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Response of the European mammalian fauna to the mid-Pleistocene transition

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Abstract: The end of the Early Pleistocene is intriguing particularly for mammalian palaeontologists. In Eurasia, this interval has a faunal turnover caused by both the evolution and migration of species. It is the time in which the famous end-Villafranchian 'event' takes place, a phenomenon characterized by a faunal turnover resulting mainly from the migration of larger mammals. The smaller mammal record reveals in particular an important radiation in medium-sized voles. Different *Microtus* species evolve rapidly from species of the genus *Allophaiomys*, and various lineages can be observed. This radiation finally leads to the diversity seen today.

In eastern Europe, particularly on the Russian Plain and the Taman Peninsula, a number of localities occur where faunal assemblages from well-dated stratigraphic sequences can be analysed. These assemblages show the mid-Pleistocene evolution of rodent faunas within eastern Europe. Identical and synchronous changes in the mammalian faunas are found in other parts of Europe. However, a fauna from Untermassfeld in Germany does not fit this general picture, and serious doubts about its published age must be considered.

The onset of the Pleistocene, about 2.6. Ma ago, marks a change in the mammalian fauna of north-western and central Europe. The change in climate led, for example, to the extinction of the tapir, a reduction in the variety of insectivores and flying squirrels, and an increased number of voles. The composition of the mammalian fauna changed gradually, however, over a restricted period of time representing about 0.5 Ma, approximately between 2.4 and 1.9 Ma. A second well-known alteration of the mammalian fauna took place during the later phase of the Late Pleistocene and the early Holocene when the megafauna in particular, mostly large herbivores and some carnivores, became extinct. However, the mid-Pleistocene interval, covering the later part of the Early Pleistocene and the early Middle Pleistocene, is an intriguing time for mammalian palaeontologists. This is the period during which the famous end-Villafranchian 'event' (Azzaroli *et al*. 1988) takes place, as well as the radiation within the voles (Rabeder 1981). How gradual or abrupt were these changes in the mid-Pleistocene mammalian fauna? And if there were obviously abrupt changes, can they be used in continental deposits to mark, or at least recognize, a boundary between the Early and Middle Pleistocene?

In eastern Europe, particularly on the Russian Plain and the Taman Peninsula, there are a number of localities where faunal assemblages from well-dated stratigraphic sequences can be analysed. These assemblages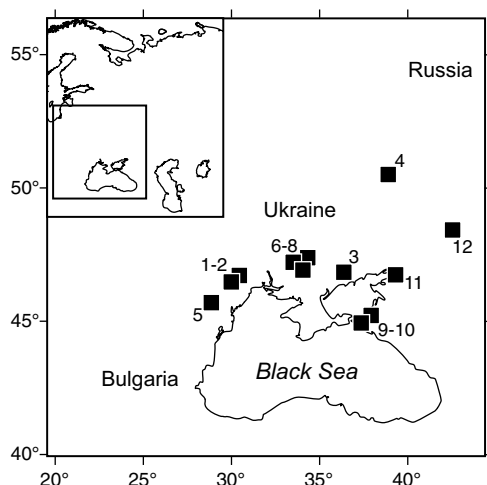 reveal the mid-Pleistocene evolution of faunas within rodent associations in eastern Europe, and are treated first. Can identical and synchronous changes in the mammalian faunas be observed in other parts of Europe? This question and others are addressed.

The mid-Pleistocene rodent history in eastern Europe

Mid-Pleistocene sequences that yield faunal assemblages and are constrained by good palaeomagnetic stratigraphy are known from a number of localities on the Russian Plain and the Taman Peninsula. These localities form the basis of current knowledge on the faunal history in the region during the period from the Jaramillo Subchron to the early Brunhes Chron.

