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OUT OF ASIA: A PALEOECOLOGICAL SCENARIO OF MAN AND HIS CARNIVOROUS COMPETITORS IN THE EUROPEAN LOWER PLEISTOCENE

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Summary
When early man entered Europe during the Lower Pleistocene, staying at the southeastern gate of the continent on the Pliocene/Pleistocene boundary, he had to compete successfully with the large carnivorous species, as he depended on animal food resources. The paleoecological scene of the rich predator guild and large herbivore community of the Epivillafranchian reference horizon at Untermassfeld (Germany) provide an excellent basis for developing a plausible scenario for man's placement in European Lower Pleistocene habitats. Only with possession of a deadly weapon would man have been able to ensure himself a place in the carnivore interspecific hierarchy enabling him to enjoy nearly unlimited large mammal food resources. Without it, no niche existed. No mammalian predator species in the Upper Villafranchian and Epivillafranchian faunas has possible African roots much later than the Middle Pliocene. In contrast, there was obvious penetration of large carnivore elements from east Asia ending in the European Epivillafranchian, as well as herbivore dispersal events from the Eurasian east to the west. For man, as an integrated member of this large mammal fauna, there should not be any real doubt that his way into Europe was out of Asia, but not out of Africa. The specific mosaic morphological pattern of early man at the southeastern gate of Europe may easily be understood in terms of a common archaic ancestor population dispersed from roots in Africa and Asia not later than about 2.5 myr ago and undergoing geographically different progressive evolution before finally starting from Asia to Europe.

Introduction

Survival of early man in temperate Eurasia, whatever was the time of his arrival, depended in a year-round view on sufficient animal food resources. As there is general agreement on this point, no new reasoning may be necessary (e.g., Turner 1992, who considers terrestrial mammals likely to have been a key resource). An obligatory carivory, even if contributing only partially and seasonally to man's food spectrum, is putting man inevitably in the role of a member of the guild of larger terrestrial carnivores. He was forced to stay in competition with them, whether mainly as a hunter or mainly as a scavenger (e.g., Blumenschine, 1987 and comments in this paper, also Schüle & Schuster, 1996).

Therefore, the early dispersal of man into any region of temperate Eurasia in general, and into Europe in particular, had to meet the requirements of being successfully competitive within the interspecific carnivore hierarchy. The earliest undebatable evidence of man at the gates of Europe is the Dmanisi mandible (Caucasia Minor, Georgia). It is actually dated to within the Olduvai paleomagnetic event at about 1.9-1.7 myr (Sologasvili *et al.*, 1996, Schmincke & van den Bogaard, 1996), at the boundary of the Pliocene and Pleistocene. The fauna essentially corresponds to the Upper Villafranchian mammal age of the Lower Pleistocene (Vekua, 1996). In the west of Europe it is obvious that man did not disperse before the end of the Upper Villafranchian, as traces remain in sites with an Epivillafranchian faunal complex, such as Venta Micena (Orce, Granada, south-eastern Spain, Palmqvist *et al*., 1996, Gibert *et al*., 1998) or Vallonet (south-eastern France, de Lumley *et al*., 1988). The fossil-bearing sands of Untermassfeld (Thuringia, Germany), free of human remains and dated at about 1 myr to the onset of the Jaramillo paleomagnetic event, were chosen as the reference horizon of this Late Villafranchian/early Middle Pleistocene transitional zone (Kahlke, this volume). The paleoecology of the rich carnivore guild of the Untermassfeld site has been broadly discussed within the framework of a study of the felid species (Hemmer, in press). This provides the basis for the development of a scenario for man's fitting into the interspecific hierarchy of his competitors in the late Lower Pleistocene. Looking at the felid species at the paleo-population level adds to the knowledge of geographic affiliations of large mammals in Europe at the time of the arrival of man, and also indicates his possible way in.

