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Similarity and regional differences in Quaternary arvicolid evolution in Central and Eastern Europe

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Abstract

Because of their rapid evolution and abundant fossil record, arvicolid molars are commonly employed in Quaternary biostratigraphy. In addition, with their extensive geographical ranges these fossils often permit interregional faunal correlations. However, as a precondition for such correlations it has to be established that the occurrences are really time parallel in the different regions. This paper deals with the particular comparison of arvicolid records from Central and Eastern Europe. In most of the earliest and latest records of the species investigated similarities in the spectrum of accompanying species can be observed. In some cases endemism (*Ungaromys*, *Ellobius*, *Eolagurus*, *Villanyia*, several *Pliomys* species) or different taxonomic interpretations do not provide a sufficient base for comparison. Only for a few taxa can clear biostratigraphical differences of ranges be recognised (mainly *Mimomys savini-Arvicola* and various lineages within the genus *Microtus*). In some cases, differences in the chronostratigraphical ranges are possibly caused by the lack of a geological and palaeomagnetic framework for most of the Central European localities.

1. Introduction

For decades, arvicolid molars have been commonly employed for biostratigraphical purposes within the Pliocene and Quaternary, as a result of their rapid and well-documented dental evolution and abundant fossil record. Furthermore, it has long been accepted that many arvicolid taxa have extensive geographical ranges and they have therefore been used as biozonational markers in interregional faunal correlations throughout Europe and beyond. However, it is also well known that possible geographical differences in the occurrences of species and morphological clines throughout the continent (e.g. Röttger, 1987) have to be taken into account. Therefore, the question of whether and by how much, such differences can influence the biostratigraphical correlations arises. The increased spatial density of the arvicolid fossil record from Central and Eastern Europe provides a good basis for the assessment of similarities and differences between the regions. However, several general problems have to be faced, such as the limited number of independently dated sites, different opinions about particular correlations between faunas, sediments, climatic cycles, equivalent marine isotope stages, absolute ages and palaeomagnetic units and different taxonomic approaches to nomenclature and discrimination of morphotypes and species.

Despite all these problems, the authors have attempted to provide an overview of cases where arvicolid occurrences in Central and Eastern Europe can be considered to be time parallel and to indicate the level of certainty. The authors also attempt to indicate the remaining uncertainties, in order to contribute a small step forwards in overcoming these problems.

2. Methodology

In this paper, Central Europe is taken as the area of The Netherlands, Germany, Poland, Austria, Czechia, Slovakia, Hungary, Romania and parts of Italy and France. Eastern Europe is considered to be Belarus, Ukraine, Moldova and the European part of Russia. Some East Romanian localities may be transitional in this respect,

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since they display more affinities to Eastern Europe (see Sections 3.2 and 3.19).

Various biostratigraphical subdivisions and correlations with chronostratigraphy exist for the different regions of Europe. Here the biostratigraphical schemes of Fejfar et al. (1998) are employed for Central Europe, and of Markova (2004a) for Eastern Europe (Figs. 1–3). The genus *Microtus* is one of the most dominant and rapidly evolving elements in small mammal faunas of the Quaternary, and its first occurrence sets a fixed point for any biostratigraphical zonation and is therefore of crucial importance. However, the relationship between the first appearance of *Microtus* and the Plio-Pleistocene boundary (just above the top of the Olduvai Subchron) is still a matter of debate. Its first occurrence is variously placed (a) near (Chaline, 1977), (b) clearly below (Pevzner et al., 2001) or (c) clearly above (Rabeder, 1981) this boundary. The majority of arguments support variants (a) or (b) (see also notes 1–4 below), and therefore we refer to both correlation options.

Here current knowledge of the assumed stratigraphical ranges is discussed species by species. Using data from the literature the possibilities of different taxonomic considerations are presented. Therefore, occasional short notes about the criteria for species discrimination that are applied are given in this paper. In some cases the taxonomic problems are simplified by grouping several species. For occlusal surface elements, the nomenclature of Van der Meulen (1973) is followed. For the enamel differentiation the terms of Martin (1987) are used: 'negative' for anterior edges thinner than posterior ones in the lower molars, and the reverse in the upper molars and 'positive' for anterior edges thicker than posterior ones in the lower molars, and the reverse in the upper molars. For morphometric comparisons the following indexes are used in arvicolid $M/1$: A/L for the length of the anteroconid complex (A) in relation to the tooth length (L) (Van der Meulen, 1973), SDQ (abbreviation of the German term: 'Schmelzband-Differenzierungs-Quotient', English: 'enamel differentiation quotient') for the ratio of the thickness of each posterior to the each related anterior enamel cutting edge (Heinrich, 1978), Hsd/L for the relation of the height of the posterior buccal linea sinuosa (Hyposinuid–Hsd) to the tooth length (L) (Rabeder, 1981; Maul et al., 1998).

To compare the earliest (EO) and latest occurrences (LO) in both regions it is first considered whether accompanying taxa are similar or not, since the inclusion of several taxa reduces possible circular reasoning. Consequently, the available dating from sources related to chronostratigraphy is compared. In order to reduce repetitions only the numbers of the following interpretations are quoted in the text:

(1) The small mammal fauna of Tegelen does not contain *Microtus* and originates from a horizon referred to Tegelen pollen zone c5 with normal magnetisation, interpreted as the Olduvai Subchron (Van Kolfschoten, 1990a). On the basis of this observation, Central European faunas containing *Microtus* cannot be older than the upper part of the Olduvai Subchron.
(2) According to Tesakov (1998, Fig. 54) the small mammal fauna of Tegelen originates from a unit that predates the Olduvai Subchron. It therefore appears that Central European faunas containing *Microtus* can be of Olduvai or even older age.
(3) The *Microtus pliocaenicus* remains from the Brielle 1 borehole originate from a unit interpreted as of Eburonian age (Van der Meulen and Zagwijn, 1974). This indicates that the EO of *Microtus pliocaenicus* cannot be younger than the Eburonian.
(4) The fossiliferous strata of Kryzhanovka 4, and of Tizdar, contain *Microtus deucalion* and are related to reverse-magnetised sediments interpreted as of pre-Olduvai age (Pevzner et al., 1998). The implication of this is that *Microtus* appears at least in Eastern Europe before the Olduvai Subchron.
(5) The fossiliferous strata of Untermaßfeld are normally magnetised and interpreted as of Jaramillo Subchron age (Wiegank, 1997). The Untermaßfeld *Microtus* sample is more evolved than advanced *Allophaiomys*, since it is characterised by the predominance of hintoni morphotypes, the absence of morphotypes with closed T4–T5 and very rare allophaiomyid morphotypes and A/L of 48.7 (Maul, 2001). This indicates that Central European faunas with more evolved *Microtus* must be younger than the onset of the Jaramillo Subchron, faunas with more primitive *Microtus* must be older than the termination of this subchron.
(6) The fossiliferous strata of the Korotoyak/Ostrogozhsk suite are normally polarised, and are correlated with the Jaramillo Subchron. They contain *Microtus pliocaenicus* (Iosifova and Semenov, 1998; Markova, 2005).
(7) The fossiliferous units at Karaj Dubina, Petropavlovka 2, Krasnyj Log and Shamin are reverse magnetised. On the basis of both geological and palaeomagnetic evidence they are correlated to the very end of the Matuyama Chron. They include *M. protoeconomus* (Agadjanian, 1992; Markova, 1992, 2004a; Rekovets, 1994). These results indicate that at least in Eastern Europe, less advanced *Microtus* samples cannot be younger than the Matuyama/Brunhes Chron boundary.
(8) The fossil locality Zapadnye Kairy, which yields advanced *Allophaiomys*, is part of a complicated loess–palaeosol sequence. Between the fossiliferous stratum and the M/B (Matuyama/Brunhes) boundary in sediments above the fossil-bearing unit two palaeosols and two loess horizons are recorded (thus, at least two temperate and two cooler climatic events are represented) (Markova, 2005).
(9) According to Koenigswald and Van Kolfschoten (1996), *Mimomys* still occurs in 'Cromerian