Faunas correlated to the Jaramillo Subchron

The earliest faunas from this time interval have been found in fluvial deposits at the Roksolany locality (lower Dniester basin; Figs 1–3). The fossiliferous strata occur below a thick loess–soil sequence where the Matuyama–Brunhes boundary and the Jaramillo Subchron have been indicated (Dodonov *et al*. 1998). The bones were found in alluvial deposits in the Dniester terrace just below the floodplain loam, the latter yielding a positive (normal) magnetic

Fig. 1. Map showing the geographical position of eastern European mammal localities. 1, Morosovka 1; 2, Roksolany; 3, Nogaisk; 4, Korotoyak; 5, Nagornoe 1; 6–8, Zapadnye Kairy, Ushkalka, Karai-Dubina; 9–10, Litvin, Priozernoe; 11, Port-Katon; 12, Shamin.

signal (the Jaramillo Subchron). The rodent fauna from the Roksolany site is marked by the first appearance of the lagurid *Prolagurus pannonicus*. Remains of the ancestral form *Prolagurus ternopolitanus* are absent here. *Allophaiomys pliocaenicus* molars from this site show advanced enamel differentiation and a rather low *A/L* ratio (*A* = length of the anteroconid complex of the first lower molar, *L* = length of the first lower molar) (Markova & Kozharinov 1998). *Eolagurus argyruloi, Lagurodon arankae* and *Clethrionomys sokolovi* still occur in this fauna and the genus *Mimomys* is represented by *M. savini* as well as by *M. pusillus*.

Two other eastern European faunas (from the Ushkalka and Zapadnye Kairy localities, lower Dnieper basin; Figs 1–3) are very similar in species composition to that described above (Markova 1998). The *A/L* ratios of *Allophaiomys* first lower molars from these localities are slightly higher than the ratios of molars from the Roksolany locality, indicating a younger age (Markova & Kozharinov 1998). Palaeomagnetic analysis of the loess–palaeosol series at the Zapadnye Kairy locality show the Matuyama–Brunhes boundary occurring above a sequence with two fossil soils and intercalated loamy deposits (Fig. 2). These sediments overlie alluvial deposits bearing a small mammal assemblage. A similar situation can be observed in the Ushkalka locality (Markova 1982; Velichko *et al.* 1983; Fig. 2).
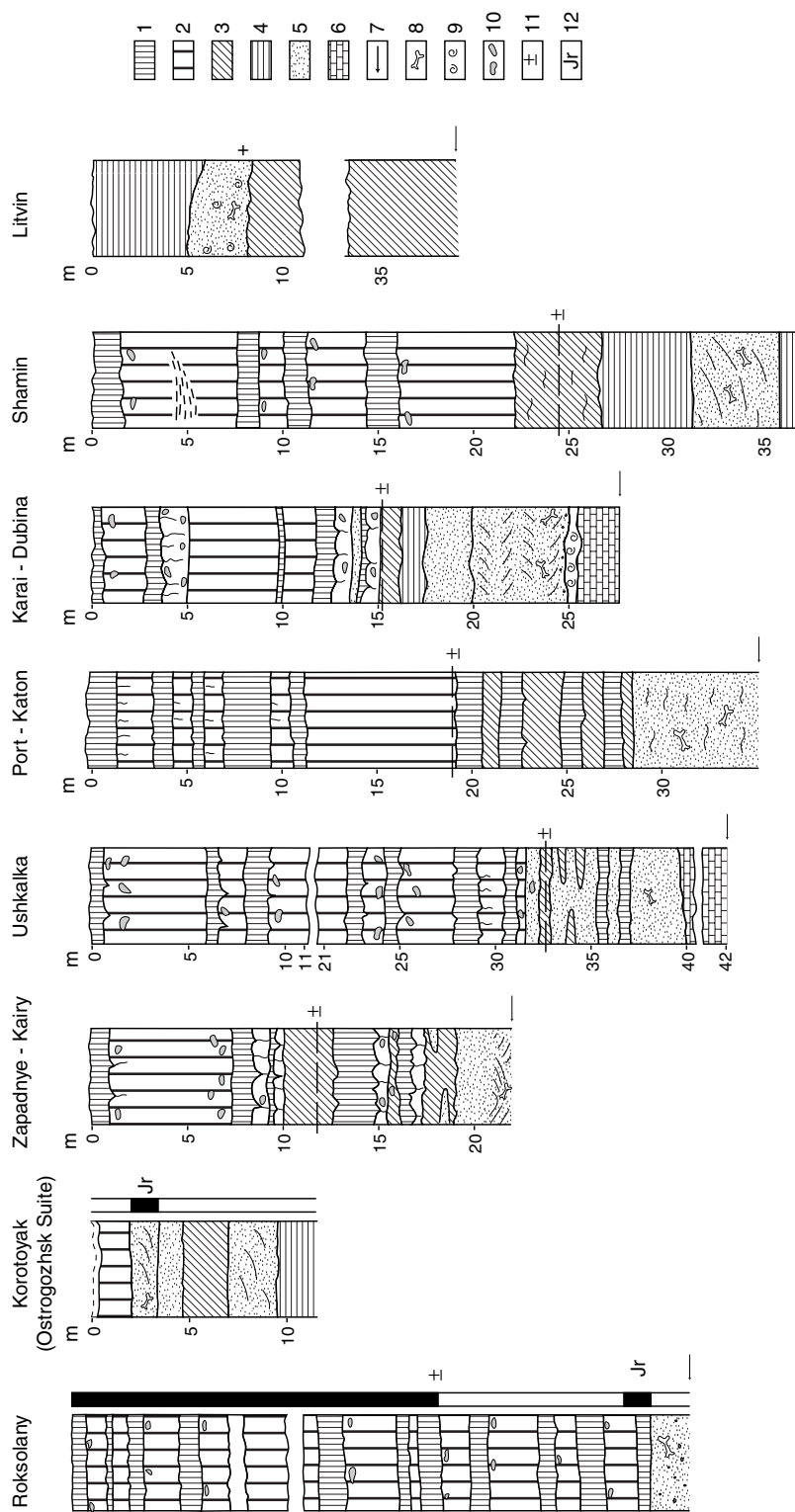
A very important section, that contains faunal remains of the same age, is at Korotoyak (Don River basin; Fig. 2). One stratum of this complicated