The paleoecological scene of European Epivillafranchian large carnivores

The Untermassfeld site comprises all large felid species of the European Lower Pleistocene, with well-preserved dentition, skull and postcranial specimens. Abundant in the river valley was the European jaguar (*Panthera onca gombaszoegensis*, revised at the specific level by Hemmer, in press), a huge-sized pantherine cat with a body weight range between 90 and 180kg for the Untermassfeld remains, and 70 to 210kg over all European sites. This makes that population comparable with modern Indo chinese tigers (100-195kg) or modern Indian lions (110-190kg) (for methods and details of body weight estimations and for references concerning this species as well as the following ones see Hemmer, in press). The second felid species was the giant European cheetah (*Acinonyx pardinensis*). The body weight estimates for this species span between 60 and 130kg during its late Pliocene and Lower Pleistocene history, the Untermassfeld specimen occupying the largest size. This is just double the weight of the modern African cheetah (35-65kg). A leopard-sized cat was for a long time the most enigmatic felid of the European Villafranchian. Now it is understood as an European puma (*Puma pardoides*, syn. *Viretailurus schaubi*) representing a basic level of puma evolution and a forerunner of the modern American pumas. This species is represented in Untermassfeld by a 40-45kg animal. The weights of Villafranchian European pumas altogether are to be estimated as 35-45kg for females and 60-100kg in males, which equals the size of the American puma. The lynx of Untermassfeld (*Lynx issiodorensis* ssp. ex aff. *spelaeus*) was smaller than the earlier European Villafranchian lynxes, with a body weight in the range of 15-25kg; comparable in weight to the actual northern lynx, but with a somewhat more stocky stature. The sabertooth cats are represented by two species. The dirktooth cat (*Megantereon cultridens*) was a very stocky, short-limbed, small-headed cat with extremely long dirk-like canines and powerful forelimbs. Its body weight, compiled over the whole Villafranchian and Epivillafranchian time span, obviously varied between 60 and 210kg, comparable to the modern, now extinct, Turkmenian tiger. The second sabertooth species of the Untermassfeld site and other European Villafranchian and Epivillafranchian faunas was the mighty scimitar cat (*Homotherium crenatidens*), larger than the Siberian tiger, with body weights to be estimated from 210 up to 400kg for the Untermassfeld specimens. This species was characterized by a somewhat hyena-like and also - in its massiveness - a bear-like stature with elongated forelimbs and a sloping back and by large, flattened and recurved canines with sharp serrated edges.

There were no other great cat species in Villafranchian and Epivillafranchian European faunas. The report of the lion (*Panthera leo*) from Vallonet (de Lumley *et al*., 1988) is based on an upper canine that could well have belonged to a jaguar, reports of a leopard (*Panthera pardus*) from Vallonet (de Lumley *et al*., l.c.) and from Venta Micena (Pons Moyá, 1987) look rather to be based on puma and jaguar remains (Hemmer, in press).

In addition to the felids, a giant hyena (*Pachycrocuta brevirostris*) is common in the Epivillafranchian faunas, being very abundant at Untermassfeld (Kahlke, this volume). This species of lion-like size was obviously extremely powerful, but seemingly less well-equipped for running than the modern hyenas (Turner & Antón, 1996). A body weight in the region of 100 to 150kg seems not to be unrealistic (Hemmer, in press). A related, but smaller species, *Pachycrocuta perrieri* (possibly conspecific with the modern brown hyena, *Hyaena brunnea*: Turner, 1990), disappeared in Europe for the time being in the early Lower Pleistocene. Besides the giant hyena lived, a very large canid, the European hunting dog (*Xenocyon lycaonoides*), comparable in size to a large modern wolf. The true wolf (*Canis lupus mosbachensis*), a frequent element of the Untermassfeld fauna (Kahlke, this volume), was a relatively small canid, to be compared with the modern southern wolves of the Arabian Peninsula and India. The bear frequently occurring at this site is placed into the ancestry of brown bears (Musil, see Kahlke, this volume).

For those carnivores that have near living relatives, the spectrum of favored prey species can be outlined with a high degree of reliability. The size of the ideal prey follows the size of the predator within each type of functional specialization. Looking at the hunting biology of the modern felids and taking into account the factor body weight and specific functional correlates in the modern counterparts, the main target species of jaguar, puma, cheetah and lynx within the series of large herbivores of the Untermassfeld fauna (for the list see Kahlke, this volume) become obvious

