ASPECTS OF THE MIGRATION OF MAMMALS TO NORTHWESTERN EUROPE DURING THE PLEISTOCENE, IN PARTICULAR THE REIMMIGRATION OF *ARVICOLA TERRESTRIS*

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Abstract

The migration of mammals is a major causal factor in the frequent faunal changes of Northwest Europe. Most important in this context is that migrations are due to climatic changes characteristic of the Pleistocene period. In addition, there are more incidental migrations of groups of species (e.g. the 'end-Villafranchian' dispersal event) or single species (e.g. *Coelodonta antiquitatis*) which affect the faunal composition of Northwest Europe. Study of the Northwest European fossil record of *Arvicola terrestris* indicates a re-immigration of less derived populations from the south(east) during the Eemian, after the species disappears during the Late Saalian due to the southerly extension of the ice-sheet. This re-immigration resulted in a distinct fluctuation in the general evolutionary trend. Such fluctuations restrict the applicability of evolutionary stages for biostratigraphical purposes.

Zusammenfassung

Ein wichtiger Faktor für die Änderungen der pleistozänen Faunenspektren in Nordwesteuropa sind die Ein- und Auswanderungen der Säuger. Dies sind vor allem Wanderbewegungen, die durch die charakteristischen klimatischen Wechsel im Pleistozän hervorgerufen wurden. Die Zusammensetzungen der Faunen werden daneben
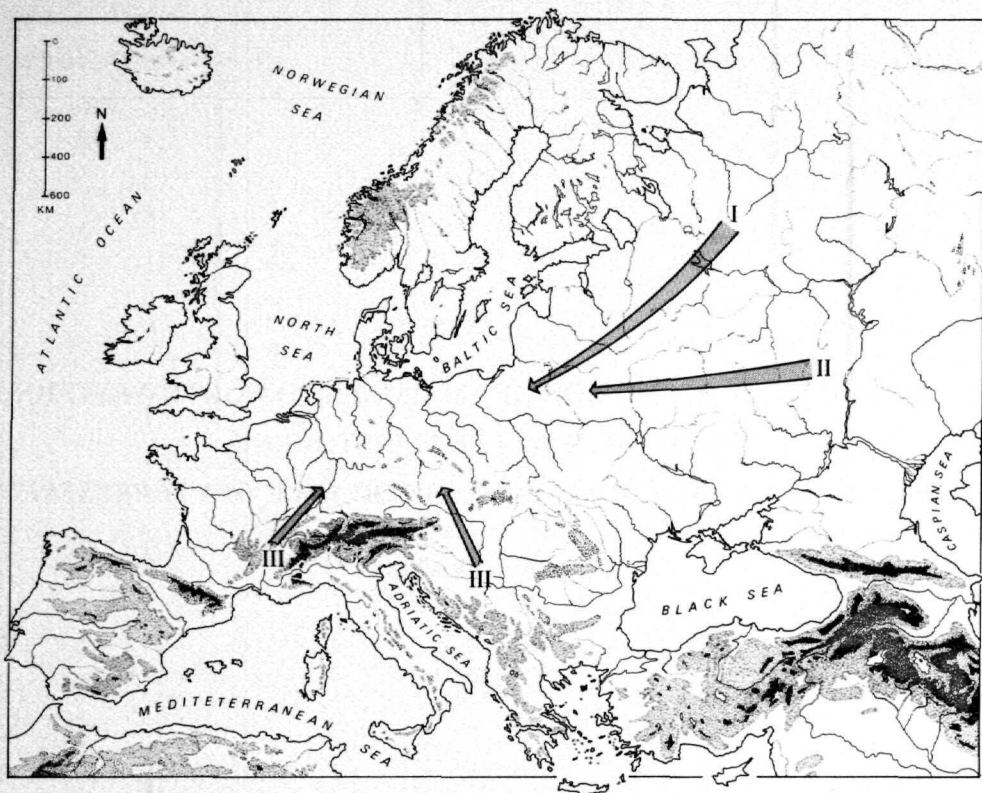
Fig. 1: The major migration routes of the mammals which invaded Northwest Europe during a cold stage (I and II), during a steppic phase (II) and during an interglacial (III).

durch eher einmalige Wanderungen von Artengruppen (z. B. am Ende des Villafranchiums) oder von einzelnen Arten (etwa *Coelodonta antiquitatis*) beeinflußt. Detailliert wurde die Entwicklung von *Arvicola terrestris* untersucht: In der späten Saale-Kaltzeit war die Art mit der südlichen Verbreitung des Inlandeises in Nordwesteuropa verschwunden; während des Eems wanderten weniger entwickelte Populationen aus dem süd-östlichen Raum ein. Diese Wiedereinwanderung läßt sich an einer ausgeprägten Schwankung des generellen Evolutionstrends ablesen. Die Verwendung von Evolutionsstufen der Tierart für biostratigraphische Zwecke wird durch diese Schwankungen eingeschränkt.

