

MAMMALIAN REMAINS IN A PALAEOOLITHIC CONTEXT

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Summary

Palaeolithic industries are often associated with fossil mammalian remains which can inform us not only on the subsistence of our Palaeolithic ancestors but can also be used for a reconstruction of the palaeoenvironment and for relative dating of the Palaeolithic sites. The applicability of fossil mammals to a reconstruction of the palaeoenvironment is however hampered by a number of restrictions. The distribution of homoithermic mammals depends more on food than on external temperatures. Smaller mammals may even be less dependent on environmental conditions than larger mammals as they have the capacity to live under micro-climatic conditions. The use of fossil mammals for inferring former ecological conditions is also hampered by the fact that mammals have the capacity to adapt to various environments and to tolerate other circumstances than those under which they live today. The evolution as observed in the Pleistocene Arvicolidae is most likely not restricted to changes in morphology as the morphological changes may be the result of adaptations to a different environment. There may even be adaptations to a different environment which are not reflected in morphological changes.

When interpreting a fossil assemblage and translating the data into a palaeoenvironmental reconstruction we have to be aware of taphonomical biases. The fossil record is very often not a true reflection of the original fauna of the region. Birds of prey, carnivores and human activity but also hydrodynamic sorting and hibernation act on the composition of the fossil faunal assemblage. Despite these restricting factors we can, in general, use mammal fossils for our conclusions on palaeoclimatic and palaeoenvironmental conditions as we are able to recognise temperate, interglacial and interstadial faunas as well as cold stage, glacial faunas. It has, however, so far not been possible to differentiate the mammal faunas into associations which are characteristic of very specific environmental conditions.

Mammalian fossils can also contribute to the dating and correlation of deposits and to the establishment of a biozonation because most mammals have an extensive distribution area and a number of species also show a rapid evolution and/or migratory shift within the Quaternary. The smaller mammal biostratigraphical subdivision of the Quaternary is based on the Arvicolidae succession and has three well defined biozones for the Pleistocene: Villányian, Biharian and Toringian. The larger mammal faunas are subdivided into Villafranchian and Galerian faunas. However, the late Villafranchian - Galerian boundary is not well defined. The terms late Villafranchian or Galerian are, therefore, of little biostratigraphical value and lead to confusion. This confusion is rooted in the inaccurate dating of the fauna from Isernia. The Arvicola fauna from Isernia has, in my opinion, a late Cromerian age instead of an Early Pleistocene age. Despite this shift in age, the site is nevertheless one of the

oldest Palaeolithic sites in Europe and for that reason very important in a palaeontological as well as an archaeological sense.

Riassunto

Le industrie paleolitiche sono spesso associate a resti di mammiferi fossili che possono da un lato offrire informazioni sul tipo di alimentazione dei nostri predecessori e dall'altro essere utilizzati per una ricostruzione paleoambientale e per datare i siti paleolitici. L'impiego dei mammiferi fossili per una ricostruzione paleoambientale è tuttavia ostacolata da un certo numero di fattori. La distribuzione dei mammiferi omeotermi dipende più dal cibo che dalla temperatura esterna. I mammiferi più piccoli potrebbero anche essere meno dipendenti dalle condizioni ambientali rispetto ai mammiferi più grandi, poiché hanno la capacità di vivere in condizioni microclimatiche. L'utilizzo dei mammiferi fossili per ricostruire le condizioni ecologiche del passato è ostacolato anche dal fatto che i mammiferi hanno la capacità di adattarsi a vari ambienti e di tollerare situazioni molto diverse da quelle in cui vivono oggi. L'evoluzione, come osservato nelle Arvicolidae del Pleistocene, è probabilmente non limitata ai cambiamenti nella morfologia perché questi potrebbero essere il risultato di adattamenti ad un ambiente diverso. Ci potrebbero inoltre essere stati degli adattamenti ad ambienti diversi che non hanno riflessi sui mutamenti morfologici.

Quando interpretiamo una raccolta fossile e traduciamo i dati in una ricostruzione paleoambientale, dobbiamo essere a conoscenza delle sistematiche tassonomiche. L'insieme fossile molto spesso non è una vera rappresentazione della fauna originale della regione. I rapaci, i carnivori e l'attività umana, ma anche la selezione idrodinamica influenzano la composizione della raccolta faunistica fossile. Nonostante questi fattori restrittivi possiamo, in generale, utilizzare i mammiferi fossili per le nostre conclusioni sulle condizioni paleoclimatiche e paleoambientali poiché possiamo riconoscere le faune temperate, interglaciali e interstadiali e anche le faune glaciali. Non è stato, però, possibile differenziare le faune dei mammiferi in associazioni che sono caratteristiche di condizioni ambientali molto specifiche. I mammiferi fossili possono anche contribuire alla datazione e alla correlazione dei depositi e alla ricostruzione di una biozonazione poiché la maggioranza dei mammiferi hanno un'estesa area di distribuzione e un numero di specie mostrano anche una rapida evoluzione e/o uno spostamento migratorio nel Quaternario. La suddivisione biostratigrafica più raffinata dei mammiferi è basata sulla successione di Arvicolidae e ha tre biozone ben definite per il Pleistocene: Villaniano, Bihariano e Toringiano. Le faune dei mammiferi più grandi sono suddivise nelle faune Villafranchiane e Galeriane. Nonostante ciò il limite tra il Villafranchiano superiore e il Galeriano non è ben definito. I termini Villafranchiano superiore e Galeriano sono, inoltre, di modesto valore biostratigrafico e inducono alla confusione. Questa incertezza si ha nella datazione della fauna di Isernia. La fauna ad Arvicola di Isernia è, secondo la mia opinione, del Cromeriano superiore e non del Pleistocene inferiore. Nonostante questa variazione di età, il giacimento è nondimeno uno dei siti paleolitici più antichi d'Europa e per questo motivo molto importante sia in senso paleontologico che archeologico.