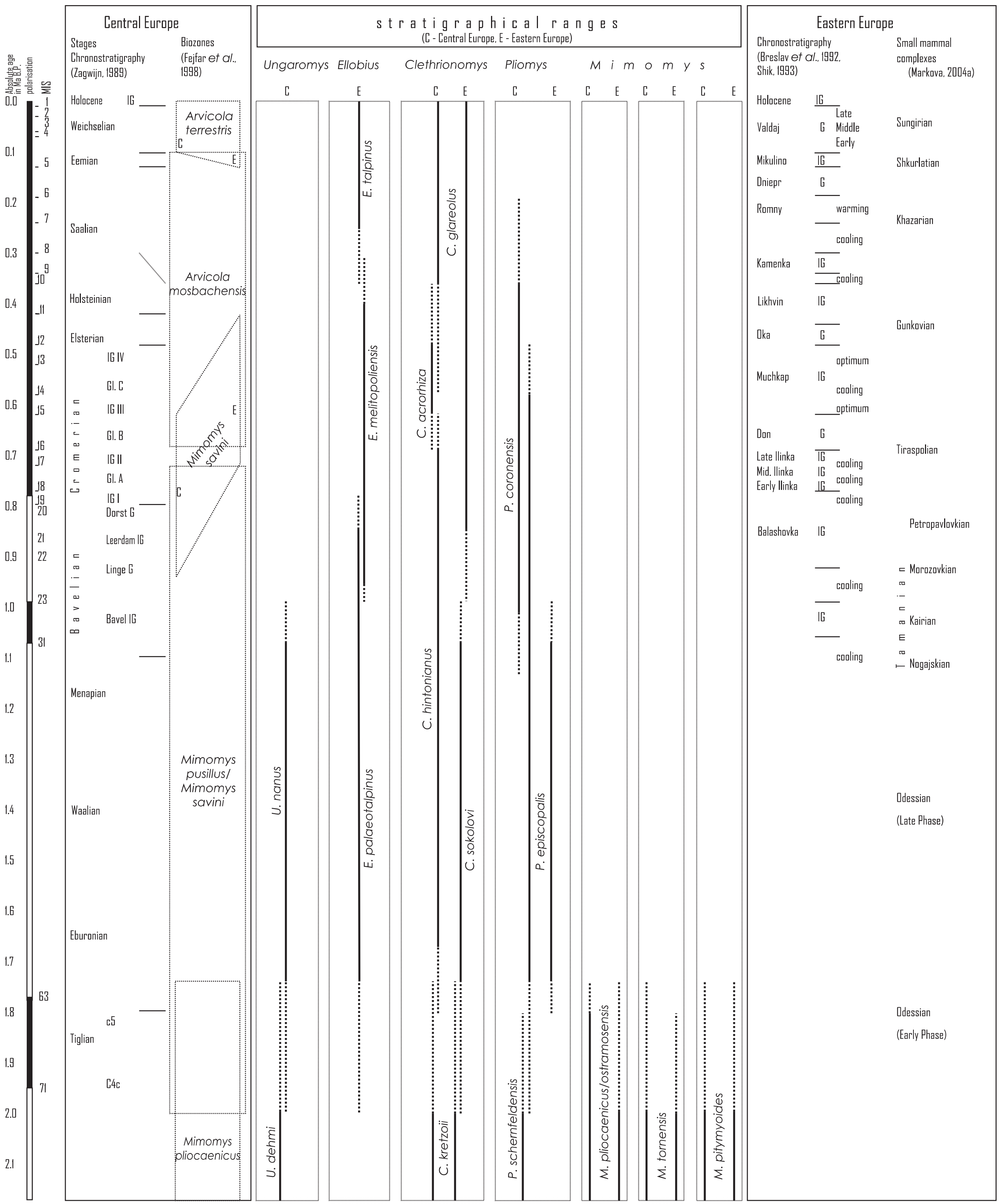

Fig. 1. Presumed ranges of various arvicolid taxa (*Ungaromys*, *Ellobius*, *Clethrionomys*, *Pliomys*, *Mimomys*) in Central and Eastern Europe. Abbreviations: C4c, c5—pollen zones of Zagwijn (1989), G—glacial, IG—interglacial, MIS—Marine Isotope Stages.

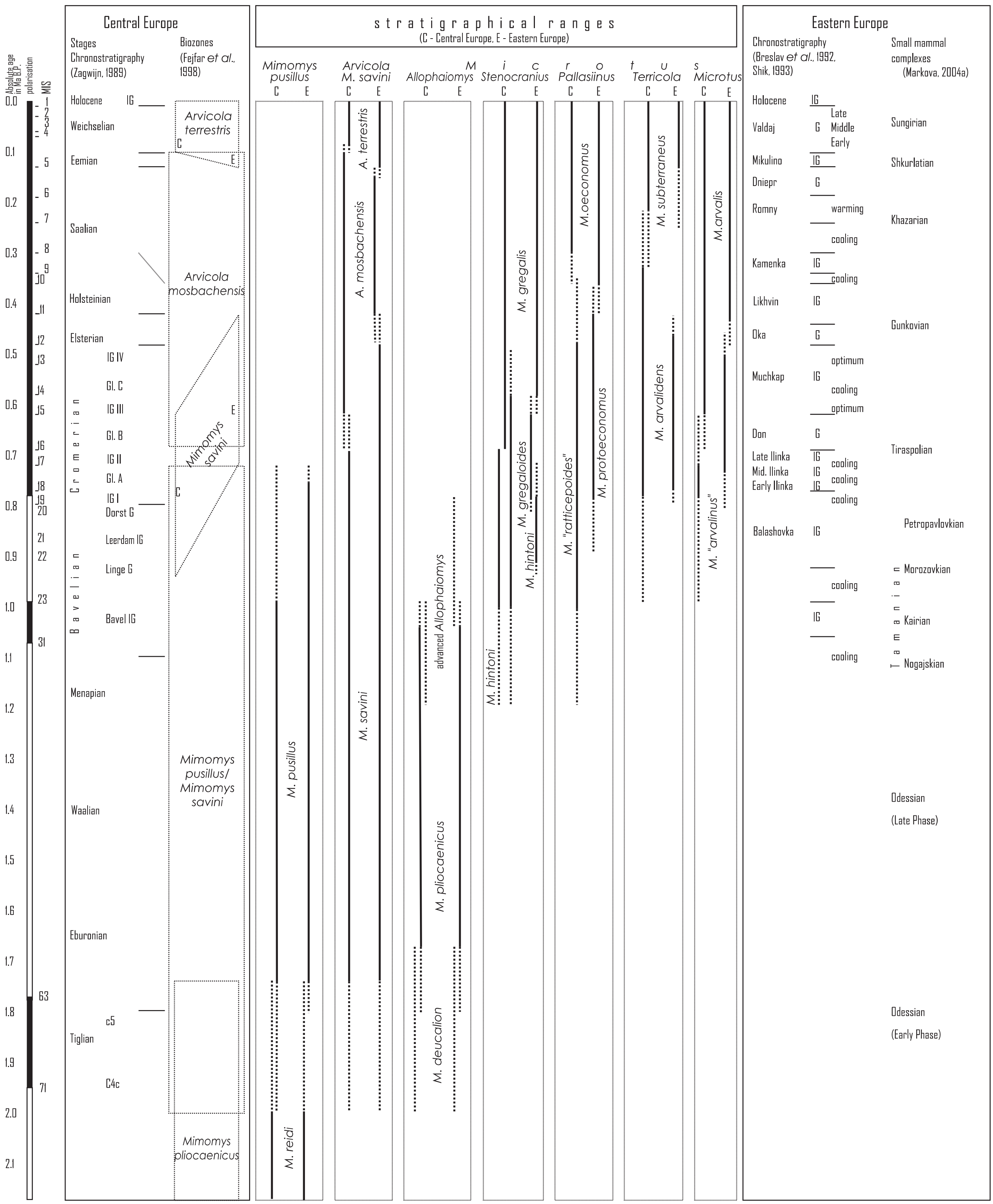

Fig. 2. Presumed ranges of various arvicolid taxa (*Mimomys*, *Microtus*) in Central and Eastern Europe. Abbreviations: C4c, c5—pollen zones of Zagwijn (1989), G—glacial, IG—interglacial, MIS—Marine Isotope Stages.

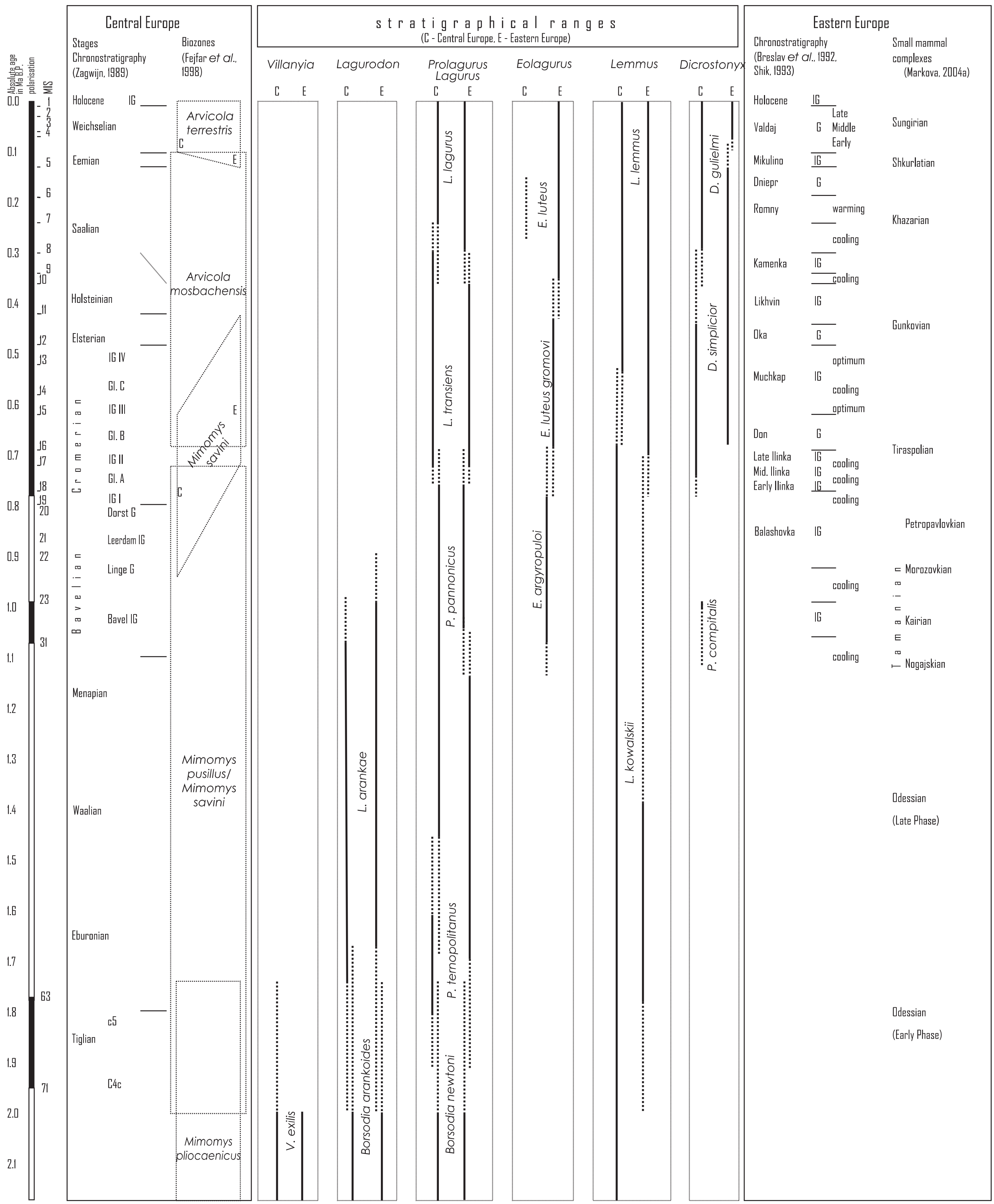

Fig. 3. Presumed ranges of various arvicolid taxa (*Villanyia*, *Borsodia*, *Lagurodon*, *Prolagurus*, *Eolagurus*, *Lemmus*, *Dicrostonyx*) in Central and Eastern Europe. Abbreviations: C4c, c5—pollen zones of Zagwijn (1989), G—glacial, IG—interglacial, MIS—Marine Isotope Stages.