section – the Ostrogozhsk suite – contains a small mammal fauna similar to those from the localities of Roksolany, Zapadnye Kairy and Ushkalka (Iosifova & Krasnenkov 1994; Iosifova *et al* 1992; Markova 1998). Palaeomagnetic evidence indicates that the Ostrogozhsk suite should be correlated with the Jaramillo Subchron (Iosifova & Semenov 1998). The rodent fauna from this suite includes the remains of *Mimomys pusillus*, *M. savini*, *Mimomys* sp., *Clethrionomys* ex gr. *sokolovi*, *Eolagurus argyruloi*, *Prolagurus pannonicus* and an advanced *Allophaiomys pliocaenicus* (Agadjanian & Kazantseva 1994). The remnants of more evolved species of the *Allophaiomys–Microtus* phylogenetic lineage, such as *Microtus* (*Terricola*)*, Microtus* (*Pallasiinus*) and *Microtus* (*Stenocranius*), have not been found in this stratum.
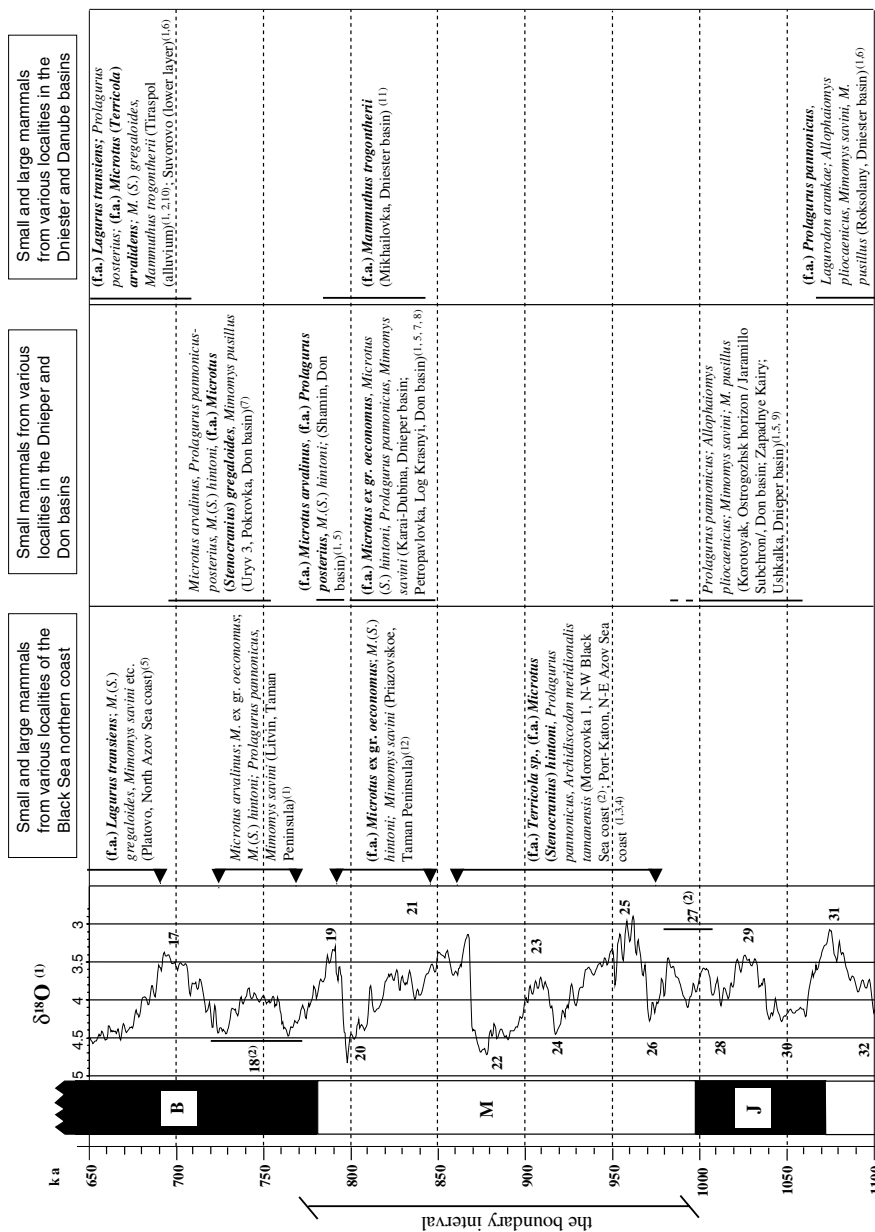
The small mammal faunas listed above are characterized by the first appearance of the lagurid *Prolagurus pannonicus*, the presence of *Allophaiomys pliocaenicus* with an advanced molar morphology, as well as the occurrence of *Eolagurus argyruloi, Lagurodon arankae*, *Clethrionomys sokolovi*, *Mimomys savini* and *M. pusillus*. Faunas with these characteristics have been referred to as the Kairian assemblage, after the fossil record from Zapadnye Kairy (Markova 1998). Lagurid molars with a '*praepannonicus'* morphology (broadly confluent triangles T4–T5) prevail in earlier faunas (for example in the fauna from Nogaisk, Azov Sea coast) (Topachevski 1965). The *A/L* index of the first lower molars of *Prolagurus* from the Nogaisk locality is lower (47.7) than the *A/L* index of the *Prolagurus* molars from Zapadnye Kairy (50.0), indicating that the Nogaisk fauna is older (Rekovets 1994).