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Introduction

The intensive search for Palaeolithic remains in Europe has resulted in the discovery of a large number of Lower, Middle and Upper Palaeolithic sites scattered all over the continent. The Palaeolithic industries are often associated with fossil mammalian remains which may not only inform us on the subsistence of our Palaeolithic ancestors but can also be used for a reconstruction of the palaeoenvironment as well as for the relative dating of Palaeolithic sites.

The applicability of mammalian remains to a reconstruction of the palaeoenvironment will be discussed briefly in the first part of this paper. The second part will present a review of our knowledge of the terrestrial mammal fauna evolution during the Middle and Late Pleistocene. The faunal evolution is translated into a biostratigraphical framework which is correlated with the continental chronostratigraphical subdivision of the Pleistocene.

A well-established correlation between the biostratigraphical data and the chronostratigraphical subdivision offers the possibility of dating mammalian remains and the associated Palaeolithic industries. However, the biostratigraphical data do not always correspond with the results of other methods of dating, such as absolute dating methods and palaeomagnetism. A famous example of conflicting data is the locality of Isernia (Italy). The results of palaeomagnetic research and absolute dating of volcanic deposits indicate a deposition before the Brunhes/Matuyama boundary with an age of 783 Kyr BP, whereas the mammal fossils strongly suggest a much younger age, probably not older than 500,000 BP. This contradiction will be discussed extensively in the concluding part of this paper.

Palaeoenvironmental reconstruction

The results of different research disciplines inform us about the palaeoenvironmental conditions in the past. Sedimentological data help us to reconstruct the geological and environmental conditions at and near the site. The local vegetation, in the vicinity of the site, can be deduced from palaeobotanical macro-remains whereas palynological data can inform us about the vegetation at larger distances.

Land and freshwater molluscs can be very valuable in the reconstruction of the palaeoenvironment, in particular if they are from oxidised sediments where fossil remains such as pollen and insects are missing. They are often well represented and the number of specimens, as well as the number of species, can be high in Quaternary deposits. An advantage of fossil molluscs is that they can nearly always be identified to species level which implies that more meaningful palaeoenvironmental conclusions can be drawn. Furthermore, their presence in large numbers allows a quantitative assessment of changes in species compositions over time.

Fossil insects are, according to Lowe & Walker (1984), "one of the most valuable sources of evidence at our disposal for inferring former ecological conditions". Insect remains are often associated with plant debris and are abundant in sediments accumulated in e.g. ponds, backwaters and peats. Many different orders of insects have been found in these deposits. The Coleoptera (beetles), however, have shown to be by far the most useful palaeoenvironmental indicators and therefore dominate the interest of Quaternary entomologists. Many parts of the chitinous exoskeletons of beetles are diagnostic and a large number of species have a clearly marked preference for particular, restricted environments. Coleoptera show furthermore a morphological, physiological and evolutionary stability; only a few species may have changed their ecological tolerance (Lowe & Walker, 1984). Climate is the dominant factor governing their regional distribution and the high mobility of these insects

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results in rapid changes in the composition of assemblages due to climatic changes. However, insect remains from Palaeolithic sites have not been investigated thoroughly so far. This applies in particular to sites outside the British Isles. In addition we have to realise that many sites are found in sediments which are not conducive to the preservation of insect remains.

Vertebrate fossils are often found in association with Palaeolithic artefacts. The excavation of large areas and wet screening of large quantities of sediment may result in extensive collections of vertebrate fossils representing fishes, reptiles, amphibians, birds and mammals. Fish remains are not very suitable for a reconstruction of the Pleistocene palaeoenvironment because most species are not indicative of specific environmental or climatic conditions and do not tell us more than the existence of slowly or rapidly flowing bodies of water or more open or densely vegetated ones. In many cases fish remains are therefore not studied in great detail.

Heterothermic reptiles and amphibians depend more than the homoiothermic mammals on environmental conditions such as humidity and temperature and can therefore be more informative. The European pond tortoise *Emys orbicularis* (Linnaeus, 1758) for instance, requires a minimum number of hot days for the eggs to hatch and thereby to maintain populations in a certain area. Hence the species is indicative of a mean July temperature of 17°C or more (Stuart, 1979, 1982). The parsley frog *Pelodytes punctatus* and the smooth snake *Coronella austriaca* also have a restricted distribution and their occurrence in the northwestern European fossil record indicates warm conditions (Holman, 1993). However, the fossil herpeto fauna of Europe has only been studied haphazardly and is therefore hardly known, and the lack of accurate data precludes the application of the herpeto fauna to a reconstruction of the palaeoenvironment.

In many cases we therefore have to rely on the use of the homoiothermic animals. The distribution of these animals depends more on the availability of food than on external temperatures. Smaller mammals may be even less dependent on environmental conditions than larger mammals as they may have the capacity to live under microclimatic conditions. Some of the smaller mammals are able to protect themselves against external factors by hiding in burrows or to survive the winter period under a snow cover, e.g. *Dicrostonyx* and *Lemmus*. The latter two species tolerate very cold climatic conditions provided that there is a cover of snow during the cold period. The actual habitat of mammal species depends, however, not only on temperature and humidity. A complex of other factors, such as ethology, competition and predation, also determines and restricts the distribution of mammals.

The applicability of fossil mammals to a reconstruction of the palaeoenvironment is also hampered by the fact that mammals have the capacity to adapt to various environments and to tolerate other circumstances than those under which they live today. Some Arvicolidae, for example, evolved rapidly during the Pleistocene period and the evolution is most likely not restricted to changes in morphology as the morphological changes may be the result of adaptations to a different environment. There may even be adaptations to a different environment which are not reflected in morphological changes. A famous example is provided by the Norway Lemming *Lemmus lemmus* which nowadays inhabits a limited, (sub)arctic biotope, whereas its Early and Middle Pleistocene relatives, which hardly show any morphological differences from the extant species, lived under temperate conditions in a more wooded environment (Koenigswald, 1970). Habitat changes can also be assumed in larger mammal lineages such as the *Alces* lineage: *Alces latifrons* is supposed to be confined to an open steppe-like habitat whereas *Alces alces* prefers coniferous forests (Lister, 1993).