Interglacial II' in Central Europe, whereas the first appearance of *Arvicola* is in 'Cromerian Interglacial III'.

(10) *Mimomys savini* is unknown from sites referred to the Okian Stage Glaciation (c. MIS 12) or younger deposits (Agadjanian, 1992; Markova, 2004a). Moreover, *Arvicola mosbachensis* remains have not been found in the deposits correlated to this glaciation, e.g. at Likhvin and Mikhailovka 2 (Agadjanian and Glushankova, 1986; Alexandrova, 1982).

(11) According to *Arvicola* SDQ values from Central Europe given by Heinrich (1987), independently dated Weichselian and Holocene samples have SDQ <100, Eemian to Holsteinian samples SDQ <135 and Elsterian and Cromerian samples SDQ >130.

Figs. 1–3 display all the interpreted ranges mentioned in the text and correlations with the stratigraphical schemes of Fejfar et al. (1998) and Markova (2004a). For species record, morphometric values and other information the authors have used the following references for the sites mentioned (Table 1). These references are not subsequently repeated in the text. In addition we refer to the bibliography of Quaternary rodents by Kowalski (2001).

Table 1
Sites mentioned in the text

Country	Locality	Reference
Austria	Deutsch Altenburg	Rabeder (1981)
Austria	Hundsheim	Heinrich (1987)
Belarus	Korchevo	Motuzko (1985)
Czechia	Chlum	Fejfar and Horáček (1983)
Czechia	Dobrkovice	Fejfar in Bartolomei et al. (1975)
Czechia	Holštejn	Fejfar and Horáček (1983)
Czechia	Koněprusy	Fejfar in Bartolomei et al. (1975)
Czechia	Mokrá	Fejfar and Horáček (1983)
Czechia	Včeláre	Fejfar and Horáček (1983); Horáček (1985)
England	West Runton	Stuart (1981)
France	Les Valerots	Chaline (1972)
Germany	Ariendorf	Van Kolfschoten (1990b)
Germany	Bilzingsleben	Heinrich (2004)
Germany	Burgtonna	Heinrich (1987)
Germany	Hohensülzen	Storch et al. (1973)
Germany	Kärlich	Koenigswald and Van Kolfschoten (1996)
Germany	Kerspleben	Maul et al. (1998)
Germany	Mahlis	Fuhrmann et al. (1977)
Germany	Miesenheim	Van Kolfschoten (1990b)
Germany	Mosbach	Maul et al. (2000)
Germany	Neuleiningen	Maul (1996); Maul et al. (1998)
Germany	Sackdillingen	Heller (1930)
Germany	Schambach	Koenigswald (1977)
Germany	Schernfeld	Carls and Rabeder (1988)
Germany	Untermaßfeld	Maul (2001)
Germany	Voigtstedt	Maul (2002)
Hungary	Nagyharsányhegy	Jánossy (1986)
Hungary	Osztramos	Jánossy (1986)
Hungary	Somssich hegy	Jánossy (1986)
Hungary	Süttö	Jánossy (1986)
Hungary	Tarkö	Jánossy (1986)
Hungary	Villány	Jánossy (1986)
Italy	Castelfranco di Sopra	Masini and Torre (1990)
Italy	Colle Curti	Abbazzi et al. (1998)
Italy	Monte Peglia	Van der Meulen (1973)
Italy	Pirro Nord	Masini and Torre (1990)
Poland	Kadzielnia	Nadachowski (1998)
Poland	Kamyk	Nadachowski (1998)
Poland	Kielniki	Nadachowski (1998)
Poland	Koži Grzbiet	Nadachowski (1985); Abramson and Nadachowski (2001)
Poland	Żabia	Nadachowski (1998)
Poland	Zalesiaki	Nadachowski (1998)
Romania	Betfia	Méhely (1914); Terzea (1994)
Romania	Braşov	Terzea (1995)
Romania	Sândominic	Terzea (1995)
Russia	Akkulaevo	Sukhov (1970); Tesakov (2004)

Table 1 (*continued*)

Country	Locality	Reference
Russia	Bogdanovka	Markova (1982)
Russia	Chigirin	Markova (1982)
Russia	Gunki	Markova (1982, 2004b)
Russia	Ilinka	Agadjanian (1977, 1992); Krasnenkov et al. (1992)
Russia	Korotoyak/Ostrogozhsk suite	Markova (2005)
Russia	Krasnyj Log	Agadjanian (1992)
Russia	Likhvin	Alexandrova (1982)
Russia	Liventsovka	Tesakov (2004)
Russia	Malutino	Markova (2000)
Russia	Melekino	Markova (1982, 1998)
Russia	Mikhailovka	Agadjanian and Glushankova (1986)
Russia	Perevoz	Markova (1992)
Russia	Petropavlovka	Agadjanian (1977, 1992)
Russia	Pivikha	Markova (1982)
Russia	Platovo	Agadjanian (1977, 1992)
Russia	Port Katon	Markova (1990)
Russia	Posevkino	Markova (1992)
Russia	Priluki	Markova (1982)
Russia	Psekups	Tesakov (2004)
Russia	Rybinsk	Agadjanian and Erbaeva (1983)
Russia	Shamin	Markova (1998)
Russia	Shkurlat	Markova (2000)
Russia	Tizdar	Tesakov (2004)
Russia	Uryv	Agadjanian (1977, 1992)
Russia	Ushkalka	Markova (1982, 2005)
Slovakia	Koliňany	Fejfar and Horáček (1983)
The Netherlands	Maastricht-Belvedere	Van Kolfschoten (1990b)
The Netherlands	Tegelen	Van Kolfschoten (1990a); Tesakov (1998)
Ukraine	Bolshevik	Rekovets et al. (1990); Rekovets (1994)
Ukraine	Cherevychnoe	Rekovets (1994)
Ukraine	Chortkov	Rekovets (1994)
Ukraine	Karaj Dubina	Markova (1982)
Ukraine	Khadzhimus	Markova (1998)
Ukraine	Kolkotova Balka	Alexandrova (1976); Mikhailesku and Markova (1992); Markova (1992, 2004a)
Ukraine	Kryzhanovka	Rekovets (1994); Tesakov (2004)
Ukraine	Matveevka	Rekovets (1994)
Ukraine	Morozovka	Rekovets (1994)
Ukraine	Nogajsk	Topachevskij (1965); Rekovets (1994)
Ukraine	Roksolany	Mikhailesku and Markova (1992); Markova (1998)
Ukraine	Suvorovo	Mikhailesku and Markova (1992)
Ukraine	Tarkhankut	Topachevskij (1973); Rekovets (1994)
Ukraine	Tikhonovka	Rekovets (1994)
Ukraine	Tiligul	Topachevskij and Skorik (1977)
Ukraine	Zapadnye Kairy	Markova (1982, 2004a)
Ukraine	Zhevakhova Gora	Rekovets (1994)

3. Ranges of arvicolids

3.1. *Ungaromys*

Ungaromys dehmi is the ancestor of *U. nanus*. The type material of *U. dehmi* from Schernfeld has an Hsd/L (relation of hyposinuid height to molar length) of c. 80; the type of *U. nanus* from Betfia 2 has an Hsd/L of c. 100. Rabeder (1981) bases *U. meuleni* on the figure of a molar from Monte Peglia with a higher Hsd/L (definition see chapter 'Methodology')(c. 120). The writers agree with this opinion but since there are no other data available, in this paper *U. meuleni* will be included in *U. nanus*.

3.1.1. *Central Europe*

In faunas of the early range of *U. dehmi* (e.g. Tegelen, Schernfeld, Neuleiningen 7, Kielniki 3/B) *Microtus* is still absent, whereas in faunas of the later range of *U. dehmi* (e.g. Kadzielnia, Neuleiningen 2) as well as in faunas with the EO (earliest occurrence) of *U. nanus* (Kamyk, Betfia 13) *Microtus deucalion* and *Mimomys pitymyoides* occur. This implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). The LO (latest occurrence) of *Ungaromys* is recorded in the faunas of Zalesiaki 1/A, Les Valerots, and Monte Peglia, which all contain advanced *Allophaiomys*, and are therefore no younger than the Jaramillo Subchron (5).

3.1.2. Comparison

Ungaromys is probably the sister taxon of *Ellobius* (see below) that independently evolved from the same ancestor beginning in the Pliocene (Rabeder, 1981). *Ungaromys* has never been recorded from Pleistocene sites of Eastern Europe.