Faunas from the interval between the Jaramillo Subchron and the Matuyama–Brunhes Chron boundary

Small mammal faunas of this interval can be divided into two distinct assemblages. The oldest, the Morozovian assemblage (Alexandrova 1976; Markova 1992, 1998), is characterized by the first appearance of the more advanced voles *Microtus* (*Stenocranius*) *hintoni* and *M.* (*Terricola*) sp. Both evolved from voles of the genus *Allophaiomys*. They are absent from the Kairian faunas. The faunas of this assemblage also feature the presence of an advanced type of *Allophaiomys* and the occurrence of *Mimomys savini*, as well as *M. pusillus*. Steppe lemmings are represented by *Prolagurus pannonicus, Lagurodon arankae* and *Eolagurus argyruloi*. These faunas were described from the Morozovka 1 locality near the city of Odessa (Alexandrova 1976) and from Port-Katon on the Azov Sea coast (Markova 1990; Fig. 1). The fossiliferous beds are

Fig. 2. Stratigraphic columns of the sections at Roksolany, Korotoyak, Zapadnye-Kairy, Ushkalka, Port-Katon, Karai-Dubina, Shamin and Litvin. 1, palaeosol; 2, loess; 3, loam; 4, clay; 5, sand; 6, limestone; 7, water level; 8, mammal remains; 9, mollusc remains; 10, mole courses; 11, Matuyama–Brunhes Chron boundary; 12, Jaramillo Subchron.

Fig. 3. The stratigraphic position of eastern European mammal localities. Data sources (superscripts): 1, Markova (1998); 2, Alexandrova (1976); 3, Markova (1990); 4, Markova (1992); 5, Agadjanian & Erbajeva (1983); 6, Mikhailesku & Markova (1992); 7, Agadjanian & Kazantseva (1994); 8, Iosifova & Semenov (1998); 9, Iosifova et al. (1992); 10, Nikiforova & Nigodaev-Nikonov (1971); 11, Dubrovo & Chepalyga (1967); 12, Markova (2002). B, Brunhes Chron; M, Matuyama Chron; J, Jaramillo Subchron.

located below the Matuyama–Brunhes boundary. In the Port-Katon section, four soils with hydrogenic features occur between the subjacent fossiliferous bed and the position of the Matuyama–Brunhes boundary (Velichko *et al*. 1983; Fig. 2).

The more advanced faunas are attributed to the Petropavlovkian assemblage, which is characterized by the first appearance of *Microtus (Pallasiinus)* ex gr. *oeconomus*. The faunas have been named after the locality of Petropavlovka in the Don drainage basin, described by Alexandrova (in Krasnenkov *et al*. 1970) and Agadjanian (in Agadjanian & Erbaeva 1983). A small, rich mammal fauna with a composition similar to that from Petropavlovka has been collected from the Dnieper River basin, near the village of Karai-Dubina (Markova 1982, 1998; Markova & Kozharinov 1998; Rekovets 1994; Figs 1 & 2). Another fauna of similar composition has been discovered on the Taman Peninsula at the Priozernoe locality (Markova 2002; Fig. 1). All these faunas have been attributed to the Petropavlovkian assemblage, with the steppe and yellow lemmings *Prolagurus pannonicus* and *Eolagurus argyropuloi* and the vole *Microtus* (*Stenocranius*) *hintoni* as the most important species. The presence of rhizodont voles *Mimomys savini* and *M. pusillus*, as well as very few remnants of late representatives of the genus *Borsodia* (*B. fejervaryi*), characterize these faunas. The scarce *Allophaiomys* molars recovered from these localities are distinct because of their advanced morphologies (Fig. 3). The first appearance of *Microtus* ex gr. *oeconomus* was also discovered in these localities. In the Karai-Dubina and Petropavlovka sections the Matuyama–Brunhes boundary is found in the alluvial floodplain deposits overlying the channel deposits with the small mammals (Velichko *et al*. 1983).

The Shamin locality (Don basin; Figs 1 & 2) has yielded teeth of *Microtus arvalinus* as well as remains of *Microtus* (*Stenocranius*) *hintoni* and *Prolagurus posterius*. This site is correlated to the very end of the Matuyama Chron. The Shamin fauna is apparently more advanced than the faunas correlated to the Petropavlovkian assemblage because it includes an additional species of the genus *Microtus*, *M. arvalinus*, and the more advanced lagurid, *P. posterius* (Markova 1998).