Introduction

The composition of the Pleistocene mammalian fauna of Northwestern Europe has been influenced by a number of factors. These are: a) the evolution of species; b) the extinction of species (due to the evolution of species or to the extinction of lineages), and c) the migration of species. The evolution of species can be observed in the lineages of, e.g., *Mammuthus (Archidiskodon) meridionalis - Mammuthus (Mammuthus) trogontherii - Mammuthus (Mammuthus) primigenius, Dicerorhinus etruscus - Dicerorhinus hemitoechus, Mimomys savini - Arvicola terrestris* and *Microtus (Allophaiomys) -Microtus (Microtus)*. Several examples demonstrate the extinction of species or their disappearance from Northwest European faunas. 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;
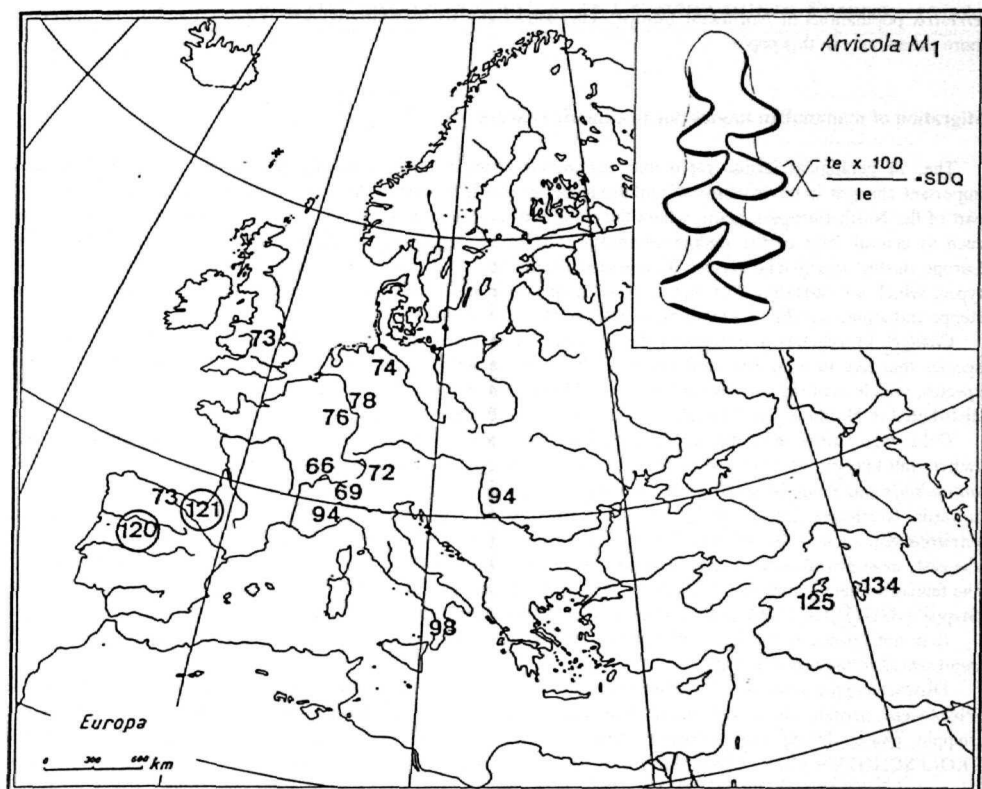
Fig. 2: Geographical variation in the morphological cline of the enamel thickness quotient in extant populations of *Arvicola terrestris* and *Arvicola sapidus* (circled) throughout Europe. More primitive forms occur in the Mediterranean region, whereas most northern populations are highly derived. (te = trailing edge; le = leading edge; SDQ = enamel thickness quotient [Schmelz-Dicken-Quotient]) (after RÖTTGER 1987).