(Hemmer, in press). The ideal prey for the European jaguar were surely the medium-sized and large deer species *Cervus nestii* and *Eucladoceros giulii*, and the wild pig (*Sus scrofa*). Less importance should be given to the larger moose (*Alces carnutorum*) and bison (*Bison menneri*), and to the smaller roe deer (*Capreolus* sp.) and the large rodents *Castor fiber* and *Troqontherium cuvieri*. Calves of elephant (*Mammuthus troqontherii*), rhino (*Stephanorhinus etruscus*) and hippopotamus (*Hippopotamus amphibius antiquus*) are to be considered as of only marginal interest for this predator. The European puma would have favored small and medium-sized ungulates, represented in the Untermassfeld fauna by *Cervus nestii*, *Capreolus* sp. and *Sus scrofa*, also by calves of the larger deer species. Foals of the equid (*Equus* sp.) and hares may mark the boundary of the usual puma prey size range. The main victims of the European cheetah would have been ungulates dwelling in more open landscapes and weighing between 30 and 120kg. In the Untermassfeld herbivore fauna, these requirements were best met by *Cervus nestii* and foals of *Equus* sp. The main pillars of the prey spectrum of the lynx are roe deer and hares, additionally calves of the medium-sized deer species and piglets of *Sus scrofa*, as well as different rodents.

The problems arising from ideas of the hunting or scavenging behavior of the sabertooth cats have been widely discussed. Conclusions reached by the author (Hemmer, in press) by integrating knowledge of felid ethology with the results of studies on comparative functional morphology of dentition, skull and postcranial elements allow the drawing of a consistent picture. The dirktooth cat, as a sturdy, short-limbed forest hunter may not have been able to attain a balanced energy budget and to minimize the risk of canine breakage when regularly hunting herbivores of the same size category as favorable by the European jaguar of comparable body weight. Adult bison and especially rhino meet the functional requirements of *Megantereon cultridens* more satisfactorily. The same should hold true for young hippos on the riverbank, or for elephant calves approaching the forest-edge. The scimitar cat was obviously adapted to a more cursorial life than the modern felids, roaming over a broad range of habitats. It seems that this species was a prime predator of elephant calves and other pachyderms and well adapted to deal with fresh carcasses of these large-sized mammals.

There are no convincing arguments (vs. Turner & Antón, 1996) that the feeding behavior of the giant hyena was not the same one as that shown today by the brown hyena, feeding as a scavenger with only a few exceptions (Mills, 1978). A quantitative paleoecological study of the Venta Micena large mammal assemblage does in fact suggest that *Pachycrocuta brevirostris* was a bone-cracking scavenger that fed largely on the carcasses of ungulates preyed upon and partially consumed by fresh-meat-eating carnivores (Palmqvist *et al*., 1996). For a well-founded opinion on the predatory behavior of the great hunting dog in the Epivillafranchian faunas, it is crucial to know relative brain size, as a correlate of grouping ability. With the African wild dog (*Lycaon pictus*), pack size decides not only the upper size limit of the prey to be hunted down, but also its position in the interspecific carnivore hierarchy (Eaton, 1979). The ability of *Xenocyon lycanoides* likewise to hunt in large packs is assumed here. On that basis, the reach of this large canid could have been extended to the smaller pachyderms (again in comparison with the broad prey spectrum of the much smaller modern African wild dog). The small wolf of the Epivillafranchian faunas may not have attacked herbivores larger than the medium-sized deer. Opportunistic scavenging as found in the living southern wolves, coyotes and jackals, also cannot be denied for this early wolf. Finally, the bears of Epivillafranchian sites should be considered as occasional and opportunistic predators as are most modern bear species in addition to their vegetable diet. Compared with actual brown bears, the upper limit of prey size may have been that of the large cervids. Carrion feeding surely played some role, too.

Taking the favored prey spectra of the large carnivores of Untermassfeld outlined above together, we see a picture of the different rates the herbivore species had to pay to the predator guild, also of the different rates paid by immature and mature animals. This picture correlates well with the minimum number of individuals of these species and their age stages in the herbivore fossil assemblage of this site (Hemmer, in press). Thus, a well-functioning and balanced large mammal community is indicated despite the considerable number and diversity of predator species. Looking at their probable interspecific behavioral rank as deduced from the comparative study of modern carnivore guilds, from the size range of the species in question and from their functional specializations, there is a clear picture of a well-balanced community of all the carnivores involved (Hemmer, in press). Without doubt, the large

European jaguar dominated the European puma, resulting in a low-density puma population when jaguars were plentiful. On the other hand, an accumulation of pumas may have lowered the lynx density. In more open landscapes, the giant cheetah could have played a limiting role for the puma population. A confrontation of jaguar and cheetah would usually have resulted in a lower rank for the latter, if this happened despite the different habitat preferences of the species. Different prey-size ranges of the jaguar and the dirktooth cat surely allowed their coexistence. In cases of conflict, the dirktooth cat was probably superior to the jaguar of comparable size, allowing the former to take jaguar prey in active confrontation. Such behavior may have negatively influenced jaguar density, when there was not enough supply of typical *Megantereon* prey. Finally, there should be no doubt of the top position held by the mighty scimitar cat in the felid interspecific hierarchy, allowing the presumably widely roaming *Homotherium*. opportunistic confrontational scavenging.