When we interpret a fossil assemblage and translate the data into a palaeoenvironmental reconstruction we have to be aware of taphonomical biases. The fossil record is very often not a reflection of the original fauna of a particular region. Smaller mammal remains are

usually transported to the locality by birds of prey, and the composition of these faunas will therefore be affected by the diet of these birds. The fauna of a Palaeolithic site, particularly the larger mammal fauna, may be affected by the activities of humans and animals. Hyenas are known to accumulate bones and their selection results in an abnormal composition of the mammal fauna. Furthermore phenomena such as hydrodynamic sorting and hibernation act on the composition of the fossil faunal assemblage.

The taphonomical aspects mentioned above restrict the applicability of fossil mammals to the reconstruction of a climate and the environment. The proportional representation of a species is less important than its actual presence and should therefore be handled with care. This applies to many assemblages but especially to smaller mammal assemblages. The diet of birds of prey differs from one species to another but also varies during the year (Andrews, 1990). Changes in the abundance of smaller mammal species (cf. Cordy, 1991) are, therefore, not necessarily a reflection of climatic developments.

Despite these restricting factors we can generally use mammal fossils for our conclusions on palaeoclimatic and palaeoenvironmental conditions. We are able to recognise temperate, interglacial and interstadial faunas as well as cold stage, glacial faunas in Northwestern Europe (Kolfschoten, 1995).

Interglacial and interstadial faunas from northwestern Europe

The term interglacial can, according to the original definition by Jessen and Milters (1928), only be used if we can recognise, in Northwestern Europe, a phase with a clear expansion of thermophilous trees. Only the mammal species which are related to such an expansion are indicative of interglacial conditions. However, most of the present-day woodland inhabitants occur in deciduous woods, mixed-oak forests as well as coniferous ones. Another problem is that a species such as *Glis glis*, which is nowadays mainly restricted to deciduous and mixed-oak forests, may have had a broader ecological range as is indicated by the co-occurrence with *Dicrostonyx* in Late Pleistocene assemblages (Storch, 1973; Kolfschoten & Roth, in press). The capacity to adapt to other environments also applies to other mammal species such as *Erinaceus europaeus*, *Erinaceus concolor*, *Apodemus flavicollis*, *Felis catus*, *Sus scrofa* and *Bison bonasus* which are nowadays mainly restricted to deciduous and mixed-oak forests. It cannot be excluded that these species also occurred in Northwestern Europe during temperate phases - referred to as interstadials - without a clear expansion of thermophilous trees. Thus the number of mammal species indicative of interglacial conditions in the sense of Jessen and Milters' original definition is low. Only *Hippopotamus* and *Bubalus* require very specific conditions as physiological factors restrict their distribution to areas with open water, i.e. without long periods of frost. Hence, no single mammalian species, apart from *Hippopotamus* and *Bubalus*, is a convincing indication of an interglacial fauna (Kolfschoten, 1995).

Cold stage faunas from Northwestern Europe

A characterisation of glacial faunas seems to be much easier. If species such as *Dicrostonyx*, *Alopex lagopus*, *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Rangifer tarandus*, *Ovibos moschatus* and *Capra ibex* are present, we speak of glacial faunas. The composition of these faunas (characterised by a dominance of large herbivores) seems to confirm Guthrie's views on the presence of a more steppe-like environment (the 'Mammoth Steppe') (Guthrie, 1990) rather than more tundra-like conditions as suggested by e.g. Zagwijn (1989).

Hence, the 'Mammoth Steppe' fauna is indicative of glacial conditions. However, there appears to be a problem in distinguishing faunas from glacial maxima - which lasted for about 12% of the total timespan - from those faunas which date to episodes between real interglacials and glacial optima (75% of the total timespan). Guthrie assumes that the 'Mammoth Steppe' environment also dominates the episode between the real interglacials and the glacial maxima; an assumption which is underlined by the fossil record from the Late Pleistocene and the second half of the Middle Pleistocene in Central and Northwestern Europe (Kolfschoten, 1995). Hence it is difficult to differentiate the cold stage faunas.

The application of fossil mammals to dating

The terrestrial mammal faunas of Europe did, in a geological sense, change almost continuously during the Quaternary, due to the extinction or evolution of species but most of all due to the migration or dispersal of species as a reaction to the extreme climatic fluctuations which characterise the history of the past 2.5 million years.

Migration and dispersal

The migration of mammal species is certainly the major factor in the changing composition of the Pleistocene faunas of Northwestern Europe. These migrations are first of all caused by the alteration of the available habitats due to the changes in climate and environment. Cold stage faunas from the last (Weichselian) and penultimate (Saalian) glacial period are composed of a group of species (e.g. *Dicrostonyx gulelmi*, *Lemmus lemmus*, *Mammothus primigenius*, *Coelodonta antiquitatis* and *Rangifer tarandus*) with a northeastern origin (Fig. 1) which often occur together with species which prefer a more steppic environment such as *Spermophilus undulatus*, *Cricetulus migratorius* and *Cricetus cricetus*. The latter species migrated from the east, probably from areas which they inhabit nowadays (Storch, 1969; Chaline, 1972; Kolfschoten, 1992).

After every cold stage we observe a rise in temperature and above all an increase in oceanic influences resulting in a climate which induces a dominance of forests in the North European plain (Zagwijn, 1989). During the cold stages the thermophilous broad-leaved and coniferous vegetation survived only in restricted condensation zones and deep, moist valleys of the Southern European mountains (Zagwijn, 1992). Species such as *Eliomys quercinus*, *Muscardinus avellanarius*, *Sus scrofa*, *Cervus (Dama) dama* and *Capreolus capreolus*, inhabiting a forest biotope, probably survived in these refuge areas and migrated to Northwestern Europe during the interglacial phases.