Early Brunhes Chron faunas

In a few sections, small mammal remains have been recovered from deposits just above the Matuyama–Brunhes boundary. The earliest assemblage is an early Tiraspolian fauna from the locality of Litvin (Taman Peninsula; Fig. 1). This fauna occurs in the Chauda marine deposits dated to the beginning of the Brunhes Chron. It yields the remains of small

mammals such as *Mimomys savini, Allophaiomys pliocaenicus, Prolagurus pannonicus, Eolagurus simplicidens gromovi, Microtus* (*Stenocranius*) *hintoni* and *Microtus* (*Microtus*) *arvalinus* (Markova 1992). The rodent fauna closely resembles the Shamin fauna that predates the Matuyama–Brunhes boundary. Early Brunhes faunas, younger than that from Litvin, include for example the faunas of Uryv 3 and Pokrovka (Don Basin), which are characterized by the occurrence of a significant quantity of *Microtus* (*Stenocranius*) molars of the 'gregaloides' morphotype (Agadjanian and Erbaeva 1983; Agadjanian & Kazantseva 1994).

The evidence presented above indicates that the eastern European rodent faunas show a clear evolution in the interval from the Jaramillo Subchron to the beginning of the Brunhes Chron. *Allophaiomys pliocaenicus*, a dominant component of the earliest faunas, disappears and is replaced by *Microtus* (*Terricola*) sp. and *Microtus* (*Stenocranius*) *hintoni*. The latter species evolved gradually into *Microtus* (*Stenocranius*) *gregaloides* during the early Brunhes Chron. *Prolagurus pannonicus*, a species that first occurred during the Jaramillo Subchron, is succeeded by *Prolagurus posterius* just before the Matuyama–Brunhes reversal. A remarkable event in the mid-Pleistocene evolution of the rodent faunas is the first appearance of *Microtus* ex gr. *oeconomus* just before the Matuyama–Brunhes boundary. This event corresponds in age with the first appearance of *Mammuthus trogontherii* as indicated in the early Tiraspolian fauna from the Mikhailovka locality (Dniester basin). The earlier larger mammal faunas (those that correspond in age to the Kairian and Morozovian rodent assemblages) are referred to the Tamanian Mammalian age, being characterized for example by the occurrence of *Archidiskodon meridionalis tamanensis*.

Evidence from western and central Europe

In northwestern and central Europe there are no long continental sequences that have yielded mammalian faunas spanning the Jaramillo Subchron to the early Brunhes Chron. Only a few geographically scattered localities contain mid-Pleistocene faunal remains. One of the longer sequences that include a mammalian record is the Kärlich section in the Neuwied Basin (Germany). The Quaternary strata, which overlie Tertiary deposits, consist of basal gravels overlain by loess or loess-like deposits, alternating with ash and pumice. A number of palaeosols are present in the loess-like deposits. Two palaeomagnetic reversals have been recognized in the lower part of the section: the Matuyama–Brunhes boundary and a reversal that might correspond to the Jaramillo Subchron (Brunnacker *et al*. 1976). The lowermost

smaller mammal assemblages are from deposits just above the Matuyama–Brunhes boundary. The fauna is characterized by the absence of *Allophaiomys pliocaenicus* and the presence of *Microtus (Terricola) arvalidens* and *Microtus* (*Stenocranius*) *hintoni/ Microtus* (*Stenocranius*) *gregaloides*. *Mimomys savini* is also present in the lowermost smaller mammal faunas. Of particular note in the larger mammal associations from the Kärlich section is the occurrence of molars referred to as cf. *Mammuthus trogontherii* in deposits situated below the Matuyama–Brunhes boundary and above the level that is correlated with the Jaramillo Subchron.

Mammuthus trogontherii has also been recorded from the Dorn-Dürkheim 3 locality together with rodents referred to *Microtus* (*Stenocranius*) *hintoni* and *Mimomys savini*. Palaeomagnetic investigations have indicated reversed magnetization of the deposits. The fauna is therefore correlated with the latest phase of the Matuyama Chron, postdating the Jaramillo Subchron (Franzen *et al*. 2000).

Bavel in The Netherlands is the type locality of the Bavelian Interglacial Substage which is correlated to the Jaramillo Subchron. Vertebrate remains from this site are rare and the faunal information is very poor. A molar of *Allophaiomys pliocaenicus* was recorded from the interglacial deposits (unfortunately the molar is lost). However, this molar, referred to as *Microtus arvalis* (Van Kolfschoten 1990), appears to be from a level younger than the Bavelian Interglacial and predating the Matuyama– Brunhes boundary.