With the situation for the modern African pair of leopard and brown hyena, the European jaguar may have been higher ranking than the giant hyena, if this species was not group-living like also the modern *Hyaena* species. In terms of the modern brown hyena and cheetah pair, *Pachycrocuta brevirostris* should have been dominant over the giant cheetah, allowing the hyena to take cheetah prey in active confrontation. The European hunting dog was surely the top carnivore of the whole Epivillafranchian predator guild, if it did hunt in large packs. As a solitary hunter, it was presumably dominated even by the large cheetah.

Integrating these concepts of habitat, of favored prey and of the mutual relations within the guild of large predators, a scenario of carnivore feeding biology can be outlined for the Untermassfeld assemblage (Hemmer, in press). A very high hunting success rate of the giant cheetah as a sprinter in open landscapes, allowed this species the position of the most important carcass producer. An occasional loss of prey through encounters with predators ranking higher in the interspecific hierarchy was presumably quite tolerable. The cheetah must be considered to be a typical flesh eater, in contrast to the less specialized pantherine cats with some bone-crushing capabilities (Marean, 1989), and so its hunting activity always provided partially consumed carcasses to be used by less specialized felids, by wolves and by the bone-crunching giant hyena in the role of carcass destroyers. The dirktooth and scimitar cat would surely have seized any opportunity of taking large to medium-sized fresh kills by active confrontation with other carcass producers. This being the case, in addition to pachyderm hunting, the two sabertooth species in their role of extremely specialized flesh eaters with a complete inability to process bone must have left a considerable quantity of scavengeable flesh and bones to be used by most of the other carnivores (Blumenschine, 1987; Marean, 1989; Turner, 1992). In the riparian woodlands and forested areas, the European jaguar must be considered as an important carcass producer, as was the giant cheetah in more open landscapes. What was left by this cat was available for further processing, especially by wolves and bears. The large hunting dog also seems to have ranged among the top carcass producers, especially in open habitats. It should not be assumed that there was much scavengeable food left by their pack activity. The solitary living cat species ranging near the end of the interspecific predator hierarchy had to eat smaller prey animals immediately, or safeguard carcasses against competing carcass destroyers. In the case of the European puma, this could have been effected by covering them with movable materials found nearby as is done by the American puma or by carrying them up into trees as is favored by the leopard. The left-overs of puma and lynx kills was then available for wolves, and also for small carnivores, wild pigs and birds.

Fitting man into the carnivore scenario

Man the carnivore must now be fitted into this community. In the role of man the hunted, he may possibly have been part of the prey spectrum of the tiger-sized European jaguar and also of the giant cheetah, as the latter was much larger and therefore more inclined to attack man than is its modern relative. The European puma may have been inclined to prey upon man more sporadically. Lower down the chain, man surely did not fit well into the prey specifications of the two sabertooth cat species. The large hunting dog, on the other hand, is assumed to have been a formidable threat if hunting in pack, whereas the small wolf only may have been dangerous for small children alone. Despite its mighty dentition and powerful stature, the giant hyena may not have been a great problem, at least as long as scavenging.

This scene will have changed dramatically when man became a carcass-owner. Attracting roaming carnivores with the smell of flesh would have provoked confrontational scavenging, making especially the hyenas abundant in the more open landscapes and likewise the bears in the woodlands formidable rivals. Without the possession of deadly weapons pointed to each actually relevant competing predator man would have not been able to survive long within this large predator guild, being himself a carnivore and thus repeatedly a carcass owner. Without such weapons also to employ for hunting, it would already have been very hard to gain enough fresh flesh through scavenging. Dietary considerations meant that only relatively fresh meat could be consumed by man without the risk of serious disorder (Schüle & Schuster, 1996). The considerable habitat difference of carcass availability as shown for East African ecosystems by Blumenschine (1987, 1989) must not be expected for Epivillafranchian Europe. The rate of decomposition of carcasses left by the great cats in East Africa corresponds to the density of spotted hyenas, who prefer open vegetation habitats to riparian woodlands (Blumenschine l.c.). A large carcass destroyer superior in competition with unarmed man in woodland habitats is lacking in this African model, but was of course present in the form of the bear in Europe, leaving there no distinct scavenging niche to be occupied by man.