The general picture of migrations due to climatic changes is completed by a more incidental invasion of species. Contemporary migrations of a number of species characterise the so-called major dispersal events like the "Wolf" event and the "end-Villafranchian" dispersal event (Azzaroli, 1983 and Azzaroli *et al.*, 1988). Apart from these major dispersal events there are also incidental immigrations of single species. Examples are *Coelodonta antiquitatis*, *Elephas (P.) antiquus* and *Hippopotamus amphibius*, species which invaded Europe during the Pleistocene and which form a regular part of the European fauna since their first invasion. However, there are also exotic species, such as *Bubalus murrensis*, which invaded Northwestern or Central Europe twice, as far as we can ascertain (Koenigswald, 1988).

Another aspect is the migration and dispersal at subspecies level: the migration and dispersal of populations to areas already inhabited by the same species. To trace these migra-

tions requires significant morphological differences between the "new" population and the "old", as for instance between the Late Saalian and Eemian *Arvicola terrestris* populations of Northwestern Europe (for more detailed information see Kolfschoten, 1990).

Extinction of species

Several examples demonstrate the phenomenon of the extinction of a species, either worldwide or more locally. Well-known are the extinctions of larger mammals such as *Ursus spelaeus*, *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus hydruntinus* and *Megaloceros giganteus* at the end of the Late Pleistocene or the beginning of the Holocene (Kurtén, 1968; Martin, 1984; Stuart, 1991). Other larger mammals, such as *Dicerorhinus kirchbergensis* and *Dicerorhinus hemitoechus* became extinct in an earlier phase of the Late Pleistocene (Guerin, 1980; Stuart, 1991). Stuart's data show a geographical gradient in the extinction of the latter species. They became extinct in the northern regions earlier than in Southern Europe. Another example of a geographical difference in the extinction of species forms is the arvicolid *Pliomys lenki* which became extinct in Northwestern Europe during the Elsterian, but which still inhabited Southwestern Europe until the Early Weichselian (Bartolomei *et al.*, 1975).

The extreme reduction in the number of larger mammal species at the end of the Late Pleistocene cannot be observed in the smaller mammal fauna. The smaller mammals appear to have survived both the climatic changes and the changes in the Late Pleistocene biome. A number of smaller mammals (*Drepanosorex savini*, *Talpa minor*, and *Trogotherium cuvieri*) became extinct in Europe during the second part of the Middle Pleistocene, in the early Saalian (Kolfschoten, 1990).

Evolution of species

The Pleistocene fossil record indicates that a number of species e.g. *Sorex minutus* hardly evolved during that period, whereas other species clearly show morphological changes in for instance the molars or antlers. Lister (1993) presented and discussed e.g. the evolution in the *Mammuthus* (*Archidiskodon*) *meridionalis* - *M. trogontherii* - *M. primigenius* lineage, in which an increase in hypsodonty and the number of plates as well as a reduction in the thickness of the enamel can be observed.

The evolution of species can also be observed in other lineages e.g. *Dicerorhinus etruscus* - *Dicerorhinus hemitoechus*, *Miomys savini* - *Arvicola terrestris* and *Microtus* (*Allophaiomys*) - *Microtus* (*Microtus*). These lineages form the basis for a biozonation of the Pleistocene.

Biozonation

Mammalian fossils are valuable for dating and correlating deposits and for establishing a biozonation because most mammals have an extensive distribution area and a number of them show a rapid evolution and/or migratory shift within the Quaternary. Many palaeontologists use the biostratigraphical subdivision of the Quaternary based on the Arvicolidae succession as proposed by Fejfar and Heinrich (1981). These two authors established three well-defined biozones (stages in their terminology) for the Pleistocene: Villányian, Biharian and

Toringian (Fig. 2).

Villányian - Biharian - Toringian

The Biharian faunas differ from the preceding Villányian faunas by the occurrence of *Microtus*. The Villányian faunas can be recognised by the dominance of *Mimomys*, the Biharian faunas by the co-occurrence of *Microtus* and *Mimomys*, and the Toringian "Stage" by *Arvicola* - *Microtus* assemblages. The Biharian Stage is divided into two substages: the Early Biharian with *Microtus* (*Allophaiomys*) and the Late Biharian with *Microtus* (*Microtus*).

The transition from the Villányian to the Biharian in the Early Pleistocene corresponds, more or less, with the Tiglian/Eburonian transition. Faunas such as those from Tegelen (the Netherlands) belong to the Villányian; the Early Biharian comprises faunas such as those from Le Vallonnet (France), Monte Peglia (Italy) and Betfia 2 (Romania).

The transition from *Microtus* (*Allophaiomys*) to *Microtus* (*Microtus*), marking the transition from the Early to the Late Biharian, dates to the early part of the Bavelian complex, roughly correlated with the Jaramillo (see Fig. 3).

Faunas such as those from West Runton, Stránská Skála, Prezletice (Czech Republic), Tarkó (Layer 16) (Hungary), Ilynka I-II and Ilynka IV (Russia) belong to the Late Biharian. The genus *Mimomys* is represented by only one species, the large *Mimomys savini*, in most of these faunas. A second *Mimomys*, a smaller form often referred to as *Mimomys* (*Cseria*) *pusillus*, occurs only in the faunas from Kärlich C and Ilynka IV and I-II. The presence or absence of this smaller *Mimomys* is probably a stratigraphical marker which can be used to subdivide the Late Biharian faunas into an older group with and a younger group without the smaller *Mimomys*. The faunas from Kärlich C and E date to the Brunhes Epoch which indicates that the smaller *Mimomys* disappeared after the Brunhes/Matuyama boundary.

A very important stratigraphical marker is the transition from *Mimomys savini* to *Arvicola terrestris* during the second half of the Cromerian Complex (Kolfschoten, 1990; Koenigswald and Kolfschoten, in press). As the most primitive representative of the genus *Arvicola*, *Arvicola t. cantiana* (often cited as e.g. *Arvicola cantiana* or *Arvicola mosbachensis*), is known from Cromerian Interglacial IV deposits in Noordbergum (The Netherlands) (Kolfschoten, 1990), the transition took place before the end of the Cromerian Complex.

