDVEDEV G. I., SAVEL'EV N. A., SVININ V. V., 1990: *Stratigrafyia, paleogeografyia i arkheologyia iuga sredney Sibiri.* Nauka, Irkutsk.

MOCHANOV Y. A., 1977: *Drevneyshye etapy zaselenyia chelovekom severo-vostochnoy Azii.* Nauka, Novosibirsk.

MOCHANOV Y. A., 1992: *Drevnejshyi paleolit Diuringa i problema vnetropicheskoy prarodiny chelovechestva.* Nauka, Novosibirsk.

PRASLOV N. D., 1969: Domustierskye i Mustierskye pamyatniki iuga russkoy ravniny, In: I. P. Gerasimov (Ed.): *Priroda i razvitie pervobytnogo obschestva na territorii evropeyskoy chasti SSSR.* Pp. 119–127. Nauka, Moscow.

PRASLOV N. D., 1982: Rasselenye cheloveka v Evrope v pozdniem pleystotsene. In: I. P. Gerasimov, A. A. Velichko (Eds.): *Paleogegrafia Evropy za poslednye sto tysiatch let.* Pp. 113–115. Nauka, Moscow.

RUKANG W., OLSEN, J. W. (Eds.), 1985: *Paleoanthropology and Paleolithic archaeology in the People's Republic of China.* Academic Press, Orlando.

SOFFER O., 1985: *The Upper Paleolithic of the Central Russian Plain.* Academic Press, Orlando.

SWISHER C. G., RING W. J., ANTON S. C., SHWARCZ H. P., CURTIS C. H., SUPRIJO A, WIDIASMORO, 1996: Last *Homo erectus* of Java: potential contemporaneity with *Homo sapiens* in southeast Asia. *Science* 274: 1870–1874.

TSEJTLIN S. M., 1979: *Geologyia paleolita severnoy Azii.* Nauka, Moscow.

VELICHKO A. A., 1971a: Svyaz' dinamiki prirodnykh izmeneniy v pleystotsene s razvityem pervobytnogo cheloveka. *Voprosy antropologii* 37: 3–18.

VELICHKO A. A., 1971b: Relazione fra modificazioni dell'ambiente ed evoluzione dell'uomo primitivo. In: A. Mondadoi (Ed.): *Scienza ed tecnica* 71. Pp. 269–280. Milano.

VELICHKO A. A., 1973: *Prirodnyi protsess v pleystotsene*. Nauka, Moscow.

VELICHKO A. A., 1985: Priroda u kolybeli chelovechestva. *Priroda* 3: 35–45.

VELICHKO A. A., 1988: Geoecology of the Middle Paleolithic in East Europe and the adjacent areas. In: M. Otte (Ed.): *L'homme de Néandertal*. Vol.2. Pp. 181–206. ERAUL 28. Liège.

VELICHKO A. A., 1993: Koevoliutsia Cheloveka i Okruzhaiuschej Sredy. *Izvestiia RAN, ser. geogr.* 5: 18–31.

VELICHKO A. A., GVOZDOVER M. D., 1969: Rol' prirodnoy sredy v razvitiy pervobytnogo obschestva. In: I. P. Gerasimov, A. A. Velichko (Eds.): *Pervobytnyi chelovek i prirodnaya sreda*. Pp. 227–237. Nauka, Moscow.

VELICHKO A. A., GREKHOVA L. V., GUBONINA Z. P., 1977: *Sreda obitaniya pervobytnogo cheloveka timonovskikh stoyanok*. Nauka, Moscow.

VELICHKO A. A., KURENKOVA E. I., 1990: Environmental conditions and human occupation of Northern Eurasia during the Late Valdai. In: O. Soffer, C. Gamble (Eds.): *The World at 18,000 B.P.* Vol. 1. Pp. 254–265. Plenum Press, New York.

Andrej A. Velichko
Laboratory of Evolutionary Geography
Institute of Geography
Russian Academy of Sciences
Staromonetny Per. 29
Moscow 109017
Russia
Fax: 7 095 230 2090
E-mail: paleo@glas.apc.org