STUART 1991) are well known. Other large mammals, such as *Dicerorhinus kirchbergensis* and *Dicerorhinus hemitoechus*, became extinct in an earlier phase of the Late Pleistocene (GUÉRIN 1980; STUART 1991).

An extinction-related change in the small mammal fauna can be observed in the Middle Pleistocene. Species such as *Drepanosorex savini*, *Talpa minor* and *Trogontherium cuvieri* are well represented in the late Cromerian faunas, whereas they are absent in the Early Saalian and younger faunas. A number of species were no longer present in Northwest Europe but survived in more southerly areas. For example, *Pliomys lenki* became extinct in Northwest Europe during the Elsterian, but still inhabited Southwest Europe until the Early Weichselian (BARTOLOMEI et al. 1975).

The migration of mammal species is certainly the major factor behind the changes in composition of the Pleistocene faunas of Northwest Europe. These migrations are mainly caused by alternations of the available habitats due to changes in climate and environment. However, one can also distinguish migrations that are more or less independent of climatic changes. Both aspects of migration will be discussed briefly in this paper.

Another aspect is migration and dispersal at the subspecific level; the migration and dispersal of populations into areas once inhabited by the same species. To trace these migrations demands significant morphological differences between the 'new' population and the 'old' one, such as between the Late Saalian and Eemian *Arvicola*

terrestris populations of Northwest Europe. This aspect and its biostratigraphical implications will be discussed more extensively in this paper.

Migration of mammalian faunas due to climatic changes

The, in geological terms, rapid and continuous climatic changes during the Pleistocene period induced important changes in environmental conditions and available habitats. This is particularly the case in the western part of the North European plain, where the conditions are more uniform, in comparison with mountainous areas such as central Italy or the Balkan peninsula. The forest vegetation which dominated the flora of Northwest Europe during interglacial phases disappeared during the cold stages and was replaced by treeless vegetation types, which are 'analogous to, but in plant-composition not necessarily identical with, the present-day tundra, steppe and alpine meadows' according to ZAGWIJN this volume)).

Changes in vegetation influenced the presence of mammal species in Northwest Europe. The presence of species that live in a confined habitat (e.g. the arctic lemming) is restricted in temporal extent, whereas other species, which occur in various biotopes (e.g. *Talpa europaea* and *Cervus elaphus*) or in biotopes that are widely distributed in Northern and Central, as well as Southern Europe, have a greater stratigraphic range.

Cold stage faunas from the last (Weichselian) and penultimate (Saalian) glacial periods are characteristic and rather well known; species such as *Dicrostonyx gulielmi, Lemmus lemmus, Mammuthus primigenius, Coelodonta antiquitatis* and *Rangifer tarandus* are well represented in these faunas. These species migrated from the northeast towards Northwest Europe (Fig. 1). They often occur together with species that prefer a more steppic environment, such as *Spermophilus undulatus, Cricetulus migratorius* and *Cricetus cricetus*, which migrated from the east, most probably from areas they still inhabit today (STORCH 1969; CHALINE 1972). The composition of the faunas seems to confirm GUTHRIE's idea of the presence of a more steppe-like environment (his 'Mammoth-Steppe') (GUTHRIE 1990) instead of more tundra-like conditions as suggested by, e.g., ZAGWIJN (1989).

It is not known if the Early Pleistocene cold stage faunas show the same composition, as they are poorly represented in the fossil record.

Distinct steppic conditions have been indicated in Northwest and Central Europe during different phases of the Pleistocene period. The fossil record from the section Maastricht-Belvédère demonstrates the occurrence of a steppic phase during the transition from an Early Saalian cold stage to a full interglacial interval (KOLFSCHOTEN 1985, 1990). Late Saalian steppic phases are known from, e. g., Tönchesberg, Plaidter-Hummerich Fauna I (KOLFSCHOTEN 1990; KOLFSCHOTEN & ROTH in prep.), whereas Early Weichselian steppe faunas are known from, e. g., Burgtonna (HEINRICH & JANOSSY 1973; KOENIGSWALD & HEINRICH in prep.).