3.2. *Ellobius*

There are several *Ellobius* species and subspecies described (Topachevskij and Rekovets, 1982). The most frequently recorded taxa are *E. palaeotalpinus*, *E. melitopoliensis* and the modern species *E. talpinus*. The species can be discriminated by differences in tooth size and the height of the linea sinuosa.

3.2.1. Eastern Europe

The EO of *E. palaeotalpinus* is recorded in faunas including *Microtus deucalion* (e.g. Zhevakhova Gora 5), referable to the earliest Pleistocene (1, 3) or latest Pliocene (2, 4). The latest record is known from Petropavlovka 2 where it occurs together with *Mimomys savini* and *Microtus* '*arvalinus*' and is comparable to the fauna of Karaj Dubina. The latter is referred to the very end of the Matuyama Chron (7). The EO of *E. melitopoliensis* is at Tikhonovka 2, here it co-occurs with *Microtus pliocaenicus*, *Microtus hintoni*-*gregaloides* and *L. arankae*. This species composition is recorded in faunas of the Morozovkian Small Mammal Complex (Markova, 2004a), which is correlated to the early part between the Jaramillo Subchron and the M/B boundary (Markova, 2004a). The latest records are known from the Bolshevik 2/1 sequence, where it is accompanied by *Arvicola* (SDQ c. 132), comparable to values from the Chigirin and Gunki sites. The latter are referred to the Likhvin Stage Interglacial (Markova, 2004a, b). The earliest *E. talpinus* is known from Matveevka, where it occurs with *Arvicola* (SDQ 102). These assemblages are typical for sites younger than the Kamenka Stage Interglacial (Markova, 2004a).

3.2.2. Comparison

Ellobius, probably the sister taxon of *Ungaromys* (see above), is restricted in Pleistocene sites in Eastern Europe, except for the East Romanian site Gura Dobrogei that is of Saalian age, and which includes *E.* cf. *talpinus* (Radulescu and Samson, 1995). This record matches the species range in Eastern Europe.

3.3. *Clethrionomys*

According to Carls and Rabeder (1988), the *C. kretzoii*–*C. hintonianus*–*C. acrorhiza*–*C. glareolus* lineage can be traced in Central Europe during the Quaternary. The species differ in their $M/1$ occlusal surface (especially the LRA3 shape) and sinuid height. However, *C. hintonianus*, *C. acrorhiza* and *C. glareolus* are sometimes difficult to distinguish, since they are defined by percentages of morphotypes (Carls and Rabeder, 1988). Thus, finds of this age are often generally referred to as *C. glareolus* (or *C.* ex gr. *glareolus*). The Eastern European *C. sokolovi* is assumed to be a synonym of *C. hintonianus* (Tesakov, 1996).

3.3.1. Central Europe

C. kretzoii appears for the first time in faunas that lack *Microtus* (Tegelen, Schernfeld, etc.). The latest records are known from *Microtus deucalion* assemblages (at sites including Kamyk, Kadzielnia), which implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). The EO of *C. hintonianus* is at Deutsch Altenburg 2C1, together with *Microtus pliocaenicus*. The appearance cannot therefore predate the Eburonian (3). The latest *C. hintonianus* is probably recorded in the normally polarised sediments at Voigtstedt, where it co-occurs with *Mimomys savini*, *Microtus* '*arvalinus*' and *Microtus* '*ratticepoides*'. These sediments are equated with 'Cromerian Interglacial II' (9). The EO of *C. glareolus* must post-date the *C. acrorhiza* occurrences, the EO of which is represented at Braşov and Hundsheim. These faunas contain *Arvicola* and therefore are no older than 'Cromerian Interglacial III' (9).

3.3.2. Eastern Europe

The latest *C. kretzoii* occurs in the *Microtus deucalion* fauna from Kryzhanovka 4 and also the EO of *C. sokolovi* in Tiligul is characterised by a co-occurrence with *Microtus deucalion*, which in both cases implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). The LO of *C. sokolovi* is recorded in *Microtus pliocaenicus* assemblages from Nogajsk and Petropavlovka 1, and therefore cannot post-date the Jaramillo Subchron (6). The EO of *C. glareolus* (*C.* ex gr. *glareolus*) is recorded from Karaj Dubina and Cherevychnoe. There it occurs together with *Mimomys savini*, *Microtus hintoni* and *Microtus protoeconomus*, and should be referred to the very end of Matuyama Chron (7).

3.3.3. Comparison

On the basis of the sequence of to the accompanying *Microtus* remains, the LO of *C. kretzoii* might be synchronous in both regions. The synonymy of *C. sokolovi* with *C. hintonianus* may not be completely confirmed since *Microtus* in the earliest faunas with *C. sokolovi* is more primitive than in those with the earliest *C. hintonianus*. The differences of the EO of *C. glareolus* are very probably a matter of different interpretation of the discrimination between *C. hintonianus*, *C. acrorhiza* and *C. glareolus*.

3.4. *Pliomys*

Pliomys schernfeldensis branches into *P. episcopalis* and *P. coronensis* (= *P. lenki*, priority discussed by Terzea, 1983). *P. simplicior* is not considered here as a separate species, although the crown height of specimens referred to this taxon are clearly intermediate (Hsd/L of type materials: c. 80 in *P. schernfeldensis* from Schernfeld c. 100 in *P. simplicior* from Nagyharsányhegy 2, >110 in *P. episcopalis* from Betfia 2). Many records in the literature do not describe this character. What was probably a more local branch developed into *P. hollitzeri*.

3.4.1. Central Europe

P. schernfeldensis has been described from the Schernfeld fauna, which also lacks *Microtus* and is therefore of Pliocene age. The first *P. episcopalis* is recorded from Kadzielnia, Včeláre 3*B*/1, etc., together with *Microtus deucalion*, *Mimomys pitymyoides* and *Mimomys tornensis*, which implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4) for these assemblages. The latest *P. episcopalis* specimens are known from Mosbach 2 and Hundsheim, where they occur with ancient *Arvicola* (SDQ 133 and 135). These assemblages were equated to the period spanning from late Cromerian to Holsteinian (9, 11). The EO of *P. coronensis* is known from Betfia 5 and Holštejn, where it is associated with advanced *Allophaiomys*. This find indicates that the assemblages must be older than the termination of the Jaramillo Subchron (5). The latest records of *P. coronensis* occur at Tarkö/units 2–15 and Dobrkovice 2, again associated with *Arvicola*, the SDQ (Tarkö: 129; Dobrkovice: 123) indicates that it must date from the period spanning the Eemian to the Holsteinian age (11).

3.4.2. Eastern Europe

In Eastern Europe *P. episcopalis* is restricted to faunas dominated by *Microtus pliocaenicus*, such as Akkulaevo, Nogajsk, Melekino and Bolshevik.

3.4.3. Comparison

During the Quaternary, *Pliomys* is rare in Eastern Europe. In Central Europe, the first *P. episcopalis* specimens are recorded earlier, co-occurring with *Microtus deucalion* and continuing until the Middle Pleistocene, whereas in Eastern Europe they are exclusively recorded in *Microtus pliocaenicus* assemblages.

3.5. Mimomys pliocaenicus/ostramosensis

Mimomys ostramosensis is commonly considered to be the more advanced descendant of *Mimomys pliocaenicus*. Comparisons between these species have involved *Mimomys ostramosensis* from its type locality Osztramos 3 and samples that were referred to *Mimomys pliocaenicus*, e.g. from Tegelen (Jánossy and Van der Meulen, 1975), East Anglian sites (Mayhew and Stuart, 1986) or Schernfeld (Carls and Rabeder, 1988; Kościów and Nadachowski, 2002). However, a more important comparison is with *Mimomys pliocaenicus* from the type locality Castelfranco di Sopra, figured by Masini and Torre (1990, pl. II Fig. 8). The height of the linea sinuosa (Hsd/*L*) in the single worn specimen from this locality can only be considered as >110. Two specimens of the *Mimomys ostramosensis* type material have an Hsd/*L* of 111 and 141 (Kościów and Nadachowski, 2002). Since *Mimomys pliocaenicus* is a valid species and *Mimomys ostramosensis* cannot be distinguished from it, the latter species should therefore be a synonym (cf. Maul et al., 1998). However, the use of *Mimomys ostramosensis* would be more practicable since it consists of a series of molars from which various measurements can be taken. As a compromise, in this paper the authors apply the name *Mimomys pliocaenicus/ostramosensis*.

3.5.1. Central Europe

The type locality of *Mimomys pliocaenicus* should be referred to the Olduvai Subchron (*cf*. Maul et al., 1998). The latest remnants of *Mimomys pliocaenicus/ostramosensis* occur in faunas together with *Microtus deucalion*, *Mimomys pitymyoides* and *Borsodia* (Koliňany 3, Villány 5, Včeláre 3*B*/1). This association implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4).

3.5.2. Eastern Europe

Earlier records of this taxon are mentioned from the Pliocene locality of Psekups. The latest records occur at Tizdar 1 and Kryzhanovka 4, together with *Mimomys reidi*, *Mimomys pitymyoides*, *Borsodia newtoni* and *Microtus deucalion*. This implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4).

3.5.3. Comparison

Assemblages that include the latest occurrence of members of *Mimomys pliocaenicus/ostramosensis* are similar to those based on the common presence of *Microtus deucalion*, *Mimomys pitymyoides* and *Borsodia* and are therefore probably time parallel.

3.6. Mimomys tornensis

Carls and Rabeder (1988) consider *Mimomys tornensis* to be the rooted toothed ancestor of *Microtus*, but Garapich and Nadachowski (1996) confirmed the specific distinctness between the two species in Polish localities.