Toringian faunas can be subdivided into at least three groups: an older one with *Arvicola terrestris cantiana* co-occurring with so-called relict species (such as *Talpa minor*, *Sorex* (*Drepanosorex*), *Trogontherium cuvieri*, *Pliomys episcopolis*). This group comprises faunas from for instance Miesenheim I, Kärlich G, Mauer (Germany), Boxgrove, Westbury-sub-Mendip (Great Britain), Sprimont (Belle Roche) (Belgium) and Tarkó (Hungary). Faunas from e.g. Swanscombe (Great Britain), Neede (The Netherlands), Schöningen and Bilzingsleben (Germany) are younger in age. *Arvicola terrestris cantiana* still occurs but without the co-occurring relict species.

Arvicola terrestris ssp. A and B accompanied by a modern smaller mammal fauna, characterise the third group of Toringian faunas. From the early Saalian the *Arvicola* molars from Northwestern Europe show a thinning of the convex sides of the dentine triangles which has resulted in changes in the relative thickness of the enamel band of the molars (Koenigswald, 1973; Heinrich, 1978, 1987; Kolfschoten, 1990). This development can be used for stratigraphical correlations of younger, i.e. post-"Holsteinian" smaller mammal faunas, such as those from Caune de l'Arago (Desclaux, 1992a, 1992b), Maastricht-Belvédère and Weimar-Ehringsdorf (cf. Kolfschoten 1990).

Villafranchian - Galerian

The biostratigraphical subdivision of the larger mammal faunas into Villafranchian and Galerian faunas, as proposed by Italian palaeontologists, is widely used. The Villafranchian, starting about 3 million years ago, covers part of the Pliocene and the Early Pleistocene. It has been subdivided into an early, a middle and a late phase, a subdivision refined by Azzaroli (1977), who divided the Villafranchian faunas into six more or less well defined faunal units. The beginning of the Villafranchian itself, of some of its units and its end are characterised by pronounced dispersal events (Azzaroli *et al.*, 1988; Sala *et al.*, 1992). Azzaroli *et al.* (1988) state that the Villafranchian-Galerian transition (the end-Villafranchian event, 1.0-0.9 million years ago) corresponds with a complete faunal turnover, with massive extinctions and new, previously unknown, adaptations. Late Villafranchian taxa such as *Eucladoceros*, *Dama nestii*, *Leptobos etruscus*, *Sus strozzii* and *Archidiskodon meridionalis* became extinct whereas many taxa (*Megaceros*, *Soergelia* sp., *Praeovibos priscus*, *Bison schoetensacki*, *Equus süssenbornensis*, *Ursus deningeri*) appear during the Early Galerian.

However, the transition from the late Villafranchian to the Galerian did not take place at once or during a geologically short period of time as assumed by Azzaroli *et al.* (1988). This assumption is partially based on the inferred Early Pleistocene age of Isernia. The end-Villafranchian 'event' in the sense of e.g. Azzaroli *et al.* (1988) has in my opinion a very long stratigraphical range and may have lasted for more than 500 Kyr. The fauna from Venta Micena dates to around 1.2 million years ago (Agusti, 1986), yet already contains several Galerian immigrants (*Megaloceros*, *Praeovibos*, *Soergelia* and *Bison*) (Agusti *et al.*, 1987), whereas the faunas from West Runton and Voigtstedt which date between 500 and 700 Kyr still contain late Villafranchian elements. If the assumption that the end-Villafranchian faunal turnover appeared to have taken place more gradually over a period of several 100 Kyr is correct then it will be necessary and very important to re-define the late Villafranchian - Galerian boundary. With the current state of knowledge the terms late Villafranchian or Galerian are of little biostratigraphical value. In order to be able to propose a new definition we will have to clarify the stratigraphical position of important larger mammal faunas such as the fauna from Isernia.

The age of the Palaeolithic fauna from Isernia

The assumption that the Villafranchian - Galerian faunal turnover transition was rather rapid is partially based on the inferred Early Pleistocene age of Isernia; an age based on radiometric and poor palaeomagnetic data (Coltorti *et al.*, 1981; McPherron and Schmidt, 1983). Isernia has yielded fossil remains of *Arvicola terrestris cantiana* (assigned to the junior synonym *Arvicola mosbachensis* by Sala, 1983; Coltorti *et al.*, 1982). The fauna with *Arvicola*, *Elephas (P.) antiquus*, *Stephanorinus hundsheimensis* and without *Mimomys savini*, *Mimomys pusillus* and *Microtus (Allophaiomys)* sp. suggests a Middle Pleistocene age, as it is comparable to the Central European faunas from Mosbach and Mauer (cf. Sala and Fortelius, 1993).

A study of the *Arvicola* molars, including those sampled in the period after 1982, showed that we are dealing with a primitive population of the genus *Arvicola*. Only 80% of the molars (only a few of which are juvenile) are rootless, whereas 20% show indications of root formation but are still rootless. One of the earliest appearances of *Arvicola* in Northwestern and Central Europe is in the Kärlich section, in the fauna from Kärlich G, a level with a Cromerian Interglacial III/IV age (Kölschoten and Turner, in press). Hence, the *Mimomys*-

Arvicola transition took place in the second half of the Cromerian Complex. This also seems to have been the case in other areas, as for instance documented by the occurrence of *Arvicola terrestris* before the Elsterian in Central Europe (Terzea, in press) and the occurrence of very advanced *Mimomys savini* in faunas from the Don Basin, dated to the second interglacial before the Oka-Elsterian glaciation (Kasantseva, 1987; Kolfshoten, in prep.).