One of the most important mid-Pleistocene localities in central Europe is Untermassfeld in Germany. This site has yielded a very rich, well documented fauna and a huge quantity of vertebrate fossils from a large variety of taxa (Kahlke 2001). The smaller mammal assemblage includes *Mimomys savini* and *Mimomys pusillus*; *Allophaiomys* is absent and a more evolved vole described as *Microtus thenii* is represented (Maul 2001). The fossils are from deposits with normal magnetization; reversed polarization is indicated in levels just below the fossil-bearing horizon. The palaeomagnetic transition is regarded as the base of the Jaramillo Subchron, and hence the Untermassfeld assemblage is assigned to the Jaramillo Subchron (Maul 2001; Kahlke 2001). The assumption is based on the fact that the early Brunhes faunas from sites such as Voigtstedt and West Runton are more advanced than that from Untermassfeld (Maul 2001).

Other faunas included within the interval of the Jaramillo Subchron are those from Le Vallonet (France) and Colle Curti (Italy). The Colle Curti small mammal remains have been found in deposits with normal polarity, and located between deposits bearing the reversed polarity of the Matuyama Chron. The Colle Curti fauna includes the remains of the genus *Allophaiomys*, but *Microtus* (*Terricola)* and *Microtus (Stenocranius)* are absent. In addition, the Trinchera Dolina site at Atapuerca, Spain, has yielded mid-Pleistocene faunal remains from deposits with reversed polarity referred to the very end of the Matuyama Chron. The rodent assemblage from the levels TD 3–6 at this site comprises *Microtus (Stenocranius) gregaloides* and *Microtus (Terricola) arvalidens* (Cuenca Bescos *et al*. 1995). However, the pictures of *Microtus (S.) gregaloides* molars (Cuenca Bescos *et al*. 1995) indicate a rather primitive morphology (i.e. a simple anterior loop and broad confluent triangles T4 and T5) comparable to the morphology of molars that also could be referred to *M*. (*S*.) *hintoni*. The late Biharian vertebrate fauna from the lacustrine succession of San Lorenzo (Italy) with *Microtus* (*Terricola*) *arvalidens* is referred to the early Brunhes Chron of the early Middle Pleistocene (Masini *et al*. 2005).

A combined picture

Evidence from the regions discussed above indicates that the mid-Pleistocene rodent faunas of eastern, central and western Europe are very similar in a number of aspects. However, there is one important difference: the lagurids. These mammals are well represented in both eastern European and Asian faunas and offer additional information concerning the biostratigraphic position of faunal assemblages. However, they are absent from the western part of the Eurasian continent. Fortunately, representatives of the *Allopahaiomys–Microtus* lineage occur in eastern as well as central and western Europe, and therefore offer the possibility to correlate between east and west. A comparison of the faunal evolution observed in eastern Europe with that in the west, based on scattered data, indicates that the general picture in both regions is more or less identical. The rodent faunas show a clear pattern of evolution during the interval from the Jaramillo Subchron to the beginning of the Brunhes Chron. *Allophaiomys pliocaenicus*, which had been dominant in the earliest faunas, disappeared and was replaced by *Microtus* (*Terricola*) sp. and *Microtus* (*Stenocranius*) *hintoni*. The latter species evolved into *Microtus* (*Stenocranius*) *gregaloides* during early Brunhes time. The first appearance of *Mammuthus trogontherii*, in faunas predating the Matuyama–Brunhes boundary, can be traced in both regions. It is remarkable that the mid-Pleistocene evolution of widely dispersed rodent species, such as voles and lagurids, occurs more or less simultaneously in western Transbaikalia (Alexeeva & Erbajeva 2005) and Europe. Foronova (2005) describes the larger mammal evolution in the Kuznetsk basin (southwestern Siberia) and mentions the first appearance

of the steppe mammoth *Mammuthus trogontherii* just before the Matuyama–Brunhes boundary. The mid-Pleistocene faunal evolution can apparently be traced all over Eurasia. This conclusion can be drawn only because of the good palaeomagnetic time-control available in many of the sections described.