3.6.1. Central Europe

Mimomys tornensis mainly occurs in latest Pliocene faunas (Osztramos 3, Schernfeld) that lack *Microtus deucalion*. However, the latest *Mimomys tornensis* occur in Deutsch Altenburg 10, Neuleiningen 2, 3 and 13, Kamyk, Koliňany 3, Kadzielnia and Kielniki 3/A, together with *Borsodia newtoni*, *Lagurodon* and *Microtus deucalion*. The implication is that they date from the earliest Pleistocene (1, 3) or latest Pliocene (2, 4).

3.6.2. Eastern Europe

In Eastern Europe, the latest record of *Mimomys tornensis* is in the Kryzhanovka 3 assemblage, which lacks *Microtus deucalion*. This fauna is older than those from Tizdar 1, 2 and Kryzhanovka 4. It is correlated to the Pliocene.

3.6.3. Comparison

Mimomys tornensis possibly disappears a little earlier in Eastern than in Central Europe, where it is still present in *Microtus deucalion* faunas.

3.7. *Mimomys pitymyoides*

The common opinion is that *Mimomys pitymyoides* is a species, which becomes extinct around the Plio-Pleistocene boundary, whereas Carls and Rabeder (1988) consider *Mimomys pitymyoides* as the ancestor of *Mimomys pusillus*. The present authors cannot contribute to this discussion but only consider the latest fossil records.

3.7.1. Central Europe

Mimomys pitymyoides is recorded from older faunas (Tegelen, Osztramos 3) that lack *Microtus deucalion* and in younger faunas (Neuleiningen 2, 3 and 13, Kadzielnia, Kamyk, Deutsch Altenburg 10, Včeláre 3*B*/1, Kolinany 3, Villány 5 and Betfia 13) that include it, where it also co-occurs with *Mimomys tornensis*, *Mimomys reidi*/*pusillus*, *V. exilis*, *B. newtoni* and *B. arankoides*. The LO is probably represented at Betfia 13 where it is associated with *L. arankae*. The occurrence of *Microtus deucalion* implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4).

3.7.2. Eastern Europe

Mimomys pitymyoides has its latest occurrences at Kryzhanovka 4, Tizdar 1 and 2, where it is associated with *Mimomys* cf. *pliocaenicus*, *Mimomys reidi*, *Microtus deucalion*, *B. arankoides*, and at Tizdar 2 and Khadzhimus with *L. arankae*. The occurrence of *Microtus deucalion* implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4).

3.7.3. Comparison

The LO seems to be similar in both regions, since the species occurs in the same associations — in the very latest assemblages together with *L. arankae*.

3.8. *Mimomys reidi–Mimomys pusillus*

Mimomys reidi is commonly considered to be the ancestor of *Mimomys pusillus. Mimomys reidi* has a lesser linea sinuosa and an islet persisting until deeper parts of the *M*/1. However, there is no discrimination level defined between the two species. According to Van der Meulen (1973), *Mimomys blanci* is a more evolved descendant of *Mimomys pusillus*, but every character described as being typical of *Mimomys blanci* can also be found in *Mimomys pusillus*. Neither can one demonstrate that *Mimomys blanci* has a higher linea sinuosa, since specimens from both Betfia 2 (the type locality of *Mimomys pusillus*) and Monte Peglia (the type locality of *Mimomys blanci*) have such high crowns that their complete sinuids cannot be measured. Therefore the authors consider *Mimomys blanci* as a synonym of *Mimomys pusillus*.

3.8.1. Central Europe

Mimomys reidi without *Mimomys pusillus* is recorded from assemblages from which *Microtus* is absent (Tegelen, Schambach), which are considered to be of Pliocene age (1, 3). The earliest *Mimomys pusillus* together with, or as a transitional form of *Mimomys reidi*, have been found at Kadzielnia, Mokrá 1 and Betfia 13, associated with *Mimomys pitymyoides*, *B. newtoni*, *P. ternopolitanus*, *B. arankoides* and *L. arankae*. The presence of *Microtus deucalion* in these assemblages implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). The latest *Mimomys pusillus* are recorded from Hohensülzen and Sackdillingen associated with *Mimomys savini*, *Microtus* '*arvalinus*' and *Microtus* '*ratticepoides*', and also with *P. pannonicus* at Villány 6. Because of the assumed age of Untermaßfeld (5) it post-dates the Jaramillo Subchron. On the other hand, *Mimomys pusillus* is unknown from *Mimomys savini* faunas (West Runton, Voigtstedt) of 'Cromerian Interglacial II' (9) since it probably disappeared before this event.

3.8.2. Eastern Europe

Early occurrences of *Mimomys reidi* are known from sites of pre-Olduvai Subchron age (Psekups, Kryzhanovka 3) that lack *Microtus*. The LO is known in faunas with *Microtus deucalion*, *Mimomys pitymyoides*, accompanied by *B. arankoides* and *B. newtoni* (Tizdar 1, Kryzhanovka 4), or *L. arankae* and *P. ternopolitanus* (Tizdar 2). The EO of *Mimomys pusillus* is found (together with or as a transitional form of *Mimomys reidi*) in the upper unit at Akkulaevo, where it is associated with *Microtus pliocaenicus* (*A*/*L* c. 44). The latest *Mimomys pusillus* are still found in assemblages such as that from Ilinka, accompanied by *Mimomys savini*, *Microtus protoeconomus*, *Microtus hintoni*, *Microtus* '*arvalinus*' and *L. transiens*. This fauna is referred to the Early Ilinka Stage Interglacial (Markova, 2004a).

3.8.3. Comparison

The transition *Mimomys pusillus–Mimomys reidi* is recorded in Central Europe in *Microtus deucalion* faunas and in Eastern Europe in a *Microtus pliocaenicus* fauna. The authors hesitate to place too much emphasis on this difference, because subjective differences in the discrimination between the rather similar *Mimomys* species might be unavoidable. Therefore, they conclude that this transition was coeval in both regions. However, *Mimomys pusillus* probably became extinct later in Eastern than in Central Europe. In Eastern Europe it occurs until the first part of Ilinka Interglacial, which is equated with Marine Isotope Stage (MIS) 17–18. Here it is already accompanied by *Prolagurus posterius* and *Lagurus transiens*, whereas in Central Europe the latest *Mimomys pusillus* faunas still contain *P. pannonicus*. West Runton and Voigtstedt, probably equivalent to 'Cromerian Interglacial II' and MIS 17, do not yield *Mimomys pusillus*. However, a synchronous LO in MIS 18 cannot be excluded.

3.9. Mimomys savini–Arvicola mosbachensis–Arvicola terrestris

These three species undergo continuous changes and are commonly considered to belong to one lineage. This is certainly correct in general, and in this paper the authors consider only these three species. However, the geographical patterns of this evolution are much more complex. The discrimination is clear between the rooted *Mimomys savini*, and the rootless *Arvicola*, between *A. mosbachensis* with negative and *A. terrestris* with positive enamel differentiation. Further evolutionary levels of *Arvicola* can be distinguished by use of the SDQ ratio devised by Heinrich (1978). *A. chosaricus* is a transitional form with SDQ c. 100 and is not distinguished separately here.

3.9.1. Central Europe

The earliest *Mimomys savini* occurs at Villány 5 together with *Microtus deucalion*, which implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). The latest *Mimomys savini* are known from faunas of Brunhes Chron-age (Kärlich F, West Runton, Voigtstedt), referred to 'Cromerian Interglacial II' and the earliest occurrence of *A. mosbachensis* is recorded in Kärlich G dated as 'Cromerian Interglacial III' (9). The EO of *A. terrestris* is recorded in faunas from the Early Weichselian, such as Burgtonna 2 (SDQ c. 99) (11).

3.9.2. Eastern Europe

The earliest *Mimomys savini* occur at Tiligul and Zhevakhova Gora sites 5 and 9 together with *Microtus deucalion*, which implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). The latest *Mimomys savini* specimens occur in the Muchkap Stage Interglacial (Markova, 2004a). *A. mosbachensis* is found at sites including Gunki, Pivikha, Chigirin, Ozernoe and Uzmari which are correlated to the Likhvin Stage Interglacial, after a record gap (neither *Mimomys savini* nor *Arvicola* records) in the Okian Stage Glaciation sites with *Dicrostonyx simplicior okaensis* and *Lagurus transiens* (Markova, 2004a, b). SDQ$<$100 at the Shkurlat and Malutino sites indicate the first *A. terrestris* occurrence during the Mikulino (= Eemian Stage) Interglacial.

3.9.3. Comparison

The first *Mimomys savini* occurs in both regions in similar faunal associations. The *Mimomys savini–Arvicola* transition occurs earlier in Central Europe (after 'Cromerian Interglacial II', therefore possibly in MIS 16), than in Eastern Europe (after the Muchkap Stage Interglacial, therefore possibly in MIS 12). The *A. mosbachensis–A. terrestris* transition is recorded earlier in Eastern Europe, in the Mikulino (= Eemian) Interglacial, whereas in Central Europe it only occurs during the following Weichselian Stage. Finds of *A. terrestris* (SDQ$<$100) are mentioned from Central European assemblages referred to the Saalian Stage and in which they are interpreted as immigrants from Eastern Europe (Van Kolfschoten, 1990b). However, during the Saalian (Dniepr) Stage Eastern European *Arvicola* samples also have SDQ values of $>$100.

3.10. Microtus

The palaeoecology, as well as the origin, of early *Microtus* taxa is still obscure. This could be of biostratigraphical importance since the possibility that this taxon was absent from some localities for ecological reasons cannot be excluded. The interrelationships between early *Microtus* taxa are often unclear and a polyphyletic origin is possible. The *Microtus* radiation into recent groups becomes clearly visible approximately within the Jaramillo Subchron. For the purpose of this paper matters are therefore simplified to distinguish only 5 groups (subgenera): *Allophaiomys*, *Pallasiinus*, *Stenocranius*, *Terricola* and *Microtus*. Members of the subgenus *Chionomys* are excluded for the scope of this paper, since they are often not considered in the fossil record. For extensive discussion on the fossil and recent members of this group, refer to Nadachowski (1991). A/L is a valuable index for determination of the evolutionary level within each *Microtus* group.