These steppic conditions lead to an increase in the relative number of steppic elements. Lemmings and other cold stage indicators withdraw to the northeast and species such as *Lagurus lagurus* invade Northwest Europe, as indicated by the faunas from, e. g., Fontéchevade and Régourdou (France) (CHALINE 1972, 1973), Tornewton Cave (England) (SUTCLIFFE & KOWALSKI 1976), Burgtonna (Germany) (HEINRICH & JANOSSY 1973) and Tönchesberg, Plaidter-Hummerich, Wannen, Schweinskopf (Germany) (KOLFSCHOTEN & ROTH in prep.).

The rise in temperature and above all the increase in oceanic influences results in a climate which induces a dominance of forests on the North European plain (ZAGWIJN 1989). The thermophilous broad-leaved and coniferous vegetation survived during the cold stages only in restricted condensation zones and deep moist valleys of the southern European mountains (ZAGWIJN 1992 (this volume)). Species such as *Eliomys quercinus, Muscardinus avellanarius, Sus scrofa, Cervus (Dama) dama* and *Capreolus capreolus*, which inhabit a forest biotope, most probably survived in these refugia and migrated to Northwest Europe (Fig. 1) during the interglacial phases.

This is a general picture of the faunal changes and the migration during the late Middle and Late Pleistocene. It may be applicable to the earlier cold stages as well.

Incidental migrations

The general picture of migrations due to climatic changes is completed by the more incidental invasion of species. The contemporary migration of a number of species characterizes the so-called major dispersal events. AZZAROLI et al. (1988) distinguish four major events: the *'Leptobos'* event, the elephant-*Equus* event, the 'Wolf' event and the 'end-Villafranchian' dispersal event. The 'end-Villafranchian event', described by
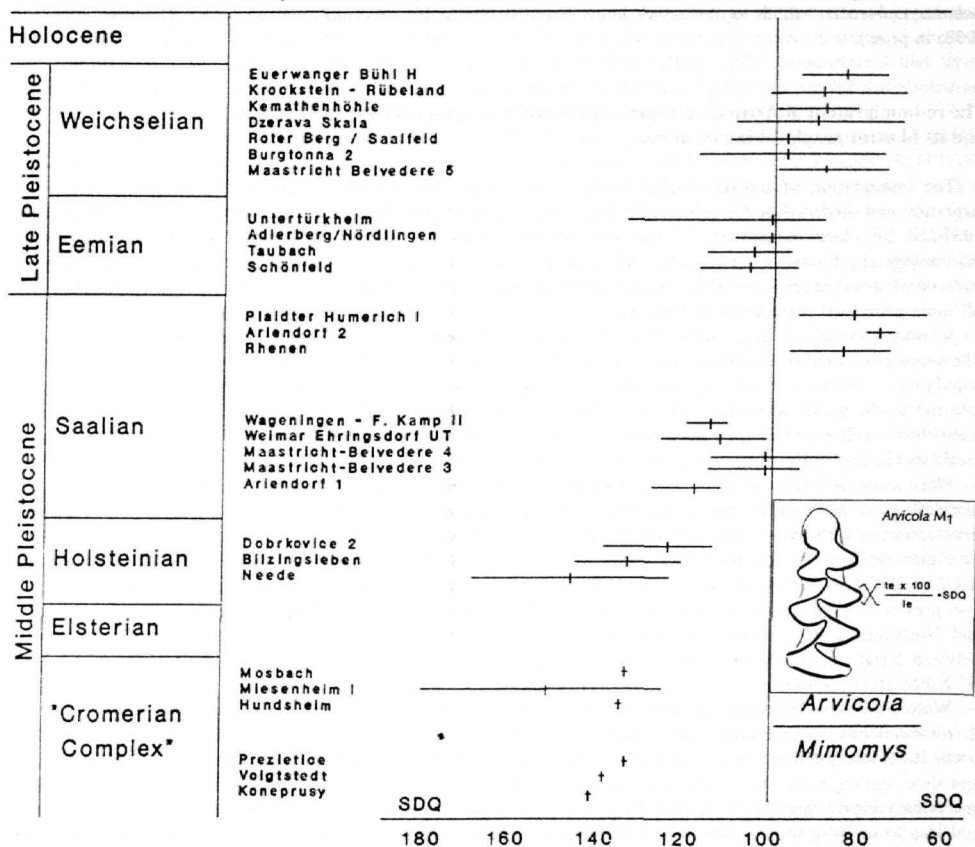
Fig. 3: The range and mean of the enamel thickness quotient (SDQ) of several *Mimomys* populations and several Middle and Late Pleistocene populations of *Arvicola* from Central and Northwestern Europe. The figure shows that there is a gradual decrease, interrupted by an important fluctuation at the Saalian-Eemian transition due to immigration of less derived populations after the Saalian ice-advance. (Figure taken from KOENIGSWALD & KOLFSCHOTEN in press).