One could accept a late Early Pleistocene age for Isernia only by suggesting an earlier occurrence of *Arvicola* in Italy, in a more or less isolated area of Europe. This is not a plausible argument, however, as there are no indications of a barrier isolating the mammalian faunas in Italy from those of Central and Western Europe during the Pleistocene. On the contrary, the numerous similarities in the composition of the Early, Middle and Late Pleistocene faunas of Italy and Eastern, Central and Western Europe show a general and almost continuous faunal exchange between these areas during the Quaternary.

Summarising it can be stated that it is most likely that the fauna from Isernia has an early Middle Pleistocene age. The site is nevertheless, despite the younger age, one of the oldest Palaeolithic sites in Europe (see Roebroeks and Kolfshoten, 1994) and for that reason very important in a palaeontological as well as an archaeological sense.

Acknowledgements

The research of the author has been made possible by a fellowship from the Royal Netherlands Academy of Arts and Sciences, for which I am grateful. Furthermore I would like to thank Mrs. Kelly Fennema for the linguistic improvements.

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References

Agusti, J., 1986: Synthèse biostratigraphique du plio-pléistocène de Guadix-Baza (Province de Granada, sud-est de l'Espagne). *Geobios* 19, 4, 505-510.

Agusti, J., S. Moyà-Solà, J. Pons-Moyà, 1987: La sucesión de Mamíferos en el Pleistoceno inferior de Europa: proposición de una nueva escala bioestratigráfica. *Paleont. I Evol., Mem. Esp.* 1, 287-295.

Andrews, P., 1990: *Owls, Caves and Fossils*. British Museum Natural History, London.

Azzaroli, A., 1977: Evolutionary Patterns of Villafranchian Elephants in central Italy. *Lincei Memorie Sc. Fisiche S. VIII*, vol. XIV, Sez. II, 4, 149-169.

Azzaroli, A., 1983: Quaternary mammals and the "End-Villafranchian" dispersal event - a turning point in the history of Eurasia. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 44, 117-139.

Azzaroli, A., Giuli, C. de, Ficarelli, G. and Torre, D., 1988: Late Pliocene to early mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 66, 77-100.

Bartolomei, G., Chalaine, J., Fejfar, O., Jánossy, D., Jeannet, M., v. Koenigswald, W. and Kowalski, K., 1975: *Pliomys lenki* (Heller 1930) (Rodentia, Mammalia) en Europe. *Acta Zool. Cracov.*, 10, 393-468.

Chalaine, J., 1972: *Les Rongeurs du Pléistocène moyen et supérieur de France (Systématique, biostratigraphie, paléoclimatologie)*. Cahiers de Paléontologie, Ed. C.N.R.S., 410: Paris.

Coltorti, M., Cremaschi, M., Delitala, M. C., Esu, D., Fornaseri, M., McPherron, A., Nicoletti, M., Otterloo, R. van, Peretto, C., Sala, B., Schmidt, V., Sevink, J., 1981: *Isernia La Pineta: Lower Paleolithic with Fauna before 0.7 MY in the upper Volturno basin, Central Italy; first report*. 58-63.

Coltorti, M., Cremaschi, M., Delitala, M. C., Esu, D., Fornaseri, M., McPherron, A., Nicoletti, M., Otterloo, R. van, Peretto, C., Sala, B., Schmidt, V., Sevink, J., 1982: Reversed magnetic polarity at Isernia La Pineta, a new lower paleolithic site in Central Italy. *Nature*, 300, 5888, 173-176.

Cordy, J.-M., 1991: Palaeoecology of the Late Glacial and early Postglacial of Belgium and neighbouring areas. In: (eds.: Barton *et al.*) *The Late Glacial in north-west Europe: human adaptation and environmental change at the end of the Pleistocene*. CBA Research Report 77, 40-47.

Desclaux, E., 1992a: *Les petits vertèbres à la Caune de l'Arago (Tautavel, Pyrénées Orientales)*. Paléontologie, paléocologie, taphonomie. Thèse de Doctorat. Paris: M.N.H.N.

Desclaux, E., 1992b: Les petits vertèbres de la Caune de l'Arago à Tautavel. *Bulletin du*

Musée d'Anthropologie Préhistorique de Monaco 35, 35-64.

Fejfar, O. & Heinrich, W. D., 1981: Zur biostratigraphischen Untergliederung des kontinentalen Quartärs in Europa anhand von Arvicoliden (Rodentia, Mammalia). *Eclogae Geol. Helv.*, 74/3, 997-1006.

Guérin, C. 1980: *Les Rhinocerotidae (Mammalia, Perissodactyla) de Miocène supérieur au Pléistocène terminal en Europe occidentale. Comparaison avec les espèces actuelles*. Thèse Doctorat d'Etat en Sciences Univ. Lyon I, Doc. Lab. Géol. Lyon, no. 79, 3 fasc., 1185 p.

Guthrie, R.D., 1990: *Frozen Fauna of the Mammoth Steppe, The Story of Blue Babe*. Chicago University Press, Chicago.

Heinrich, W.-D., 1978: Zur biometrischen Erfassung eines Evolutionstrends bei Arvicola (Rodentia, Mammalia) aus dem Pleistozän Thüringens. *Säugetierkdl. Inform.*, 2, p. 3-21.

Heinrich, W.-D., 1987: Neue Ergebnisse zur Evolution und Biostratigraphie von Arvicola (Rodentia, Mammalia) im Quartär Europas. - *Z. Geol. Wiss.* 15, 3, 389-406.

Holman, J.A., 1993: Pleistocene herpetofauna of Westbury-Sub-Mendip Cave, England. *Cranium*, 10, 2, 87-96.

Jessen, K. & Milters, V., 1928: Stratigraphical and palaeontological studies of interglacial freshwater deposits in Jutland and north-west Germany. *Denmarks Geologiske Undersgelse*, 2, 48.

Kasantseva, N.E., 1987: *Paleogeograficeskie uslovija obitanija nizneplejstocenovykh faun melkix mlekopitajuscix bassejna srednego Dona*. Dissertation, University of Moscow, Moscow.