3.11. Microtus (Allophaiomys) deucalion–M. pliocaenicus–advanced Allophaiomys

Traditionally, the specimens with primitive ACC are grouped in the subgenus *Allophaiomys. Microtus* (*A.*) *deucalion* with an $A/L<42$ is the ancestor of *Microtus* (*A.*) *pliocaenicus* with an A/L between 42 and 44.5 (Van der Meulen, 1974). Polymorphic samples, including allophaiomyid morphotypes (T4–T6 confluent) with $44.5<A/L<47$, are considered in this paper as 'advanced' *Allophaiomys*, independent of the original taxonomic referral.

3.11.1. Central Europe

At Kamyk, Kadzielnia, Včeláre $3B/1$, Neuleiningen, 2, 3 and 13 *Microtus deucalion* is associated with *Mimomys ostramosensis*, *Mimomys tornensis*, *Mimomys pitymyoides* and *Borsodia*. Only at Betfia 13 is it associated with *L. arankae*. The EO of *Microtus deucalion* is referred to the earliest Pleistocene (1, 3) or latest Pliocene (2, 4). The first *Microtus pliocaenicus* faunas (Deutsch Altenburg 2C1, Betfia 9) are characterised by associations with *C. hintonianus*, *P. pannonicus* and *L. arankae* (but never *Borsodia*) and are no younger than the Eburonian (3). The LO of a *Microtus* (*Allophaiomys*) sp., which could be referred to *pliocaenicus* due to its A/L value, occurs at Colle Curti, and occurs during the Jaramillo Subchron. However, these finds have a progressive positive enamel differentiation. The latest advanced *Allophaiomys* are recorded together with *Mimomys pusillus* for example at Holštejn, Zalesiaki $1A/13$, Les Valerots and Monte Peglia. The LO of advanced *Allophaiomys* is considered to be not later than the Jaramillo Subchron (5).

3.11.2. Eastern Europe

Faunas with *Microtus deucalion* (Chortkov, Zhevakhova Gora, Tiligul, Tizdar, Mikhailovka 1, etc.) are associated with *Mimomys pitymyoides*, *Mimomys reidi*, *Mimomys* cf. *pliocaenicus*, *B. arankoides* and *B. newtoni*. The EO of *Microtus deucalion* is related to the earliest Pleistocene (1, 3) or the latest Pliocene (2, 4). The latest *Microtus deucalion* (Khadzhimus, Melekino) is associated with *P. ternopolitanus* and *L. arankae*. The first *Microtus pliocaenicus* faunas also are characterised by associations with *L. arankae* and *P. ternopolitanus* (Nogajskian faunas). An advanced *Microtus pliocaenicus* is recorded from the Korotoyak/Ostrogozhsk Suite accompanied by *P. pannonicus*, *Mimomys pusillus* and *C. sokolovi*. These deposits also accumulated during the Jaramillo Subchron (6). Zapadnye Kairy and Ushkalka have yielded advanced *Allophaiomys* together with *L. arankae* and *P. pannonicus* and are significantly older than the M/B boundary. They are also very similar to the Korotoyak/Ostrogozhsk Suite fauna, which also corresponds to the Jaramillo Subchron. The latest very advanced *Allophaiomys* were discovered in Petropavlovkian faunas, together with the first *Microtus protoeconomus* and correlated to the very end of Matuyama Chron.

3.11.3. Comparison

It seems to be more probable that the first *Microtus* arrived by an immigration wave into Europe rather than that it autochthonously evolved from *Mimomys tornensis*, as suggested by Carls and Rabeder (1988). The authors share the view of Garapich and Nadachowski (1996) that *Mimomys tornensis* and *Microtus*, co-occurring in several faunas, are different in morphology, which excludes a direct ancestor-descendant relationship of the two species. An appearance by immigration would cause a somewhat simultaneous first occurrence in the fossil record in many parts of the Continent. According to the fossil record, the oldest *Microtus deucalion* occur in Eastern and Central Europe, with similar associations. Moreover, the oldest *Microtus pliocaenicus* display striking similarities to the accompanying fauna (*P. pannonicus* and *L. arankae*). Both appearances therefore might be time parallel, which would support the immigration theory. However, the earliest and latest occurrences of advanced *Allophaiomys* are probably slightly later in Eastern than in Central Europe.

3.12. *Microtus (Stenocranius) hintoni*–*Microtus (S.) gregaloides*–*Microtus (S.) gregalis*

Microtus hintoni seems to belong to the earliest *Microtus* taxa derived from the *Allophaiomys* group. It differs from *Microtus gregaloides* by its shorter ACC ($A/L<$c. 50). Both these taxa typically display a *Pitymys*-like rhombus, which is closed in the descendant *Microtus gregalis* ($A/L>$c. 53).

3.12.1. Central Europe

Microtus hintoni first appears in Central Europe at Holštejn and Deutsch Altenburg 4A, where it co-occurs with *P. pannonicus*, *L. arankae* and advanced *Allophaiomys*. These assemblages are older than the termination of the Jaramillo Subchron (5) and younger than the Eburonian Stage (3). *M. hintoni* survives at least until 'Cromerian Interglacial II' based on its record in the *Mimomys savini* fauna of Koněprusy C 718 (9). *Microtus gregaloides* appears for the first time at Zalesiaki 1A/13, Villány 6, Somssich hegy 2, and Betfia 5, where it is associated with *P. pannonicus*, *L. arankae* and an *Allophaiomys* that is more advanced than in the faunas mentioned before. It seems that because of (5) all these localities do not predate the Jaramillo Subchron. However, independent geological and palaeomagnetic evidence is necessary to prove these assumptions. The LO of *Microtus gregaloides* is probably at Hundsheim, which is correlated with 'Cromerian Interglacial III or IV' (9, 11). The oldest records of *Microtus gregalis* are known from Koněprusy C 718 and Villány 8, where they are accompanied by *Mimomys savini*, and therefore cannot be younger than 'Cromerian Interglacial II' (9).

3.12.2. Eastern Europe

The first *M. hintoni* is recorded, together with *P. pannonicus* and advanced *Allophaiomys*, at the Morozovka site (Morozovkian faunas). *M. hintoni* became abundant at Karaj Dubina, Petropavlovka 2, Shamin. These Petropavlovkian faunas are referred to the very end of the Matuyama Chron on the basis of geological and palaeomagnetic evidence (7). *M. gregaloides* occurs in small number together with *Mimomys savini*, *M. pusillus* and *P. pannonicus* at Uryv 3 (Early Tiraspolian) which is referred to the beginning of the Brunhes Chron (Agadjanian, 1992). They became abundant in later Tiraspolian faunas (Veret'e, Ilinka, Beresovka, Zaplatino and others: Agadjanian, 1992). *M. gregalis* first appears at Suvorovo (middle and upper units), Kolkotova Balka (Vorona palaeosol), Posevkino and Perevoz (Vorona palaeosol), in sediments of the Muchkap Stage Interglacial (Markova, 2004a).

3.12.3. Comparison

All members of this group possibly occur earlier in Central than in Eastern Europe. In Central Europe, *Microtus hintoni* occurs before the termination of the Jaramillo and in Eastern Europe, that species appears after this event in the Morozovkian faunas. Likewise *M. gregaloides* occurs earlier in Central Europe, because of its association with *L. arankae* and the referral to the Jaramillo. In Eastern Europe, *M. hintoni* appears in the early part between the Jaramillo Subchron and the M/B boundary and is typical at the end of the Matuyama Chron period. *M. gregaloides* faunas are placed at the beginning of the Brunhes Chron as indicated by both palaeomagnetic and geological evidence. It therefore, seems that *M. gregalis* appeared earlier in Central Europe in the

'Cromerian Interglacial II' (probably MIS 17) and in Eastern Europe during Muchkap Stage Interglacial (probably MIS 15).

3.13. *Microtus (Pallasiinus) protoeconomus–Microtus (P.) 'ratticepoides'–Microtus (P.) oeconomus*

The morphotype eoratticeps is already present in Deutsch Altenburg 2C1 — not as a separate species but within the spectrum of *Microtus pliocaenicus*. In addition the specimens from Colle Curti and Korotoyak, both referred to *Allophaiomys*, resemble oeoconomid morphology. However, not all these finds are referred to the *Pallasiinus* group. The name *Microtus ratticepoides* is commonly used for the primitive members of the group, but according to Nadachowski (1990), the type of *Microtus nivalinus* has the same oeoconomid morphology and should be used for reasons of priority. As a compromise, the authors retain the traditional nomenclature, but in quotation marks: *Microtus* '*ratticepoides*'. Since the relationship between the Central European *Microtus* '*ratticepoides*' and the Eastern European *Microtus protoeconomus* is unclear the writers consider both species distinct. Rekovets and Nadachowski (1995) proposed to set the limit for *Microtus oeconomus* at 50.

3.13.1. *Central Europe*

The oldest records of *Microtus* '*ratticepoides*' are known from Holstein where it occurs together with *Mimomys pusillus* and advanced *Allophaiomys* and because of (5) predate the termination of the Jaramillo Subchron. The LO is known from Tarkö/unit 2–15, where associated with *Arvicola*, the SDQ (129, respectively, 123) of which is in the range between Eemian to Holsteinian samples (11). The first *M. oeconomus* occurs at Solymár. Its *Arvicola* SDQ of 108 indicates a Saalian age.