There are, however, minor discrepancies if the faunas from the different regions are compared in detail. Based on morphological features (e.g. the *A/L* index) it can be concluded that the *Allophaiomys* remnants from the Ostrogozhsk suite of the Korotoyak locality are more evolved than the *Allophaiomys* sp. from Colle Curti (Coltorti et al. 1998). The voles of the Colle Curti fauna are more similar to those from Roksolany, recovered from deposits just below the Jaramillo Subchron (Markova 2005). The Colle Curti fauna might date from the earlier part of the Jaramillo Subchron, whereas the fauna from the Ostrogozhsk suite might be of late Jaramillo age. This conclusion is justified if it is assumed that there is no geographical bias when assigning an age based on faunal evolution. However, one should be careful with such an assumption. The late Middle Pleistocene evolution of the genus *Arvicola* clearly shows a geographical gradient (Van Kolfschoten 1990): *Arvicola* species in the north are more advanced than those in the south.

Untermassfeld, an outlier

Regional differences in the mid-Pleistocene faunal evolution, however, do not explain the outlier in the general picture described above. The rodents from Untermassfeld (Germany) do not fit into the consistent stratigraphical picture. The voles from Untermassfeld, correlated to the Jaramillo Subchron, are similar to those of the fauna from Podumci 1 (Croatia) described by Malez & Rabeder (1984). *Microtus thenii* from Untermassfeld and Podumci includes abundant molars with a morphology close to that of *Microtus (Stenocranius) hintoni*, and a few molars resemble *Microtus ratticepoides* (= *M*. ex gr. *oeconomus*) morphology. However, we emphasize that *M. thenii*, *M. hintoni* and *M. ratticepoides* represent different lineages that all originate from and therefore postdate *Allophaiomys*. *Microtus (Stenocranius) hintoni* is abundant in the faunas from Karai-Dubina and Petropavlovka, in which *M*. ex gr. *oeconomus* appears for the first time. Correlation between these faunas and that from Untermassfeld, as indicated by Maul (2001) and Markova (2005), however, is problematic since the faunas from Karai-Dubina and Petropavlovka are much younger and postdate the Jaramillo Subchron. Furthermore, *Allophaiomys*, which characterizes the faunas of the Jaramillo Subchron in many regions, is not present in the Untermassfeld vole assemblage. If we assume that the supposed stratigraphic age of the Untermassfeld fauna is correct, then there is a clear discrepancy with other sites. Instead, we prefer to consider the Untermassfeld fauna as younger, and close to the age of the Matuyama–Brunhes boundary.

Discussion and conclusions

Apart from the exception mentioned above, there appears to be a more or less uniform and simultaneous evolution in the mid-Pleistocene rodent fauna of Eurasia. The onset of changes began immediately before the Jaramillo Subchron, with evolution within the genus *Allophaiomys*. This radiation in the *Allopahiomys–Microtus* lineage, resulting in the appearance of *Microtus (Terricola)* and *Microtus (Stenocranius)*, is a post-Jaramillo phenomenon. *Microtus* ex gr. *oeconomus* (= *M. praeratticeps* = *M. protoeconomus*) first appeared during the latest part of the Matuyama Chron, together with the steppe mammoth *Mammuthus trogontherii*. These steps in faunal evolution are most certainly related to climate changes and probably coincide with changes in other climate proxies such as the pollen record, data on sea surface temperature and the occurrence of permafrost features.

The climate changes that triggered the steps in faunal evolution also play a role in the debate on the definition of the Early–Middle Pleistocene boundary. Can one of these mid-Pleistocene climate events be used for the definition of the boundary? Since voles underwent a more or less simultaneous evolution in an area covering most of Eurasia, one of their evolutionary stages could be a useful biostratigraphical marker for the boundary. The first appearance of *Microtus* ex gr. *oeconomus* (= *M. praeratticeps* = *M. protoeconomus*) just before the Matuyama–Brunhes reversal has a particular potential for recognizing the Early–Middle Pleistocene boundary.

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