In summary, it seems obvious that there was no good place for man, dependent on large terrestrial mammals as a key food resource, in the large carnivore guild in Epivillafranchian Europe, as long as he had no weapon at his disposal suited to deal successfully with his carnivore competitors.

Having such a weapon, however, allowed man to rise to the top of the carnivore hierarchy and ensured him enough animal food resources by active hunting as well as by confrontational scavenging, even in conflict with large sabertooth cats on fresh kills. As, in the Lower Pleistocene, man succeeded in dispersing from the southeastern gate of Europe into the Iberian southwest, thereby making himself part of the carnivore community, he must have been able to integrate, i.e., he must have possessed a suitable weapon, advocated by Schüle & Schuster (1996) to be a wooden spear.

Martinez-Navarro & Palmqvist (1996, Palmqvist *et al*., 1996) present the idea that only the presence of the dirktooth cat, considered to be a hypercarnivorous felid generating large amounts of carrion, made the first dispersal of hominids to Eurasia in the Lower Pleistocene possible. In principle, they consider early man to be a scavenger dependent on the hunting activity of the dirktooth cat, following it over the continent. They don't attempt to explain how man, who, if forced to earn his animal food resources by scavenging only, must be considered unarmed, could have managed to survive side-by-side with his mighty carnivorous competitors in the Lower Pleistocene predator guild. Man able to drive off sabertooth cats from their kills must also have been able to do a good bit of hunting himself, making him independent of any carnivore species. Indeed, in the long run, man may possibly have influenced *Megantereon cultridens* populations in a negative sense, if frequently disturbing the dirktooth cat by confrontational scavenging. This species is characterized by a relative small flesh processing dentition in relation to body weight. To meet its energy needs it therefore had to stay longer at the kill than other cat species of the same size, e.g., the European jaguar. Within the interspecific predator hierarchy this was surely no problem for a species with top rank in its woodland habitat, just as long as man didn't enter the scene with weapons (Hemmer, in press).

Looking for indications of man the hunter at Epivillafranchian sites with human traces seems to be in vain in Venta Micena, where hyenas were obviously responsible for the bone assemblage (Palmqvist *et al*., 1996). Biotic origin is also assumed for bone layers of the Vallonet cave. An unusually large number of well-preserved rhino postcranial elements is one of the characteristics of this assemblage (de Lumley *et al*., 1988). The most frequent carnivores at this site, bears, were hardly the rhino killers. The sabertooth cats as pachyderm specialists are not represented in that fauna and they surely were not inclined to drag bodies weighing a ton to a cave. Their dentition was also not very useful in disarticulating rhino legs before a transport. Rhino don't fit the prey spectrum of the European jaguar for such a high percentage. The giant hyena surely didn't prey on rhino, but may well be responsible for bone transport. It seems improbable that rhinos moved themselves into the cave to die. Only man the hunter can indeed provide a plausible explanation of rhino killing and subsequent transport of the disarticulated fleshy parts to the cave.

Biogeographic implications of the carnivore guild

Martinez-Navarro & Palmqvist (1995, 1996) advocated the arrival of an African dirktooth cat (*Megantereon whitei*) in Europe towards the end of the Villafranchian, immediately followed by man feeding on the remnants of the kills of this cat. Unfortunately, the statistics used by these authors to separate an African species *Megantereon whitei* from the Eurasian species *M. cultridens* and *M. falconeri* accomplished this result by omitting an African specimen that would have reduced the basic problem to sexual dimorphism, not to different clades. The specific traits of the dentition of dirktooth cats found at Untermassfeld, Venta Micena and Dmanisi may be interpreted as the end of a chronocline beginning in the European Lower Villafranchian as well as by descent from east Asian relatives (*M. cultridens nihowanensis*), this being by no means less probable than a relationship with an African population (Hemmer, in press).