AZZAROLI (1983) and AZZAROLI et al. (1988), marks a total faunal turnover, with massive extinctions and replacements. The event did not take place at once but its duration seems to have been geologically short (AZZAROLI 1983; AZZAROLI, et al. 1988).

Apart from such major dispersal events there are also incidental immigrations of single species. *Coelodonta antiquitatis* has its origin in Asia (GUÉRIN 1980) and migrated to Europe during the Middle Pleistocene, together with other cold stage faunal elements. Since its appearance the species has been a permanent element of the European cold stage faunas. *Elephas (P.) antiquus* migrated to Northwest Europe for the first time during the Late Cromerian and occurs during every interglacial period since. *Hippopotamus amphibius* also invaded Europe in the Late Cromerian, most probably during the same warm phase during which *Elephas (P.) antiquus* appeared. However, *Hippopotamus* did not return until the Eemian, after its withdrawal at the end of the Late Cromerian *sensu lato*. A comparable hiatus in the presence of *Hippopotamus* can be observed between its first occurrence during the late Early Pleistocene and the Late Cromerian invasion (KOLFSCHOTEN & VERVOORT-KERKHOFF in prep).

Apart from species which are regularly part of the European faunas, there are also exotic species such as *Bubalus murrensis*, which as far as we know invaded Northwest or Central Europe twice (KOENIGSWALD 1988; in press).

The re-immigration of *Arvicola terrestris* into Northwest Europe during the Eemian, and its biostratigraphical implications

The immigration of species is often rather easy to trace in the fossil record. It is more difficult to track migration and dispersal at the subspecific level; the migration and dispersal of populations to areas which were inhabited by other populations of the same species. This can only be indicated if there are significant morphological differences between the 'old' inhabitants and the 'new' immigrants. The observed changes in fossil material of *Arvicola terrestris* at the Saalian/Eemian transition are interpreted as being the result of the migration of 'more primitive' populations to Northwest Europe.

Mimomys savini, a water vole with rooted molars, is the ancestor of the living water vole *Arvicola terrestris*. The species occurred in European faunas during the late Early and the early Middle Pleistocene. The transition of populations of water voles with rooted molars to populations with more hypsodont, unrooted molars, which are referred to the genus *Arvicola*, took place during the second half of the 'Cromerian Complex'. This transition seems to be well established, since populations with a small percentage of rooted molars are known from several localities (Isernia, Italy; Prezletice, Czechoslovakia).

Pleistocene *Arvicola* remains from Northwest and Central Europe show a variability in size, in the morphology of M^3 and M_1 and in the differentiation of the enamel. However, distinct intraspecific evolutionary developments, with the exception of the changes in the differentiation of the enamel band, have not been observed in either the general morphology or the size of the fossil molars from Central and Northwest Europe (KOLFSCHOTEN 1990). The observed variability of the enamel band in the fossil record is also present in populations of living *A. terrestris*. This implies that the fossil *Arvicola* populations from Central and Northwest Europe should be referred to *A. terrestris* because of the lack of distinct specific differences between fossil *Arvicola* populations from Northwest and Central Europe and the living water vole *A. terrestris* (KOLFSCHOTEN 1990).

Water voles are, because of their great climatic tolerance, widely distributed during the Pleistocene. The living *A. terrestris* has been divided into a number of subspecies, each with its own geographical distribution. These occur in various habitats: *A. terrestris amphibius* from England is closely associated with water and lives in lakes and slow-moving rivers with well vegetated banks, whereas the populations of Central Europe are more terrestrial and mainly inhabit grasslands. RÖTTGER (1986, 1987) studied extant *Arvicola* populations from Europe, Turkey and Iran to investigate interspecific variation in the molars. Her results show that there is some variation in size and, more importantly, a large variation in the relative thickness of the enamel band, especially the thickness of the convex sides of the dentine triangles of the upper and lower molars. RÖTTGER (1986, 1987) quantified the relative thickness by calculating the so called SDQ-values, using the method proposed by HEINRICH (1978, 1982). She demonstrated that living *Arvicola* populations show a strong geographical cline in the development of the enamel differentiation. The southern populations have high SDQ-values whereas the Northwest and Central European populations have lower values (Fig. 2).