3.13.2. *Eastern Europe*

The oldest representatives in Eastern Europe, which can be clearly referred to this group, are *Microtus protoeconomus* from Karaj Dubina (A/L 45). Markova (2004a) refers this as to *Microtus* ex gr. *oeconomus* and dates it to the very end of Matuyama Chron (MIS 20–21) within the Petropavlovkian assemblage. According to Pevzner et al. (2001) Petropavlovka 2 ranges from the base of MIS 21 to that of MIS 18. Here *Microtus protoeconomus* is associated with *Prolagurus pannonicus*. The transition to modern *Microtus oeconomus* is difficult to define. Based on the proposal of Rekovets and Nadachowski (1995) to use the A/L for the differentiation, Gunki (A/L 49) would be the latest *Microtus protoeconomus*. Markova (2004a) correlates the site of Gunki with MIS 11.

3.13.3. *Comparison*

The *Pallasiinus* group possibly appears in Central Europe before and in Eastern clearly after the Jaramillo Subchron. European faunas with the earliest *M. protoeconomus* also yield very advanced *Allophaiomys* and abundant *P. pannonicus*. They are referred to the very end of Matuyama Chron. Since Polish (Nadachowski, 1982) and German (Maul et al., 1998) *M. oeconomus* have A/L values of 48 and the Late Pleistocene and modern *M. oeconomus* from Ukraine have A/L values of 51 (Rekovets and Nadachowski, 1995), it is not possible to correlate the transition *M.* '*ratticepoides*'–*M. oeconomus* in the two regions by means of this parameter.

3.14. *Microtus (Terricola) arvalidens–Microtus (T.) subterraneus*

Members of the group are referred to *Pitymys* or *Terricola* (discussion see Martin, 1987). The *Pitymys* rhombus seems to be a plesiomorphy and probably all *Microtus* lineages passed a level with such a structure during their evolution. *Microtus arvalidens* has a more primitive ACC than *Microtus subterraneus*, but the discrimination between the species is not clearly defined.

3.14.1. *Central Europe*

The earliest record of *Microtus arvalidens* has been found in the *Microtus pliocaenicus* fauna from Pirro Nord 1. Since it is a single specimen, contamination may be possible. The next earliest record originates form Villány 6, where *M. arvalidens* co-occurs with *Mimomys pusillus*. Since the latter species disappears in Central Europe after the Jaramillo Subchron (5) and before 'Cromerian Interglacial II' (9), the EO of *Microtus* '*arvalidens*' must also lie within this time frame. The earliest finds referred to *Microtus subterraneus* are recorded from Maastricht-Belvedere 4, which is of Early Saalian age (Van Kolfschoten, 1990b).

3.14.2. *Eastern Europe*

In Eastern Europe the earliest *M. arvalidens* appears in the Middle Ilinka Stage Interglacial (MIS 18) (Ilinka 1 and 2, Veret'e, Trosnianka, the Zaplatino sites), which corresponds to the interval after the so-called Pokrovka cool event (MIS 19). Clear finds of *M. subterraneus* were made in the Mikulino Stage Interglacial (= Eemian) in Mikhailovka 5 site (MIS 5) (Agadjanian and Glushankova, 1986; Agadjanian, 1992; Markova, 2004a), but an earlier appearance cannot be excluded.

3.14.3. *Comparison*

Microtus arvalidens possibly appears in Central Europe before the M/B boundary and therefore earlier than in Eastern Europe (Middle Ilinka Stage Interglacial, MIS 18). However, independent geological and palaeomagnetic data will be necessary to prove these assumptions. The first appearance of *Microtus subterraneus* seems to be earlier in Central than in Eastern Europe.

3.15. *Microtus (Microtus) 'arvalinus'–Microtus (Microtus) arvalis*

The name *Microtus arvalinus* is commonly used for the primitive members of this group, but according to Nadachowski (1990), the type of *Microtus nivaloides* has the same arvalid morphology and should be used for priority reasons. As a compromise, the authors follow the traditional nomenclature, but in quotation marks: *Microtus* '*arvalinus*'. The discrimination between *Microtus arvalis* and its ancestor *Microtus* '*arvalinus*' is not clearly defined. Small A/L values seem to be typical for *Microtus* '*arvalinus*' (Hohensülzen: 48.1, Somssich hegy 2: 50.4, Voigtstedt: 50.9) in comparison to modern samples (Poland: 54, Nadachowski, 1982; Germany: 54, Maul et al., 1998). Here the authors do not consider *Microtus hyperboreus* because records in Central Europe are too rare and uncertain (cf. Nadachowski, 1992).

3.15.1. *Central Europe*

The earliest records of *Microtus* '*arvalinus*' have been found at Villány 6, Sackdillingen and Hohensülzen together with *Mimomys pusillus*. Since the latter species disappears in Central Europe after the Jaramillo Subchron (5) and before 'Cromerian Interglacial II' (9), the EO of *Microtus* '*arvalinus*' must also lie within these limits. Possibly the earliest *Microtus arvalis* is known from Hundsheim (A/L 53.0) and Miesenheim 1. Here a very ancient *A. mosbachensis* also occurs, as well as *Pliomys*. This record implies a correlation with 'Cromerian Interglacial III or IV' (c. MIS 13 or 15) (9).

3.15.2. *Eastern Europe*

Microtus '*arvalinus*' probably has its earliest record in Shamin. The fossiliferous horizon is reversely magnetised, and is therefore referred to the very end of the Matuyama Chron (7). *Microtus arvalis* is present at Gunki, Chigirin, Pivikha, Rybnaya Sloboda, Ozernoe, Uzmari and Verkhnaya Emancha (Gunkovian: MIS 11-12, Markova, 2004a). Since the Gunki sample is already developed (A/L 56), the EO of this species might be a little earlier.

3.15.3. *Comparison*

The earliest occurrence of *Microtus* '*arvalinus*' is recorded from Central Europe during the period between the Jaramillo Subchron and the M/B boundary, and in Eastern Europe at the very end of the Matuyama Chron. There few records with A/L values allow only a vague comparison of the first appearance of *Microtus arvalis*, which seems to be time parallel.

3.16. *Villanyia exilis*

Villanyia remains are generally rare in the fossil record but are more common in Central, rather than in Eastern Europe. Its oldest records are found in Pliocene faunas that lack *Microtus* (e.g. Koliňany 1, Liventsovka). *Villanyia exilis* exists longer in Central Europe since its LO is here recorded in faunas such as Mokrá 1, Villány 5, Kadzielnia, Kamyk and Betfia 13 together with *Mimomys tornensis*, *Mimomys pitymyoides*, *Borsodia* and *Microtus deucalion*, which implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). In Eastern Europe *Villanyia* occurs only in Pliocene faunas that lack *Microtus* (e.g. Korotoyak 2).

3.17. *Borsodia arankoides–Lagurodon arankae*

Both species differ mainly only in the possession of rooted (*Borsodia*) or rootless (*Lagurodon*) molars.

3.17.1. *Central Europe*

In Koliňany 3 and Villány 5 *B. arankoides* co-occurs with *Mimomys pitymyoides* and *Microtus deucalion*, and is therefore of earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). Assemblages that include both *Borsodia* and *Lagurodon* are recorded from Deutsch Altenburg 10 and Mokrá 1. These sites also yield *Microtus deucalion*, the find of which implies an earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). *Lagurodon*, without the rooted toothed *Borsodia*, occurs in *Microtus pliocaenicus* faunas (Betfia 2, Deutsch Altenburg 2) that are no younger than Eburonian Stage (3) whilst the latest *L. arankae* are recorded from faunas with advanced *Allophaiomys* (Deutsch Altenburg 4B, Chlum 6, Holštejn and Betfia 5, all with A/L 45–46). These assemblages are therefore older than the Jaramillo Subchron termination (5).

3.17.2. *Eastern Europe*

B. arankoides occurs together with *Microtus deucalion* and *Mimomys pitymyoides* at Tizdar 1 and Kryzhanovka 4. The earliest records of *L. arankae* (Zhevakhova Gora 5, 9, Chortkov, Khadzhimus and Melekino) are also found together with *Microtus deucalion*, and are therefore of earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). *L. arankae* has its latest records during the Morozovkian (Port Katon, *Microtus* A/L c. 46) and is older than Petropavlovkian faunas without *L. arankae* such as Karaj Dubina, Petropavlovka 2 and Krasnyj Log, and therefore referred to the very end of Matuyama Chron (7).

3.17.3. *Comparison*

The latest *B. arankoides* occurs in both regions in *Microtus deucalion* faunas, the first *L. arankae,* without *Borsodia* in *Microtus pliocaenicus* faunas in Central, and in *Microtus deucalion* faunas in Eastern Europe. Because of the problematic discrimination between rootless *Lagurodon* and rootless juvenile *Borsodia*, the authors hesitate to stress this difference and consider the transition in similar faunal assemblages. The LO of *L. arankae* is recorded from both regions in assemblages together with advances *Allophaiomys* (A/L c. 46) before the end of the Jaramillo in Central Europe, and shortly after this event but before the M/B boundary in Eastern Europe.

3.18. *Borsodia newtoni–Prolagurus ternopolitanus–P. pannonicus–Lagurus transiens–L. lagurus*

These species differ in their possession of rooted (*Borsodia*) or rootless (*Prolagurus*, *Lagurus*) molars and in the occlusal surface. The primitive rootless lagurid *L. praepannonicus* is considered as *P. ternopolitanus. P. posterius*, with a typical rounded LSA5, is not considered separately here, since there are no records from Central Europe, except from Gura Dobrogei 4 in Eastern Romania.