Turner (1992), when discussing European carnivore immigration events around 1.0 myr, stresses the presence of the lion and the leopard in the Vallonet fauna for a possible African origin. Indeed, these scanty remains may rather be attributed to the European jaguar and the European puma, excluding the lion and the leopard from the Epivillafranchian European scene (Hemmer, in press).

The jaguar was obviously a holoarctic species in the Lower Pleistocene. Its dispersal over Europe took place in the uppermost Pliocene. An ancestor of the European puma, living here since the Lower Villafranchian, may have existed in Africa as early as in the Lower Pliocene (Hemmer, in press). No Lower Pleistocene African connection can be demonstrated with these two species. From the Lower Pleistocene on, the lynxes separated in regional evolutionary lineages. Giant cheetahs dispersed worldwide in the Pliocene at about 3 myr ago. Nevertheless the cheetah of the Epivillafranchian Untermassfeld so clearly matches the east Asian Middle Villafranchian-lower Middle Pleistocene cheetah, that at least a Lower Pleistocene transpalearctic gene flow from east to west must be assumed, if not a new European colonization from the east (Hemmer, in press). Obviously a fully comparable situation existed for the scimitar cat-distributed nearly world-wide during the Upper Pliocene, but having in the European Epivillafranchian population extremely flattened saber canines, present before only in central and east Asian populations (Hemmer, in press).

The giant hyena entered Europe at the end of the Upper Pliocene, but was present earlier in Asia as well as in Africa, in both continents reaching back to about 3.0 myr (Turner & Antón, 1996) . The European hunting dog may have evolved from a pool of large canids dispersing in Europe in the Lower Pleistocene but distributed in Asia since 2.5 myr and settling in Africa at the end of the Pliocene (Torre *et al*., 1992). Wolves never had an African connection. The same is true of the evolutionary line of the modern bears.

This short survey of the large carnivore competitors of earliest man in Europe clearly shows that there was no species with a possible African origin much later than the Lower Villafranchian in the Middle Pliocene. Indeed, looking at the population level of such far-roaming species as the giant cheetah and the scimitar cat, possibly also the dirktooth cat, clear morphological connections of the European populations to older east Asian relatives show up just at the time of the dispersal of man in Europe in the Lower Pleistocene. It seems insignificant to this basic statement whether these connections were only from gene flow from the east within existing populations or from new colonizations of Europe by new waves of these species in areas previously depleted of them. Be this as it may, there was obviously a penetration of large carnivore elements into Europe that may have started in east Asia in the Middle Villafranchian, reaching the eastern gates of Europe possibly during the Upper Villafranchian and ending in the west in the Epivillafranchian. This movement in the carnivore community paralleled the same movement in large herbivore species, which also have clear Asian connections in the Lower Pleistocene of Europe. The most striking seem to be the so-called *Megaloceros* (*Megaceroides*) dispersal events, but the appearance of primitive bisons, of caprines and ovibovines from the east also marked this period (Torre *et al*. 1992). There seems no conclusive reason why man, ecologically integrated in the carnivore guild and in the large mammal community in general, should not have been a member during the dispersal from Asia to and over Europe. Only the hippopotamus obviously reached Europe from Africa as an active swimmer or by drift from coast to coast over the

Mediterranean Sea (Kahlke, 1997). Man lacked the evolutionary adaptations to follow suit.

Finally, we turn to the evolution of man himself. The oldest specimen of *Homo* at the southeastern gate of Europe, the Dmanisi mandible shows a mosaic of archaic features of early African *Homo* of roughly the same absolute age and even, though it is less pronounced, of *Australopithecus*. This is combined with progressive characteristics already foreshadowing the late *erectus* morphotype (Bräuer *et al*., 1996). Such a pattern may easily be understood on the basis of a common archaic *Homo* population dispersing over Africa and Asia not later than the Middle Villafranchian, beginning at about 2.5 myr ago and afterwards undergoing geographically different progressive evolution. The first traces of early man at the base of the Middle Villafranchian in Africa as well as in southwestern Asia (up-to-date tabulated compilation of sites: Henke & Rothe, 1999) fits well in the framework of a broad faunal exchange at that time.

Dedication

This paper is dedicated to Prof. Dr. Dr. Hans-Dietrich Kahlke, nestor of Eurasian Quaternary Paleontology, on the occasion of his 75th birthday on May 27, 1999.

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