Koenigswald, W. von, 1970: Mittelpleistozäne Kleinsäuger aus der Spaltenfüllung Petersbuch bei Eichstätt. *Mitt. Bayer. Staatssamml. Paläont. Hist. Geol.*, 10, 407-432.

Koenigswald, W. von, 1973: Veränderungen in der Kleinsäugerfauna von Mitteleuropa zwischen Cromer und Eem (Pleistozän). *Eiszeitalter und Gegenwart*, 23/24, 159-167.

Koenigswald, W. von, 1988: Paläoökologische Aussage letzterinterglazialer Säugetiere aus der nördlichen Oberrheinebene. In Koenigswald, W. von (ed.): *Zur Paläoklimatologie des letzten Interglazials im Nordteil der Oberrheinebene*. *Paläoklimaforschung* 4, 205-314.

Koenigswald, W. von & Kolschoten, T. van, in press: The *Miomys*-*Arvicola* boundary and the enamel thickness quotient (SDQ) of *Arvicola* as stratigraphic markers in the Middle Pleistocene. *Proceedings of the SEQS Cromer Symposium*, 1990.

Kolschoten, T. van, 1990: The evolution of the mammal fauna in the Netherlands and the middle Rhine Area (Western Germany) during the late Middle Pleistocene. *Meded. Rijks Geol. Dienst*, 43, 3, 1-69.

Kolfschoten, T. van, 1992: Aspects of the migration of mammals to Northwestern Europe during the Pleistocene, in particular the reimmigration of *Arvicola terrestris*. *Courier Forsch.-Inst. Senckenberg*, 153: 213-220.

Kolfschoten, T. van, 1995: On the application of fossil mammals to the reconstruction of the palaeoenvironment of northwestern Europe. *Acta Zool. Cracov.*, 38 (1). (in press.).

Kolfschoten, T. van & Roth, G., in press: Die mittel- und spätpleistozäne Mollusken und Kleinsäuger von Schlackenkegeln der Osteifel. *Jahrbuch Römisch Germanisch Zentral Museum, Mainz*.

Kolfschoten, T. van & E. Turner, in press: "Early Middle Pleistocene Mammalian Faunas from Kärlich and Miesenheim I and their biostratigraphical implications". *Proceedings of the SEQS Cromer Symposium*, 1990.

Kurtén, B., 1968: *Pleistocene Mammals of Europe*. London (Weidenfeld and Nicolson).

Lister, A.M., 1993: Evolution of mammoths and moose: the Holarctic perspective. In: (R.A. Martin & A.D. Barnosky, eds.) *Morphological Change in Quaternary Mammals of North America*, 178-204, Cambridge University Press: New York.

Lowe, J.J. & Walker, M.J.C., 1984: *Reconstructing Quaternary Environments*. London (Longman).

Martin, P. S., 1984: Prehistoric overkill: The global model. *Quaternary Extinctions* (Martin and Klein, eds.), Univ. Ariz. Press., 354-403.

McPherron & Schmidt, V. (1983): Paleomagnetic dating at Isernia La Pineta. *Isernia La Pineta*, 67-69, 1 fig.; Museo Nazionale Isernia.

Roebroeks, W. & T. van Kolfschoten, 1994: The earliest occupation of Europe: a short chronology. *Antiquity* 68, 489-503.

Sala, B. (1983): La Fauna del giacimento di Isernia La Pineta. *Isernia La Pineta*, 71-79, 4 fig.; Museo Nazionale Isernia.

Sala, B., F. Masini, G. Ficcarelli, L. Rook & D. Torre, 1992: Mammal dispersal events in the Middle and Late Pleistocene of Italy and Western Europe. *Courier Forsch.-Inst. Senckenberg*, 153: 59-68, 1 Fig.; Frankfurt a.M.

Sala, B. & M. Fortelius, 1993: The rhinoceroses of Isernia La Pineta (early Middle Pleistocene, Southern Italy). *Palaeontographia Italica*, 80, 157-174: Pisa.

Storch, G., 1969: Über Kleinsäuger der Tundra und Steppe in jungeszeitlichen Eulengewöhlen aus dem nordhessischen Löß. *Natur und Museum*, 99 (12): Frankfurt a. M.

Storch, G., 1973: Jungpleistozäne Kleinsäugerfunde (Mammalia: Insectivora, Chiroptera, Rodentia) aus der Brillenhöhle. G. Riek: *Das Paläolithikum der Brillenhöhle von Blaubeuren*, II, 106-123.

Stuart, A. J., 1979: Pleistocene occurrences of the European pond Tortoise (*Emys orbicularis* L.) in Britain. *Boreas*, 8. 359-371.

Stuart, A. J., 1982: *Pleistocene Vertebrates in the British Isles*. Longman, London/New York.

Stuart, A.J., 1991: Mammalian extinctions in the Late Pleistocene of Northern Eurasia and north America. *Biol. Rev.*, 66. 453-562.

Terzea, E., in press: Mammalian events in the Quaternary of Romania and correlations with climatic chronology of Western Europe. *Acta Zool. Cracov.*, 38 (1). (1995)

Zagwijn, W. H., 1989: The Netherlands during the Tertiary and the Quaternary: A case history of Coastal Lowland evolution. *Geologie en Mijnbouw*, 68, 107-120, 23 fig.: Dordrecht.

Zagwijn, W. H., 1989: Vegetation and climate during warmer intervals in the late Pleistocene of Western and Central Europe. *Quaternary International*, 3/4. 57-67.

Zagwijn, H.W., 1992: Migration of vegetation during the Quaternary in Europe. *Courier Forsch.-Inst. Senckenberg*, 153: 9-20.