3.18.1. Central Europe

B. newtoni appears in faunas that lack *Microtus* but is also recorded in *Microtus deucalion* faunas (Kamyk, Kadzielnia, Mokrá 1, Koliňany 3 and Villány 5). It is therefore of earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). In Včeláre 3*B*/1 *B. newtoni* is associated with *P. ternopolitanus* and *Microtus deucalion* (A/L c. 42) and *Mimomys pitymyoides*, and is therefore of earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). *P. pannonicus* appears in Central Europe for the first time in *Microtus pliocaenicus* faunas, such as Deutsch Altenburg 2, Betfia 2 and Včeláre 4*A*/7 (A/L 42.3–43.7), and thus cannot predate the Eburonian Stage (3). The oldest *L. transiens* originate from Tarkö/unit 16 from an assemblage together with *Mimomys savini*. It therefore cannot post-date 'Cromerian Interglacial II' (9). The earliest records of *L. lagurus* is known from Bilzingsleben 2, accompanied by *Arvicola* (SDQ c. 132) and correlated with late Holsteinian Stage (Heinrich, 1987).

3.18.2. Eastern Europe

B. newtoni is found in faunas again lacking *Microtus* and survives into faunas where it co-occurs with *Microtus deucalion*. It is therefore of earliest Pleistocene (1, 3) or latest Pliocene age (2, 4). The rootless *P. ternopolitanus* appears in the Late Odessa faunas associated with an archaic *Microtus pliocaenicus* (A/L c. 42), like Melekino and Khadzhimus. The latter site also contains *Mimomys pitymyoides* and has been dated by Thermoluminescence Dating to 1.3 Ma B.P. (Markova, 2004a). *P. pannonicus* appears together with *Microtus pliocaenicus* (A/L 43–45) in the Kairian faunas, such sites as Zapadnye Kairy, Ushkalka, the Korotoyak/Ostrogozhsk Suite (correlated with the Jaramillo Subchron) and Roksolany (immediately beneath the Jaramillo Subchron) (7). The earliest *L. transiens* are found in sediments of the Late Ilinka Stage Interglacial (Agadjanian, 1992; Markova, 2004a). The earliest record determined as *L.* ex gr. *lagurus* (with the predominant morphotype lagurus) was recovered from the localities Priluki and Kolkotova Balka (within a soil of the Kamenka Stage Interglacial) (MIS 9, Mikhailesku and Markova, 1992; Markova, 2004a).

3.18.3. Comparison

The transition from the rooted toothed *Borsodia* to the rootless *P. ternopolitanus* occurs in Central Europe in faunas that include *Microtus deucalion*, and in Eastern European faunas with very archaic *Microtus pliocaenicus*. Because of the problematic discrimination between the rootless *Prolagurus* and rootless juvenile *Borsodia* the authors hesitate to stress this difference and consider the transition in similar faunal assemblages. First *P. pannonicus* co-occurs in both regions in *Microtus pliocaenicus* faunas. *L. transiens* appears in Central and Eastern Europe at around MIS 16 or 17. *L. lagurus*, by contrast, appears both in Central and Eastern Europe during the late Holsteinian Stage or just after (Kamenka Stage Interglacial).

3.19. *Eolagurus argyropuloi–E. luteus*

Remains of this genus are restricted to Eastern Europe, with the exception of some records from eastern Romania (Terzea, 1995). The authors distinguish only *E. argyropuloi* (with *Pitymys* rhombus and $A/L < 54$) and *E. luteus* (without rhombus, $A/L > 54$). An increase in size with time can be recognised.

3.19.1. Eastern Europe

The possibly oldest *E. argyropuloi* originates from Tarkhankut, in association with *Microtus pliocaenicus*. The subspecies *E. luteus gromovi* is restricted to Tiraspolian faunas. The transition to *E. luteus* occurs at Gunki, with *A. mosbachensis* (SDQ 125), referred to the Likhvin Stage Interglacial (Markova, 1990).

3.19.2. Comparison

The records of *Eolagurus luteus* from Eastern Romania are of Saalian age (La Adam: Terzea, 1995) and therefore occur within the stratigraphical range of this species in neighbouring Russia and Ukraine.

3.20. *Lemmus kowalskii–L. lemmus*

Lemmus kowalskii and *L. lemmus* are distinguished by the morphology of all molars, mainly that of upper $M/3$. Many records only refer to *L.* sp. (cf. Kowalski, 2001).

3.20.1. Central Europe

L. kowalskii was first described from Schernfeld. Similar evolutionary stages are seen in the records of Kadzielnia, Kamyk, Včeláre 3B1 and Včeláre 5, where they co-occur with *Microtus deucalion* and are therefore younger than Schernfeld. The latest occurrence is probably known from the *Mimomys savini* fauna Koži Grzbiet ('Cromerian Interglacial II' because of (9)). Miesenheim 1 ('Cromerian Interglacial IV') and Kärlich G ('Cromerian Interglacial III') contain the oldest *L. lemmus*, together with the earliest *Arvicola*.

3.20.2. Eastern Europe

Lemmus cf. *kowalskii* is known from only a few sites, e.g. Chertkov in Ukraine (together with *Microtus pliocaenicus*). The oldest record of *L. lemmus* is probably that of

Bogdanovka in association with *Mimomys savini* (Donian Stage Glaciation, c. MIS 16).

3.20.3. Comparison

The few records of *L. kowalskii* in Eastern Europe do not permit a comparison with Central European sites. *L. lemmus* probably appears a little earlier in Central Europe.

3.21. Predicrostonyx compitalis–Dicrostonyx simplicior–D. gulielmi/torquatus

All the species mentioned can be distinguished using specific morphotype frequencies (due to the numbers of enamel fields) of all molars. Because of various problems arising from the distinction between *D. gulielmi* and *D. torquatus* these species are here lumped together.

3.21.1. Central Europe

P. cf. *compitalis* from Zalesiaki 1*A*/13 site and the related (possibly conspecific) *P. antiquitatis* at Les Valerots are recorded together with advanced *Allophaiomys*. Both localities are probably older than the termination of the Jaramillo Subchron (5). The EO of *D. simplicior* occurs in units that include evidence of cold climatic conditions in the Koněprusy Jk and C 718 and in the Koži Grzbiet profiles. In these units it co-occurs with *Mimomys savini* and is probably referable to 'Cromerian Glacial b' (5). *D. gulielmi/torquatus* is present from after the Early Saalian Substage (Ariendorf 1).

3.21.2. Eastern Europe

Possibly the earliest *D.* cf. *simplicior* was recorded in sediments of the Donian Stage Glaciation (c. MIS 16, Markova, 2004a) at Bogdanovka. The oldest record of *D. gulielmi/torquatus* (mentioned as *D.* ex gr. *simplicior*) is from Rybinsk (Saalian Stage).

3.21.3. Comparison

Pleistocene *Predicrostonyx* is still unknown from Eastern Europe. *D. simplicior* occurs in older faunas in Central than in Eastern Europe, where it appears shortly after the M/B boundary. *D. gulielmi/torquatus* is present in both regions during the Saalian Stage but possibly in Eastern Europe persists slightly later.

4. Discussion

The comparison of the arvicolid occurrence dates is rather consistent in most cases, although several taxon occurrences are not comparable possibly because of endemism or extreme differences of record density. These problems are particularly evident in the case of *Ungaromys*, *Ellobius*, *Pliomys*, *Villanyia*, *Eolagurus*, *Lemmus* and *Dicrostonyx*. Other taxa are not comparable because of differences in taxonomy, as in the case of the *Clethrionomys hintonianus–C. glareolus*, and *M. protoeconomus–M. oeconomus* transitions. Species-specific characters should be defined in further investigations to overcome these problems. Discrepancies in chronostratigraphical correlation of arvicolid occurrence were recognised in nearly all *Microtus* groups and in the LO of *Lagurodon arankae*. However, these differences could be artificial and possibly arise from the insufficient number of Central European sites from which geological and palaeomagnetic evidence is available. More independent biostratigraphical ages are available from Eastern Europe, particularly for faunas older than the Cromerian. These sites are often situated in loess regions and can be correlated with particular palaeosol or loess horizons, and in some cases, they can also be correlated with particular terraces, tills or palaeomagnetic boundaries.

One of the few complex sites in Central Europe is Untermaßfeld, which has a rich fauna and has been dated by several geological and palaeontological techniques (Kahlke, 1997, 2001a, b). In this paper it was used as a fixed point for the chronostratigraphical age estimation of other Central European sites where the geological context is uncertain. However, a change in the assumed age of Untermaßfeld would influence all other interpreted ages of the localities concerned. Because of the similarities between the Karaj Dubina and the Untermaßfeld *Microtus* samples, the second author (A.K. Markova), disagrees with the first author (L.C. Maul), in suggesting that the normal magnetopolarity recorded at Untermaßfeld should be interpreted as falling just above the M/B boundary rather than within the Jaramillo Subchron. If this interpretation is accepted, then several discrepancies in the present paper between Central and Eastern European arvicolid ranges would certainly be reduced (LO of advanced *Allophaiomys* and of *L. arankae*, EO of *M.* (*Stenocranius*), *M.* (*Pallasiinus*), *M.* (*Terricola*) and *M.* (*Microtus*)), as discussed by Van Kolfschoten and Markova (2005). Vice versa, also a slight older position of Karaj Dubina could reduce these disagreements (cf. Maul, 2001, Abb. 56).

However, a re-positioning of the Untermaßfeld sequence close to the M/B boundary would create striking problems. It would then be only slightly older than Voigtstedt, which contains a much more evolved small mammal fauna, and the interpretation of other fossil groups would become very difficult. This problem requires further complex investigations to provide an explanation for these discrepancies.

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