The Pleistocene *Arvicola* remains from Northwest and Central Europe, all referred to *A. terrestris*, show an evolution in the relative thickness of the enamel band (KOENIGSWALD 1973; HEINRICH 1978, 1987; KOLFSCHOTEN 1990). The enamel differentiation appears to be an important marker to indicate the evolutionary stage of *Arvicola* in the area discussed. Fig. 3 shows the range and mean of the enamel thickness quotient (SDQ) of some of the latest *Mimomys* populations and several Middle and Late Pleistocene populations of *Arvicola* from Central and Northwest Europe. The figure shows that the SDQ-values of the latest *Mimomys* molars are very similar to those of the earliest *Arvicola* populations. Furthermore, the diagram clearly indicates a gradual decrease in the SDQ-values, interrupted by an important fluctuation at the Saalian-Eemian transition. The data presented by HEINRICH (1978, 1987) showed the gradual decrease, but his diagrams did not indicate the fluctuation. This is most probably due to a large hiatus in the fossil record (late Saalian faunas are not represented in the associations investigated by HEINRICH). Moreover, these fluctuations can only be recognized if independent detailed stratigraphical information is available, as in the case of the fauna from Rhenen, where pre-Eemian age is indicated by the fact that the sediments were pushed by the Saalian ice-sheet.

The fluctuation in the SDQ-values during the Saalian-Eemian transition is unlikely to be the result of a partial return to an older phylogenetic stage, but rather results from an invasion of less derived populations. *Arvicola*

terrestris disappeared from the northern areas which were covered by inland ice and along the edge of the inland ice shield during the Late Saalian. Re-immigration into that area took place through the invasion of populations which survived in areas located further to the south(east). The presence of more primitive features in southern populations during the Pleistocene is very plausible, since RÖTTGER (1986, 1987) demonstrated that living *Arvicola* populations also show a strong morphological cline in the development of the enamel differentiation. The southern populations are in this respect much more primitive than the northern populations.

The fact that the southern populations differ from the northern ones in the development of their enamel differentiation cannot be exclusively explained as a result of adaptation to different environments (RÖTTGER 1987). *Arvicola* populations with high SDQ-values (*A. terrestris persicus*) prefer an aquatic environment, as does *Arvicola sapidus*, which also has high SDQ-values. *A. terrestris amphibius* from England, however, also lives semi-aquatic environments, but is much more advanced in its differentiation of the enamel band (Fig. 2). These geographical differences in development are more the result of differences in the rate of evolution. The evolutionary pressure on the *Arvicola* populations was apparently greater in Northwest and Central Europe where the climatic changes during the Middle and Late Pleistocene were more extreme than in Southern Europe. The impulse to survive under extreme conditions led to such adaptations as the thinning of the convex sides of the salient angles which, in combination with a more rapid tooth growth, is advantageous when abrasive food is chewed.

The strong geographical cline and the migration of populations have important implications for the applicability of evolutionary stages as biostratigraphical markers. The geographical cline makes correlations between northern and southern populations very dubious and the migrations of populations might cause fluctuations in the general evolutionary trend. The geographical differences in the rate of evolution, as indicated for the *Arvicola* populations, are most probably not only restricted to that species. The evolution of *Microtus (Allophaiomys)*, with a comparable development in its enamel differentiation, might show an identical geographical variation. This can explain the occurrence of *Microtus (Allophaiomys)* with advanced enamel differentiation in a Late Tiglian fauna from the Zuurland Borehole.

Discussion

The phenomenon of local re-immigration, as demonstrated for the Northwest European *Arvicola* population, shows that the migration and dispersal of species at the local level is dynamic and complex. Conclusions as to small scale migration, but also the occurrence of major dispersal events, requires a very complete fossil record and detailed stratigraphical information.

Intensive studies of the Quaternary during the last few decades have resulted in more detailed knowledge of climatic history and have shown the presence of a large number of climatic fluctuations. The Pleistocene period is very complex. The lack of detailed stratigraphical information hampers the development of a more or less complete picture of migration and dispersal of Pleistocene mammals. We have to obtain more stratigraphical information in the near future in order to be able to draw more reliable conclusions.

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