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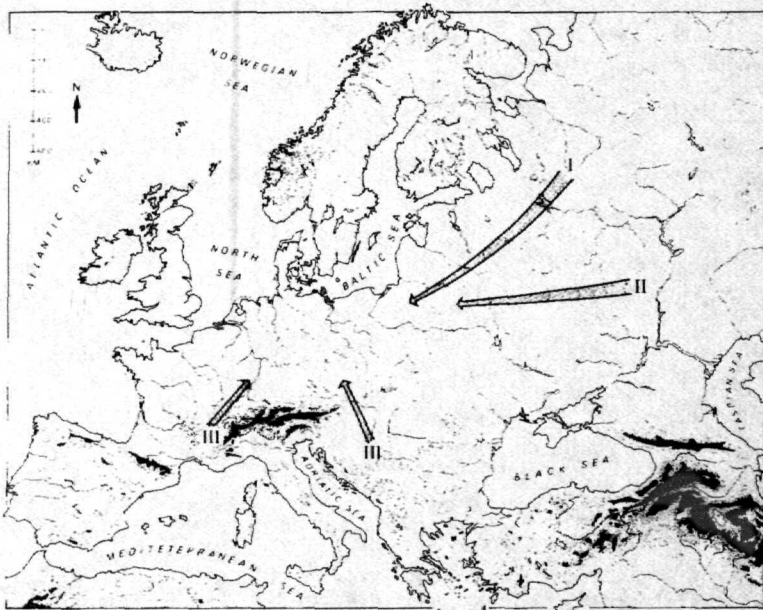


Fig. 1: The major migration routes of the mammals which invaded northwest Europe during a cold stage (I and II), during a steppic phase (II) and during an interglacial (III).

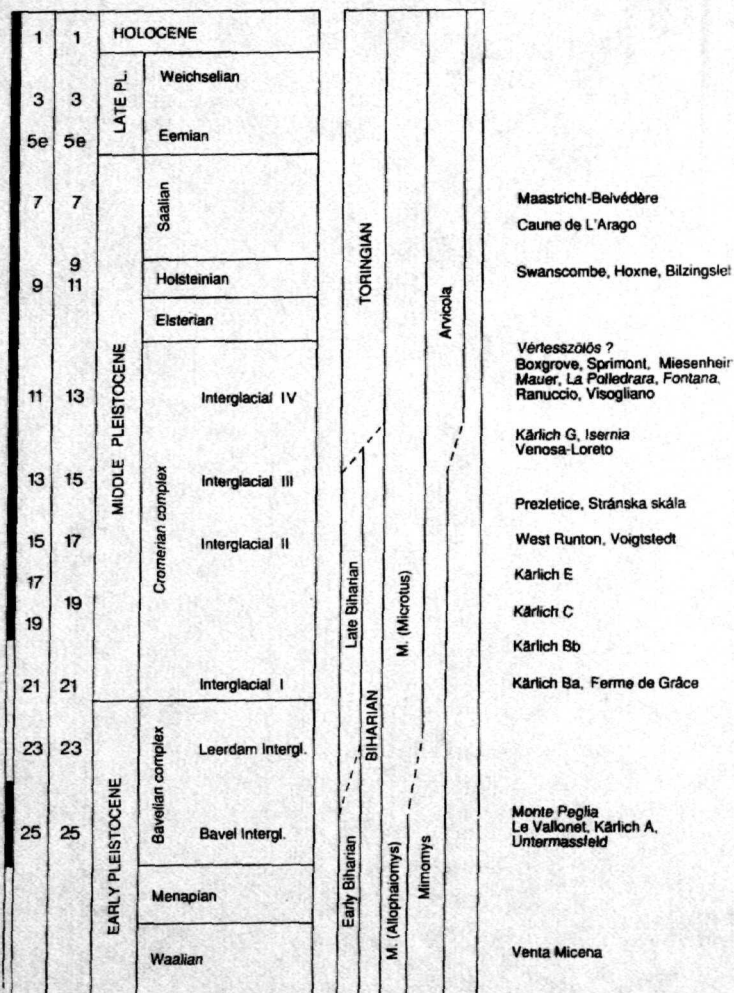


Fig. 2: Correlation of small mammal faunas to the biozones discussed in the text.

	TORINGIAN	<i>A. terrestris</i> ssp. A and B	Maastricht-Belvédère (The Netherlands), Weimar-Ehringsdorf (Germany), Blach-Saint-Vaast, Caune de L'Arago (France)
Belvédère Arago		<i>A. t. cantiana</i> - <i>Talpa minor</i>	Swanscombe, Hoxne (Great Britain), Bilzingsleben, Schöningen 12B (Germany), Vértesszöllös II (Hungary)
de, Hoxne, Bilzingsle!		<i>A. t. cantiana</i> - <i>Pl. episcopalis</i>	Miesenheim I, Kärlich G, Mauer (Germany), Boxgrove, Westbury-Sub-Mendip (Great Britain), Sprimont (Belgium), Cullar de Baza I (Spain), Venosa-Notachirico, Visogliano, Isernia (Italy), Tarkó (Hungary)
is ? Sprimont, Miesenheim Polledrara, Fontana, Visogliano	BIHARIAN	Late Biharian	West Runton (Upper Freshwater Bed), Little Oakley, Sugworth (Great Britain), Zuurland 5 (The Netherlands), Ferme de Grâce (France), Atapuerca TD 4 (Spain), Kärlich C and E, Voigtstedt, Süssenborn (Germany), Kozł Grzbiet (Poland), Stránská Skála, Prezletice (Czech Republic)
ernia eto		Early Biharian	Les Valerots, Le Vallonet (France), Venta Micena (Spain), Monte Peglia, Pirro Nord-1 (Italy), Untermaassfeld (Germany), Deutsch-Altenburg 2 (Austria), Betfia 2 (Roumania)
Stránská skála on, Voigtstedt	VILLANYIAN		Tegelen (The Netherlands), St. Vallier (France), Stranzendorf (Austria), Villány 3, 4 and 11 (Hungary)
Ferme de Grâce			
ilia t. Kärlich A, sifeld			
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Fig. 3: Tentative correlation of small mammal biozones and faunal assemblages to the northwest European standard subdivision of the Quaternary and to various oxygen isotope stages (after Roebroeks & Van Kolfschoten, 1994).